fiddlehead forum

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Clubmosses (Lycopodium) in North America by Joseph Beitel*

The clubmoss genus Lycopodium, in the broad sense (sensu lato), is best defined as homosporous vascular plants exhibiting a pteridophytic mode of life (alternation of generations) with a dominant sporophyte generation possessing spirally-arranged microphylls (single-veined leafy appendages), reniform sporangia in the axils of the microphylls, and protosteles. This will serve to distinguish clubmosses from the related genera of lycopods, which are either heterosporous (Isoetes, Stylites, and Selaginella) or possess a pith (Phylloglossum).

The members of this large genus (over 400 species) are found on every continent (except Antarctica), ranging from 81° 43' N (Ellesmere Island) south to Tierra del Fuego. In elevation they occur from the lowland tropics up to the alpine zone of most mountain chains. They live in almost every conceivable land habitat except deserts. They occur in bogs, swamps, forests, cliffs, and tundra, and live on trees in the tropics as epiphytes.

Like other pteridophytes, the clubmosses exhibit alternation of generations with the spore-bearing plant (sporophyte) being the dominant generation, the one that most people are familiar with. The morphology of the sporophyte is extremely diverse, and a representative sample of the diversity is found in the North American species. The spores germinate under proper conditions to produce the gametophyte, the generation that produces the gametes. The diversity in gametophyte morphology in Lycopodium is as great as the diversity in sporophyte morphology, with five basic types of gametophytes.

The taxonomic categories in Lycopodium s.1. have been the subject of much controversy, both at the species and at the generic level. There have been many attempts at organizing the diverse members of the genus Lycopodi- $\mathit{um}\ s.l.$ into natural groups, whose status has ranged from sections within subgenera up to separate families. There will always be differing opinion among taxonomists as to what constitutes a genus. The taxonomists who recognize the various splinter genera point out the great diversity, especially in the tropics, in sporophyte morphology, spore type, gametophyte morphology and chromosome number among the members of the genus Lycopodium s.1. The only other families of pteridophytes which possess both members with superficial, green gametophytes and members with subterranean, mycorrhizal gametophytes, are the Schizaeaceae and Gleicheniaceae. It can be argued that the profoundly different biologies of the various groups are obscured by submerging those differences at the subgeneric level and are better reflected in treating them as separate genera.

These arguments are countered by the conservative element among ${\it Lycopodium}$ taxonomists who feel that the differences do not warrant generic recognition. The

genus Lycopodium as it stands can be recognized at a glance. According to these taxonomists, the minor specializations in vegetative morphology need not be given generic rank, differing chromosome numbers are not a sufficient basis for splinter genera, and the entire range of spore types seen in Lycopodium s.1. can be found in a single genus, Isoetes.

Various authors have felt that gametophyte type is not a significant taxonomic character, a view bolstered by the experiment of Freeberg and Wetmore (1957) in which the gametophyte differences in Lycopodium were shown to be environmentally controlled. However, when Whittier (1975) cultured L. obscurum spores in sterile medium, the gametophytes retained the morphology of the subterranean, mycorrhizal gametophytes found in nature. A careful re-evaluation of the Freeberg-Wetmore experiment, examining actual material from the experiment and comparing gametophytic and sporophytic characters (Bruce, 1975), showed the Freeberg-Wetmore conclusions to be in error. Thus, for almost twenty years, one of the biologically more significant taxonomic characters had been down-played to the point of complete discredit.

The gametophytic differences, when viewed in concert with the differences in sporophytic morphology, chromosome number, and spore morphology, provide a strong case for generic recognition. The fact that the differences in almost every stage of the life cycle are correlated makes even a stronger case. This raises the other problem which has contributed to the rejection of consideration of the splinter genera in Lycopodium s.1. The bulk of the species in this large genus are tropical and little is known about such characters as gametophyte type or chromosome number. The fact that most temperate botanists are not familiar enough with the diversity of the tropical lycopods, coupled with the uncommonness of Lycopodium gametophytes, accounts for some of the unwillingness to accept the segregate genera. Much more work needs to be done before our knowledge is even close to being complete, but that does not seem a tenable reason to ignore the biological diversity already observed. The diversity exhibited in the adaptive radiation of the lycopods can be used to teach valuable biological lessons if presented in an orderly and manageable system. In the interest of doing that, I will discuss the separate genera, followed by consideration of the individual species contained within that genus.

