

APPENDIX TO BE MADE AVAILABLE ONLINE

APPENDIX 3. (All references are in Literature Cited of printed manuscript, except for those that appear **only** in Appendix 3—see below). Characters and character states considered here, but excluded from this study either for lack of accessible information, highly ambiguous homology concepts, or because they were not informative in a maximum parsimony analysis. Characters derived from published studies are indicated in parentheses by an author abbreviation followed by the character number. 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). Additional characters excluded from this study, but pertinent only to seed plants or "bryophytes", are not listed below. For examples, see Garbary et al. (1993), Mishler et al. (1994), Nixon et al. (1994), Doyle (1996), Kenrick and Crane (1997), and Garbary and Renzaglia (1998).

I. SPOROPHYTE

I. A. LEAF

137. (SL 34) Ligule: absent (0); present (1). Not informative with this dataset.

The presence of a scale-like structure on the adaxial surface of the leaf is known only from Selaginellaceae and Isoëtaceae in living plants. The structure is also known from fossil Lycopsida (Kenrick and Crane 1997). Structures on leaves of some monocots (e.g., palms, grasses) that are also called ligules are not homologous to ligules of *Isoëtes* and *Selaginella*. Goebel (1930), Bierhorst (1971), Kubitzki (1990), Kenrick and Crane (1997).

138. (PSS 10) Blade hairs: absent (0); present (1). In nearly all euphyllophytes, young euphylls possess hairs, but the adult leaves vary from naked to densely covered with hairs. The density of hairs may be relatively constant for species and sometimes for genera too, but higher taxa, such as families, are mostly polymorphic. The persistence of hairs probably reflects adaptations to dry environments and other environmental stresses. Hairs are of interest for studies focusing on the phylogeny of genera and families, but the character does not offer suitable information for deep level phylogeny. Kubitzki (1990).

139. (PSS 18; S 112) Trophopods: absent (0); present (1). This character is informatively variable at the genus level. Wagner and Johnson (1983), Kubitzki (1990).

140. (PSS 86) Non-appendicular leaves: absent (0); present (1). Not informative because non-appendicular leaves occur in very few species that are not closely related. Bierhorst (1968, 1969, 1973, 1974), Kaplan (1977).

141. (R 18) Planation of vegetative leaves: absent (0); present (1). Not informative with this dataset.

142. (R 19) Biseriate vegetative leaves: absent (0); present (1). Not informative with this dataset.

143. (R20) Quadriseriate branching of vegetative leaves: absent (0); present (1). Not informative with this dataset.

144. (PSS 88) Winged petiole and/or rachis: absent (0); present (1). Not informative with this dataset. Kubitzki (1990).

145. (SL 33) Laminar buds: absent (0); present (1). This character is variable within genera and may reflect ecologically-induced convergence. Kubitzki (1990).

146. (PSS 6) Secondary vein form: isotomous, dichotomous (0); anisotomous, dichotomous (1). Secondary and tertiary veins tend to be dichotomously branched. This character may be highly influenced by environmental and developmental constraints. Bower (1923, 1926).

147. (SL 39) Paracostal commissure: absent (0); present (1). Not informative with this dataset. Kubitzki (1990).

148. (SL 50) Submarginal commissure: absent (0); present (1). Not informative with this dataset. Bower (1923, 1926, 1928), Kubitzki (1990).

149. (SL 53) Vascular commissure: absent (0); present (1). Not informative with this dataset. Bower (1923, 1926, 1928), Kubitzki (1990).

150. (PSS 8; SL 38) Vein areoles: with free included veinlets (0); without free included veinlets (1). Not informative with this dataset. Bower (1923, 1926), Kubitzki (1990).

151. (PSS 40) Hypodermis: absent (0); present (1). Insufficient information. This character is difficult to discern. Davis (1991), Ogura (1972), Payne and Peterson (1973).

152. (PSS 87; SL 41) **Hippocampus-shaped bundles in petiole:** absent (0); present (1). Interesting character for derived fern groups only. Ogura (1972).

153. (New) **Aerophores:** absent (0); present (1). Aerophores are modified pneumathodes that extend as knob-like to peg-like structures from the petiole and rachis. They are often not well-preserved in herbarium material. Aerophores are reported for various groups of leptosporangiate ferns (e.g., Blechnaceae, Cyatheaceae, Plagiogyriaceae, Thelypteridaceae). Knoblike structures in *Culcita* and *Thyrsopteris* may be related. However, the homology of all these structures is unclear and needs further investigation. Bower (1923, 1926), Kubitzki (1990), Davis (1991).

154. (PSS 20) **Sclerenchyma coloration on petiole and rachis:** not dark-pigmented (0); dark-pigmented (1). Not informative with this dataset; probably correlated with environmental constraints. Ogura (1972), Kubitzki (1990).

155. (New) **Palisade parenchyma in mesophyll:** absent (0); present (1). In contrast to angiosperms, the mesophyll is not always differentiated into palisade and spongy parenchyma in ferns. The suppression of palisade parenchyma may be induced by environmental constraints. Ogura (1972).

