

GENERIC CLASSIFICATION OF MODERN NORTH AMERICAN LYCOPODIACEAE¹

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ABSTRACT

Generic classification of North American Lycopodiaceae is analyzed in terms of the general factors that govern the recognition of the rank of genus, the character states that determine affinities, the hypothetical common ancestral groundplan, a tree based on these data, and a translation of this information into a classification scheme. The genera segregated here are based primarily on numerous characters of anatomy, chromosomes, spores, and gametophytes. Those groups that are recognized as genera have many distinguishing features, strong gaps separating them from other groups, monophyly, uniquely derived states, inability to hybridize, and a level of segregation consistent and comparable with generic division in other pteridophytes. The classification adopted is as follows: subfamily Huperzioideae (*Phlegmariurus*, *Huperzia*), subfamily Lycopodioideae (*Lycopodium*, *Diphasiastrum*), and subfamily Lycopodielloideae (*Pseudolycopodiella*, *Lycopodiella*, and *Palhinhaea*).

At the species level, the classification of North American clubmosses, all formerly placed in a single genus *Lycopodium*, has been altered radically since the eighth edition of *Gray's Manual* (Fernald, 1950). More rigorous definitions of species, and the inclusion of data from population biology, anatomical characters, cytogenetics, and interspecific hybridization, have been important factors in this change. Recently, a new question has arisen: What should be the classification at the generic level? The traditional classification has been challenged by such recent European workers as Pichi Sermolli (1977), Holub (1975, 1983), and Øllgaard (1987). The generic interpretation of Lycopodiaceae has also been influenced by researchers in North America including Beitel, Britton, Bruce, Hickey, F. Wagner, Whittier, and Wilce, who have contributed valuable new information on anatomy, spores, chromosomes, life cycles, habitats, and interspecific hybridization. In the following report we attempt to interpret this information.

We have asked the following questions: What criteria are used for recognition of genera in pteridophytes overall? What characters can be used to differentiate the groups of Lycopodiaceae in particular? What, if any, directionality can be deduced for each character trend? What were the character states of the probable ancestral source of modern Lycopodiaceae? How do the character

changes fit into a tree of relationships? And how should this body of information be translated into an acceptable classification scheme?

For nearly 20 years pteridologists were under the impression that the different gametophytic types reported in Lycopodiaceae were merely results of environmental modifications, as proposed by Freeberg & Wetmore (1957). The gametophyte was therefore considered unreliable as an indicator of relationships. However, Bruce (1976b) and Whittier (1981) showed that this conclusion was based on experimental error. For the past decade and a half, the gametophytic differences between species groups of Lycopodiaceae have proved to be valuable taxonomic characters (Bruce, 1972, 1976a, b, 1979; Bruce & Beitel, 1979). Other characters such as spore sculpture (Wilce, 1972; Tryon & Lugardon, 1990) and chromosome numbers (see F. Wagner, 1992) became available only during the past several decades. Also, Bruce (1975) provided data on mucilage canals, and Øllgaard (1975, 1979) new insights into the structure of the sporangium wall. Altogether, we now have a substantial array of new comparative data to aid us in classification.

In North America there are nearly 50 recognized species. Remarkably, approximately two-fifths of these are nothospecies as opposed to orthospecies, i.e., taxa of reticulate origin as opposed to

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those of normal divergent origin. For such a small clubmoss flora, there is, nevertheless, profound diversity, and as will be seen below seven discrete groups can be readily distinguished. The largest number of species in this family is in the tropics, where the family is made up largely of species related to *Phlegmariurus phlegmaria*. Only one of these is in North America, where it is found locally in southern Florida.

GENERIC DELIMITATION IN PTERIDOPHYTES

For generic delimitation there are far more gross morphological characters that can be used in angiosperms than in pteridophytes. Perhaps for this reason, workers familiar primarily with flowering plants have tended to lump Lycopodiaceae into one catch-all genus, simply because they all seem to look alike. However, when the plants are examined in detail, including many micromorphological characters, we rapidly become aware of multiple and often striking differences between pteridophyte groups. There are far more demonstrable differences between the groups of living Lycopodiaceae than between such filicean genera as *Dryopteris*, *Rumohra*, *Arachniodes*, *Polystichum*, and *Phanerophlebia* (Kramer & Green, 1990). If workers with Dryopteridaceae deal with the species groups of clubmosses and firmosses at the same level of generic discrimination, to maintain consistency they should accept seven genera of Lycopodiaceae in North America.

