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Phylogenetic Relationships of Extant Ferns Based on Evidence from Morphology and *rbcL* Sequences

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ABSTRACT.—We present the first cladistic analysis of extant ferns based on morphological characters. Our data set consisted of 77 vegetative and reproductive morphological/anatomical characters recorded on a broad sampling of 50 extant pteridophyte taxa, with representatives of all major fern groups, and one seed plant (*Cycas*). An annotated list of both retained and excluded morphological characters is presented. Results from the morphological analysis are compared with an independent analysis of *rbcL* data carried out here for the same set of pteridophyte taxa. Finally, we analyze a combined (morphological and molecular) data set. All three data sets were analyzed using maximum parsimony. Two separate sets of analyses using different taxon combinations were conducted on each of the three data sets. Analysis 1 focused on phylogenetic relationships of ferns only (Filicopsida, *Botrychium*, and *Angiopteris*), using *Cycas* as an outgroup representative from the seed plants. Analysis 2 focused on phylogenetic relationships of pteridophytes (Filicopsida, *Angiopteris, Botrychium, Equisetum, Psilotum*), using *Lycopodium* as the outgroup. In both sets of analyses, the combined data set provided the most robustly supported hypothesis of relationships. Results from the combined data set in Analysis 1 provided strong bootstrap support for the monophyly of the following clades: leptosporangiate ferns (with *Osmunda* as the most basal leptosporangiate fern), heterosporous ferns, *Cheiropleuria-Dipteris, Diplopterygium-Stromatopteris,* tree ferns, schizaeoid ferns, pteridoid ferns, and a large clade consisting of a derived group of leptosporangiate ferns that excludes dennstaedtioids and pteridoids. Various smaller clades within some of these larger clades also have strong support. The dennstaedtioid ferns are paraphyletic. We use the results of the combined data set in Analysis 1 to examine character evolution within the leptosporangiate ferns. Results from the combined data set in Analysis 2 indicated robust support for essentially the same fern clades as the combined data set in Analysis 1. In both Analyses 1 and 2, bootstrap support for the leptosporangiate fern clade is much greater using the combined data set than when either the morphological or, particularly, the molecular data set is analyzed separately. Relationships among major groups of pteridophytes at the base of the tree (*Botrychium, Angiopteris, Psilotum, Equisetum, Lycopodium*) were poorly supported by the combined data in Analysis 2, except for a weak association between *Botrychium* and *Psilotum*. We are convinced from this study of the value of using both molecular and morphological data sets in combination as well as separately. A synthetic approach that integrates paleobotanical and neobotanical data will be of greatest interest in further elucidating the phylogenetic relationships of pteridophytes.

Our understanding of the phylogeny of pteridophytes has lagged behind the considerable progress made recently in clarifying the phylogenetic relationships of other green plants, especially seed plants (Crane, 1985a, 1985b; Doyle

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and Donoghue, 1986a, 1986b, 1992; Doyle et al., 1994; Loconte and Stevenson, 1990, 1991; Nixon et al., 1994; Rothwell and Serbet, 1994). Often-cited reasons for this discrepancy are that ferns have, relatively speaking, far fewer morphological characters, and that determining homologous character states, particularly when dealing with organisms with such a long geological record, is not feasible. These arguments have become less persuasive since the publication of a number of comprehensive studies on bryophytes and green algae and their relationships to tracheophytes (Garbary et al., 1993; Graham et al., 1991; Mishler and Churchill, 1984, 1985; Mishler et al., 1994).

An overview of extant tracheophyte relationships based on recent analyses of green plant phylogeny is shown in Figure 1, indicating major clades that are resolved and areas of greatest uncertainty (unresolved polychotomies). Although numerous phylogenetic studies have been devoted to the seed plants (spermatophytes), higher-level relationships among some of the major extant lines (cycads, *Ginkgo,* conifers, gnetales, angiosperms) still are not resolved convincingly (Doyle et al., 1994). For example, the position of the cycads as the most basal group in the spermatophytes is supported by Crane (1985b), Loconte and Stevenson (1990), and Nixon et al. (1994), whereas *Ginkgo* is the most basal spermatophyte in the analysis by Rothwell and Serbet (1994). Other authors have obtained still different arrangements.

Within tracheophytes, relationships among pteridophytes are the least understood (Kenrick and Crane, 1991; Nayar, 1970; Rothwell, 1994). The major clades of extant pteridophytes are: lycopodiophytes (Lycopodiaceae, Selaginellaceae, Isoetaceae); psilotophytes (*Psilotum, Tmesipteris*); equisetophytes (*Equisetum*); and ferns (Fig. 1). Ferns comprise three classes: the Ophioglossopsida and Marattiopsida (eusporangiate ferns), and the Filicopsida (leptosporangiate ferns). It has been hypothesized that the psilotophytes are the most basal lineage of extant pteridophytes, and indeed of all extant tracheophytes (Bremer, 1985; Bremer et al., 1987; Parenti, 1980; Pichi Sermolli, 1959). However, more recent evidence supports the placement of the lycopodiophytes at the base of the extant tracheophyte clade (DiMichele and Skog, 1992; Donoghue, 1994; Kenrick and Crane, 1991; Raubeson and Jansen, 1992).

Contemporary estimates of higher-level relationships in ferns are mostly intuitive and founded largely on the phenetic concept of overall similarity of morphological/anatomical characters. These characters most often include the sorus and its associated structures (sporangia, indusia, spores), leaf architecture and venation, rhizomes, stipes, and chromosome numbers. In 1969, Wagner attempted a more objective approach to resolving fern phylogeny by applying his "ground plan/divergence method" to homosporous ferns. This method consisted of first inferring the primitive and advanced states of various characters based on the assumption that the commonest character state is usually also that which is primitive. How these states were correlated was then determined so as to organize the taxa graphically in an evolutionary pattern (Wagner, 1969, 1980). A slightly modified version of Wagner's scheme of evolutionary relationships is still presented in morphology and evolution textbooks (e.g., Gifford and Foster, 1988). Smith (1995) reviewed modern ideas on

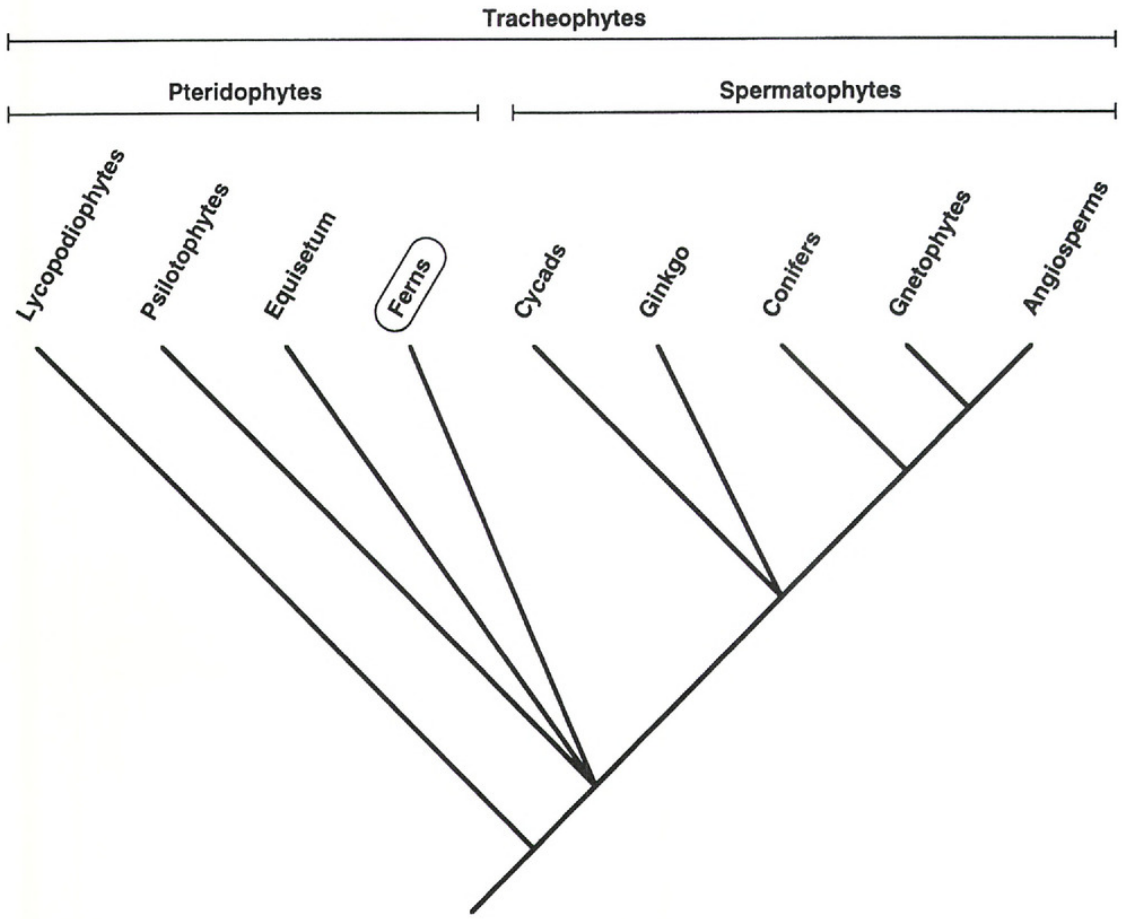


FIG. 1. Simplified summary of current understanding of phylogenetic relationships among extant tracheophytes (based primarily on the recent analyses of Crane, 1985; Donoghue, 1994; Doyle and Donoghue, 1992; Doyle et al., 1994; Garbary et al., 1993; Mishler et al., 1994; Nixon et al., 1994; Raubeson and Jansen, 1992; Rothwell, 1994; Rothwell and Serbet, 1994). The monophyly of spermatophytes has been supported in all recent studies, although relationships of major extant lines (cycads, *Ginkgo*, conifers, gnetophytes, and angiosperms) still have not been resolved convincingly. Major clades of extant pteridophytes are: lycopodiophytes, psilotophytes, *Equisetum*, and ferns. The relationships of the pteridophytes are the least well known among tracheophytes.

fern relationships as depicted by Holttum (1973), Mickel (1974), Pichi Sermolli (1977), and Wagner (1969).

A comprehensive cladistic evaluation of relationships among extant pteridophytes has never been attempted using morphological characters. Pteridophytes are the only large group of green plants for which phylogenetic relationships have not been analyzed using a rigorous and explicit approach to interpret morphological character patterns. Very few studies of ferns have used cladistic methodology (e.g., marattialean ferns: Hill and Camus, 1986; subfamily Drynarioideae of the Polypodiaceae: Roos, 1985). Resistance to such an approach has most likely been fueled by the belief that homoplasy (parallelism or convergence) is too pervasive in ferns to permit a meaningful phylogenetic analysis of morphological characters. There is certainly considerable homoplasy in ferns, but it remains to be demonstrated whether there is more than

in other plant groups. In addition, homoplasy, even a large amount, does not in itself invalidate a phylogenetic hypothesis. This is especially true of large scale studies, which tend to have high levels of homoplasy simply by virtue of the number of taxa involved (Donoghue and Sanderson, 1992; Sanderson and Donoghue, 1989). Other factors, such as polyploidy and hybridization, common mechanisms of speciation in ferns, have led many pteridologists to conclude that phylogeny reconstruction for the ferns is an impossible task (e.g., Kramer and Tryon, 1990). However, we do not anticipate these factors to influence phylogenetic reconstruction at the higher taxonomic levels investigated here. With the exception of McDade (1990, 1992), who demonstrated that hybrids were not likely to cause the breakdown of cladistic structure unless they are between distantly related parents, there have been no empirical studies that test the criticism of using cladistics in groups that have undergone hybridization. McDade (1995) convincingly argued that hybridization has almost always been between close relatives and that the much heralded difficulties posed by hybrids for resolving plant phylogenies (Cronquist, 1987) may have been overstated.

As with systematists studying other plant groups, pteridologists are increasingly turning to molecular data, specifically DNA sequences and chloroplast DNA restriction site variation, as a potential arbiter of phylogenetic relationships among ferns. A common assumption is that molecular characters are superior to and less homoplasious than morphological characters and therefore, more reliable indicators of phylogeny. The greater number of characters and the less subjective nature of molecular character analysis adds to their appeal. It is important to note, however, that when the number of possible character states is highly constrained, as is the case with DNA sequence data, the chance that mutations at a particular site will result in homoplasy is quite high (Mishler et al., 1988; Smith and Littlewood, 1994). Furthermore, molecular data are beset with other difficulties that impact phylogenetic reconstruction (e.g., secondary molecular structure, transition-transversion bias, saturated nucleotide sites, base composition bias, long branch attraction; Felsenstein, 1988; Lanyon, 1988).

Because a sequence-based molecular phylogeny is necessarily a gene phylogeny, it may not agree with the organismal phylogeny due to such biological processes as introgression, lineage sorting, and gene duplication (Doyle, 1992; Hillis, 1987). Phylogenetic trees derived from different data sets may also differ due to sampling error, or to the use of an inappropriate evolutionary model for a given data set (Bull et al., 1993; Rodrigo et al., 1993). Because our primary interest is the phylogeny of organisms rather than of genes, this problem of differential phylogenetic history among data sets argues for the use of multiple data sets. Increased efforts are now being made to include both morphological and molecular data sets (or multiple molecular data sets) in phylogenetic studies (Doyle et al., 1994; Eernisse and Kluge, 1993; Lutzoni and Vilgalys, 1995; Mishler et al., 1994; Olmstead and Sweere, 1994). However, this practice is not without controversy regarding how best to integrate phylogenetic information from disparate sources (Barrett et al., 1991; Bull et al., 1993; Chippin-

dale and Wiens, 1994; de Queiroz 1993; Eernisse and Kluge, 1993; Huelsenbeck et al., 1994; Lutzoni and Vilgalys, 1995; Mishler, 1994; Rodrigo et al., 1993; Swofford, 1991a).

In this paper we present the first cladistic analysis of extant ferns based on morphological characters. We also compare results from the morphological analysis with an independent analysis of molecular data carried out here for the same set of taxa, examining the strengths and weaknesses of the data with bootstrap methods. Finally, we analyze a combined morphological and molecular data set. Our aim is to examine empirically the hypothesis that morphological and molecular data may be more complementary than contradictory (Doyle et al., 1994). However, this paper is not intended as a comprehensive examination of how best to analyze and integrate morphological and molecular data (see references cited in previous paragraph). This study encompasses two main goals. The first is to provide a highly resolved and well-supported phylogeny of ferns based on a careful evaluation of information currently available from morphology and chloroplast sequence data. The second is to use the phylogeny to examine morphological character transitions involved in the evolution of ferns. While we believe that we have provided some new insights, we fully expect that integrating information from fossils, molecular sequence data from both the chloroplast and nuclear genomes, as well as improved methods of analysis that can be applied to large data sets, will further refine future analyses.

Materials and Methods

Terminal Taxa.—Pteridophytes were sampled to ensure representation of all major groups. Appendix 1 lists the 51 terminal taxa for which we recorded morphological character state information and the set of voucher exsiccatae compiled at UC to verify morphological characters. Vouchers selected were of the same species as those utilized in a broad-scale molecular analysis by Hasebe et al. (1995) and in the molecular aspects of this study. See also Table 1 for a list of taxa and the complete morphological data matrix.

We made use of a relatively strict exemplar method, coding morphological information for the same species for which we had *rbcL* sequence data. This differs from the "consensus coding" or "compartmentalization" used in many other analyses of higher taxonomic level relationships (e.g., Doyle et al., 1994; Mishler et al., 1994; Nixon et al., 1994). In those studies, many of the terminals are "summary taxa" and characters are scored for supraspecific groups rather than for exemplar samples (e.g., in Doyle et al. (1994) the terminal taxon "Magnoliales" is based on *Degeneria,* Myristicaceae, Annonaceae, and Magnoliaceae). When characters vary within composite terminal taxa, they can be scored either as polymorphic or as having the hypothesized ancestral states for the entire composite taxon (often based on results from previous analyses). Problems with the use of polymorphic characters are discussed fully by Nixon and Davis (1991). In our study, we used species as terminal taxa, scoring them directly for character states present. However, our scores are consensus-based

TABLE 1. Morphological data matrix. Taxon vouchers are listed in Appendix 1. Characters and character states are described in Appendix 2. ?=character state unknown or not applicable (these are distinguished in footnotes of the MacClade version of the matrix, which is available from the first author). A unique character state was assigned to each taxon for most characters. For certain characters, some taxa were assigned multiple character states because they were polymorphic (character varied among individuals): A=0&1; B=1&2; C=0&1&2; D=0&3; E=1&3; F=2&3. For a few characters, we were partially uncertain about the state that a particular taxon possessed, but some of the potential states could be excluded as possibilities: G=2/3; H=0/1. It is not possible to mix the two "multistate" interpretations at the same time in PAUP, so all multistate taxa were treated as polymorphisms rather than uncertainties (Swofford and Begle, 1993, p. 95).

	1	2	3	4	5	6	7	
Character number	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
Anemia mexicana	1211210?01	0011000010	1010001001	0?110000??	1000110??0	?0???10001	0000011211	0011110
Asplenium filipes	1011210?11	0021000111	1022012000	1211000??	1001221112	1110113100	0011001?21	0011110
Azolla caroliniana	02100?0?01	002?000000	0011011000	0?110300??	101A22A0?1	11?120??21	0011001400	01?0110
Blechnum occidentale	1011210?11	1021000010	1030002000	1A1100001?	1001221112	1110013100	0010011211	0011110
Cheiropleuria bicuspis	1300211100	011?000000	1000010001	0?110000??	1000110?12	?0???13001	0000100201	1011000
Cyathea lepifera	1011310?11	1020021010	1033002100	10110010??	1010121011	10???13001	0011000211	0011000
Blotiella pubescens	1011311011	0021020010	1130002001	0?110000??	1001221102	1100013100	0011001201	0011110
Dennstaedtia punctilobula	1011310?11	0020020010	1110011101	0?110000?0	1000221001	01A1213101	011?001201	0011110
Histiopteris incisa	1011311011	1020000010	1130011001	10110000??	1001221102	1100013100	0000011201	0011110
Lindsaea odorata	1011100?10	0021000010	1010010000	10110000??	1001221102	?110113100	0010001201	0011110
Lonchitis hirsuta	1011310?11	0020000010	1030011001	0?110000??	1000221102	1100013101	0011001201	0011110
Microlepia strigosa	1011310?11	0021020010	1010011001	0?11000000?	1011221001	1110113101	0001001201	0011110
Monachosorum henryi	1011310?11	0020000010	102001B001	0?110000??	1001221010	10???13101	0011011301	0011110
Pteridium aquilinum	1011310?01	0020020010	1130011101	0?1100011A	1001221102	1100013101	0001001201	0011110
Calochlaena dubia	1011310?01	0111020010	1010001001	0?110010??	1010121001	11A1213001	0000010201	0011000
Dicksonia antarctica	1011310?01	0021020000	1033002001	0?11000001?	1011121001	11A1213001	0000010201	0011000
Dipteris conjugata	1010211101	011?000010	1000011000	1011000?0	1001121012	10???13100	0000100201	0011000
Davallia mariesii	1011310?10	0021021010	1030012000	1A110100??	1001221012	1110113100	0000011211	0011110
Elaphoglossum hybridum	1301100?01	102?020010	10300?2000	10110000??	1001220?12	?0???13100	0011001G11	0011110
Nephrolepis cordifolia	1011210?10	1022001010	1030002000	1011000001?	1001221012	1110113100	0011001211	0011110
Onoclea sensibilis	1311311011	1021000100	1020012000	10110000?0	1011221011	1110113100	1011001211	0011110
Rumohra adiantiformis	1011310?00	1021020010	1030012000	10110000??	1001221012	1112313100	0011001211	0011110
Diplopterygium glaucum	1010310?00	1021000000	1010010000	10110000??	1000?11010	00???12001	0000100211	1011000
Stromatopteris moniliformis	1011100?01	0021000011	10100?0001	1010000?0	1010111010	10???12000	000011?000	1011000
Micropolypodium okuboi	1001110?11	0021000000	1010001000	10110100??	1001221012	10???13101	100001H311	0011111

TABLE 1. Continued.

Character number	1 1234567890	2 1234567890	3 1234567890	4 1234567890	5 1234567890	6 1234567890	7 1234567890	1234567
Cephalomanes thysanostomum	1011310?01	0??1000000	?011000001	0?110000??	1020?11001	11A0112001	1000110101	?0110?1
Lygodium japonicum	1111310?01	0020000000	1011010001	0?110000?0	1000110?10	?110110001	0011011201	0011110
Angiopteris evecta	1011310?00	1200110000	1034A02100	1011101?1	0110001110	00???0??01	0010112201	1000010
Marsilea quadrifolia	12100?1001	002?100000	0010011001	0?11020110	101A221101	01A140??2B	0010001400	01??110
Matonia pectinata	1011310?00	0020000010	1010011101	0?110000??	1000121010	0112312101	0011102201	0011000
Metaxya rostrata	1011210?01	01B1020010	1110011001	0?110000??	1000121010	10???13001	001100?201	0011000
Botrychium strictum	0311310?01	0201000000	003010B010	0?100000??	0100000??0	?0???0??01	0000111000	1001000
Osmunda cinnamomea	1311310?01	0200000010	101000B001	0?11000?0	1000110??0	?0???11201	1001111201	1011000
Ceratopteris thalictroides	1311311000	0020000000	0030002100	10110200??	1000?21102	1100013101	0001011201	?001110
Plagiogyria japonica	1311210?00	002?020010	1010002000	0?110000??	1001121112	1100013001	0011001201	0011000
Loxogramme grammitoides	1001111000	002?000000	?011012000	12110000??	1000221112	10???13100	100001O3?1	0011111
Polypodium australe	1001210?11	1022001000	1030012000	10110000??	1001221012	10???13100	000001H211	0011110
Psilotum nudum	030?????00	020?0000?0	10??A0A001	0?0??A000?	0100010?0	00???0??00	0000111000	1011012
Acrostichum aureum	1111211001	0021000010	103400B100	10110200?1	1001220?02	?0???13101	0001001201	0011110
Adiantum raddianum	1011310?00	0021000011	102001B000	10110000??	1000221102	1100013101	0011001201	0011110
Coniogramme japonica	1011311011	102C000010	101001B000	10110000?1	1000221112	10???13101	00000?1201	0011110
Platyzoma microphyllum	1D11210?01	002?001011	1010011001	0?110000??	1000221112	00???13111	0000011E01	0011110
Pteris fauriei	1011310?01	0021000010	101000B100	11110000??	1000221102	1100013101	0100011201	0011110
Taenitis blechnoides	1011211001	002?000010	10?001B001	0?110000??	1000221112	10???13101	0101011201	0011110
Salvinia cucullata	0F01211001	002?000000	0011011001	0?0??300??	103A2210?1	11?120??21	0011001401	01?0110
Actinostachys digitata	11020???00	002?000000	1010001001	0?110000??	1000110??0	?100010000	0000012000	1011110
Thelypteris beddomei	1011310?01	0022020010	1020002000	10110000??	1000221012	1110113100	0011011211	0011110
Vittaria flexuosa	1001111000	002?000011	102001B000	12110000??	1000221102	10???13100	0000001301	0011111
Equisetum arvense	0?020?0?10	011?0000??	00??101001	0?110001?1	0100?0???0	?0???0??04	100100?301	0011010
Lycopodium digitatum	03020?0?00	020?0000??	10??100000	0?11001020	0100000?2?	?0???0??01	0000010000	1001000
Cycas circinalis	0311110?01	020?000000	?030103011	0?1?1010??	2100000?10	?0???0??23	00??20?400	01?0?10

for some characters, especially gametophytic and spore characters, for which it was sometimes not possible to obtain information for individual species.

There are assumptions, benefits, and drawbacks inherent in using composite taxa versus exemplar species as terminal taxa. We chose the exemplar method because we wished to construct comparable morphological and molecular data sets with the same taxa. The exemplar approach is used in molecular studies, where a DNA sequence from an individual frequently represents its species, genus, or even family. The exemplar method reduces the level of polymorphism in a data set. One result of this is that specific ancestral states can more frequently be hypothesized. A drawback to this method is the possibility of "concealed polymorphisms," when one extrapolates from an exemplar taxon to the genus or family level. In addition, autapomorphies that happen to be convergences with other taxa can lead to misplacement of exemplars. Because the *rbcL* data set was available first, our choice of species to include in our morphological data set was dictated by those for which this gene already had been sequenced. Had we begun first with selecting "representative" species for the morphological and molecular data sets, we likely would have chosen different species in some cases. Character state coding may sometimes be different for a particular species than if one were coding for the entire genus (e.g., *Sphaeropteris lepifera* [in this data set] is exindusiate and therefore was not scored for indusial characters, whereas many species of *Sphaeropteris* [formerly included in *Cyathea*] are indusiate). We made efforts to mitigate this problem by choosing the most representative taxon of a particular genus or family whenever a choice was available in the *rbcL* data set.

Pteridophytes: The final data sets included 50 pteridophyte taxa, which are listed in Table 1 and Appendix 1. Thirteen additional taxa for which we had *rbcL* data were also scored for morphological data: *Hypolepis punctata* (Thunb.) Mett., *Odontosoria scandens* (Desv.) C. Chr., *Paesia scaberula* (Rich.) Kuhn, *Sphenomeris chinensis* (L.) Maxon, *Cibotium barometz* (L.) J. Smith, *Athyrium filix-femina* (L.) Roth ex Mertens, *Dryopteris dickinsii* (Fr. & Sav.) C. Chr., *Oleandra pistillaris* (Sw.) C. Chr., *Tectaria fauriei* Tagawa, *Crepidomanes birmanicum* (Bedd.) K. Iwats., *Pilularia americana* A. Br., *Tmesipteris tannensis* Bernh., *Doryopteris concolor* (Langsd. & Fisch.) Kuhn. These were eventually eliminated from the analysis because their scores were very similar to other fern taxa already in the data set. This allowed us to decrease significantly the computer time required for the analyses.

Cycas: Because of the incomplete nature of cycad specimens in herbaria, we relied primarily on literature references (Bierhorst, 1971; Crane, 1988; Dehgan and Dehgan, 1988; Gifford and Foster, 1988; Jones, 1993; Kubitzki, 1990; Nixon et al., 1994; Rothwell and Serbet, 1994; Stevenson, 1990) and observations on living material of *Cycas* for information on morphological characters.

DATA SETS.—Three data sets were assembled; all comprised 51 taxa: 50 pteridophytes and 1 seed plant (*Cycas*). Two separate sets of analyses (explained under "Analyses"), involving different combinations of taxa, were carried out on these data sets. The morphological data set included 77 parsimony-infor-

mative characters for each taxon. A list of characters and character states is given in Appendix 2, and the data matrix is shown in Table 1. The molecular data set included 1206 bp (potential characters) of the *rbcL* gene for each taxon. All sequence data were taken from Hasebe et al. (1995), except for *Lycopodium digitatum* and *Equisetum arvense* (Manhart, 1994), and *Cycas circinalis* (Chase et al., 1993). Sequence data were easily aligned without any insertions or deletions. The molecular data matrix is not shown, but is available on request as a PAUP file from the first three authors of Hasebe et al. (1995). In Analysis 1 (see "Analyses" section below), 589 molecular characters were invariant, 128 were variable but parsimony-uninformative (i.e., autapomorphic), and 489 were parsimony-informative. Of the informative sites, 377 (77%) were in the third codon position. In Analysis 2, 584 molecular characters were invariant, 132 were variable but parsimony-uninformative, and 490 were parsimony-informative (380 [78%] were in the third codon position). The third data set was produced by combining the morphological and molecular data sets.

MORPHOLOGICAL CHARACTERS.—A total of 115 morphological characters was initially considered (Appendix 2). Of these, 77 proved parsimony-informative, 8 were autapomorphic and may be useful in future studies, and 30 were excluded for reasons detailed in Appendix 2. Each of the 77 morphological characters used in this study (Appendix 2) shows discrete variation among taxa that is heritable and that we believe is independent of other characters, and passes the criteria of homology described below (see "Theoretical Issues"). These characters sample vegetative and reproductive morphology and anatomy. Of the 77 characters, 49 were binary, 17 were 3-state, 7 were 4-state, and 4 were 5-state. Character state assignments reflect character state distribution among the study taxa and do not convey a priori judgments about character polarity (i.e., "0" does not necessarily indicate that the character state is primitive). Hypotheses of character state ordering (adjacency without any implied directionality) are often inferred from observations of character state transformations in ontogeny (see Mabee, 1989, for discussion of assumptions involved). Because we had no ontogenetic or a priori information on transformation series in the multistate characters, we chose to leave them unordered for these analyses. Without such information, the most reliable criterion for determining the evolutionary sequence of a multistate character is congruence with other presumably independent characters on the cladogram itself (Hauser, 1992; Hauser and Presch, 1991; Mabee, 1989). Characters were weighted equally and unpolarized, and trees were rooted via the outgroup method (Maddison et al., 1984; Watrous and Wheeler, 1981).

These morphological/anatomical data were, in large part, derived from the vast pteridological literature of the past century. Fortunately there are several comprehensive and seminal compendia from which we were able to extract data. Most notable were the works of Bierhorst (1971), Bower (1923, 1926, 1928), Eames (1936), Flora of North America Editorial Committee (1993), Gifford and Foster (1988), Kubitzki (1990), Ogura (1972), Stewart and Rothwell (1993), Tryon and Lugardon (1991), and Tryon and Tryon (1982). Whenever

possible, we also examined the primary references found therein. Other references that we consulted are cited under the relevant characters (Appendix 2). Additional references were consulted for *Equisetum* (Brown, 1976; Duckett, 1973; Hauke, 1957, 1979; Johnson, 1937) and for *Lycopodium* (Bruce, 1979; Øllgaard, 1987; Rolleri, 1972; Wagner and Beitel, 1992; Whittier, 1981). In addition, we assembled a voucher study set of herbarium specimens (UC) for each of the taxa in this analysis (Appendix 1). Insofar as we were able, we used these specimens, and some garden and greenhouse plants, to corroborate data taken from the literature. Following each character description (Appendix 2), we cite the sources from which particular data were extracted and we use the University of California (Berkeley) herbarium designation "UC" to indicate that vouchers were checked. The morphological data set was compiled using MacClade, version 3.05 (Maddison and Maddison, 1992). Using the footnote feature available in MacClade, the matrix cells were annotated to document sources, indicate controversies, and explain decisions about homology and character states. This annotated morphological data matrix is available on request from the first author.

