Systematic Botany (2009), 34(3): pp. 455–475

Is Morphology Really at Odds with Molecules in Estimating Fern Phylogeny?

Harald Schneider,[1,2,5] Alan R. Smith,[3] and Kathleen M. Pryer[4]

[1]Department of Botany, Natural History Museum, London SW7 5BD U.K.

[2]Albrecht-von-Haller-Institut für Pflanzenwissenschaften, Abteilung Systematische Botanik, Georg-August-Universität, 37073 Göttingen, Germany

[3]University Herbarium, University of California, Berkeley, California 94720 U.S.A.

[4]Department of Biology, Duke University, Durham, North Carolina 27708 U.S.A.

[5]Author for correspondence (h.schneider@nhm.ac.uk)

Communicating Editor: Mark P. Simmons

Abstract—Using a morphological dataset of 136 vegetative and reproductive characters, we infer the tracheophyte phylogeny with an emphasis on early divergences of ferns (monilophytes). The dataset comprises morphological, anatomical, biochemical, and some DNA structural characters for a taxon sample of 35 species, including representatives of all major lineages of vascular plants, especially ferns. Phylogenetic relationships among vascular plants are reconstructed using maximum parsimony and Bayesian inference. Both approaches yield similar relationships and provide evidence for three major lineages of extant vascular plants: lycophytes, ferns, and seed plants. Lycophytes are sister to the euphyllophyte clade, which comprises the fern and seed plant lineages. The fern lineage consists of five clades: horsetails, whisk ferns, ophioglossoids, marattioids, and leptosporangiate ferns. This lineage is supported by characters of the spore wall and has a parsimony bootstrap value of 76%, although the Bayesian posterior probability is only 0.53. Each of the five fern clades is well supported, but the relationships among them lack statistical support. Our independent phylogenetic analyses of morphological evidence recover the same deep phylogenetic relationships among tracheophytes as found in previous studies utilizing DNA sequence data, but differ in some ways within seed plants and within ferns. We discuss the extensive independent evolution of the five extant fern clades and the evidence for the placement of whisk ferns and horsetails in our morphological analyses.

Keywords—Equisetaceae, horsetails, leptosporangiate ferns, lycophytes, monilophytes, Ophioglossaceae, Psilotaceae, seed plants.

Our general understanding of phylogenetic relationships across vascular plants has increased enormously in recent years, due in large part to numerous molecular systematic studies focused on the green branch of the tree of life (Mishler et al. 1994; Bowe et al. 2000; Nickrent et al. 2000; Pryer et al. 2001, 2004; Burleigh and Mathews 2004; Dombrovska and Qiu 2004; Wikström and Pryer 2005; Qiu et al. 2006, 2007). A parallel development has been the increasingly unpopular use of morphological data to reconstruct phylogenetic relationships (Hillis and Wiens 2000; Wiens 2004). Largely forgotten are arguments for the precedence of morphology in studies on ancient rapid radiations (Bateman 1998, 1999). Instead, DNA sequence data are seen as better suited to reconstruct the evolutionary history of deep radiations because of their universality, stochastic behavior, and abundance (Bromham 2003; Whitfield and Lockhart 2007). Some have argued that the increasing ambiguity of homology assessments in compilations of ever-larger morphological data matrices renders morphology a poor indicator of phylogeny (Scotland et al. 2003). Others are willing to accept a limited role for morphology in phylogenetic reconstruction, one where more rigorous and critical studies of fewer, but unambiguous, morphological characters are integrated with molecular data (Scotland et al. 2003; Olmstead and Scotland 2005). The ongoing discussion tends to ignore the needs of researchers working primarily with extinct taxa or those who strive to integrate fossil and extant taxa into a single phylogeny. For these kinds of studies, there is either no choice, or little choice, other than to continue to add to and attempt to improve upon morphological data matrices (Jenner 2004; Lee 2004; Wiens 2004; Smith and Turner 2005; Magallón 2007; Schneider 2007; Hermsen and Hendricks 2008).

Our objective in this paper is to explore empirically to what degree incongruence and conflict between morphological and molecular data pose a problem in estimating a phylogeny for extant ferns and their relatives. For the molecular component of this study we use our published phylogeny for which we have sequenced more than 5,000 base pairs of nucleotide data from four genes (three plastid and one nuclear) for 21 taxa of ferns, plus six species of seed plants, three species of lycophytes, and five species of "bryophytes" as outgroup taxa (Pryer et al. 2001). This phylogeny is viewed as among the most robust for green plants (Palmer et al. 2004). For the same set of taxa, we critically reevaluate the available morphological data. Most of these characters were considered in previous cladistic analyses (Garbary et al. 1993; Mishler et al. 1994; Pryer et al. 1995; Schneider 1996; Stevenson and Loconte 1996; Kenrick and Crane 1997; Garbary and Renzaglia 1998; Rothwell 1999).

The hypothesis of a congruent phylogenetic signal in molecular and morphological data is fostered by the fact that lycophytes have been found to be sister to all other vascular plants using molecules alone, as well as using morphological data alone (Kenrick and Crane 1997; Nickrent et al. 2000; Renzaglia et al. 2000; Pryer et al. 2001; Qiu et al. 2006, 2007). Similarly, a clade comprising horsetails and ferns was first proposed on the basis of morphological data (Kenrick and Crane 1997), and this relationship was recovered subsequently with molecular data (Nickrent et al. 2000; Pryer et al. 2001; Dombrovska and Qiu 2004; Wikström and Pryer 2005; Qiu et al. 2006, 2007; Rothwell and Nixon 2006; Schuettpelz et al. 2006). Conflicting results have been reported in some, but not all, studies utilizing mitochondrial DNA markers. Peculiarities of mitochondrial genome evolution, such as the frequent horizontal transfer of mitochondria among lineages, are most likely the cause for these conflicts (Bergthorsson et al. 2003, 2004; Dombrovska and Qiu 2004; Knoop 2004; Davis et al. 2005; Wikström and Pryer 2005). Since Kenrick and Crane (1997), only two studies have found evidence for an alternative interpretation of relationships, one that does not support ferns as including horsetails (Rothwell 1999; Rothwell and Nixon 2006). These two studies utilized a morphological dataset for living and fossil plants. Therefore, one could argue that the more commonly found relationship of "ferns

plus horsetails" is an artifact caused by excluding extinct taxa, although the original concept of "monilophytes", ferns plus horsetails, was based strictly on fossil evidence (Stein et al. 1984; Stein 1993; Kenrick and Crane 1997; Berry and Stein 2000; Cordi and Stein 2005).

Using maximum parsimony (Fitch 1971) and Bayesian MCMC inference (Yang and Rannala 1997) approaches, we independently reconstruct the phylogeny of ferns and horsetails from a morphological dataset, the same dataset used by Pryer et al. (2001). This data matrix was also employed in a study inferring the evolution of the vascular plant body plan (Schneider et al. 2002), as well as in a paper on the limits of approaches integrating fossil evidence in a phylogenetic framework that is based mainly on extant taxa (Schneider 2007). Our dataset comprises morphological characters, as well as various anatomical, biochemical, cytological, and DNA structural characters (e.g. absence/presence of introns and inversions). The classification used throughout this study is based on Smith et al. (2006) for ferns and Kenrick and Crane (1997) for other land plants. Our results are compared to those from independent analyses of molecular data (Pryer et al. 2001; Wikström and Pryer 2005; Schuettpelz et al. 2006; Qiu et al. 2006, 2007). We were particularly interested in ascertaining whether morphological data may be misleading in the phylogenetic placement of whisk ferns (Psilotales) and horsetails (Equisetopsida).

Materials and Methods

Taxon and Character Selection——We sampled 30 representatives from all major lineages of vascular plants (ingroup), including most early-diverging fern genera, as well as five outgroup taxa from all three "bryophyte" lineages (Appendix 1). We restricted this dataset to extant taxa to be able to take full advantage of all information provided by living organisms and to avoid potentially compromising our results by including extinct taxa, which can be scored for fewer than 20% of the characters used in our analysis (see Schneider 2007, for a more comprehensive study on the influence of fossil taxa on the results). Of the 258 morphological characters examined, we selected 136 that were parsimony informative for this study (Appendix 2). The remaining 122 characters were excluded (electronic supplement: Appendix 3) because information was either highly incomplete or unavailable, thereby preventing us from confidently defining unambiguous character states. The majority of characters were adopted or modified from previous phylogenetic studies of land plants (Parenti 1980; Garbary et al. 1993; Mishler et al. 1994; Kenrick and Crane 1997; Garbary and Renzaglia 1998), ferns (Hill and Camus 1986; Pryer et al. 1995; Schneider 1996; Stevenson and Loconte 1996; Pryer 1999; Rothwell 1999) and seed plants (Crane 1985, 1988; Doyle and Donoghue 1986, 1987, 1992; Loconte and Stevenson 1990; Doyle et al. 1994; Nixon et al. 1994; Rothwell and Serbet 1994; Doyle 1996; Nandi et al. 1998). Newly adopted characters were critically studied using primary literature and, whenever possible, also checked against herbarium specimens (F, UC). The dataset of 136 parsimony informative characters is deposited in TreeBASE (study number S2277).

Phylogenetic Analyses——We used equal-weighted maximum parsimony (MP), as implemented in PAUP* 4.0 b10 (Swofford 2002), and Bayesian inference (BI), as implemented in MrBayes 3.1 (Ronquist and Huelsenbeck 2003). Maximum parsimony analyses were performed as heuristic searches with 1,000 random-addition-sequence (RAS) replicates and tree bisection and reconnection (TBR) branch swapping until completion. All characters were included and designated as unordered. Polymorphic characters were treated as such. Equally most parsimonious trees were summarized using a strict consensus approach. The five taxa representing the three extant lineages of the paraphyletic bryophytes were assigned either as a multiple outgroup or each of the three lineages assigned independently as outgroup taxa, but all analyses recovered the same set of most parsimonious trees insofar as the relationships among tracheophytes. For MP, we estimated branch support using 1,000 bootstrap (BS; Felsenstein 1985) replicates with 100 RAS and TBR. Decay index (DI) values were estimated as outlined by Bremer (1988). The number of unambiguous and ambiguous character state changes, as well as apomorphic character state changes, were identified for critical clades using MacClade 4.0 (Maddison and Maddison 2000). By excluding critical clades from MP analyses and visually comparing the strict consensus trees obtained with and without the taxa under consideration, we were able to explore the influence of taxon sampling. We report the statistics of the most parsimonious trees by using established measurements: ensemble consistency index (CI), ensemble retention index (RI), and ensemble rescaled consistency index (RC) (Kluge and Farris 1969; Farris 1989).

Bayesian methodology is applicable to morphological evidence due to the development of appropriate models for character evolution (Lewis 2001). Bayesian inference (BI) was performed using the standard discrete model with gamma shape (1-MkΓ; Yang 1993; Lewis 2001) implemented in MrBayes 3.1. Three independent Bayesian MCMC analyses were conducted using this model and four chains. Each chain was run for 5 million generations, and trees were sampled every 500 generations. Following completion, the sampled trees from each analysis were examined by estimating the standard deviation of all model-parameters in MrBayes and by determining convergence of parameters using Tracer v. 12.1 (Rambaut and Drummond 2005). All trees prior to convergence (< 1,500 generations in each analysis) were discarded as the "burn-in" phase. Each of the three analyses showed the same convergence diagnostics. A majority-rule consensus tree was calculated from a tree set in which all trees were pooled from the three independent analyses after discarding all trees from the "burn-in" phase.

The results of our analyses of the morphological dataset were compared for congruence to those recovered with DNA sequence data, as well as tested for competing hypotheses using the Kishino-Hasegawa (KH) test (Kishino and Hasegawa 1989) as implemented in PAUP*. A value of $p < 0.05$ was considered to be a significant difference between alternative hypotheses fitted to a given dataset. We designed reduced datasets to explicitly test for incongruence between the morphological dataset and various published phylogenetic hypotheses proposed for the fern clade (e.g. Pryer et al. 2001; Qiu et al. 2006, 2007). In particular, we tested for the following relationships among the major lineages of ferns (cf. Table 2): i) horsetails sister to whisk ferns (EQ:PS); ii) horsetails sister to leptosporangiate ferns (EQ:PO); iii) horsetails sister to the Ophioglossales plus Psilotales clade (EQ(OP:PS)); iv) horsetails sister to marattioids (EQ:MA); and v) horsetails sister to marattioids, this clade sister to a monophyletic Psilotopsida (Ophioglossales plus Psilotales), and leptosporangiate ferns (Polypodiopsida) sister to all (((EQ:MA)(PS:OP))PO).

To localize conflicting signals within our morphological dataset, we performed Neighbor-Net (NNet) analyses (Bryant and Moulton 2004) and reconstructed consensus networks (Holland and Moulton 2003; Holland et al. 2004) to generate split graphs in which alternative relationships are visible. These analyses were performed using SplitsTree 4.0 beta (Huson 1998). Split graph approaches have been applied recently to explore controversial phylogenetic results based on molecular data, especially when long-branch attraction is suspected (Huson and Bryant 2005; Kennedy et al. 2005; Martin et al. 2005). Distance matrices were calculated in PAUP* using either "mean character difference" or "total character difference" and used to perform Neighbor-Net analysis with the following settings: edge fitting as ordinary least squares; splits transformation as convex hull; modify weights as least squares; and filtering splits via maximum dimension set to either two or four. Alternative settings were explored to determine the influence of these settings on the recovered split graphs. Consensus networks were reconstructed with a threshold value of x = 0.1 and using all trees recovered in the plateau phase of the BI or in the bootstrap analyses using MP.

Results

Seven equally most parsimonious trees were found with a tree length of 348 steps (trees not shown; CI = 0.5401, RI = 0.8218, RC = 0.4558). Bayesian inference found the same topology as maximum parsimony (Fig. 1), except for some relationships within leptosporangiate ferns (Fig. 2, morphological-only topolgy). Tracheophytes are found to be monophyletic with BS = 100% and DI = 11 from MP, and a Bayesian posterior probability (PP) = 1.00; this clade is supported by a broad range of character states such as the presence of vascular tissue and the occurrence of more than one apical meristem per sporophyte (Appendix 2: characters 23, 36, 52, 111, 112,

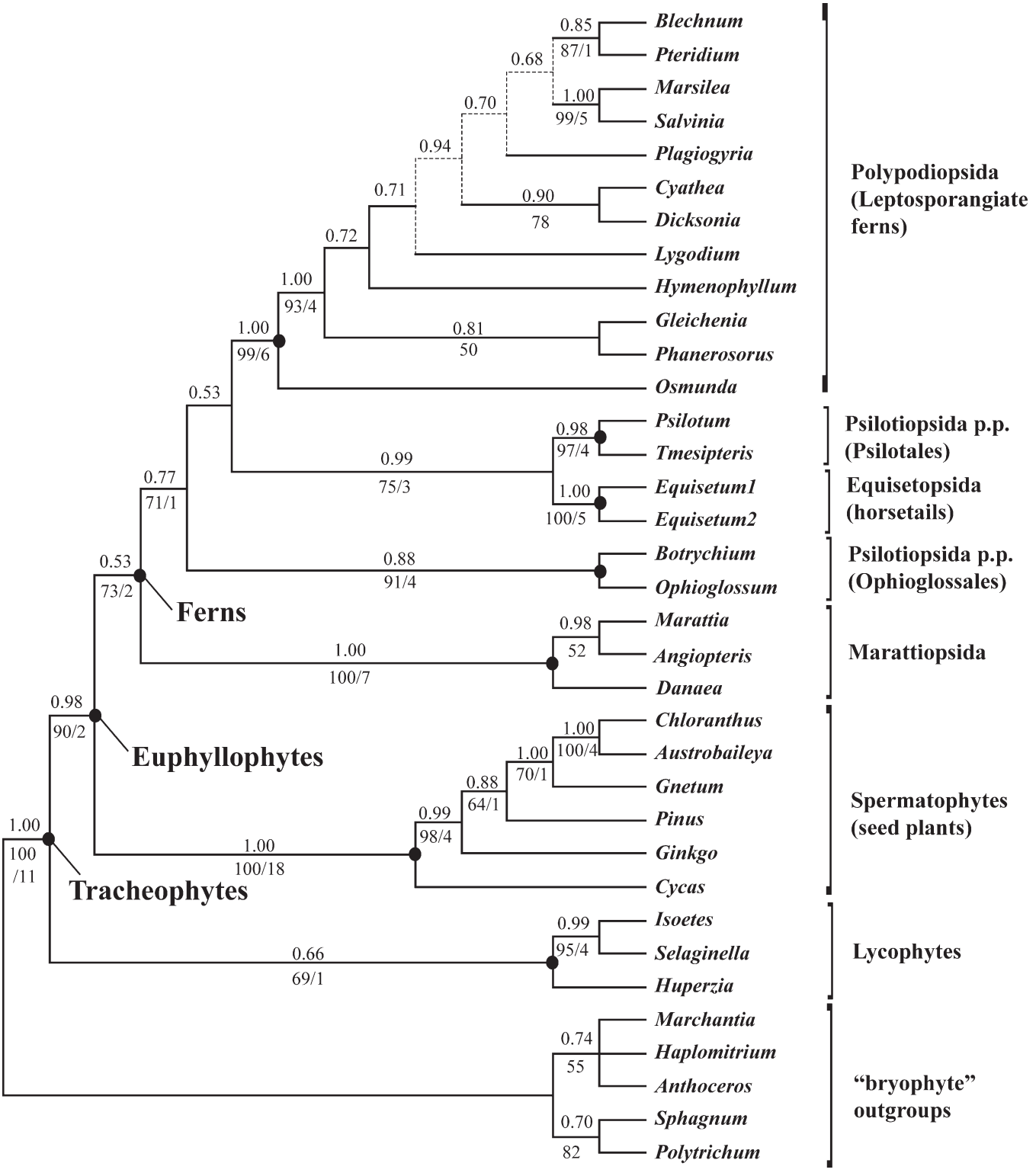

FIG. 1. Relationships among vascular plants (tracheophytes) based on morphological evidence (cf. Appendix 2). The topology shown is the majority-rule consensus tree obtained from Bayesian inference (BI) analysis. A nearly identical topology was recovered from a maximum parsimony (MP) analysis of the same dataset. Dashed lines indicate where there were topological differences between the BI majority-rule consensus tree and the strict consensus of the eight equally most parsimonious trees recovered from MP. Numbers above branches correspond to Bayesian posterior probabilities (PP), whereas numbers below branches correspond to the MP bootstrap support value/decay index (BS/DI). Large dots at nodes indicate higher taxonomic units discussed in text. The classification follows Smith et al. (2006) for ferns and Kenrick and Crane (1997) for other plants.

and 121). The lycophytes (BS = 69%, DI = 1, PP = 0.66) are strongly supported as sister to the remaining vascular plants, the euphyllophytes. The euphyllophyte clade (BS = 89%, DI = 2, PP = 0.98) is characterized by the following putative apomorphic character states: a 30-kb inversion in the chloroplast genome, monoplastidic sperm cells, and the position of the basal body in sperm cells (characters 83, 115, 116, 118, and 136). Euphyllophytes include two sister clades, the ferns

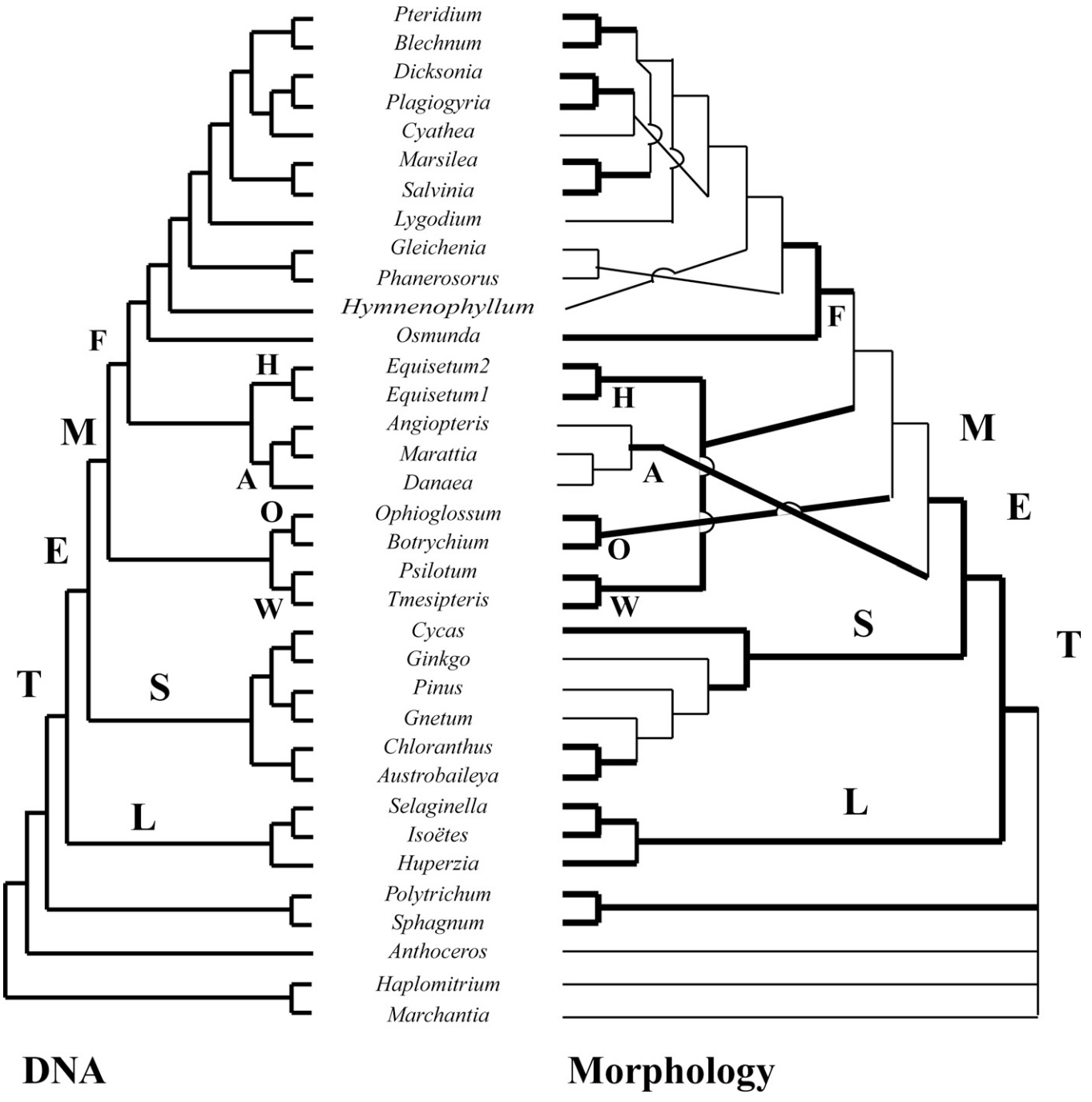

FIG. 2. Comparison of relationships among vascular plants. A) Morphology-only topology (this study) vs. B) molecular-only topology as recovered in various DNA based studies such as Fig. 1 in Pryer et al. 2001, Fig. 3 in Pryer et al. 2004; Figs. 3, 4 in Wikström and Pryer 2005). The topology shown as morphology-only corresponds to the topology of the strict consensus tree estimated in the maximum parsimony analyses of the morphological dataset. Taxon names are deleted but corresponding taxa are connected between both cladograms using thin lines. Thickened branches within the cladograms indicate good bootstrap support in MP (> 75%) and posterior probability in BI (PP ≥ 0.95). Abbreviations: E = Euphyllophytes, EQ = Equisetopsida, F = Ferns, L = Lycophytes, MA = Marattiopsida, OPH = Ophioglossales, PO = Polypodiopsida, PSI = Psilotales, S = Spermatophytes, T = Tracheophytes.