Problems in Lycopodium are not restricted to the generic level, but are rampant on the level of species

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recognition. There are three basic reasons for confusion at the level of species. One is the nature of the characters which are used to distinguish species. These characters are often extremely subtle, such as the size of ventral leaves compared to the lateral leaves. The second reason deals with the effects of environment on the various characters. Sun and shade forms in Lycopodium are well known. The species growing in the sun will be more upright, in the shade more lax and spreading. This can be observed in a single clone in which a portion is in the sun and a portion is in the shade. Unless one is familiar with the range of variation found in the species in various environments, the species may appear to overlap.

The third problem is that of hybridization which has occurred to various degrees among the clubmosses. Due to the predominance of vegetative reproduction over sexual reproduction, once a hybridization event occurs, the hybrid, no matter how sterile it is, may outnumber either of its parents by sheer vegetative propagation. The chances of a hybridization even occurring are increased by the fact that most clubmosses reproduce best in disturbed situations and often form genus communities in those situations. Thus, the subtle species characters, whose natural variability has already been compounded by environmental effects, have another level of variation added, that of hybrid intermediacy. It is often difficult to sort out which effect is which, especially if one is looking at a dried specimen on a herbarium sheet. Herbarium specimens reveal little about the variation in the population or the environmental situation where it was collected. Careful field studies of the species in various environments and how they interact with other species are necessary when dealing with clubmosses.

LYCOPODIUM s.s. (sensu stricto)

The sporophytes of this group are characterized by successive unequal forkings, or dichotomies (anisodichotomies), of the shoot, resulting in a creeping horizontal stem (rhizome) and upright branched stems, which are covered with spirally arranged leaves in 6-10 ranks. These leaves are not fused along their length to the stems, and the plants are evergreen. The sporangia are borne in the axils of modified leaves (sporophylls) aggregated into strobili (cones), which are either sessile or on long, naked stems (peduncles). The spores are covered with high ridges which join to form a network (reticulum). The gametophytes which have been found in this group (L. annotinum, L. obscurum, L. dendroideum) are subterranean (and therefore mycorrhizal) and basically disc-shaped. The edges of this disc become convoluted with age, producing what looks like a brownish walnut meat. The chromosome numbers in this group are based on n=34.

Lycopodium clavatum L.

(Staghorn clubmoss, wolf's claw clubmoss, common clubmoss)

Range: Circumboreal and isolated populations in tropical and subtropical mountain ranges of both New and Old Worlds; w. to Alaska, e. to Greenland, s. to n.w. Calif., n.w. Mont., Minn., Wisc., Mich., and in Appalachians s. to N.C. & Tenn.

Habitat: Acidic soils in open coniferous and deciduous woods, thickets, and swamp margins.

Surficial rhizome with forked upright branches, resembling deer antiers. Leaves in 10 ranks, giving the branches a cylindrical look. Each leaf tipped with a long (3 mm), colorless hair. Strobili borne on long, naked peduncles produced at the tips of upright branches. Each peduncle in the typical variety bears two to several strobili. \underline{n} =34.

One of the most common clubmosses, this species is

the type for the genus Lycopodium. The major problem with the species in North America is the status of the var. monostachyon Hook. & Grev. The question of whether this northern taxon should be considered as a species, variety, or merely a form points out a problem common to many species of Lycopodium. There is often a zone of overlap between the northern taxon and its southern counterpart in which the two remain distinct. The northern taxon, which ranges only as far south as n. Mich., n. Minn., and n. New England, characteristically has one strobilus per peduncle, shorter peduncles, and more appressed leaves. In the northern part of Canada it becomes the dominant taxon.

Lycopodium annotinum L.

(Bristly clubmoss, stiff clubmoss)

Range: Circumboreal; w. to Alaska, e. to Greenland, s. to n.e. Oregon; n.w. Wyo. (disjunct in Colorado 8,000-11,000 ft), Minn., Wisc., Mich., and in Appalachians to s.w. Va.

 ${\it Habitat:}$ Acidic soils in moist coniferous and deciduous woods, rocky barrens.

Surficial rhizome with simple or few-forked upright branches showing annual constrictions. Serrate leaves broadest in middle, in 8 ranks and spreading widely from stem. Strobili solitary and borne at the tips of upright branches. n=34.

Vying with L. clavatum as the most common clubmoss in many parts of its range, it is often confused with L. lucidulum (which neither branches anisodichotomously nor has a strobilus). The variety pungens (La Pylaie) Desv. ranges south to n. New England at high elevation, becoming more prevalent further north. This variety has appressed leaves that are smaller (3-6 mm) and entiremargined. This parallels the problem in L. clavatum and deserves careful study.

Lycopodium obscurum L.