156. (PSS 78; SL 29) **Blade thickness:** three or more cells thick (0); one to two (rarely three) cells thick (excluding veins) (1). The second character state is correlated with the absence of a differentiated epidermis and the absence or strong degradation of the cuticle. Reduction of blade thickness (cell layers) occurs in several groups of ferns (e.g., Hymenophyllaceae, *Hymenophyllopsis* in Cyatheaceae, Marattiaceae, and Osmundaceae). This is combined with the loss of differentiation of blade tissues (e.g., palisade parenchyma, spongy parenchyma), but the lamina is usually not so extremely

reduced to three or fewer layers. Ferns with reduced but three or more cell layers are found in Aspleniaceae (few species), Marattiaceae (*Danaea* pro parte), Osmundaceae (*Leptopteris*), Pteridaceae (*Adiantum diaphanum*). Absence of stomata in Hymenophyllaceae, *Hymenophyllopsis* (Cyatheaceae), and *Leptopteris* (Osmundaceae) is correlated with the reduction of blade thickness and cuticle loss. In contrast to seed plants, blade tissue structure is very variable in ferns. Information is incomplete, but the presence or absence of palisade parenchyma may reflect ecologically induced convergence. Ogura (1972), Kubitzki (1990).

157. (NCSF 22; PSS 89; R 26; SL 28) **Stipules:** absent (0); present (1). Stipules are found in many angiosperms, and similar structures are found also in Ophioglossaceae and Marattiaceae. Their homology is doubtful and the structures may simply be analogous. Bower (1923, 1926), Goebel (1930), Eames (1936), Hill and Camus (1986), Kato (1988), Nixon et al. (1994).

158. (PSS 9; S 98; SL 55) **Hydathodes:** absent (0); present (1). Not informative with this dataset. Presence and absence of hydathodes may correlate with ecological constraints. Ogura (1972), Kubitzki (1990).

159. (PSS 90; SL 36) **Idioblasts:** absent (0); present (1). The term idioblast is used for various kinds of specialized cells. In ferns, spicular cells are the most remarkable type of idioblast. These are sclereids or sclereid-like cells in the epidermis of the leaf. Such cells are found in different, not closely related, groups of ferns (Hymenophyllaceae, Marsileaceae, Pteridaceae—including vittarioids). Esau (1977), Wagner (1978), Fahn (1990), Kubitzki (1990).

I. B. SHOOT

160. (R 4) Model of growth: psilotoid (0); selaginelloid (1); cotyledonoid (2).

Composite character based on five criteria (Rothwell 1995); each criterion is reflected by a separate character in this study.

161. (PSS 91; R 9; SL 10) Shoot branching: dichotomous (0);

pseudodichotomous (1); anisotomous, sympodial (2); anisotomous, monopodial (3).

Branching patterns are very variable in ferns and are often correlated with growth form and ecological constraints. The particular pattern does not appear to be informative, although careful comparative observations are lacking. Bell (1994), Bierhorst (1971), Bower (1923), Hagemann (1980), Goebel (1930), Kaplan (1977), Kubitzki (1990), Roth (1963).

162. (New) Origin of lateral branches: exogenous (0); endogenous (1). An

unusual origin of the lateral branches, which can be named *endogenous*, was described for *Equisetum* by Hofmeister (1851) and recently confirmed by Stützel and Jädicke (2000). Lateral branches are developed exogenously in all other vascular plants, but the sporophytes of some vascular plants, such as in Marattiales and Ophioglossales, are generally unbranched. So far, endogenous branching appears to be an apomorphy for *Equisetum*; therefore the character was excluded as uninformative for judging relationships among vascular plants. Hofmeister (1851), Stützel and Jädicke (2000).

163. (R 7; SL 7) Trunk: absent (0); present (1). Trunk-like shoots have evolved

in various unrelated groups of vascular plants. The character reflects ecological constraints. Presence of trunks is usually correlated with secondary growth, although

trunks of palms and ferns show that this is not always true. Rothwell (1999) used the term arborescent for the same character. Kubitzki (1990), Kubitzki et al. (1993).

164. (SL 9) Stem filiform: absent (0); present (1). Filiform stems are present in various unrelated groups of vascular plants. The character reflects ecological constraints. Kubitzki (1990).

165. (R 6) Growth as a liana: absent (0); present (1). The liana growth form has evolved independently in various groups of seed plants. Gifford and Foster (1988), Goebel (1930).

166. (R 14) Unvascularized enations: absent (0); present (1). Not informative with this dataset. Various structures such as scales and thorns are classified as unvascularized enations. Bierhorst (1971).

167. (PSS 32; S 83; SL 44) Shoot scales: uniformly colored (0); sharply bicolored (1); clathrate (2). Not informative with this dataset. Kubitzki (1990).

168. (R 36) Peripheral loops in the shoot vascular tissue: absent (0); present (1). Not informative with this dataset. Stein (1993).

169. (PSS 82; R 52) Vascular cambium directionality: unifacial (0); bifacial (1). Not informative with this dataset. Unifacial cambia are described for *Botrychium*, *Isoetes*, and some fossil tracheophytes (non-seed plants) with secondary growth. Ogura (1972), Esau (1977), Khandelwal and Goswami (1977), Kato (1988), Fahn (1990), Bhambie (1994).

170. (R 51) Xylem rays: absent (0); present (1). Not informative with this dataset. Martens (1971), Esau (1977), Fahn (1990), Kubitzki (1990), Stevenson (1990), Norstog and Nicholls (1997).