(monilophytes) and the seed plants (spermatophytes). The fern clade (BS = 72%, DI = 2, PP = 0.53) is supported by several apomorphic character states, including lateral roots borne from endodermal cells, a plasmodial tapetum, the presence of a pseudoendospore, and an exclusively centrifugal sporoderm development (characters 40, 92, 94, and 95). The seed plant lineage (BS = 100%, DI = 18, PP = 1.00) has an impressive number of apomorphies (Table 1); several of these correlate with the derived reproductive biology of seed plants.

The topology of the seed plant lineage is identical to results found in previous cladistic morphological studies (Crane 1985; Nixon et al. 1994; Doyle 1996). *Cycas* is sister to all other seed plants (seed plants without *Cycas*: BS = 98%, DI = 4, PP = 0.99), and *Ginkgo* is the subsequent sister to the remaining seed plants (Fig. 1). These two taxa differ from all other living seed plants in having free-swimming sperm cells and by depositing nutrients into the ovule prior to fertilization. Conifers are sister to a clade including *Gnetum* and the angiosperms.

TABLE 1. Morphological character state changes for selected clades. Numbers of unambiguous (before slash) and ambiguous (after slash) character state changes were reconstructed by plotting characters onto topologies obtained in the cladistic analysis of morphology (morphological topology, Figs. 1 and 2A) and analyses using either DNA sequence data alone or in combination with morphological evidence (molecular topology, Fig. 2B). For the latter, a topology was chosen in which Marattiopsida and Equisetopsida are sister clades and the gymnosperms are monophyletic (as found in Pryer et al. 2004). In both topologies (morphology and molecular), mosses are sister to tracheophyes. [1]Clade with Psilotales and Ophioglossales sister (topology obtained in analyses using DNA only or combined evidence); [2]clade with Psilotales sister to Equisetopsida (topology found in analyses using morphology only); [3]apomorphic character state changes found only with the molecular topology are in italics, all others are in both the morphological and molecular topologies.

Clade	Morphological topology (Figs. 1 and 2A)	Molecular topology (Fig. 2B)	Unambiguous apomorphic character state changes for selected clades
Tracheophytes	12 / 8	10 / 9	
Lycophytes	3 / 7	3 / 9	
Euphyllophytes	6 / 6	7 / 5	
Seed Plants	17 / 14	18 / 17	
Ferns (monilophytes)	4 / 8	5 / 12	59: 0 → 1 / 92: 0 →1 / 94: 0 → 1 / 95: 0 → 1 / *121: 0 → 1*[3]
Marattiopsida	10 / 11	15 / 14	
Psilotales	5 / 3	7 / 3	
Ophioglossales	4 / 7	3 / 5	
Equisetopsida	6 / 4	10 / 11	
Polypodiopsida	9 / 7	10 / 9	
Psilotopsida[1]	NA	1 / 10	*102: 0 → 1*
Psilotales + Equisetopsida[2]	5 / 7	NA	5: 1 → 0 / 8: 2 → 0 / 9: 1 → 0 / 19: 0 → 1 / 25: 0 → 2

Similarities in the leaves (reticulate venation, stomatal development) and reproductive biology (embryo development) support *Gnetum* as sister to angiosperms (BS = 70%, DI = 1, PP = 1.00). Although several characters (presence of short shoots, pit structure of tracheids, and similar parenchymatous cells in the phloem) potentially could have supported an alternative topology with *Gnetum* as part of a clade comprising *Pinus* and *Ginkgo*, this topology is not found with either MP or BI.

Three out of four extant classes of ferns are well supported: Marattiopsida (BS = 100%, DI = 7, PP = 1.00), Equisetopsida (BS = 100%, DI = 5, PP = 1.00), and Polypodiopsida (BS = 99%, DI = 6, PP = 1.00). The Psilotopsida was not recovered as monophyletic. Although the orders Ophioglossales and Psilotales are each strongly supported lineages (Psilotales with BS = 97%, DI = 4, PP = 0.98 and Ophioglossales with BS = 89%, DI = 4, PP = 0.88) they are not sister to one another. Although the Psilotaceae and Equisetaceae differ radically in their gametophyte morphology, they appear here as sister taxa (BS = 75%, DI = 3, PP = 0.99), united by similarities in their sporophytes, especially the simplified leaves and similarities of the shoot system organization (see Table 1). Other deep relationships among the extant lineages of ferns, however, lack statistical support (BS < 75%, PP < 0.95).

Leptosporangiate ferns are supported by several synapomorphies, such as the reduction in sporangium size, spore output per sporangium, number of sperm cells, and structure of the archegonial neck (characters 72, 75, 112, and 122). The earliest diverging order of leptosporangiates, Osmundales (Fig. 1), represented here by *Osmunda*, is somewhat intermediate between the eusporangiate and leptosporangiate condition in having about 1,000 spores per sporangium. All other leptosporangiate ferns produce fewer than 500 spores per sporangium. *Osmunda* is well supported as sister to all other extant leptosporangiate ferns (BS = 91%, DI = 4, PP = 1.00), but weak support was found for relationships among the remaining fern groups. Our results indicate that there are six other distinct lineages, of which two are represented by a single genus. In relative branching order, these clades are: (1) Gleicheniales represented by *Gleichenia* and *Phanerosorus*; (2) Hymenophyllales represented by *Hymenophyllum*; (3) Schizaeales represented by *Lygodium*; (4) Cyatheales represented by *Cyathea*, *Dicksonia*, and *Plagiogyria*; (5) Salviniales represented by *Marsilea* and *Salvinia*; and (6) Polypodiales represented by *Blechnum* and *Pteridium* (Fig. 1). The results of the MP and BI analyses differed with respect to the monophyly of two orders of leptosporangiate ferns: Cyatheales were monophyletic in MP but not in BI, whereas Gleicheniales were monophyletic in BI but not in MP.

DISCUSSION

Comparing Phylogenetic Hypotheses: Morphology vs. Molecules——Our analysis based on morphology resulted in a phylogenetic hypothesis (Fig. 1) that is quite similar to those derived from a combined dataset [as on p. 5] that included four genes, *atpB*, *rbcL*, *rps4*, nrSSU (cf. Fig. 2; Pryer et al. 2001), the same four genes plus one mitochondrial gene (Wikström and Pryer 2005), and the same Pryer et al. (2001) genes plus plastid *atpA* (Schuettpelz et al. 2006). All major lineages previously recovered with molecular data were also recovered using morphological data alone (Fig. 2), including tracheophytes (T), lycophytes (L), euphyllophytes (E), spermatophytes (S), ferns (F), marattioids (MA), horsetails (EQ), and leptosporangiate ferns (PO), except for the Psilotopsida (Ophioglossales + Psilotales). The last group was not resolved as monophyletic based on morphological characters (Figs. 1 and 2A), but rather it collapsed into two distantly related lineages, Ophioglossales (OPH) and Psilotales (PSI).

Our morphology data alone strongly support the phylogenetic classification proposed by Kenrick and Crane (1997), in which the fern clade (called Infradivision Moniliformopses by them) was proposed on the basis of a unique stelar pattern (Stein et al. 1984; Stein 1993; Kenrick and Crane 1997). However, the more common topology found in independent analyses of molecular plus morphological data differs substantially with respect to (1) relationships among seed plants, (2) relationships among lineages of leptosporangiate ferns, and (3) relationships among the four to five major lineages of ferns. Similar differences have also been observed between phylogenetic reconstructions based on single genes and combined genes (Pryer et al. 2001, 2004; Wikström and Pryer 2005; Schuettpelz et al. 2006; Qiu et al. 2006, 2007), as well as in other molecule- and morphology-based phylogenetic analyses within ferns (Pryer et al. 1995; Pryer 1999). Our KH tests

for incongruence between datasets and conflicting hypotheses indicated that the overall hypotheses based on molecular data do not fit very well with those derived from our morphological dataset ($p < 0.05$). The same KH test for a single incongruence, the relationships among the five lineages of ferns recovered in the morphological vs. the molecular analyses, did not find significant differences ($p > 0.05$). Comparison of differences among the hypotheses, using Fitch optimization, showed that the morphological hypothesis is more parsimonious with regard to characters describing leaf morphology (up to seven characters), whereas hypotheses generated using DNA sequence data, as published in previous studies (see Table 2), are more parsimonious with respect to several other characters, e.g. mycorrhizae of gametophytes and the presence of a foot in early embryo development. Overall, the inferred five hypotheses differ only slightly from each other with respect to the interpretation of character evolution, as indicated by their similar tree statistics (Table 2).

Two recent morphological studies are similar to ours in their selection of representatives of the same major lineages of land plants for the ingroup, but the authors reached different conclusions. Stevenson and Loconte (1996) included only living taxa, whereas Rothwell (1999) included both extant and extinct taxa. Both of these studies resulted in different overall topologies, and both placed the whisk ferns (Psilotales) between lycophytes and all other euphyllophytes. This phylogenetic position of whisk ferns is most congruent with a general assumption of a progressive evolution from simple to more complex growth forms in a series of evolutionary steps from the apparent low morphological complexity of bryophytes, to the increasingly more complex lycophytes, whisk ferns, horsetails, ferns, different lineages of gymnosperms, and finally to the most derived clade, the angiosperms. The position of whisk ferns as part of a grade leading to derived vascular plants reflects the simplicity of their leaves and absence of roots. However, this hypothesis is inconsistent with ultrastructural characters observed in the spore wall (Tryon and Lugardon 1991; Lugardon and Piquemal 1993), haustorial placentas (Duckett and Ligrone 2003; Hilger et al. 2005), and sperm cells (Renzaglia et al. 2000, 2001), which suggest instead a close relationship of whisk ferns to other ferns. Another major difference between the results of our morphological study and others is in the phylogenetic position of the horsetails. Stevenson and Loconte (1996) placed horsetails close to whisk ferns as part of the grade leading to seed plants. Rothwell (1999) proposed an alternative hypothesis in which horsetails are sister to seed plants, which resulted from his interpretation that the equisetostele shares some similarities with the eustele, the latter being one of the major apomorphic character states of the seed plant lineage. Rothwell (1999) also stressed that the problem of comparing the elaborate stelar structure of extant and extinct horsetails in making homology assessments was difficult to address. According to other authors (e.g. Schmid 1982), the equisetostele differs from the eustele in the position of the protoxylem (centrarch in eustele, mesarch in equisetostele). The mesarch position of the protoxylem poles in mature steles was proposed as an apomorphic character state for the ferns plus horsetail clade (Stein et al. 1984; Stein 1993; Kenrick and Crane 1997; Berry and Stein 2000; Cordi and Stein 2005). In addition, Stevenson and Loconte (1996) interpreted the leaf-like structures of horsetails and whisk ferns (only *Tmesipteris*) as microphylls and contrasted this character state to macrophylls in ferns and seed plants.

Differences between our results and those of other phylogenetic morphological studies (e.g. Mishler et al. 1994; Stevenson and Loconte 1996; Garbary and Renzaglia 1998; Rothwell 1999) are more likely caused by differences in character selection and homology assessments rather than by differences due to taxon sampling. Of the studies discussed here (Mishler et al. 1994; Stevenson and Loconte 1996; Garbary and Renzaglia 1998; Rothwell 1999; our study), only Rothwell's (1999) included fossil taxa, and the incompleteness of these fossils resulted in a large number of unknown character states, thereby reducing phylogenetic resolution (see Schneider, 2007 and Wiens 1998, for discussion on the impact of incomplete data). Reduced resolution in phylogenetic reconstructions often diminishes the potential advantage of fossils to show character combinations that will benefit the discovery of the true phylogeny (see Schneider 2007).

Similar to other studies exploring the relationships among all major lineages of land plants (e.g. Garbary et al. 1993), we employed many ultrastructural characters, including the pattern of cell divisions, the structure of sperm cells, and spore wall ultrastructure. These characters appear to be highly conserved, and transformations of their character states have rarely occurred in the evolution of land plants. Interpretation of these characters derives from relatively few studies (Carothers and Duckett 1979; Brown and Lemmon 1990, 1991a, 1991b, 1997, 2001a, b; Renzaglia and Maden 2000; Renzaglia et al. 2000, 2001; Duckett and Ligrone 2003; Hilger et al. 2005). By comparison, Rothwell (1999) and Stevenson and Loconte (1996) focused more on gross morphology and as a result assessed several characters of controversial homology. In particular, two homology assessments in our dataset require a more detailed explanation to enable the reader to compare our results with the hypotheses obtained in those two studies.

Table 2. Comparison of tree statistics obtained for alternative relationships among ferns (monilophytes). Five hypotheses were superimposed on the morphological dataset. We used a reduced dataset including only two representatives for each of the five included lineages to avoid the influence of other nodes that conflict among the different hypotheses. EQ = Equisetopsida including *Equisetum 1* and *Equisetum 2*, MA = Marattiopsida including *Angiopteris* and *Danaea*, OP = Ophioglossales including *Botrychium* and *Ophioglossum*, PO = Polypodiopsida including *Osmunda* and *Phanerosorus*, and PS = Psilotales including *Psilotum* and *Tmesipteris*. Measurements: CI = ensemble consistency index, RC = ensemble rescaled consistency index, RI = ensemble retention index, TL = tree length.

Hypothesis	TL	CI	RI	RC	Name and source
MA(OP((EQ:PS)PO)	114	0.80	0.78	0.63	morphological hypothesis reported here
(OP:PS)(MA(EQ:PO)	116	0.78	0.76	0.60	molecular hypothesis 1 *Pryer et al. 2001*
((OP:PS)EQ)(MA:PO)	117	0.78	0.75	0.59	molecular hypothesis 2 *Qiu et al. 2006*
(OP:PS)((MA:EQ)PO)	120	0.76	0.73	0.55	molecular hypothesis 3 *Pryer et al.2001*
PO((OP:PS)(MA:EQ))	120	0.76	0.73	0.55	molecular hypothesis 4 *Qiu et al. 2007*

The first issue is the interpretation of the homology among different stelar types. We accept the interpretations put forth in studies that have taken morphological evidence from both fossil and extant species into account (Schmid 1982; Stein et al. 1984; Stein 1993; Kenrick and Crane 1997). We appreciate that different homology assessments for the organization of vascular tissues in plants are still to be considered as viable alternatives; however, we propose that the interpretation we have employed here is most congruent with existing anatomical, developmental, and phylogenetic evidence.

The second controversial issue involves the interpretation of leaves. We accept the distinctness of leaves in lycophytes (lycophylls) from superficially similar structures of horsetails and whisk ferns (euphylls), which differ substantially in their developmental biology (Kaplan 2001; Schneider et al. 2002; Harrison et al. 2005; Floyd and Bowman 2006, 2007; Beerling and Fleming 2007; Bowman et al. 2007; Gola et al. 2007; Harrison et al. 2007). It is now widely accepted that the term microphylls has been applied to an assemblage of nonhomologous structures (e.g. Kaplan 2001; Floyd and Bowman 2006; Beerling and Fleming 2007). Lycophylls have a shared developmental origin of the venation and meristem organization, as well as having simple, usually unforked veins and a usually unstructured scale-like shape. Crane and Kenrick (1997) discussed a putative scenario for the independent origin of "microphylls" in lycophytes from sterilized sporangia.

Most recent authors have suggested multiple and independent origins of so-called megaphylls (Beerling 2005; Boyce 2005; Beerling and Fleming 2007). Here, we adopt an alternative concept, the euphyll, which differs from Zimmermann's (1952) telome theory in that it does not invoke assumptions about the evolution of dorsiventrally organized leaves that are differentiated into lamina and petiole. We agree with most authors (Beerling 2005; Boyce 2005; Beerling and Fleming 2007) who have concluded that structures that differentiate into a petiole and lamina likely evolved independently in various groups of euphyllophytes. However, we propose that leaves across euphyllophytes are homologous based on shared developmental and structural characters, including apical/marginal growth, apical origin of the venation, the usual presence of leaf gaps in the stele, and determinate growth. This interpretation is similar to one suggested by Donoghue (in Judd et al. 2002), which he called pseudodichotomous branching, and is comparable to the proto-leaf concept suggested by Beerling and Fleming (2007). Our interpretation is consistent with a phylogenetic scenario in which euphylls evolved in the common trimerophyte ancestor of euphyllophytes by transforming lateral shoots (Floyd and Bowman 2006, 2007). Understandably, this may be seen as reductionist, because it considers only some criteria usually used to define leaves and invokes only the first step in the evolutionary sequence proposed in the telome theory of Zimmermann (1952).

Can Morphological Datasets be Positively Misleading?—Misleading results in studies using DNA sequence data are well known and can be attributed to several factors, including insufficient taxon sampling, long-branch attraction, saturation, and lineage-specific substitution rate changes (Felsenstein 1978; Hendy and Penny 1989; Magallón and Sanderson 2002; Burleigh and Mathews 2004; Martin et al. 2005). Less attention has been given to possibly misleading results in phylogenetic analyses utilizing morphological evidence. Phylogenetic hypotheses based on single genes are, in reality, "gene-trees" that may or may not be identical to the true phylogeny of a group of organisms (Doyle 1992). A parallel argument can be applied to many phylogenetic studies using morphological evidence, because many datasets are biased toward particular organs. This is especially true in studies based exclusively or partly on fossil data, which rely in general on characters that are preserved in the incomplete fossil record. Such studies are more appropriately considered "organ phylogenies" (Bateman et al. 1998).

With regard to our dataset, the possibility of long-branch attraction needs to be considered. Assembling morphological apomorphic characters for each of the five lineages of ferns, as well as for other land plants, results in each extant lineage having a unique combination of characters that allows for easy identification. The low number of characters that are putatively shared across all taxa, which are further fractioned into homoplastic and plesiomorphic character states, adds to our concern for a possible misleading bias that associates Psilotales with Equisetopsida (Fig. 1). Our Neighbor-Net analyses to explore alternative signals within the morphological dataset found evidence for a different relationship, one that places Psilotales more closely to Ophioglossales (Fig. 3). In addition, we performed separate parsimony analyses that sequentially excluded each one of the five lineages of ferns. Only the exclusion of horsetails (Equisetopsida) altered the PSI + EQ topology, and in that case the Psilotales were sister to the Ophioglossales. The five lineages of ferns show strikingly different growth forms and share only a few anatomical and ultrastructural characters (Table 1). The placement of Psilotales as sister to Equisetopsida in our parsimony and Bayesian analyses may be the result of shared homoplastic character states and thus could be interpreted as a consequence of long-branch attraction. Molecular data suggest a sister relationship between Ophioglossales and Psilotales, a hypothesis that is consistent with some morphological characters, including heterotrophic gametophytes with multicellular rhizoids, the reduction of the root systems, and a peculiar placement of the sporangia on an elongate axis of uncertain homology (Pryer et al. 2001; Schneider et al. 2002). This last character was not included in the data matrix and needs further exploration.

