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

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Homosporous or heterosporous, seedless vascular plants with *microphylls* (small leaves with a single vein and a single leaf trace, not associated with a leaf gap). *Sporangia* borne in the axils of normal or reduced foliage leaves. *Gametophytes* free-living and photosynthetic to symbiotic, or retained within the spore.

Though treelike species flourished during the Carboniferous, all 1,000 or so modern species are herbaceous. In addition to the two families present at La Selva, this division includes the monotypic Isoetaceae (quillworts), occurring elsewhere in Costa Rica.

KEY TO THE FAMILIES

1. Leaves numerous, all more or less alike, in several ranks around the stem; sporangia borne in axils of typical leaves, or in cylindrical strobili; epiphytic or terrestrial. ..... 1. *LYCOPODIACEAE.*
1. Leaves (in ours) of two kinds: spreading lateral leaves, and appressed median leaves, each in two ranks along the stems; sporangia borne in tetragonal strobili; plants at La Selva generally terrestrial, occasionally epilithic or on logs. ..... 2. *SELAGINELLACEAE.*

1. LYCOPODIACEAE

Perennial herbs, terrestrial or epiphytic, erect, pendent, repent or scandent, simple or dichotomously branched. *Leaves* numerous, small, simple, 1-veined, in four to many ranks, all similar in ours, lacking ligules. *Sporophylls* similar to the foliage leaves, or modified and forming strobili. *Sporangia* solitary in axils of sporophylls, of a single kind (the plants homosporous). *Gametophytes* free-living, photosynthetic to symbiotic.

There are two extant genera of Lycopodiaceae: *Lycopodium* and *Phylloglossum* Kunze, a monotypic genus of Australia and New Zealand.

1. LYCOPODIUM L.

NESSEL, H. 1939. Die Barläppgewächse. Gustav Fischer, Jena. 404 pp.

ØLLGAARD, B. 1983. Lycopodiaceae. Pp. 20–44 *in* R. G. STOLZE, Ferns and fern allies of Guatemala. Part III. Marsileaceae, Salviniaceae, and the fern allies (including a comprehensive index to Parts I, II, and III). Fieldiana, Bot. n.s. 12: 1–91.

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UNDERWOOD, L. M. AND F. E. LLOYD. 1906. The species of *Lycopodium* in the American tropics. Bull. Torrey Bot. Club 33: 101–124.

Characters of the family. A cosmopolitan genus of about 250 species, best represented in south temperate zones and tropical montane areas. Roughly half of the species occur in the New World, where the genus ranges from New England and the Pacific Northwest to Tierra del Fuego; 40–45 species are known from Costa Rica, mostly from above 1,000 m.

KEY TO THE SPECIES

1. Plants terrestrial, sprawling or scandent; leaves less than 5 mm long; sporangia borne in terminal, well-differentiated, unbranched strobili. ..... 1. *L. cernuum.*
1. Plants epiphytic, suberect to pendent; leaves more than 5 mm long; sporangia borne in the upper axils.
   2. Leaves ovate to oblong or obovate, less than 4 times as long as broad; sporangia borne in terminal, simple to branched strobili (i.e., in the axils of much reduced leaves); very rare. ..... 2. *L. dichaeoides.*
   2. Leaves linear, more than 4 times as long as broad; sporangia borne in axils of unmodified foliage leaves.
      3. Stems relatively stout, more than 1.5 mm in diameter throughout; dichotomous branching pattern obvious. ... 3. *L. dichotomum.*
      3. Stems very slender, less than 1.5 mm in diameter throughout; dichotomous branching pattern not usually obvious. ..... 4. *L. linifolium.*

1. **Lycopodium cernuum** L.
(=*Lycopodiella cernua* (L.) Pichi-Serm.)

Terrestrial, the main *stems* long and usually arching to scandent, bearing erect, determinate stems 30–100 cm tall, the latter with numerous spreading branches that are themselves repeatedly branched. *Ultimate branches* nodding, terminating in sessile strobili. *Leaves* subulate, many-ranked, entire, more or less similar, 2.5–4 mm long. *Strobili* pointing downwards, cylindrical, 3–15 mm long and 2–3 mm wide, the sporophylls somewhat scarious and pale. A pantropical species, widespread in Costa Rica from 0 to 3,200 m.

A weedy species, abundant in the Puerto Viejo region along roadsides, but uncommon at La Selva. It occurs in open disturbed sites, such as on landslides along the rivers.