(Tree clubmoss, princess pine)

Range: Eastern North America; s. to Alabama & S.C., w. to Minn., n. to Ont., Que., & Nova Scotia.

Habitat: Acidic soils in deciduous and coniferous woods, less commonly in thickets and swamp margins.

Subterranean rhizome with much-branched upright portions, resembling small trees. Leaves needle-like in 6 ranks (1 dorsal, 1 ventral, and 4 lateral ranks). Leaves of lower portion of main aerial axis closely appressed. Strobili 1-10 per aerial shoot, sessile on main axis or lateral branch systems. <u>n=34</u>.

The Lycopodium obscurum complex, consisting of this species, a newly described var., L. obscurum var. isophyllum, and the long-confused taxon Lycopodium dendroideum, has recently been studied by James Hickey (1977) and is discussed with the following species.

Lycopodium dendroideum Michx.
(Tree clubmoss, princess pine)

Range: Northern North America and Asia; n. to Alaska, N.W.T., and Labrador, e. to Newfoundland, s. to Wash., Mont., Iowa, Ill., Mich., & W.Va.

Habitat: Acidic soils in coniferous and deciduous woods, swamps, bogs, and barrens.

Similar to *L. obscurum* in form, except for arrangement of the 6 ranks of leaves (2 dorsal, 2 lateral, and 2 ventral ranks) and widely spreading leaves on the lower portion of the main aerial stem. n=34.

This species and the preceding have long been confused; the widespread, more northern L. dendroideum considered a variety of the eastern North American endemic L. obscurum. Imagining the branch section to be the clock face with 12 representing the upper surface of the branch and 6 the lower surface of the branch, L. obscurum has its leaf ranks at the even positions, whereas L. dendroideum has them at the odd positions. The upper surface of the branch of L. obscurum will show a single rank of leaves running its length, whereas L. dendroideum has two ranks running the length of the upper surface of the branch. L. obscurum var. isophyllum differs in having all 6 ranks of leaves equal in size, whereas L. obscurum var. obscurum has the ventral rank of leaves reduced. L. obscurum and L. dendroideum overlap in range, remaining distinct in the common area, often growing side by side.

DIPHASIASTRUM Holub

The sporophytes of this group are anisodichotomously branched with a creeping rhizome and upright branches, and are evergreen. The bulk of the species have 4 ranks of leaves (I dorsal, 2 lateral, I ventral) which are fused to the stem for much of their length, forming the flattened branches characteristic of this group. The primitive condition of 5-6 ranks is retained in the fertile branches and the rhizome leaves of all species, but is found in the vegetative branches of only a few species. The strobili are either sessile or on long. naked peduncles. The spores have a reticulate pattern. The gametophytes that have been found (L. complanatum, L. alpinum, and L. flabelliforme) are of the subterranean, mycorrhizal type, cone-shaped like tiny carrots. Chromosome number is based on $\underline{n}=23$. This segregate genus is most closely related to Lycopodium s.s. and is often combined with that group.

Lycopodium complanatum L. (Northern running-pine)

Range: Circumboreal; s. to Wash., n.w. Mont., n. Minn., n. Mich., n. N.Y., n. Vermont, & n. N.H., n.e. to Greenland, n.w. to Alaska.

Habitat: Acidic soils in coniferous and deciduous woods, tundra, alpine slopes.

Rhizome surficial to shallowly buried. Plants greenish in color. Branch dichotomies at irregular angles producing a "spidery" look. Branches 2-4 mm wide and showing annual constrictions where growth was renewed from previous year. Leaves in four ranks, fused for most of their length to stem. Ventral rank much reduced as compared to lateral ranks. Strobili produced on naked peduncles in groups of 1-4, with no sterile tips. n=23.

The members of the *L. complanatum* complex are best identified on the basis of a suite of characters rather than one distinctive character. This situation is compounded by the presence of hybrids between the various taxa. Hybrids of *L. complanatum* with *L. flabelliforme*, *L. tristachyum* and *L. alpinum* have been reported. *L. alpinum X complanatum* (*L. X issleri* (Rouy) Lawalrée) is an uncommon hybrid known only from scattered localities in Europe and one record in n. Maine. The hybrid *L. complanatum X tristachyum* (Diphasiastrum X zeilleri (Rouy) Holub) is common in the northern part of the range of *L. tristachyum*, such as n. Minnesota and Finland, where the hybrid far outnumbers *L. tristachyum*. It appears as a wide, spidery *L. tristachyum* with somewhat reduced ventral leaves or a narrow, bluish-green *L. complanatum* with large ventral leaves.