A general issue in morphological studies is the problem of polarization of character states. In our study, about 40% of the characters scored were not applicable for the outgroup taxa (bryophytes) and thus were scored as missing data. Most of these nonapplicable characters describe gross morphological features; ultrastructural data, on the other hand, provide a much higher percentage of the characters that are applicable to the outgroups. A high percentage of nonapplicable characters are also found among the sexual reproductive characters, because all extant members of the seed plants have a highly modified reproductive system in comparison to other land plants. Several informative characters, such as the ultrastructure of sperm cells, were applicable to only two seed plant lineages, *Cycas* and *Ginkgo*, which show several plesiomorphic character states in their reproductive biology. The correct polarization of seed character states using extant land plants is likely impossible and will need to rely on the integration of fossil taxa (Schneider 2007). Unfortunately, correct polarization is hampered in two ways by the incompleteness of the fossil record. First, many critical taxa are not preserved or still await discovery by specialists. Second, preserved organisms are incomplete and critical structures are often not attached to each other (Kemp 1999; O'Leary 2001). In many cases, a

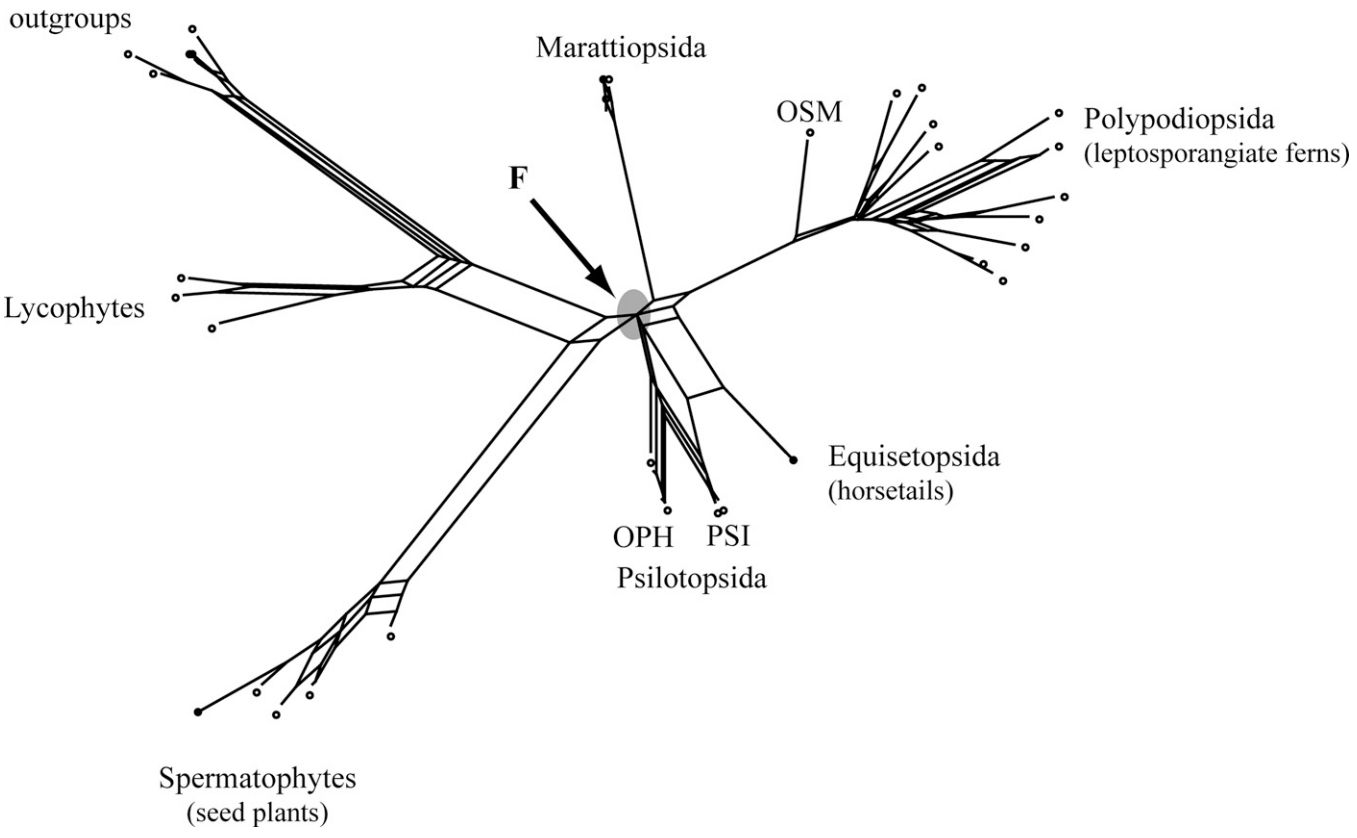

FIG. 3. Neighbor-Net graph generated using SplitsTree4. The analysis was performed using Convex Hull as the chosen splits transformation, least squares as modify weights, and two maximum dimensions as the filter for selected splits. Abbreviations: F = Ferns, OPH = Ophioglossales, OSM = Osmundales, PSI = Psilotales. The arrow indicates the fern node (F) that is marked with a gray circle.

detailed study of the evolution of particular structures (not organisms) may be the best and only approach that will lead to the integration of fossil evidence into phylogenetic hypotheses dealing with whole organisms. Studies by Stein and coworkers on the evolution of vascular tissue in Devonian land plants are outstanding examples of this approach (Stein 1993; Berry and Stein 2000; Cordi and Stein 2005). The alternative, relying on whole plant reconstruction, may offer much less information because of the ambiguities in these reconstructions and the scarcity of taxa with an adequate fossil record.

Why are Morphological Studies Needed?—It is common for morphological data to be considered less important than DNA sequence data in phylogenetic studies (Endress 2002). Arguments against the use of morphological data include the high amount of homoplasy and the notorious problems associated with making homology assessments (Bowe et al. 2000), but objections to these arguments are raised in several contributions to this important discussion (Sanderson and Donoghue 1996; de Queiroz 2000; Donoghue and Ree 2000; Hillis and Wiens 2000). Morphological characters differ substantially from DNA sequence characters in their complexity and their frequency of evolutionary change. Many morphological characters show a much lower mutational rate than nucleotides and thus may be less-prone to problems such as saturation. Most especially, the conservation of developmental pathways and functional aspects can contribute to the persistence of certain character states in major lineages of organisms (Raff 1996; Arthur 1997; Donoghue and Ree 2000; Endress 2002). Therefore, some morphological characters are likely to be ideal phylogenetic characters because they allow us to identify single (and hence rare) evolutionary events (Bateman 1998, 1999; Endress 2002). For example, characters associated with critical steps in plant life cycles are more likely to be conserved in major lineages. Several studies demonstrate that certain anatomical and morphological characters, e.g. sperm cell ultrastructure and spore wall ultrastructure, are informative for phylogenetic studies focused at deep nodes (Kenrick and Crane 1997; Graham et al. 2000; Renzaglia et al. 2000; Schneider et al. 2002). Other morphological characters, such as the density of leaf indument, have been modified frequently during land plant evolution in response to various environmental factors, and they may be more informative in studies focused on species-level relationships. As we demonstrate with this study, morphological studies based on a careful evaluation of all potentially informative characters can generate well-supported phylogenetic results.

Four additional arguments can be put forth to support the use of morphological data in phylogenetic reconstruction. First, many theoretical and empirical studies have shown that all accessible information should be used to obtain the most robust phylogenetic hypotheses (Kluge 1989; Mishler et al. 1994; de Queiroz et al. 1995; Pryer et al. 1995, 2001; Bateman 1998; de Queiroz 2000; Hillis and Wiens 2000; Magallón 2007; Schneider 2007; Hermsen and Hendricks 2008). Second, morphological data are the only set of characters that are observable in both fossil and living taxa (Donoghue et al. 1989; Smith 1998; Springer et al. 2001; Teeling et al. 2005; Hermsen and Hendricks 2008), although many informative morphological structures (e.g. the ultrastructure of meristems and the spindle apparatus controlling cell divisions) are rarely or never

preserved in the fossil record. Similarly, fossilized DNA is certainly exceptional in phylogenetic studies (Smith 1998; Wills and Fortey 2000). The inclusion of fossils in phylogenetic studies enables an increased taxon sampling that is especially critical in studies that address assembling the tree of life. This is particularly notable given that Jablonski (2004) estimated that more than 99% of species that ever lived are now extinct. Third, recent attempts to integrate developmental genetics and evolutionary biology in a new approach, called "evolutionary developmental genetics" (Hall 1992; Raff 1996; Arthur 1997), relies on explicit statements about character state changes in the evolution of the inferred group (Bang et al. 2000; Endress 2002; Schneider et al. 2002; Cracraft 2005). The explicit definition of discrete character states and the careful scoring of all taxa in a particular study are critical components in the reconstruction of character evolution, whether morphological data, molecular data, or both, are used in phylogenetic reconstruction. This procedure is preferred over the simple mapping of characters loosely obtained from the literature without a strict consideration of character states. Plotting morphological character states onto a phylogeny without detailed studies is adequate if explicit statements about the character states and data for all critical taxa can be obtained from the literature. However, character state definitions that are suitable for phylogenetic studies are rarely found in traditional botanical literature. In addition, without undergoing the process of collecting data for an extensive morphological matrix, important characters can be easily overlooked. Several critical but cryptic character state changes (e.g. exclusively centrifugal spore wall development) have been ignored in the past, and we have shown in this study that they can be important apomorphies of clades and thus are critical for the circumscription of taxonomic units. They may also point to major changes in developmental pathways that were involved in the formation of a particular character state. Transformation statements generated using a phylogenetic framework will provide critical information about morphological innovations and the corresponding changes in developmental programs in the evolution of land plants (e.g. Graham et al. 2000; Renzaglia et al. 2000; Schneider et al. 2002; Bowman et al. 2007; Floyd and Bowman 2007).

The last argument for the continued use of morphology when reconstructing phylogeny recalls Hennig's concept of reciprocal illumination (Hennig 1950; Daly et al. 2001). Each cycle of recompiling and reanalyzing matrices will provide us with new insights as the result of critical reflection on previous studies using morphology or other kinds of evidence, as well as the consideration of newly obtained evidence. This iterative process ultimately results in improved concepts of homology, which in turn result in the discovery of apomorphic characters that are not only critical to phylogenetics but also to a natural classification of organisms.

Acknowledgments. The authors are grateful to many colleagues who contributed ideas to this paper, especially William Burger, Ray Cranfill, Andrew Douglas, Jim Doyle, John Engel, Rick Lupia, Susanna Magallón, and Rolf Rutishauser. This work was supported by NSF grants DEB-9615533 and DEB-0347840 to KMP, DEB-0089909 to KMP and HS, and DEB-9616260 to ARS.

Literature Cited

Arthur, W. 1997. *The origin of animal body plans: a study in evolutionary developmental biology*. Cambridge, U. K.: Cambridge University Press.

Atkinson, L. R. 1973. The gametophyte and family relationships. Pp. 73–90 in *The phylogeny and classification of the ferns*, eds. A. C. Jermy, J. A. Crabbe, and B. A. Thomas. *Botanical Journal of the Linnean Society* 67 (*Supplement* 1): 1–284.

Atkinson, L. R. and A. G. Stokey 1964. Comparative morphology of the gametophyte of homosporous ferns. *Phytomorphology* 14: 51–70.

Baayen, P. R. and E. Hennipman 1987. The paraphyses of the Polypodiaceae (Filicales). *Beiträge zur Biologie der Pflanzen* 62: 251–347.

Bang, R., R. DeSalle, and W. Wheeler. 2000. Transformalism, taxism, and developmental biology in systematics. *Systematic Biology* 49: 19–27.

Baranova, M. 1992. Principles of comparative stomatographic studies of flowering plants. *Botanical Review* 58: 49–99.

Barlow, P. W. 1994a. Cell divisions in meristems and their contribution to organogenesis and plant form. Pp. 169–194 in *Shape and form in plants and fungi*. eds. D. S. Ingram and A. Hudson. London: Academic Press.

Barlow, P. W. 1994b. From cell to system: repetitive units of growth in the development of roots and shoot. Pp. 19–58 in *Growth patterns in vascular plants*, ed. M. Iqbal. Portland: Dioscorides Press.

Bateman, R. M. 1998. Integrating molecular and morphological evidence for evolutionary radiations. Pp. 432–471 in *Molecular systematics and plant evolution*, eds. P. M. Hollingsworth, R. M. Bateman, and R. J. Gornall. London: Taylor and Francis.

Bateman, R. M. 1999. Architectural radiations cannot be optimally interpreted without morphological and molecular phylogenies. Pp. 221–250 in *The evolution of plant architecture*, eds. M. H. Kurmann and A. R. Hemsley. Kew: Royal Botanic Gardens.

Bateman, R. M., P. R. Crane, W. A. DiMichele, P. Kenrick, N. P. Rowe, T. Speck, and W. E. Stein 1998. Early evolution of land plants: phylogeny, physiology, and ecology of the primary terrestrial radiation. *Annual Review of Ecology Evolution and Systematics* 29: 263–292.

Beck C. B., R. Schmid, and G. W. Rothwell 1982. Stelar morphology and the primary vascular system of seed plants. *Botanical Review* 48: 691–815.

Beerling ,D. J. 2005. Leaf evolution: gases, genes, and geochemistry. *Annals of Botany (Oxford)* 96: 345–352.

Beerling, D. J. and A. J. Fleming. 2007. Zimmerman's telome theory of megaphyll leaf evolution: a molecular and cellular critique. *Current Opinion in Plant Biology* 10: 4–12.

Behnke, H.-D. and E. D. Sjolund. 1990. *Sieve elements: comparative structure, induction, and development*. Berlin: Springer-Verlag.

Bell, P. R. 1979. The contribution of the ferns to an understanding of the life cycles of vascular plants. Pp. 57–85 in *The experimental biology of ferns*, ed. A. F. Dyer. London: Academic Press.

Bergthorsson, U., K. L. Adams, B. Thomason, and J. D. Palmer. 2003. Widespread horizontal transfer of mitochondrial genes in flowering plants. *Nature* 424: 197–201.

Bergthorsson, U., A. O. Richardson, G. J. Young, L. R. Goertzen, and J. D. Palmer. 2004. Massive horizontal transfer of mitochondrial genes from diverse land plant donors to the basal angiosperm *Amborella*. *Proceedings of the National Academy of Sciences USA* 101: 17747–17752.

Berry, C. M. and W. E. Stein 2000. A new iridopteridalean from the Devonian of Venezuela. *International Journal of Plant Sciences* 161: 807–827.

Bhambie, S. 1994. Secondary growth in pteridophytes. Pp. 185–210 in *Growth patterns in vascular plants*, ed. M. Iqbal. Portland: Dioscorides Press.

Bierhorst, D. W. 1968. On the Stromatopteridaceae (fam. nov.) and on the Psilotaceae. *Phytomorphology* 18: 232–268.

Bierhorst, D. W. 1969. On *Stromatopteris* and its ill-defined organs. *American Journal of Botany* 56: 160–174.

Bierhorst, D. W. 1971. *Morphology of vascular plants*. New York: Macmillan Press.

Bierhorst, D. W. 1977. The systematic position of *Psilotum* and *Tmesipteris*. *Brittonia* 29: 3–13.

Blackmore, S. 1990. Sporoderm homologies and morphogenesis in land plants, with discussion of *Echinops sphaerocephala* (Compositae). *Plant Systematics and Evolution* 5(Supplement): 1–12.

Boros, A. and M. Járai-Komlódi. 1975. *An atlas of recent European moss spores*. Budapest: Akadémiai Kiadéo.

Boullard, B. 1957. La mycotrophie chez les ptéridophytes. Sa fréquence, ses caractères, sa signification. *Botaniste* 41: 1–185.

Boullard, B. 1979. Considérations sur la symbiose fongique chez les ptéridophytes. *Syllogeus* No. 19. Ottawa: National Museum of Natural Sciences.

Bowe, L. M., G. Coat, and C. W. DePamphilis 2000. Phylogeny of seed plants based on all three genomic compartments: extant gymnosperms are monophyletic and Gnetales' closest relatives are conifers. *Proceedings of the National Academy of Sciences USA* 97: 4092–4097.

Bower, F. O. 1923. *The ferns (Filicales) vol. 1*. Cambridge: Cambridge University Press.

Bower, F. O. 1926. *The ferns (Filicales) vol. 2*. Cambridge: Cambridge University Press.
Bower, F. O. 1928. *The ferns (Filicales) vol. 3*. Cambridge: Cambridge University Press.
Bowman, J. L., S. K. Floyd, and K. Sakaibara. 2007. Green genes – comparative genomics of the green branch of life. *Cell* 129: 229–234.
Boyce, C. K. 2005. Patterns of segregation and convergence in the evolution of fern and seed plant leaf morphologies. *Paleobiology* 31: 117–140.
Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42: 795–803.
Bromham, L. 2003. Molecular clocks and explosive radiations. *Journal of Molecular Evolution* 57: 513–520.
Brown, R. C. and B. E. Lemmon 1990. Sporogenesis in bryophytes. Pp. 55–94 in *Microspore evolution and ontogeny*, eds. S. Blackmore and R. B. Knox. London: Academic Press.
Brown, R. C. and B. E. Lemmon. 1991a. Plastid polarity and meiotic spindle development in microsporogenesis of *Selaginella*. *Protoplasma* 161: 168–180.
Brown, R. C. and B. E. Lemmon. 1991b. Sporogenesis in simple land plants. Pp. 9–24 in *Pollen and spores, patterns of diversification*, eds. S. Blackmore and S. H. Barnes. *Systematic Association Special Volume 44.* Oxford: Clarendon Press.
Brown, R. C. and B. E. Lemmon 1997. The quadripolar microtuble system in lower land plants. *Journal of Plant Research* 110: 93–106.
Brown, R. C. and B. E. Lemmon 2001a. Sporogenesis in eusporangiate ferns: I. Monoplastidic meiosis in *Angiopteris* (Marattiales). *Journal of Plant Research* 114: 223–235.
Brown, R. C. and B. E. Lemmon 2001b. Sporogenesis in eusporangiate ferns: II. Polyplastidic meiosis in *Ophioglossum* (Ophioglossaceae). *Journal of Plant Research* 114: 237–246.
Bryant, D. and V. Moulton 2004. NeighborNet: an agglomerative algorithm for the construction of planar phylogenetic networks. *Molecular Biology and Evolution* 21: 255–265.
Burleigh, J. G. and S. Mathews 2004. Phylogenetic signal in nucleotide data from seed plants: implications for resolving the seed plant tree of life. *American Journal of Botany* 91: 1599–1613.
Campbell, D. H. 1895. *The structure and development of the mosses and ferns*. London: Macmillan and Co.
Carothers, Z. B. and J. G. Duckett. 1979. Spermatogenesis in the systematics and phylogeny of the Hepaticae and Anthocerotae. Pp. 425–445 in *Bryophyte systematics*, eds. G. C. S. Clarke and J. G. Duckett. *Systematic Association Special Volume 14*. London: Academic Press.
Churchill, H., R. Tryon, and D. S. Barrington. 1998. Development of the sorus in the tree ferns: Dicksoniaceae. *Canadian Journal of Botany* 76: 1245–1252.
Cook, M. E. and W. E. Friedman. 1998. Tracheid structure in a primitive extant plant provides an evolutionary link to earliest fossil tracheids. *International Journal of Plant Sciences* 159: 881–890.
Cooper-Driver, G. 1977. Chemical evidence for separating the Psilotaceae from the Filicales. *Science* 198: 1260–1262.
Cooper-Driver, G. and M. Bhattacharya. 1998. Role of phenolics in plant evolution. *Phytochemistry* 49: 1165–1174.
Cordi, J. and W. E. Stein. 2005. The anatomy of *Rotoxylon dawsonii* comb. nov. (*Cladoxylon dawsonii*) from the Upper Devonian of New York State. *International Journal of Plant Sciences* 166: 1029–1045.
Cracraft, J. 2005. Phylogeny and evo-devo: characters, homology, and the historical analysis of the evolution of development. *Zoology (Jena, Germany)* 108: 345–356.
Crane, P. R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. *Annals of the Missouri Botanical Garden* 72: 716–793.
Crane, P. R. 1988. Major clades and relationships in the "higher" gymnosperms. Pp. 218–272 in *Origin and evolution of gymnosperms*, ed. C. B. Beck. New York: Columbia University Press.
Crane, P. R. and P. Kenrick. 1997. Diverted development of reproductive organs: a source of morphological innovation in land plants. *Plant Systematics and Evolution* 206: 161–174.
Daly, D. C., K. M. Cameron, and D. W. Stevenson. 2001. Plant systematics in the age of genomics. *Plant Physiology* 127: 1328–1333.
Darnell-Smith, G. P. 1917. The gametophyte of *Psilotum*. *Transactions of the Royal Society of Edinburgh* 52: 79–91.
Davis, C. C., W. R. Anderson, and K. J. Wurdack. 2005. Gene transfer from a parasitic flowering plant to a fern. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 272: 2237–2242.
Davis, K. L. 1991. A brief comparative survey of aerophore structure within the Filicopsida. *Botanical Journal of the Linnean Society* 107: 115–137.
De, B., D. Samanta, and U. Sen. 1991. Stomatal structure as an indicator of affinity among vascular plants. Pp. 43–51 in *Perspectives in pteridology: present and future*, eds. T. N. Bhardwaja and C. B. Gena. *Aspects of Plant Science* 11: 1–342.
Dehgan, B. and N. B. Dehgan. 1988. Comparative pollen morphology and taxonomic affinities in Cycadales. *American Journal of Botany* 75: 1501–1516.
de Queiroz, A., M. J. Donoghue, and J. Kim. 1995. Separate versus combined analysis of phylogenetic evidence. *Annual Review of Ecology Evolution and Systematics* 26: 657–681.
de Queiroz, K. 2000. Logical problems associated with including and excluding characters during tree reconstruction and their implications for the study of morphological character evolution. Pp. 192–212 in *Phylogenetic analysis of morphological data*, ed. J. J. Wiens. Washington: Smithsonian Institution Press.
DiMichele, W. A., J. I. Davis, and R. G. Olmstead 1989. Origins of heterospory and the seed habit: The role of heterochrony. *Taxon* 38: 1–11.
Dombrovska, O. and Y.-L. Qiu. 2004. Distribution of introns in the mitochondrial gene *nad1* in land plants: phylogenetic and molecular evolutionary implications. *Molecular Phylogenetics and Evolution* 32: 246–263.
Donoghue, M. J. and R. H. Ree. 2000. Homoplasy and developmental constraint: a model and an example from plants. *American Zoologist* 4: 759–769.
Donoghue, M. J., J. A. Doyle, J. Gauthier, A. G. Kluge, and T. Rowe. 1989. The importance of fossils in phylogeny reconstruction. *Annual Review of Ecology Evolution and Systematics* 20: 431–460.
Doyle, J. A. 1996. Seed plant phylogeny and the relationships of Gnetales. *International Journal of Plant Sciences* 157(Supplement 6): S3–S39.
Doyle, J. A. and M. J. Donoghue. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *Botanical Review (Lancaster)* 52: 321–431.
Doyle, J. A. and M. J. Donoghue. 1987. The origin of angiosperms: a cladistic approach. Pp. 17–50 in *The origins of angiosperms and their biological consequences*, eds. E. M. Friis, W. G. Chaloner, and P. R. Crane. Cambridge: Cambridge University Press.
Doyle, J. A. and M. J. Donoghue. 1992. Fossils and seed plant phylogeny reanalyzed. *Brittonia* 44: 89–106.
Doyle, J. A., M. J. Donoghue, and E. A. Zimmer. 1994. Integration of morphological and ribosomal RNA data on the origin of angiosperms. *Annals of the Missouri Botanical Garden* 81: 419–450.
Doyle, J. J. 1992. Gene trees and species trees: molecular systematics as one-character taxonomy. *Systematic Botany* 17: 144–163.
Duckett, J. G. 1973. Comparative morphology of the gametophytes of the genus *Equisetum* subgenus *Equisetum*. *Botanical Journal of the Linnean Society* 66: 1–22.
Duckett, J. G. 1979. Comparative morphology of the gametophytes of *Equisetum* subgenus *Hippochaete* and the sexual behavior of *E. ramosissimum* subsp. *debile* (Roxb.) Hauke, *E. hyemale* var. *affine* (Engelm.) A. Br., and *E. laevigatum* A. Br. *Botanical Journal of the Linnean Society* 79: 179–203.
Duckett, J. G. and P. R. Bell. 1977. An ultrastructural study of the mature spermatozoid of Equisetum. *Philosophical Transactions of the Royal Society of London, series B* 277: 131–158.
Duckett, J. G. and Z. B. Carothers. 1979. Spermatogenesis in the systematics and phylogeny of the Musci. Pp. 385–423 in *Bryophyte systematics*, eds. G. C. S. Clarke and J. G. Duckett. *Systematics Association Special Volume 14.* London: Academic Press.
Duckett, J. G. and R. Ligrone. 2003. The structure and development of haustorial placentas in leptosporangiate ferns provide a clear-cut distinction between euphyllophytes and lycophytes. *Annals of Botany (Oxford)* 92: 513–521.
Duckett, J. G. and W. C. Pang. 1984. The origins of heterospory: A comparative study of sexual behaviour in the fern *Platyzoma microphyllum* R. Br. and the horsetail *Equisetum giganteum* L. *Botanical Journal of the Linnean Society* 88: 11–34.
Duckett, J. G., R. Ligrone, and K. S. Renzaglia. 1996. Plastid-dividing rings in pteridophytes. Pp. 471–487 in *Pteridology in perspective*, eds. J. M. Camus, M. Gibby, and R. J. Johns. Kew: Royal Botanic Gardens.
Eames, A. J. 1936. *Morphology of vascular plants, lower groups*. London: McGraw-Hill.
Endress, P. K. 2002. Morphology and angiosperm systematics in the molecular era. *Botanical Review (Lancaster)* 68: 545–570.
Esau, K. 1977. *Anatomy of seed plants*, 2nd ed. New York: John Wiley and Sons.
Fahn, A. 1990. *Plant anatomy*, 4th ed. Oxford: Pergamon Press.
Farris, J. S. 1989. The retention index and the rescaled consistency index. *Cladistics* 5: 417–419.
Felsenstein, J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. *Systematic Zoology* 27: 401–410.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