The reasons why taxonomists separate and recognize plant genera are numerous, and there is no widespread agreement on how to go about it. We have used the most dependable and objective criteria that we can adopt in delimiting the genera of Lycopodiaceae. They include the following: (a) The characters used for generic separation should be numerous, not only one or several. (b) It is imperative that there be strong gaps in the character patterns. There should be no intermediate taxa, whether these intermediates are produced by gradation in ordinary phylogenetic divergence or intermediates produced by interspecific hybridization. (c) No genus should be recognized if it can be shown that that genus arose from two or more sources, i.e., is polyphyletic whether by convergence or some form of reticulation. A genus should be monophyletic, with strong evidence for an immediate common ancestry of its species. (d) Lines should be based on uniquely derived character states. Parallelisms, convergences, and reversals can be used to bolster generic validity so long as their patterns and incidence show them clearly to

be separate, though similar, derived states. (e) More and more pteridologists regard the presence of "intergeneric" hybridization as evidence for not separating genera. If hybridization does occur between members of "different" genera, that is evidence for their taxonomic unity. In the case of Lycopodiaceae, there is no evidence of intergeneric hybridization, even though in some groups (e.g., *Diphasiastrum*, *Huperzia*, *Lycopodiella*) intra-generic hybridization is rampant. (f) Above all, good genera in one group of pteridophytes should be approximately equivalent to and comparable with genera in other groups. One family of pteridophytes should not be finely split and another be grossly lumped. The character states involved in generic separations in the Lycopodiaceae should be reasonably similar in number and kind to those used in other families of pteridophytes. For example, if we keep the following pairs separate, *Marattia* and *Angiopteris* (Marattiaceae), *Pellaea* and *Cheilanthes* (Adiantaceae), *Athyrium* and *Diplazium* (Dryopteridaceae), then, as will be mentioned below, we should certainly keep *Palhinhaea* separate from *Lycopodiella*, or *Diphasiastrum* from *Lycopodium*. There should be some consistency.

CHARACTERS USED FOR GENERIC PHYLOGENY AND CLASSIFICATION

In trying to develop a consistent taxonomy for Lycopodiaceae there are, of course, pitfalls. Dealing only with North American taxa could lead to erroneous conclusions because links in other parts of the world might be overlooked. However, we believe that the taxa elsewhere on the earth will either fit the generic system given here and can be easily accommodated within it, or new ones can be added to it (Holub, 1991; Øllgaard, 1987). Because of the gaps in the divergence patterns (Fig. 1), it is no problem to delimit the genera. Another potential pitfall in this, as in all, systematic syntheses, is incompleteness or lack of data. The fossil record, although perhaps rich in comparison with the majority of other plant orders, is still replete with vast lacunae. And the living record has not been completely examined, especially in the tropics and Southern Hemisphere. We recognize that future research may change our understandings and even our basic conclusions.

For determining character state polarities there is no single living genus or family that we can use for comparison outside of the Lycopodiaceae. The Lycopodiaceae as we know them are diverse modern survivors of an ancient lineage. We used for outgroup comparison mainly three of the well known

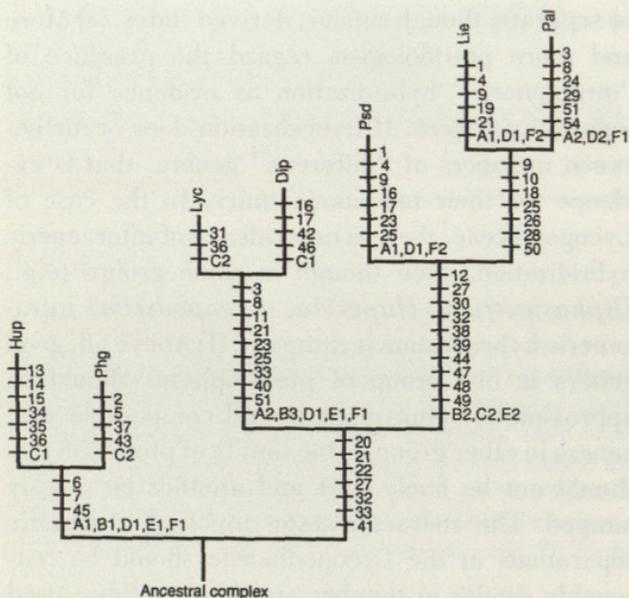


FIGURE 1. Wagner tree of characters in North American Lycopodiaceae. Abbreviations of taxa are as follows: Hup = *Huperzia*; Phg = *Phlegmariurus*; Lyc = *Lycopodium*; Dip = *Diphasiastrum*; Pd = *Pseudolycopodiella*; Lie = *Lycopodiella*; Pal = *Palhinhaea*.

early genera: *Asteroxylon*, *Drepanophycus*, and *Baragwanathia*, all from Lower to Middle Devonian strata. The ligulate, heterosporous lycosids, Lepidodendrales, Selaginellales, Pleuromeiales, and Isoetales, apparently constitute separately derived assemblages of evolutionary lines that became established by the Carboniferous. The Devonian elements, commonly known as Protolepidodendrales, eligulate and homosporous, are more logical outside groups for comparison with the modern Lycopodiales and include the three genera listed. The original evolutionary progression probably began in the Upper Silurian: Rhyniopsids apparently gave rise to zosterophylloids, and these to lycopodiophytes, and the first two groups became extinct. The most primitive were the Protolepidodendrales, and they too became extinct, as did the ligulate orders Lepidodendrales and Pleuromeiales. These changes are discussed in numerous textbooks of paleobotany (e.g., Bierhorst, 1971; Taylor, 1981, Thomas & Spicer, 1987). Although there are disagreements on the details of the history of lycosids, there is a fair consensus regarding the broad outlines. In addition to outside comparison, we examined trends within and between the subgroups of the present-day Lycopodiaceae. The highly complex and specialized propagative branches of the gemma firmosses, *Huperzia* sens. str., are uniquely derived and found only in this genus; comparisons within (and outside) the family support the conclusion that such bizarre shoots involving a number of character changes represent distinct and mul-