Lycopodium flabelliforme* (Fernald) Blanchard (Common running-pine)

Range: Eastern North America; n.e. to Newfoundland, w. to Minn. & Ky., n. to Ont. & Que., s. to n. Alabama & Ga.

Habitat: Acidic soils in woods and abandoned fields.

Rhizome surficial. Plants greenish in color. Branching dichotomous at regular angles creating a flattened, fan-shaped branch system. Branches 2-4 mm wide, growing only one season (no annual constrictions). Leaves in 4 ranks, fused for most of their length to the stem. Ventral rank much reduced as compared to lateral ranks. Strobili produced on long, naked peduncle, usually in groups of 3-4 with sterile tips on ca. 50% of specimens. n=23.

This eastern North American endemic was long considered a variety of *L. complanatum* although it is one of the most distinct species in this group. It rarely hybridizes with *L. complanatum* in the region of overlap with that species, the most common hybrid being with *L. tristachyum* (*L. X habereri* House), which occurs throughout the range of *L. flabelliforme. L. X habereri* has the constrictions, large ventral leaves, and slight bluish-green color of *L. tristachyum*. The branches are wider than those of *L. tristachyum* and fan-shaped as in *L. flabelliforme*.

Lycopodium tristachyum Pursh (Ground Cedar)

Range: Eastern North America and Europe; n. to Newfoundland & James Bay, w. to Minn. & Mo., s. to n. Ga. & n. Ala.

Habitat: Acidic soils in open woods, abandoned fields and pine barrens.

Rhizome deeply buried. Plants bluish-green (glaucous) in color. Branches strongly ascending (in sun) to spreading (in shade). Branches narrow (1-2 mm), showing annual constrictions where growth was renewed from previous year. Leaves in 4 ranks; ventral rank similar in size and shape to lateral ranks. Strobili produced on long, naked peduncle in groups of 3-4. n=23.

This species occurs in the most xeric habitats of all the clubmosses, living in dry oak woods and pine barrens as well as overgrown fields. It is known to hybridize with L. complanatum, L. flabelliforme, and L. sitchense (see discussion of hybrids under those those species.)

Lycopodium sitchense Ruprecht (Sitka clubmoss)

Range: Boreal and arctic North America and n.e. Asia, s. to Japan; s. in western mountains to Ore., Idaho, & Mont., s. in eastern North America to north shore of Lake Superior (Ont.), N.H. & Me., e. to w. Greenland, w. to Aleutians.

Habitat: Acidic soils in alpine meadows, sub-alpine forests, tundra, and boreal forest.

Rhizome surficial to shallowly buried. Branches ascending (in sun) to widely spreading (in shade), round in cross section with leaves free from stem for most of their length. Leaves spirally arranged in 5 ranks, equal in size. Strobili sessile on long fertile branches (not on naked peduncles). n=23.

Due to its northern distribution and most botanists' lack of familiarity with it, L. sitchense is confused with L. alpinum or L. sabinifolium. L. sabinifolium (cf.) is considered to be the natural hybrid between L. sitchense and L. tristachyum, which might explain some of the confusion.

^{*} An earlier name for this common species has recently been found and therefore must be used --Lycopodium digitatum A. Braun.

Lycopodium sabinifolium Willdenow (Savin-leaved clubmoss)

Range: North temperate and boreal eastern North America; w. to north shore of Lake Superior (Ont.), e. to Newfoundland, s. to Penn. and Mich.

Habitat: Open, disturbed areas in boreal forests and mountainous temperate regions.

Rhizome surficial to shallowly buried. Plants slightly bluish-green in color. Branches ascending (in sun) to widely spreading (in shade), flattened in cross section. Leaves free from stem for half of their length and arranged in 4 ranks. Ventral and dorsal surfaces of branch identical. Strobilus base indistinct; scattered sporophylls and sporangia straggling down naked peduncles, 1-2 strobili per peduncle. n=23 (questionable count; voucher identity not confirmed).

This eastern North American endemic is now considered to be the hybrid of L. sitchense and L. tristachyum, occurring where the ranges of the two parents overlap and possessing an intermediate morphology. The characteristic "vague" distinction between strobilus base and naked peduncle (i.e., the straggling sporangia) is the product of the hybridization of a sessile-coned species (L. sitchense) and a species with a distinct peduncle (L. tristachyum). The species characters of the three taxa involved are maintained in both their sun and shade forms. In gross form the sun form of L. sabinifolium is similar to that of L. sitchense and would most likely be confused with it if the species characters were not noticed. The same holds true for the shade form of L. sabinifolium and that of L. tristachyum. Common only in Que. & e. Ont.; rare in U.S. portion of range.