171. (NCSF 11) Xylem rays structure: uniseriate/biseriate (0); some multiseriate (1). Not informative with this dataset. Esau (1977), Fahn (1990), Kubitzki (1990), Stevenson (1990), Norstog and Nicholls (1997).

172. (R 47) Cortical sclerenchyma: continuous cylinder (0); absent (1); scattered nests or bundles (2); discontinuous cylinder (3). Insufficient information. Ogura (1972).

173. (R 48) Pith sclerenchyma: absent (0); present (1). Insufficient information. Ogura (1972).

174. (R 49) Sclerenchyma accompanying vascular tissue of stele: absent (0); present (1). Insufficient information. Ogura (1972).

175. (R 12) Branches alternating with leaves at nodes: absent (0); present (1). Not informative with this dataset. Bierhorst (1971).

I. C. ROOT

176. (PSS 95) Root hair distribution pattern: scattered (0); densely matted (1). Not informative with this dataset.

177. (PSS 96) Sporophyte fungal associations: absent (0); present, facultative (1); present, obligate (2). Few careful observations are published. Mycorrhizae appear to be correlated with habitat and are absent mainly in epiphytes, aquatics, and xerophytes. New information is also required to improve the definition of character states. Boullard (1957, 1979), Gemma et al. (1992), Moteete et al. (1996), Schmid et al. (1996).

178. (S 17) Root cortex cells with spiral cell wall thickenings: absent (0); present (1). Not informative with this dataset. Schneider (1996).

**I. D. ANATOMICAL AND MORPHOLOGICAL CHARACTERS THAT ARE
APPLICABLE TO MORE THAN ONE SPOROPHYTE ORGAN**

179. (PSS 36, R 1, 2, 3) **Habitat:** terrestrial (0); epiphytic (1); rooted aquatic (2); floating aquatic (3). Each character state reflects a suite of anatomical and morphological characters that may be the result of adaptation. The character is not independent from other characters that are included in this study (e.g., 36, 46). Scoring of actual morphological features rather than ecological features is preferred here for phylogenetic studies because they reflect inherited genetic information and are less likely to be excluded due to assumed ecological functions. Kubitzki (1990).

180. (D 14; NCSF 3) **Apical meristems divided into corpus and tunica:** absent (0); present (1). Loconte and Stevenson (1990) and Doyle and Donoghue (1992) discuss this character, which is not applicable to meristems with a single apical cell. It is not known if layers in the apical meristems of Lycopsidea correspond to the corpus/tunica divisions in seed plants. Guttenberg (1960, 1961), Gifford and Corson (1977), Halperin (1978), Gifford and Foster (1988).

181. (PSS 39) **Intranuclear paracrystals:** absent (0); present (1). Insufficient information. Fabri and Menicanti (1970).

182. (SL 113) **Pyrenoids:** absent (0); present (1). Insufficient information. Gifford and Foster (1988).

183. (New) **Structure of starch grains:** pteridophyte-type (0); other types (1). Starch grains of the pteridophyte-type are known for all groups of "pteridophytes" but also for Gingkoatae, Coniferidra, and Gnetidra (Czaja 1978). They are rare in

Magnolidra, which possess starch grains with a more complex structure. Complex starch grains are also found in Cycadatae. Little is known about the ultrastructure of starch grains in mosses. Further studies are needed because this character may be phylogenetically informative.

184. (New) Secondary xylem differentiated into tracheary elements and fibers: absent (0); present (1). This character is informative only for plants with secondary growth. The primary difference between angiosperm wood and all other woods is the differentiation of two cell types (vessels and fibers). Martens (1971), Esau (1977), Fahn (1990).

185. (D 19; NCSF 12; PSS 38, 93) Vessel perforation (= true vessels or tracheary elements): imperforate (0); scalariform or foraminate (1). It has long been accepted that tracheary elements are almost restricted to angiosperms. However, recent studies (e.g., Carlquist and Schneider 1999) have shown their widespread distribution in ferns. Tracheary elements may be absent in only a few groups of tracheophytes, but many taxa are insufficiently studied. Absence of tracheary elements is certain only for *Ginkgo* and *Pinus*. The degree of specialization in tracheary elements may not correlate with phylogenetic position as much as it depends on ecological and physiological factors (Carlquist and Schneider 1999, 2001). Bierhorst (1958, 1971), White (1961, 1963a, b), Martens (1971), Esau (1977), Fahn (1990), Kim et al. (1993), Li et al. (1999), Schneider and Carlquist (1999, 2000).

186. (R 54) Periderm: absent (0); present (1). The formation of a periderm is correlated with secondary growth. Peterson (1971), Esau (1977), Khandelwal and Goswami (1979), Fahn (1990), Bhambie (1994).

187. (New) Sieve tubes: absent (0); present (1). Sieve tubes are reported only from angiosperms, but detailed studies may find similar structures in other groups of land plants. As with vessels/tracheids the distinction between sieve cells and sieve tubes is not clear. Esau (1969), Behnke and Sjolund (1990).