Leaves: Several sources were useful in guiding us in defining leaf characters. Those that were especially helpful with regard to interpreting venation were Doyle and Donoghue (1986a, 1986b, 1987) and Nixon et al. (1994). For *Platyzoma* and *Salvinia,* which have 2 types of sterile leaves (see character 2: fertile-sterile leaf differentiation), blade dissection and venation characters were scored for the larger, sterile, photosynthetic blades.

Rhizomes: The rhizome scores for *Equisetum, Lycopodium,* and *Psilotum* apply to the underground rhizome, not the aerial stem, so as to correspond most closely with the scores for the underground rhizomes of ferns, which in general do not have aerial stems.

Sporangia and Spores: Spore characters were scored only for spores that are shed. The term "free-sporing" was used by Stewart and Rothwell (1993) to describe plants with sporangia that upon maturity dehisce and shed their spores. All pteridophytes are free-sporing. In heterosporous ferns, both microspores and megaspores are released from the sporangia, and so these taxa were scored for both types of spores. In the outgroup *Cycas,* primarily the microspores and the microsporangial tissues were scored for the sporangia and spore characters because they are "free-sporing," whereas the megaspores remain within the protective layer of the megasporangium on the parent plant. Because tissues of the indehiscent sporangia remain homologous to their dehiscent counterparts, we omitted scoring only those megasporangium characters that were no longer applicable because of the indehiscense. For example, for spore output we scored *Cycas* for microspores only, since the megasporangia do not dehisce.

Gametophytes: There exists a substantial body of detailed information on the gametophyte morphology of numerous ferns, due in large part to the individual and collaborative research efforts of L. R. Atkinson, B. K. Nayar, and A. G. Stokey. Stokey (1951), Wagner (1952a), and others recognized that knowledge of the gametophyte would make an important contribution to understand-

ing relationships among ferns. Stokey (1951) suggested where useful information might be found: spore germination patterns; manner of development of the cell plate and the meristematic regions; form of the adult thallus; type, position, and time of appearance of hairs when present; and reproductive structures, especially the antheridium. Atkinson, Nayar, and Stokey working alone and in collaboration (see below and literature cited therein) provided consistent data on these topics for numerous fern gametophytes. We were able to extract enough information about gametophytes to score our study taxa confidently for eleven gametophytic characters from Atkinson (1962, 1970, 1973), Atkinson and Stokey (1964), Bierhorst (1968, 1971), Bower (1923, 1926, 1928), Eames (1936), Kubitzki (1990), Nair and Sen (1974), Nayar (1963, 1967), Nayar and Kaur (1968, 1971), Qiu et al. (1995), Stokey (1950, 1960), Stokey and Atkinson (1954, 1956, 1957, 1958), Tryon and Tryon (1982), and M. D. Turner (pers. comm. to KMP, *Calochlaena, Metaxya*).

THEORETICAL ISSUES.—*Missing Data vs. Missing Characters:* The risks involved in coding non-applicable characters as missing data in computer-assisted phylogenetic analyses with parsimony are explicitly discussed in Maddison (1993), and referred to in Maddison and Maddison (1992), Nixon and Davis (1991), Nixon et al. (1994), and Swofford and Begle (1993). Data are missing when characteristics are not known but presumed to be knowable if complete material and thorough studies were available. Non-applicable characters occur when taxa lack the structures in question (e.g., for plants in which the megaspore is retained, it is nonsensical to contemplate characteristics involved in spore dispersal). A common solution to this problem is to code those taxa lacking a particular structure as having missing data. This practice can be safe in some circumstances (Maddison, 1993), but may not be in others; there is, however, no algorhithmic solution to the problem at present. For example, in our morphological data set, roots were scored as absent for *Psilotum* and *Salvinia*. Consequently, for the two characters, "root hairs" and "root anatomy," these taxa were scored with a ? (Table 1). In the footnotes of the MacClade version of the matrix, we reported that these characters are not applicable in these taxa (and not simply that the character state information is unknown); however, this distinction is not evident in the way the matrix is presented (Table 1) or analyzed. However much as we would prefer to distinguish between these two concepts, it is not yet possible, because currently available phylogenetic computer programs have yet to resolve the issue computationally. Another general solution to this dilemma is to fuse these characters into a single multistate character that encompasses all the relevant features of that character; however, this is not always practical and can quickly become unwieldy and perhaps even meaningless. Furthermore, the resolving power of such multistate characters is seriously reduced. On the other hand, splitting one large comprehensive character (e.g., root characteristics) into several characters might result in correlated (non-independent) characters. This did not appear to be the case in this study, because none of these characters had the same pattern of character state distributions among taxa. For the moment, we

assume that scoring non-applicable characters and missing data in a similar fashion will not lead to unexpected and undesirable results. It is unfortunate, however, that there is no method to incorporate uncertainty vs. inapplicability into the analysis. This topic is in critical need of theoretical investigation.

Homology: Assessment of homology among divergent taxa is a serious consideration in a phylogenetic study of higher level taxa. Taking the view that homologues are the product of descent from a common ancestor, we followed Remane's criteria (Wiley, 1981) for identifying homologous character states: 1) position; 2) quality of resemblance; and 3) continuity of similarity through intermediate forms, based on developmental or across-species comparisons. Every statement of homology is a hypothesis subject to testing, and individual hypotheses of putative homology are built up on a character-by-character basis. It is now generally accepted that testing homologies is a 2-step process. First, similarity in position, structure, and development are used as evidence for homology. These hypotheses are then tested for congruence against the pattern of phylogenetic relationships based on all characters. Cladistics provides a critical test of homology—it relates information from all characters to questions of homology of particular characters. If one hypothesizes that a certain character is homologous for a certain group (i.e., that it is a synapomorphy that specifies a monophyletic group) and this is congruent with the phylogeny, then this is corroboration for a homologous character. A true homology will circumscribe a group that is congruent with those specified by other character homologies. Cladistic analyses take all informative characters into account in determining the topology. We can then map character transformations onto the tree and determine which characters support which monophyletic groups and are therefore homologous for that group, and which groups show a homoplasious event with regard to a particular character. An incongruence between hypotheses of synapomorphy and phylogeny identifies homoplasy. In other words, homoplasy is determined by conflict with other independent characters and is manifested in the final tree(s). For example, the development of similar adaptations in the Euphorbiaceae and the Cactaceae is interpreted as homoplasy, rather than homology, because all of the evidence together (floral features and other characters) points to different ancestry and thus independent development of their similar features. In every cladistic analysis some uncertainty exists in assessment of homology. Whether or not we have succeeded in this effort will be evaluated by future character and cladistic analyses. For useful discussions of the relationships between homology, cladistics, and systematics see: Donoghue and Sanderson (1994), Mishler (1986, 1994), Nelson (1994), Patterson (1982, 1988), Roth (1984, 1988, 1994), Stevens (1984), Wiley (1981), and references cited therein.

ANALYSES.—The data sets were compiled using MacClade, version 3.05 (Maddison and Maddison, 1992). Phylogenies were reconstructed using equal-weighted maximum parsimony as implemented in PAUP, version 3.1.1 (Swofford, 1991b). Generally a unique character state was assigned to each taxon for each character. For some characters, however, it was necessary to assign

multiple states to certain taxa. This was either because the taxa were polymorphic and the character varied among individuals, or because we were partially uncertain about the state that a particular taxon possessed, but some of the potential states could be excluded as possibilities. When taxa were "multistate" for certain morphological characters and were coded as either polymorphisms (e.g., 0&2) or partial uncertainties (e.g., 0/2), PAUP interpreted all these as polymorphisms (rather than uncertainties). A current limitation of PAUP is that it cannot mix the two multistate interpretations at the same time (Swofford and Begle, 1993, p. 95). Multistate characters were unordered and uninformative characters were ignored in all analyses. Accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) were used to investigate character state optimization.

Due to the large number of taxa included in the data sets, a branch-and-bound analysis, which guarantees finding all most parsimonious trees, could not be carried out. The heuristic search algorithm was used in a two-step process, first finding some of the shortest trees and then using these as starting points to find all the shortest trees [modified from Maddison et al., 1992; Olmstead and Palmer, 1994; with suggestions from D. Maddison (pers. comm. to KMP)]. The first step was to get a sample of the shortest trees by initiating 100 searches each using random addition starting trees, with TBR swapping and MULPARS selected, but saving no more than 2 of the shortest trees from each search (saving trees of length $\geq$"2", or some number smaller than the shortest possible tree). The tree length of the shortest trees was noted from this analysis, and in the second step at least 1000 searches were initiated in the same manner as above, but saving no more than 25 trees of length $\geq$"X", where "X" was a number one step longer than the shortest tree discovered in the first step of this heuristic search process. This restricted the number of trees that were saved that were longer than the minimal length thus far achieved, but not the number of shorter trees that were saved. This is a very effective method for finding all the most parsimonious trees that belong to different "islands" of shortest trees (Maddison, 1991). For instance, when the search locates some of the shortest length trees, it finds all of the trees belonging to that particular island of shortest trees; then it goes on to another random addition starting tree for the next search. After 1000 replicates most of the smallest islands of shortest trees had been discovered at least 5 times, and the larger islands had been discovered many more times, strongly suggesting that the shortest possible trees were found (D. Maddison, pers. comm. to KMP).

Equally most parsimonious trees from all analyses were summarized using strict consensus, except for trees from the morphology data, which were summarized using majority rule consensus. Bootstrap analyses (Felsenstein, 1985; Hillis and Bull, 1993; Sanderson, 1989) were conducted to provide a measure of support for the phylogenetic results presented here. Bootstrapping of the molecular data set and the combined data set used 100 replicates, with 10 random addition starting trees implemented for each replicate, and TBR branch swapping and MULPARS selected. Bootstrapping of the morphological data set used 1000 replicates, with 10 random addition starting trees imple-

mented for each replicate, and TBR branch swapping, and MULPARS selected, but saving no more than 10 trees of length ≥"n" (a number smaller than the shortest possible tree) for each random addition sequence. A decay analysis (Bremer, 1988; Donoghue et al., 1992) was attempted using the HyperCard 2.1 "Auto Decay version 2.4 program" kindly provided by Torsten Eriksson. Given the large size of the data sets, however, the computer time required to conduct the appropriate PAUP searches that would result in reliable decay values with the constraint tree definitions derived from the Auto Decay program was prohibitive.

The analyses that were carried out in this study are presented below and are numbered in the Results and the Discussion for ease of reference.

Analysis 1: The goal of Analysis 1 was to determine the phylogenetic relationships of ferns only (*Botrychium, Angiopteris,* and Filicopsida) by analyzing the three data sets (Analyses 1A, 1B, and 1C). All recent phylogenetic analyses that have included pteridophyte representatives indicate that ferns shared a most recent common ancestor with seed plants (Fig. 1; Bremer, 1985; Bremer et al., 1987; Garbary et al., 1993; Kenrick and Crane, 1991; Manhart, 1994; Mishler and Churchill, 1985; Mishler et al., 1994; Parenti, 1980). The cycads are often resolved as the most basal group in recent phylogenetic analyses of the seed plants (Crane, 1985a, 1985b; Nixon et al., 1994; but see also alternate resolutions in Doyle et al., 1994; Rothwell, 1994; Rothwell and Serbet, 1994); therefore, we chose *Cycas* as the outgroup terminal taxon in this analysis. Forty-seven fern taxa were included in Analysis 1, with *Cycas* as outgroup; *Equisetum, Lycopodium,* and *Psilotum* were excluded. With this combination of terminal taxa, two characters (33: roots, and 39: intranuclear paracrystals) were parsimony-uninformative (autapomorphic) and were excluded from the analysis.

Analysis 1A: Parsimony analysis of morphological characters only. All characters were unordered and weighted equally.

Analysis 1B: Parsimony analysis of *rbcL* characters only. All characters were unordered and weighted equally. Giving all categories of molecular change equal weight (i.e., weighting transitions and transversions equally) is an assumption. Albert et al. (1993) found equal weighting to be adequate if sampling effects are not a factor. We analyzed the *rbcL* data set using the differential character-state weights calculated by Albert et al. (1993) and also with differential a priori character-state weights empirically calculated from this data set. A single most parsimonious tree resulted from each of these differentially weighted analyses, and these disagreed only in minor respects from each other and from trees obtained in the equal weighted analysis. We do not show these results, primarily because the use of a differential character-state weighting model for molecular data in a combined analysis results in favoring the molecular data so greatly that morphological characters are effectively ignored.

Analysis 1C: Parsimony analysis of morphological and *rbcL* characters combined. All characters were unordered and weighted equally. When the results from different data sets are each well resolved, but in conflict, combining the data sets could support erroneous conclusions if the data sets have sufficiently

TABLE 2. Comparison of bootstrap support for selected clades between Analysis 1A (morphology), Analysis 1B (*rbcL*), and Analysis 1C (morphology and *rbcL* combined). Numbers are percentage (%) values. A dash indicates bootstrap support is <50% for a clade that occurs in the consensus trees shown in Figs. 2–4. NA indicates a clade not observed in the consensus trees (Figs. 2–4) of a particular analysis.

Clade	1A	1B	1C
Heterosporous ferns: *Azolla-Salvinia-Marsilea*	98	95	98
Leptosporangiate ferns (including *Osmunda*) = all taxa except *Botrychium, Angiopteris,* and *Cycas*	73	NA	89
Leptosporangiate ferns (excluding *Osmunda*) = all taxa except *Osmunda, Botrychium, Angiopteris,* and *Cycas*	—	NA	71
Loxogramme-Vittaria	67	NA	NA
Dipteroid ferns: *Cheiropleuria-Dipteris*	60	100	100
Gleichenioid ferns: *Diplopterygium-Stromatopteris*	NA	100	100
Tree ferns: *Calochlaena-Dicksonia-Metaxya-Cyathea* + *Plagiogyria*	—	93	89
Pteridoid ferns: *Platyzoma-Pteris-Taenitis-Ceratopteris-Acrostichum-Adiantum-Vittaria-Coniogramme*	NA	96	100
Dennstaedtioid ferns (in part): *Blotiella-Histiopteris-Pteridium*	—	94	93
Micropolypodium-Polypodium-Loxogramme-Davallia-Nephrolepis-Elaphoglossum-Rumohra-Blechnum-Onoclea-Thelypteris-Asplenium	NA	100	99
Ceratopteris-Acrostichum	—	93	99
Schizaeoid ferns: *Anemia-Actinostachys-Lygodium*	NA	78	91
Calochlaena-Dicksonia	56	NA	74
35 fern taxa (excluding *Matonia, Lygodium, Anemia, Actinostachys, Cheiropleuria, Dipteris, Diplopterygium, Stromatopteris, Cephalomanes, Osmunda, Botrychium, Angiopteris, Cycas*)	NA	77	NA
Pteridoid ferns: (*Platyzoma-Pteris-Taenitis-Ceratopteris-Acrostichum-Adiantum-Vittaria-Coniogramme*) + Dennstaedtioid ferns sensu stricto (*Blotiella-Histiopteris-Pteridium-Monachosorum-Dennstaedtia-Microlepia*) + *Micropolypodium-Polypodium-Loxogramme-Davallia-Nephrolepis-Elaphoglossum-Rumohra-Blechnum-Onoclea-Thelypteris-Asplenium*	NA	75	72
All taxa in above row + *Lonchitis*	NA	67	NA
All taxa in above row + *Lindsaea*	NA	73	86
Polypodioid ferns: *Micropolypodium-Polypodium-Loxogramme*	NA	60	89
Vittaria-Adiantum	NA	78	90
Elaphoglossum-Rumohra	—	79	85
Micropolypodium-Polypodium-Loxogramme-Davallia-Nephrolepis	NA	74	88
All taxa in above row + *Elaphoglossum-Rumohra*	NA	79	82
Tree ferns: *Calochlaena-Dicksonia-Metaxya-Cyathea*	NA	77	75
Dennstaedtioid ferns sensu stricto: *Blotiella-Histiopteris-Pteridium-Monachosorum-Dennstaedtia-Microlepia*	NA	—	NA
All taxa in above row + *Micropolypodium-Polypodium-Loxogramme-Davallia-Nephrolepis-Elaphoglossum-Rumohra-Blechnum-Onoclea-Thelypteris-Asplenium*	NA	51	NA

different modes of evolution (Bull et al., 1993). Due to the relatively poor resolution of results based on the morphological data set alone, it was not possible for us to test for combinability of data sets (Rodrigo et al., 1993). When the results from one data set are poorly resolved and in conflict with the more resolved results from another data set, as is the case shown here, discrepancies between the two are very likely due to character sampling error suggesting that the data sets be combined.

Analysis 2: The goal of Analysis 2 was to determine the phylogenetic relationships of pteridophytes (Filicopsida, *Angiopteris, Botrychium, Equisetum, Lycopodium, Psilotum*) by analyzing the three data sets (Analyses 2A, 2B, and 2C). Recent evidence supports the placement of the lycopodiophytes at the base of the extant tracheophyte clade (Donoghue, 1994; Kenrick, 1994; Kenrick and Crane, 1991; Raubeson and Jansen, 1992), and so we used *Lycopodium* as the outgroup terminal taxon in this analysis. Forty-seven fern taxa, *Psilotum,* and *Equisetum* were included in Analysis 2, with *Lycopodium* as the outgroup; *Cycas* was excluded. This combination of terminal taxa resulted in two characters (29: vascular cambium, and 35: root anatomy) being parsimony-uninformative (autapomorphic), and they were excluded from this analysis.

An analysis that included all 50 pteridophytes and *Cycas* was not pursued here. Coding morphological characters across this broad spectrum of plants is difficult since fewer homologous comparisons can be made due to the major phenotypic differences. A future paper will address the question of which pteridophyte group is most closely related to the spermatophytes, using more comprehensive data sets (including data from fossils) for these groups.

Analysis 2A: Parsimony analysis of morphological characters only. All characters were unordered and weighted equally.

Analysis 2B: Parsimony analysis of *rbcL* characters only. All characters were unordered and weighted equally.

Analysis 2C: Parsimony analysis of morphological and *rbcL* characters combined. All characters were unordered and weighted equally.

Results

Analysis 1A.—Ten islands of most parsimonious trees were found. These varied in size from 1512 trees to 2 trees and included a total of 3326 most parsimonious trees at 449 steps (CI = 0.325; RI = 0.541). Because the CI value is highly correlated with the number of taxa included in an analysis (homoplasy increases as the number of taxa increases), we used the formula of Sanderson and Donoghue (1989) to estimate if homoplasy was higher than expected. We determined that the observed CI is very close to the expected CI=0.335, indicating that the level of homoplasy is not greater than would be expected for a study with 48 taxa. The majority rule consensus tree, with bootstrap values, is shown in Figure 2. Thickest branches are those with bootstrap support exceeding 70%. This value was chosen because Hillis and Bull (1993, p. 189) demonstrated through computer simulation and laboratory manipulation of a known phylogeny that, "Almost every internal branch with a bootstrap pro-

portion above 70% defines a true clade." Bootstrap support for selected clades is also shown in Table 2. The monophyly of the heterosporous ferns (*Azolla, Salvinia,* and *Marsilea*) is robustly supported by this data set (98% bootstrap value). The Filicopsida (leptosporangiate ferns) are a reasonably well supported group with 73% support. Note that *Loxogramme* and *Vittaria* have some bootstrap support as a monophyletic group (67%). All other clades shown here without bootstrap support (or asterisks) were found only in the majority rule consensus and not the strict consensus.

ANALYSIS 1B.—Only 1 tree island was found of 3 most parsimonious trees at 3639 steps (CI = 0.235; RI = 0.464). The observed CI is lower than the expected CI = 0.335, as calculated by the formula of Sanderson and Donoghue (1989), indicating that the level of homoplasy in *rbcL* is greater than would be expected for an average study with 48 taxa. It is interesting to note that the level of homoplasy is higher here than in the morphological data set (Analysis 1A). The three most parsimonious trees differ only in their placement of three tree fern taxa (*Calochlaena, Dicksonia,* and *Cyathea*); all other portions of their topologies are identical. The strict consensus tree is shown in Figure 3. Bootstrap support for selected clades is also indicated in Table 2. High bootstrap support (>85%) is shown for several clades throughout the tree: *Cheiropleuria-Dipteris,* 100%; gleichenioid ferns (*Diplopterygium-Stromatopteris,* 100%); tree ferns (*Calochlaena* to *Plagiogyria,* 93%); heterosporous ferns (*Azolla* to *Marsilea,* 95%); pteridoid ferns (*Platyzoma* to *Coniogramme,* 96%); *Dennstaedtia-Microlepia,* 100%; *Blotiella* to *Pteridium,* 94%; and a clade including some of the most derived ferns (*Micropolypodium* to *Asplenium,* 100%). Smaller clades within some of these major clades also have high bootstrap support (e.g., *Ceratopteris-Acrostichum,* 93%, in the pteridoid ferns). Other monophyletic groupings that show relatively high bootstrap support (≤85%, >70%) are: the schizaeoid ferns (*Anemia* to *Lygodium,* 78%) and a large clade that includes many of the leptosporangiate ferns in this study (*Micropolypodium* to *Plagiogyria,* 77%). A smaller clade (*Micropolypodium* to *Coniogramme*) that includes the pteridoids, the dennstaedtioids, and the robustly supported *Micropolypodium* to *Asplenium* group, has 75% bootstrap support, with *Lonchitis* and *Lindsaea* basally attached to it with 67% and 73% support, respectively. The leptosporangiate ferns do not form a monophyletic clade in this analysis, with the leptosporangiate, filmy fern *Cephalomanes* grouping with the eusporangiate fern *Botrychium* near the base of the tree (<50% bootstrap support).

ANALYSIS 1C.—Only one tree island was found of 34 most parsimonious trees at 4128 steps (CI=0.242; RI=0.466). The observed CI is slightly higher in the combined analysis than with the *rbcL* data alone (Analysis 1B). The strict consensus tree is shown in Figure 4 and bootstrap support for selected clades is also indicated in Table 2. The general result of the combined analysis is that the two data sets tend to reinforce each other in cases where they were congruent. Many of the branches that had high bootstrap support (>85%) in Analysis 1B show bootstrap values that are about the same, e.g., tree ferns (*Caloch-*

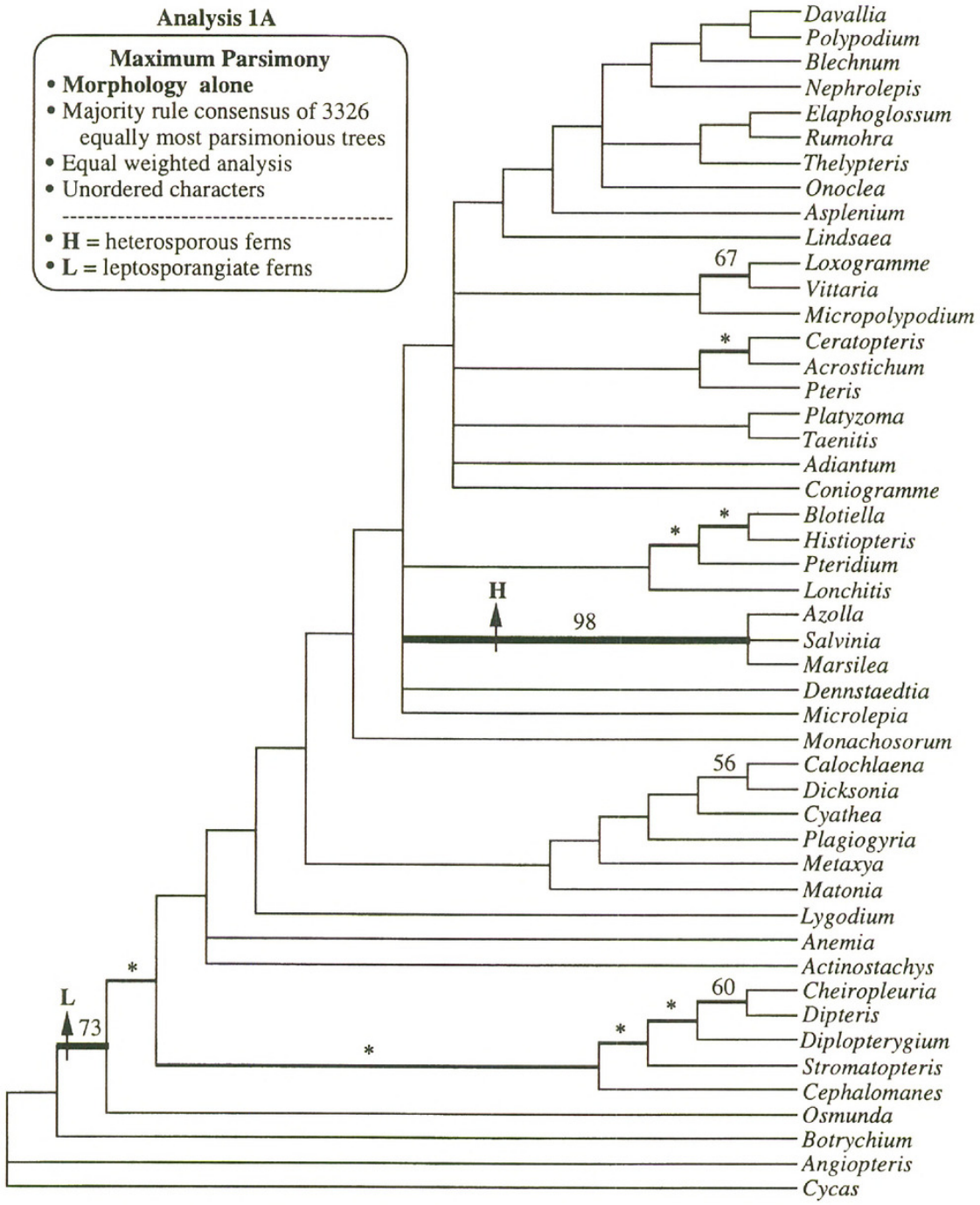


FIG. 2. Majority rule consensus of 3326 most parsimonious trees at 449 steps based on 75 parsimony-informative morphological characters that were equally weighted and unordered. Numbers above branches indicate bootstrap percent values. Thickest branches are those with bootstrap support exceeding 70%. All clades with bootstrap support greater than 56% were found in the strict consensus. Asterisks on medium-thick branches indicate clades also found in the strict consensus, but not in the bootstrap majority rule tree. Thinnest branches without numbers were resolved in the majority rule consensus tree but had bootstrap values <50%. The tree was rooted with *Cycas*. CI=0.325; RI=0.541.

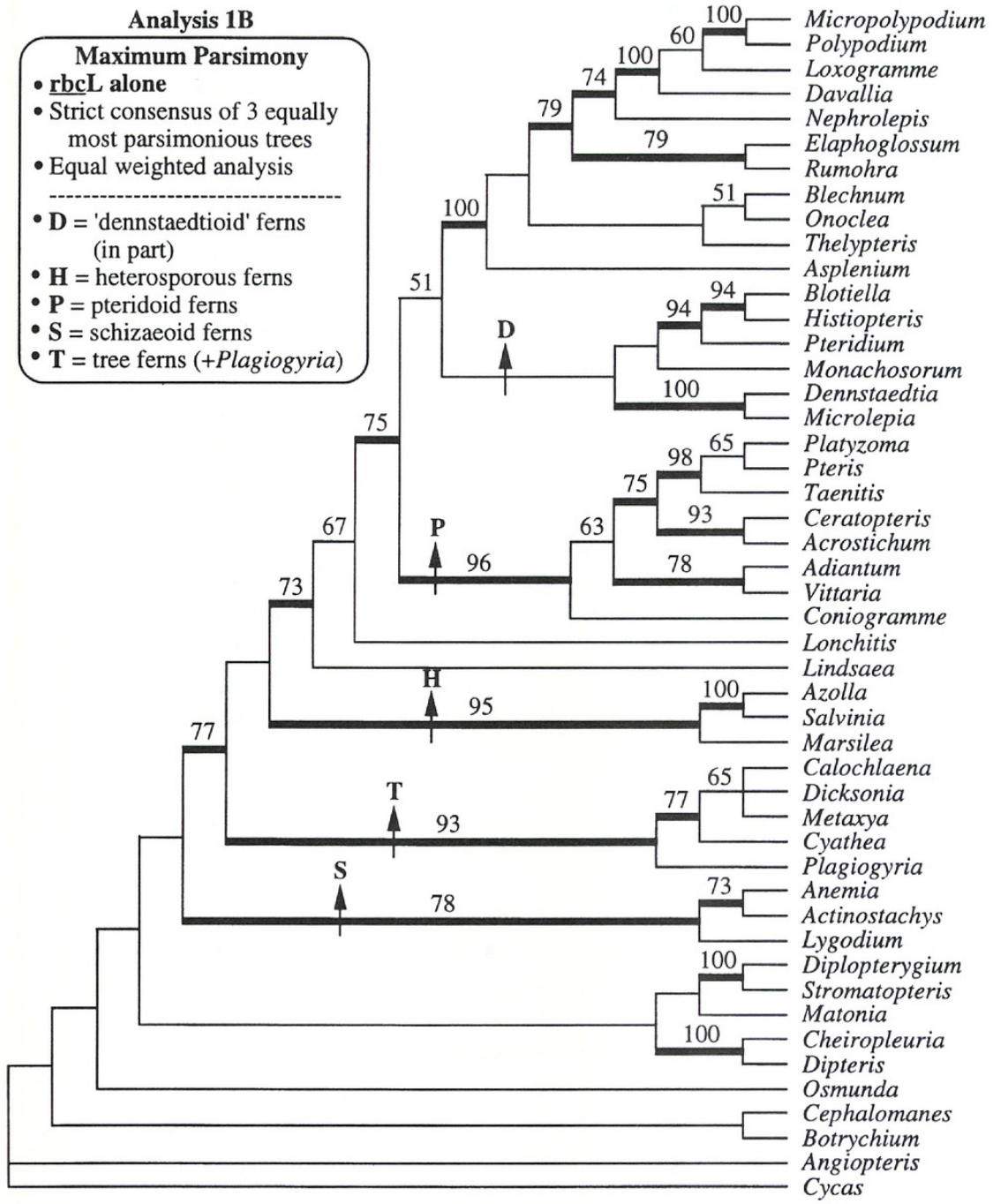


FIG. 3. Strict consensus of 3 most parsimonious trees at 3639 steps based on 489 parsimony-informative *rbcL* characters that were equally weighted and unordered. Numbers above branches indicate bootstrap percent values. Thicker branches are those with bootstrap support exceeding 70%. Branches without numbers were resolved in the strict consensus tree but had bootstrap values <50%. The tree was rooted with *Cycas*. CI=0.235; RI=0.464.

laena to *Plagiogyria*), 89%; *Micropolypodium* to *Asplenium,* 99%; *Diplopterygium-Stromatopteris,* 100%; *Blotiella* to *Pteridium,* 93%. More often, the bootstrap values are higher in the combined analysis, e.g., heterosporous ferns (*Azolla* to *Marsilea*), 98%; pteridoid ferns (*Platyzoma* to *Coniogramme*), 100%; *Ceratopteris-Acrostichum,* 99%. Bootstrap support for the leptosporangiate fern clade (including *Osmunda*) in the combined analysis was 89%, higher than in Analysis 1A (73%) and in Analysis 1B (not a monophyletic clade). In addition, there is good bootstrap support for branches in the combined analysis that did not have support in either separate analysis, e.g., 71% for all leptosporangiate ferns (excluding *Osmunda*), providing support for *Osmunda* being the most basal leptosporangiate fern. These results demonstrate that morphological data can provide support at the base of the tree, which *rbcL* data alone could not.