Lycopodium alpinum L. (Alpine clubmoss)

Range: Circumpolar in arctic and alpine areas; w. to Alaska, s. in western mountains to n. Wash. (Mt. Baker) and n.w. Mont. (Glacier Nat'l Park), s. in eastern North America to mountains of Gaspé (Que.), e. to Greenland.

Habitat: Acidic, alpine talus slopes and meadows, and arctic tundra.

Rhizome surficial to shallowly buried. Plants bluish-green (glaucous) in color. Aerial branches tufted and dwarfed. Leaves in 4 ranks and free from stem for much of their length. Ventral leaves trowel-shaped, lateral leaves with broad flange-like bases. Strongly recurved margins of lateral leaves meeting margins of trowel-like ventral leaves give the branches a rounded look. Strobili sessile on fertile branches (not on naked peduncle). n=23.

This northern species barely gets into the continental U.S. having been reported at high elevations at two localities in Glacier Nat'l Park, Montana, and one locality on Mt. Baker, Washington. Frequently confused with L. sitchense(cf.), the peculiar 4-ranked leaves of L. alpinum are easily distinguished from the isomorphic, 5-ranked leaves of L. sitchense. A hybrid with L. complanatum (L. X issleri) has been reported in Europe and n. Maine.

LYCOPODIELLA Holub

The species included in Lycopodiella (in the broad sense) share a certain number of features, but are highly diverse in others. These divergent features have been the basis for the segregation of the species into sections or even additional genera.

The sporophytes in *Lycopodiella* are found typically in open, sandy acidic marshes and wet meadows; they commonly occur in moist, roadside ditches and borrow pits. The sporophyte is deciduous, except for the rhizome tip

which over-winters as a swollen, subterranean storage organ. The spores are covered with shallow, rolling ridges (rugulate type). The gametophytes which have been described (L. inundatum, L. alopecuroides, L. carolinianum and L. cernuum) all resemble tiny, green pincushions growing on wet, mineral surfaces.

In the interest of clarity, the distinct features of the three species groups found in North America will be enumerated below.

Lycopodium inundatum group

The sporophytes of this group are anisodichotomously branched, with a creeping rhizome and unbranched, upright fertile branches. Both the creeping rhizome and fertile branches are covered with numerous ranks of spirally arranged leaves. The sporophylls are only slightly differentiated from the photosynthetic leaves, and are loosely aggregated into a strobilus at the end of the unbranched fertile branch. The chromosome number is based on \underline{n} =78.

The systematics of this group, which is extremely complex at the species level, is currently being studied by Dr. James Bruce (Univ. of Georgia). The species, other than L. inundatum, rarely grow alone and hybridization is rampant. The hybrids are intermediate in morphology and occur in most populations. Two new tetraploid species have been detected in the Great Lakes region and at least one of the undescribed tetraploids occurs along the northern Atlantic Coastal Plain (Bruce, 1975). The Coastal plain from Long Island, NY to Cape Cod, Mass. has one of the largest numbers of taxa in this group: four species (L. inundatum, alopecuroides, appressum & the new tetraploid) and the 6 possible hybrid combinations.

Lycopodium inundatum L. (Bog clubmoss)

Range: Circumboreal; w. to Alaska, e. to Labrador, s. in western North America to n.w. Calif. & Mont., s. in eastern portion of range to ill. & Mich., n.e. N.J. (on coastal plain) and Va. (in the Appalachians).

 ${\it Habitat:}\ {\it Acidic, sandy shores of ponds, wet meadows and sphagnum bogs.}$

Creeping rhizome thin, 0.6-1.2 mm wide without leaves, prostrate. Upright fertile branches up to 10 cm tall, usually less than 8 cm; strobilus accounting for ca. $\frac{1}{2}$ the height of fertile branch. Peduncle leaves and sporophylls widely spreading, strobilus 6-10 mm wide. \underline{n} =78.

The taxon segregated in the past as *L. inundatum* var. *bigelovii* has been shown to be the northern populations of *L. appressum* (cf.). *L. inundatum* var. *robustum* probably represents the hybrid combination *L. alopecur-oides X inundatum*.

Lycopodium appressum (Chapman) Lloyd and Underwood
 (Appressed bog clubmoss, southern clubmoss, Chapman's clubmoss)

Range: Eastern North America, chiefly Gulf and Atlantic coastal lowlands; w. to Texas & Ark., s. to Fla., n. to Newfoundland (disjunct population in w. Kentucky).

Habitat: Acidic, sandy shores of ponds, wet meadows, and sphagnum bogs.