188. (PSS 37; S 20; SL 14) Mucilage canals and/or cavities: absent (0); present (1). Stevenson and Loconte (1996) combined mucilage-producing hairs and schizogenous tissues into one character, but they are certainly not homologues. Cavities and canals occur in Marattiaceae and some seed plants. The differences between mucilage ducts and laticifers are rather unclear. Ogura (1972), Esau (1977), Hill and Camus (1986), Fahn (1990), Kubitzki (1990), Mahlberg (1993), Datta and Iqbal (1994).

189. (KC 3.15) Stomata: absent (0); present (1). Loss of stomata is a sporadic, but widespread, phenomenon in ferns and other land plants. In filmy ferns (Hymenophyllaceae), the character appears to be related to reduction of blade thickness and loss of cuticle. Kubitzki (1990).

190. (PSS 104; S 79, 80, 81, SL 114) Chromosome numbers: These are highly variable in some groups while constant in others. No obvious groupings could be made. Duncan and Smith (1977), Löve et al. (1977).

191. (PSS 115) Apogamous life cycle: absent (0); present (1). Apogamous life cycles have evolved independently in various groups of vascular plants. Asexual life cycles may be an advantage in different ecological conditions. Sheffield and Bell (1987), Bell (1979).

I. E. SORI/SPORANGIA/SPORES

192. (M et al. 106; R 56) **Sporangia borne on leaves:** absent (0), present (1).

Character correlated with euphylls. Crane and Kenrick (1997), Kenrick and Crane (1997).

193. (SL 46) **Sporophyll shape:** bifacial (0); peltate or pseudopeltate (1). Not informative with this dataset. Character correlated with presence of lycophylls or euphylls. Kenrick and Crane (1997).

194. (SL 45) **Strobili:** absent (0); present (1). Sporophyll arrangement into strobili may evolve independently. Bierhorst (1971), Page (1972), Taylor (1981), Gifford and Foster (1988), Kato (1988), Stewart and Rothwell (1993), Crane and Kenrick (1997).

195. (R 63, 64) **Sporangia attached to a modified part of adaxial leaf surface:** absent (0); present (1). All sporangia of Ophioglossaceae are attached to a stalk-like structure (sporangiphore) that has its origin in an early division of the apical meristem of the leaf (Imaichi and Nishida 1986). A very similar condition is found in Psilotaceae (Siegert 1964, 1965, 1967, 1969, 1970, 1973; Rouffa 1978). This structure may be a synapomorphy for the Ophioglossaceae/Psilotaceae clade, but this arrangement of sporangia could also be the basal condition for the Euphyllphytina. It is not possible to interpret the arrangement of the sporangia of extant Equisetopsida without a detailed study that includes the sporangia of fossil sphenopsid groups. Similar studies are needed to determine the condition of early-diverging extinct seed plants. Bierhorst (1971), Page (1972), Taylor (1981), Kato (1988), Stewart and Rothwell (1993), Crane and Kenrick (1997), Gifford and Foster (1988), Grauvogel-Stamm and Ash (1999).

196. (New) **Schizaeoid sorophores:** absent (0); present (1). Sporangia assembled on strongly modified leaf segments or leaf lobes. The character appears to be a putative synapomorphy of schizaeoid ferns (Anemiaceae, Lygodiaceae, Schizaeaceae).

Sori on modified segments occur, however, sporadically in many families, e.g., Tectariaceae, Dryopteridaceae, Woodsiaceae (*Deparia*), and Polypodiaceae. Bower (1926), Kubitzki (1990), Gandolfo et al. (2000).

197. (R 58) Sporocarps: absent (0); present (1). Critical investigations have led to a reassessment of the homology of structures associated with sporangia and sori in heterosporous ferns (Marsileaceae, Salviniaceae), leading to a redefinition of sporocarps. The character is an apomorphy of the heterosporous fern clade. Nagalingum et al. (2006).

198. (R 59) Monosporangiate sporocarps: absent (0); present (1). Character based on non-homologous structures (Nagalingum et al. 2006).

199. (SL 62) Sporocarp germination: fragmentation (0); gelatinous (1). Informative only for heterosporous ferns (Marsileaceae, Salviniaceae).

200. (SL 58) Acrostichoid sporangia: absent (0); present (1). Not informative with this dataset. Kubitzki (1990).

201. (SL 59) Involucre: absent (0); present (1). An involucre sensu stricto is restricted to Hymenophyllaceae, but assessment of its homology relative to true indusia, or false indusia, is unclear. Bower (1926). Bierhorst (1971).

202. (PSS 99) Stomium cell differentiation: Insufficient information. In derived leptosporangiate ferns, the annulus does not form a continuous bow. It is interrupted by parenchymatous cells that are arranged in three groups: hypostomium, stomium, epistomium. The number of stomium cells differs among the major groups of derived leptosporangiate ferns and this character may be very important in a phylogenetic analysis directed at their relationships. Wilson (1959), Kubitzki (1990), Edwards (1996).

203. (PSS 102) Spore dimensions: Dimension of spores is usually correlated with ploidy and no trend was observed that might be pertinent at deeper phylogenetic levels. Tryon and Lugardon (1991).

204. (PSS 100; R 86; SL 70) Spore shape: globose (0); tetrahedral (1); monolete (1). Correlated with the shape of laesura. Monolete spores have a linear laesura, while tetrahedral spores have a triradiate laesura. Globose spores have triradiate, circular, or sulcate laesura, but this is not informative for this dataset. Tryon and Lugardon (1991).