Fitch, W. M. 1971. Toward defining the course of evolution: minimum change for a specific tree topology. *Systematic Zoology* 20: 406–416.

Floyd, S. K. and J. L. Bowman. 2006. Distinct developmental mechanisms reflect the independent origins of leaves in vascular plants. *Current Biology* 16: 1911–1917.

Floyd, S. K. and J. L. Bowman. 2007. The ancestral developmental tool kit of land plants. *International Journal of Plant Sciences* 168: 1–35.

Freeberg, J. A. and R. H. Wetmore. 1967. The Lycopsida - a study in development. *Phytomorphology* 17: 78–91.

Fryns-Claessens, E. and W. van Cotthem. 1973. A new classification of the ontogenetic types of stomata. *Botanical Review* 37: 71–138.

Garbary, D. J. and K. S. Renzaglia. 1998. Bryophyte phylogeny and the evolution of land plants: evidence from development and ultrastructure. Pp. 45–63 in *Bryology for the twenty-first century*, eds. J. W. Bates, N. W. Ashton, and J. G. Duckett. Leeds: Maney and the British Bryological Society.

Garbary, D. J., K. S. Renzaglia, and J. G. Duckett. 1993. The phylogeny of land plants: a cladistic analysis based on male gametogenesis. *Plant Systematics and Evolution* 188: 237–269.

Gifford, E. M. 1983. Concept of apical cells in bryophytes and pteridophytes. *Annual Review of Plant Physiology* 34: 419–440.

Gifford, E. M. 1985. The apical cell of fern roots and shoots: an appraisal of its functional role in development. *Proceedings of the Royal Society of Edinburgh, section B* 86: 237–243.

Gifford, E. M. 1991. The root apical meristem of *Asplenium bulbiferum*, structure and development. *American Journal of Botany* 78: 370–376.

Gifford, E. M. 1993. The root apical meristem of *Equisetum diffusum*: structure and development. *American Journal of Botany* 80: 468–473.

Gifford, E. M. and G. E. Corson. 1977. The shoot apex in seed plants. *Botanical Review* 37: 143–229.

Gifford, E. M. and A. S. Foster. 1988. *Morphology and evolution of vascular plants*. 3rd ed. New York: Freeman Press.

von Goebel, K. 1930. *Organographie der pflanzen. 3. Aufl. Zweiter Teil. Bryophyten und Pteridophyten*. Jena: Gustav Fischer Verlag.

Gola, E. M., J. A. Jernstedt, and B. Zagórska-Marek. 2007. Vascular architecture in shoots of early divergent vascular plants, *Lycopodium clavatum* and *Lycopodium annotinum*. *The New Phytologist* 174: 774–786.

Gottlieb, O., M. A. C. Kaplan, D. H. T. Zocher, and K. Kubitzki. 1990. A chemosystematic overview of pteridophytes and gymnosperms. Pp. 2–10 in *The families and genera of vascular plants. Vol. I. Pteridophytes and gymnosperms*, ed. K. Kubitzki. Vol. eds., K. U. Kramer and P. S. Green. Berlin: Springer-Verlag.

Graham, L. E., M. E. Cook, and J. S. Busse. 2000. The origin of plants: body plan changes contributing to a major evolutionary radiation. *Proceedings of the National Academy of Sciences USA* 97: 4535–4540.

Groff, P. A. and D. R. Kaplan. 1988. The relation of root systems to shoot systems in vascular plants. *Botanical Review* 54: 387–423.

von Guttenberg, H. 1947. *Die physiologischen Scheiden.* Handbuch der Pflanzenanatomie. Band VII, Teil 2, Histologie. Berlin: Gebrüder Bornträger.

von Guttenberg, H. 1960. *Grundzüge der Histogenese höherer Pflanzen. I. Die Angiospermen.* Handbuch der Pflanzenanatomie. Band VIII, Teil 3, Spezieller Teil. Berlin: Gebrüder Bornträger.

von Guttenberg, H. 1961. *Grundzüge der Histogenese höherer Pflanzen. II. Gymnospermen.* Handbuch der Pflanzenanatomie. Band VIII, Teil 4, Spezieller Teil. Berlin: Gebrüder Bornträger.

von Guttenberg, H. 1966. *Histogenese der pteridophyten*. Handbuch der Pflanzenanatomie. Band VII, Teil 2. Spezieller Teil. Berlin: Gebrüder Bornträger.

von Guttenberg, H. 1968a. *Der primäre Bau der Angiospermen Wurzel.* Handbuch der Pflanzenanatomie. Band VIII, Teil 5, Spezieller Teil. Berlin: Gebrüder Bornträger.

von Guttenberg, H. 1968b. *Der primäre Bau der Gymnospermen Wurzel.* Handbuch der Pflanzenanatomie. Band VIII, Teil 6, Spezieller Teil. Berlin: Gebrüder Bornträger.

Hagemann, W. 1984. Morphological aspects of leaf development in ferns and angiosperms. Pp. 301–349 in *Contemporary problems in plant anatomy*, eds. R. A. White and W. C. Dickinson. Orlando: Academic Press.

Hagemann, W. 1989. Aerogenous branching in pteridophytes. Pp. 245–258 in *Proceedings of the international symposium on systematic pteridology*, eds. K. H. Shing and K. U. Kramer. Beijing: China Science and Technology Press.

Hall, B. K. 1992. *Evolutionary developmental biology*. New York: Academic Press.

Halperin, W. 1978. Organogenesis at the shoot apex. *Annual Review of Plant Physiology* 29: 239–262.

Harrison, C. J., S. B. Corley, E. C. Moylan, D. L. Alexander, R. W. Scotland, and J. A. Langdale. 2005. Independent recruitment of a conserved developmental mechanism during leaf formation. *Nature* 434: 509–514.

Harrison, C. J., M. Rezvani, and J. A. Langdale. 2007. Growth from two transient apical initials in the meristem of *Selaginella kraussiana*. *Development* 134: 881–889.

Hartman, M. E. 1931. Antheridial dehiscence in the Polypodiaceae. *Botanical Gazette (Chicago, Ill.)* 91: 252–276.

Hasegawa, J. 1994. New classification of Anthocerota. *The Journal of the Hattori Botanical Laboratory* 76: 21–34.

Hauke, R. L. 1957. The stomatal apparatus of *Equisetum*. *Bulletin of the Torrey Botanical Club* 84: 178–181.

Hébant, C. 1976. Evidence for the presence of sieve elements in vascularised gametophytes of *Psilotum* from Holoway's collections. *New Zealand Journal of Botany* 14: 187–191.

Hébant, C. 1979. Conducting tissue in bryophyte systematics. Pp. 365–383 in *Bryophyte systematics*, eds. G. C. S. Clarke and J. G. Duckett. *Systematics Association Special Volume 14.* London: Academic Press.

Hébant-Mauri, R. 1972. Le genre Trichomanes L. (fougères leptosporangiées). *Adansonia, series 2* 12: 469–495.

Hébant-Mauri, R. 1993. Cauline meristems in leptosporangiate ferns: structure, lateral appendages and branching. *Canadian Journal of Botany* 71: 1612–1624.

Hendy, M. D. and D. Penny. 1989. A framework for the quantitative study of evolutionary trees. *Systematic Zoology* 38: 297–309.

Hennig, W. 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin: Deutscher Zentralverlag.

Hermsen, E. J. and J. R. Hendricks. 2008. W(h)ither fossils? Studying morphological character evolution in the age of molecular sequences. *Annals of the Missouri Botanical Garden* 95: 72–110.

Hilger, H. H., N. Kapuskar, and W. Frey. 2005. The gametophyte-sporophyte junction in *Selaginella martensii* Spring (Selaginellales, Lycopodiophyta). *Phyton* 45: 1–8.

Hill, C. R. and J. M. Camus. 1986. Evolutionary cladistics of marattialean ferns. *Bulletin of the British Museum, Natural History. Botany* 14: 219–300.

Hillis, D. M. and J. J. Wiens. 2000. Molecules versus morphology in systematics: conflicts, artifacts, and misconceptions. Pp. 1–19 in *Phylogenetic analysis of morphological data*, ed. J. J. Wiens. Washington: Smithsonian Institution Press.

Holland, B., T. K. Huber, V. Moulton, and P. Lockhart. 2004. Using consensus networks to visualize contradictory evidence for species phylogeny. *Molecular Biology and Evolution* 21: 1459–1461.

Holland, B. and V. Moulton. 2003. Consensus networks: a method for visualizing incompatibilities in collections of trees. Pp. 165–176 in *Algorithms in bioinformatics, 3rd international workshop, WABI 2003*, eds. G. Benson and R. D. M. Page. Berlin: Springer-Verlag.

Holloway, J. E. 1939. The gametophyte, embryo, and young rhizome of *Psilotum triquetrum* Swartz. *Annals of Botany* 3: 313–336.

Hori, T., R. W. Ridge, W. Tulecke, P. Del Tredici, J.Trémouillaux-Guiller, and H. Tobe. 1997. *Ginkgo biloba - a global treasure, from biology to medicine*. Berlin: Springer-Verlag.

Huson, D. H. 1998. SplitsTree: A program for analyzing and visualizing evolutionary data. *Bioinformatics* 14: 68–73.

Huson, D. H. and D. Bryant. 2005. Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution* 23: 254–267.

Imaichi, R. 1977. Anatomical study on the shoot apex of *Osmunda japonica* Thunb. *Botanical Magazine (Tokyo)* 90: 129–141.

Imaichi, R. 1986. Surface-viewed shoot apex of *Angiopteris lygodiifolia* Ros. (Marattiaceae). *Botanical Magazine (Tokyo)* 99: 309–317.

Imaichi, R. and M. Kato 1991. Developmental study of branched rhizophores in three *Selaginella* species. *American Journal of Botany* 78: 1694–1703.

Imaichi, R. and M. Nishida 1986. Developmental anatomy of the three-dimensional leaf of *Botrychium ternatum* (Thunb.) Sw. *Botanical Magazine (Tokyo)* 99: 85–106.

Jablonski, D. 2004. Extinction: past and present. *Nature* 427: 589.

Jarzen, D. M. and D. J. Nichols. 1996. Pollen. Pp. 261–291 in *Palynology: principles and applications vol. 1*, eds. J. Jansonius and D. C. McGregor. *American Association of Stratigraphic Palynologists Foundation*. Salt Lake City: Publishers Press.

Jenner, R. A. 2004. Accepting partnership by submission? Morphological phylogenetics in a molecular millenium. *Systematic Biology* 53: 333–342.

Jernstedt, J. A., E. G. Cutter, E. M. Gifford, and P. Lu. 1992. Angle meristem origin and development in *Selaginella martensii*. *Annals of Botany* 69: 351–363.

Judd, W. S., D. C. S. Campbell, E. A. Kellogg, P. F. Stevens, and M. J. Donoghue. 2002. *Plant systematics: a phylogenetic approach*. 2nd ed. Sunderland: Sinauer Associates.

Kaplan, D. R. 1977. Morphological status of the shoot systems of Psilotaceae. *Brittonia* 29: 30–53.

Kaplan, D. R. 2001. The science of plant morphology: definition, history, and role in modern biology. *American Journal of Botany* 88: 1711–1741.

Karrfalt, E. E. 1977. The comparative morphology and development of *Isoetes tuckermanii*. *American Fern Journal* 67: 68–72.

Karrfalt, E. E. 1981. The comparative and developmental morphology of the root system of *Selaginella* (L.) Link. *American Journal of Botany* 68: 244–253.

Karrfalt, E. E. 1982. Secondary development in the cortex of *Isoetes*. *Botanical Gazette (Chicago, Ill.)* 143: 439–445.

Karrfalt, E. E. 1984. The origin and early development of the root-producing meristem of *Isoetes andicola* L. D. Gómez. *Botanical Gazette (Chicago, Ill.)* 138: 357–368.

Kato, M. 1988. The phylogenetic relationships of Ophioglossaceae. *Taxon* 37: 381–386.

Kato, M. and R. Imaichi. 1997. Morphological diversity and evolution of vegetative organs in pteridophytes. Pp. 27–43 in *Evolution and diversification of land plants*, eds. K. Iwatsuki and P. H. Raven. Berlin: Springer-Verlag.

Keating, R. C. 1968. Trends of specialization in the stipe anatomy of *Dennstaedtia* and related genera. *American Fern Journal* 58: 126–140.

Kemp, T. S. 1999. *Fossils and evolution*. Oxford: Oxford University Press.

Kennedy, S. M., B. R. Holland, D. G. Russell, and H. G. Spencer 2005. Untangling long branches: identifying conflicting phylogenetic signals using spectral analysis, neighbor-net, and consensus networks. *Systematic Biology* 54: 620–633.

Kenrick, P. 1994. Alternation of generations in land plants: new phylogenetic and palaeobotanical evidence. *Biological Reviews of the Cambridge Philosophical Society* 69: 293–330.

Kenrick, P. and P. R. Crane. 1991. Water-conducting cells in early fossil plants: implications for the evolution of tracheophytes. *Botanical Gazette (Chicago, Ill.)* 152: 335–356.

Kenrick, P. and P. R. Crane. 1997. *The origin and early diversification of land plants: a cladistic study*. Washington: Smithsonian Institution Press.

Khandelwal, S. and K. Goswami. 1977. Periderm in Ophioglossaceae. *Acta Societatis Botanicorum Poloniae* 46: 641–645.

Kishino, H. and M. Hasegawa. 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea. *Journal of Molecular Evolution* 29: 170–179.

Klekowski, E. J. 1985. Mutations, apical cells, and vegetative reproduction. *Proceedings of the Royal Society of Edinburgh, section B* 86: 67–73.

Kluge, A. G. 1989. A concern for evidence and a phylogenetic hypothesis for relationships among *Epicrates* (Boidae, Serpentes). *Systematic Zoology* 38: 7–25.

Kluge, A. G. and J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. *Systematic Zoology* 18: 1–32.

Knoop, V. 2004. The mitochondrial DNA of land plants: peculiarities in phylogenetic perspective. *Current Genetics* 46: 123–129.

Knox, R. B. and S. C. Ducker. 1991. The evolution of gametes - from motility to double fertilization. Pp. 345–361 in *Pollen and spores*, eds. S. Blackmore and S. H. Barnes. *Systematics Association Special Volume 44*. Oxford: Clarendon Press.

Kondo, T. 1962. A contribution to the study of fern stomata. *Research Bulletin of the Faculty of Education of Shizuoka University* 13: 239–267.

Kramer, K. U. 1987. A brief survey of the dromy in fern leaves, with an expanded terminology. *Botanica Helvetica* 97: 219–228.

Kubitzki, K., ed. 1990. *The families and genera of vascular plants. Vol. 1. Pteridophytes and gymnosperms*, vol. eds. K. U. Kramer and P. S. Green. Berlin: Springer-Verlag.

Kubitzki, K., J. G. Rohwer, and V. Bittrich, eds. 1993. *The families and genera of vascular plants. Vol. 2. Flowering plants*, vol. eds. K. U. Kramer and P. S. Green. Berlin: Springer-Verlag.

Labouriau, L. G. 1958. Studies on the initiation of sporangia in ferns. *Arquivos do Museu Nacional, Rio de Janeiro* 46: 119–201.

Leavitt, R. G. 1904. Trichomes of the root in vascular cryptogams and angiosperms. *Proceedings of the Boston Society of Natural History* 31: 273–313.

Lee, M. S. Y. 2004. Molecular and morphological datasets have similar numbers of relevant phylogenetic characters. *Taxon* 53: 1019–1022.

Lewis, P. O. 2001. A likelihood approach to estimating phylogeny from discrete morphological data. *Systematic Biology* 50: 913–925.

Ligrone, R., J. G. Duckett, and K. S. Renzaglia. 1993. The gametophyte-sporophyte junction in land plants. *Advances in Botanical Research* 19: 231–317.

Ligrone, R., J. G. Duckett, and K. S. Renzaglia. 2000. Conducting tissues and phyletic relationships of bryophytes. *Philosophical Transactions of the Royal Society of London, series B* 355: 795–813.

Lin, B.-L. and C. E. DeVol. 1977. The use of stipe characters in fern taxonomy I. *Taiwania* 22: 91–99.

Lin, B.-L. and C. E. DeVol. 1978. The use of stipe characters in fern taxonomy II. *Taiwania* 23: 77–95.

Loconte, H. and D. Stevenson. 1990. Cladistics of the Spermatophyta. *Brittonia* 42: 197–211.

Logan, K. J. and B. A. Thomas 1985. Distribution of lignin derivatives in plants. *The New Phytologist* 99: 571–585.

Lugardon, B. 1990. Pteridophyte sporogenesis: a survey of spore wall ontogeny and fine structure in a polyphyletic plant group. Pp. 95–120 in *Microspores: evolution and ontogeny*, eds. S. Blackmore and R. B. Knox. London: Academic Press.

Lugardon, B. and C. Brousmiche-Delcambre. 1994. Exospore ultrastructure in Carboniferous sphenopsids. Pp. 53–66 in *Ultrastructure of fossil spores and pollen*, eds. M. H. Kurman and J. A. Doyle. Kew: Royal Botanic Gardens.

Lugardon, B. and P. Piquemal. 1993. Ultrastructure exosporale et phylogenie chez les ptéridophytes. *Gaussenia* 8: 16–24.

Maddison, W. P. and D. R. Maddison. 2000. MacClade 4: analysis of phylogeny and character evolution. Version 4. Sunderland: Sinauer Associates.

Maden, A. R., D. P. Whittier, D. J. Garbary, and K. S. Renzaglia 1997. Ultrastructure of the spermatozoid of *Lycopodiella lateralis* (Lycopodiaceae). *Canadian Journal of Botany* 75: 1728–1738.

Magallón, S. 2007. From fossils to molecules: phylogeny and the core eudicot floral groundplan in Hamamelioideae (Hamamelidaceae, Saxifragales). *Systematic Botany* 32: 317–347.

Magallón, S. and M. J. Sanderson. 2002. Relationships among seed plants inferred from highly conserved genes: sorting conflicting phylogenetic signals among ancient lineages. *American Journal of Botany* 89: 1991–2006.

Markham, K. E. 1988. Distribution of flavonoids in the lower plants and its evolutionary significance. Pp. 427–468 in *The flavonoids*, ed. J. B. Harborne. London: Chapman and Hall.

Martens, P. 1971. *Les Gnétophytes*. Handbuch der Pflanzenanatomie. Band XII, Teil 2, Spezieller Teil. Berlin: Gebrüder Borntträger.