Creeping rhizome thick, 1-4 mm wide without leaves, prostrate. Upright fertile branches up to 30 cm tall; strobilus accounting for less than $\frac{1}{4}$ the height of fertile branch. Peduncle leaves and sporophylls tightly appressed, strobilus 3-4 (5) mm wide. n=78.

The northern populations of this species were formerly segregated as *L. inundatum* var. *bigelovii* due to their smaller stature. The records of this species from the Great Lakes region as well as some of the records of *L. appressum* from the n. Atlantic Coastal Plain represent the two undescribed tetraploid species (Bruce, 1975). The disjunct population of *L. appressum* in w. Kentucky occurs with the hybrid combinations *L. alopecuroides X appressum* (*L. X copelandii*) and *L. appressum X prostratum*, with neither of the parents present (Bruce, 1975).

Lycopodium alopecuroides L. (Foxtail clubmoss)

Range: Eastern North America (chiefly Atlantic and Gulf coastal lowlands), Central and South America; w. to Tex., s. to Fla., n. to Cape Cod, Mass.

Habitat: Acidic, sandy shore, wet meadows and pineland swamps.

Creeping rhizome thick, 2.5-3.5 mm wide without leaves, usually strongly arching. Upright fertile branches up to 25 cm tall, shorter in northern part of range; strobilus usually accounting for less than 4 the height of fertile branch. Peduncle leaves and sporophylls widely spreading, strobilus 15-20 mm wide. n=78.

Disjunct population of L. alopecuroides X appressum (L. X copelandii Eiger) occurs in w. Kentucky with L. appressum, but without L. alopecuroides.

Lycopodium prostratum Harper (Meadow clubmoss, prostrate clubmoss)

Range: Southeastern coastal plain of North America, Gulf and Atlantic lowlands; w. to Texas, n. to N.C.

Habitat: Acidic, sandy shores of ponds, wet meadows, and pineland swamps.

Creeping rhizome thin, 1-2 mm wide without leaves, prostrate. Upright fertile branches up to 25 cm tall; strobilus accounting for less than $\frac{1}{4}$ the height. Peduncle leaves ascending, sporophylls widely spreading; strobilus 12-20 mm wide. n=78.

Disjunct population of *L. appressum X prostratum* occurs in w. Kentucky with *L. appressum*, but without *L. prostratum*.

Lycopodium carolinianum group

Only one species in this pantropical coastal species complex occurs in North America. See *Lycopodiella* for common features.

Lycopodium carolinianum L. (Carolina clubmoss, slender clubmoss)

Range: Part of pantropical species complex; w. to Tex., s. to Fla., n. to Mass., confined chiefly to coastal plain.

Habitat: Acidic, sandy shores, wet meadows, and roadside
ditches.

Creeping rhizomes with unbranched fertile branches. Rhizome leaves in 3-5 ranks; 2 lateral rows of large, falcate leaves and 1-3 dorsal rows of smaller leaves. Fertile shoots slender, straw-colored at maturity, 10-25 cm tall; with scattered, reduced leaves in pseudo-whorls of three. One compact strobilus produced per fertile shoot. $\underline{n}=35$, 70.

The compact strobili, naked peduncle, strongly dimorphic rhizome leaves and differing chromosome number separate this group from the members of the L. inundatum

group. Diploid and tetraploid races exist, with triploid plants having abortive spores produced when two different ploidy levels hybridize.

Lycopodium cernuum group

Only one member of this pantropical complex of weedy species occurs in the southern U.S. See *Lycopodiella* for common features. This group has been segregated from *Lycopodiella* as the genus *Palhinhaea* Holub.

Lycopodium cernuum L. (Nodding clubmoss)

Range: Pantropical; scattered colonies in Fla., s. Ga., s. Ala., s. Miss., central and s.e. La.

Habitat: Acidic streambanks, roadside ditches and disturbed, moist roadbanks.

Erect, Christmas tree-like stem, much branched to 30 cm tall. Aerial stolons rooting at intervals, creating vine-like growth. Leaves spirally arranged in many ranks. Sessile, compact strobili (5-10 mm long) produced at drooping tips of branches of erect stem. n=104, 110, 136, 156, ca. 165, ca. 170, 208 (chromosome counts from entire species complex).

The rare, scattered populations of *L. cernuum* represent the northern limit of this pantropical weed. It is commonly seen in tropical regions forming dense growths on disturbed roadbanks.