Some clades with moderate support (≤85%, >70%) in Analysis 1B and <50% support (or not resolved) in Analysis 1A had strikingly higher support in the combined analysis: schizaeoid ferns, 91%; the large clade including the pteridoids (*Platyzoma* to *Coniogramme*), dennstaedtioids (*Blotiella* to *Lindsaea*), and *Micropolypodium* to *Asplenium,* 86%. *Loxogramme* was basal to the *Micropolypodium-Polypodium* clade in Analysis 1B, but with low bootstrap support (60%). In Analysis 1A it grouped with *Vittaria* (67%). In the combined analysis, it is basal to the *Micropolypodium-Polypodium* clade with high bootstrap support (89%). Likewise, the support for the grouping of *Vittaria* with *Adiantum* in Analysis 1B is increased in the combined analysis, from 78% to 90%. A number of branches in the *Micropolypodium* to *Rumohra* clade with moderate bootstrap support in Analysis 1B and none in Analysis 1A were more strongly supported in the combined analysis (e.g., the *Micropolypodium* to *Nephrolepis* clade went from 74% to 88% support).

Conversely, some relationships that conflicted but were weakly supported in both Analyses 1A and 1B are less resolved in the combined analysis (Table 2). This effect of the combined analysis is also evident in the reduced resolution of the strict consensus from the combined analysis compared to the strict consensus from Analysis 1B. For example, within the *Micropolypodium* to *Monachosorum* clade in Fig. 4 there are several robustly supported clades with greater than 90% bootstrap values, e.g., pteridoids (*Platyzoma* to *Coniogramme*), 100%; *Dennstaedtia-Microlepia,* 100%; *Blotiella* to *Pteridium,* 93%. However, the relationship of these clades to one another is unresolved in the combined analysis. By contrast, in Analysis 1B (Fig. 3), these same clades are resolved with respect to one another, but mostly with <50% bootstrap support (e.g., *Dennstaedtia-Microlepia* is sister group to other dennstaedtioids [*Blotiella* to *Monachosorum*]; *Blotiella* to *Microlepia* clade is sister group to *Micropolypodium* to *Asplenium* clade; and also the *Platyzoma* to *Coniogramme* clade is weakly supported at the base of this larger clade). Likewise, the larger *Micropolypodium* to *Plagiogyria* clade that has 77% bootstrap support in Analysis 1B has <50% support in the combined analysis.

Analysis 1—Summary of results and a hypothesis for morphological character evolution in ferns: The increased support for most clades in Analysis 1C

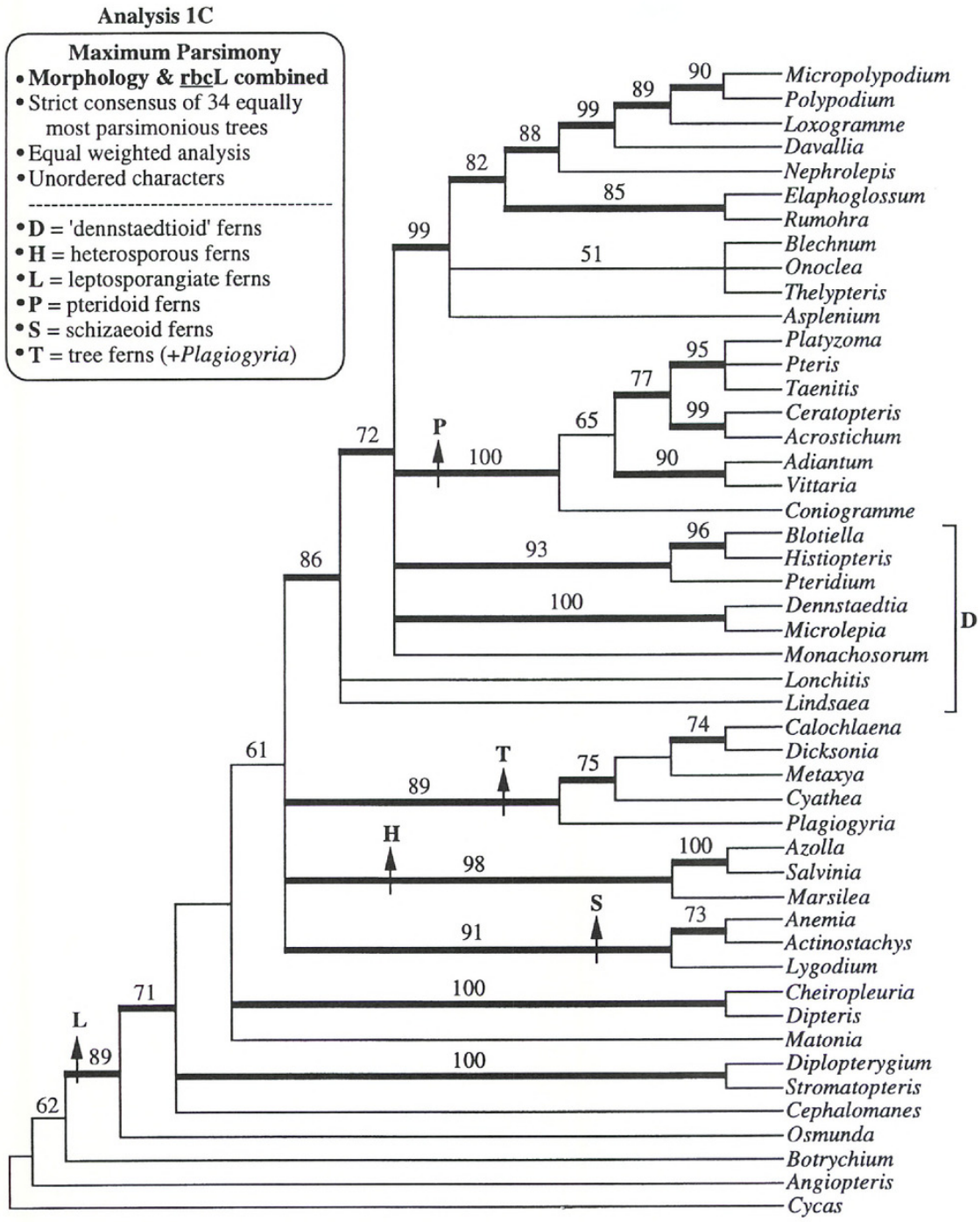


FIG. 4. Strict consensus of 34 most parsimonious trees at 4128 steps based on 564 parsimony-informative characters (489 from *rbcL* and 75 from morphology) that were equally weighted and unordered. Numbers above branches indicate bootstrap percent values. Thicker branches are those with bootstrap support exceeding 70%. Branches without numbers were resolved in the strict consensus tree but had bootstrap values <50%. The tree was rooted with *Cycas*. CI=0.242; RI=0.466.

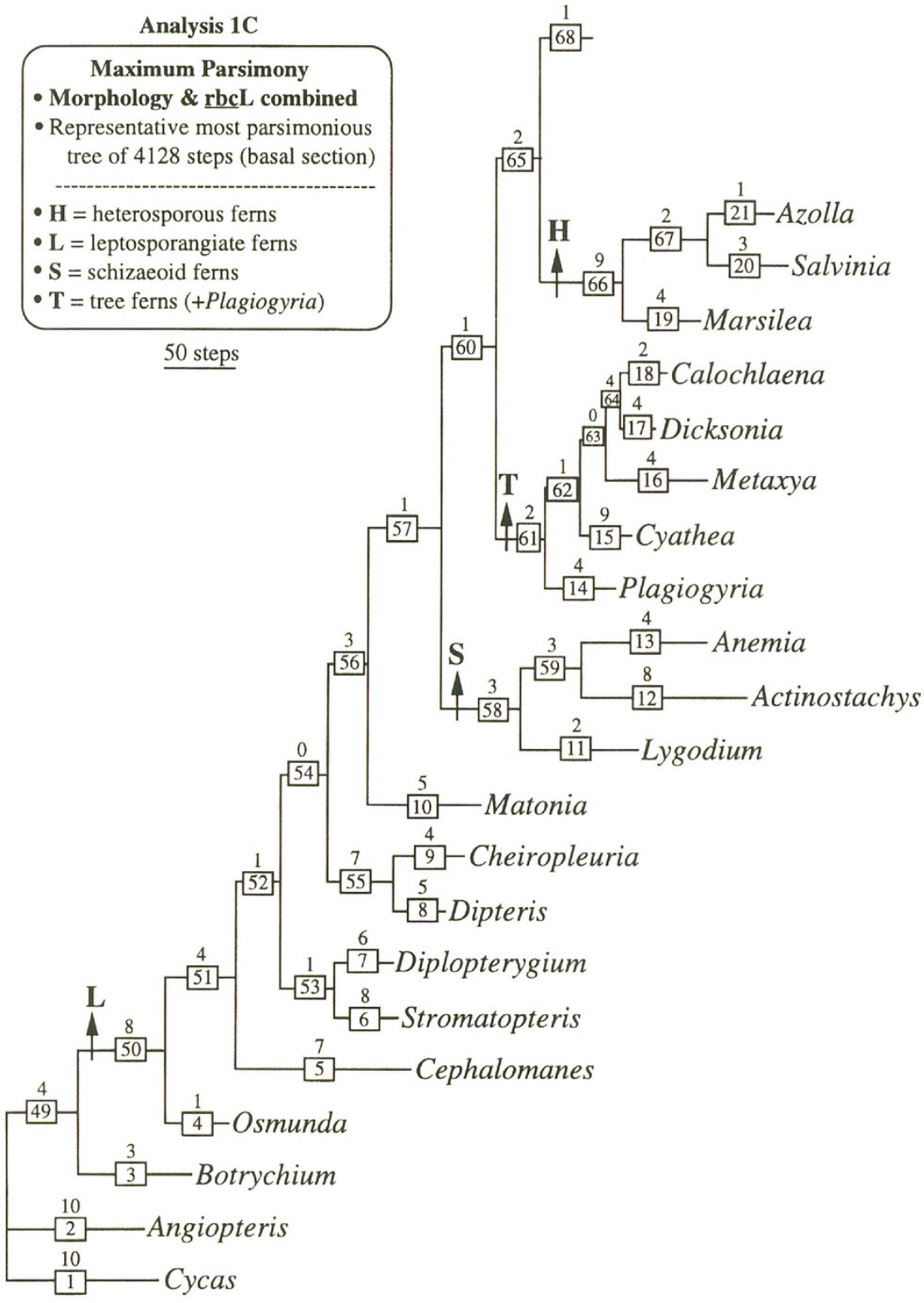
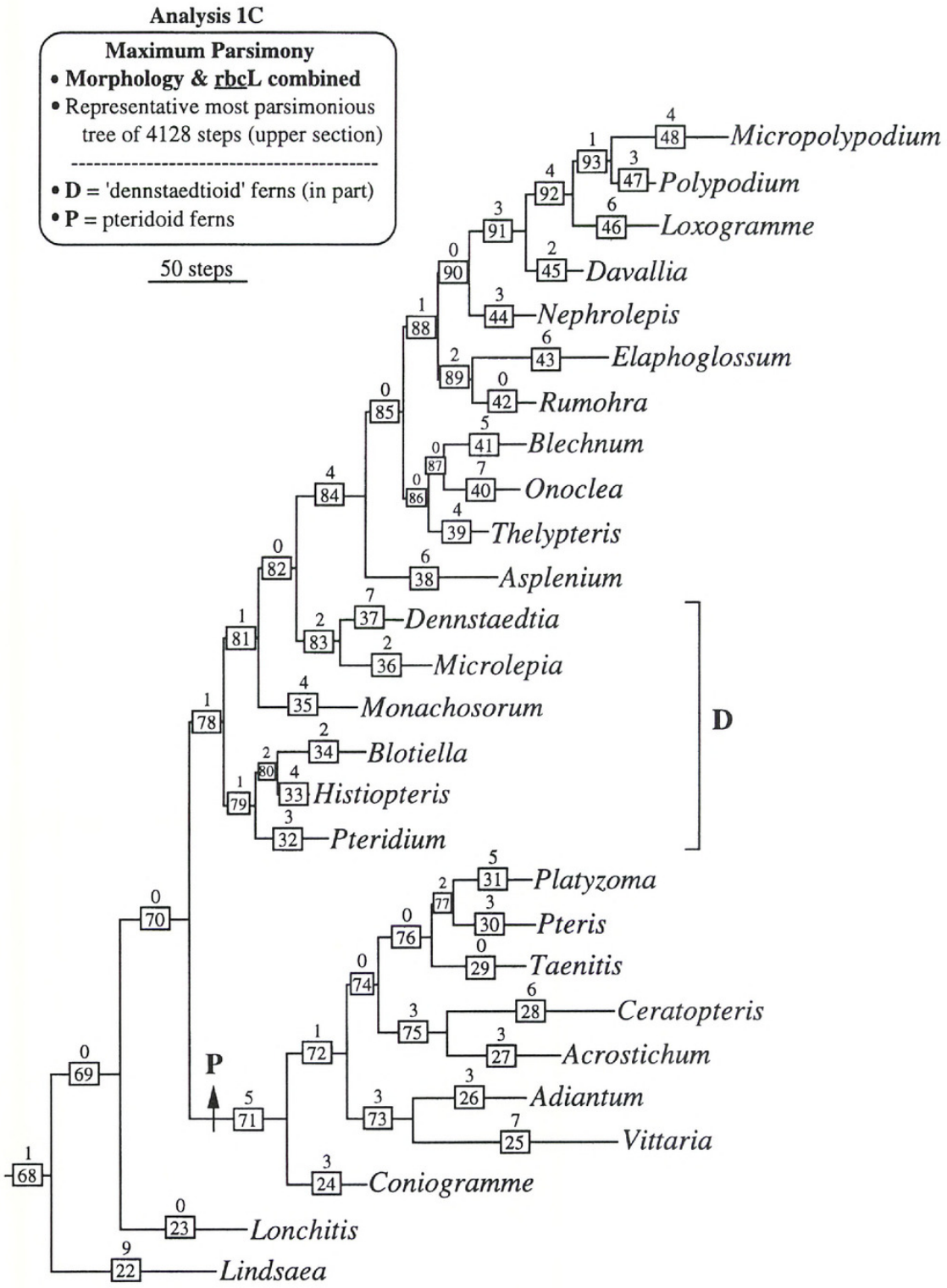


FIG. 5. Representative most parsimonious tree at 4128 steps from the results of the combined analysis (Analysis 1C). Boxed numbers are branch numbers as listed in Table 3. Numbers above boxes are the number of unambiguous morphological character state changes on that branch. Branch lengths on the phylogram are indicative of the total number of molecular and morpholog-



ical changes (unambiguous and ambiguous). The number of unambiguous molecular and morphological character state changes on each branch and a tabulation of the morphological character state changes (indicating those that are non-homoplasious) are provided in Table 3. The upper and lower portions of the tree are connected along branch 68.

controvert the concern that conflicting patterns of homoplasy will significantly lower overall resolution when data are combined, suggesting instead that, in this case, both separate analyses (1A and 1B) are reflecting the same real phylogenetic signal. To present more clearly the results of the three different subanalyses, bootstrap support is compared between Analyses 1A–1C for selected clades in Table 2. In addition, a representative tree was chosen from the 34 most parsimonious trees that resulted from the combined analysis (Analysis 1C), and is shown as a phylogram in Figure 5. Each branch in Figure 5 is numbered to correspond to those listed in Table 3. The number of unambiguous morphological and molecular character state changes on each branch and a tabulation of the morphological changes are provided in Table 3. These are changes that occur both in ACCTRAN and DELTRAN reconstructions.

As shown in Fig. 5, the number of unambiguous morphological character state changes for terminal taxa ranges from zero (only in *Lonchitis, Taenitis,* and *Rumohra*) to ten; on internal branches the number ranges from zero to nine. As indicated in Table 3, the internal branches with the highest number of unambiguous morphological character state changes are: 1) branch 66 supporting the heterosporous ferns as a monophyletic clade with nine changes, 2) branch 50 supporting the leptosporangiate ferns (including *Osmunda*) with eight changes (six of which are non-homoplasious), 3) branch 55 below the *Cheiropleuria-Dipteris* clade with seven changes, and 4) branch 71 supporting the pteridoid ferns (*Platyzoma* to *Coniogramme* clade in Fig. 5), with 5 changes. Several internal branches have no unambiguous morphological changes (branches 54, 63, 69, 70, 74, 76, 82, 85–87, 90); all the unambiguous support for these particular branches is provided by molecular character state changes (Table 3).

Unambiguous morphological character state changes that are non-homoplasious (i.e., do not occur elsewhere on the tree) are shown in bold in Table 3, with more than 25% of these mapped on branch 50 (supporting leptosporangiate ferns clade; Fig. 5A). It is important for the reader to note that similar but non-homologous character state changes (homoplasies) in different parts of the tree do not necessarily confound or negate phylogenetic information. For example, on branch 66 (Fig. 5A and Table 3), the heterosporous condition is an unambiguous synapomorphy for *Azolla, Salvinia,* and *Marsilea.* It is homoplastic, however, because the heterosporous condition is also an unambiguous character state for the outgroup *Cycas* (branch 1 in Fig. 5A and Table 3). Although homoplastic in the context of the tree as a whole, character state changes such as these do still contribute important phylogenetic information in more localized areas of the tree (within which one infers they are homologous).

MacClade allows one to map characters onto the most parsimonious topology based on all the evidence to learn something about patterns of character evolution (Analysis 1C). To illustrate the sequence of morphological character change in ferns, samples of a few sporophytic vegetative (Fig. 6) and sporangial (Fig. 7) characters, as well as spore and gametophytic (Fig. 8) characters, were selected and mapped onto the representative most parsimonious tree topology

TABLE 3. Distribution of unambiguous molecular and morphological character state changes on representative most parsimonious tree (1 of 34 trees) from Analysis 1C of combined data set. These changes occur in both ACCTRAN and DELTRAN reconstructions. Branch numbers correspond to those in Figs. 5A and 5B. The number of unambiguous character state changes are given for both molecular and morphological characters. Morphological character numbers and names are provided, along with the character state change and an abridged statement of the derived character state for each branch. Morphological character numbers and names correspond to those in Appendix 2. Unambiguous character state changes that are non-homoplasious (i.e., do not occur elsewhere on the tree) are shown in bold.

Branch number	No. unambiguous molecular character state changes	No. unambiguous morphological character state changes	Number and name of unambiguous morphological character: Character state change on branch; character state at node above (if internal branch) or of terminal taxon (if terminal branch). Non-homoplasious character state changes are indicated in bold.	
1	71	10	(5)	Vein orders: 3 → 1; Two
			(27)	**Rhizome stele type: 2 → 3; Eustele**
			(41)	**First zygote division: 0 → 2; Free-nuclear division**
			(59)	Sporogenesis: 0 → 2; Heterosporous
			(60)	**Spore laesura: 1 → 3; Furrow**
			(65)	**Exospore structure: 1 → 2; 5-layered**
			(66)	Exospore surface: 1 → 0; Smooth
			(68)	Gametophyte form: 2 → 4; Reduced
			(71)	Gametophytic fungal association: 1 → 0; No
			(72)	Dependent gametophyte: 0 → 1; Yes
2	54	10	(2)	Fertile-sterile leaves: 3 → 0; Monomorphic
			(10)	Blade hairs: 1 → 0; Absent
			(11)	Blade scales: 0 → 1; Present
			(15)	Pulvini: 0 → 1; Present
			(16)	**Pneumathodes: 0 → 1; Present and scattered**
			(24)	Stipe xylem configuration: 0 → 4; Polycyclic
			(28)	Rhizome stele cycles: 0 → 1; Polycyclic
			(31)	Rhizome scales: 0 → 1; Present
			(43)	Sporangium receptacle: 0 → 1; Convex
			(47)	Sori: 0 → 1; Present
3	63	3	(21)	Sclerenchyma fibers: 1 → 0; Absent
			(34)	Root hairs: 1 → 0; Absent
			(68)	Gametophyte form: 2 → 0; Tuberous
4	33	1	(64)	Perispore surface: 0 → 1; Smooth
5	94	7	(24)	Stipe xylem configuration: 0 → 1; Solid form in center
			(43)	**Sporangium receptacle: 0 → 2; Elongate and bristle-like**
			(49)	Sporangium position: 1 → 0; Marginal
			(50)	Sporangium/sorus maturation: 0 → 1; Gradate
			(52)	Indusia: 0 → 1; Present
			(68)	Gametophyte form: 2 → 1; Filamentous
			(77)	Gametophyte gemma-producing: 0 → 1; Yes, on thallus
6	30	8	(5)	Vein orders: 3 → 1; Two
			(6)	Secondary vein form: 1 → 0; Dichotomous
			(20)	Sclerenchyma coloration: 0 → 1; Dark-pigmented
			(34)	Root hairs: 1 → 0; Absent

TABLE 3. Continued.

Branch number	No. unambiguous molecular character state changes	No. unambiguous morphological character state changes	Number and name of unambiguous morphological character: Character state change on branch; character state at node above (if internal branch) or of terminal taxon (if terminal branch). Non-homoplasious character state changes are indicated in bold.	
			(43)	Sporangium receptacle: 0 → 1; Convex
			(60)	Spore laesura: 1 → 0; Linear
			(68)	Gametophyte form: 2 → 0; Tuberous
			(70)	Gametophyte photosynthetic: 1 → 0; No
7	25	6	(4)	Primary vein form: 1 → 0; Dichotomous
			(10)	Blade hairs: 1 → 0; Absent
			(11)	Blade scales: 0 → 1; Present
			(30)	Rhizome hairs: 1 → 0; Absent
			(51)	No. sporangia/sorus: 1 → 0; Few (<12)
			(69)	Gametophyte hairs: 0 → 1; Present
8	27	5	(30)	Rhizome hairs: 1 → 0; Absent
			(31)	Rhizome scales: 0 → 1; Present
			(44)	Sporangium stalk length: 0 → 1; Long
			(58)	Annulus span: 0 → 1; Interrupted bow
			(60)	Spore laesura: 1 → 0; Linear
9	33	4	(2)	Fertile-sterile leaves: 0 → 3; Dimorphic
			(3)	Blade dissection: 1 → 0; Simple to pinnatifid
			(10)	Blade hairs: 1 → 0; Absent
			(47)	Sori: 1 → 0; Absent
10	61	5	(10)	Blade hairs: 1 → 0; Absent
			(28)	Rhizome stele cycles: 0 → 1; Polycyclic
			(51)	No. sporangia/sorus: 1 → 0; Few (<12)
			(54)	Indusium attachment: 0 → 2; Central
			(58)	Annulus span: 0 → 1; Interrupted bow
11	63	2	(24)	Stipe xylem configuration: 0 → 1; Solid form in center
			(27)	Rhizome stele type: 1 → 0; Protostele
12	78	8	(3)	Blade dissection: 1 → 0; Simple to pinnatifid
			(4)	**Primary vein form: 1 → 2; Solitary/unbranched**
			(10)	Blade hairs: 1 → 0; Absent
			(60)	Spore laesura: 1 → 0; Linear
			(67)	Spore germination pattern: 1 → 2; Amorphous
			(68)	Gametophyte form: 2 → 0; Tuberous
			(70)	Gametophyte green: 1 → 0; No
			(71)	Gametophytic fungal association: 0 → 1; Yes
13	57	4	(2)	Fertile-sterile leaves: 1 → 2; Hemidimorphic, leaf base fertile
			(13)	Origin of cells surrounding guard cells: 2 → 1; Mesogenous
			(52)	Indusium: 1 → 0; Absent
			(69)	Gametophyte hairs: 0 → 1; Present
14	39	4	(2)	Fertile-sterile leaves: 0 → 3; Dimorphic
			(5)	Vein orders: 3 → 2; Three
			(10)	Blade hairs: 1 → 0; Absent
			(44)	Sporangium stalk length: 0 → 1; Long

TABLE 3. Continued.

Branch number	No. unambiguous molecular character state changes	No. unambiguous morphological character state changes	Number and name of unambiguous morphological character: Character state change on branch; character state at node above (if internal branch) or of terminal taxon (if terminal branch). Non-homoplasious character state changes are indicated in bold.	
15	19	9	(9)	Hydathodes: 0 → 1; Present
			(11)	Blade scales: 0 → 1; Present
			(17)	Blade articulation: 0 → 1; Present
			(23)	Stipe stele number: 1 → 3; Polystele
			(24)	Stipe xylem configuration: 0 → 3; Three arcs
			(28)	Rhizome stele cycles: 0 → 1; Polycyclic
			(31)	Rhizome scales: 0 → 1; Present
			(37)	Mucilage canals: 0 → 1; Present
			(69)	Gametophyte hairs: 0 → 1; Present
16	61	4	(5)	Vein orders: 3 → 2; Three
			(22)	Epipetiolar branches: 0 → 1; Present
			(26)	Rhizome symmetry: 0 → 1; Dorsiventral
			(50)	Sporangium/soral maturation: 1 → 0; Simultaneous
17	14	4	(19)	Stipe adaxial outline: 1 → 0; Convex to flat
			(23)	Stipe stele number: 1 → 3; Polystele
			(24)	Stipe xylem configuration: 0 → 3; Three arcs
			(44)	Sporangium stalk length: 0 → 1; Long
18	26	2	(13)	Origin of cells surrounding guard cells: 2 → 1; Mesogenous
			(37)	Mucilage canals: 0 → 1; Present
19	37	4	(15)	Pulvini: 0 → 1; Present
			(38)	True vessels: 0 → 1; Present
			(51)	No. sporangia/sorus: 1 → 0; Few (<12)
			(64)	Perispore surface: 1 → 0; Smooth
20	37	3	(3)	Blade dissection: 1 → 0; Simple to pinnatifid
			(5)	Vein orders: 0 → 2; Three
			(43)	**Sporangium receptacle: 1 → 3; Elongate and highly branched**
21	31	1	(30)	Rhizome hairs: 1 → 0; Absent
22	66	9	(5)	Vein orders: 3 → 1; Two
			(6)	Secondary vein form: 1 → 0; Dichotomous
			(10)	Blade hairs: 1 → 0; Absent
			(27)	Rhizome stele type: 1 → 0; Protostele
			(30)	Rhizome hairs: 1 → 0; Absent
			(31)	Rhizome scales: 0 → 1; Present
			(44)	Sporangium stalk length: 0 → 1; Long
			(60)	Spore laesura: 1 → 0; Linear
			(64)	Perispore surface: 1 → 0; Smooth
23	56	0	NA	
24	30	3	(11)	Blade scales: 0 → 1; Present
			(49)	Sporangium/sorus position: 0 → 1; Abaxial
			(64)	Perispore surface: 1 → 0; Smooth
25	88	7	(3)	Blade dissection: 1 → 0; Simple to pinnatifid
			(5)	Vein orders: 3 → 1; Two
			(32)	Rhizome scale pattern: 0 → 2; Clathrate

TABLE 3. Continued.