iple advancements (cf. Stevenson, 1976, and references therein). So it is with such character states as cortical roots, plectosteles, ring meristems in gametophytes, napiform gametophyte thalli, nodular sporangial wall cells, unequal sporangial valves, and many of the other states summarized below. However, a number of obvious specializations found in North American Lycopodiaceae are useless at the generic level since they involve only individual species. These "peripheral" or "autapomorphic" states are obviously advanced within their phylads, but they cannot be used for delimitation of whole genera. They include such advancements as leaf margins toothed, leaf tips hair-tipped, stomates only on abaxial leaf surfaces, blade surfaces glaucescent with epicuticular wax, or rhizome subterranean.

At the generic level there are some striking alternative states for which we can assign no polarity at present. We have no basis for judgment either within or outside of the family. These include the patterns of the root base stele, sculpture of spores, extent of the triradiate groove on the proximal spore face, and the sculpture of the proximal face. A particular problem involves the chromosome base number: The chromosome numbers seem to concentrate around $x = 22, 33, 55, 66,$ and $77,$ with various aneuploidal additions and subtractions (F. Wagner, 1992). Intuitively it might seem reasonable to say that lower ploidal levels are more primitive than higher ones and that fewer aneuploidal changes are more primitive than more, but we cannot be sure that this is so in any particular case. We have been forced, therefore, to use base numbers as they are, as a classificatory tool but without applying phylogenetic directionality. These unpolarized trends are summarized at the end of Table 1 and are represented by letters and numbers there and in the character tree, Figure 1.

POLARIZED CHARACTER TRENDS

The character polarizations we have deduced (numbered in Table 2 and Fig. 1, and in parentheses below) come primarily from comparisons with the members of the outside groups given above, supported by data presented by various authors (e.g., Bruce, 1975, 1976b; Holub, 1975, 1983, 1985; Øllgaard, 1975, 1979, 1987; Wilce, 1965, 1972), as well as by ourselves. The basis for determining directionality is outside comparison (Wagner, 1962, 1969, 1980). The terrestrial habitat is considered primitive. Two trends have occurred away from it: to semiaquatic, i.e., inundated for part of the growing season, (1) and to epiphytic

(2). The former is characteristic of *Lycopodiella* and *Pseudolycopodiella*, the latter the dominant condition of *Phlegmariurus*, some species of which have no doubt experienced reversal. Simple, dichotomous aerial branching is considered ancestral by outside comparison, and there are two different transformations: amplification to extremely complex dendroid habit of the aerial shoots (e.g., *Palhinhaea*) (3), and reduction to simple, unbranched aerial shoots (e.g., *Lycopodiella*) (4). The erect habit of terminal aerial branches is considered basic, and the pendent derived (5). The presence of a well-defined creeping rhizome is presumably the initial state, while the loss of a distinct rhizome is considered derived (6), as illustrated by *Huperzia* and *Phlegmariurus*. The emergence of roots close to their position of origin in the stem stele is the most probable ancestral condition, and the extensive basal migration of roots from the shoot apex downward through the cortex to the level of the substratum before emergence is specialized (7), as in the *Huperzia* group. The branching of the roots themselves was initially most likely isodichotomous and gave way to anisodichotomous (8), as is represented in *Palhinhaea*. In all Lycopodiaceae, evergreen condition of the vegetative aerial shoots is evidently the original one; deciduous components like the upright shoots of *Lycopodiella* are thus advanced (9). The lack of hairs and other emergences is the generalized primary condition, and their presence on stems and/or leaves is specialized and secondary (10). From the most likely original stele, the actinostele, there have been two major directions of change: to a meshed actinostele (like that of *Lycopodiella* and its nearest allies) (12), and to the peculiar and unique condition known as plectostele (like that of *Lycopodium* and *Diphasiastrum*) (11).