205. (PSS 101) Laesura length: A highly variable character. Tryon and Lugardon (1991).

206. (SL 80) Exine (= exospore) type: *Lycopodium*-type (0); *Selaginella*-type (1); *Psilotum*-type (2); *Equisetum*-type (3); *Ophioglossum*-type (4); *Osmunda*-type (5); *Gleichenia*-type (6); Filicean-type (7). Insufficient information. Tryon and Lugardon (1991).

207. (R 91) Fine structure of meio/microspore perine (= perispore): solid (0); filamentous (1); lamellar (2). Insufficient information. Tryon and Lugardon (1991).

208. (PSS 62; S 43; SL 82) Spore equatorial flange (cingulum): absent (0); present (1). Not informative with this dataset. Tryon and Lugardon (1991).

209. (R 90) Perine forming elaters: absent (0); present (1). This character is an autapomorphy of the extant genus *Equisetum*. The fossil record of the *Equisetum* lineage indicates that not all members of the lineage formed elaters. In general, elaters were present in various genera of the horsetail lineage but these structures were lacking in others (Taylor and Taylor 1990). The evolution of this character in the horsetail lineage requires further study. Tryon and Lugardon (1991).

210. (SL 83) Spore proximal flange: absent (0); present (1). Not informative with this dataset. Tryon and Lugardon (1991).

211. (R 92) Meio/microspore massulae: absent (0); present (1). Informative only for heterosporous ferns (Marsileaceae, Salviniaceae).

212. (PSS 103) Intine: absent (0); present (1). Intine (= endospore) appears to be present in all vascular plants, but its development may differ in ferns. Tryon and Lugardon (1991).

213. (New) Mesospore: absent (0); present (1). Among extant plants, a true mesospore is known only from megaspores of *Selaginella*. The character is of great interest for studies focused on the relationships of Lycopsidea. Taylor (1994).

214. (D 29) Ovule-bearing structure: pinnate (0); simple (1). Informative only for seed plants. Gifford and Foster (1988), Kubitzki (1990).

215. (D 33) Closed carpel with stigmatic pollen germination: absent (0); present (1). Informative only for seed plants. Gifford and Foster (1988).

216. (D 55) Integument: free from nucellus (0); fused more than halfway from the base of the ovule (1). Informative only for seed plants. Gifford and Foster (1988).

II. *GAMETOPHYTE*

217. (PSS 105) Gametophyte cell plate formation: Insufficient information. Atkinson and Stokey (1964), Nayar and Kaur (1971).

218. (SL 87) Gametophyte development: *Marattia*-type (0); *Osmunda*-type (1); *Drynaria*-type (2); *Adiantum*-type (3); *Ceratopteris*-type (4); *Aspidium*-type (5); polar

Anemia-type (6); polar *Vittaria*-type (7). Insufficient information. Nayar and Kaur (1971).

219. (PSS 106) Gametophyte duration: Insufficient information. This character may be correlated with growth form and various other characters (e.g., 97, 102, 103, 131).

220. (PSS 107) Gametophyte growth conditions: This character may be correlated with growth form and various other characters (e.g., 97, 102, 103, 131).

221. (PSS 69; S 137; SL 92) Gametophyte hairs: absent (0); present (1). This character includes various types of hairs, perhaps not homologous, found on gametophytes. Two specialized types of gametophyte hairs are scored here as independent characters (characters 100-101), but a general classification of gametophyte hairs is not possible without detailed ontogenetic evidence. The presence of unicellular or multicellular hairs may reflect certain environmental conditions, although multicellular hairs are restricted to few fern families. Gametophytes of many early-diverging fern lineages are naked. Nayar and Kaur (1971), Schuster (1967, 1992).

222. (PSS 70) Gametophytes green: no (0); yes (1). This character is correlated with gametophyte dependence. Independent gametophytes are green, whereas gametophytes dependent on mycorrhizae, a megaspore, or a sporophyte, are not green. Absence of chlorophyll in the gametophyte signals a change from an autotrophic to a heterotrophic life style. Bierhorst (1971), Nayar and Kaur (1971), Tryon and Tryon (1982), Gifford and Foster (1988), Kubitzki (1990), Tryon and Lugardon (1991).

223. (GR 10; KC 3.24; M et al. 79; PSS 108; SL 99) Multicellular rhizoids: absent (0); present (1). Insufficient information. Multicellular rhizoids are reported to

occur occasionally on the gametophytes of *Botrychium*, *Psilotum*, and *Stromatopteris*. Their occurrence may be related to the obligate mycorrhizae of these gametophytes. Similarly, the lack of early rhizoid development may be correlated with the presence of mycorrhizae (e.g., young gametophytes of *Botrychium*, *Huperzia*, *Ophioglossum*, *Psilotum*, *Stromatopteris*, *Tmesipteris*), or to endospory (e.g., Marsileaceae). Insufficient information precludes the use of other characters of rhizoids, such as forked rhizoids of Hymenophyllaceae. Atkinson and Stokey (1964), Bierhorst (1971), Nayar and Kaur (1971), Whittier and Pintaud (1999).