Martin, W., O. Deusch, N. Stawski, N. Grünheit, and V.Goremykin. 2005. Chloroplast genome phylogenetics: why we need independent approaches to plant molecular evolution. *Trends in Plant Science* 10: 203–209.

McAlpin, B. W. and R. A. White. 1974. Shoot organization in the Filicales: the promeristem. *American Journal of Botany* 61: 562–579.

Mishler, B. D., L. A. Lewis, M. A. Buchheim, K. S. Renzaglia, D. J. Garbary, C. F. Delwiche, F. W. Zechman, T. S. Kantz, and R. L. Chapman. 1994. Phylogenetic relationships of the "green algae" and "bryophytes". *Annals of the Missouri Botanical Garden* 81: 451–483.

Nagalingum, N. S., H. Schneider, and K. M. Pryer. 2006. Comparative morphology of reproductive structures in heterosporous water ferns and a reevaluation of the sporocarp. *International Journal of Plant Sciences* 167: 805–815.

Nandi, O. I., M. W. Chase, and P. K. Endress. 1998. A combined cladistic analysis of angiosperms using *rbcL* and non-molecular data sets. *Annals of the Missouri Botanical Garden* 85: 137–212.

Nayar, B. K. and S. Kaur. 1968. Spore germination in homosporous ferns. *Journal of Palynology* 4: 1–14.

Nayar, B. K. and S. Kaur. 1971. Gametophytes of homosporous ferns. *Botanical Review* 37: 295–396.

Neidhart, H. V. 1979. Comparative studies of sporogenesis in bryophytes. Pp. 251–280 in eds. G. C. S. Clarke and J. G. Duckett. *Systematics Association Special Volume 14*. London: Academic Press.

Nickrent, D. L., C. L. Parkinson, J. D. Palmer, and R. J. Duff. 2000. Multigene phylogeny of land plants with special reference to bryophytes and the earliest land plants. *Molecular Biology and Evolution* 17: 1885–1895.

Nixon, K. C., W. L. Crepet, D. W. Stevenson, and E. M. Friis. 1994. A reevaluation of seed plant phylogeny. *Annals of the Missouri Botanical Garden* 81: 484–533.

Norstog, K. J. and T. J. Nicholls. 1997. *The biology of the cycads*. Ithaca: Cornell University Press.

Ogura, Y. 1938. *Anatomic der Vegetationsorgane der Pteridophyten*. Handbuch der pflanzenanatomie. Abt. II, Bd.VII, Tr 2. Berlin: Gebrüder Bornträger.

Ogura, Y. 1972. *Comparative anatomy of vegetative organs of pteridophytes.* Handbuch der pflanzenanatomie. Band VII, Teil 3, Spezieller Teil. Berlin: Gebrüder Bornträger.

O'Leary, M. A. 2001. The phylogenetic position of Cetaceans: further combined data analyses, comparisons with the stratigraphic record and a discussion of character optimization. *American Zoologist* 41: 487–506.

Olmstead, R. G. and R. W. Scotland. 2005. Molecular and morphological datasets. *Taxon* 54: 7–8.

Pacini, E. 1990. Harmomegathic characters of Pteridophyta spores and Spermatophyta pollen. *Plant Systematics and Evolution* 5 (Supplement): 53–69.

Pacini, E. 1997. Tapetum character states: analytical keys for tapetum types and activities. *Canadian Journal of Botany* 75: 1448–1459.

Pacini, E. and G. G. Franchi. 1991. Diversification and evolution of tapetum. Pp. 301–316 in *Pollen and spores, patterns of diversification*, eds. S. Blackmore and S. H. Barnes. *Systematics Assocation Special Volume 44.* Oxford: Clarendon Press.

Pacini, E., G. G. Franchi, and M. Ripaccioli. 1999. Ripe pollen structure and histochemistry of some gymnosperms. *Plant Systematics and Evolution* 217: 81–99.

Pahnke, J., V. Goremykin, V. Bobrova, A. L. Toitsky, A. Antonov, and W. Martin. 1996. Utility of rDNA internal transcribed spacer sequences from the inverted repeat of chloroplast DNA in pteridophyte molecular phylogenetics. Pp. 217–230 in *Pteridology in perspective*, eds. J. M. Camus, M. Gibby, and R. J. Johns.Kew: Royal Botanic Gardens.

Palmer, J. D., D. E. Soltis, and M. W. Chase. 2004. The plant tree of life: an overview and some points of view. *American Journal of Botany* 91: 1437–1445.

Pant, D. D. 1965. On the ontogeny of stomata and other homologous structures. *Plant Science Series of Allahabad University* 1: 1–24.

Pant, D. D. and P. K. Khare. 1971. Epidermal structure of Psilotales and stomatal ontogeny of *Tmesipteris tannensis* Bernh. *Annals of Botany* 35: 151–157.

Paolillo, D. J. 1982. Meristems and evolution: developmental correspondence among the rhizomorphs of the lycopsids. *American Journal of Botany* 69: 1032–1042.

Parenti, L. R. 1980. A phylogenetic analysis of the land plants. *Biological Journal of the Linnean Society* 13: 225–242.

Parkinson, B. M. and E. Pacini. 1995. A comparison of tapetal structure and function in pteridophytes and angiosperms. *Plant Systematics and Evolution* 198: 55–88.

Payne, W. W. 1979. Stomatal patterns in embryophytes: their evolution, ontogeny and interpretation. *Taxon* 28: 117–132.

Perry, J. W. and R. F. Evert. 1975. Structure and development of the sieve elements in *Psilotum nudum*. *American Journal of Botany* 62: 1038–1052.

Peterson, R. L., M. J. Howarth, and D. P. Whittier. 1981. Interactions between a fungal endophyte and gametophyte cells in *Psilotum nudum*. *Canadian Journal of Botany* 59: 711–720.

Philipson, W. R. 1990. The significance of apical meristems in the phylogeny of land plants. *Plant Systematics and Evolution* 173: 17–38.

Pickett-Heaps, J. D., B. E. S. Gunning, R. C. Brown, B. E. Lemmon, and A. L. Cleary. 1999. The cytoplast concept in dividing plant cells: cytoplasmic domains and the evolution of spatially organized cell division. *American Journal of Botany* 86: 153–172.

Playford, G. and M. E. Dettmann. 1996. Spores. Pp. 227–260 in *Palynology:principles and applications vol. 1*, eds. J. Jansonius and D. C. McGregor. *American Association of Stratigraphic Palynologists Foundation.* Salt Lake City: Publishers Press.

Pryer, K. M. 1999. Phylogeny of marsileaceous ferns and relationships of the fossil *Hydropteris pinnata* reconsidered. *International Journal of Plant Sciences* 160: 931–954.

Pryer, K. M., H. Schneider, A. R. Smith, R. Cranfill, P. G. Wolf, J. S. Hunt, and S. D. Sipes. 2001. Horsetails and ferns are a monophyletic group and the closest living relatives to seed plants. *Nature* 409: 618–622.

Pryer, K. M., E. Schuettpelz, P. G. Wolf, H. Schneider, A. R.Smith, and R.Cranfill. 2004. Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate divergences. *American Journal of Botany* 91: 1582–1598.

Pryer, K. M., A. R. Smith, and J. E. Skog. 1995. Phylogenetic relationships of extant ferns based on evidence from morphology and *rbcL* sequences. *American Fern Journal* 85: 205–282.

Qiu, Y.-J., R. A. White, and M. D. Turner. 1995. The developmental anatomy of *Metaxya rostrata* (Filicales: Metaxyaceae). *American Journal of Botany* 82: 969–981.

Qiu, Y.-L., C. Yangrae, J. C. Cox, and J. D. Palmer. 1998. The gain of three mitochondrial introns identifies liverworts as the earliest land plants. *Nature* 394: 671–673.

Qiu, Y.-L., L. Li, B. Wang, Z. Chen, V. Knoop, M. Groth-Malonek, O. Dombrovska, J. Lee, L. Kent, J. Rest, G. F. Estabrook, T. A. Hendry, D. W. Taylor, C. M. Testa, M. Ambros, B. Crandall-Stotler, R. J. Duff, M. Stech, W. Frey, D. Quant, and C. C. Davis. 2006. The deepest divergences in land plants inferred from phylogenomic evidence. *Proceedings of the National Academy of Sciences USA* 103: 15511–15516.

Qiu, Y.-L., L. Li, B. Wang, Z. Chen, O. Dombrovska, J. Lee, L. Kent, R. Li, R. W. Jobson, T. A. Hendry, D. W. Taylor, C. M. Testa, and M. Ambros. 2007. A nonflowering land plant phylogeny of seven chloroplast, mitochondrial, and nuclear genes. *International Journal of Plant Sciences* 168: 691–708.

Raff, R. A. 1996. *The shape of life: genes, development, and the evolution of animal form*. Chicago: University of Chicago Press.

Rambaut, A. and A. Drummond. 2005. Tracer version 1.21. Computer program distributed by the authors. Oxford, England: Department of Zoology, University of Oxford.

Raubeson, L. A. and R. K. Jansen. 1992. Chloroplast DNA evidence on the ancient evolutionary split in vascular land plants. *Science* 255: 1697–1699.

Raubeson, L. A. and D. B. Stein. 1995. Insights into fern evolution from mapping chloroplast genomes. *American Fern Journal* 85: 193–204.

Rausher, M. D., R. E. Miller, and O. Tiffin. 1999. Patterns of evolutionary rate variation among genes of the anthocyanin biosynthetic pathway. *Molecular Biology and Evolution* 16: 266–274.

Renzaglia, K. S. 1978. A comparative morphology and developmental anatomy of the Anthocerotophyta. *The Journal of the Hattori Botanical Laboratory* 44: 31–90.

Renzaglia, K. S. and D. J. Garbary. 2001. Motile gametes of land plants: diversity, development, and evolution. *Critical Reviews in Plant Sciences* 20: 107–213.

Renzaglia, K. S. and A. R. Maden. 2000. Microtubule organizing centers and the origin of centrioles during spermatogenesis in the pteridophyte *Phylloglossum*. *Microscopy Research and Technique* 49: 496–505.

Renzaglia, K. S., D. L. Bernhard, and D. J. Garbary. 1999. Developmental ultrastructure of the male gamete of *Selaginella*. *International Journal of Plant Sciences* 160: 14–28.

Renzaglia, K. S., R. J. Duff, D. L. Nickrent, and D. J. Garbary. 2000. Vegetative and reproductive innovations of early land plants: implications for a unified phylogeny. *Philosophical Transactions of the Royal Society of London, series B* 355: 769–793.

Renzaglia, K. S., T. H. Johnson, H. D. Gates, and D. P. Whittier. 2001. Architecture of the sperm cell of *Psilotum*. *American Journal of Botany* 88: 1151–1163.

Ronquist, F. and J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.

Rothwell, G. W. 1984. The apex of *Stigmaria* (Lycopsida), rooting organ of Lepidodendrales. *American Journal of Botany* 71: 1031–1034.

Rothwell, G. W. 1995. The fossil history of branching: implications for the phylogeny of land plants. Pp. 71–86 in *Experimental and molecular approaches to plant biosystematics*, eds. P. C. Hoch and A. G. Stephenson. *Monographs in Systematic Botany from the Missouri Botanical Garden 53.* St. Louis: Missouri Botanical Garden Press.

Rothwell, G. W. 1999. Fossils and ferns in the resolution of land plant phylogeny. *Botanical Review (Lancaster)* 65: 188–218.

Rothwell, G. W. and D. M. Erwin. 1985. The rhizomorph apex of *Paurodendron*: implications for homologies among the rooting organs of Lycopsida. *American Journal of Botany* 72: 86–98.

Rothwell, G. W. and K. C. Nixon. 2006. How does the inclusion of fossil data change our conclusions about the phylogenetic history of euphyllophytes? *International Journal of Plant Sciences* 167: 737–749.

Rothwell, G. W. and R. Serbet. 1994. Lignophyte phylogeny and the evolution of spermatophytes: a numerical cladistic analysis. *Systematic Botany* 19: 443–482.

Rowley, J. R. 1996. Exine origin, development and structure in pteridophytes, gymnosperms, and angiosperms. Pp. 443–462 in *Palynology: principles and applications vol. 1*, eds. J. Jansonius and D. C. McGregor. *American Association of Stratigraphic Palynologists Foundation.* Salt Lake City: Publishers Press.

Sanderson, M. J. and M. J. Donoghue. 1996. The relationship between homoplasy and confidence in a phylogenetic tree. Pp. 67–89 in *Homoplasy: the recurrence of similarity in evolution*, eds. M. J. Sanderson and L. Hufford. San Diego: Academic Press.

Schmid, E. and F. Oberwinkler. 1995. A light- and electron-microscopic study on a vesicular-arbuscular host-fungus interaction in gameto-

phytes and young sporophytes of the Gleicheniaceae (Filicales). *The New Phytologist* 129: 317–324.
Schmid, R. 1982. The terminology and classification of steles: historical perspective and the outlines of a system. *Botanical Review (Lancaster)* 48: 817–931.
Schneider, H. 1996. *Vergleichende Wurzelanatomie der Farne*. Aachen: Shaker-Verlag.
Schneider, H. 2000. Morphology and anatomy of roots in the filmy fern tribe Trichomaneae H. Schneider (Hymenophyllaceae, Filicatae) and the evolution of rootless taxa. *Botanical Journal of the Linnean Society* 132: 29–46.
Schneider, H. 2007. Plant morphology as the cornerstone to the integration of fossils and extant taxa in phylogenetic analyses. *Species. Phylogeny and Evolution* 1: 65–71.
Schneider, H. and K. M. Pryer. 2002. Structure and function of spores in the aquatic heterosporous fern family Marsileaceae. *International Journal of Plant Sciences* 163: 485–505.
Schneider, H., K. M. Pryer, R. Cranfill, A. R. Smith, and P. G. Wolf. 2002. The evolution of vascular plant body plans – a phylogenetic perspective. Pp. 330–364 in *Developmental genetics and plant evolution*, eds. Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins.London: Taylor and Francis.
Schuettpelz, E., P. Korall, and K. M. Pryer. 2006. Plastid *atpA* data provide improved support for deep relationships among ferns. *Taxon* 55: 897–906.
Schuster, R. M. 1967. Studies on Hepaticae XV: Calobryales. *Nova Hedwigia* 13: 1–63.
Schuster, R. M. 1992. *The Hepaticae and Anthocerotae of North America vol. VI*. Chicago: Field Museum of Natural History.
Scotland, R. W., R. G. Olmstead, and J. R. Bennett. 2003. Phylogeny reconstruction: the role of morphology. *Systematic Biology* 52: 539–548.
Sen, U. and B. De. 1992. Structure and ontogeny of stomata in ferns. *Blumea* 37: 239–261.
Smith, A. B. 1998. What does palaeontology contribute to systematics in a molecular world? *Molecular Phylogenetics and Evolution* 9: 437–447.
Smith, A. R., K. M. Pryer, E. Schuettpelz, P. Korall, H.Schneider, and P. G.Wolf. 2006. A classification of extant ferns. *Taxon* 55: 705–731.
Smith, N. D. and A. H. Turner. 2005. Morphology's role in phylogeny reconstruction: perspectives from paleontology. *Systematic Biology* 54: 166–173.
Soeder, R. W. 1985. Fern constituents: including occurrence, chemotaxonomy and physiological activity. *Botanical Review* 51: 442–536.
Springer, M. S., E. C. Teeling, O. Madsen, M. J. Stanhope, and W. W. de Jong. 2001. Integrated fossil and molecular data reconstruct bat echolocating. *Proceedings of the National Academy of Sciences USA* 98: 6241–6246.
Stein, W. E. 1993. Modeling the evolution of the stelar architecture in vascular plants. *International Journal of Plant Sciences* 154: 229–263.
Stein, W. E., D. C. Wight, and C. B. Beck. 1984. Possible alternatives for the origin of Sphenopsida. *Systematic Botany* 9: 102–118.
Stevenson, D. W. 1976. The cytohistological and cytohistochemical zonation of the shoot apex of *Botrychium multifidum*. *American Journal of Botany* 63: 852–856.
Stevenson, D. W. 1978. Observations on shoot apices of eusporangiate ferns. *Kew Bulletin* 33: 279–282.
Stevenson, D. W. 1980. Ontogeny of the vascular system of *Botrychium multifidum* (S. G. Gmelin) Rupr. (Ophioglossaceae) and its bearing on stelar theories. *Botanical Journal of the Linnean Society* 80: 41–52.
Stevenson, D. W. 1990. Morphology and systematics of Cycadales. *Memoirs of the New York Botanical Garden* 57: 8–55.
Stevenson, D. W. and H. Loconte. 1996. Ordinal and familial relationships of Pteridophyta genera. Pp. 435–467 in *Pteridology in perspective*, eds. J. M. Camus, M. Gibby, and R. J. Johns.Kew: Royal Botanic Gardens Kew.
Stewart, W. N. 1947. A comparative study of stigmarian appendages and *Isoetes* roots. *American Journal of Botany* 34: 315–324.
Stewart, W. N. and G. W. Rothwell. 1993. *Paleobotany and the evolution of plants*, 2nd ed. Cambridge: Cambridge University Press.
Stokey, A. G. 1951. The contribution by the gametophyte to the classification of homosporous ferns. *Phytomorphology* 1: 39–58.
Swofford, D. L. 2002. PAUP*: phylogenetic analysis using parsimony (* and other methods), version 4.0, b10. Sunderland: Sinauer Associates.
Takiguchi, Y., R. Imaichi, and M. Kato. 1997. Cell division patterns in the apices of subterranean axis and aerial shoot of *Psilotum nudum* (Psilotaceae): morphological and phylogenetic implications for the subterranean axis. *American Journal of Botany* 84: 588–596.
Teeling, E. C., M. S. Springer, O. Madsen, P. Bates, S. J. O'Brien, and W. J. Murphy. 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. *Science* 307: 580–584.
Troll, W. 1935. *Vergleichende morphologie der höheren pflanzen*. Band 1. Teil 1. Berlin: Gebrüder Borntträger.
Troop, J. E. and J. T. Mickel. 1968. Petiolar shoots in the dennstaedtioid and related ferns. *American Fern Journal* 58: 64–70.
Tryon, A. F. and B. Lugardon. 1991. *Spores of the Pteridophyta: surface, wall structure, and diversity based on electron microscope studies*. Berlin: Springer-Verlag.
Tryon, R. M. and A. F. Tryon. 1982. *Ferns and allied plants, with special reference to tropical America*. Berlin: Springer-Verlag.
Van Cotthem, W. R. J. 1970. A classification of stomatal types. *Botanical Journal of the Linnean Society* 63: 235–246.
Van Cotthem, W. R. J. 1973. Stomatal types and systematics. Pp. 59–71 in *The phylogeny and classification of ferns*, eds. A. C. Jermy, J. A. Crabbe, and B. A. Thomas. *Botanical Journal of the Linnean Society* 67: 1–284.
Van Fleet, D. S. 1961. Histochemistry and function of the endodermis. *Botanical Review* 27: 165–220.
Wagner, W. H. Jr. 1952. Types of foliar dichotomy in living ferns. *American Journal of Botany* 39: 578–592.
Wagner, W. H. Jr. 1964. Paraphyses: Filicineae. *Taxon* 13: 56–64.
Wagner, W. H. Jr. 1979. Reticulate veins in the systematics of modern ferns. *Taxon* 28: 87–95.
Wallace, J. W. 1991. A phytochemical approach for gaining insight into pteridophyte phylogeny. Pp. 117–135 in *Perspectives in pteridology: present and future*, eds. T. N. Bhardwaja and C. B. Gena. *Aspects of Plant Science* 11: 1–342.
Wardlaw, C. W. 1955. *Embryogenesis in plants*. London: Methuen.
Wardlaw, C. W. 1965. *Organization and evolution of plants*. London: Longmans.
Warmbrodt, R. D. 1980. Characteristics of structure and differentiation in the sieve element of lower vascular plants. *Berichte der Deutschen Botanischen Gesellschaft* 93: 13–28.
White, R. A. 1963a. Tracheary elements of the ferns. I. Factors which influence tracheid length; correlation of length with evolutionary divergence. *American Journal of Botany* 50: 447–455.
White, R. A. 1963b. Tracheary elements in ferns. II. Morphology of tracheary elements: conclusions. *American Journal of Botany* 50: 514–522.
White, R. A. 1979. Experimental investigations of fern sporophyte development. Pp. 505–549 in *The experimental biology of ferns*, ed. A. F. Dyer. London: Academic Press.
White, R. A. and M. D. Turner. 1988. *Calochlaena*, a new genus of dicksonioid ferns. *American Fern Journal* 78: 86–95.
Whitfield, J. B. and P. J. Lockhart. 2007. Deciphering ancient rapid radiations. *Trends in Ecology & Evolution* 22: 258–265.
Whittier, D. P. and J.-C. Pintaud. 1999. Spore germination and early gametophyte development in *Stromatopteris*. *American Fern Journal* 89: 142–148.
Wiens, J. J. 1998. Does adding characters with missing data increase or decrease accuracy? *Systematic Biology* 47: 625–640.
Wiens, J. J. 2004. The role of morphological data in phylogeny reconstruction. *Systematic Biology* 53: 653–661.
Wikström, N. and K. M. Pryer. 2005. Incongruence between primary sequence data and the distribution of a mitochondrial *atp1* group II intron among ferns and horsetails. *Molecular Phylogenetics and Evolution* 36: 484–493.
Wills, M. A. and R. A. Fortey. 2000. The shape of life: how much is written in stone? *BioEssays* 22: 1142–1152.
Wolf, P. G., S. D. Sipes, M. R. White, M. L. Martines, K. M. Pryer, A. R. Smith, and K. Ueda. 1999. Phylogenetic relationships of the enigmatic fern families Hymenophyllopsidaceae and Lophosoriaceae: evidence from *rbcL* nucleotide sequences. *Plant Systematics and Evolution* 219: 263–270.
Yang, Z. 1993. Maximum-likelihood estimation of phylogeny from DNA sequences with substitution rates differ over sites. *Molecular Biology and Evolution* 10: 1396–1401.
Yang, Z. and B. Rannala. 1997. Bayesian phylogenetic inference using DNA sequences: a Markov chain Monte Carlo method. *Molecular Biology and Evolution* 14: 717–724.
Yi, S.-Y. and M. Kato. 2001. Basal meristem and root development in *Isoëtes asiatica* and *Isoëtes japonica*. *International Journal of Plant Sciences* 162: 1225–1235.
Zimmermann, W. 1952. The main results of the telome theory. *Palaeobotanist* 1: 456–470.