HUPERZIA Bernhardi

The sporophytes of this group characteristically divide equally into two branches (isodichotomous); consequently, there is no differentiation within this group of creeping rhizome and erect branches (except in a few primitive species). Leaves are in many ranks and are spirally arranged. New roots are produced near the tip of the stem and burrow through the stem cortex, emerging at the soil level. The sporangia are borne either in the axils of unmodified or slightly modified sporophylls arranged in zones on the stem, or in dangling tassels (in some rainforest epiphytes). Spores are ornamented with small pits (foveolate-fossulate). The subterranean, mycorrhizal gametophytes have sterile, multicellular hairs (paraphyses) associated with the gametangia.

This large group is in need of study since much basic knowledge, such as chromosome number and gametophyte morphology, remains unknown for the bulk of the species. For example, the gametophytes of only seven species in this group of over 300 species have been reported. There is also great diversity within <code>Huperzia</code> which is evident even in the two groups found in North America, with many more groups in the tropics.

Lycopodium selago group

Members of this group are terrestrial or epipetric. Plants are evergreen. Branches strictly isodichotomous. Extensive vegetative reproduction is achieved by means of 3-lobed bulblets (gemmae), produced in zones near the apex. They are dislodged by rain or wind, and subsequently root. The gametophytes described (L. selago, L. lucidulum) are unbranched, bilateral rods which are subterranean and mycorrhizal.

Much of the confusion in the systematics of this group comes with sorting out the variation caused by inheritance, environment, and hybridization. Abortive-spored hybrids (which are presumed to be sterile) are commonly found, often with only one of the parents.

These hybrids can reproduce vegetatively by gemmae, and even outnumber their parents. Many hybrids have been dismissed in the past as environmental forms, such as the catch-all taxa L. selago var. patens and L. lucidulum var. occidentale, into which L. porophilum, L. selago, L. lucidulum X porophilum and L. lucidulum X selago have been lumped in the past. The classification presented here is a tentative system based on research in progress on the L. selago complex as part of my doctoral thesis.

Lycopodium lucidulum Michaux (Shining clubmoss)

Range: Eastern North America; w. to Minn. & Ark., e. to Newfoundland, n. to north shore of Lake Superior (Ont.) and Gaspé (Que.), s. to n. Ala. & n. Ga.

Habitat: Deciduous and coniferous forests.

Erect shoots becoming decumbent and rooting, often forming large colonies. Plants dark green in color. Leaves spreading to highly reflexed. Pronounced difference in size of sporophylls and vegetative leaves, causing shoot to have undulating outline. Leaves up to 12 mm long, broadest in middle with toothed margins. No stomates on upper surface of leaf. Lateral lobes of gemmae broad with apiculate tips.

Commonly found in rich, temperate and boreal forests, often forming large fairy rings with 15-20 years of growth evident on stems. Hybrids with *L. selago* and *L. porophilum* usually found with rarer parent, even if *L. lucidulum* is not evident. Hybrids not usually found if *L. lucidulum* is only parent present.

Lycopodium porophilum Lloyd & Underwood (Rock clubmoss)

Range: Central eastern U.S.; n.w. to Driftless Area (Wisc. & Iowa), n. to Ohio & Penn., s. to n. Alabama, w. to Missouri. Colonies disjunct throughout entire range due to scattered nature of specialized habitat.

Habitat: Moist, moss-covered, acidic sandstone cliffs and ledges; usually in the shade of an evergreen, such as hemlock or white pine.

Erect shoots forming a tuft, shoots on older individuals becoming somewhat decumbent. Plants green in color, becoming yellowish at base of older plants. Leaves spreading, shoot 10 mm in diameter. Slight undulation in outline of shoot due to difference in sporophyll size. Leaves ca. 8 mm long, parallel-sided (linear-lanceolate); few, if any teeth. Stomates on upper surface of leaf. Lateral lobes of gemmae narrow with acute tips.

This taxon has been badly confused with *L. lucidulum* and *L. selago*, having been made a variety of each at one time or another. *L. porophilum* is rare due to the rarity of acidic sandstone cliffs, such as those found in the Hocking Valley (Ohio), the Driftless Area (Wisc.), the Red River Gorge (Ky.) or the Sipsey River area (Alabama). Hybrids with *L. lucidulum*, intermediate in morphology and abortive-spored, may actually outnumber *L. porophilum* on sandstone cliffs.

Lycopodium selago L. (Fir clubmoss, mountain clubmoss)

Range: Arctic, boreal and alpine North America and Eurasia; w. to Alaska, e. to Greenland, s. in western mountains to Ore., Mont., & Colo., s. in eastern portion of range to n. Minn., n. Wisc., n. Mich. and widely scattered colonies at high elevation in Appalachians from New England south to n. Ga.