Branch number	No. unambiguous molecular character state changes	No. unambiguous morphological character state changes	Number and name of unambiguous morphological character: Character state change on branch; character state at node above (if internal branch) or of terminal taxon (if terminal branch). Non-homoplasious character state changes are indicated in bold.	
			(60)	Spore laesura: 1 → 0; Linear
			(64)	Perispore surface: 1 → 0; Smooth
			(68)	Gametophyte form: 2 → 3; Elongate-thalloid
			(77)	Gametophyte gemmae-producing: 0 → 1; Yes, on thallus
26	36	3	(7)	Vein fusion: 1 → 0; Anastomosing
			(52)	Indusium: 0 → 1; Present
			(63)	Perispore prominence: 0 → 1; Prominent
27	48	3	(24)	Stipe xylem configuration: 0 → 4; Polycyclic
			(44)	Sporangium stalk length: 0 → 1; Long
			(47)	Sori: 1 → 0; Absent
28	68	6	(10)	Blade hairs: 1 → 0; Absent
			(14)	Dromy at base of blade: 1 → 0; Catadromous
			(19)	Stipe adaxial outline: 1 → 0; Convex to flat
			(21)	Sclerenchyma fibers: 1 → 0; Absent
			(52)	Indusium: 0 → 1; Present
			(73)	Antheridium position: 1 → 0; Embedded or slightly projecting
29	44	0	NA	
30	28	3	(26)	Rhizome symmetry: 1 → 0; Radial
			(28)	Rhizome stele cycles: 0 → 1; Polycyclic
			(52)	Indusium: 0 → 1; Present
31	31	5	(17)	Blade articulation: 0 → 1; Present
			(20)	Sclerenchyma coloration on stipe: 0 → 1; Dark-pigmented
			(51)	No. sporangia/sorus: 1 → 0; Few (<12)
			(59)	**Sporogenesis: 0 → 1; Anisosporous**
			(68)	Gametophyte form: 2 → 1&3; Filamentous and elongate-thalloid
32	31	3	(9)	Hydathodes: 1 → 0; Absent
			(28)	Rhizome stele cycles: 0 → 1; Polycyclic
			(38)	True vessels: 0 → 1; Present
33	10	4	(11)	Blade scales: 0 → 1; Present
			(31)	Rhizome scales: 0 → 1; Present
			(64)	Perispore surface: 1 → 0; Smooth
			(66)	Exospore surface: 0 → 1; Sculptured
34	40	2	(26)	Rhizome symmetry: 1 → 0; Radial
			(27)	Rhizome stele type: 1 → 2; Dictyostele
35	43	4	(50)	Sporangium/sorus maturation: 2 → 0; Simultaneous
			(52)	Indusium: 1 → 0; Absent
			(66)	Exospore surface: 0 → 1; Sculptured
			(68)	Gametophyte form: 2 → 3; Elongate-thalloid
36	40	2	(43)	Sporangium receptacle: 0 → 1; Convex
			(63)	Perispore prominence: 1 → 0; Not prominent
37	18	7	(22)	Epipetiolar branches: 0 → 1; Present
			(28)	Rhizome stele cycles: 0 → 1; Polycyclic
			(44)	Sporangium stalk length: 1 → 0; Sessile to short

TABLE 3. Continued.

Branch number	No. unambiguous molecular character state changes	No. unambiguous morphological character state changes	Number and name of unambiguous morphological character: Character state change on branch; character state at node above (if internal branch) or of terminal taxon (if terminal branch). Non-homoplasious character state changes are indicated in bold.	
			(51)	No. sporangia/sorus: 1 → 0; Few (<12)
			(54)	Indusium attachment: 0 → 1; Basal
			(55)	Indusium opening: 1 → 2; Suprasoral
			(62)	Spore equatorial flange: 0 → 1; Present
38	62	6	(5)	Vein orders: 3 → 2; Three
			(18)	Trophopods: 0 → 1; Present
			(20)	Sclerenchyma coloration in stipe: 0 → 1; Dark-pigmented
			(24)	**Xylem configuration in stipe: 0 → 2; X-shape**
			(32)	Rhizome scale pattern: 0 → 2; Clathrate
			(48)	Sorus outline: 0 → 1; Elongate
39	24	4	(9)	Hydathodes: 1 → 0; Absent
			(14)	Dromy at base of blade: 1 → 2; Isodromous
			(16)	Pneumathodes: 0 → 2; Present in discrete lines or patches
			(44)	Sporangium stalk length: 1 → 0; Sessile to short
40	26	7	(2)	Fertile-sterile leaves: 0 → 3; Dimorphic
			(7)	Vein fusion: 0 → 1; Anastomosing
			(18)	Trophopods: 0 → 1; Present
			(19)	Adaxial outline of stipe: 1 → 0; Convex to flattened
			(43)	Sporangium receptacle: 0 → 1; Convex
			(50)	Sporangium/sorus maturation: 2 → 1; Gradate
			(61)	Spores chlorophyllous: 0 → 1; Yes
41	37	5	(5)	Vein orders: 3 → 2; Three
			(23)	Stipe stele number: 2 → 3; Polystele throughout
			(48)	Sorus outline: 0 → 1; Elongate
			(55)	Indusium opening: 1 → 0; Introrse
			(64)	Perispore surface: 1 → 0; Smooth
42	29	0	NA	
43	60	6	(2)	Fertile-sterile leaves: 0 → 3; Dimorphic
			(3)	Blade dissection: 1 → 0; Simple to pinnatifid
			(5)	Vein orders: 3 → 1; Two
			(6)	Secondary vein form: 1 → 0; Dichotomous
			(47)	Sori: 1 → 0; Absent
			(52)	Indusium: 1 → 0; Absent
44	28	3	(5)	Vein orders: 3 → 2; Three
			(14)	Dromy at base of blade: 1 → 2; Isodromous
			(26)	Rhizome symmetry: 1 → 0; Radial
45	26	2	(16)	Pneumathodes: 0 → 2; Present in discrete lines or patches
			(36)	Growth habit: 0 → 1; Epiphytic
46	36	6	(7)	Vein fusion: 0 → 1; Anastomosing
			(9)	Hydathodes: 1 → 0; Absent
			(24)	Xylem configuration in stipe: 0 → 1; Solid form in center
			(32)	Rhizome scale pattern: 0 → 2; Clathrate
			(44)	Sporangium stalk length: 1 → 0; Sessile to short
			(48)	Sorus outline: 0 → 1; Elongate

TABLE 3. Continued.

Branch number	No. unambiguous molecular character state changes	No. unambiguous morphological character state changes	Number and name of unambiguous morphological character: Character state change on branch; character state at node above (if internal branch) or of terminal taxon (if terminal branch). Non-homoplasious character state changes are indicated in bold.	
47	10	3	(5)	Vein orders: 1 → 2; Three
			(11)	Blade scales: 0 → 1; Present
			(14)	Dromy at base of blade: 1 → 2; Isodromous
48	52	4	(26)	Rhizome symmetry: 1 → 0; Radial
			(27)	Rhizome stele type: 2 → 1; Solenostele
			(36)	Growth habit: 0 → 1; Epiphytic
			(60)	Spore laesura: 0 → 1; Triradiate
49	22	4	**(35)**	**Root anatomy: 1 → 0; 2–5 arch**
			(37)	**Mucilage canals: 1 → 0; Absent**
			(74)	**Archegonium position: 0 → 1; Partially to fully exposed**
			(76)	No. archegonium neck cell tiers: 1 → 0; 6 cells high
50	16	8	(23)	Stipe stele number: 3 → 1; Monostele throughout
			(25)	**Primary xylem bordered pits: 1 → 0; Scalariform**
			(41)	**First division of zygote: 0 → 1; Vertical**
			(42)	**Sporangium wall thickness: 1 → 0; Single cell layer**
			(45)	**Sporangium stalk width: 0 → 1; 4–6 cell rows wide**
			(46)	Spore output/sporangium: 0 → 1; >100 <1000
			(56)	**Annulus: 0 → 1; Present**
			(73)	**Antheridium position: 0 → 1; Partially to fully exposed**
51	20	4	(2)	Fertile-sterile leaves: 3 → 0; Monomorphic
			(27)	Rhizome stele type: 2 → 0; Protostele
			(47)	Sori: 0 → 1; Present
			(67)	Spore germination pattern: 1 → 0; Equatorial
52	8	1	(26)	Rhizome symmetry: 0 → 1; Dorsiventral
53	32	1	(31)	Rhizome scales present: 0 → 1; Present
54	9	0	NA	
55	32	7	(4)	Primary vein form: 1 → 0; Dichotomous
			(5)	Vein orders: 3 → 2; Three
			(7)	Vein fusion: 0 → 1; Anastomosing
			(12)	Guard mother cell division: 0 → 1; Parameristic
			(13)	Origin of cells surrounding guard cells: 2 → 1; Mesogenous
			(23)	**Stipe stele number: 1 → 0; Monostele at base, polystele above**
			(50)	Sorus/sporangium maturation: 0 → 2; Mixed
56	10	3	(52)	Indusium: 0 → 1; Present
			(63)	Perispore prominence: 0 → 1; Prominent
			(64)	Perispore surface: 0 → 1; Sculptured
57	14	1	**(65)**	**Exospore structure: 1 → 0; 2-layered**

TABLE 3. Continued.

Branch number	No. unambiguous molecular character state changes	No. unambiguous morphological character state changes	Number and name of unambiguous morphological character: Character state change on branch; character state at node above (if internal branch) or of terminal taxon (if terminal branch). Non-homoplasious character state changes are indicated in bold.	
58	15	3	(2)	Fertile-sterile leaves: 0 → 1; Hemidimorphic, leaf tip fertile
			(47)	Sori: 1 → 0; Absent
			(66)	Exospore surface: 0 → 1; Sculptured
59	26	3	(26)	Rhizome symmetry: 1 → 0; Radial
			(63)	Perispore prominence: 1 → 0; Not prominent
			(64)	Perispore surface: 1 → 0; Smooth
60	12	1	(50)	Sporangium/sorus maturation: 0 → 1; Gradate
61	12	2	(16)	Pneumathodes: 0 → 2; Present in discrete lines or patches
			(26)	Rhizome symmetry: 1 → 0; Radial
62	13	1	(67)	Spore germination: 1 → 0; Equatorial
63	5	0	NA	
64	4	4	(49)	Sporangium/sorus position: 1 → 0; Marginal
			(63)	Perispore prominence: 1 → 0; Not prominent
			(64)	Perispore surface: 1 → 0; Smooth
			(66)	Exospore surface: 0 → 1; Sculptured
65	4	2	**(45)**	**Sporangium stalk width: 1 → 2; 1–3 cell rows wide**
			(49)	Sporangium/sorus position: 1 → 0; Marginal
66	23	9	(2)	Fertile-sterile leaves: 0 → 2; Hemidimorphic, leaf base fertile
			(5)	Vein orders: 3 → 0; One
			(21)	Sclerenchyma fibers: 1 → 0; Absent
			(43)	Sporangium receptacle: 0 → 1; Convex
			(54)	Indusium attachment: 0 → 1; Basal
			(56)	Annulus: 1 → 0; Absent
			(59)	Sporogenesis: 0 → 2; Heterosporous
			(68)	Gametophyte form: 2 → 4; Reduced
			(72)	Dependent gametophyte: 0 → 1; Yes
67	38	2	(1)	Circinate vernation: 1 → 0; No
			(24)	Xylem configuration in stipe: 0 → 1; Solid form in center
68	20	1	(9)	Hydathodes: 0 → 1; Present
69	15	0	NA	
70	14	0	NA	
71	29	5	(7)	Vein fusion: 0 → 1; Anastomosing
			(30)	Rhizome hairs: 1 → 0; Absent
			(31)	Rhizome scales: 0 → 1; Present
			(40)	Hypodermis: 0 → 1; Present
			(52)	Indusium: 1 → 0; Absent
72	8	1	(9)	Hydathodes: 1 → 0; Absent
73	18	3	(10)	Blade hairs: 1 → 0; Absent
			(20)	Sclerenchyma coloration in stipe: 0 → 1; Dark-pigmented
			(23)	Stipe stele number: 1 → 2; Distele at base, monostele above

TABLE 3. Continued.

Branch number	No. unambiguous molecular character state changes	No. unambiguous morphological character state changes	Number and name of unambiguous morphological character: Character state change on branch; character state at node above (if internal branch) or of terminal taxon (if terminal branch). Non-homoplasious character state changes are indicated in bold.	
74	6	0	NA	
75	20	3	(26)	Rhizome symmetry: 1 → 0; Radial
			(28)	Rhizome stele cycles: 0 → 1; Polycyclic
			(36)	Growth habit: 0 → 2; Rooted aquatic
76	13	0	NA	
77	8	2	(7)	Vein fusion: 1 → 0; Non-anastomosing
			(64)	Perispore surface: 1 → 0; Smooth
78	8	1	(44)	Sporangium stalk length: 0 → 1; Long
79	10	1	(22)	Epipetiolar branches: 0 → 1; Present
80	8	2	(7)	Vein fusion: 0 → 1; Anastomosing
			(60)	Spore laesura: 1 → 0; Linear
81	4	1	(48)	Sorus outline: 1 → 0; Round
82	4	0	NA	
83	16	2	(16)	Pneumathodes: 0 → 2; Present in discrete lines or patches
			(50)	Sporangium/sorus maturation: 2 → 1; Gradate
84	25	4	(27)	Rhizome stele type: 1 → 2; Dictyostele
			(30)	Rhizome hairs: 1 → 0; Absent
			(31)	Rhizome scales: 0 → 1; Present
			(60)	Spore laesura: 1 → 0; Linear
85	10	0	NA	
86	4	0	NA	
87	8	0	NA	
88	6	1	(23)	Stipe stele number: 2 → 3; Polystele throughout
89	10	2	(9)	Hydathodes: 1 → 0; Absent
			(16)	Pneumathodes: 0 → 2; Present in discrete lines or patches
90	9	0	NA	
91	16	3	(63)	Perispore prominence: 1 → 0; Not prominent
			(64)	Perispore surface: 1 → 0; Smooth
			(66)	Exospore surface: 0 → 1; Sculptured
92	5	4	(3)	Blade dissection: 1 → 0; Simple to pinnatifid
			(5)	Vein orders: 3 → 1; Two
			(19)	Adaxial outline of stipe: 1 → 0; Convex to flattened
			(52)	Indusium: 1 → 0; Absent
93	16	1	(10)	Blade hairs: 0 → 1; Present

illustrated in Figure 5. These character patterns can be viewed as hypotheses of character evolution in ferns based on parsimony considerations. For example, the transition to anastomosing veins (Fig. 6A) appears to have arisen independently in six different lineages of leptosporangiate ferns, and is shown as a single occurrence for pteridoid ferns (having been lost in *Adiantum, Platyzoma,* and *Pteris*). The transition to hydathodes (Fig. 6B) is hypothesized to

have occurred once in the common ancestor of the most highly derived ferns (between *Lindsaea* and the heterosporous ferns), having been subsequently lost in five lineages, most notably in the pteridoid ferns (except for *Coniogramme*); hydathodes are shown also to have originated independently in *Cyathea.* Finally, rhizome scales (Fig. 6C) are shown to have evolved several times among ferns, and in some cases the character is a synapomorphy for large clades, such as the *Micropolypodium* to *Asplenium* clade.

Patterns in sporangial character evolution are shown in Figure 7. An annulus on the sporangium capsule (Fig. 7A) distinguishes all leptosporangiate ferns (except for the heterosporous ferns, *Azolla* to *Marsilea,* where it was lost). Sporangium stalk width (Fig. 7B) shows a defined sequence of origin, with massive stalks (>6 cells wide) in the eusporangiate ferns, followed by a transition to stalks 4–6 cells wide on the branch leading to *Osmunda* and other leptosporangiate ferns, and yet another transition to slender sporangial stalks (1–3 cells wide) on a branch between tree ferns and all the more derived ferns. Annulus span (Fig. 7C) across the sporangium capsule appears as a transition to a continuous bow at the base of the leptosporangiate fern clade; an interrupted bow originated at least three times, once on the branch between tree ferns and all the more derived ferns (heterosporous ferns lack an annulus), and independently in both *Matonia* and *Dipteris. Osmunda* is unique with a lateral patch annulus. Finally, the transition to long sporangium stalks (Fig. 7D) occurred once in a derived clade of leptosporangiate ferns (*Micropolypodium* to *Pteridium*), but this character also arose independently at least five times along isolated basal lineages.

Some patterns in the evolution of spore and gametophytic characters are shown in Figure 8. A clearly defined sequence of character evolution is shown by the exospore structure (Fig. 8A), with a 3-layered exospore shown at the base of the ferns, followed by a single transition to a 2-layered exospore on the branch leading to the *Micropolypodium* to *Lygodium* clade. A transition to hairy gametophytes (Fig. 8B) appears to have occurred on a branch leading from the dennstaedtioid ferns to the derived *Micropolypodium* to *Asplenium* clade (hairs on *Asplenium* gametophytes was scored as unknown); they also evolved independently in *Cyathea, Anemia,* and *Diplopterygium.* Antheridium position is shown in Figure 8C. At the base of the leptosporangiate fern clade there was a single transition to exposed antheridia; this character was reversed only in the aquatic fern *Ceratopteris.* Finally, the transition from antheridia with ≥5 wall cells to 3–5 cells is ambiguously placed. It may have arisen a single time on the branch leading to the *Micropolypodium* to *Lygodium* clade, and then was reversed on the branch leading to the tree ferns (*Calochlaena* to *Plagiogyria*), or it arose twice: once on the branch leading to the schizaeoid ferns, and once on the branch leading to the derived *Micropolypodium* to *Marsilea* clade.

All of the above scenarios about morphological character evolution are hypothetical and based on the assumption that this representative, most parsimonious tree from the combined analysis (Fig. 5) is the correct topology. The

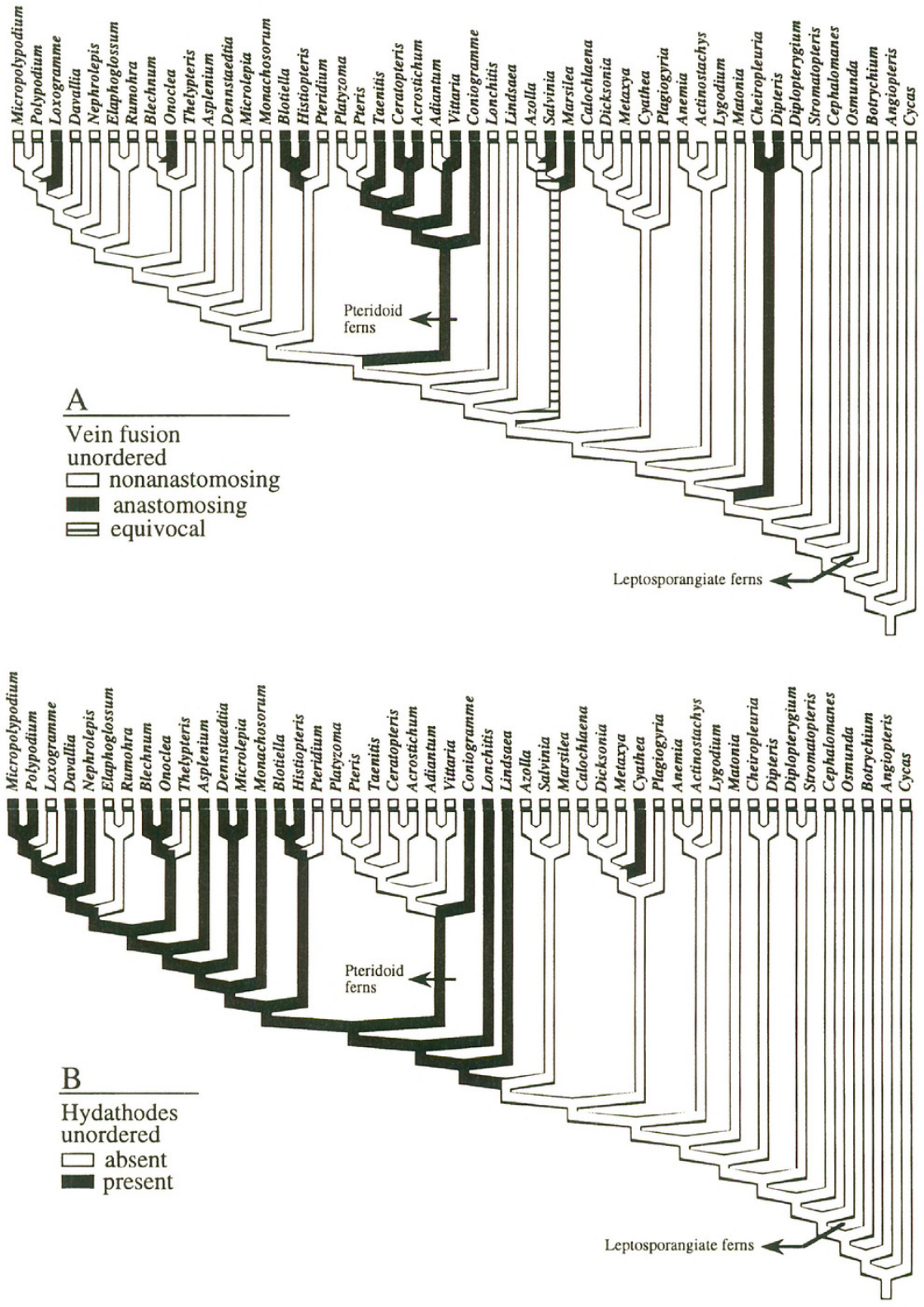


FIG. 6. Distribution of selected sporophytic vegetative characters plotted on representative most parsimonious tree from Analysis 1C (cf. Fig. 5 and Table 3). A) Vein fusion in sterile blades (character 7); B) Hydathodes (character 9); C) Rhizome scales (character 31).

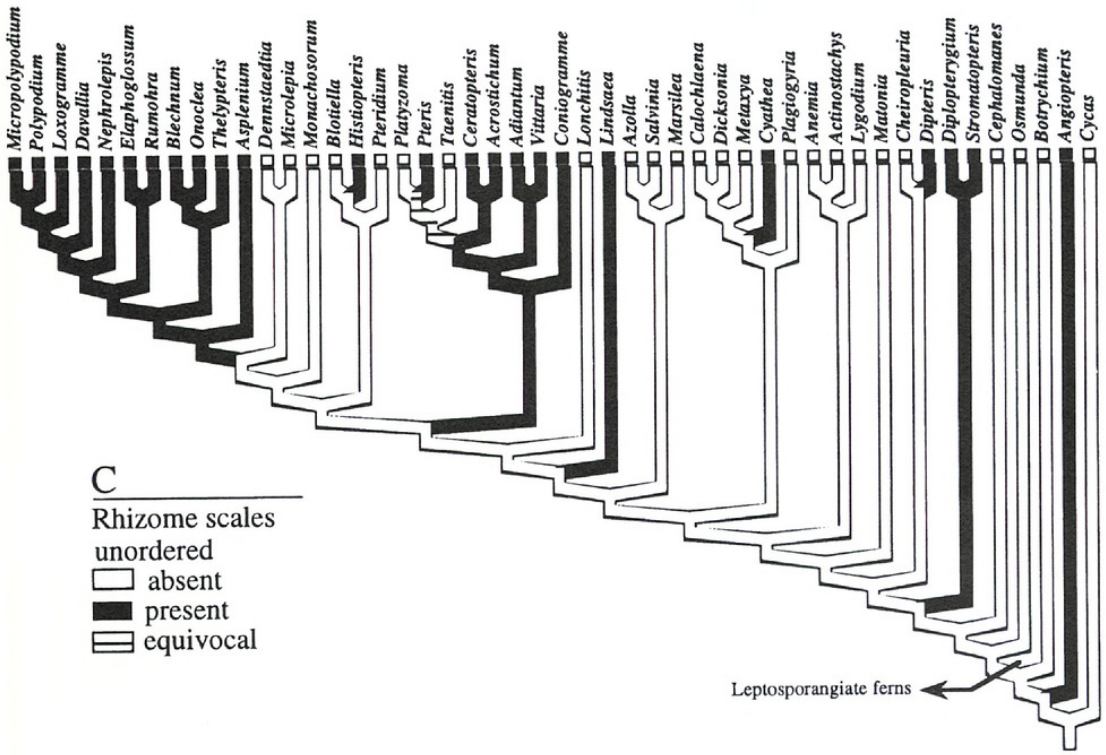


FIG. 6. Continued.

inclusion of additional taxa might, of course, alter the precise location on the topology of hypothesized character changes.

ANALYSIS 2A.—When all pteridophyte taxa were included in the morphological analysis, seven islands of most parsimonious trees were found. These varied in size from 1720 trees to 2 trees and included a total of 2682 most parsimonious trees at 469 steps (CI=0.316; RI=0.549). The observed CI is slightly lower than the expected CI=0.332, as calculated by the formula of Sanderson and Donoghue (1989), indicating that the level of homoplasy is not much greater than would be expected for an average study with 50 taxa. The majority rule consensus tree, with bootstrap values, is shown in Figure 9. Bootstrap support for selected clades is also indicated in Table 4. Only the clade for heterosporous ferns (*Azolla* to *Salvinia*) had robust bootstrap support (99%). Clades lacking bootstrap values or asterisks were found in the majority rule consensus but not the strict consensus. Overall the relationships resolved among the ferns in Analysis 2A are essentially the same as in Analysis 1A; there is lower bootstrap support (57%), however, for the leptosporangiate fern clade in this analysis than in Analysis 1A. The relationships shown among the non-leptosporangiate pteridophytes (*Lycopodium, Equisetum, Psilotum, Botrychium, Angiopteris*) have bootstrap values <50%.

ANALYSIS 2B.—Only 1 tree island was found of 3 most parsimonious trees at 3843 steps (CI=0.228; RI=0.466). The observed CI is considerably lower than the expected CI=0.332, as calculated by the formula of Sanderson and Dono-

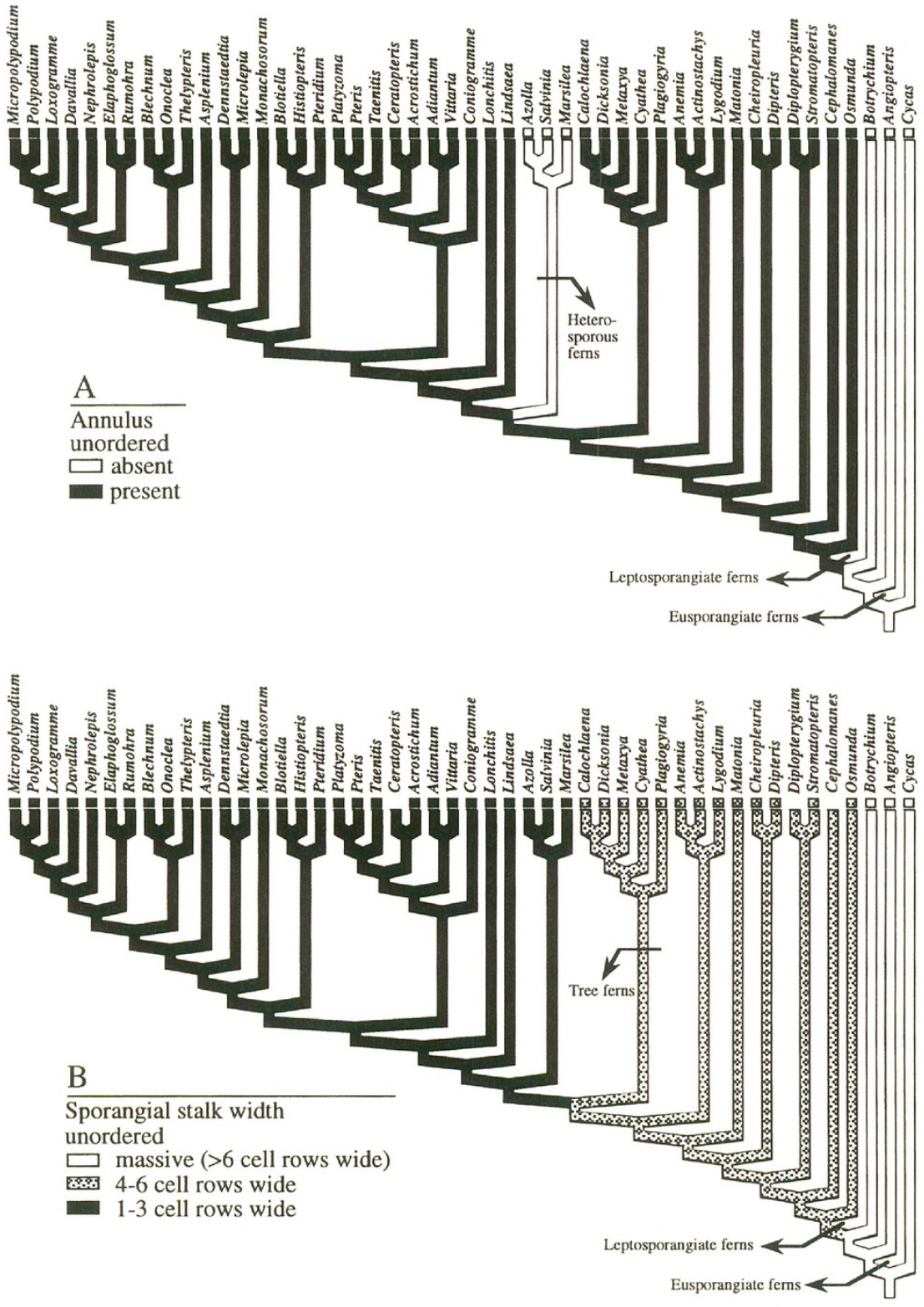


FIG. 7. Distribution of selected sporophytic reproductive characters plotted on representative most parsimonious tree from Analysis 1C (cf. Fig. 5 and Table 3). A) Annulus (character 56); B) Sporangium stalk width (character 45); C) Annulus span across sporangium (character 58); D) Sporangium stalk length (character 44).