Appendix 1. The 35 taxa included in morphological and molecular analyses. Classification follows Kenrick and Crane (1997) for non-ferns and Smith et al. (2006) for ferns. Genera follow Smith et al. (2006) for ferns and lycophytes, Kubitzki (1990) for gymnosperms, Kubitzki et al. (1993) for angiosperms.

***Outgroup Taxa*—Marchantiophyta.** *Haplomitrium* Nees, *Marchantia* L.; **Anthocerophyta.** *Anthoceros* L.; **Bryophyta.** *Polytrichum* Hedw., *Sphagnum* L.

***Ingroup Taxa*—**Lycophytina. **Lycopodiales.** *Huperzia* Bernh. **Selaginellales.** *Selaginella* P. Beauv. **Isoëtales.** *Isoëtes* L. Ferns [Monilifo rmopses]. **Equisetopsida.** *Equisetum* L. subg. *Equisetum* (= *Equisetum 1*), *Equisetum* L. subg. *Hippochaete* (Milde) Baker (= *Equisetum 2*). **Marattiopsida.** *Angiopteris* Hoffm., *Danaea* Sm., *Marattia* Sw. **Psilotopsida.** *Psilotum* Sw., *Tmesipteris* Sw., *Botrychium* Sw., *Ophioglossum* L. **Polypodiopsida.** *Blechnum* L., *Cyathea* Sm, *Dicksonia* L'Hér., *Gleichenia* Sm., *Hymenophyllum* Sm., *Lygodium* Sw., *Marsilea* L., *Osmunda* L., *Phanerosorus* Copel., *Plagiogyria* (Kunze) Mett., *Pteridium* Scop., *Salvinia* Ség. Spermatophytata. **Coniferidra.** *Pinus* L. **Cycadatae.** *Cycas* L. **Ginkgoatae.** *Ginkgo* L. **Gnetidra.** *Gnetum* L. **Magnolidra**. *Austrobaileya* C. D. White, *Chloranthus* Sw.

Appendix 2. Description of characters, character states, and scoring criteria used in this study. Characters derived from published studies are indicated in parentheses by an author abbreviation followed by the character number. Underlined abbreviations indicate a character that has been modified here from the original publication. New characters are indicated by "New" following the character number. Unless otherwise stated, for characters and states defined in the same manner as in Pryer et al. (1995), the same character state arguments and definitions apply. References useful in coding taxa and defining characters are given if appropriate. Abbreviated publications: D - Doyle (1996); GRD - Garbary et al. (1993); GR - Garbary and Renzaglia (1998); KC - Kenrick and Crane (1997); M et al. - Mishler et al. (1994, Table 3); NCSF - Nixon et al. (1994); PSS - Pryer et al. (1995); R - Rothwell (1999); S - Schneider (1996); SL - Stevenson and Loconte (1996).

***I. Sporophyte*—**I. A. Leaf. The term *leaf* is used here as a synonym for euphyll (= megaphyll), which is consistent with the morphological literature (Bierhorst 1971; Gifford and Foster 1988; von Goebel 1930; Troll 1935). The leaflike structures of Lycophytina are considered as lycophylls (specialized microphylls) and non-homologous to euphylls (von Goebel 1930; Kenrick and Crane 1997). Lycophylls develop differently than euphylls (von Guttenberg 1966; R. Imaichi, pers. comm.) and they may be derived from sterile sporangia (Crane and Kenrick 1997). Characters of euphylls do not apply to lycophylls, since they are not homologous. In pteridological literature, the term "frond" is often used. The distinction between fronds and leaves may be based on differences in ptyxis and growth patterns (acropetal versus basipetal) that result in fern-like leaves. Leaves of Equisetaceae and Psilotaceae are often regarded as microphylls, and similar to the leaves of Lycopsida. They share with lycophylls their small size, the absence of blade/petiole differentiation and reduced vascular tissue, but they differ in their development. The leaves of Equisetaceae and Psilotaceae have a differentiated apical meristem with a single apical cell (Bierhorst 1971; von Guttenberg 1966). Lycophylls lack apical meristems (von Guttenberg 1966) and they differ from euphylls in their development (Freeberg and Wetmore 1967; Kaplan 2001; Imaichi, pers. comm.). Apical meristems are found in all euphylls, but a single apical cell is known only from Filicopsida and Equisetopsida. Another criterion of euphylls is the presence of leaf gaps, which are found in Equisetaceae and *Tmesipteris* (Psilotaceae, but are lacking in *Psilotum*). In comparison, leaves of *Tmesipteris* are larger and more complex. Forking or branching is also mentioned as a criterion of euphylls. Sporophylls of both living genera of Psilotaceae are forked, and extinct relatives of Equisetaceae had forked or branched leaves. These three criteria (development, leaf gap, and branching) suggest that leaves of Equisetaceae and Psilotaceae be regarded as euphylls.

1. (M et al. 102) **Sporophyte with lycophylls:** absent (0); present (1). Lycophylls are not homologous to euphylls, resulting in "not applicable" scores for leaf (= euphyll). von Goebel (1930), Kenrick and Crane (1997), Kaplan (2001).

2. (M et al. 101; R 8) **Sporophyte with euphylls:** absent (0); present (1). This character reflects the absence/presence of leaf gaps. In contrast to euphylls, lycophylls do not introduce gaps in the stele, and they typically have a single, simple vascular strand (Kenrick and Crane 1997). However, leaf gaps are also not present in protostelic leptosporangiate ferns, for example, many Hymenophyllaceae and Lindsaeaceae. The reduced leaves of Psilotaceae may be interpreted as euphylls because the sporophylls are often branched; however, they do not introduce leaf gaps in the stele. Leaves of Equisteaceae are also interpreted as reduced euphylls because the fossil record gives evidence for the presence of euphylls in Equisetopsida (Stein et al. 1984; Stewart and Rothwell 1993). The presence of gaps in the stele of *Equisetum* is consistent with this interpretation. von Goebel (1930), Stewart and Rothwell (1993), Kenrick and Crane (1997), Kaplan (2001).

3. (PSS 1; R 21; SL 26) **Leaf ptyxis:** erect (0); circinate, folded in same direction as the primary axis (1); circinate, but folded at a 90° angle to the primary axis (2); convolute or conduplicately folded (3). The development of leaves is a complex process and the developmental pattern is strongly influenced by leaf size. Pryer et al. (1995) stated that *Cycas* does not have the same vernation as ferns, because the orientation of the bud to the leaf axis is different. Stevenson and Loconte (1996) considered also the vernation of other seed plants and treated Cycadales as polymorphic with both circinate and conduplicate ptyxis. However, they considered the vernation of *Cycas* as circinate and excluded the differences in the orientation of the bud. The condition of *Cycas* represents a state between circinate vernation, as in ferns, and the convolute or conduplicate vernation found in Anthophytatae. This character reflects the change from a mainly acropetal growth of the leaf blade to a basipetal one (see Hagemann 1984). von Goebel (1930), Bierhorst (1971), Gifford and Foster (1988), Kubitzki (1990), Stevenson (1990), Hori et al. (1997), Norstog and Nicholls (1997).

4. (PSS 2; R 57; S 108; SL 42) **Fertile-sterile leaf differentiation:** (nearly) monomorphic (0); hemidimorphic (1); dimorphic (2). Bower (1923, 1926, 1928), Eames (1936), Bierhorst (1971), Tryon and Tryon (1982), Gifford and Foster (1988), Kubitzki (1990).

5. (D 6; PSS 3; S 104, 105; SL 20, 21, 22) **Blade dissection:** simple to deeply pinnatifid (0); compound (1). This character applies to mature, photosynthetic blades only. Blade dissection differs remarkably among ferns, but further states do not improve the quality of the analysis at the phylogenetic level under study here. Only trends toward compound or simple blades are informative. von Goebel (1930), Bierhorst (1971), Gifford and Foster (1988), Tryon and Tryon (1982), Kubitzki (1990).

6. (PSS 14; SL 37) **Dromy at base of blade (proximal pair of pinnae):** catadromous (0); anadromous (1); isodromous (2). Dromy applies only to compound leaves. This character describes the position of secondary veins/pinnae to primary ones. Geometrically, one of two positions is usually favored, catadromous or anadromous (see Kramer 1987 for definition). The patterns are fixed in most fern genera and only a few taxa show intermediate or mixed dromy patterns (isodromous). The character has switched between both states more than once in the evolution of derived taxa. Therefore, it introduces a significantly homoplastic signal in the deeper branches of fern phylogeny. It may, however, be an informative character in analyses focused on family-level relationships. Kubitzki (1990).

7. (SL 27) **Leaf architecture:** monopodial, primary rachis longer than secondary (0); sympodial, secondary rachis longer than primary rachis (1); sympodial, secondary rachis longer than primary rachis, dormant bud terminating the primary rachis (2). Leaf architecture of Gleicheniaceae is unique among extant vascular plants. The growth of the apical meristem of the main rachis slows down or stops and the two lateral apical meristems (secondary order) accelerate their growth. This character is applicable only to leaves with small apical cell groups and not to leaves with a broad leaf meristem, as in angiosperms. Wagner (1952), Bierhorst (1971), Kubitzki (1990).

8. (PSS 4) **Primary blade vein form:** solitary/unbranched (0); dichotomous/isotomous (1); non-dichotomous/anisotomous (2). The Marsileaceae were scored as in Pryer (1999). Bower (1923, 1926), Kubitzki (1990).

9. (D 9; PSS 5)**Vein orders:** one (0); two or more (1). This character is used as in Doyle (1996). Vein orders higher than two reflect the width of the blade. Bower (1926), Kubitzki (1990).

10. (D 8; PSS 7; R 22; S 110; SL 38) **Vein fusion (in sterile blades):** non-anastomosing (0); anastomosing (1). Bower (1923, 1926), Kubitzki (1990), Wagner (1979).

11. (PSS 11) **Blade scales:** absent (0); present (1). Scales are interpreted here as not homologous to scalelike structures in seed plants, which are mostly reduced leaves. Scales are modified hairs that are developed by a group of epidermal cells; these cells ultimately produce a planar (flattened) structure. True scales are absent in seed plants. Leaves with scales are found only in plants that also possess scales on the shoot. Therefore, the character is not independent from the character describing the presence or absence of scales on the shoot. Kubitzki (1990).

12. (PSS 15; S 113; SL 32) **Pulvini:** absent (0); present (1). The pulvini in Marattiaceae are not similar or homologous to structures called pulvini in Marsileaceae. The term is used here only for pulvini as in Marattiaceae. Hill and Camus (1986), Kubitzki (1990).

13. (PSS 16; S 115, 117; SL 30) **Pneumathodes:** absent (0); present and scattered all around petiole and/or rachis (1); present and borne in discrete lines or patches on petiole and/or rachis (2). Bower (1923, 1926), Davis (1991), Kubitzki (1990), Wolf et al. (1999).
14. (PSS 17; SL 23, 24, 25) **Blade/leaf/pinna articulation:** absent (0); present (1). Leaf articulation is common in seed plants. In ferns, blade/leaf articulation regularly occurs in Davalliaceae and Polypodiaceae (including grammitids), and it occurs occasionally in some other families (e.g., Cyatheaceae, Dryopteridaceae, Osmundaceae (*Osmunda*), Lygodiaceae (*Lygodium*), and Thelypteridaceae). von Goebel (1930), Bierhorst (1971), Gifford and Foster (1988), Kubitzki (1990).
15. (PSS 19; R 55; S 95; SL 31) **Adaxial outline of petiole and rachis:** convex to flattened (0); sulcate (1). Kubitzki (1990).
16. (PSS 21) **Sclerenchyma fibers:** absent (0); present (1). Sclerenchyma fibers are scored as absent in *Angiopteris* and *Marattia,* even though they sometimes possess isolated sclereids in the hypodermis of the petiole. These cells, however, are never arranged in bundles or fibers. Ogura (1972), Hill and Camus (1986), Kubitzki (1990).
17. (PSS 22, R 13) **Epipetiolar branches:** absent (0); present (1). Troop and Mickel (1968), Ogura (1972), Qiu et al. (1995), Kubitzki (1990).
18. (PSS 23; R 11, 40; S 90, 91; SL 40) **Petiole stele number (from base to apex):** monostele at base, polystele above (0); monostele throughout (1); distele at base, monostele above (2), polystele throughout (3); distele throughout (4). Bower (1923, 1926), Keating (1968), Bierhorst (1971), Ogura (1972), Lin and DeVol (1977, 1978), White and Turner (1988), Kubitzki (1990).
19. (PSS 24; R 41, 43, 44, 45, 46) **Xylem configuration in petiole (from base to apex):** horseshoe-shape variation (C, U, V, Q, , or low arc) with petiole center parenchymatous (0); solid T, O or -shape in petiole center (1); X-shape (sometimes becoming V towards petiole apex) (2); three arcs: two 7-shaped abaxial strands and one arc-shaped adaxial strand (3); polycyclic (4). Bower (1923, 1926), Keating (1968), Bierhorst (1971), Ogura (1972), Lin and DeVol (1977, 1978), White and Turner (1988), Kubitzki (1990).
20. (SL 15) **Leaf vascular bundle:** amphicribal (0); collateral (1). The similarity between vascular bundles in the leaves of Ophioglossaceae and seed plants has often been used as an argument to support a close relationship between them (Kato 1988). Ogura (1972), Esau (1977), Gifford and Foster (1988), Fahn (1990).
21. (NCSF 23; D 12) **Leaf trace:** mesarch (0); endarch (1). Ogura (1972), Esau (1977), Gifford and Foster (1988), Fahn (1990).
22. (New) **Intercalary meristem:** absent (0); present (1). Intercalary growth is reported only for the euphylls of seed plants (Hagemann 1984) but not for euphylls of other tracheophytes. It is often interpreted as a primary difference between leaves of ferns and derived seed plants. Intercalary growth plays an important role in the development of lycophylls in Lycopsida (Freeberg and Wetmore 1967; R. Imaichi pers. comm.), and it is also reported for Anthocerotopsida (Kenrick and Crane 1997). This indicates that intercalary growth may be more widespread in Embryophyta.

I. B. Shoot. The terms shoot and rhizome are used synonymously in this section.—

23. (M et al. 82; KC 3.2, 3.3; SL 4, 5, 6) **Independent, branched sporophyte with multiple sporangia:** absent (0); present (1). This character combines the independence and branching of sporophytes. Further division of this character might be useful only if some fossil taxa were included. Sporophytes of some vascular plants are generally unbranched, as in Ophioglossales and Marattiales, but mature sporophytes are independent and have multiple sporangia. In some groups of vascular plants, especially Lycopodiales, Psilotales, and Ophioglossales, the gametophyte is long-lived and it is attached to the sporophyte for a long time. von Goebel (1930), Gifford and Foster (1988), Rothwell (1995).
24. (D18; GR 122; NCSF 7; PSS 92; R 35; SL 18) **Position of protoxylem:** exarch (0); mesarch (1); endarch (2). Pryer et al. (1995) excluded this character, stating that data were insufficient or unreliable for many fern taxa. The position of protoxylem poles is determined by the direction of xylem differentiation. Xylem maturation information is available for all major basal land plant groups. It is not clear if all leptosporangiate ferns have mesarch protoxylem, as suggested by Stevenson and Loconte (1996), or if some may be endarch. The difference between endarch and mesarch may reflect the size of the protoxylem poles. Reduction of the vascular tissue may lead from endarch to mesarch protoxylem poles, or, in extreme cases, to the exarch maturation pattern (Hymenophyllaceae). Bierhorst (1971), Ogura (1972), Esau (1977), Fahn (1990).
25. (PSS 26; R 5; S 122; SL 8) **Shoot symmetry:** radial (0); dorsiventral (1); both (2). Semi-erect to erect shoots are treated as radial, while creeping shoots are interpreted as dorsiventral. *Equisetum* and *Psilotum* have two different kinds of shoots, a creeping subterranean shoot and an erect aerial shoot. This is treated as a combination of dorsiventral and radial shoot symmetry, rather than as a polymorphism, because both growth forms are observed consistently and uniformly in all individuals and species of both genera. Bower (1923, 1926, 1928), Kaplan (1977), Kubitzki (1990), Kato and Imaichi (1997), Takiguchi et al. (1997).
26. (PSS 27; R 27, 28, 29, 30, 31, 32, 33, 39; S 119-121; SL 19; NCSF 4; D 16) **Mature shoot stele type:** eustele (0); protostele (1); ectophloic siphonostele (2); amphiphloic siphonostele or solenostele (3); dictyostele (4). Pryer et al. (1995) treated this character as four states, which was certainly useful in their attempt to analyze the relationships of ferns. Stevenson and Loconte (1996) defined seven states, because they had a more diverse dataset. Based on treatments by Schmid (1982) and Stein (1993), the character states are redefined here to reflect developmental aspects observed in various groups of vascular plants. Distinction of further types (e.g., equisetostele) appears to be non-informative for our dataset. Ogura (1972), Stevenson (1980), Beck et al. (1982), Tryon and Tryon (1982), Hill and Camus (1986), White and Turner (1988), Kubitzki (1990), Stein (1993), Qiu et al. (1995).
27. (PSS 28; R 34; S 123) **Vascular stele cycles:** monocyclic (0); polycyclic (1). Ogura (1972), Hill and Camus (1986), Kubitzki (1990).
28. (PSS 29; R 50; SL 16) **Vascular cambium in shoot:** absent (0); present (1). Bierhorst (1971), Ogura (1972), Esau (1977), Khandelwal and Goswami (1977), Gifford and Foster (1988), Kato (1988), Fahn (1990), Stevenson (1990), Bhambie (1994), Nixon et al. (1994), Doyle (1996).
29. (M et al. 107; R 23) **Shoot indumentum:** absent (0); present (1). Primary shoots possessing any trichome-like structures (hairs, scales) are scored as present. Indument may be ephemeral (or transient) in some taxa. Bierhorst (1971), Martens (1971), Gifford and Foster (1988), Kubitzki (1990), Stevenson (1990), Kenrick and Crane (1997), Norstog and Nicholls (1997).
30. (M et al. 107; PSS 30, 31; R 24; S 82; SL 43) **Shoot indumentum type:** hairs (0); scales (1). Pryer et al. (1995) separated hairs and scales into two characters. Scales are defined here as modified hairs. Hairs are also found in taxa with scales. Furthermore, transitions between hairs and scales are known, such as the bristles in some Pteridaceae and "hair-scales" in Gleicheniaceae. Kubitzki (1990).
31. (New) **Hairs with a swollen, multicellular base:** absent (0); present (1). Hairs with a swollen, multicellular base are restricted to Loxomataceae. Ogura (1972), Kubitzki (1990).
32. (SL 11) **Stem sclerenchyma:** absent (0); present (1). Sclerenchymatous cells are absent in some highly specialized plant groups such as Isoëtaceae, Marattiaceae, Ophioglossaceae, and Psilotaceae (*Tmesipteris*). Sclerenchyma is defined here as groups of elongated cells with remarkably thick cell walls and without cytoplasm when mature. Ogura (1972), Esau (1977), Hill and Camus (1986), Fahn (1990).
33. (NCSF 1, R 10) **Axillary buds:** absent (0); present (1). Axillary buds are known only in seed plants. Reports by Hébant-Mauri (1972) and Hagemann (1989) for ferns (*Trichomanes*) are based on an inadequate distinction between the shoot construction of ferns and seed plants. Ferns lack axillary buds. von Goebel (1930), Gifford and Foster (1988).
34. (NCSF 2) **Short shoots:** absent (0); present (1). Plant architecture with short shoots (dwarf shoots, spur shoots) is restricted to seed plants. Highly modified lateral shoots are found in some filmy ferns (Hymenophyllaceae) (Schneider 2000), but they are not homologous to short shoots in seed plants. von Goebel (1930), Gifford and Foster (1988).
35. (New) **Shoot with extensive system of lacunae/canals:** absent (0); present (1). *Equisetum* has a unique shoot organization. This character combines the arrangement of leaves in whorls of six or more and a system of three kinds of lacunae/canals in the shoot (medullary canal, vallecular canal, protoxylem canal). Ogura (1972), Kubitzki (1990).

I. C. Root.

36. (GR 115; PSS 33; R 15; S 2; SL 1) **Roots:** absent (0); present (1). Roots are absent in a few highly specialized plant groups. Some authors (e.g., Rothwell and Erwin 1985) have expressed doubts that roots of Lycophytina and Euphyllophytina are homologous, but rather that they are the product of convergent evolution. The fossil record does not provide the necessary evidence to answer this question (Kenrick and Crane 1997). Structural similarities indicate a common origin. von Goebel (1930), Gifford and Foster (1988), Schneider (1996).
37. (New) **Rhizomorphs (rhizophores):** absent (0); present (1). Roots of *Selaginella* and *Isoëtes* originate in a modified shoot structure, the rhizomorph or rhizophore (Paolillo 1982). This structure is sometimes

confused with roots, because the modified shoot is located in a similar position to roots on the shoot. Roots of all other tracheophytes originate from an unmodified part of the shoot. Stewart (1947), Karrfalt (1977, 1981, 1982, 1984), Paolillo (1982), Rothwell (1984), Rothwell and Erwin (1985), Imaichi and Kato (1991), Jernstedt et al. (1992), Yi and Kato (2001).