2. **Lycopodium dichaeoides** Maxon
(=*Urostachys dichaeoides* (Maxon) Herter ex Nessel)

Epiphytic, the main *stems* generally pendent, the plants mostly 15–45 cm long and 1–several times dichotomously branched. *Foliage leaves* 4-ranked, spreading, mostly 6–8 mm long and 2–5 mm wide, ovate to oblong or obovate, minutely apiculate apically, inaequilateral at base, with basal lobe on one side overlapping the stem. *Sporophylls* appressed and imbricate, ovate, acute at apex with median keel, about 0.8 mm long. *Strobili* simple or 1–several times dichotomously forked. *Sporangia* about 1 mm broad. Guatemala to Ecuador; from about 50 to 900 m on the Atlantic slope of Costa Rica.

Lycopodium dichaeoides is known from a single collection at La Selva, in upland primary forest.

3. **Lycopodium dichotomum** Jacq.
(=*Huperzia dichotoma* (Jacq.) Trev. St. Léon; *Urostachys dichotomus* (Jacq.) Herter)

Epiphytic, often pendent (but rigidly so), the plants mostly 8–25(–50) cm long. *Stems* 2–5 mm thick, 2–6 times dichotomously branched. *Leaves* uniform, numerous and in many ranks, linear, 10–20 mm long and 0.7–1.4 mm broad. *Sporangia* reniform, 1.5–2 mm broad, borne in upper axils. Southern Mexico to Brazil, Florida, West Indies; from 50 to 1,100 m in Costa Rica, on both slopes. Occasional as a canopy epiphyte in primary upland or alluvial forest; a squatter, darker green, relatively leafier and less flaccid plant than *Lycopodium linifolium.*

4. **Lycopodium linifolium** L.
(=*Huperzia linifolia* (L.) Trev. St. Léon; *Urostachys linifolius* (L.) Herter)

Epiphytic, limply pendulous, the plants 10–80 cm long. *Stems* 0.7–1.4 mm thick, obscurely 2–8 times dichotomously branched. *Leaves* uniform, linear and often slightly falcate, spiraled in few ranks and comparatively distant, light green, 12–25 mm long and 1–3 mm broad. *Sporangia* reniform, 1–1.5 mm broad, borne in upper axils. Southern Mexico to Brazil, West Indies; widespread in Costa Rica from 0 to 2,100 m.

Occasional at La Selva as a high canopy epiphyte, sometimes found low down as on boughs overhanging creeks.

This is our most familiar *Lycopodium* species; large specimens of *L. linifolium* are quite striking, and are sometimes gathered as household decorations by local people.

2. SELAGINELLACEAE

Generally terrestrial or epilithic plants, creeping to erect or (elsewhere) scandent, usually much branched. *Rhizophores* produced from at least the lowermost nodes. *Leaves* numerous, tiny and

1-veined, monomorphic and spirally arranged or (in ours) dimorphic and dorsiventrally two-ranked (with larger, spreading "lateral leaves" and smaller, appressed "median leaves"). Minute *ligule* borne in the axil of each leaf. *Sporophylls* somewhat dissimilar from foliage leaves, arranged in terminal, four-ranked strobili. *Sporangia* borne in axils of sporophylls, of two kinds (the plants heterosporous, usually monoecious). *Gametophytes* retained within spore walls. A single genus.

1. SELAGINELLA P. Beauv.

ALSTON, A. H. G. 1955. The heterophyllous *Selaginellae* of continental North America. Bull. Brit. Mus. (Nat. Hist.), Bot. 1: 219–274.

Characters of the family. A huge, chiefly tropical genus of 600–700 species, about 270 of which occur in the New World from Alaska to Argentina. About 33 species are known from Costa Rica. *Selaginella potaroensis* Jenman has been collected from Finca El Bejuco, near Chilamate.

KEY TO THE SPECIES

1. Plants erect, with a distinct stem on which the leaves are appressed, spiraled and monomorphic; rhizophores borne only at the base of the stem, never from above the lowest branching point.
   2. Branching pattern generally simply pinnate at La Selva; leaves bicolored, with a silvery-satiny sheen below; both lateral and median leaves long-ciliate along the margins; rare, along creeks. . . . . 4. *S. bombycina.*
   2. Branching pattern bipinnate to tripinnate; leaves not strongly bicolored; median leaves never long-ciliate.
      3. Main stem and secondary stems articulated, with conspicuous, swollen, reddish nodes; very common. . . . . 2. *S. arthritica.*
      3. Stems lacking swollen nodes.
         4. Main stems strongly reddened, less than 2 mm thick at the base; plants small, less than 30 cm tall. . . . . 9. *S. umbrosa.*
         4. Main stems green, more than 2 mm thick at the base; plants large, generally more than 30 cm tall.
            5. Lateral leaves strongly ciliate, at least toward base; ultimate branches (including leaves) less than 4 mm wide. . . . . 1. *S. anceps.*
            5. Lateral leaves obscurely denticulate; ultimate branches more than 4 mm wide. . . . . 7. *S. oaxacana.*
1. Plants creeping to weakly ascending, without a well defined stem; leaves dimorphic and two-ranked throughout; rhizophores borne along the stem to well above the lowest branching point.
   6. Plants delicate, creeping to horizontal or arching, less than 15 cm long; lateral leaves toward base of main axis less than 3.5 mm long; ultimate branches less than 4 mm wide (including leaves).
      7. Median leaves long-acuminate at the apex, symmetrical at the base, without basal auricles; main axis often much prolonged. . . . . 6. *S. flagellata.*
      7. Median leaves merely acute at the apex, very asymmetrical at the base, with the auricle on one side much enlarged; plants creeping. . . . . 3. *S. atirrensis.*
   6. Plants coarser, weakly erect, more than 15 cm long; lateral leaves toward the base of the main axis more than 3.5 mm long; ultimate branches more than 4 mm wide.
      8. Median leaves very asymmetrical at base, with one auricle much longer than the other; lateral leaves broad at the base, with very short, ciliolate auricles; common. . . . . 5. *S. eurynota.*
      8. Median leaves symmetrically attached, the auricles very short and subequal; lateral leaves constricted basally, exauriculate; very rare. . . . . 8. *S. silvestris.*