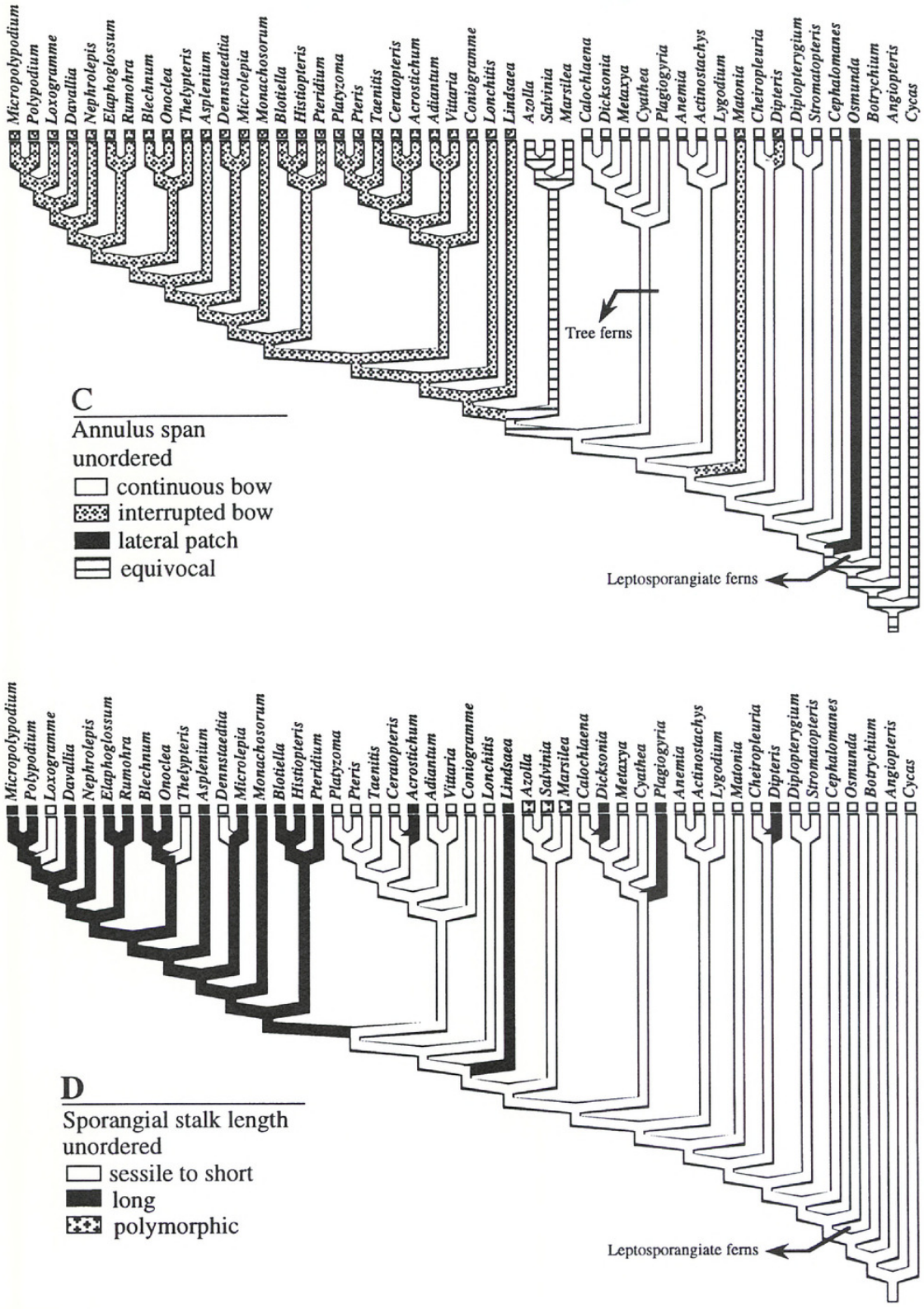


FIG. 7. Continued.

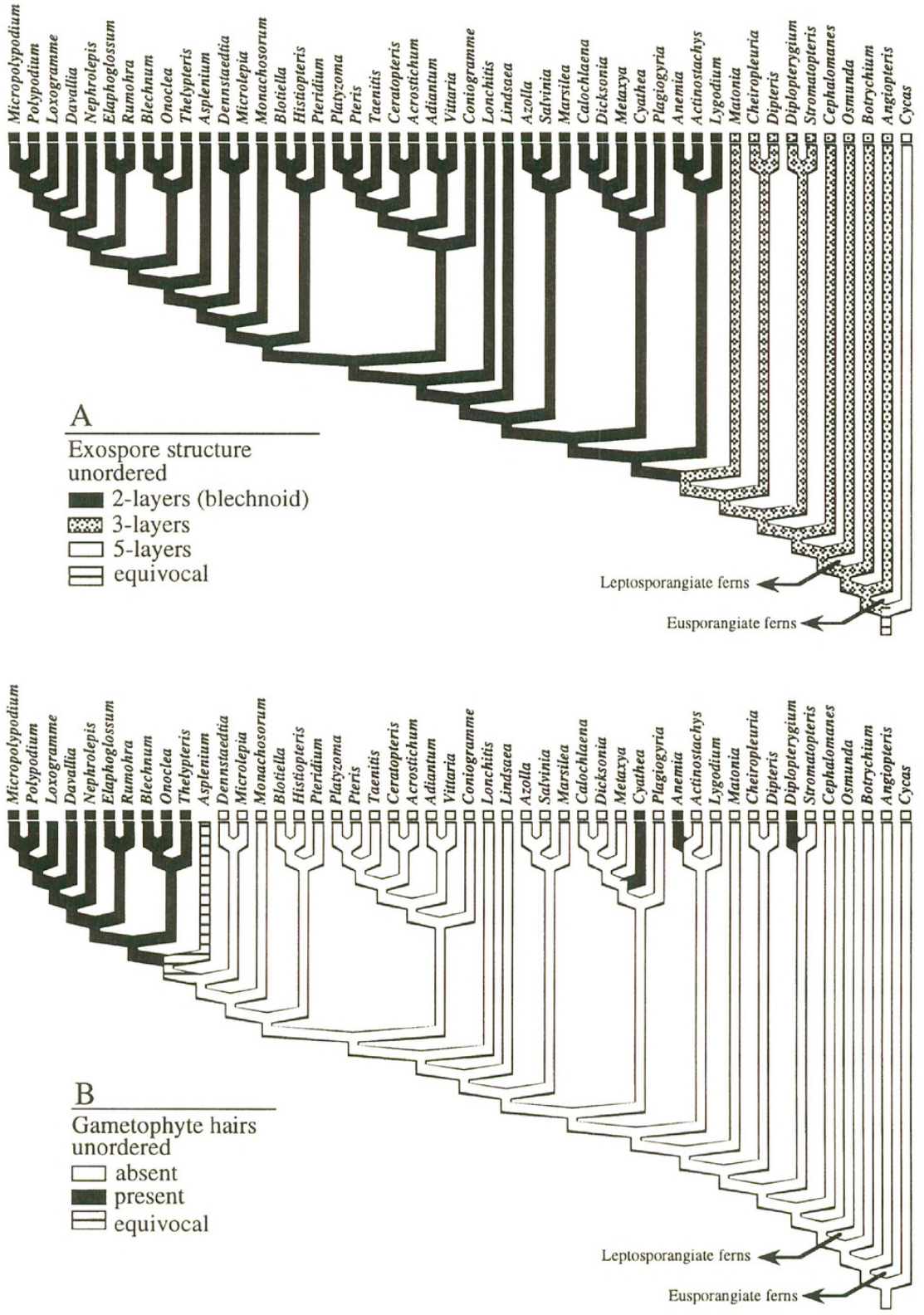


FIG. 8. Distribution of selected spore and gametophytic characters plotted on representative most parsimonious tree from Analysis 1C (cf. Fig. 5 and Table 3). A) Exospore structure (character 65); B) Gametophyte hairs (character 69); C) Antheridium position (character 73); D) Number of antheridium wall cells (character 75).

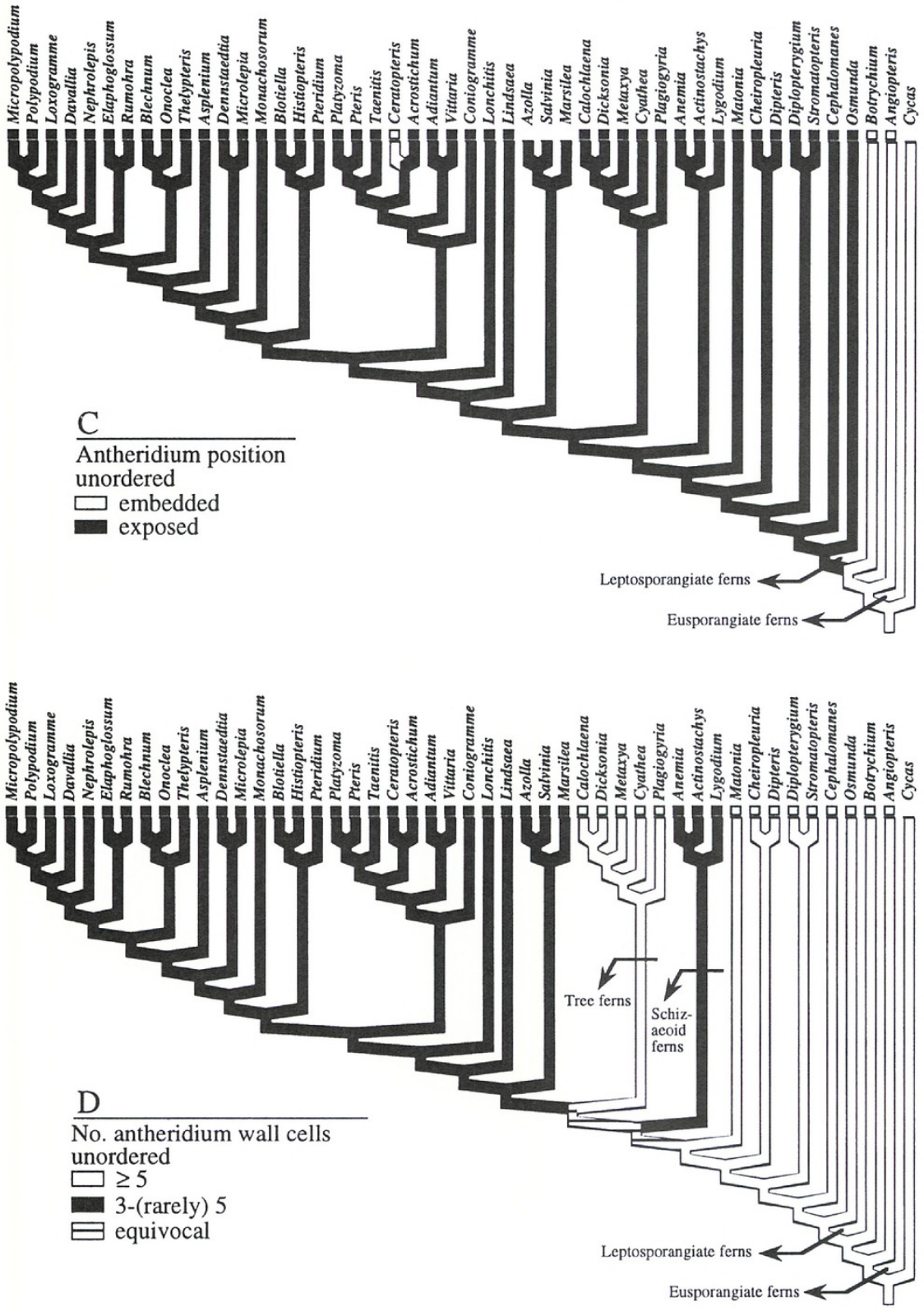


FIG. 8. Continued.

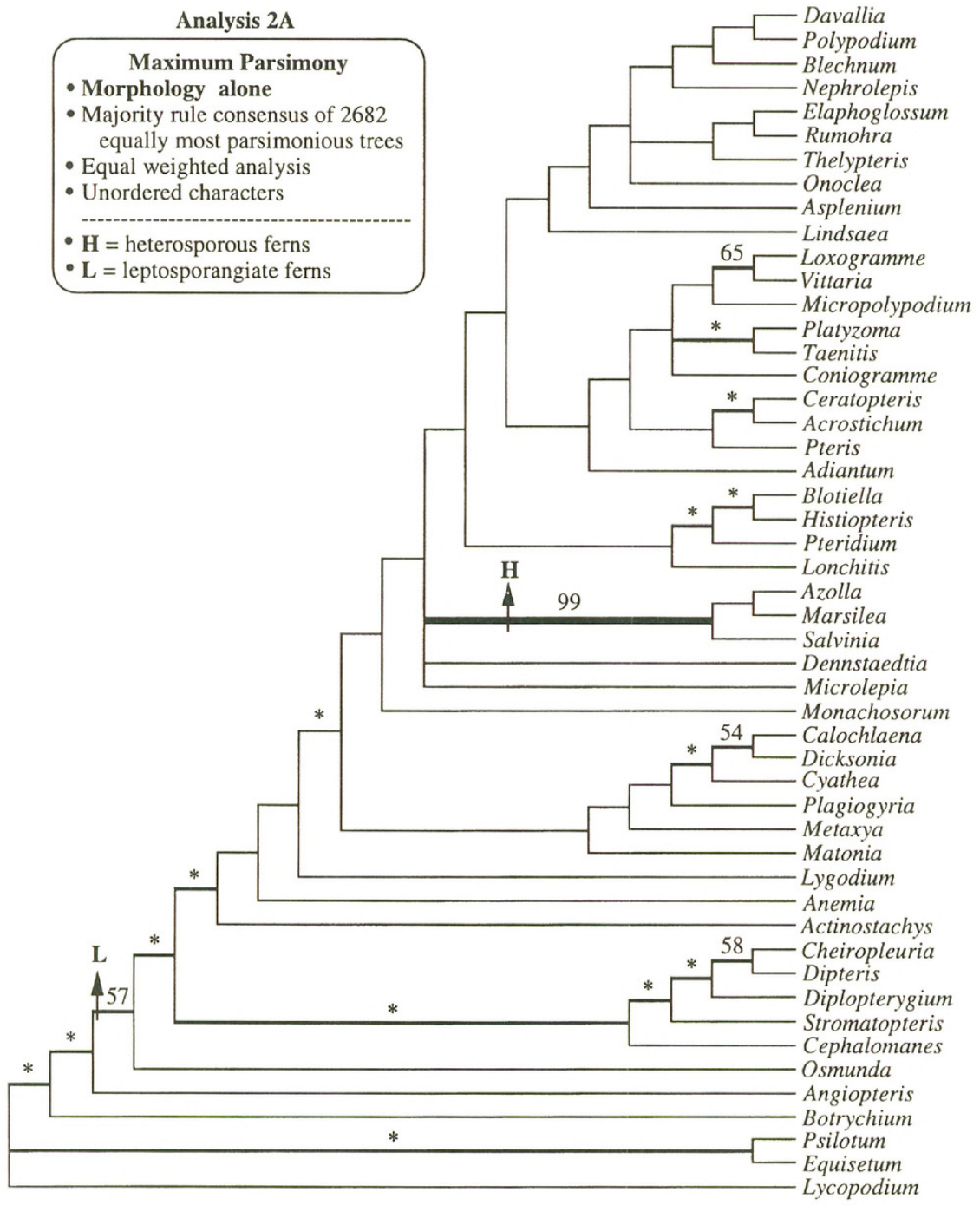


FIG. 9. Majority rule consensus of 2682 most parsimonious trees at 469 steps based on 75 parsimony-informative morphological characters that were equally weighted and unordered. Numbers above branches indicate bootstrap percent values. Thickest branches are those with bootstrap support exceeding 70%. All clades with bootstrap support greater than 50% were found in the strict consensus. Asterisks on medium-thick branches indicate clades also retained in the strict consensus, but not in the bootstrap majority rule tree. Thinnest branches without numbers were resolved in the majority rule consensus tree but had bootstrap support values <50%. The tree was rooted with *Lycopodium*. CI=0.316; RI=0.549.

ghue (1989). This indicates that the level of homoplasy in *rbcL* is greater than would be expected for an average study with 50 taxa; it is also higher here than in the morphological data set (Analysis 2A). As in Analysis 1B, the three most parsimonious trees here differ only in their placement of three tree fern taxa: *Calochlaena, Dicksonia,* and *Cyathea*; all other portions of their topologies are identical. The strict consensus tree is shown in Figure 10 and bootstrap support for selected clades is also indicated in Table 4. High bootstrap support (>85%) is shown for the same clades as in Analysis 1B (compare Table 4 with Table 2). With few exceptions, the clades with relatively strong support (≤85%, >70%) in this analysis had about the same support in Analysis 1B (compare bootstrap values in Tables 2 and 4). The only striking difference was the support for the schizaeoid ferns which was 78% in Analysis 1B and 90% in Analysis 2B. As in Analysis 1B, the leptosporangiate ferns did not form a monophyletic clade. The most basal branches of the tree (i.e., the placement of *Cephalomanes* with *Equisetum, Botrychium* with *Psilotum,* and of these four taxa together in a clade) had bootstrap values <50%.

ANALYSIS 2C.—Only 1 tree island was found of 12 most parsimonious trees at 4360 steps (CI=0.235; RI=0.468). The observed CI is slightly higher in the combined analysis than with the *rbcL* data alone (Analysis 2B). The strict consensus tree is shown in Figure 11, and bootstrap support for selected clades is also indicated in Table 4. These 12 trees differ in topology in minor respects from one another only within the derived clade *Micropolypodium* to *Monachosorum.* The base of the tree (from *Lonchitis* to *Lycopodium*) is identical in topology in all 12 trees. Once again, the general result of the combined analysis is that the two data sets tend to reinforce each other in cases where they were congruent (Table 4). Many of the branches that had high bootstrap support (>85%) in Analysis 2B show bootstrap values that are about the same in the combined analysis, e.g., tree ferns (*Calochlaena* to *Plagiogyria*), 88%; *Micropolypodium* to *Asplenium,* 99%. Several branches also have increased bootstrap support in the combined analysis, e.g., heterosporous ferns (*Azolla* to *Marsilea*), 100%.

There is good bootstrap support for branches in the combined analysis that did not have support in either separate analysis, e.g., 80% for all leptosporangiate ferns (including *Osmunda*), much higher than in Analyses 2A (57%) and 2B (not a monophyletic clade). Morphology makes a strong contribution to resolving the base of the tree in the combined analysis, whereas the *rbcL* data alone provided little information regarding relationships in this part of the tree.

Some clades with moderate support (≤85%, >70%) in Analysis 2B and <50% support in Analysis 2A were more strongly supported in Analysis 2C (Table 4), e.g., the large clade including the pteridoids (*Platyzoma* to *Coniogramme*), dennstaedtioids (*Blotiella* to *Lindsaea*), and *Micropolypodium* to *Asplenium,* 86%. Other relationships that were weakly or moderately supported by Analyses 2A and 2B were often less resolved in the combined analysis (Table 4), e.g., the *Blotiella* to *Microlepia* clade that was resolved with 55%

TABLE 4. Comparison of bootstrap support for selected clades between Analysis 2A (morphology), Analysis 2B (*rbcL*), and Analysis 2C (morphology and *rbcL* combined). Numbers are percentage (%) values. A dash indicates bootstrap support is <50% for a clade that occurs in the consensus trees shown in Figs. 9–11. NA indicates a clade not observed in the consensus tree (Figs. 9–11) of a particular analysis.

Clade	2A	2B	2C
Heterosporous ferns: *Azolla-Salvinia-Marsilea*	99	91	100
Leptosporangiate ferns (including *Osmunda*) = all taxa except *Botrychium, Angiopteris, Psilotum, Equisetum,* and *Lycopodium*	57	NA	80
Leptosporangiate ferns (excluding *Osmunda*) = all taxa except *Osmunda, Botrychium, Angiopteris, Psilotum, Equisetum,* and *Lycopodium*	—	NA	NA
Loxogramme-Vittaria	65	NA	NA
Dipteroid ferns: *Cheiropleuria-Dipteris*	58	100	100
Gleichenioid ferns: *Diplopterygium-Stromatopteris*	NA	100	100
Tree ferns: *Calochlaena-Dicksonia-Metaxya-Cyathea* + *Plagiogyria*	—	89	88
Pteridoid ferns: *Platyzoma-Pteris-Taenitis-Ceratopteris-Acrostichum-Adiantum-Vittaria-Coniogramme*	NA	99	98
Dennstaedtioid ferns (in part): *Blotiella-Histiopteris-Pteridium*	—	92	96
Micropolypodium-Polypodium-Loxogramme-Davallia-Nephrolepis-Elaphoglossum-Rumohra-Blechnum-Onoclea-Thelypteris-Asplenium	NA	99	99
Ceratopteris-Acrostichum	—	99	97
Schizaeoid ferns: *Anemia-Actinostachys-Lygodium*	NA	90	88
Calochlaena-Dicksonia	54	NA	63
35 fern taxa (excluding *Matonia, Lygodium, Anemia, Actinostachys, Cheiropleuria, Dipteris, Diplopterygium, Stromatopteris, Cephalomanes, Osmunda, Botrychium, Angiopteris, Psilotum, Equisetum,* and *Lycopodium*)	NA	76	NA
Pteridoid ferns (*Platyzoma-Pteris-Taenitis-Ceratopteris-Acrostichum-Adiantum-Vittaria-Coniogramme*) + Dennstaedtioid ferns sensu stricto (*Blotiella-Histiopteris-Pteridium-Monachosorum-Dennstaedtia-Microlepia*) + *Micropolypodium-Polypodium-Loxogramme-Davallia-Nephrolepis-Elaphoglossum-Rumohra-Blechnum-Onoclea-Thelypteris-Asplenium*	NA	85	68
All taxa in above row + *Lonchitis*	NA	68	59
All taxa in above row + *Lindsaea*	NA	76	86
Polypodioid ferns: *Micropolypodium-Polypodium-Loxogramme*	NA	59	91
Vittaria-Adiantum	NA	85	86
Elaphoglossum-Rumohra	—	82	84
Micropolypodium-Polypodium-Loxogramme-Davallia-Nephrolepis	NA	83	85

TABLE 4. Continued.

Clade	2A	2B	2C
All taxa in above row + *Elaphoglossum-Rumohra*	NA	81	81
Tree ferns: *Calochlaena-Dicksonia-Metaxya-Cyathea*	NA	83	73
Dennstaedtioid ferns sensu stricto: *Blotiella-Histiopteris-Pteridium-Monachosorum-Dennstaedtia-Microlepia*	NA	55	NA
All taxa in above row + *Micropolypodium-Polypodium-Loxogramme-Davallia-Nephrolepis-Elaphoglossum-Rumohra-Blechnum-Onoclea-Thelypteris-Asplenium*	NA	—	NA

support in Analysis 2B was unresolved in both Analyses 2A and 2C. Another example is the *Micropolypodium* to *Plagiogyria* clade with 76% support in Analysis 2B, but that was not resolved in either Analyses 2A or 2C.

Analysis 2—Summary of results: Bootstrap support is compared among Analyses 2A–2C for selected clades in Table 4. Most importantly, although the monophyly of the leptosporangiate ferns is only weakly supported in Analysis 2A and not supported in Analysis 2B, it is strongly supported in the combined analysis (80%), with the increased resolution at this basal node of the tree provided mostly from the morphological data set. Within the leptosporangiate ferns the tree topologies obtained in Analyses 1C and 2C are substantially similar. It therefore would be unnecessarily repetitive to choose one of the most parsimonious trees from Analysis 2C to illustrate the unambiguous morphological and molecular character state changes on each of the branches (cf. Fig. 5 and Table 3 for Analysis 1). However, two differences between Analyses 1 and 2 deserve further discussion. Firstly, all of the most parsimonious trees from the combined data in Analysis 2C (Fig. 11) show the heterosporous ferns (*Azolla* to *Marsilea*) and the schizaeoid ferns (*Anemia* to *Lygodium*) grouped together as a monophyletic group, whereas Analysis 1C does not. However, there is <50% bootstrap support for the heterosporous and schizaeoid ferns forming a monophyletic group in Analysis 2C. The branch supporting this clade has a single unambiguous morphological change (character 19 [adaxial outline of stipe]: 1→0; sulcate→convex to flat) and 8 unambiguous molecular changes in all 12 most parsimonious trees. Secondly, *Cephalomanes* is shown as the most basal leptosporangiate fern in Analysis 2C (Fig. 11), essentially changing places with *Osmunda* in Analysis 1C (Fig. 4). However, there is <50% bootstrap support for the placement of *Cephalomanes* as the most basal leptosporangiate fern.

The relationships among the non-leptosporangiate pteridophytes (*Lycopodium, Psilotum, Botrychium, Angiopteris,* and *Equisetum*) are weakly resolved. The only branch among these taxa with >50% bootstrap support is one weakly supporting *Botrychium* and *Psilotum* as sister taxa. This branch has a single unambiguous morphological change (character 67 [spore germination pattern]:

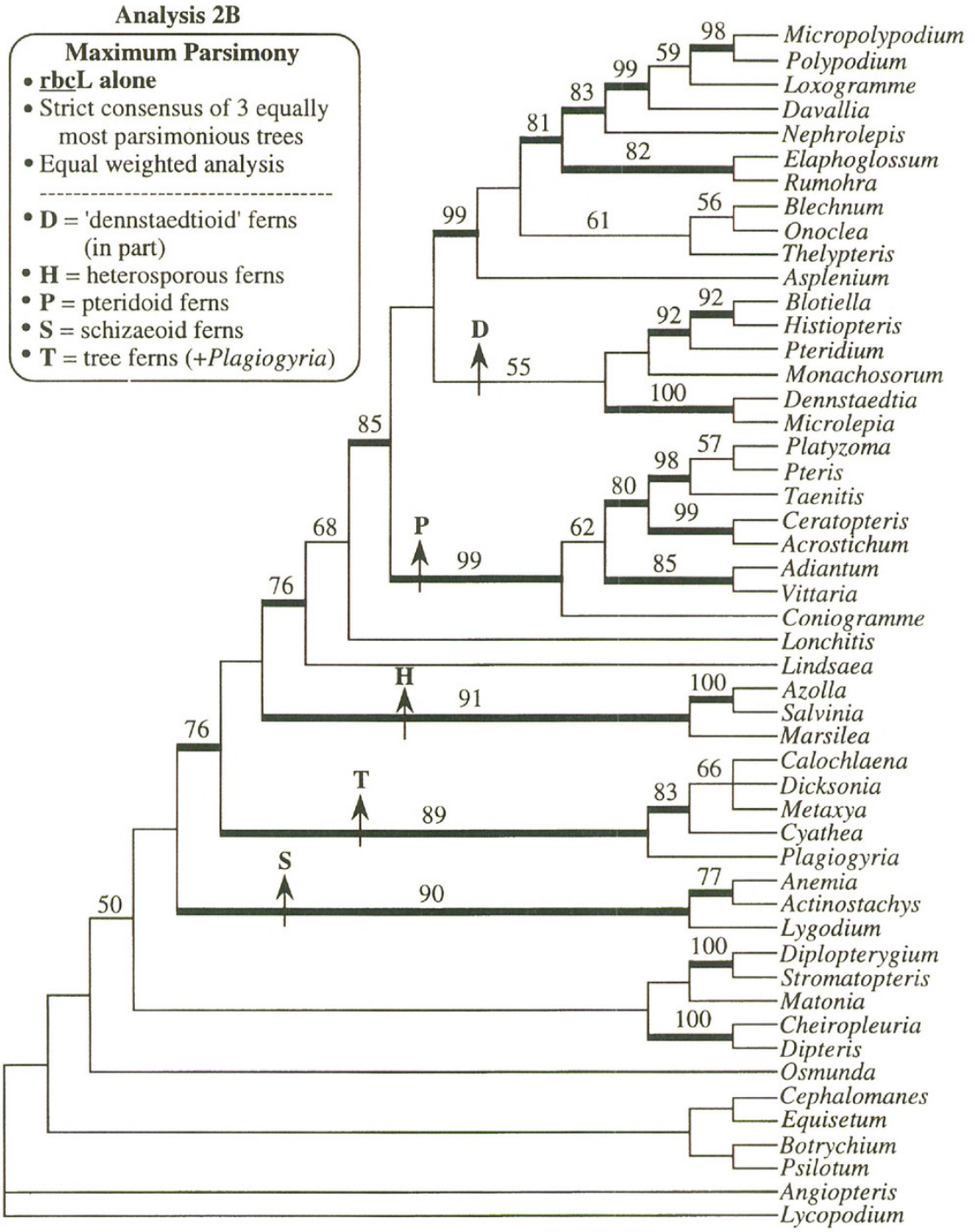


FIG. 10. Strict consensus of 3 most parsimonious trees at 3843 steps based on 490 parsimony-informative *rbcL* characters that were equally weighted and unordered. Numbers above branches indicate bootstrap percent values. Thicker branches are those with bootstrap support exceeding 70%. Branches without numbers were resolved in the strict consensus tree but had bootstrap values <50%. The tree was rooted with *Lycopodium*. CI=0.228; RI=0.466.