38. (PSS 79; SL 1) **Root origin:** primary allorhizic (0); homorhizic or secondarily allorhizic (1). Character reflects the embryonic orientation of the root pole to the shoot pole. Primary allorhizic patterns are the result of the root pole not in opposition to the shoot pole (unipolar embryo). Embryos of homorhizic plants have shoot poles in opposition to root poles (bipolar embryo). The first root is short-lived in Magnolidra, especially Liliopsida. Their root systems are classified as secondarily allorhizic. von Goebel (1930), Gifford and Foster (1988), Groff and Kaplan (1988).

39. (PSS 80; SL 2) **Root branching:** dichopodial, exogenous origin (0); monopodial, endogenous origin (1). von Goebel (1930), von Guttenberg (1960, 1961, 1966), Gifford and Foster (1988).

40. (New) **Lateral root origin in endodermis:** absent (0); present (1). Character is applicable only to taxa with monopodial, branching roots. Lateral roots in leptosporangiate ferns, Marattiaceae, and Ophioglossaceae originate in the endodermis, while their place of origin in seed plants is the pericycle/pericambium. The endodermis is part of the inner cortex and the pericycle is part of the vascular tissue. In *Equisetum*, lateral roots originate in a layer internal to the endodermis, which is formed by a division of the initial cells of the endodermis. von Guttenberg (1960, 1961, 1966, 1968a, b), Gifford (1993).

41. (PSS 34; R 17; S 4, SL 3) **Root hairs:** present (0); absent (1). Root hairs are absent only in Ophioglossaceae, but they are sometimes rare or uncommon in water plants such as *Isoëtes* and Marsileaceae. The expression of root hairs in aquatic taxa is influenced by environmental conditions. Therefore, root hairs are treated as present in aquatic taxa, but scored as absent in Ophioglossaceae (terrestrial). von Guttenberg (1968a, b), Ogura (1972), Schneider (1996).

42. (S 6, SL 3) **Root hair structure:** non-septate (0); septate (1). Root hairs are always unicellular, though they appear multicellular in Marattiaceae. This is the result of septae formed by the cell walls. Septate root hairs also occur occasionally in some species of *Actinostachys* and *Oleandra*. Ogura (1972), Hill and Camus (1986), Schneider (1996).

43. (S 3) **Rhizodermis cells:** undifferentiated (0); differentiated into long and short cells (1). Trichoblasts (rhizodermis cells that develop root hairs) and atrichoblasts (rhizodermis cells without root hairs) do not differ in shape and size in most land plants, but they are differentiated in some taxa (e.g., *Anemia* pro parte, *Azolla*, *Equisetum*, *Huperzia*, *Lygodium* pro parte, *Schizaea*). Leavitt (1904), von Guttenberg (1968a, b), Ogura (1972), Schneider (1996).

44. (S 8) **Root pith:** absent (0); present (1). In leptosporangiate ferns, the vascular tissue forms a compact circle with a central pith in the center of the root cross-section, whereas non-vascular tissue is central in Equisetopsida, Marattiopsida, and Ophioglossopsida. A pith is also present in most gymnosperms, such as *Cycas*, and some angiosperms (monocots) but absent in eudicots. von Guttenberg (1968a, b), Ogura (1972), Esau (1977), Fahn (1990), Stevenson (1990), Norstog and Nicholls (1997), Schneider (1996).

45. (PSS 35; R 16; S 9) **Number of protoxylem poles in root:** variable, ranging from monarch to 18-arch (0); variable, ranging from monarch to hexarch, rarely non-arch (1); usually diarch, rarely triarch (2). This character describes the number of protoxylem poles in the vascular tissue of a root of a mature plant. Roots of young plants tend to have fewer protoxylem poles than roots of mature plants. Derived leptosporangiate ferns always possess diarch vascular bundles in roots. The number of protoxylem poles is more variable in eusporangiate ferns and seed plants and often corresponds to size of the plant. More than two protoxylem poles usually are found in Hymenophyllaceae, Gleicheniaceae, and some other early-diverging fern families. von Guttenberg (1968a, b), Schneider (1996).

46. (S 18) **Aerenchyma in root cortex:** absent (0); present, septate cells not differentiated (1); present, septate cells differentiated (2). Aerenchymatous tissue is found only in *Azolla*, *Acrostichum*, *Ceratopteris*, *Equisetum*, *Isoëtes*, *Marsilea*, *Pilularia*, and *Selaginella*. Cells separating the lacunae are defined as septate cells. The septae of marsileaceous aerenchyma are composed of parenchymatous cells with a unique shape (Schneider 1996). von Guttenberg (1968a, b), Ogura (1972).

47. (PSS 94, S 12) **Inner root cortex:** parenchymatous (0); sclerenchymatous (1). The root cortex of ferns is divided into an inner and outer cortex, which is the product of two different cell lineages. The majority of modern leptosporangiate ferns possess a sclerenchymatous inner root cortex. von Guttenberg (1968a, b), Schneider (1996).

48. (PSS 94, S 10) **Outer root cortex:** parenchymatous (0); sclerenchymatous (1). A sclerenchymatous outer root cortex is common in Osmundaceae, Gleicheniaceae, and some close relatives. von Guttenberg (1968a, b), Schneider (1996).

49. (S 15) **Cells of the innermost cell layer of the root cortex:** not different in size, shape, and/or number from the adjacent cell layers (0); remarkably different in size, shape, and/or number (1). Cells of the innermost cell layer of the root cortex can obviously differ from the adjacent cell layers in size and shape in some fern families (e.g., Lindsaeaceae, Pteridaceae, Schizaeaceae, sensu Smith et al. 2006). Schneider (1996).

I. D. Anatomical and morphological characters that are applicable to more than one sporophyte organ.

50. (PSS 81; S 1) **Apical meristem of root and shoot:** with single apical cell or up to 4 initial cells (0); more than 4 initial cells, complex meristem (1). A salient feature of all ferns except Marattiaceae and Osmundaceae is that a single, conspicuous apical cell is present in the zone of surface initials, and this cell can usually be identified at some point in the development of the apex (Gifford 1983, 1985). This single cell may be replaced by up to four conspicuous cells in Marattiaceae and Osmundaceae, though Imaichi (1986) has shown that the shoot apex of *Angiopteris lygodiifolia* possesses a single apical cell. This information supports the presence of a monoplex apex (with a single initial) in all fern groups, including Equisetaceae, Ophioglossaceae, and Psilotaceae. Monoplex apical meristems are also known from some species of *Selaginella* (von Guttenberg 1966; Philipson 1990), but Lycopodiaceae and Isoëtaceae have a more complex apical meristem. Complex apical meristems are also known from Spermatophytata, but these differ in their structure from those of Lycopsida. Additionally, each order of Lycopsida (Isoëtales, Lycopodiales, Selaginellales) has a unique type of apical meristem. Karrfalt (1977) reported the exceptional occurrence of a single apical cell in *Isoëtes*, but the genus usually possesses complex apical meristems. Bower (1923), von Guttenberg (1960, 1961), Bierhorst (1971, 1977), McAlpin and White (1974), Gifford and Corson (1977), Stevenson (1976, 1978), Imaichi (1977), Halperin (1978), White (1979), Gifford (1983, 1985, 1991, 1993), Klekowksi (1985), Imaichi and Nishida (1986), Gifford and Foster (1988), Hébant-Mauri (1993), Barlow (1994a, b).

51. (S 7) **Endodermal cells in root and shoot:** primary type (0); secondary type (1); tertiary type (2). The endodermal cells of all land plants show a similar development. Initially, a Casparian strip is formed (primary), followed by a suberin lamella that develops to cover all cell walls (secondary). Only in angiosperms does the cell wall thickness increase in an additional step (tertiary). Lycopsida, Equisetopsida, eusporangiate ferns (Marattiaceae, Ophioglossaceae, Psilotaceae) and some leptosporangiate ferns (Osmundaceae, Salviniaceae, vittarioid ferns in the Pteridaceae, and a few Hymenophyllaceae) possess only the primary stage, while all other ferns and gymnosperms form endodermal cells with a suberin lamella. Most species of Hymenophyllaceae have a secondary endodermis, but the primary type is known in some species of *Vandenboschia*. Their occurrence is considered an apomorphy for this taxon. Ogura (1938), von Guttenberg (1947), Van Fleet (1961), Schneider (1996).

52. (M et al. 83; SL 12, 13) **Xylem and phloem differentiation:** absent (0); present (1). Specialized cells with a conductive function (hydroids and leptoids) in some Bryopsida (Polytrichaceae) are often described as "precursors" to tracheids and sieve cells. Hydroids/tracheids and leptoids/sieve cells do share functional features, but they may represent convergent structures. Tracheids occurring in the gametophyte of *Psilotum* (Bierhorst 1971; Hébant 1976) may be present only because of the longevity of this phase, and they do not provide phylogenetic information. Esau (1977), Hébant (1979), Fahn (1990), Kenrick and Crane (1991), Cook and Friedman (1998), Ligrone et al. (2000).

53. (D 14; NCSF 8; PSS 25; R 37, 38; SL 17) **Primary xylem bordered pits:** scalariform (0); circular (1); conifer-type (2). Kato (1988) pointed out the presence of bordered pits in Ophioglossaceae as a shared similarity with conifers. Pryer et al. (1995) and Stevenson and Loconte (1996) interpreted this character in two different ways, but both with two character states. Stevenson and Loconte (1996) scored only for the presence or absence of conifer-like bordered pits, while Pryer et al. (1995) scored differences in the shape of the pits. These are regularly scalariform in most ferns, but more circular pits (without borders of the conifer-type) are found in Lycopsida, Equisetaceae, Psilotaceae, Marattiaceae, and Cycadaceae. White (1963a, b), Esau (1977), Fahn (1990).

54. (D 25; NCSF 15) **Companion cells:** absent (0); present (1). Companion cells are known only in angiosperms. Companion cells occurring in

flowering plants differ in their ultrastructure from Strassburger cells found in the phloem of Coniferidra, Cycadatae, Ginkgoatae, and Gnetidra, which could be a synapomorphy of a gymnosperm clade. However, neither Strassburger cells nor companion cells are found in lycophytes and ferns. Presence of Strassburger cells is not scored as an independent character state, and detailed studies are needed to confirm the homology assessment given in Behnke and Sjolund (1990). Perry and Evert (1975), Warmbrodt (1980), Kubitzki et al. (1993).

55. (New) **Sieve cells with refractive spherules:** absent (0); present (1). A detailed comparative study is lacking for the ultrastructure of sieve elements in ferns; however, refractive spherules appear to be a common character in Euphyllophytina but absent in Lycophytina. Perry and Evert (1975), Warmbrodt (1980), Behnke and Sjolund (1990), Kenrick and Crane (1997).

56. (D 11; PSS 12; SL 35) **Guard mother cell division:** diameristic (0); parameristic (1); anomomeristic (2). Hauke (1957), Kondo (1962), Pant (1965), Van Cotthem (1970, 1973), Pant and Khare (1971), Fryns-Claessens and van Cotthem (1973), Kubitzki et al. (1993), Payne (1979), De et al. (1991), Baranova (1992), Sen and De (1992).

57. (PSS 13) **Origin of cells surrounding guard cells:** perigenous (0); mesogenous (1); mesoperigenous (2). Kondo (1962), Pant (1965), Van Cotthem (1970, 1973), Pant and Khare (1971), Fryns-Claessens and van Cotthem (1973), De et al. (1991), Baranova (1992), Sen and De (1992), Kubitzki et al. (1993).

58. (SL 14) **Mucilage-producing hairs:** absent (0); present (1). Mucilage-producing hairs are present in various groups of ferns. The character may reflect ecological constraints. Tryon and Tryon (1982), Kubitzki (1990).

I. E. Sorus/Sporangia/Spores.

59. (PSS 47; R 65) **Sorus:** absent (0); present (1). Eames (1936), Bierhorst (1971), Tryon and Tryon (1982), Hill and Camus (1986), Kubitzki (1990).

60. (PSS 48) **Sorus outline:** round (0); elongate (1). As in *Azolla* (Salviniaceae), the Marsileaceae possesses an elongate receptacle, which is attached to the sporocarp wall only at the receptacle base. Eames (1936), Bierhorst (1971), Tryon and Tryon (1982), Hill and Camus (1986), Kubitzki (1990), Nagalingum et al. (2006).

61. (PSS 49; R 60, 61, 62; SL 47) **Sporangial position on bladed fertile leaf-segments:** abaxial, marginal to dorsal (0); adaxial (1). Sporangia are located either on the abaxial or the adaxial side of leaves. Some ferns show a marginal position of the sporangia, but they are located closer to the abaxial than to the adaxial side. The distinction between the dorsal and marginal position of sporangia that is used for the identification of fern genera is informative only for phylogenetic analyses focused on derived families or genera, but not for relationships across all ferns. The identification of dorsal position is blurred in some taxa because the blade is highly reduced in the fertile part of the leaf (e.g., *Osmunda*, *Plagiogyria*). Marginal versus dorsal position of the sporangia may be the result of developmental changes reflecting different dispersal strategies. Bower (1923, 1926, 1928), Eames (1936), Kubitzki (1990), Qiu et al. (1995), Churchill et al. (1998).

62. (PSS 50; R 68; S 30, 31; SL 49) **Sporangial maturation within sori:** simultaneous (0); gradate (1); mixed (2). This character refers to the maturation of sporangia either within sori, or with respect to adjacent sporangia on a fertile leaf, or part of a leaf, if sporangia are not arranged in sori. Bower (1923, 1926, 1928), Eames (1936), Kubitzki (1990).

63. (PSS 51; R 67) **Number of sporangia per sorus:** few, 1 to 12 (0); many, usually more than 20 (1). Bower (1923, 1926, 1928), Eames (1936), Kubitzki (1990).

64. (PSS 97; S 56; SL 52, 54) **Hairs/scales associated with receptacle and/or sporangium (paraphyses):** absent (0); present (1). Paraphyses are specialized hairs that, when present, are associated with sporangia, or at least with the receptacle. Soral structure is often not well studied, and paraphyses are used in a broad sense to identify hairs or glands associated with sporangia and/or sori. All taxa scored for paraphyses in this dataset have hairs. Modified sporangia, sometimes considered paraphyses, are better treated as a separate character. Modified sporangia are found only in some mostly derived leptosporangiate ferns (e.g., Cyatheaceae, Polypodiaceae) and therefore appear uninformative in this study. In addition, we consider hairs attached to capsules as paraphyses. This condition could also be treated as a separate character. Wagner (1964), Baayen and Hennipman (1987), Kubitzki (1990).

65. (PSS 52, 53; R 70; S 49; SL 57) **False indusium (= Pseudoindusia):** absent (0); present (1). Any protective covering of sori or sporangia formed by a strongly reflexed or otherwise modified leaf margin is identified here as a false indusium. In some cases, false indusia cover sporangia not clustered in sori (e.g., *Lygodium*). The sporangia covering lobes of *Lygodium* are the outgrowth of the lamina of the sporangia bearing digits. This unqiue organization is either homologous to false-indusia or a unique structure evolved independently in this lineage of ferns. Slightly reflexed and largely unmodified marginal leaf tissues are not considered to be false indusia. In some cases, indusia are made up of components that are derived from both the receptacle (abaxial leaf surface) and the leaf margin (e.g., some Dicksoniaceae), forming a "cup-like" structure. The lips of the indusial "involucre" in some Hymenophyllaceae are flared outward on both the adaxial and abaxial sides. The involucre of filmy ferns 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 components of indusia in Hymenophyllaceae may be unique in ferns. It is unclear if this structure is homologous to false indusia and it is scored here as unknown. Bower (1923, 1926, 1928), Eames (1936), Bierhorst (1971), Tryon and Tryon (1982), Kubitzki (1990), Churchill et al. (1998).

66. (PSS 52, 53; R 69; S 48; SL 56) **True indusium:** absent (0); present (1). This character includes any protective covering of sori that is attached to the receptacle/abaxial leaf surface. Indusia of Marsileaceae and Salviniaceae are the most complex and difficult to interpret; however, Nagalingum et al. (2006) have shown that these heterosporous ferns possess true indusia. Bower (1923, 1926, 1928), Bierhorst (1971), Tryon and Tryon (1982), Churchill et al. (1998), Kubitzki (1990), Nagalingum et al. (2006).

67. (PSS 54) **Attachment of true indusium relative to sori:** lateral (0); basal (1); central (2). Bower (1923, 1926, 1928), Bierhorst (1971), Tryon and Tryon (1982), Kubitzki (1990).

68. (PSS 55) **Opening of true indusium:** introrse (0); extrorse (1); suprasoral (2); circumsoral (3); none (4). Bower (1923, 1926, 1928), Bierhorst (1971), Tryon and Tryon (1982), Kubitzki (1990).

69. (PSS 83; R 66; SL 51; D 41) **Sporangial fusion resulting in a synangium:** none (0); sporangia wholly or partly fused (1). Fused microsporangia (Doyle, 1996), as in Gnetidra and Magnolidra, are interpreted here as a type of synangium. Synangia have likely evolved several times independently in homosporous and heterosporous lineages. Bierhorst (1971), Tryon and Tryon (1982), Hill and Camus (1986).

70. (PSS 43; SL 60) **Sporangium receptacle:** none or flat (0), convex (1); columnar to elongate, attached to lamina only at receptacle base (2). The receptacle is a difficult character to code, and developmental and comparative studies are required to understand this character. Our coding reflects what we know. Campbell (1895), Eames (1936), Bierhorst (1971), Kubitzki (1990), Churchill et al. (1998).

71. (SL 61) **Sporangial shape:** reniform (0); globose to elongate (1). Sporangial shape of heterosporous ferns is based on the microsporangium. von Goebel (1930), Gifford and Foster (1988), Kenrick and Crane (1997), Nagalingum et al. (2006).

72. (PSS 42; R 73, 79; S 23; SL 48) **Sporangial wall thickness/development:** more than two cell layers, eusporangiate development (0); one cell layer, leptosporangiate development (1). The sporangia of Osmundaceae differ from other leptosporangiate ferns in several characters. The outer layers of the tapetum are persistent, which is why the sporangial wall has sometimes been reported as two-layered (Bower 1923, 1926). They also differ slightly in their development from other leptosporangiate ferns (Bierhorst 1971). Detailed comparative studies that illustrate the changes in the development of sporangia in early-diverging leptosporangiate ferns are lacking. In spite of the differences, the sporangia in Osmundaceae are clearly leptosporangiate, but with some similarities to conditions found in eusporangiate ferns, especially Marattiaceae. von Goebel (1930), Gifford and Foster (1988).

73. (PSS 44; R 72; S 32) **Sporangial stalk length:** sessile to short, as long as wide and up to twice as long as wide (0); long, 3 to 10 times longer than wide (1), extremely long, 50-80 times longer than wide (2). This character may be influenced by the presence of indusia. Campbell (1895), Bierhorst (1968, 1969, 1971), Kubitzki (1990).

74. (PSS 45; R 71; S 33; SL 63) **Sporangial stalk width:** more than six cell rows wide (0); four to six cell rows wide (1); one to three cell rows wide (2). Campbell (1895), Bierhorst (1968, 1971), Kubitzki (1990).

75. (PSS 46; R 78; SL 67) **Spore output per sporangium:** one thousand or more (0); more than one hundred, but fewer than one thousand (1); fewer than one hundred (2). Bower (1923, 1926, 1928), Bierhorst (1971), Tryon and Tryon (1982), Kubitzki (1990), Tryon and Lugardon (1991).

76. (PSS 56; R 74; S 24; SL 64) **Annulus:** absent (0); present (1). Bower (1923, 1926, 1928), Bierhorst (1971), Tryon and Tryon (1982), Kubitzki (1990), Qiu et al. (1995).

77. (PSS 57; R 74, 75, 76, 77; S 26, 27; SL 64) **Annulus aspect on sporangium:** apical (0); lateral (1); oblique to transverse (2); vertical to slightly

oblique (3). Bower (1923, 1926, 1928), Bierhorst (1971), Tryon and Tryon (1982), Kubitzki (1990), Qiu et al. (1995).

78. (PSS 58; R 74, 76, 77; S 28; SL 64) **Annulus span across sporangium:** continuous bow (0); interrupted bow (1); restricted patch (2). Bower (1923, 1926, 1928), Bierhorst (1971), Tryon and Tryon (1982), Kubitzki (1990), Qiu et al. (1995).

79. (PSS 98; R 77; SL 65) **Orientation of sporangial dehiscence:** longitudinal (0); transverse (1). Orientation of the dehiscence line is relative to the point of attachment of the sporangial capsule. Bower (1923, 1926, 1928), Kubitzki (1990).

80. (D 42; R 83; SL 66) **Mechanisms of sporangial dehiscence:** ectokinetic (0); endokinetic (1). The dehiscence of microsporangia is used here to code seed plants. Endothecial dehiscence of angiosperm microsporangia is scored as a subset of endokinetic dehiscence, as discussed in Nixon et al. (1994) and Doyle (1996).

81. (PSS 59; R 80; S 35; SL 68) **Sporogenesis:** homosporous (0); heterosporous (1). Labouriau (1958), Bell (1979), Tryon and Lugardon (1991).

82. (M. et al. 100; SL 112) **Seeds:** absent (0); present (1). Gifford and Foster (1988), Kubitzki (1990).