224. (PSS 109; SL 92, 93, 94) **Gametophyte hair types:** Insufficient information. Atkinson and Stokey (1964), Nayar and Kaur (1971).

225. (PSS 77; SL 89) **Gametophytes gemma-producing:** absent (0); borne from gametophyte thallus (1); borne from gametophyte rhizoids (2). In land plants, gametophytic gemmae differ in their structure and location. Gametophytic gemmae need to be studied using a comparative approach so as to clarify their homologies. Bierhorst (1971), Farrar (1967, 1974), Nayar and Kaur (1971), Farrar and Johnson-Groh (1990), Kubitzki (1990), Dassler and Farrar (1997).

226. (PSS 110; SL 102) **Antheridial dehiscence:** Insufficient information. Bower (1923), Atkinson and Stokey (1964), Bierhorst (1971), Nayar and Kaur (1971).

227. (SL 95) **Antheridium size:** massive (0); minute (1). Needs re-evaluation. This character is likely correlated with the number of cells making up the antheridium and the number of sperm cells per antheridium. Atkinson and Stokey (1964), Nayar and Kaur (1971).

- 228. (SL 97) Antheridial basal cell origin:** antheridial initial (0); thallus (1).
Insufficient information. Atkinson and Stokey (1964), Nayar and Kaur (1971).
- 229. (GRD 72; M et al. 53) Mitochondria associated with plastids in young spermatids:** absent (0); present (1). Insufficient information. Duckett and Bell (1977), Garbary et al. (1993), Maden et al. (1997), Garbary and Renzaglia (1998), Renzaglia et al. (1999).
- 230. (GRD 74; M et al. 54) Specialized anterior mitochondrion in spermatids:** present (0); absent (1). Insufficient information for this dataset. Duckett and Bell (1977), Garbary et al. (1993), Maden et al. (1997), Garbary and Renzaglia (1998), Renzaglia et al. (1999).
- 231. (M et al. 55) Specialized posterior mitochondrion in spermatids:** present (0); absent (1). Insufficient information for this dataset.
- 232. (GRD 75; M et al. 56) Additional mitochondria in anterior of cell in spermatids:** absent (0); row of mitochondria behind anterior mitochondrion (1); numerous, unspecialized mitochondria (2). Insufficient information. Duckett and Bell (1977), Garbary et al. (1993), Maden et al. (1997), Garbary and Renzaglia (1998), Renzaglia et al. (1999).
- 233. (M et al. 57) Origin of anterior mitochondrion:** fusion (0); elongation (1).
Insufficient information. Duckett and Bell (1977), Garbary et al. (1993), Maden et al. (1997), Garbary and Renzaglia (1998), Renzaglia et al. (1999).
- 234. (GRD 77; M et al. 58) Osmophilic material underneath anterior mitochondrion:** absent (0); present (1). Insufficient information. Duckett and Bell

(1977), Garbary et al. (1993), Maden et al. (1997), Garbary and Renzaglia (1998),
Renzaglia et al. (1999).

235. (PSS 113, SL 107) Archegonial neck curvature: Insufficient information.
Atkinson and Stokey (1964), Nayar and Kaur (1971).

236. (R 81) Coenocytic development of megagametophyte: absent (0); present
(1). Not informative with this dataset.

237. (R 82) Number of megaspores: more than two (0); one to two (1). Not
informative with this dataset.

238. (R 84) Nonhydrasperman pollen chamber: present (0); absent (1). Not
informative with this dataset.

239. (R 86) Integument with micropyle: absent (0); present (1). Not
informative with this dataset.

240. (D 83) Fusion of sperm cells: fusion of only one sperm cell with a female
gametophyte nucleus (0); regular fusion of both sperm cells (1). These processes appear
to be quite distinct in angiosperms and Gnetales and various authors have expressed their
doubts about a common origin of the character in both seed plant lineages (Doyle 1998b,
Friedman and Floyd 2001). Friedman and Carmichael (1996), Gifford and Foster (1988).

III. EMBRYO

241. (New) Polyembryony: present (0); absent (1). Insufficient information.
Bierhorst (1971), Nayar and Kaur (1971).

242. (M et al. 98, 99) Gametophyte-sporophyte junction: Insufficient
information. The presence and structure of transfer cells on the gametophyte and/or

sporophyte may be important conditions in the evolution of land plants. Wardlaw (1965), Bierhorst (1971), Gifford and Foster (1988), Ligrone et al. (1993).

IV. LIFE CYCLE

243. (New) Life cycle length (spore to spore): more than two years (0); one to two years (1); less than one year (2). Some early-diverging fern groups have a very long life cycle length with more than three to five years (e.g., *Botrychium*) required from spore to spore. This is also the case for Lycopodiaceae. In contrast, most leptosporangiate ferns complete their life cycle in one or two years. Not enough data are available at this time, and taxa with long life cycles may have a heterotrophic gametophyte with obligate mycorrhizae. The length of the life cycle is influenced by the plant habit, especially in large arborescent sporophytes, which need years before they produce spores. The time-span of the sporophytic generation is very variable in some lineages of seed plants. Kubitzki (1990).

V. BIOCHEMISTRY

244. (New) Auxin metabolism: low IAA conjugate level (0); high IAA conjugate level (1). Insufficient information. Modifications of the auxin metabolism pathway may be important in the evolution of plant development. Stein et al. (1999).