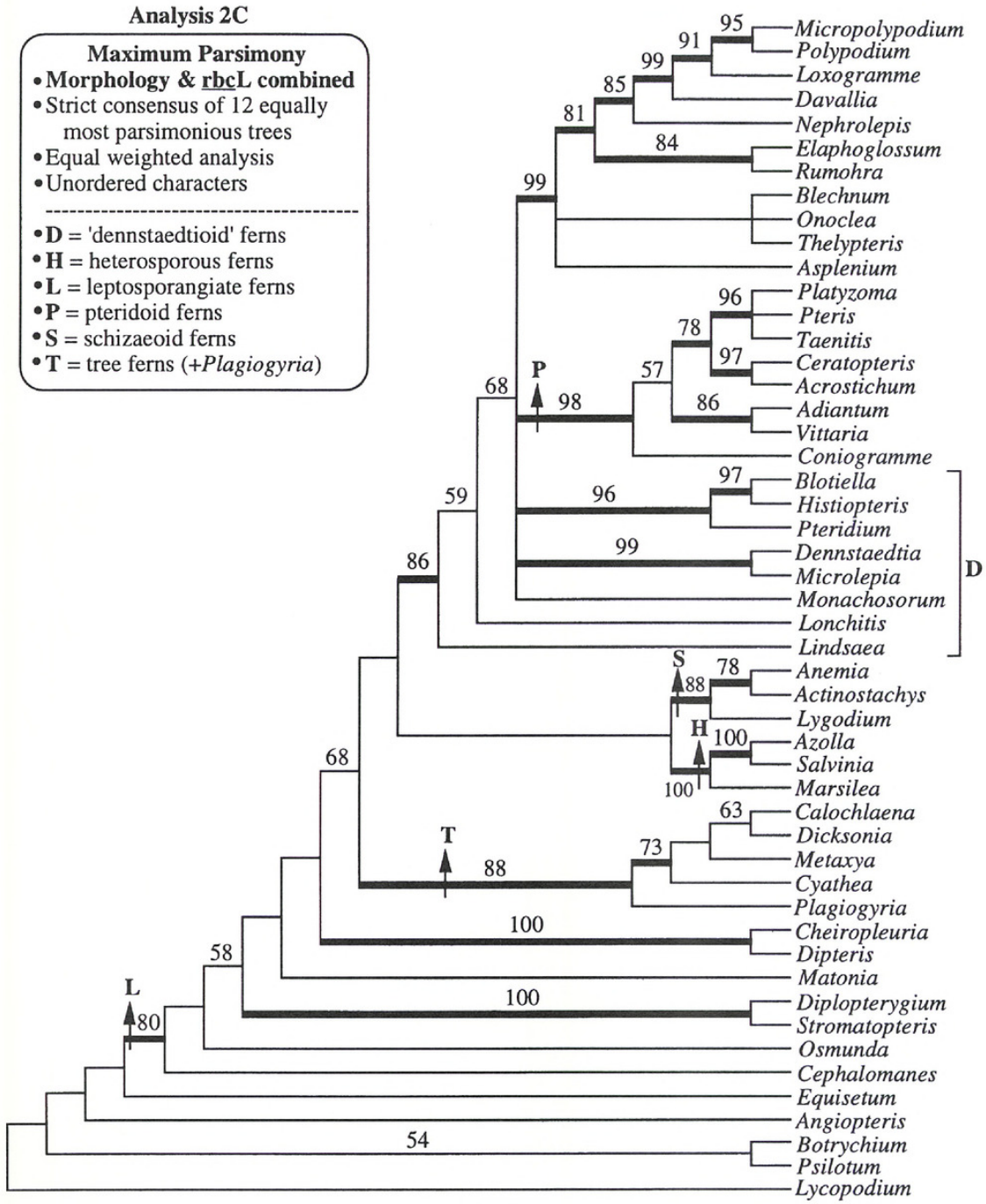


FIG. 11. Strict consensus of 12 most parsimonious trees at 4360 steps based on 565 parsimony-informative characters (490 from *rbcL* and 75 from morphology) that were equally weighted and unordered. Numbers above branches indicate bootstrap percent values. Thicker branches are those with bootstrap support exceeding 70%. Branches without numbers were resolved in the strict consensus tree but had bootstrap values <50%. The tree was rooted with *Lycopodium*. CI=0.235; RI=0.468.

0→1; equatorial→polar) and 24 unambiguous molecular changes in all 12 most parsimonious trees.

Discussion

The most robustly supported results of these analyses are those provided by the combined analysis of morphological and molecular data. Most notably, in both combined analyses (Analyses 1C and 2C) the leptosporangiate ferns have strong bootstrap support as a monophyletic clade (Figs. 4 and 11). This result is moderately supported by the morphological data alone, but is not resolved when the *rbcL* data are analyzed alone (cf. bootstrap values in Tables 2 and 4). In addition, in Analysis 1C (Fig. 4) there is good bootstrap support for all leptosporangiate ferns (excluding *Osmunda*), providing support for *Osmunda* being the most basal leptosporangiate fern. Even in the parsimony analysis of *rbcL* data by Hasebe et al. (1995), which included many more taxa, there was only weak bootstrap support (66%) for the monophyly of leptosporangiate ferns. These are important results in that they demonstrate the capability of morphological data to provide support at the base of the tree, where *rbcL* data alone were not able to confer strong resolution. These basal internodes are critical to resolving fern phylogeny. For divergences so long ago, it is possible that some codon positions in *rbcL* are saturated with change and therefore unable to provide useful phylogenetic information. On the other hand, some morphological characters are stable over long periods of time (see branch 50, Table 3). Other studies that have similarly shown increased support for phylogenetic hypotheses when morphological and molecular data are combined are: Yoder (1994), where morphological and molecular evidence together yield compelling support for monophyly of Malagasy primates; Mishler et al. (1994), where combined data offer the greatest potential for resolving phylogenetic relationships of green plants; and Kim et al. (1992), where data combined from *rbcL*, morphology, and restriction sites reinforce each other to give a more fully resolved pattern of tribal relationships in the Asteraceae.

What is known about the first appearance of the various fern groups in the geological record (Stewart and Rothwell, 1993) does not contraindicate the phylogenetic relationships revealed here. Future studies can use the fossil record of first occurrences to explore how rates of evolution have varied in the past (Smith and Littlewood, 1994).

Relationships Among the Most Derived Ferns.—A clade that is not resolved in the morphological analyses, but that has good support (73–76%) in the molecular analyses, is one that includes all the dennstaedtioid ferns (*Blotiella, Histiopteris, Pteridium, Dennstaedtia, Microlepia, Lonchitis,* and *Lindsaea*), the pteridoid ferns (*Platyzoma, Pteris, Taenitis, Ceratopteris, Acrostichum, Adiantum, Vittaria,* and *Coniogramme*), and a diverse lineage (11 families, according to Pichi Sermolli, 1977) that includes *Micropolypodium* to *Asplenium* (Figs. 3 and 10). This large clade has strong support (86%) in the combined analyses (Figs. 4 and 11). All other ferns included in this study were

consistently and strongly excluded from this clade. The *Micropolypodium* to *Asplenium* lineage has robust support as a monophyletic group, within which *Polypodium* (Polypodiaceae) and *Micropolypodium* (Grammitidaceae) are strongly supported as sister taxa. This finding upholds arguments presented by Jarrett (1980) and runs counter to a hypothesis of a close relationship of polypodioids and grammitidoids with the gleichenioid ferns, which was based primarily on these taxa sharing the exindusiate condition (Bierhorst, 1971; Bower, 1928; Holttum, 1973; Lovis, 1977; Wagner, 1969). This character is hypothesized here to have arisen several times (Table 3; character 52). Likewise, *Thelypteris* is more closely related to other members of this large, well supported clade, which is in agreement with Mickel (1974), Pichi Sermolli (1977), and Smith (in Kubitzki, 1990), and not to the cyatheoids as was suggested by Holttum (1973) and Lovis (1977).

Despite being quite heterogeneous, the pteridoid ferns (seven families, as treated by Pichi Sermolli, 1977) also form a group with robust support within this larger clade. Although it is ambiguous whether this broadly circumscribed pteridoid clade is more closely related to the *Asplenium* to *Micropolypodium* clade, or to the dennstaedtioid ferns, it is certain that, contrary to previous hypotheses (Holttum, 1973; Lovis, 1977; Mickel, 1974; Pichi Sermolli, 1977; Wagner, 1969), these results indicate that they are only very distantly related to the schizaeoid ferns.

Another heterogeneous group of taxa that is commonly referred to as the dennstaedtioid ferns, is clearly not a monophyletic group. In the molecular analyses, the Dennstaedtiaceae sensu stricto (not including *Lonchitis* and *Lindsaea*) form a weakly supported group that is not corroborated in the combined analyses. *Blotiella, Histopteris,* and *Pteridium* form a well supported clade, as do *Dennstaedtia* and *Microlepia.* The relationship of these clades and of *Monachosorum, Lonchitis,* and *Lindsaea* are unresolved within the larger clade to which they are robustly assigned.

Loxogramme (Polypodiaceae) and *Vittaria* (Vittariaceae) were scored similarly in the morphological data matrix for many characters. This similarity included not only vegetative characters, but cryptic characters related to reproductive and gametophytic features. In the morphological analyses these two taxa were consistently sister taxa, although the bootstrap support for the association was not strong (ca. 65%). Convergence for a large number of morphological characters in these exemplar species of *Loxogramme* and *Vittaria* caused them to be placed together. In the molecular analyses, *Loxogramme* invariably grouped with *Polypodium* and *Micropolypodium,* and *Vittaria* grouped with *Adiantum.* It was interesting to observe that in the combined analyses these same groupings occurred, but with much stronger bootstrap support. The addition of the morphological data caused the support for the placement of *Loxogramme* with *Polypodium* and *Micropolypodium* to soar from 60% in Analysis 1B to 89% in Analysis 1C, and from 59% in Analysis 2B to 91% in Analysis 2C. Therefore, a strong "minority" signal from the morphology for the correct placement of these taxa was congruent with the molecular signal, so that when these data were combined the signal from con-

vergence was swamped and a common historical signal was detected. The phylogenetic signal from at least part of the morphological data clearly had a notable impact in increasing the confidence levels that could be placed on these clades in the combined analyses.

RELATIONSHIPS AMONG BASAL LEPTOSPORANGIATE FERNS.—In Analysis 1C, there is good support for *Osmunda* being the most basal leptosporangiate fern. This is concordant with the fossil record for Osmundaceae, which extends into the late Permian, one of the oldest known extant leptosporangiate fern families (Stewart and Rothwell, 1993; Tidwell and Ash, 1994). This result is not so strongly upheld in Analysis 2C, where the relationships between *Osmunda* and other ferns at the base of the leptosporangiate clade lack convincing bootstrap support. The strong bootstrap support for the leptosporangiate clade (including *Osmunda*) indicates that despite its few eusporangiate-like features, *Osmunda* is more closely related to leptosporangiate ferns than it is to any other group.

Within the gleichenioid ferns (sensu Jarrett, 1980, who included *Diplopterygium, Stromatopteris, Cheiropleuria, Dipteris,* and *Matonia*), there is robust support for two subclades, *Diplopterygium-Stromatopteris* and *Cheiropleuria-Dipteris.* How these clades are related to one another and to *Matonia* is unclear. It is noteworthy that *Stromatopteris* is indeed a leptosporangiate fern, and did not group with *Psilotum* in any of the analyses (including morphology alone), which is concordant with the conclusion of Wagner (1977) and counter to Bierhorst (1977b).

Although relationships among schizaeoid ferns (*Anemia, Actinostachys,* and *Lygodium*) are not so clearly resolved in the morphological analyses as in the molecular analyses, the combined analysis (Analysis 1C) raises the confidence level for this clade. This is not the case in Analysis 2, where the addition of morphological data does not alter the strong bootstrap support found from molecular data alone. In view of the long-standing hypothesis of a relationship between the schizaeoid ferns and the Marsileaceae (Bower, 1926; Bierhorst, 1971; Campbell, 1904; Lovis, 1977; Pichi Sermolli, 1977), it is interesting to note that in Analysis 2C the schizaeoid and heterosporous ferns come together as a monophyletic group; however, there is <50% bootstrap support for this association.

The monophyly of the heterosporous ferns (*Azolla, Salvinia,* and *Marsilea*) is the most strongly supported result from all analyses in this study. In some early classifications (Bower, 1926; Copeland, 1947), Salviniaceae (*Azolla* and *Salvinia*) and Marsileaceae (*Marsilea, Regnellidium,* and *Pilularia*) were maintained as separate families within the Filicopsida. In other classifications (e.g., Engler and Diels, 1936), the families were segregated as the order Hydropteridales, to emphasize the fact that they are both aquatic and heterosporous. These characters were later thought not to be due to a shared common ancestry, but to convergence. Therefore, more recently, they have been maintained as separate orders, Marsileales and Salviniales, to emphasize their structural differences. It has been hypothesized that the Marsileales may be more closely

related to the Schizaeaceae (Kramer in Kubitzki, 1990) and the Salviniaceae to the Hymenophyllaceae than either is to each other (Bierhorst, 1971; Gifford and Foster, 1988; Pichi Sermolli, 1977). Rothwell and Stockey (1994) reported fossil evidence for a new heterosporous fern genus, *Hydropteris.* Their cladistic analysis of heterosporous ferns demonstrated that these plants are a monophyletic group, which led these authors to readopt the order Hydropteridales. Hasebe et al. (1994, 1995) demonstrated the monophyly of the heterosporous ferns based on *rbcL* sequences. The results of our study strongly corroborate a single origin of heterospory in leptosporangiate ferns.

The tree ferns (*Calochlaena, Dicksonia, Metaxya, Cyathea*), together with *Plagiogyria,* come together in a robustly supported clade (Analyses 1C and 2C). *Plagiogyria* has been placed previously with *Osmunda* (Holttum, 1973; Mickel, 1974; Pichi Sermolli, 1977). In both Analyses 1 and 2, the most parsimonious *rbcL* trees differed only in their placement of *Calochlaena, Dicksonia,* and *Metaxya.* The strict consensus of these *rbcL* trees yielded a trichotomy for these taxa. Relationships among the tree ferns in the larger *rbcL* analysis by Hasebe et al. (1995) were also poorly resolved. In the analyses of the morphological data alone (Analyses 1A and 2A), there was weak support for *Calochlaena* and *Dicksonia* as sister taxa. With the combined data (Analyses 1C and 2C), this relationship was upheld with increased bootstrap support provided mostly from at least part of the morphological data. The recent suggestion by Qiu et al. (1995) that *Metaxya* does not share any derived characters with the cyatheoid or dicksonioid ferns is not upheld here. Even in the analyses of morphological data alone, both *Plagiogyria* and *Metaxya* grouped with the tree ferns. This outcome indicates the usefulness of an explicit cladistic approach to determining phylogenetic relationships based on all available data, as opposed to making intuitive systematic judgments based primarily on concepts of overall morphological similarity. Although the tree ferns, the heterosporous ferns, and the schizaeoid ferns are each well supported clades, their interrelationships remain unresolved.

Relationships of Non-Leptosporangiate Pteridophytes.—Relationships among *Lycopodium, Psilotum, Botrychium, Angiopteris,* and *Equisetum* were not well resolved in Analysis 2, even in the combined analysis, except for a weak association between *Botrychium* and *Psilotum.* For future analyses to resolve better these relationships, we suggest including fossil and other extant taxa pertinent to this area of the tracheophyte clade. Molecular data from other genes are also desirable.

Hypotheses of Morphological Character Evolution in Ferns.—Figures 6–8 display the most parsimonious hypotheses of evolutionary history for several sporophytic and gametophytic characters on one of our best estimates of fern phylogeny. These are presented to illustrate that explicit cladistic analyses, which include morphological data, not only permit generation of hypotheses of relationship among groups of ferns, but also permit study of character evolution. If comparative studies of ferns are to yield evolutionary explanations, rather than simply descriptions of variation and covariation, they need to con-

sider phylogenies (Donoghue, 1989; Harvey and Pagel, 1991; Hufford, 1995; Maddison and Maddison, 1992). In studies of character evolution, a phylogeny allows estimation of the number of times that a trait evolved and the direction or temporal sequence of character transformation. Taking advantage of MacClade's (Maddison and Maddison, 1992) interactive environment for exploring phylogeny, Donoghue (1989) provided examples of how a phylogeny might be used to elucidate sequences of morphological character change. Establishing the order of evolution of traits is critical in choosing among alternative evolutionary explanations. Donoghue (1989) used a phylogeny of seed plants to test the hypothesis that fleshy, animal-dispersed propagules promote the evolution of dioecy. More recently, Friedman (1993) and Rothwell and Serbet (1994), using phylogenies of seed plants, hypothesized a sequence of character origins to evaluate current hypotheses of microgametophyte evolution. Their studies provide insight into the origin of a suite of male gametophyte characters (e.g., sulcus, pollen tube, and siphonogamy) that were key events in the early evolution of seed plants. In our future thinking about the evolution of traits in ferns, cladograms can help to identify not only the context in which a feature evolved, but also whether it may have been strictly correlated with the evolution of some other character or performance advantage (Maddison, 1990; Pagel, 1994). The availablity of phylogenetic trees will permit explicit studies of a wide variety of characters (e.g., heterospory, breeding systems) of interest to fern biologists, and may yield new insights regarding the role morphological innovations have played in influencing the evolution of ferns.

Conclusions

Morphological data have to some extent been eclipsed in phylogenetic work by advances in molecular sequencing. The analyses carried out in this study clearly show the value of combining molecular and morphological data sets, as well as analyzing them separately. Rather than the many molecular characters "swamping" a few morphological characters, it is apparent that the sheer number of characters of different types is not as important in determining the tree topology as is the distribution of character support and homoplasy (Donoghue and Sanderson, 1992). The addition of morphological characters to the molecular data set is shown here to influence not only the topology based on molecular data alone, but to alter substantially the support for various clades within the topology. Most importantly, morphological data provided increased support at the base of the tree and in this sense are complementary to the *rbcL* data, which alone did not confer strong support for relationships among the most basal taxa. Ignoring morphological data would be justified if they provided no evidence whatsoever about phylogenetic relationships. We believe we have demonstrated the utility of taking morphology into account in formulating hypotheses of phylogenetic relationships of pteridophytes. Indeed, would the concept of "pteridophytes" even exist were it not for morphological data? The advantage of a well supported hypothesis of phylogenetic

relationships that is based also on an extensive morphological data set is that it can in turn lead to a modern classification of pteridophytes that utilizes morphological synapomorphies to circumscribe the monophyletic groups that are recognized. This cannot be achieved with a phylogeny based only on molecules.

Although the phylogenetic hypotheses that we present in this study are not conclusive about many questions, we believe that the cladistic analyses on which they are based enable a much clearer evaluation of the relative merits of competing hypotheses on fern phylogeny, and will help to focus attention on several issues that require further consideration. On the neobotanical front, continued emphasis on gathering DNA sequence data using a multiple gene approach from both nuclear and organellar genomes will be essential to resolve better various portions of the phylogeny. Another worthwhile approach to understanding fern relationships would be comparative developmental studies of morphology. Such work would likely yield additional characters, as well as insight into the potential ordering of certain multistate characters and the identification of homoplasies. On the paleobotanical front, we are confident that adding information from the fossil record of pteridophytes will influence our current understanding of relationships (Smith and Littlewood, 1994) and will have important implications for hypotheses of homology (Doyle and Donoghue, 1992; Huelsenbeck, 1991; Kenrick, 1994), as it has in recent studies of seed plants (Crane, 1985b; Doyle et al., 1994; Nixon et al., 1994; Rothwell and Serbet, 1994). Future cladistic analyses of pteridophytes using a synthetic approach that integrates paleobotanical and neobotanical data will help to resolve outstanding problems of pteridophyte phylogeny and will lead to a better understanding of character evolution among these early vascular plants.

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APPENDIX 1

Taxa included in study, with voucher exsiccatae compiled to verify morphological character data. All specimens are at UC. For some taxa, more than one specimen was selected to permit study of all vital information. When no collector's number was available the UC accession number was noted. The classification used here generally follows Kramer (in Kubitzki, 1990), except for a few modifications, as given in Flora of North America Editorial Committee (1993), to reflect more recent publications.

ANEMIACEAE

Anemia mexicana Klotzsch—Mexico (Veracruz), *Purpus 5482*

ASPLENIACEAE

Asplenium filipes Copel.—Borneo (Mt. Kinabalu), *Clemens and Clemens 27292*

AZOLLACEAE

Azolla caroliniana Willd.—USA (Texas), *Kessler 6814*

BLECHNACEAE

Blechnum occidentale L.—Mexico (Oaxaca), *Mickel 6964*

CHEIROPLEURIACEAE

Cheiropleuria bicuspis (Blume) C. Presl—Taiwan (Miaoli Co.), *Peng 1748*

CYATHEACEAE

Sphaeropteris lepifera (J. Smith ex Hook.) R. Tryon [formerly *Cyathea*]—Taiwan, *Hutchison 2749,* cultivated in Hawaii

CYCADACEAE

Cycas circinalis L.—Guam, *Moran 4375*

DENNSTAEDTIACEAE

Blotiella pubescens (Kaulf.) R. Tryon—Tanzania, *Peter 15*
Dennstaedtia punctilobula (Michx.) T. Moore—USA (Massachusetts), *Morris s.n.* (UC 181497)
Histiopteris incisa (Thunb.) J. Smith—Costa Rica (San José), *Smith 2014;* Mexico (Oaxaca), *Mickel 4631*
Lindsaea odorata Roxb.—Ceylon (Uva), *Faden and Faden 77/19*
Lonchitis hirsuta L.—Mexico (Veracruz), *Herb. Copeland 80;* Ecuador (Napo), *Fay and Fay 2763*
Microlepia strigosa (Thunb.) C. Presl—USA (Hawaii), *Degener et al. 35718*
Monachosorum henryi H. Christ—Bhutan, *Bartholomew 231;* Taiwan, *Moran 5461*
Pteridium aquilinum (L.) Kuhn—USA (California), *Hall 9241*

DICKSONIACEAE

Calochlaena dubia (R. Br.) M.D. Turner & R.A. White—Australia (New South Wales), *Constable P7803*
Dicksonia antarctica Labill.—Australia (New South Wales), *Coveny 12161*

DIPTERIDACEAE

Dipteris conjugata Reinw.—Philippines (Luzon), *Pterid. Philipp. Exs. s.n.* (UC 350921), *Loher s.n.* (UC 229495)

DRYOPTERIDACEAE

Davallia mariesii T. Moore ex Baker—Taiwan (Taitung Co.), *Zogg and Gassner 6265*
Elaphoglossum hybridum (Bory) T. Moore—Tanzania (Kilimanjaro), *Daubenberger s.n.* (UC 398041)
Nephrolepis cordifolia (L.) C. Presl—China (Fukien), *Chung 3694*
Onoclea sensibilis L. USA (Connecticut), *Hill 21664*
Rumohra adiantiformis (G. Forster) Ching—Brazil (São Paulo), *Ulbricht 78*

EQUISETACEAE

Equisetum arvense L.—USA (Minnesota), *Moore 20505*

GLEICHENIACEAE

Diplopterygium glaucum (Houtt.) Nakai [formerly *Gleichenia japonica*]—Japan (Hitachi Hondo), *Furuse s.n.* (UC 1291856)
Stromatopteris moniliformis Mett.—New Caledonia, *Buchholz 1726*

GRAMMITIDACEAE

Micropolypodium okuboi (Yatabe) Hayata [formerly *Xiphopteris*]—Japan (Kyushu), *Tagawa 8303*

HYMENOPHYLLACEAE

Cephalomanes thysanostomum (Makino) Iwatsuki—Philippines (Luzon), *Topping 715*

LYCOPODIACEAE

Lycopodium digitatum Dill. ex A. Br.—USA (Vermont), *Moldenke 8863*

LYGODIACEAE

Lygodium japonicum (Thunb.) Sw.—Japan (Ryukyu Isl.), *Iwatsuki 4694*

MARATTIACEAE

Angiopteris evecta (G. Forster) Hoffm.—Fiji (Ngau), *A. C. Smith 7844*

MARSILEACEAE

Marsilea quadrifolia L.—Italy, *collector unknown* (UC 679271)

MATONIACEAE

Matonia pectinata R. Br.—Malaya, *Norris s.n.* (UC 678755)

METAXYACEAE

Metaxya rostrata (Kunth) C. Presl—Brazil (Amazonas), *Maguire et al. 60318*

OPHIOGLOSSACEAE

Botrychium strictum Underw. [formerly *Botrypus*]—China (Hubei), *1980 Sino-Amer. Exped. No. 1686*

OSMUNDACEAE

Osmunda cinnamomea L.—Canada (Québec), *Louis-Marie s.n.* (UC 1072541)

PARKERIACEAE

Ceratopteris thalictroides (L.) Brongn.—Japan (Honshu), *Seto 7330;* Venezuela (Delta Amacuro), *Steyermark et al. 114557*

PLAGIOGYRIACEAE

Plagiogyria japonica Nakai—China (Kwangsi), *Ching 5898;* (Anhwei), *Ching s.n.* (UC 261788)

POLYPODIACEAE

Loxogramme grammitoides (Baker) C. Chr.—Japan (Honshu), *Seto 12727*
Polypodium australe Fée—Italy (Sardinia), *Reichardt s.n.* (UC 398130)

PSILOTACEAE

Psilotum nudum (L.) P. Beauv.—Tahiti, *Setchell and Parks 302*

PTERIDACEAE

Acrostichum aureum L.—Aldabra Isl. (South Isl.), *Fosberg 49192;* Costa Rica (Puntarenas), *Mickel 2761*
Adiantum raddianum C. Presl—Brazil (Paraná), *Kummrow 1685*
Coniogramme japonica (Thunb.) Diels—Japan (Kanagawa), *Suzuki s.n.* (UC 953991)
Platyzoma microphyllum R. Br.—Australia (New South Wales), *Coveny 11675*
Pteris fauriei Hieron.—Hongkong, *Kao 6383*
Taenitis blechnoides (Willd.) Sw.—Sumatra, *Rahmat Si Toroes 1562*

SALVINIACEAE

Salvinia cucullata Roxb. ex Bory—Japan (Honshu), *Tagawa 8395*

SCHIZAEACEAE

Actinostachys digitata (L.) Wall. [formerly *Schizaea*]—Sumatra, *Winkler s.n.* (UC 391724)

THELYPTERIDACEAE

Thelypteris beddomei (Baker) Ching—Japan (Kyushu), *Tagawa and Iwatsuki 3938*

VITTARIACEAE

Vittaria flexuosa Fée—Japan (Honshu), *Konta 4853*

APPENDIX 2

Morphological character list and discussion

Note that whenever UC appears after a character description, this indicates that the voucher study set at UC (Appendix 1) was consulted to corroborate data taken from the literature.

Sporophyte: Vegetative Morphology and Anatomy

1. CIRCINATE VERNATION OF LEAVES: (0) no, (1) yes. This character describes the form of the entire leaf in the bud. Although in *Cycas* the vernation of the young leaflets is distinctly circinate (coiled) as in many ferns, the primary leaf axis is erect or only slightly bent (Gifford and Foster, 1988). Kubitzki (1990), Stevenson (1990), Tryon and Tryon (1982).

2. FERTILE-STERILE LEAF DIFFERENTIATION: (0) (nearly) monomorphic, (1) hemidimorphic—leaf tip fertile, (2) hemidimorphic—leaf base fertile, (3) dimorphic. The monomorphic condition is defined here as the lack of differentiation between fertile and sterile leaves (other than the latter lacking sporangia), i.e., fertile leaves are essentially similar in shape and size to sterile leaves, though they may be slightly contracted. Dimorphism entails significant differentiation, where fertile and sterile leaves are clearly dissimilar. If differentiation appears in separate parts of the same leaf, the term "hemidimorphism" is applied (Wagner and Wagner, 1977). Either the tip of the blade, the middle of the blade, or the base may be fertile. For example, the presence of sporocarps modifies the leaf base in Marsileaceae to form a hemidimorphic leaf (Wagner and Wagner, 1977). *Actinostachys,* on the other hand, is hemidimorphic at the blade tip. In our particular data set, there was no hemidimorphism in the middle of the blade, and so this state was not included. *Platyzoma* has small, sterile, filiform leaves; large, sterile, 1-pinnate leaves; and fertile leaves that are similar in size and shape to the large, sterile leaves. It was scored as both monomorphic (fertile leaves are not distinguishable in size and shape from the large, sterile leaves) and dimorphic (fertile leaves completely different in size and shape from small, sterile, filiform leaves). *Salvinia* has two green, floating, entire leaves and one submerged, highly branched leaf at every node. It was scored as both hemidimorphic (at the base) and dimorphic. Hemidimorphic differentiation is observed in the submerged leaf when it is sterile vs. when fertile, since the sporocarps are borne upon only some of the "inner" segments of the submersed leaves (Eames, 1936), thereby changing the morphology of only those segments. Dimorphic differentiation is observed between the fertile, highly branched, submerged leaf and the sterile, green, floating leaves. In Psilotaceae, the tips of the "foliar appendages" are forked or bilobed when associated with sporangia, and therefore they were scored as dimorphic. The fertile spike of *Botrychium* is regarded here as a separate leaf fused to the sterile leaf, with the "petiole" of the leaf complex being stemlike; others may regard it as a single leaf with fertile and sterile segments (see Bierhorst, 1971; Gifford and Foster, 1988 for references and overview of historical interpretations). UC; Bierhorst (1971), Eames (1936), Gifford and Foster (1988), Kubitzki (1990), Tryon (1961, 1964, 1967), Tryon and Tryon (1982).

3. BLADE DISSECTION: (0) simple to deeply pinnatifid, (1) compound (once-pinnate or more divided). This character applies to mature, sterile, photosynthetic blades only (i.e., does not include the narrow, filiform, sterile leaves of *Platyzoma,* or the highly dissected, sterile leaves of *Salvinia*). UC; Kubitzki (1990), Warmbrodt and Evert (1978).

4. PRIMARY BLADE VEIN FORM: (0) dichotomous, (1) anisotomous (pinnate), (2) solitary/unbranched. This character refers to the primary vein system only. It is a combination of Nixon et al.'s (1994) characters 25 and 26. In seed plants, some leaves with an anisotomous primary vein form were then scored as having either parallel, pinnate, or palmate veins. In our data set, all fern leaves with an anisotomous primary vein form had pinnate leaf venation; therefore we combined these two characters into one. The palmately veined condition is apparently unknown in extant ferns and there are no palmately divided fern leaves (Mickel, pers. comm.). The terms trichotomously-pedate and pseudodichotomous have been applied to the branching observed in leaves of *Matonia* (Kubitzki, 1990). We agree with Wagner (1952b) that the leaf of *Matonia* is similar to the pedate leaves of certain pteridoid ferns (e.g., *Adiantum*), where the early leaves are clearly pinnate, but the pinnae of mature leaves are re-oriented so as to give the impression of being dichotomously

branched; hence the primary vein form is scored here as anisotomous. UC; Bower (1923, 1926), Jarrett (1980), Kubitzki (1990), Wagner (1952b), Warmbrodt and Evert (1978).

5. VEIN ORDERS: (0) one, (1) two, (2) three, (3) four or more. Size classes of veins were used to determine vein order. All taxa in this data set have at least one order of venation, except for *Psilotum nudum*, which has no vascular bundle in the "leaf." Two vein orders occur by branching off from the midvein in leaves with anisotomous primary venation (the rachis of pinnate compound leaves was considered to be the primary vein), or by branching off from the primary dichotomous veins. UC; Bower (1926).