83. (New) **Monoplastidic meiosis:** present (0); absent (1). Monoplastidic cell division is common in algae and monoplastidic mitosis is known only from Anthocerotopsida. Monoplastidic meiosis is reported for Bryopsida, Selaginellaceae, and Isoëtaceae. Mitosis and meiosis always seem to be polyplastidic in leptosporangiate ferns and seed plants. The spindle construction is different from polyplastidic divisions in Marchantiopsida, and both conditions are not homologous. Both monoplastidic and polyplastidic meiosis are known in Lycopodiaceae and Marattiaceae. No studies exist for Ophioglossaceae, Equisetaceae, and Psilotaceae. Additional information is also needed for some early-diverging taxa of leptosporangiate ferns and seed plants. The presence of plastid-dividing rings may be correlated with this character (Duckett et al. 1996). Brown and Lemmon (1991a, b, 1997, 2001a, b), Pickett-Heaps et al. (1999).

84. (D 65) **Arrangement of cell plates in homospore and/or megaspore tetrad:** monolete (0); tetrahedral (1); linear (2). Doyle (1996) defined this character for the megaspore tetrad, but it is also applicable to homospore development. Tryon and Lugardon (1991).

85. (GR 102; PSS 60; R 86; SL 71) **Spore laesura:** linear (0); triradiate (1); circular (2); sulcate (3). The laesura is an exine (= exospore) structure that is sometimes covered by the perine (perispore). In heterosporous ferns (Marsileaceae, Salviniaceae), the perine is strongly modified above the laesura, but the exine shows a trilete mark, as in many other ferns. The modification of the perine to a papilla-like structure (also called acrolamella) is an independent character that is scored separately from laesura shape (see character 86). Boros and Járai-Komlódi (1975), Dehgan and Dehgan (1988), Tryon and Lugardon (1991), Hasegawa (1994), Schneider and Pryer (2002).

86. (New) **Spores with acrolamella:** absent (0); present (1). The perine (= perispore) is modified into an enlarged structure above the exine (= exospore) laesura. Such structures, called acrolamellae, are found in Marsileaceae and Salviniaceae. In previous analyses (Pryer et al. 1995, Stevenson and Loconte 1996), this character was scored as a modification of the laesura, but, as discussed above (character 85), it is more accurately defined as a transformation of the perine. Tryon and Lugardon (1991), Schneider and Pryer (2002).

87. (KC 3.13; M et al. 76; R 89; PSS 84, SL 73) **Perine/Perispore:** absent (0); solid perine present (1); reduced perine, orbicules/ubisch bodies present (2). Seed plants are often interpreted as lacking a perine, but we follow Blackmore's (1990) argument that the perine (of spores) and the outer layers of the ectexine (of pollen) are homologous. Tapetal globules that build the perispore in ferns are considered to be homologous to the orbicules or ubisch bodies produced by gymnosperms and some angiosperms. Boros and Járai-Komlódi (1975), Neidhart (1979), Blackmore (1990), Tryon and Lugardon (1991), Jarzen and Nichols (1996), Playford and Dettmann (1996), Pacini et al. (1999).

88. (PSS 63; SL 75, 76, 77, 78, 79) **Perine (= perispore) prominence relative to exine (= exospore):** absent to not prominent (0); prominent, but not cavate (1); prominent and cavate (2). This character is modified from Pryer et al. (1995) to reflect the more complex perispore of derived leptosporangiate ferns. Boros and Járai-Komlódi (1975), Neidhart (1979), Dehgan and Dehgan (1988), Brown and Lemmon (1990), Lugardon (1990), Tryon and Lugardon (1991), Lugardon and Brousmiche Delcambre (1994), Playford and Dettmann (1996).

89. (PSS 64, SL 74) **Perine (= perispore) surface:** smooth or plain (0); obviously patterned or sculptured (1). Boros and Járai-Komlódi (1975), Neidhart (1979), Tryon and Lugardon (1991).

90. (PSS 65; R 87; S 36, 37; SL 80, 84) **Exine/exospore structure:** 1- to 2-layered (0); 3-layered (1); 5-layered (2). Homology assessments of spore and pollen walls follow Blackmore (1990). Boros and Járai-Komlódi (1975), Neidhart (1979), Brown and Lemmon (1990), Lugardon (1990), Tryon and Lugardon (1991), Lugardon and Piquemal (1993), Lugardon and Brousmiche Delcambre (1994), Jarzen and Nichols (1996), Playford and Dettmann (1996), Rowley (1996).

91. (PSS 66; R 88; S 38; SL 81) **Exine/exospore surface:** smooth (0); obviously patterned or sculptured (1). Boros and Járai-Komlódi (1975), Neidhart (1979), Dehgan and Dehgan (1988), Tryon and Lugardon (1991).

92. (New) **Pseudoendospore:** absent (0); present (1). Tryon and Lugardon (1991) reported the presence of a pseudoendospore for most ferns. This structure is not homologous to the intine (= endospore). Tryon and Lugardon (1991).

93. (New) **Paraexospore:** absent (0); present (1). A unique structure of Selaginellaceae and Isoëtaceae. Tryon and Lugardon (1991).

94. (SL 72) **Spore wall development:** centripetal (0); centrifugal (1). Neidhart (1979), Rowley (1996), Tryon and Lugardon (1991).

95. (New) **Tapetum type:** parietal (0); plasmodial (1). Tapetum type is highly conserved in major groups of land plants and tapetum evolution may reflect important divergence events in land plant evolution. Detailed studies are lacking for many ferns, but all reports support the presence of a plasmodial tapetum. Comparative studies may provide evidence for further subdivision of the character states. Pacini and Franchi (1991), Parkinson and Pacini (1995), Pacini (1997).

96. (New) **Harmomegathic character of spores/pollen:** maximum size in water (0); maximum size in sucrose concentrations (1). The term *harmomegathic* (Pacini 1990) describes the behavior of spores and pollen in water. Spores of "pteridophytes" and "bryophytes" have their maximum size in water, whereas pollen of seed plants achieves a maximal size in sucrose solutions. This character reflects a change in chemical composition of the spore wall between "pteridophytes" and seed plants.

97. (PSS 61; S 46; SL 69) **Spores chlorophyllous:** no (0); yes (1). Kubitzki (1990), Tryon and Lugardon (1991).

II. Gametophyte—

98. (PSS 67; S 140, 141; SL 85) **Spore germination pattern:** equatorial (0); polar (1); amorphous (2). Data missing for several taxa. Campbell (1895), Nayar and Kaur (1968, 1971), Bierhorst (1971), Duckett and Pang (1984), Whittier and Pintaud (1999).

99. (KC 3.16; PSS 68; R 93; S 132, 133, 134, 135; SL 90) **Gametophyte form:** tuberous (0); filamentous (1); cordate to elongate thalloid (2); reduced to relatively few cells (3). Pryer et al. (1995) coded *Equisetum* as elongate thalloid. Similarly, Stevenson and Loconte (1996) coded *Equisetum* as ribbon-like. Neither assessment fits well with the descriptions by Duckett (1973, 1979). *Equisetum* gametophytes are more adequately described as tuberous-cylindrical with filamentous to lamellar appendages; we treat them here as tuberous. Gametophytes of bryophytes are more complex and therefore more difficult to characterize. For purposes of our analysis, we compare the juvenile gametophyte stages of bryophytes with the adult gametophytes of tracheophytes, since they are developmentally homologous to one another. Darnell-Smith (1917), Bower (1923, 1926, 1928), Holloway (1939), Stokey (1951), Atkinson and Stokey (1964), Schuster (1967, 1992), Bierhorst (1971), Nayar and Kaur (1971), Atkinson (1973), Duckett (1973, 1979), Tryon and Tryon (1982), Kubitzki (1990), Whittier and Pintaud (1999).

100. (New) **Gametophyte with *Gleichenia*-type club-shaped hairs:** absent (0); present (1). Only club-shaped hairs that develop from special wedge-shaped initial cells are scored. This kind of hair development is known only from gametophytes of Gleicheniaceae. Club-shaped gametophytic hairs found in other fern groups differ in their development. Nayar and Kaur (1971).

101. (New) **Gametophyte with bristle- to scale-like hairs:** absent (0); present (1). Gametophytes with bristle-like hairs are known only from Loxomataceae and Cyatheaceae. These hairs are large, pluricellular, thin-walled, chlorophyllous, 2 to several cells wide, and several cells long. Nayar and Kaur (1971).

102. (GR 4; PSS 71; SL 88) **Obligate mycorrhizae in gametophytes:** absent (0); present (1). Obligate mycorrhizae are restricted to non-green gametophytes. Mycorrhizae are known also from different groups of vascular land plants with green, autotrophic gametophytes (e.g., Marattiaceae, Osmundaceae). Pryer et al. (1995) included the presence of facultative mycorrhizae in this character, but the occurrence of facultative types of mycorrhizae is insufficiently studied. Spores of taxa with non-green gametophytes germinate in dark, while light induces germination of taxa with green gametophytes (Whittier and Pintaud 1999). Boullard (1957, 1979), Peterson et al. (1981), Kubitzki (1990), Schmid and Oberwinkler (1995).

103. (KC 6.37; PSS 72; SL 88) **Gametophyte dependence:** independent (0); dependent megaspore, endosporic gametophyte (1); dependent on sporophyte (2). Bell (1979), Gifford and Foster (1988).
104. (KC 3.22) **Gametangia distribution:** widely distributed (non-terminal) (0); more or less terminal (1). The position of gametangia is one of the main differences between the Lycophytina and Euphyllophytina. Gifford and Foster (1988), Kubitzki (1990).
105. (KC 3.23; M et al. 93) **Paraphyses between gametangia:** absent (0); present (1). Schuster (1967, 1992), Kubitzki (1990).
106. (GRD 5; PSS 73; R 95; SL 96) **Position of antheridia on gametophyte:** embedded or slightly projecting (0); partially to fully exposed (1). This character is correlated with the development of antheridia (Kenrick and Crane 1997). Detailed investigations of the developmental processes associated with antheridia may provide important information about the evolution of early-diverging groups of ferns. Campbell (1895), Schuster (1967, 1992), Bierhorst (1971), Nayar and Kaur (1971), Renzaglia (1978).
107. (PSS 75, R 96; SL 99) **Number of antheridial wall cells:** > 5 (0); 3 - (rarely) 5 (1). Schuster (1967, 1992), Nayar and Kaur (1971), Tryon and Tryon (1982).
108. (GRD 7; PS 110; SL 98) **Antheridial operculum:** absent (0); lateral, circular (1); terminal, circular (2); triangular (3); pore (4). It is not possible to determine the character state that best applies to heterosporous taxa, which have extremely reduced antheridia. This is also the case for other antheridial characters, such as the presence of an apical cell and stalk. Hartman (1931), Atkinson and Stokey (1964), Nayar and Kaur (1971), Duckett and Bell (1977), Garbary et al. (1993), Garbary and Renzaglia (1998).
109. (GRD 2; M et al. 1) **Apical cell in antheridial ontogeny:** absent (0); present (1). Atkinson and Stokey (1964), Nayar and Kaur (1971), Duckett and Bell (1977), Garbary et al. (1993), Garbary and Renzaglia (1998).
110. (GRD 6; M et al. 5) **Antheridial stalk:** absent (0); present (1). Atkinson and Stokey (1964), Schuster (1967, 1992), Nayar and Kaur (1971), Duckett and Bell (1977), Garbary et al. (1993), Garbary and Renzaglia (1998).
111. (GRD 4; SL 101) **Spermatogenous cell arrangement:** blocks (0); random (1); single (2). Campbell (1895), Bower (1923), Garbary et al. (1993).
112. (GRD 10; M et al. 7; PSS 111; SL 102) **Number of sperm cells:** more than 1,000 (0); 100 to 1,000 (1); 16 to 64 (2); 2 to 15 (3). Bower (1923), Eames (1936).
113. (D 79; GRD 8; M et al. 6; R 97; SL 100) **Sperm transfer with pollen tube:** absent, zooidogamous (0); suspended, zooidogamous (1); penetrating, siphonogamous (2). Gifford and Foster (1988).
114. (GDR 56; M et al. 12; PSS 112; SL 103) **Sperm flagellae:** biflagellate (0); multiflagellate, 3-29 (1); multiflagellate, 30 to 100 (2); multiflagellate, (> 100) 1,000 to 10,000 (3). Detailed observations on sperm flagellae are published for only a few genera. Little is known about the constancy of flagellae number per sperm cell in leptosporangiate ferns. However, it is clear that all leptosporangiate ferns examined have between 30 and 80 flagellae and recent studies (Renzaglia et al. 2000) have shown that *Psilotum* has about 36 flagellae. Sperm cells of lycophytes differ substantially in their development from sperm cells of bryophytes and euphyllophytes (Renzaglia and Maden 2000). In addition, the development of sperm cell basal bodies is identical in taxa of ferns and seed plants (Cycadatae and Ginkgoatae) with free sperm cells. This character is not applicable to taxa that do not have suspended sperm cells (Knox and Ducker 1991). Duckett and Bell (1977), Garbary et al. (1993), Maden et al. (1997), Garbary and Renzaglia (1998), Renzaglia et al. (1999, 2000, 2001), Renzaglia and Maden (2000), Renzaglia and Garbary (2001).
115. (GRD 19; M et al. 14) **Basal body position:** side-by-side (0); staggered anterior-posterior (1); staggered continuous (2). This character reflects the relative position of basal bodies to the flagellae. Duckett and Bell (1977), Carothers and Duckett (1979), Duckett and Carothers (1979), Garbary et al. (1993), Maden et al. (1997), Garbary and Renzaglia (1998), Renzaglia et al. (1999).
116. (GRD 18; KC 3.30; M et al. 13) **Bicentriolar centrosomes:** absent (0); present (1). This character addresses the centriolar development of spermatid mother cells in antheridia. This character may be correlated with the presence of biflagellate sperm. Duckett and Bell (1977), Carothers and Duckett (1979), Duckett and Carothers (1979), Garbary et al. (1993), Maden et al. (1997), Garbary and Renzaglia (1998), Renzaglia et al. (1999).
117. (GRD 16; M et al. 11) **Point of origin of centrioles:** sperm mother cell (0); sperm mother cell progenitor (1). Duckett and Bell (1977), Garbary et al. (1993), Maden et al. (1997), Garbary and Renzaglia (1998), Renzaglia et al. (1999).
118. (GD 80; M et al. 60) **Monoplastidic sperm cells:** absent (0); present (1). Duckett and Bell (1977), Garbary et al. (1993), Maden et al. (1997), Garbary and Renzaglia (1998), Renzaglia et al. (1999).
119. (GRD 12; M et al. 8) **Nascent sperm cells:** paired (0); not paired (1). Duckett and Bell (1977), Garbary et al. (1993), Maden et al. (1997), Garbary and Renzaglia (1998), Renzaglia et al. (1999).
120. (D 77) **Number of nuclei per microgametophyte:** five or more (0); four (1); three (2). Atkinson and Stokey (1964), Schuster (1967, 1992), Bierhorst (1971), Nayar and Kaur (1971), Duckett and Bell (1977), Gifford and Foster (1988), Garbary et al. (1993), Garbary and Renzaglia (1998).
121. (KC 3.21; PSS 74; SL 106) **Position of archegonia on gametophyte:** embedded or slightly projecting (0); partially exposed (1); fully exposed (2). Coding of character states follows Pryer et al. (1995), but one more state is added here based on Kenrick and Crane (1997). Schuster (1967, 1992), Nayar and Kaur (1971), Hasegawa (1994).
122. (PSS 76; SL 108) **Number of archegonial neck cell tiers:** more than six cells high (0); one to five (rarely six) cells high (1). Bower (1926), Schuster (1967, 1992), Bierhorst (1971), Nayar and Kaur (1971), Gifford and Foster (1988).
123. (PSS 114; SL 105) **Neck canal cell:** multinucleate (0); binucleate (1). Bierhorst (1971), Nayar and Kaur (1971), Schuster (1967, 1992).
124. (D 81, SL 104) **Megagametophyte:** large, completely cellular, with cellular archegonia (0); large, apical portion with egg free-nuclear (1); eight-nucleate, central portion free-nuclear, egg cellular but without neck cells (2). Bierhorst (1971), Gifford and Foster (1988).

III. Embryo—The embryo is recognized separately from the sporophyte because its phenotypic expression may be largely influenced by the gametophyte—

125. (D 84) **Product of fertilization:** diploid zygote and embryo (0); diploid zygote and embryo plus triploid endosperm tissue (1). Gifford and Foster (1988).
126. (PSS 41; R 99) **First division of zygote:** horizontal (0); vertical (1); free-nuclear phase (2). Bierhorst (1971), Gifford and Foster (1988), Hasegawa (1994).
127. (R 101; SL 110) **Embryo orientation:** exoscopic (0); endoscopic (1); prone (2). Bierhorst (1971), Kubitzki (1990), Kenrick and Crane (1997).
128. (R 100; SL 109) **Suspensor:** absent (0); present (1). The development of a suspensor is a fixed condition in some land plant groups. von Guttenberg (1960, 1961, 1966).
129. (KC 3.6; SL 111) **Foot:** large, tapering (0); large, bulbous (1); small, bulbous (2); absent (3). The development of a foot is a fixed character in some early diverging groups of land plants. However, an accurate estimation of relative size requires morphometric studies. Wardlaw (1955, 1965), von Guttenberg (1960, 1961, 1966), Schuster (1967, 1992), Bierhorst (1971), Gifford and Foster (1988), Ligrone et al. (1993).
130. (D 86) **Embryo development:** derived from a single, uninucleate cell by cellular division (0); derived from several free nuclei (1). Wardlaw (1955, 1965), Gifford and Foster (1988), Bierhorst (1971).

IV. Life Cycle—

131. (New) **Gametophyte/sporophyte life-span:** Gametophyte phase dominant: gametophyte long-lived, sporophyte short-lived (0); gametophyte and sporophyte both long-lived (1); sporophyte phase dominant: sporophyte long-lived, gametophyte short-lived (2). The shift from an isomorphic to a heteromorphic life cycle is a crucial innovation in the evolution of land plants (Kenrick and Crane 1997; Stewart and Rothwell 1993). "Bryophytes" are distinct from all other extant embryophytes by having a dominant gametophyte phase. In all tracheophytes, the sporophyte is the dominant phase, but the duration of the gametophyte compared to that of the sporophyte varies among the major lineages. Seed plants and most ferns have a short-lived gametophyte phase, whereas Equisetaceae, Lycopodiaceae, Ophioglossaceae, and Psilotaceae have long-lived gametophytes. This is also the case in some early diverging groups of ferns (e.g., Hymenophyllaceae). An extremely short-lived gametophyte is correlated with heterosporous reproduction and may be a prerequisite for the evolution of heterospory (DiMichele et al. 1989). Kenrick (1994), Kubitzki (1990), Kenrick and Crane (1997).
132. (New) **Number of photosynthetic leaves per shoot at any given time:** two or more (0); one (1). Shoots of Ophioglossaceae develop only one photosynthetically active leaf at any given time. Future leaves are present but do not contain chlorophyll, and they are completely enclosed by the single green leaf. The leaf growth is correlated with seasonal changes in temperate and subtropical regions. Tropical Ophioglossaceae, such as *Helminthostachys*, show a similar behavior,

although a correlation with "seasons" is not obvious. All other vascular plants with euphylls possess more than one photosynthetic leaf at any given time, with the exception of the early stages of embryo development. Kubitzki (1990).

V. Biochemistry—The presence of chemical constituents reflects the activity of cellular enzymes and these could potentially provide phylogenetic information. Problems with these kinds of characters include: little is known about their biosynthesis, reports on the presence of constituents are based on doubtful identifications of taxa, not all constituents are reported, and the absence of constituents is often not noted—

133. (GR 61, 105; KC 4.36; M et al. 84) **Lignin:** absent (0); present (1). Lignin is an important component of the cell walls of tracheids. The chemical composition may differ among the major lineages of land plants, but detailed studies are lacking for many taxa. Angiosperms and Gnetales differ from other seed plants by the absence of the Mäule reaction; however, data are inconsistent and insufficient to add this as a character state. Cooper-Driver (1977), Logan and Thomas (1985), Soeder (1985), Markham (1988), Gottlieb et al. (1990), Wallace (1991), Cooper-Driver and Bhattacharya (1998), Rausher et al. (1999).

134. (GR 63, 108; M et al. 108) **Flavonoids:** absent (0); at least flavones and/or biflavonoids present (1). The flavonoid pathway is present in all tracheophytes. All reports indicate Psilotaceae and Lycopsida possess only flavones and biflavonoids, while all other tracheophytes also produce more derived constituents such as flavonols, flavanones, and flavanols. The presence of flavones reflects the activity of chalcone isomerase. Flavonoids are also known from some Marchantiopsida, but not from Anthocerotopsida and Bryopsida. Reports of flavonoid constituents (e.g., flavonols, flavanones) are incomplete and therefore it is not possible to use their presence or absence in a phylogenetic analysis at this level. Cooper-Driver (1977), Logan and Thomas (1985), Soeder (1985), Markham (1988), Gottlieb et al. (1990), Wallace (1991), Cooper-Driver and Bhattacharya (1998), Rausher et al. (1999).

135. (SL 115) **Pro-anthocyanidins:** absent (0); present (1). Anthocyanidins are among the most derived products of the flavonoid pathway. The presence of pro-anthocyanidins reflects the presence of dihydroflavonol reductase. True anthocyanins, the products of anthocyanin synthase, appear to be restricted to angiosperms. Cooper-Driver (1977), Logan and Thomas (1985), Soeder (1985), Markham (1988), Gottlieb et al. (1990), Wallace (1991), Cooper-Driver and Bhattacharya (1998), Rausher et al. (1999).

VI. Molecular Data—Certain macromolecular structural features of DNA (e.g., absence or presence of introns, see Qiu et al. 1998, Wikström and Pryer 2005) lend themselves well to being incorporated in a morphological study. It is unfortunate that these data (structural DNA characters) are available for a limited number of taxa—

136. (M et al. 105; SL 116) **Chloroplast inversion:** absent (0); present (1). Raubeson and Jansen (1992), Raubeson and Stein (1995), Pahnke et al. (1996).