1. **Selaginella anceps** C. Presl

Plants erect, 35–70 cm tall, the basal, homophyllous (unbranched) portion 14–35 cm long. *Rhizophores* produced only at base of stem. *Homophyllous leaves* appressed, lanceolate, ovate or deltate, 2–3.5 mm long, ciliate. *Lateral leaves* spreading-erect, 2–3 mm long, abruptly truncate at base, the margins ciliate toward the base. *Median leaves* asymmetrically ovate, inaequilaterally cordulate at base, acute at apex, 1–2.5 mm long. *Strobili* 0.5–3.5 cm long. Costa Rica to Bolivia; widespread in Costa Rica from 0 to 1,400 m.

Scattered and not particularly common at La Selva, though conspicuous. Known mainly from damp sites in secondary forest and disturbed primary forest on recent alluvium; in several sites, it grows side by side with *S. oaxacana,* with which it is easily confused. The latter is a somewhat coarser plant with darker green foliage.

2. **Selaginella arthritica** Alston

Plants erect, 10–40 cm tall, the *stem* often long-decumbent at base; basal, homophyllous (unbranched) portion of stem 4–27 cm long. *Rhizophores* produced only along decumbent portion and base of erect portion. *Homophyllous leaves* appressed or somewhat spreading, ovate, ca. 3 mm long, inaequilateral at base, the margins subentire. *Lateral leaves* narrowly ovate to lanceolate, 2–5 mm long, narrowly obtuse at apex, inaequilaterally truncate at base, the margins entire. *Median leaves* narrowly and inaequilaterally ovate, 2–3 mm long, acute at apex, with one enlarged basal lobe. *Strobili* 0.5–2 cm long. Nicaragua to Panama; widespread from 0 to 1,400 m in Costa Rica, on both slopes.

Common in secondary growth and abandoned

cacao and banana plantations on recent alluvium. The erect habit and reddish, swollen nodes separate *S. arthritica* from all our other species.

3. **Selaginella atirrensis** Hieron.

Stems creeping, heterophyllous and rhizophorous throughout. *Lateral leaves* lanceolate, 1.7–2.5 mm long, subacute at apex, broadly cuneate to rounded at base, the margins entire or obscurely serrulate to ciliate (larger leaves) toward base. *Median leaves* asymmetrically lanceolate, acute at apex, with one enlarged basal lobe. *Strobili* 2–12 mm long. Costa Rica to Venezuela and Peru; from 50 to 2,100 m in Costa Rica, on the wetter parts of the Caribbean slope.

A delicate, inconspicuous, creeping species, fairly common along the rivers and lower portions of the major quebradas. It is our only *Selaginella* that does not, in some manner, contrive to raise itself off the ground.

4. **Selaginella bombycina** Spring

Plants erect, 16–46 cm tall, the basal, homophyllous (unbranched) portion 1–18 cm long. *Rhizophores* produced only at base. *Leaves* bicolored, more or less silvery below. *Lateral leaves* spreading, 6–8 mm long, lanceolate, acute at apex, rounded at base, the margins villous toward base. *Median leaves* narrowly and inaequilaterally ovate, cuspidate at apex, broadly cuneate at base, the margins irregularly villous-ciliate. *Strobili* 0.5–1.5 cm (or more) long. Costa Rica to Peru; from 50 to 800 m in Costa Rica, restricted to very wet areas on the Caribbean slope.

An almost exclusively epilithic species, *Selaginella bombycina* is quite rare at La Selva, occurring only in rapid sections of quebradas in primary forest toward the back of the property. Plants from higher elevations are often larger and more extensively (bi- to tripinnately) ramified, and may rarely be seen as low trunk epiphytes.