6. SECONDARY VEIN FORM: (0) dichotomous, (1) anisotomous/non-dichotomous. Secondary vein form refers to the pattern of venation of the second order of veins. This character obviously does not apply to leaves with only one order of veins, because the form of the primary vein order has already been described in character 4. This character is modelled after character 28 in Nixon et al. (1994), but is more explicit about which vein order pattern it is describing. UC; Bower (1923, 1926), Jarrett (1980), Tryon (1961).

7. VEIN FUSION (IN STERILE BLADES): (0) nonanastomosing, (1) anastomosing. This character is defined as anastomoses consistently distributed over the leaf blade. In some taxa (e.g., *Anemia mexicana*) the veins repeatedly fork and it is common for some of the branches to run together to form, in effect, areoles. Exactly the same thing happens in some species of *Adiantum*. In such cases, the taxa were scored as nonanastomosing because the anastomoses are not consistent throughout the lamina or from leaf to leaf. In other taxa (e.g., *Coniogramme*), anastomoses occur primarily near the costa and then the veins run free to the margin; these taxa were scored as anastomosing. In *Matonia*, vein fusions occur primarily in fertile blades (around the sori) and so it was scored as nonanastomosing. UC; Bower (1923, 1926), Kubitzki (1990).

8. VEIN AREOLES: (0) with free included veinlets, (1) without free included veinlets. UC; Kubitzki (1990), Wagner (1979).

9. HYDATHODES: (0) absent, (1) present. Hydathodes are expanded or otherwise morphologically distinct vein endings visible on the adaxial surface (see Ogura, 1972, p. 124–125). They may or may not be secretory in function. Sometimes they are more conspicuous for veins ending in sori (e.g., *Microlepia*); in other cases they are equally conspicuous on both fertile and sterile vein tips (e.g., *Micropolypodium*). Interestingly, taxa with hydathodes have veins that stop short of the margin, whereas most taxa without hydathodes have veins running out to the margins. UC.

10. BLADE HAIRS: (0) absent, (1) present. Hairs are defined here as uni- to multicellular, uniseriate, epidermal outgrowths. The papillae in *Azolla* were scored as hairs. UC; Flora of North America Editorial Committee (1993), Kubitzki (1990).

11. BLADE SCALES: (0) absent, (1) present. Scales are defined here as multicellular, bi- to multiseriate epidermal outgrowths. UC; Flora of North America Editorial Committee (1993), Kubitzki (1990).

12. GUARD MOTHER CELL (GMC) DIVISION: (0) diameristic, (1) parameristic, (2) anomomeristic. Payne (1979) defined these three terms based on the manner of production and division of the GMC. These three character states are defined as the GMC dividing with a wall formed: at right angles to the preceding wall (the wall that formed the GMC); parallel to the preceding wall; or at any angle relative to the preceding wall, respectively. Where Sen and De (1992) indicated a predominance of a certain type of GMC division, we scored according to the predominant type. Baranova (1992), Kondo (1962), Mickel and Lersten (1967), Mickel and Votava (1971), Pant and Khare (1971), Sen and De (1992), Thurston (1969), Tryon (1961), Van Cotthem (1970, 1973).

13. ORIGIN OF CELLS SURROUNDING GUARD CELLS: (0) perigenous, (1) mesogenous, (2) mesoperigenous. Pant (1965) recognized three major categories of stomates, based on the origin of the cells surrounding the guard cells. These three character states are defined as: all of the cells surrounding the guard cells originated independently of the maternal cell of the guard cells; all the subsidiary cells or the single annular subsidiary cell originated from the same maternal cell as the guard cells; or the surrounding cells are of two different origins—one or more are mesogenous, and the other(s) perigenous, respectively. Where Sen and De (1992) indicated a predominance of a certain origin type for the cells surrounding the guard cells, we scored according to the predominant type. We followed Kondo (1962) for scoring certain taxa (especially Ophioglossaceae and Osmundaceae) as having anomomeristic and perigenous stomates, rather than Payne's

(1979) reference to unpublished results that argue there are no truly perigenous stomates. Baranova (1992), Kondo (1962), Mickel and Lersten (1967), Mickel and Votava (1971), Pant and Khare (1971), Sen and De (1992), Thurston (1969), Tryon (1961), Van Cotthem (1970, 1973).

14. DROMY AT BASE OF BLADE (LOWERMOST PINNAE): (0) catadromous, (1) anadromous, (2) isodromous. This character applies to the dissection pattern of the blade (in taxa that are more than once-pinnate) or to the venation (in once-pinnate taxa) displayed by the basal segment or vein(let) in the lowermost pinnae (states defined in Kubitzki, 1990, p. 16). This character was not scored for taxa with undivided blades or with dichotomous primary venation. Most taxa are relatively consistent in their blade architecture, but others, like *Coniogramme,* vary. Kramer (1987) applied the term pseudoanadromy to taxa like *Cibotium* where the basiscopic pinnules on the lowermost pinnae are suppressed but where comparison with distal pinnae or with related species indicates that the usual condition is catadromous. We prefer not to make this assumption for such taxa and so would score *Cibotium* as anadromous. UC; Kramer (1987), Kubitzki (1990).

15. PULVINI: (0) absent, (1) present. Pulvini are swellings positioned on the stipe or rachis that, through differential contraction and expansion of cells, can change the position of the blade or divisions of the blade, presumably to orient the blade in relation to sunlight. Kubitzki (1990), Johnson (1986).

16. PNEUMATHODES: (0) absent, (1) present and scattered all around stipe and/or rachis, (2) present and borne in discrete lines or patches on stipe and/or rachis. Pneumathodes (also called aerophores, pneumatophores, or respiratory lines; cf. Bower, 1923; Ogura, 1972) are ventilation lines or patches on rachis, stipe, or rhizome that allow gaseous interchange even in densely sclerotic tissues. In cross-section of stipes, pneumathodes are noted as thin areas of parenchyma on the periphery of the cortex (interrupted hypodermis). In paradermal sections, stomates are visible. Pneumathodes are more readily seen in fresh material, especially when there is a contrast with an otherwise darkened stipe, as is the case in some dennstaedtioids, cyatheoids, thelypteridoids, and dryopteridoids. UC; garden material; Bower (1923, 1926), Kramer (1957), Kubitzki (1990), Lloyd (1970), Mickel and Atehortúa (1980), D. Palmer (pers. comm.).

17. BLADE/LEAF ARTICULATION: (0) absent, (1) present. With a swollen or discolored place of separation or weakness at base of pinnae or stipe; jointed stipe or pinna. UC; Kubitzki (1990).

18. TROPHOPODS: (0) absent, (1) present. Trophopods are swollen leaf bases found in some ferns that are specialized to accumulate food and to persist as storage organs. Wagner and Johnson (1981, 1983).

19. ADAXIAL OUTLINE OF STIPE AND RACHIS: (0) convex to flattened, (1) sulcate. Taxa scored as "sulcate" have stipe and rachis that are slightly to strongly concave adaxially, or have a pronounced groove. UC; Kubitzki (1990).

20. SCLERENCHYMA COLORATION ON STIPE AND RACHIS: (0) not dark-pigmented, (1) dark-pigmented. Taxa with stipe and rachis having green pigmentation or dark pigmentation localized at the leaf base were scored as "not dark-pigmented". Taxa scored as "dark-pigmented" were so throughout the stipe and often on the rachis and costae. UC.

21. SCLERENCHYMA FIBERS: (0) absent, (1) present. Sclerenchyma fibers, when present, are found in the periphery of the stipe and rachis, and/or in the rhizome cortex, surrounding meristeles and in patches. UC; Ogura (1972).

22. EPIPETIOLAR BRANCHES: (0) absent, (1) present. Epipetiolar branching is defined here as the production of rhizomes from the leaf stipe. The production of occasional stolons from leaf stipes is scored as "absent" (e.g., *Plagiogyria*). Stolons in *Nephrolepis* are apparently borne from the rhizome. UC; Kubitzki (1990), Ogura (1972), Troop and Mickel (1968).

23. STIPE STELE NUMBER (FROM BASE TO APEX): (0) monostele at base, polystele above, (1) monostele throughout, (2) distele at base, monostele above, (3) polystele throughout, (4) distele. The number of vascular bundles in the cross-section of stipes is a relatively constant character in many taxa. *Dipteris* and *Cheiropleuria* differ from all other ferns in having a single bundle at the stipe base that divides a number of times resulting in a divided vasculature in the distal portion of the stipe; hence they were scored as "monostele at base, polystele above". Several taxa have a single vascular bundle that extends throughout the entire length of the stipe and were scored as "monostele throughout". Others, such as *Onoclea* and *Asplenium,* have two meristeles at the base that fuse to form a monostele in the distal part of the stipe and were scored as "distele at base,

monostele above". Taxa scored as "polystele throughout" have a network of more than two vascular bundles throughout their stipes. UC; Bierhorst (1971), Keating (1968), Lin and DeVol (1977, 1978), Nair and Sen (1974), Ogura (1972), Warmbrodt and Evert (1978), White and Turner (1988).

24. XYLEM CONFIGURATION IN STIPE (FROM BASE TO APEX): (0) horseshoe-shape variation (C, U, V, O, Ω, or low arc) with stipe center parenchymatous, (1) solid T, O, or Δ-shape in stipe center, (2) X-shape (sometimes becoming V towards stipe apex), (3) three arcs: two 7-shaped adaxial strands and one arc-shaped abaxial strand, (4) polycyclic. The overall configuration of the xylem in the cross-section of stipes has been of definite importance in fern identification and is quite characteristic for some groups. Most taxa were scored as having either a single vascular bundle, or several meristeles, whose overall xylem pattern is in some form of a horseshoe-shape (e.g., *Osmunda*: monostele with C-shaped xylem strand; *Pteridium*: polystele with xylem in a complex horseshoe pattern; in some gleichenioid species, the margins of the xylem arc can connect to form a ring). Several smaller taxa have a single monostele in the center of the stipe that is either a solid round, triangular, or T-shape. For most of our taxa scored as "1", there certainly is no room for more than this kind of bundle (*Lygodium* expected). *Asplenium* has two arc-shaped meristeles that come together and fuse in an X-shape (sometimes becoming a V-shape) for most of the length of the stipe (cf. Ogura, 1972, p. 110, fig. 111). Some tree ferns have a unique xylem configuration (state 3) with many meristeles arranged in two adaxial 7-shaped arcs and one abaxial arc (cf. Ogura, 1972, p. 111, p. 372). At different points along the stipe these three arcs may fuse. A polycyclic xylem configuration (state 4) consists of numerous meristeles arranged in two or more concentric rings. UC; Bierhorst (1971), Bower (1926), Keating (1968), Kubitzki (1990), Lin and DeVol (1977, 1978), Ogura (1972), Warmbrodt and Evert (1978), White and Turner (1988).

25. PRIMARY XYLEM BORDERED PITS: (0) scalariform, (1) circular. The presence of circular or slightly elliptic bordered pits (length of opening not exceeding twice the width) characterizes members of Ophioglossaceae (Bierhorst, 1960; Kim et al., 1993; White, 1963b) that have been examined, whereas scalariform bordered pits (opening more than 2 times longer than wide) predominate for the rest of the ferns. Genera of Marattiaceae appear to have mostly scalariform pitting but with occasional circular pits (see Bierhorst, 1960, fig. 52). White (1963b) illustrated "circular border pits" in *Asplenium*, but these pits have openings more than twice as long as broad. We scored a taxon as "scalariform" if the pitting type was entirely or mostly scalariform and as "circular" if a substantial number of circular bordered pits were found on the tracheids. Due to the presence of both scalariform and circular bordered pits in Marattiaceae and Psilotaceae (Bierhorst, 1960, 1971), these taxa were scored as polymorphic ("0&1"). Only in Ophioglossaceae does the pitting seem to be nearly entirely circular or slightly elliptic.

26. RHIZOME SYMMETRY: (0) radial, (1) dorsiventral. These character states roughly correspond to erect vs. creeping rhizomes, respectively. UC; Bower (1923), Holttum (1964), Kaplan (1977).

27. MATURE RHIZOME STELE TYPE: (0) protostele, (1) solenostele, (2) dictyostele, (3) eustele. There is much variation in the literature as to what these stelar terms define; therefore we indicate here exactly how we have characterized them in this study. The protostele is a solid column of vascular tissue without a pith or any parenchymatous tissue mixed with the vascular tissue. A solenostele is a tubular mass of vascular tissue with a pith and usually with non-overlapping leaf gaps or (rarely) without leaf gaps. A dictyostele is a tubular mass of vascular tissue with a pith, but with (two or more) overlapping leaf gaps. The eustele is a tubular mass of vascular tissue (with or without a definable pith) and with discrete sympodia usually in a discontinuous cylinder; it is found only in seed plants and some progymnosperms (Beck et al., 1982; Schmid, 1982). The term "*Lindsaea*-type of stele" used by Kramer (in Kubitzki, 1990) and Ogura (1972), which refers to the stele in rhizomes of most species of *Lindsaea* and *Odontosoria* with both external and internal phloem, is scored here as a protostele since it lacks a pith (Schmid, 1982). We agree with Schmid (1982) that the "medullated protostele" term used by Ogura (1972) and others is inherently contradictory in that protosteles by definition lack a pith or "medulla" and therefore it was scored here as a solenostele. Schmid (1982) termed it an ectophloic siphonostele, but for this study we have not distinguished between the ectophloic and amphiphloic siphonosteles. Although most reference works characterize *Azolla* and *Salvinia* as protostelic, we agree with Schmid's (1982, pp. 880–881) arguments that they have an ectophloic siphonostele with non-overlapping leaf gaps

(=solenostele in this paper). Similarly, we also scored *Actinostachys* as solenostelic (Schmid, 1982, p. 889). The stele in adult plants of *Pteridium* has become popularized as dictyostelic because of its apparent resemblance to the highly perforated dictyostele of polypodioids; however, we agree with Schmid's (1982, pp. 901–902) account clearly indicating its solenostelic nature. It is known that the stelar type varies within a plant during its ontogeny and continued growth, changing from protostele when young to solenostele to dictyostele, and possibly reverting to solenostele in narrower branches. Several authors stress the occurrence of transitional stelar types between solenostely and dictyostely. In some of the intermediate forms the leaf gaps overlap now and then, so that the rhizome, to a certain extent, remains in a solenostelic condition. In others, the overlapping is more general; therefore, it is impossible to state definitely whether the vascular system of the mature plant is either solenostelic or dictyostelic. This was particularly problematic in the Pteridaceae, where we scored most taxa as polymorphic ("1&2"). Beck et al. (1982), Hill and Camus (1986), Kubitzki (1990), Ogura (1972), Qiu et al. (1995), Schmid (1982), Tryon and Tryon (1982), White and Turner (1988).

28. RHIZOME STELE CYCLES: (0) monocyclic, (1) polycyclic. Monocyclic defines a rhizome that possesses a single stem cylinder, whether protostelic, solenostelic, or dictyostelic. Polycyclic rhizomes possess accessory vascular strands or cylinders in addition to the principal cylinder. Ogura (1972) used the term acyclostele to define rhizomes that, in addition to the main solenostele or dictyostele, possess some meristeles in the pith or occasionally in the cortex (accessory meristeles), which are arranged more or less irregularly. Because there are transitional forms between the polycyclostele and acyclostele, we concur with Schmid (1982, p. 901) that the latter term should be submerged under the former. Hill and Camus (1986), Kubitzki (1990), Ogura (1972), Schmid (1982).

29. VASCULAR CAMBIUM IN RHIZOME: (0) absent, (1) present. The vascular cambium in *Botrychium* is unidirectional and produces only secondary xylem centripetally. *Cycas* has a bifacial vascular cambium, typical of gymnosperm secondary growth. Bierhorst (1971), Gifford and Foster (1988), Ogura (1972), Stevenson (1980).

30. RHIZOME HAIRS: (0) absent, (1) present. UC; Kubitzki (1990).

31. RHIZOME SCALES: (0) absent, (1) present. UC; Kubitzki (1990).

32. RHIZOME SCALE PATTERN: (0) uniformly colored, (1) sharply bicolored, (2) clathrate (lattice-like). UC; Kubitzki (1990).

33. ROOTS: (0) absent, (1) present. UC; Kubitzki (1990).

34. ROOT HAIRS: (0) absent, (1) present. UC; Bierhorst (1971).

35. ROOT ANATOMY: (0) 2–5-arch, (1) polyarch. This character describes the number of simultaneously maturing protoxylem poles visible in a transverse section; the number of poles usually corresponds to the number of lobes of xylem. Taxa were scored for the usual state of main roots in their mature growth. This may vary along the axis of a given root, but in most ferns there are 2–4 (rarely 5) protoxylem points. In *Lycopodium* (*digitatum*), the roots are rhizome-like in appearance and internal anatomy, with about 6 to 9 protoxylem points in the protostele. The roots are formed near the stem apex and first appear as a crescent-shaped vascular bundle with protoxylem points along the tips and convex side. According to Bierhorst (1971), roots of *Lycopodium* are unique among vascular plants in having "protoxylem poles of different ages and in having lack of conformity between the number of protoxylem poles and shape of the xylem mass". Because the two protoxylem points at the ends of the crescent mature first, we consider *Lycopodium* as having diarch xylem. Bierhorst (1971), Gifford and Foster (1988), Johnson (1986), Kubitzki (1990), Pixley (1968).

36. GROWTH HABIT: (0) terrestrial, (1) epiphytic, (2) rooted aquatic, (3) floating aquatic. Taxa with an epipetric growth habit were scored as terrestrial. Those taxa scored as rooted aquatics grow in areas where water is commonly present only during the rainy season, or where water levels fluctuate from one season to another. UC; Burrows (1990), Kubitzki (1990).

37. MUCILAGE/LATEX CANALS: (0) absent, (1) present. Mucilage canals may be present in roots, rhizomes, and/or leaves. *Plagiogyria* and several other genera exude mucilage via mucilage-secreting trichomes. These taxa are not known to have mucilage canals or ducts. *Azolla* is reported to produce mucilage; however, this may be due to colonies of cyanobacteria that are in symbiotic

association with *Azolla* and present in its leaf cavities. Hill and Camus (1986), Kubitzki (1990), Mickel (1974), Ogura (1972), White and Turner (1988).

38. TRUE VESSELS: (0) absent, (1) present. True vessels with perforate end plates are known only from the roots in *Marsilea;* from the leaves, rhizomes, and roots in *Pteridium;* and from the rhizomes in *Equisetum.* All other taxa in our data set have tracheids. Bierhorst (1958, 1971), Gifford and Foster (1988), White (1961, 1963a, 1963b).

39. INTRANUCLEAR PARACRYSTALS: (0) absent, (1) present. Information was available for only a few taxa in our study. Fabbri and Menicanti (1970).

40. HYPODERMIS: (0) absent, (1) present. Information was available for only a few taxa in our study. Payne and Peterson (1973).

41. FIRST DIVISION OF ZYGOTE: (0) horizontal, (1) vertical, (2) free-nuclear phase. It has been a general observation in embryological studies of leptosporangiate ferns that the first division wall in the zygote is vertical, i.e., parallel to the long axis of the archegonium and at right angles to the axis of the prothallus (Bower, 1923; DeMaggio, 1977; Gifford and Foster, 1988). Bierhorst (1971) mentioned certain possible exceptions among the leptosporangiate ferns (e.g., *Stromatopteris, Actinostachys*), but the evidence is not convincing. In Marattiaceae, Ophioglossaceae, and Psilotaceae the first division wall in the zygote is horizontal, i.e., parallel to the axis of the prothallus and at right angles to the long axis of the archegonium (Bierhorst, 1971; Bower, 1923). Although the orientation of the wall of the first division differs between leptosporangiate and eusporangiate ferns, in all pteridophytes embryogenesis is cellular throughout. In embryos of extant cycads, a coenocytic phase with 250 or more nuclei may be produced before cellularization occurs. The horizontal division of single-celled fern zygotes and the horizontal developmental wall formation of cycad embryos that follows a free-nuclear phase are considered non-homologous events here, and so *Cycas* was scored as "free-nuclear phase". Gifford and Foster (1988) and Bierhorst (1971).

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42. SPORANGIAL WALL THICKNESS: (0) single cell layer, (1) 2 or more layers. This character refers to the thickness of the sterile jacket surrounding the spores in mature sporangia. Bierhorst (1971), Eames (1936), Gifford and Foster (1988).

43. SPORANGIUM RECEPTACLE: (0) (nearly) flat, (1) convex, (2) elongate and bristle-like, (3) elongate and highly branched. Many genera show a slight convexity of the receptacle, which is probably more obvious in fresh material. To be scored as convex for this study, the receptacle had to be hemispherical or more projecting, with the depth equalling or exceeding the width (diameter). UC; Bierhorst (1971), Campbell (1895), Eames (1936), Gupta (1962), Johnson (1986).

44. SPORANGIAL STALK LENGTH: (0) sessile to short, (1) long. Taxa with sporangial stalks that were barely discernable (sessile) or less than half the length of the capsule were scored as "sessile to short". Taxa with sporangial stalks that were greater than or equal to half the capsule length were scored as "long". Many fern taxa have sori with mixed maturation, hence sporangia of different ages are juxtaposed and there is considerable variation in stalk length in these sori as compared to sori with gradate or simultaneous maturation (Bower, 1923). The earliest-formed sporangia in mixed maturation sori often have shorter stalks than later-maturing sporangia. If some stalks in a given mixed sorus could be scored as "long", the taxon was scored as "long". UC; Bierhorst (1968, 1971), Campbell (1895), Eames (1936), Gupta (1962), Kubitzki (1990), Marschall (1925).

45. SPORANGIAL STALK WIDTH: (0) >6 cell rows wide, (1) 4–6 cell rows wide, (2) 1–3 cell rows wide. Taxa with sporangial stalks that were essentially sessile were scored as missing ("?") for width. UC; Bierhorst (1968, 1971), Campbell (1895), Gupta (1962), Eames (1936), Kubitzki (1990), Marschall (1925).

46. SPORE OUTPUT PER SPORANGIUM: (0) 1000+, (1) >100, <1000, (2) <100. The number of spores per sporangium is strictly correlated with the number of sporocytes that undergo meiotic division. Eusporangiate ferns have spore numbers that typically range in the thousands per sporangium. The great majority of leptosporangiate taxa have a spore output of 64 spores per sporangium, although some taxa show a reduced output of 32, 16, or even 8 spores. In the case of the heterosporous ferns, megasporangia each release a single megaspore, whereas microsporangia typ-

ically release 64 spores. A few leptosporangiate taxa have a larger spore output that ranges in the hundreds of spores per sporangium. UC; Bierhorst (1971), Bower (1923, 1926, 1928), Flora of North America Editorial Committee (1993), Kubitzki (1990), Tryon and Lugardon (1991), Tryon and Tryon (1982).

47. SORI: (0) absent, (1) present. We define sori as aggregations of sporangia arising from a "point" or discrete region on a vein into discrete clusters. *Azolla* is scored as polymorphic because the megasporangia occur singly (not in sori), whereas the microsporangia are numerous and in sori. The acrostichoid condition, with sporangia borne between as well as on the veins, is scored as sori absent (e.g., *Acrostichum, Cheiropleuria, Elaphoglossum*), as are the bladeless conditions where entire pinnae or blades are covered with sporangia (e.g., *Botrychium, Anemia, Osmunda*). *Plagiogyria,* at maturity, appears to have acrostichoid sporangia but, in actuality, the sporangia are borne only along the veins (Bower, 1923). Even though the sporangia are solitary at the ends of anastomosing veins in *Ceratopteris* (Bower, 1928), they are borne in irregular rows along the margin and protected by the reflexed segment margin. Hence, we define it as soriate. UC; Bierhorst (1971), Eames (1936), Hill and Camus (1986), Kubitzki (1990), Tryon and Tryon (1982).

48. SORUS OUTLINE: (0) round, (1) elongate. Round sori are roughly as long as wide. Elongate sori are conspicuously longer than wide and can be discrete or confluent. UC; Bierhorst (1971), Eames (1936), Hill and Camus (1986), Kubitzki (1990), Tryon and Tryon (1982).

49. SPORANGIA/SORUS POSITION ON BLADED FERTILE FRONDS/SEGMENTS: (0) marginal, (1) dorsal (abaxial), (2) adaxial. The "marginal" state refers to taxa with sporangia/sori that are restricted to the leaf margin (or nearly so). Taxa scored as "dorsal" have sporangia/sori that are well distanced from the margin on the abaxial leaf surface. Taxa with sporangia/sori on bladeless leaves or segments (e.g., *Botrychium, Anemia*) could not be scored for this character. In fertile *Azolla* plants, the lower (submersed) leaf lobe is reduced to two divisions on each of which a sporocarp is borne terminally (Bierhorst, 1971; Eames, 1936) obscuring the position of the sporangia on that segment, hence we scored it as uncertain ("?"). In Psilotaceae, the sporangia are not laminar in position and are usually interpreted as axillary (Bierhorst, 1971; Eames, 1936; Tryon and Tryon, 1982); hence we scored it as non-applicable ("?"). Fertile blade segments of *Onoclea* are very reduced, but the sori are clearly arranged on the dorsal surface (see Tryon and Tryon, 1982, p. 588). We consider the sporocarp wall of Marsileaceae taxa to be homologous to a blade, and sori are borne marginally on this blade (Eames, 1936; Johnson, 1898a, 1898b, 1933; Puri and Garg, 1953). UC; Kubitzki (1990), Qiu et al. (1995).

50. SORAL/SPORANGIAL MATURATION: (0) ± simultaneous, (1) gradate, (2) mixed. This character refers to the maturation of sporangia either within a sorus, or with respect to adjacent sporangia on a fertile leaf, or part of leaf, if sporangia are not arranged in sori. With gradate maturation, basipetal directionality is usually involved (see Bower, 1923). UC; Bower (1923, 1926, 1928), Eames (1936), Kubitzki (1990), Qiu et al. (1995), Tryon (1961).

51. NUMBER OF SPORANGIA/SORUS: (0) few (<12), (1) many (usually more than 20). UC; Bower (1926), Eames (1936), Johnson (1986), Kubitzki (1990).

52. INDUSIA: (0) absent, (1) present. This character defines a protective covering for sori, including a strongly reflexed or otherwise modified leaf margin. In some cases, indusia cover sporangia not clustered in sori (e.g., *Lygodium*). *Platyzoma,* which has pouch-like segments, is treated as lacking indusia because the margin is essentially unmodified. Slightly reflexed and largely unmodified marginal leaf tissue were not considered as indusia (e.g., *Vittaria flexuosa*). The indusia of the marsileaceous ferns are the most complex to understand; Campbell (1893) and Johnson (1898a, 1898b) are useful for interpreting these indusia, in addition to the references cited below. UC; Bierhorst (1971), Bower (1923, 1926, 1928), Eames (1936), Kubitzki (1990), Tryon and Tryon (1982).

53. ORIGIN OF INDUSIA OR INDUSIAL COMPONENTS: (0) leaf margin, (1) abaxial leaf surface. In some taxa, the indusium originates strictly from the abaxial leaf surface (e.g., *Blechnum*). In others, the indusium originates from the leaf margin (e.g., *Lonchitis*) and is clearly distinguished from a slightly reflexed and unmodified leaf margin. We regard a strongly reflexed and modified indusial leaf margin or marginal lobe (e.g., *Adiantum*) that covers sori as an indusium in this study. In some cases, the indusium is made up of components that are derived from both the abaxial leaf surface and the leaf margin (e.g., Dicksoniaceae, *Dennstaedtia*), forming a "cup-like"

structure. The lips of the indusial involucre in *Cephalomanes* (Hymenophyllaceae) are flared outward on both the adaxial and abaxial sides. The involucre is quite symmetrical and identical on both faces and it appears to be formed by abaxial and adaxial laterally fused flaps. This similarity of adaxial and abaxial appearance in hymenophylls may be unique in the ferns. UC; Bierhorst (1971), Bower (1923, 1926, 1928), Eames (1936), Kubitzki (1990), Tryon and Tryon (1982).

54. INDUSIUM ATTACHMENT RELATIVE TO SORUS: (0) lateral, (1) basal, (2) central. The indusial attachment in *Lygodium* and *Ceratopteris* is scored relative to individual sporangia, which are not in sori. A lateral indusium is attached at the edge of a sorus, and therefore covers the sorus in such a way as to resemble a flap, which can have various shapes (e.g., reniform, as in *Thelypteris;* linear, as in *Asplenium;* or 2-lipped as in Hymenophyllaceae). *Nephrolepis* and other taxa with round-reniform indusia attached to a slightly to deeply invaginated sinus in the sorus, are regarded here as having a lateral to sublateral indusial attachment. Sporangia in these sori are not found attached proximal to the point (line) of attachment of the indusium. Basally attached indusia are often cup-shaped (as in Dicksoniaceae and *Dennstaedtia*) and may completely encompass or surround sori (e.g., *Azolla*). An indusium with a central attachment point is usually peltate in shape (e.g., *Rumohra, Matonia*). UC; Bierhorst (1971), Bower (1923, 1926, 1928), Eames (1936), Kubitzki (1990), Labouriau (1958), Tryon and Tryon (1982).

55. INDUSIAL OPENING: (0) introrse, (1) extrorse, (2) suprasoral, (3) circumsoral, (4) none. An introrse indusial opening is directed toward the costa (away from the margin), whereas an extrorse opening is directed away from the costa (toward margin or segment apex). Those ferns with centrally attached, peltate indusia (e.g., *Rumohra* and *Matonia*) are scored as having a circumsoral opening, since the indusium is open all around the perimeter of the sorus and the sporangia project from the periphery of the indusium. Taxa with both segment margin and abaxial components sometimes forming a cup (e.g., *Dennstaedtia,* Dicksoniaceae) are scored as having a suprasoral (apical) indusial opening. The indusia in marsileaceous ferns form sacs with no opening; the delicate indusial tissue breaks down with the intake of water to release the spores. UC; Bierhorst (1971), Bower (1923, 1926, 1928), Eames (1936), Kubitzki (1990), Labouriau (1958), Tryon and Tryon (1982).