Habitat: Acidic soils; arctic tundra, boreal swamps and bogs, alpine meadows and open, rocky outcrops (igneous) at high elevation.

Leaves broadest at base with entire (non-toothed) margins. Many stomates present on upper surface of leaf.

Lycopodium selago in the broad sense and its varieties in North America represent a complex of species, hybrids, and environmental forms. The range, habitat and description is for the collective species. The various taxa included in L. selago are best summarized at this time as follows:

var. selago: Boreal swamps and bogs, lowlands; boreal N. America, Wash. to Newfoundland, s. to Mich., Wisc. & Minn. Erect shoots often becoming decumbent. Plants green in color. Leaves ascending (sun) to spreading (shade), 8 mm long, uniform in size with alternating zones of fertile and sterile leaves. Lateral lobes of gemmae broad.

var. appressum: Arctic tundra, alpine meadows, & open, rocky high elevation and boreal areas; arctic and alpine North America, s. in Rocky Mts. to Colo., s. to rocky coast of Lake Superior (Ont.), alpine areas of N.Y. & New England to Ga. Erect shoots densely tufted, becoming yellowish with age. Leaves 3-5 mm long, appressed except for juvenile leaves. Fertile shoot with leaves tightly appressed, ca. 5 mm in diam. Lateral lobes of gemmae narrow and acutely pointed.

var. miyoshianum: Coniferous forest, swamps, and bogs; northwestern North America, s. to Wash., e. to Mont., w. to Alaska. Erect shoots densely tufted. Leaves long (10 mm), needle-like, widely spreading to reflexed, uniform in size. Lateral lobes of gemmae narrow.

Abortive-spored hybrids between "varieties" of L. selago as well as with L. lucidulum are commonly found.

Lycopodium dichotomum group

Lycopodium dichotomum is the only representative of the group of Huperzia which has the most species: the epiphytic clubmosses. These plants root in the mosses and humus found on the trees in tropical rainforests, often dangling 5-6 feet down. Branching is strictly isodichotomous and the sporophylls may be differentiated and aggregated into pendent tassels or not. The epiphytic clubmosses for which gametophytes have been found have much-ramified, rod-shaped gametophytes, radially symmetrical in cross-section. These mycorrhizal gametophytes were growing on trees, buried in moss and humus.

Lycopodium dichotomum Jacquin (Hanging clubmoss) (not illustrated)

Range: Central America and the West Indies; found in 1934 in Collier Co., s. Florida.

Habitat: Epiphytic, on trunks and branches of trees in swamps and rainforests.

Cluster of pendent, isodichotomously branching shoots (30-60 cm long) arising from central mass of roots. Leaves lanceolate (1-2 cm), spirally arranged in many ranks. Sporophylls in zones along shoot. n=132.

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Lycopodium Identification Chart					
RUNNING PINE	FLATERANCH CLUBMOSS	GROUND CEDAR	ALPINE CLUBMOSS	SAVIN LEAF CLUBMOSS	SITKA CLUBMOSS
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Strongton U.	Sporphysis .	Sprapiyel F. T. T. T.	Sparophyll Amou	2.5.4m Spoophyll	Sperphyll 1.5-2 mm
L. flabelliforme	L.complanatum	L. tristachyum	L, alpinum	L.sabinaefolium	L.sitchense
TREE CLUBMOSS	STAGHORN CLUBMOSS	STIFF CLUBMOSS	SLENDER,CLUBMOSS	SOUTHERN CLUBMOSS	BOO CLUBMOSS
Bressilet Sterde keyl Sporophyll	Var Linderschauchguns (2) Sporophytt	Sporophyll var pungens	inverged isp Oms Horizontal storm Mailtontal storm side views Leaf of Sporohyll		Sproghyll Leaf sushus top colaryet
L.obscurum	L.clayatum	L.annotinum	L.carolinianum	L.appressum	L.inundatum
FOXTAIL CLUBMOSS	MEADOW CLUBMOSS	SHINING CLUBMOSS	ROCK CLUBMOSS	MOUNTAIN CLUBMOSS	NODDING CLUBMOSS
Sample Standard	Spaniphyll		100		Sim.
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L.alopecuroides	L.prostratum	L.lucidulum	L.porophilum	L.selago	L. cernuum



Enlargements of this chart (ca. 15x22" on ivory stock) are available at a cost of \$3, each. and extra copies of this issue of the FIDDLEHEAD FORUM can be obtained for \$1 each. Checks should be made payable to The American Fern Society and sent to John T. Mickel, New York Botanical Garden, Bronx, NY 10458.