Highly evolved lateral branches that afford vegetative propagation are observed only in the genus *Huperzia*. They are complex and involve several, apparently de novo elements—the gemmiphore, the abscission layer, gemma axis, and dorsiventral, distinctively oriented, and modified leaves. The generalized condition for Lycopodiaceae and their outside sister groups is to lack such structures entirely, so that their presence alone is apomorphic (13). The gemma apparatus in *Huperzia* evolved *sui generis* a series of other advancements, namely from radial to bilateral (14) as well as others not used here. Aerial stem branching, judging from the fossil outgroups, was almost unarguably dichotomous in the ancestors, and became unequal (anisodichotomous) in the descendants (15). The ranks of leaves on the aerial shoots have undergone re-

duction in number from 6–12 to only 3–5 (16). The vegetative leaves of the aerial parts were originally monomorphic (e.g., *Lycopodium clavatum*), but became transformed in connection with major changes in overall shoot structure so as to be heteromorphic, as in most species of *Diphasiastrum* (17), in which the branches are cordlike and flattened like *Thuja*. (This trend refers only to adult shoots; the juvenile shoots have isophylly, as illustrated by *Diphasiastrum sitchense*, which is apparently neotenic, maintaining its juvenile condition into maturity.)

Presumably, mucilage canals are derived structures absent in the progenitors. The *Huperzia-Phlegmariurus* assemblage still lacks them, but the type of mucilage duct that is basal in the fertile leaf is present in all other genera (20). Veinal mucilage canals occur only in the vegetative leaves of *Lycopodiella* and *Pseudolycopodiella* (18). However, they are absent from the sporophylls in *Pseudolycopodiella*, being present there only in *Lycopodiella* (19). These different patterns, discovered by Bruce (1975), are treated here as separate trends rather than steps in a single trend, because it is not obvious how or even if the different conditions are sequenced.

Sporophylls in the primitive lycopsids were structurally mostly like trophophylls, as they are today in typical *Selaginella selaginoides* and all species of *Isoetes*, and in the Protolapidodendrales. This condition is retained to a large extent in the firmosses, *Huperzia* and many *Phlegmariurus* species. Nevertheless, differentiated sporophylls are found in all five genera of clubmosses (21). Those of *Lycopodiella* and *Palhinhaea* are only partially transformed. The independent development of distinct sporophylls on tassel-like strobiloids that differ from typical strobili in orientation and appendage structure in *Phlegmariurus* is considered a parallelism or convergence. The attachment of the sporangia is basal in Huperzioidae as in the Devonian outgroups, but becomes pseudopeltate to peltate in all of the other groups (22), and associated with this there is a change from unstalked to stalked (23), but this is found only in Lycopodioidae. Where a true strobilus has been formed, the erect orientation is surely the ancestral one, judging from the outside evidence: the peculiar nodding strobili as found in *Palhinhaea* are derived (24). Where strobili are pedunculate, the leafy condition of the stalk as seen in *Lycopodiella* and *Palhinhaea* is exchanged for the scaly to nearly naked condition seen in *Lycopodium* (certain species), *Diphasiastrum*, and *Pseudolycopodiella* (25). The sporangial valves are primitively equal

TABLE 1. Characters and character states used in this analysis.

Character	Primitive	Advanced	Hup	Phg
1. Habitat	terrestrial	semiaquatic	0	*
2. Habitat	terrestrial	epiphytic	0	1
3. Branching	simple-dichotomous	complex-dendritic	0	0
4. Branching	simple-dichotomous	reduced-unbranched	0	0
5. Habit	erect	pendent	0	1
6. Rhizome creeping	present	absent	1	1
7. Root emergence	immediate	corticular	1	1
8. Root branching	isodichotomous	anisodichotomous	0	0
9. Aerial shoot	evergreen	deciduous	0	0
10. Indument	absent (glabrous)	absent to hairy	0	0
11. Stele	actinostele	plectostele	0	0
12. Stele	actinostele	meshed haplostele	0	0
13. Gemma occurrence	absent	present	1	0
14. Gemma shape	radial	bilateral	1	0
15. Branching	dichotomous	anisodichotomous	1	0
16. Ranks of leaves	6-12	3-5	0	0
17. Nature of leaves	monomorphic	heteromorphic	0	0
18. Veinal mucilage canal in trophophyll	absent	present	0	0
19. Veinal mucilage canal in sporophyll	absent	present	0	0
20. Basal mucilage canal in sporophyll	absent	present	0	0
21. Sporophyll	like trophophyll	reduced	0	0
22. Sporophyll attachment	basal	pseudopeltate-peltate	0	0
23. Strobilus attachment	unstaked	stalked	*	*
24. Strobilus orientation	erect	pendent	*	*
25. Peduncle appendages	leaflike	scalelike	*	*
26. Sporangial valves	equal	unequal	0	0
27. Sporangial valves	thick	thin	0	0
28. Sporangial shape	reniform	globose	0	0
29. Sporangial nature	non-enclosed	enclosed in cavity	0	0
30. Sporangium cell wall shape	sinuate	straight-walled	0	0
31. Sporangium cell wall shape	sinuate	sinuate w/invagination	0	0
32. Side wall thickenings	evenly thickened	nodular-semiannulate	0	0
33. Side wall thickenings	evenly thickened	not thickened	0	0
34. Spore sides	convex to straight	concave	1	0
35. Spore angles	rounded-pointed	truncate	1	0

TABLE 1. Continued.