245. (New) Product of chlorophyll degradation: RCCR-3 (0); RCCR-0, RCCR-1 or RCCR-2 (1). Insufficient information. Present data indicate RCCR-3 to be the product in Lycophyta, several fern lineages (including Equisetopsida, Marattiales, Psilotales), and some lineages of seed plants. RCCR-0 and RCCR-2 are found in

leptosporangiate ferns (Polypodiopsida), several genera of conifers (Coniferidra), and angiosperms (Magnolidra). Hoertensteiner et al. (2000).

VI. MOLECULAR DATA

246. (New) *ndhB* duplication in cpDNA: absent (0); present (1). Insufficient information. Raubeson and Stein (1995).

247. (New) *psbA* plus two inversions in cpDNA: absent (0); present (1). Insufficient information. Stein et al. (1992), Raubeson and Stein (1995).

248. (New) *chlL* partial duplication in cpDNA: absent (0); present (1). Insufficient information. Raubeson and Stein (1995).

249. (New) *cox2.i3* intron in mtDNA: absent (0); present (1). Insufficient information. Qiu et al. (1998) and Qiu pers. comm.

250. (New) *cox2.i4* intron in mtDNA: absent (0); present (1). Insufficient information. Qiu et al. (1998) and Qiu pers. comm.

251. (New) Group II intron in *nad5* gene in mtDNA: absent (0); present (1). Insufficient information. Vangerow et al. (1999) and Vangerow pers. comm.

252. (New) Second intron in *nad1* gene in mtDNA: absent (0); present (1). Insufficient information. Gugerli et al. (2001).

253. (New) Nuclear homeodomain-leucine zipper genes: Insufficient information to define homology and occurrence of gene copies. Aso et al. (1999), Sakakibara et al. (2001).

254. (New) Nuclear phytochromes: Insufficient information to define homology and occurrence of gene copies. Basu et al. (1999), Schmidt (2000).

255. (New) Nuclear homeodomain genes: Insufficient information to define homology and occurrence of gene copies. Bharathan et al. (2002), Champagne and Ashton (2001).

256. (New) Nuclear actin genes: Insufficient information to define homology and occurrence of gene copies. Bhattacharya et al. (2000).

257. (New) Nuclear floricaula/LEAFY: Insufficient information to define homology and occurrence of gene copies. Frohlich and Estabrook (2000), Frohlich and Parker (2000), Himi et al. (2001).

258. (New) Nuclear MADS-box genes: Insufficient information to define homology and occurrence of gene copies. Hasebe and Banks (1997), Hasebe et al. (1998), Shindo et al. (1999), Winter et al. (1999), Svensson (2000), Theissen et al. (2000).

LITERATURE CITED

[For complete Literature Cited see printed manuscript. References below appear **only** in Appendix 3].

Aso, K., M. Kato, J. A. Banks, and M. Hasebe. 1999. Characterization of homeodomain-leucine zipper genes in the fern *Ceratopteris richardii* and the evolution of the homeodomain-leucine zipper gene family in vascular plants. *Molecular Biology and Evolution* 16: 544–552.

Bharathan, G., T. E. Goliber, C. Moore, S. Kessler, T. Pham, and N. R. Sinha. 2002. Homologies in leaf form inferred from KNOXI gene expression during development. *Science* 296: 1858-1860.

- Basu, D., K. Debesh, H.-J. Schneider-Poetsch, S. E. Harrington, S. R. McCouch, and P. H. Quail. 2000. Rice *PHYC* gene: structure, expression, map position and evolution. *Plant Molecular Biology* 44: 27–42.
- Bhattacharya, D., J. Aubry, E. C. Twait, and S. Jurk. 2000. Actine gene duplication and the evolution of morphological complexity in land plants. *Journal of Phycology* 36: 813–820.
- Bell, A. D. 1994. A summary of the branching process in plants. Pp. 119–142 in *Shape and form in plants and fungi*, eds. D. S. Ingram and A. Hudson. London: Academic Press.
- Bierhorst, D. W. 1958. Vessels in *Equisetum*. *American Journal of Botany* 45: 534–537.
- Bierhorst, D. W. 1973. Non-appendicular fronds in Filicales. Pp. 45–57 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.
- Bierhorst, D. W. 1974. Variable expression of the appendicular status of the megaphyll in extant ferns with particular reference to the Hymenophyllaceae. *Annals of the Missouri Botanical Garden* 61: 408–426.
- Carlquist, S. and E. L. Schneider. 1999. SEM studies on vessels in ferns. 12. Marattiaceae, with comments on vessel patterns in eusporangiate ferns. *American Journal of Botany* 86: 457–464.
- Carlquist, S. and E. L. Schneider. 2001. Vessels in ferns; structural, ecological, and evolutionary significance. *American Journal of Botany* 88: 1–13.
- Champagne, C. E. M. and N. W. Ashton. 2001. Ancestry of *KNOX* genes revealed by bryophyte (*Physcomitrella patens*) homologs. *New Phytologist* 150: 23–36.