56. ANNULUS: (0) absent, (1) present. An annulus is defined here as a series of cells, of which at least some are indurated (thick-walled), that serve as a spore releasing or sporangial opening mechanism on the sporangium capsule. Bierhorst (1971), Bower (1923), Tryon and Tryon (1982).

57. ANNULUS ASPECT ON SPORANGIUM: (0) apical, (1) lateral (to one side), (2) oblique to transverse, (3) vertical to slightly oblique. Bierhorst (1971), Bower (1923, 1926, 1928), Kubitzki (1990), Qiu et al. (1995), Tryon and Tryon (1982).

58. ANNULUS SPAN ACROSS SPORANGIUM: (0) continuous bow, (1) interrupted bow, (2) restricted patch. A continuous bow is interrupted only by the stomium and otherwise is not disrupted by either the sporangium stalk or by non-annular sporangium wall cells (e.g., *Cibotium,* see Bower, 1926, p. 266). An interrupted bow is one that is disrupted by either the sporangium stalk (e.g., *Dipteris conjugata,* see Bierhorst, 1971, fig. 16–15, c and d) or by non-annular sporangium wall cells (e.g., *Matonia pectinata,* see Bower, 1926, p. 224), giving the annulus the appearance of being incomplete. The annular cells in *Osmunda* are a group of polygonal thick-walled cells restricted to a lateral position on the sporangium (Bower, 1926, p. 129). Bierhorst (1971), Bower (1923, 1926, 1928), Kubitzki (1990), Qiu et al. (1995), Tryon and Tryon (1982).

59. SPOROGENESIS: (0) homosporous, (1) anisosporous, (2) heterosporous. In homospory, typically all the sporogenous cells yield viable products that are of uniform size and behavior. Heterospory is restricted here to those taxa in which the production of two-sized, sexually differentiated spores is associated, during female sporogenesis, with regular abortion or degeneration of some of the spore mother cells or their meiotic products; microsporogenesis closely resembles sporogenesis in homosporous species. This differs from anisospory, where although spores of two sizes are produced, possibly differing in behavior, there is no accompanying loss or degeneration of meiotic products during the generation of the larger spores (e.g., *Platyzoma*). Bell (1979), Sheffield and Bell (1987), Tryon and Lugardon (1991).

60. SPORE LAESURA: (0) linear, (1) triradiate, (2) papilla-like, (3) furrow, (4) circular. The spore laesura is an exospore structure on the proximal face, through which the germ filament of the gametophyte emerges. Monolete spores are bilaterally symmetrical with a linear leasura and are

mostly ellipsoidal. Trilete spores are radially symmetrical with a triradiate laesura and often tetrahedral to globose. Microspores and megaspores of marsileaceous ferns differ from one another. The microspore laesura is triradiate, whereas the megaspore laesura is in the form of a proximal papilla. Microspores of *Cycas* have a single furrow (anacolpate). The circular aperture with large subapertural opturator in *Equisetum* is unique in pteridophytes. Dehgan and Dehgan (1988), Tryon and Lugardon (1991).

61. SPORES CHLOROPHYLLOUS: (0) no, (1) yes. The presence of chloroplasts within the spore is usually associated with the presence of a pseudoendospore or endospore and is indicative of precociously germinating spores. Kubitzki (1990), Tryon and Lugardon (1991).

62. SPORE EQUATORIAL FLANGE (CINGULUM): (0) absent, (1) present. A cingulum is a prominent thickening at the equator in some trilete spores. Tryon and Lugardon (1991).

63. PERISPORE (EPISPORE) PROMINENCE RELATIVE TO EXOSPORE: (0) not prominent, (1) prominent. The sporopollenin wall external to the exospore (exine) is termed an epispore (sensu Tryon and Lugardon, 1991) or perine (sensu Perkins et al., 1985) in the heterosporous ferns (Marsileaceae, *Azolla,* and *Salvinia*) and a perispore in the homosporous ferns (Tryon and Lugardon, 1991). Although developmental and ultrastructural details of this sporoderm layer are different between homosporous and heterosporous ferns (Lugardon and Husson, 1982) they are coupled here simply to refer to that spore wall layer external to the exospore. The external spore wall in *Cycas* is the exine; it does not have a perispore. Perispore (epispore) prominence was assessed relative to exospore thickness and its overall contribution to the spore wall. Perispores (epispores) that are simple, thin, and diffuse relative to the exospore were scored as "not prominent". Perispores (epispores) that are as thick as the exospore, or thicker, or make a substantial and elaborate contribution to the spore wall (e.g., *Lygodium japonicum*) were scored as "prominent". Dehgan and Dehgan (1988), Lloyd (1981), Perkins et al. (1985), Tryon and Lugardon (1991).

64. PERISPORE (EPISPORE) SURFACE: (0) (nearly) smooth or plain, (1) obviously patterned or sculptured. See character 63 for definitions of perispore and epispore. Perispore (epispore) surfaces described and depicted as smooth or finely (minutely) granulate, rugulate, or undulate by Tryon and Lugardon (1991) were scored as "smooth or plain", except where there was a distinct contrast with the exospore (e.g., *Pteridium*). Perispores (epispores) were scored as "sculptured" if their surfaces contributed an extensive, overall pattern to the spore topology that was different from the surface pattern of the exospore. This character essentially identifies whether or not the perispore layer forms conspicuous surface contours. Lloyd (1981), Perkins et al. (1985), Tryon and Lugardon (1991).

65. EXOSPORE (EXINE) STRUCTURE: (0) 2-layered, (1) 3-layered, (2) 5-layered. The exospore (or exine) is a wall formed of material derived from the tetrasporal cell and tapetum. Tryon and Lugadon (1991) define the 2-layered exospore in ferns as the blechnoid-type, with only two main zones: an inner, thin layer formed by a unique sheet, and a very broad, outer layer of amorphous sporopollenin. In fern spores with a multifoliate substructure, three structurally distinct zones can be distinguished: an inner layer of compressed sheets; a middle layer characterized by cavities between the sheets enveloped by amorphous sporopollenin; and a compact layer of sporopollenin. In *Cycas* the exine is 5-layered, with an alveolar layer called the endosexine, followed by the ectosexine (more or less smooth, porate, or foveolate on the surface) and a 3-layered nexine (Dehgan and Dehgan, 1988). Tryon and Lugardon (1991).

66. EXOSPORE (EXINE) SURFACE: (0) (nearly) smooth or plain, (1) obviously patterned or sculptured. Exospore surfaces described or depicted as finely (minutely) granulate, rugulate, or undulate were generally scored as "smooth or plain". Exospores with obvious contours or sculpturing, such as tubercles, verrucae, ridges, papillae, or pits were scored as "sculptured". Dehgan and Dehgan (1988), Perkins et al. (1985), Tryon and Lugardon (1991).

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67. SPORE GERMINATION PATTERN: (0) equatorial, (1) polar, (2) amorphous. These germination patterns were defined in detail by Nayar and Kaur (1968, 1971). In equatorial germination, the first cell division is by a wall formed parallel to the polar axis of the spore, and elongation of the thallus is in a plane parallel to the equatorial plane of the spore. In polar germination, the

first cell division in the germinating spore is by a wall formed parallel to the equatorial plane of the spore and elongation of the thallus is parallel to the polar axis of the spore. Amorphous germination is uncommon and exhibits no polarity either with regard to cell division or to the direction of thallus growth. Bierhorst (1971), Campbell (1892), Darnell-Smith (1917), Duckett and Pang (1984), Eames (1936), Nair and Sen (1974), Nayar and Kaur (1968, 1971), Tryon (1964), Whittier (1975), Whittier and Given (1987).

68. GAMETOPHYTE FORM: (0) tuberous, (1) filamentous, (2) cordate-thalloid, (3) elongate-thalloid, (4) reduced to relatively few cells. Nayar and Kaur (1971) clearly identified and defined five forms of adult prothalli (bearing sex organs) among homosporous ferns. The cordate-thalloid form is the most common. Variations in this form (i.e., symmetrical vs. asymmetrical, thick vs. thin, thallus wings ruffled vs. flat) may be useful characters to distinguish taxa at lower taxonomic ranks. The strap-like or spathulate (unbranched) and ribbon-like (branched) gametophyte forms of Nayar and Kaur (1971) were combined here into the elongate-thalloid form (state 3). The heterosporous ferns have highly reduced gametophytes with relatively few cells, as does *Cycas*. Bierhorst (1971), Bower (1923, 1926, 1928), Eames (1936), Kubitzki (1990), Nayar and Kaur (1971), Tryon and Tryon (1982).

69. GAMETOPHYTE HAIRS: (0) absent, (1) present. Nayar and Kaur (1971), Stokey (1960).

70. GAMETOPHYTES GREEN (PHOTOSYNTHETIC): (0) no, (1) yes. Bierhorst (1971), Eames (1936), Kubitzki (1990), Nayar and Kaur (1971), Tryon and Lugardon (1991), Tryon and Tryon (1982).

71. GAMETOPHYTIC FUNGAL ASSOCIATION: (0) no, (1) yes. Bierhorst (1971), Boullard (1957, 1979), Campbell (1908), Holloway (1930), Mahabale (1948), Nayar and Kaur (1971).

72. DEPENDENT GAMETOPHYTE: (0) no, (1) yes. Homosporous ferns have free-living gametophytes that are not enclosed by the spore wall (exosporic) and heterosporous ferns have endosporic gametophytes, i.e., they are entirely or mostly enclosed by the wall of the microspore or megaspore, respectively. The photosynthetic gametophytes of *Platyzoma* are exosporic and hence independent. Duckett and Pang (1985), Gifford and Foster (1988).

73. POSITION OF ANTHERIDIA ON GAMETOPHYTE: (0) embedded or slightly projecting, (1) partially to fully exposed. In heterosporous ferns, the microgametophytes are reduced to such an extent that the scoring of antheridial position is not obvious; hence the ambiguous coding for these taxa. Bierhorst (1971), Eames (1936), Gifford and Foster (1988), Nayar and Kaur (1971).

74. POSITION OF ARCHEGONIA ON GAMETOPHYTE: (0) embedded or slightly projecting, (1) partially to fully exposed. In Marsileaceae, the megagametophytes are reduced considerably and therefore the scoring of archegonial position is not obvious; hence the ambiguous coding for these taxa. In *Azolla* and especially *Salvinia* there is more cellular development of the female gametophyte, in which the archegonia are clearly embedded (Eames, 1936). Bierhorst (1971), Eames (1936), Gifford and Foster (1988), Nayar and Kaur (1971).

75. NUMBER OF ANTHERIDIAL WALL CELLS: (0) ≥ 5, (1) 3–(rarely) 5. Bierhorst (1971), Campbell (1892), Eames (1936), Gifford and Foster (1988), Nayar and Kaur (1971), Tryon and Tryon (1982).

76. NUMBER OF ARCHEGONIAL NECK CELL TIERS: (0) >6 cells high, (1) 1–5 (rarely 6) cells high. Bierhorst (1971), Bower (1926), Eames (1936), Nayar and Kaur (1971), Stokey and Atkinson (1956), M. D. Turner (pers. comm., *Metaxya*).

77. GAMETOPHYTES GEMMA-PRODUCING: (0) no, (1) yes, borne from gametophyte thallus, (2) yes, borne from gametophyte rhizoids. Gemmae are defined here as vegetative propagules that are produced by the gametophyte and should not be confused with "brood bodies" or vegetative propagules produced by the sporophyte. Bierhorst (1971), Farrar (1967, 1974), Farrar and Johnson-Groh (1990), Nayar and Kaur (1971).

Autapomorphic Morphological Characters

Initially, the following seven characters (nos. 78-84) were included in our study. They were excluded finally because they were parsimony-uninformative in this particular study in both Analysis 1 and 2. Given how we had scored these taxa for these particular characters (our scores are indicated under each character) and their transformation type (unordered), any possible dichot-

omous tree would require the same number of steps for each of these characters. Since they are irrelevant for choosing among trees using parsimony, they are considered uninformative. They are potentially useful characters with a different combination of taxa or with different assumptions about character transformation (i.e., ordered vs. unordered).

78. BLADE THICKNESS: (0) ≥ 3 cells thick, (1) 1 cell thick (excluding veins). Blades that are one cell thick lack mesophyll. Blades that are three or more cells thick have a mesophyll, and an upper and lower epidermis. Only *Cephalomanes* had leaves that were one cell thick. Although *Azolla* was polymorphic for this character, with the ventral lobe one cell thick, the character was parsimony-uninformative with the present set of taxa. UC; Ogura (1972).

79. ROOT ORIGIN: (0) allorhizic, (1) homorhizic. In allorhizic plants the root and shoot apices lie at opposite poles of the embryonic axis and the root system consists of a main root (taproot) and its lateral branches. In homorhizic plants, the first root is lateral with reference to the embryonic axis and ephemeral. All subsequent roots arise from the stem of the sporophyte. All pteridophytes have a homorhizic root origin. Seed plants are allorhizic; if more than one seed plant had been used in the analysis, this character would have been parsimony-informative. Gifford and Foster (1988, p. 519).

80. ROOT BRANCHING: (0) dichopodial, (1) monopodial. Dichopodial branching includes both isotomous and anisotomous types of dichotomous branching arising from the root apex. Monopodial branching is defined as a dominant root axis with lateral branches arising from the pericycle or endodermis. Root branching is said to be monopodial in the ferns (Ogura, 1972, especially p. 134), but dichotomous in Ophioglossaceae and some fern allies. Bower (1926, pp. 55–56) reported both bifurcating and monopodial roots in *Ophioglossum*, and monopodial branching in *Botrychium* and *Helminthostachys*. We report seeing both types of branching on specimens of *Botrychium*, which we would have scored as polymorphic ("0&1") for this character. *Lycopodium* most definitely has dichopodial branching (Ogura, 1972, p. 211, p. 134; herbarium specimens). *Cycas* has a taproot with diminutive lateral roots (Stevenson, 1990); however it also has dichotomizing "corolloid roots" (Gifford and Foster, 1988). In our data set, since only *Lycopodium* would have been scored as "0" and both *Botrychium* and *Cycas* as polymorphic ("0&1"), this character is parsimony-uninformative with this particular data set. UC; Bierhorst (1971, 1977b), Bower (1926), Gifford and Foster (1988), Johnson (1986), Kato (1983), Ogura (1972), Stevenson (1990).

81. SINGLE APICAL CELL IN SHOOT/ROOT APEX ORGANIZATION: (0) no, (1) yes. A salient feature of all ferns is that a single, conspicuous apical cell is present in the zone of surface initials and it can usually be identified at some point in the development of the apex. *Equisetum* and *Psilotum* also have a single apical cell, whereas both *Cycas* and *Lycopodium* do not. The particular combination of taxa used in Analyses 1 and 2 in this study rendered this particular character autapomorphic in both analyses. Bierhorst (1971, 1977a), Bower (1923), Gifford (1983, 1985), Gifford and Foster (1988), Imaichi (1977, 1986), Imaichi and Nishida (1986), Klekowski (1985), McAlpin and White (1974), Stevenson (1976, 1978), White (1979).

82. VASCULAR CAMBIUM DIRECTIONALITY: (0) unifacial, (1) bifacial. Only *Botrychium* in our data set has a unifacial vascular cambium and only *Cycas* has a bifacial cambium. Bierhorst (1971), Gifford and Foster (1988), Ogura (1972), Stevenson (1980).

83. SPORANGIAL FUSION: (0) none, (1) wholly or partly fused. In this data set, only the Psilotaceae had fused sporangia. Unlike those of other Marattiales, the sporangia in *Angiopteris* are not fused. Since we used only *Psilotum* in our analyses, this character was not parsimony-informative. Bierhorst (1971), Hill and Camus (1986), Tryon and Tryon (1982).

84. PERISPORE (EPISPORE): (0) absent, (1) present. This external spore wall in *Cycas* is the exine; it does not have a perispore layer (Dehgan and Dehgan, 1988). All pteridophytes have a perispore, thereby rendering this character an autapomorphy in this study. Tryon and Lugardon (1991).

Excluded Morphological and Chemical Characters

85. BIOCHEMICAL DATA: Biochemical information, mainly on flavonoids but also an a few other chemicals, was considered initially but later rejected due to a lack of comparability of data. Although some families have been examined frequently (e.g., Hymenophyllaceae, Aspleniaceae),

others have received little or no attention in this regard, thus rendering this aspect at present of little use for our study. The absence of chemical compounds in some families may be more apparent than real due to sampling methods. In addition, since most chemical compounds occur sporadically within many of the families examined, it is certainly never possible to make broad generalizations for these kinds of data. A few recent and important contributions in this area include Gottlieb et al. (1990), Richardson (1984), Soeder (1985), and Wallace et al. (1982).

86. NON-APPENDICULAR FRONDS: Kaplan (1977) argued that the fronds of *Stromatopteris* are not homologous with the shoots of Psilotaceae, a position contrary to that taken by Bierhorst (1968, 1969). By implication, Kaplan (1977, p. 48) also cast doubt on the non-appendicular origin of fronds of certain Gleicheniaceae and Hymenophyllaceae, as suggested by Bierhorst (1973, 1974). We agree with Kaplan and consider the morphogenetic and histogenetic evidence for non-appendicular origin of fern fronds as weak or at least inconclusive and reject this character from inclusion in our analysis.

87. HIPPOCAMPUS-SHAPED BUNDLES IN STIPES: For many of the species that have multiple bundles in the stipe, the two adaxial ones are larger and these have a hippocampus-shaped xylem strand (Ogura, 1972; Lin and DeVol, 1977, 1978). The smaller bundles in the same stipe have roundish or elliptic xylem strands. Although this may be of some phylogenetic or functional significance, it would require more accurate information than we have to score it in a way that might be meaningful.

88. WINGED STIPE AND/OR RACHIS: Of sporadic occurrence and thought to be of little taxonomic importance. Perhaps useful at a lower taxonomic rank.

89. STIPULES: Stipules are usually understood to be outgrowths or appendages associated with the leaf base. Stipules are diverse in appearance among those ferns that bear them and therefore we agree with Mickel (1974) that it is unlikely that they are all homologous structures. They are dilated and sheathing in *Botrychium* and fleshy, photosynthetic, and persistent in *Angiopteris*. Leaf bases are winged in *Osmunda* and expanded in *Plagiogyria*. A more detailed study of stipule-like outgrowths is required. Stipules are not to be confused with trophopods, the swollen leaf bases found in some genera (e.g., *Asplenium, Athyrium*). Trophopods are storage structures; stipules may or may not be starch-storage structures. *Diplopterygium* has stipule-like outgrowths at base of pinna forks, but not at the base of the leaf (Bower 1923, 1926; Eames, 1936; Kubitzki, 1990).

90. IDIOBLASTS: We agree with Wagner (1978) in questioning the homology of these structures in various ferns (e.g., *Trichomanes, Pteris, Marsilea*) and therefore did not score for them in this analysis.

91. RHIZOME BRANCHING: Some fern taxa have rhizomes that are commonly unbranched, whereas others regularly branch by dichotomizing (including isotomous and anisotomous patterns) or by producing lateral buds. In some ferns, both axillary and dichotomous branching undoubtedly occur in the same plant. There was insufficient information for us to score taxa for branched vs. unbranched character states; information on branching type was even more scarce. In addition, rhizome branching appears to be strongly correlated with rhizome symmetry (dorsiventral rhizomes are often branched, whereas radial rhizomes are unbranched, except under unusual circumstances). A preliminary attempt to score this character using herbarium specimens was unsatisfactory and indicated a possible bias (i.e., a collector's bias to collect unbranched specimens). Bower (1923, Chapter 4), Kaplan (1977).

92. PROTOXYLEM POSITION IN RHIZOMES: There are insufficient or unreliable data for most fern taxa on the position and maturation of protoxylem in relation to metaxylem (i.e., exarch, endarch, mesarch, centrarch). These xylem maturation patterns are potentially of considerable phylogenetic importance. Our preliminary attempt to apply what is known, however, resulted in extrapolating from one species to another and from one genus to another, which was clearly unacceptable, especially for some of the larger families (Dryopteridaceae, Pteridaceae, Dennstaedtiaceae).

93. TRACHEARY ELEMENTS: Several features of primary xylem are potentially of importance in characterizing fern families, but as yet there are insufficient comparative data available to be able to establish appropriate character states. In particular, details of tracheid size and pitting (scalariform vs. alternate or opposite) may be useful. Data presented by White (1963a) suggest that

eusporangiate and basal leptosporangiate ferns have longer tracheids in the roots than do more derived ferns. White (1963b) further suggested that the basal fern families generally had predominantly scalariform pitting in lateral walls, while more derived families had predominantly alternate or opposite pitting. Data given by White (1963a, 1963b) cannot be utilized for several reasons: 1) specific genera and species from which his divergence indices were calculated are not given; 2) circumscription of families is different in some cases than what we have used (e.g., Aspidiaceae, including our Thelypteridaceae, also Pteridaceae, which apparently includes Dennstaedtiaceae); 3) data are given only for families, not for individual species; and 4) there are no data for many of the families we have included (e.g., Matoniaceae, Dipteridaceae, and nine other families). Bierhorst (1960) provided additional data on tracheary elements in pteridophytes, but these observations are also insufficient for distinguishing informative characters and character states. There are few conclusions that he draws that can be tied with any certainty to specific families of ferns, let alone to specific genera or species. Also, some of the same problems encountered with using White's (1963a, 1963b) data are also limiting in Bierhorst's (1960) paper.

94. ROOT TYPE: A preliminary attempt was made to gather information on fleshy vs. fibrous roots in ferns. Fleshy roots are known in Ophioglossaceae, Marattiaceae, *Acrostichum*, and some *Thelypteris* (not the species in this data set), but the data were too sporadic to score this character with confidence for many of the taxa in our study set.

95. ROOT HAIR PATTERN: Root hairs scattered vs. matted was considered but excluded from this analysis due to lack of extensive comparative data for the taxa in our study set and also to the distinct likelihood that this character is correlated with ecology.

96. SPOROPHYTIC FUNGAL ASSOCIATIONS: Although Boullard (1957, 1979) made an outstanding contribution to our general knowledge of fungal associations with rhizomes or roots of sporophytes for several major fern groups, these were too vaguely known for many fern genera to be scored with confidence in this broad analysis. In addition, for many of Boullard's reports of fungal associations with fern sporophytes it is uncertain whether these are due to short-term, casual fungal infections or to obligatory symbiotic relationships. Rather than being of a constant nature, sporophytic fungal associations appear to be variable events. Gametophytic fungal associations, on the other hand, seem more predictable and constant.

97. PARAPHYSES: Paraphyses are generally defined as uni- or multicellular, sterile trichomes, which may or may not be secretory, and that are in some way associated with the sporangia. Paraphyses may be borne on soral receptacles or on sporangium stalks or capsules. Occasionally paraphyses originate from the leaf epidermis and are closely intermixed with sporangia (e.g., *Acrostichum*). The placental hairs associated with synangia in *Angiopteris* also have been called paraphyses (Hill and Camus, 1986). Several families of ferns have genera with both paraphysate and non-paraphysate sori, most notably, Thelypteridaceae, Polypodiaceae, and Grammitidaceae. Since even the positional criterion of homology could not be satisfied with regard to a definition for this character and because of the diverse nature of these structures, it is unlikely that all paraphyses are homologous. For these reasons we decided to exclude the character from our analysis. A.F. Tryon (1965), R.M. Tryon (1965), Wagner (1964).

98. SPORANGIAL DEHISCENCE ORIENTATION: The orientation in which sporangia dehisce (longitudinal, transverse) is occasionally reported (Bower, 1923, 1926, 1928; Kubitzki, 1990) however, it was too inconsistent to be useful here.

99. STOMIUM CELL DIFFERENTIATION: This feature is occasionally but inconsistently reported in the literature.

100. SPORE SHAPE: Spores were initially scored as either ellipsoidal, tetrahedral, or globose. A graded series of spore shapes between tetrahedral and globose made the task of scoring this character a difficult one. In addition, tetrahedral/globose and ellipsoidal shapes appeared directly correlated with the triradiate and linear laesurae, respectively. Consequently, the spore laesura character was selected over spore shape for the analysis because it was straightforward and easy to score.

101. LAESURA LENGTH: Many fossils keys (e.g., Moore et al., 1991) use the length of the laesura as an informative descriptive character. An attempt was made to score spores for having either short or long laesurae; however, this character was found to be too variable within taxa to be meaningful.

102. SPORE DIMENSIONS: Specific spore measurements were not readily available for many of the taxa included in this study. In addition, spore size is extremely variable depending on age of spore and ploidal level. Spore measurements in Tryon and Lugardon (1991) were given as a range with no mean or median scores, and they were usually descriptive for the genus, rather than the species.

103. ENDOSPORE: The presence of a pseudoendospore or a well-developed endospore appears to correlate with chlorophyllous spores, a character already scored in this analysis.

104. CHROMOSOME NUMBER: Although $2n$ chromosome numbers are known for most of the study taxa, we were unable to establish discrete character states that might logically represent the sequence of change in chromosome number in the evolution of ferns. Efforts to extrapolate primitive base numbers have proven illusory (Duncan and Smith, 1977). Chromosome numbers may be useful at lower taxonomic levels within the ferns.

105. GAMETOPHYTE CELL PLATE FORMATION: Atkinson and Stokey (1964) and Nayar and Kaur (1971) distinguish three and seven types of cell plate development patterns, respectively. These differ in the sequence of cell divisions, in the stage of development, in the region at which a meristem is established, and in the resultant form of the thallus. Although there certainly may be information of important phylogenetic value in these features, especially with regard to where and how meristematic regions are established, detailed studies that provided this documentation were unavailable for most of the study taxa.

106. GAMETOPHYTE DURATION: There is occasional mention in the literature as to whether the gametophytes of certain taxa are perennial or seasonal. This information was too rare to be of value to this study, and indications were that there might be considerable variation within a single taxon.

107. GAMETOPHYTE GROWTH CONDITION: The majority of pteridophytes have photosynthetic gametophytes that grow on the surfaces of soil, rocks, or rotten logs (Wagner et al., 1985). However, both genera of Psilotaceae, all of the Ophioglossaceae, many species of Lycopodiaceae, *Stromatopteris,* and *Actinostachys* have gametophytes that are non-photosynthetic and subterranean. This character appears strictly correlated with gametophyte form (all tuberous gametophytes are subterranean) and so it could not be scored as an independent character.

108. GAMETOPHYTE RHIZOIDS: Although rhizoids show much variation with regard to color, form, texture, and distribution, Stokey (1951) and Atkinson and Stokey (1964) questioned their phylogenetic significance. In addition, they stated that the rhizoids of most fern families had not been sufficiently studied and needed further investigation. Certain characteristics such as forking of the rhizoid are typical of the Hymenophyllaceae, though this might be an environmental response.

109. GAMETOPHYTE HAIR TYPES: In future studies, it would be useful to incorporate information about the various gametophyte hair types (unicellular, multicellular, unbranched, branched) that have been described (cf. Stokey, 1960). This detailed type of data is inconsistently reported in the literature and so was of limited value to this particular study.

110. ANTHERIDIAL DEHISCENCE: The antheridial wall consists of a varying pattern of curved cells, from one of which, either laterally placed or at the apex, an opercular (cap) cell is cut out (Atkinson and Stokey, 1964). In some fern groups, the antheridial cap cell is thrown off intact, whereas in others the cap cell collapses or tears apart, sometimes first forming a pore. The heterosporous ferns release their sperm via disintegration of antheridial tissues. In future analyses, it may be useful to distinguish between the position of the cap cell, if any, and the sperm release mechanisms, if this detailed information becomes available for more taxa. Bierhorst (1971), Eames (1936), Hartman (1931), Nayar and Kaur (1971).

111. SPERM OUTPUT: The number of sperm discharged by an antheridium seems to be correlated with the size of the antheridium (Bower, 1923; Eames, 1936). The 3-celled antheridia typical of most leptosporangiate ferns commonly release 16–32 sperm, whereas the 5–many-celled antherida usually release hundreds of sperm. For this analysis, the number of antheridial wall cells was chosen as a character rather than sperm output because that information was more readily accessible. Information on sperm output is only sporadic and approximate and not consistently measured or reported. Because antheridium size and sperm output are likely to be correlated and therefore not independent characters, we only scored antheridium size.

112. NUMBER OF SPERM FLAGELLAE PER MALE STRUCTURE: Information on number of sperm flagellae is known only for very few representative fern taxa and indicates there might not be much variation among ferns (Garbary et al., 1993).

113. ARCHEGONIAL NECK CURVATURE: Atkinson and Stokey (1964) and Nayar and Kaur (1971) discuss the tendency for certain fern groups to have archegonial necks that are straight, whereas others have curved necks, either towards the gametophyte apex or away from the apex. These data were too inconsistent to be recorded here with confidence, and may reflect tendencies toward inbreeding vs. outbreeding.

114. NECK CANAL CELL: The archegonial neck canal cell is binucleate in most fern groups; however, some fern groups frequently have 4-nucleate neck canal cells and *Lycopodium* may be 6+-nucleate. This information was too sporadically and inconsistently documented to be useful in this study. Bierhorst (1971), Nayar and Kaur (1971).

115. APOGAMOUS LIFE CYCLE: Approximately 10% of ferns have an apogamous life cycle (Sheffield and Bell, 1987), where a sporophyte develops from the somatic tissue of a gametophyte. The absence of fertilization results in the nuclei of gametophyte and sporophyte having the same chromosome number. Some ferns exhibit apogamy on a regular basis (obligate apogamy); apogamy can also sometimes be induced experimentally. There is insufficient or unreliable data for most fern species on the apogamous condition. Our preliminary attempt to apply what is known resulted in generalizing from one species to another and from one genus to another, which was clearly unacceptable, especially for some of the larger families (Dryopteridaceae, Pteridaceae, Dennstaedtiaceae).