Character	Primitive	Advanced	Hup	Phg
36. Allohomoploid meiosis	normal	irregular	1	0
37. Nothospeciation	common	rare or absent	0	1
38. Gametophyte nutrition	holomycotrophic	hemimycotrophic	0	0
39. Gametophyte position	subterranean	surficial	0	0
40. Gametophyte meristem	central apex	subterminal, ring	0	0
41. Gametophyte symmetry	dorsiventral	radial	0	0
42. Gametophyte shape	buttonlike	rapiform	*	*
43. Gametophyte branching	unbranched	branched	0	1
44. Apical outgrowth	absent	photosynthetic lobes	0	0
45. Apical outgrowth	absent	paraphyses	1	1
46. Gametophyte pigment	white, gray-brown	orange-brown	0	0
47. Young sporophyte form	erect	horizontal	0	0
48. First leaves	microphylls	protophylls	0	0
49. Foot	large	small	0	0
50. Protocorm	absent	present	0	0
Undirected characters				
A. Root base stele	A1. c-shaped; A2. plectostele		1	1
B. Spore sculpture	B1. foveolate-fossulate		1	1
	B2. rugulate; B3. reticulate			
C. Proximal face	C1. sculptured; C2. not sculptured		1	2
D. Triradiate groove	D1. reaching margin		1	1
	D2. not reaching margin			
E. Margo	E1. absent; E2. present		1	1
F. Equatorial ridge	F1. absent; F2. present		1	1

Abbreviations of taxa are as follows: Hup = *Huperzia*; Phg = *Phlegmariurus*; Lyc = *Lycopodium*; Dip = *Diploazium*; Lie = *Lycopodiella*; Pal = *Palhinhaea*. * = Not applicable or unknown; scored as 0.

in size, but two of the genera have developed decidedly unequal valves (26). The valves of lycopsid ancestors were probably moderately thick as seen in Devonian fossils and modern Huperzioideae, but became thin in Lycopodiodeae and Lycopodielloideae (27). The reniform sporangial type appeared in Lycopsidea as early as the Devonian (even in the more primitive Zosterophylloids) and is still maintained in most modern lycopsids; however, the advanced globose type is found in two genera, *Lycopodiella* and *Palhinhaea* (28). The sporangia are free on the surface in most taxa, but in *Palhinhaea* they are enclosed in specialized cavities (29). In two of the major groups of lycopsids, the sporangial cell walls are characteristically sinuate, but in the third they have become straight-walled (30). The sinuate-walled condition has evolved a different complication, namely, distinctive invaginations, as in typical *Lycopodium* described by Øllgaard (1975) (31). The side walls of the sporangia are typically evenly thickened, but in the Lycopodielloideae, they have specialized nodular or semiannulate thickenings, which are undoubtedly advanced (32). Typical *Lycopodium* species have side wall cells that are not thickened at all, another apparent derivation (33).

The spores of Lycopodiaceae possess many characters, some of which (see above) cannot be polarized with our present knowledge. There are, however, likely initial states for certain features. For example, the equatorial sides of lycopsid spores were most likely convex to straight, as attested by the spores of most lycopsid fossils and even *Selaginella* and *Isoetes*. In one group of extant Lycopodiaceae, *Huperzia* sens. str., the equatorial walls are concave, certainly a specialization (34). Likewise, the spore condition of truncate rather than pointed corners is a derived condition (35). Both of these conditions separate the genus *Huperzia* from *Phlegmariurus*.

Hybridization between species would be expected on theoretical grounds to produce offspring still capable of undergoing normal meiosis. Only as the species accumulate specific incompatible genetic factors does the meiotic behavior become irregular, with progressive loss of pairing ability (36). This derived condition within members of a genus, the usual state in most pteridophytes, is notable in the genus *Huperzia*. However, three other genera, *Lycopodium* sens. str., *Diphasiastrum*, and *Lycopodiella*, are conspicuous because their members can still form apparently fertile hybrids with normal meiosis and spores, i.e., the theoretical primitive state. These genera have not yet lost pairing ability. Very little is known of hybridization

in the remaining groups. There is a profound difference between the capability and results of hybridization within the groups that we do know, so we have used this as a character. If we are correct, the trend of the units within genera should be from interspecific nothospeciation with allohomoploid fertile hybrids, to interspecific nothospeciation with allopolyploid sterile hybrids, to very rare hybrids, to genera with no hybrids at all between their species. Thus, being able to form many hybrids between its component species (of any degree of fertility) is a more primitive condition within a genus than being able to form hybrids only rarely or never (37).