5. **Selaginella eurynota** A. Braun
(=*S. horizontalis* (C. Presl) Spring ssp. *eurynota* (A. Braun) Somers comb. ined.)

Plants heterophyllous throughout, arching or weakly erect to sprawling, much branched. *Rhizophores* produced from the upper stem surface, for half or more its length. *Lateral leaves* widely spreading, 3–6 mm long, narrowly lanceolate, acute, more or less cordate at the base with short, ciliolate auricles. *Median leaves* 1.5–3 mm long, peltate and very asymmetrical. *Strobili* 3–13 mm long, produced mainly from November to January. Chiapas to Panama; widespread in Costa Rica from 0 to 1,500 m.

A common, weedy species at La Selva, occurring in most of the same habitats as *S. arthritica.* These are our two most abundant *Selaginella* species in heavily frequented habitats.

6. **Selaginella flagellata** Spring

Plants heterophyllous throughout, the *stems* prostrate or arching, much branched, the main lateral branches gradually reduced to the frequently flagelliform apex. *Rhizophores* produced from the lower stem surface throughout. *Lateral leaves* 1.5–3 mm long, ovate, acute at apex, truncate to rounded or subcordulate at base, the margins serrulate toward base. *Median leaves* 1–1.5 mm long, inaequilaterally ovate, acuminate to caudate at the tip, broadly cuneate to rounded at the base. *Strobili* 3–8 mm long. Mexico to the Guianas and Bolivia, Trinidad and Tobago; widely distributed from 0 to 3,000 m in Costa Rica.

A common, weedy species along trails and in abandoned cacao groves on recent alluvium; the plants are basically terrestrial, but also grow on damp wood, stones and even concrete. They are most commonly seen along drainage ditches, the rather narrow, deep green "fronds" arching out over the void. Occasional specimens become epiphytic, ascending the trunks of understory shrubs or treelets to at least 1 meter.

7. **Selaginella oaxacana** Spring

Plants erect, bushy, 30–75+ cm tall, homophyllous below the first branching point, otherwise heterophyllous. *Rhizophores* produced from the lower surface of the stem, few and strictly basal. Basal, homophyllous (unbranched) part of *stem* about 20–50 cm long. *Homophyllous leaves* 3–4 mm long, appressed, deltate to lanceolate. *Lateral leaves* 2–7 mm long, oblong to lanceolate, subacute at the apex, rounded at base, the margins subentire. *Median leaves* 1–6 mm long, ovate, acuminate, cordate at the base. *Strobili* to 1–3.5 cm long. Oaxaca to Ecuador; from 0 to 1,500 m in Costa Rica, on both slopes.

Occasional in damp sites in secondary forest and disturbed primary (mostly swamp) forest on recent alluvium. This is our largest and most striking species of *Selaginella,* edging out *S. anceps* for that particular honor. The two species share the same habitat, and often grow intermingled. Our specimens are somewhat larger and coarser than material from higher elevations.

8. **Selaginella silvestris** Aspl.

Plants heterophyllous throughout, the *stems* arching to suberect or sprawling, much branched.

Rhizophores produced from the upper surface of the stem for ¼ to ⅔ its length. *Lateral leaves* 3–4 mm long, elliptic, obtuse to subacute at apex, rounded at base, the margins subentire. *Median leaves* 1.5–2.5 mm long, narrowly ovate, aristate at apex, cordulate at the base. *Strobili* 3–10 mm long. Southern Mexico to Bolivia; widely distributed in Costa Rica from 0 to 2,100 m.

Extremely rare or overlooked at La Selva, known from two collections in disturbed secondary forest on recent alluvium: near the Sendero Ribereño, and along the West River Road, near Discovery Woods.

9. **Selaginella umbrosa** Lemaire ex Hieron.

Plants stoloniferous, homophyllous up to the first branching point, otherwise heterophyllous, generally 20–25 cm tall at La Selva; lower (unbranched) *stem* deep reddish, 4–15 cm long. *Rhizophores* produced from the lower stem surface, strictly basal. *Lateral leaves* 1–3 mm long, ovate to lanceolate, acute at apex, inaequilaterally truncate to cordulate at base, the margins long-ciliate toward base. *Median leaves* 0.8–1.2 mm long, asymmetrically ovate, acute at apex, broadly cuneate to cordulate at the base. *Strobili* 3–20 mm long. Guatemala and Belize to Brazil, West Indies; from 0 to 300 m on the Caribbean coast of Costa Rica.

Selaginella umbrosa is abundant at La Selva along rivers and even the smaller quebradas; it is frequently epilithic, or growing on logs or trunk bases. This is the smallest and most delicate of our "arborescent" *Selaginella* species, and is easily recognized by its reddish stems.