Some of the most prominent differentiations between present-day Lycopodiaceae pertain to the gametophyte generation. It has long been known that some groups have wholly subterranean gametophytes that are mycoparasitic, while others are surficial and have photosynthesis (38). The claims of Freeberg & Wetmore (1957) that these are environmentally determined conditions are no longer accepted, as stated above. We now regard photosynthetic gametophytes in Lycopodiaceae as probably specialized for the following reasons: (a) the species that show them are mainly aquatic, or semiaquatic; (b) the aquatic habitat is not suitable for the growth of subterranean gametophytes; and (c) the basal part of the photosynthetic gametophyte is fleshy and not similar to the ferns and most liverworts. The photosynthetic function is located in special dorsal projections (44). Typically, gametophytic meristems tend to be terminal or confined to a central position, but in two lycopsid genera the meristem forms a subterminal ring (39) as shown in *Lycopodium* and *Diphasiastrum* of the Lycopodielloideae. The actual form of the gametophytes in these two genera, however, is otherwise very different. The buttonlike prothallus of the former is more like that of the outside groups than the peculiar carrot-shaped or rapiform type (42) present only in *Diphasiastrum*. Unbranched gametophytes are the widespread type in practically all pteridophytes (except the obviously specialized ones of certain schizaeas, filmy-ferns, and vittarioids). The tree inhabiting prothallia of the epiphytic *Phlegmariurus* species, where they are known, are branched (43). In this connection, the outgrowths or lobes of Lycopodielloideae, commented on above in connection with photosynthesis, are advanced (44), as they are not found elsewhere except in the (probably very remotely related) Equisetopsida. All other related groups apparently lack such outgrowths. The presence of specialized haploid trichomes or paraphyses among gametangia seems to be unique to the Huperzioideae (45).

The basic condition among Lycopodiaceae otherwise seems to be with the gametangial surfaces glabrous. The nonphotosynthetic gametophytes in the living state tend to be various shades of white, gray, and gray-brown. However, the carrotlike gametophytes of *Diphasiastrum* are usually pigmented orange or orange-brown (46).

Young sporophytes of most lycopsids and other pteridophytes tend to be erect, but in the Lycopodielloideae they are horizontal and creeping (47). In this subfamily, too, the first leaves are actually "protophylls" (48) rather than small versions of microphylls. In two of the genera of Lycopodielloideae, *Lycopodiella* and *Palhinhaea* (but not *Pseudolycopodiella*), there is a specialized structure, the protocorm (50), not found in any of the immediately related living or fossil outside groups (the tuber of *Phyllogossum* evidently not homologous (Bierhorst, 1971)). The foot of the young sporophyte is normally large in genera of Lycopodiaceae but is small (49) in the Lycopodielloideae.

ESTIMATED GROUNDPLAN OF THE ANCESTOR OF MODERN LYCOPODIACEAE

The specialized or advanced states of 50 characters are given above, as best they can be estimated, and each is given a number in parentheses. The primitive or plesiomorphous states may be used to conceptualize the hypothetical ancestral stock from which our present-day genera arose, and this is briefly summarized as follows: Habitat terrestrial; aerial stem branching simply dichotomous, upright; basal stem a horizontal rhizome; roots emerging next to their origin in stem stele, branching dichotomously, the type of root base stele unknown; aerial shoots evergreen, lacking hairs or other emergences; stem actinostelic; gemmae of any kind lacking; shoot branching dichotomous; leaves in 6–12 ranks, monomorphic. Lacking mucilage ducts of any kind. Except for presence of sporangia, sporophylls undifferentiated from trophophylls; sporangia basally attached; strobilus, if present, erect, and if pedunculate, invested by little-differentiated leaves; sporangia reniform, the valves equal, thick-walled, not enclosed in special cavities; sporangial cell walls sinuate and without invaginations, thickened evenly; spores with convex to straight sides and round-pointed angles, the type of sculpture and presence or absence of sculpture on proximal face or whether triradiate ridge reached margin unknown; hybridization between species within a genus common and chromosome pairing in hybrids normal; gametophyte holomycoparasitic,

subterranean, the meristem central and terminal, the thallus \pm dorsiventral, branching lacking; photosynthetic lobes absent; gametangial paraphyses absent; color whitish to gray-brown; young sporophyte erect, with small microphylls, foot large and protocorm absent.

TREE OF COMPARATIVE DATA

The tree shown in Figure 1 was constructed by assembling the data into what appeared to be the most parsimonious arrangement, using the manual groundplan-divergence principles of Wagner (1962, 1969, 1980), based on the operational idea that phylogeny (i.e., genetic history) is the amount, direction, and sequence of divergence from ancestral groundplans. For the initial layout, only those characters described above were used, and they are numbered on the tree to correspond with the numbers used there. These characters are believed, on the basis of outside evidence, to be uniquely derived or mostly so. Those distinctive character states that could not be assessed as to directionality were added to the tree, and are indicated by letters and numbers, as given in Table 2. The distances between the nodes of the tree are estimated on the basis of all characters, most of them polarized except for the few added later to indicate merely taxonomic differences. Thus, the tree can be used to present visually the broad picture of (systematic) relationships of all the North American Lycopodiaceae. New information can be added to the tree to embody tropical and subtropical genera, and new characters, and the polarities given here can be revised if necessary. If the number of data and taxa becomes very large, it will be necessary to resort to computer algorithms of the manual Wagner Tree.

DISCUSSION OF RESULTS

If the above arguments are valid, then we still must evaluate the traditional generic taxonomy of North American Lycopodiaceae. The application of categories is still arbitrary (Wagner, 1969). Progressively more segregated systems are shown in Table 3, starting with the classical single genus, *Lycopodium*. In order to maintain comparability and consistency of pteridophyte classification, we have kept in mind, for comparison, well-known pairs of sister genera in homosporous pteridophytes. Weak or dubious genera (cf. Table 2A) that are based upon one to few characters should probably be merged (cf. Kramer & Green, 1990): e.g., *Equisetum* and *Hippochaete* (stomates, chro-

TABLE 2. Some possible classifications for North American Lycopodiaceae. (For convenience, the same names are used for the same units, regardless of nomenclatural correctness.)

A.	Genus <i>Lycopodium</i>	E.	Genus <i>Huperzia</i>
B.	Genus <i>Huperzia</i>		Genus <i>Phlegmariurus</i>
	Genus <i>Lycopodium</i>		Genus <i>Lycopodium</i>
C.	Genus <i>Huperzia</i>		Genus <i>Diphasiastrum</i>
	Genus <i>Lycopodium</i>		Genus <i>Palhinhaea</i>
	Genus <i>Lycopodiella</i>		Genus <i>Pseudolycopodiella</i>
D.	Genus <i>Huperzia</i>		Genus <i>Lycopodiella</i>
	Subgenus <i>Huperzia</i>	F.	Subfamily Huperzioidae
	Subgenus <i>Phlegmariurus</i>		Genus <i>Huperzia</i>
	Genus <i>Lycopodium</i>		Genus <i>Phlegmariurus</i>
	Subgenus <i>Lycopodium</i>		Subfamily Lycopodioidae
	Subgenus <i>Diphasiastrum</i>		Genus <i>Lycopodium</i>
	Genus <i>Lycopodiella</i>		Genus <i>Diphasiastrum</i>
	Subgenus <i>Palhinhaea</i>		Subfamily Lycopodielloideae
	Subgenus <i>Pseudolycopodiella</i>		Genus <i>Palhinhaea</i>
	Subgenus <i>Lycopodiella</i>		Genus <i>Pseudolycopodiella</i>
			Genus <i>Lycopodiella</i>

mosome size), *Polypodium* and *Pleopeltis* (scales), *Pteris* and *Schizostege* (splitting of coenosori), *Jamesonia* and *Eriosorus* (no consistent states), *Polystichum* and *Cyrtomium* (reticulate veins), and *Asplenium* and *Camptosorus* (veins and sori). Some other, but still widely accepted, genera (Table 2B, C) are separated by only a moderate number of characters—in fact, considerably fewer than those used here in Lycopodiaceae: *Marattia* and *Angiopteris* (especially type of synangium); *Osmunda* and *Todea* (mainly sporangial arrangement); *Polypodium* and *Pyrrosia* (mainly soral arrangement); and *Dryopteris* and *Ctenitis* (especially trichomes). Few pteridologists would question their validity as genera, in spite of the relatively few characters that separate them, but most would be hesitant about dividing them into subfamilies, although they might set up subgenera (Table 2D) or separate genera (Table 2E). Further splitting is required of single or groups of genera that are so distinct from other singles or groups that they merit placement in distinct subfamilies (Table 2F). Examples from other homosporous pteridophytes are Ophioglossaceae: *Botrychium* and *Helminthostachys* (Botrychioideae) and *Ophioglossum* and *Cheiroglossa* (Ophioglossoideae); Gleicheniaceae: *Gleichenia* and *Dicranopteris* (Gleichenioideae) and *Stromatopteris* (Stromatopteridoideae); Cyatheaceae: *Dicksonia* and *Cibotium* (Dicksonioideae) and *Cyathea* and *Alsophila* (Cyatheoideae); and Dryopteridaceae: *Dryopteris*, *Davallia*, and *Tectaria* (Dryopteridoideae), and *Athyrium* and *Diplazium* (Woodsioideae). We conclude on the basis of these comparisons that the taxonomic division of modern

North American Lycopodiaceae should correspond to Table 2F, i.e., seven genera placed in three subfamilies. The distinguishing characters are numerous, they are accompanied by large gaps and no transitions, they are monophyletic, they involve a number of uniquely derived characters, they do not hybridize with each other, and the segregation level is consistent with other homosporous pteridophytes. The genera fit readily into three subfamilies defined on the basis of their separate patterns of characters and trends.

The two current leaders in the systematics of Lycopodiaceae are Josef Holub and Benjamin Øllgaard, both of whom have made extensive contributions to our understanding of these plants. Their publications (see selected papers in Lit. Cited) contain an enormous amount of information, and they summarize our current knowledge. The classification accepted here for North America conforms, in general, to their concepts except for the assignment of certain ranks. Of the two systems, the ranks of Holub (1983), with all of the genera recognized, are closer to ours; Øllgaard's (1987) treatment has three genera (*Huperzia*, *Lycopodium*, and *Lycopodiella*) in Lycopodiaceae, but includes a number of subgeneric units. Our North American *Phlegmariurus* is in Øllgaard's *Huperzia squarrosa* group; our *Huperzia* is his *Huperzia selago* group; *Lycopodium* includes his *Lycopodium* sect. *Lycopodium*, *Lycopodium* sect. *Annotina*, and *Lycopodium* sect. *Obscura*; *Diphasiastrum*, *Lycopodium* sect. *Complanata*; *Pseudolycopodiella*, *Lycopodiella* sect. *Caroliniana*; *Lycopodiella*, *Lycopodiella* sect. *Lycopodiella*; and *Palhin-*

haea, *Lycopodiella* sect. *Campylostachys*. Holub's most recent treatment (Holub, 1991) of the firmosses recognizes two subgenera under *Huperzia* rather than two genera; his subgenus *Huperzia* equals our genus *Huperzia*, and his subgenus *Subselago* our *Phlegmariurus*. Both Holub and Øllgaard describe a number of tropical and Southern Hemisphere elements, at least some of which can be raised to generic or subgeneric status. However, we believe these non-North American elements will not modify the geographically circumscribed taxonomic treatment given here. This interpretation is summarized in the key that follows:

TECHNICAL KEY TO NORTH AMERICAN
SUBFAMILIES AND GENERA

- 1a. Sporophylls like trophophylls, photosynthetic; plants epiphytic, epipetric, or terrestrial; roots running from the apex through cortex before emerging; leaves lacking mucilage canals; rhizome absent; paraphyses present among gametangia; spores foveolate-fossulate; chromosomes $x = 67-68$ *Huperzioideae*
- 2a. Plants epiphytic, mostly pendent at maturity; lacking gemmiphores and gemmae; gametophytes branched; spore angles pointed, spore sides straight or convex; proximal face unpitted, hanging firmosses *Phlegmariurus* Holub
(1 orthospecies, 0 nothospecies in North America)
- 2b. Plants terrestrial or epipetric, mostly erect at maturity; producing specialized lateral gemmiphores among the leaves bearing flattened green gemmae; gametophytes unbranched; spore angles truncate, spore sides concave; proximal face pitted, gemma firmosses *Huperzia* Bernh.
(6 orthospecies, 7 nothospecies)
- 1b. Sporophylls \pm strongly modified, unlike trophophylls, nonphotosynthetic at maturity; plants terrestrial or semiaquatic; leaves with basal mucilage canals; roots emerging immediately, scattered along rhizome; rhizome present; paraphyses absent among gametangia; spores various but not foveolate-fossulate; chromosome x numbers various.
- 3a. Spore sculpture reticulate; capsule wall cells sinuate to invaginate; root stele like rhizome stele at base; gametophyte subterranean, nonphotosynthetic, growing by a ring meristem; archegonia long, persistent *Lycopodioideae*
- 4a. Shoots round-branched, the mature leaves monomorphic and separate, in 6-8 ranks; sporangial wall cells with invaginations and evaginations; gametophytes gray or brown, flat, buttonlike and convoluted when mature; chromosomes $x = 34$, common clubmosses *Lycopodium* L.
(6 orthospecies, 0 nothospecies)
- 4b. Shoots flat-branched (with 1 exception), the leaves mostly dimorphic or

trimorphic and overlapping and (or) imbricate, in 4-5 ranks (in *D. sitchensense* leaves 5-ranked and morphologically as in juveniles); sporangial wall cells smoothly sinuate; gametophytes orange pigmented, narrowly top-shaped, nonconvoluted; chromosomes $x = 23$, flat-branched clubmosses
..... *Diphasiastrum* Holub
(5 orthospecies, 6 nothospecies)

- 3b. Spore sculpture rugulose; capsule walls straight; root stele various; gametophytes subsurficial, with photosynthetic lobes; archegonia short, ephemeral ... *Lycopodielloideae*
- 5a. Plants terrestrial; upright shoot complexly dendroidly branched; basal root stele like stem; spore laesura groove not reaching the margin; spore proximal faces not sculptured; chromosomes $x =$ ca. 55, tropical tree-like clubmosses ... *Palhinhaea* Franco & Carv.
(1 orthospecies, 0 nothospecies)
- 5b. Plants semiaquatic; upright shoot simple; basal root stele C-shaped in section; spore laesura groove reaching spore margin; spore proximal faces sculptured; chromosomes not $x =$ ca. 55.
- 6a. Peduncle leafy; sporophylls resembling trophophylls; horizontal shoot rounded, with uniform leaves \pm spreading to erect; venal mucilage canals present; $x = 78$, common bog clubmosses
..... *Lycopodiella* Holub
(6 orthospecies, 8 nothospecies)
- 6b. Peduncle mostly bare with scattered scalelike appendages; sporophylls much reduced, horizontal shoot flat, the leaves unequal, the larger ones in two rows and nearly flat on the substratum; venal mucilage canals absent; $x = 35$, Carolina bog clubmosses
..... *Pseudolycopodiella* Holub
(1 orthospecies, 0 nothospecies)

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