- Czaja, A. T. 1978. *Stärke und Stärkekörner bei Gefäßpflanzen*. Stuttgart: Gustav Fischer Verlag.
- Dassler, C. L. and D. R. Farrar. 1997. Significance of form in fern gametophytes: clonal, gemmiferous gametophytes of *Callistopteris baueriana* (Hymenophyllaceae). *International Journal of Plant Sciences* 158: 622-639.
- Datta, S. K. and M. Iqbal. 1994. The laticiferous system in vascular plants. Pp. 137–161 in *Growth patterns in vascular plants*, ed. M. Iqbal. Portland: Dioscorides Press.
- Doyle, J. A. 1998b. Molecules, morphology, fossils, and the relationship of angiosperms and Gnetales. *Molecular Phylogenetics and Evolution* 9: 448–462.
- Duncan, T. and A. R. Smith. 1977. Primary basic chromosome numbers in ferns: facts or fantasies. *Systematic Botany* 3: 105–114.
- Edwards, P. J. 1996. The leptosporangium: developing a new awareness of, and a reliable database of these neglected organs. Pp. 517–521 in *Pteridology in perspective*, eds. J. M. Camus, M. Gibby, and R. J. Johns. Kew: Royal Botanic Gardens.
- Esau, K. 1969. *The Phloem*. Handbuch der Pflanzenanatomie. Band V, Teil 2. Histology. Berlin: Gebrüder Bornträger.
- Fabri, F. and F. Menicanti. 1970. Electron microscope observations on intranuclear paracrystals in some Pteridophyta. *Caryologia* 23: 729–761.
- Farrar, D. R. 1967. Gametophytes of four tropical fern genera reproducing independently of their sporophytes in the southern Appalachians. *Science* 155: 1266–1267.
- Farrar, D. R. 1974. Gemmiferous fern gametophytes - Vittariaceae. *American Journal of Botany* 61: 146–155.

- Farrar, D. R. and C. L. Johnson-Groh. 1990. Subterranean sporophytic gemmae in moonwort ferns, *Botrychium* subgenus *Botrychium*. *American Journal of Botany* 77: 1168–1175.
- Friedman, W. E. and J. S. Carmichael. 1996. Double fertilization in Gnetales: implications for understanding reproductive diversification among seed plants. *International Journal of Plant Sciences* 157: S77-S94.
- Friedman, W. E. and S. K. Floyd. 2001. The origin of flowering plants and their reproductive biology – a tale of two phylogenies. *Evolution* 55: 217– 231.
- Frohlich, M. W. and G. F. Estabrook. 2000. Wilkinson support calculated with exact probabilities: an example using *Floricaula/LEAFY* amino acid sequences that compares three hypotheses involving gene gain/loss in seed plants. *Molecular Biology and Evolution* 17: 1914–1925.
- Frohlich, M. W. and D. S. Parker. 2000. The mostly male theory of flower evolutionary origins: from genes to fossils. *Systematic Botany* 25: 155–170.
- Gandolfo, M. A., K. C. Nixon, W. L. Crepet, and G. E. Ratcliff. 2000. Sorophore of *Lygodium* Sw. (Schizaeaceae) from the Late Cretaceous of New Jersey. *Plant Systematics and Evolution* 221: 113–123.
- Gemma, J. N., R. E. Koske, and T. Flynn. 1992. Mycorrhizae in Hawaiian pteridophytes: occurrence and evolutionary significance. *American Journal of Botany* 79: 843–852.
- Grauvogel-Stamm, L. and S. R. Ash. 1999. "*Lycostrobus*" *chinleana*, an equisetalean cone from the Upper Triassic of the southwestern United States and its phylogenetic implications. *American Journal of Botany* 86: 1391–1405.

- Gugerli, F., C. Sperisen, U. Büchler, I. Brunner, S. Brodbeck, J. D. Palmer, and Y.-L. Qiu. 2001. The evolutionary split of Pinaceae from other conifers: evidence from an intron loss and a multigene phylogeny. *Molecular Phylogenetics and Evolution* 21: 167–175.
- Hagemann, W. 1980. Über den Verzweigungsvorgang bei *Psilotum* und *Selaginella* mit Anmerkungen zum Begriff der Dichotomie. *Plant Systematics and Evolution* 133: 181–197.
- Hasebe, M. and J. A. Banks. 1997. Evolution of MADS gene family in plants. Pp. 179–197 in *Evolution and diversification of land plants*, eds. K. Iwatsuki and P. H. Raven. Tokyo: Springer-Verlag.
- Hasebe, M., S. Wen, M. Kato, and J. A. Banks. 1998. Characterization of MADS homeotic genes in the fern *Ceratopteris richardii*. *Proceedings of the National Academy of Sciences USA* 95: 6222–6227.
- Himi, S., R. Sano, T. Mishiyama, T. Tanahashi, M. Kato, K. Ueda, and M. Hasebe. 2001. Evolution of MADS-box gene induction by *FLO/LFY* genes. *Journal of Molecular Evolution* 53: 387–393.
- Hofmeister, W. 1851. *Vergleichende Untersuchungen zur Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen*. Leipzig: Engelmann.
- Hoertensteiner, S., S. Rodoni, M. Schellenberg, O. I. Nandi, Y.-L. Qiu, and P. H. Maile. 2000. Evolution of chlorophyll degradation: the significance of RCC reductase. *Plant Biology (Stuttgart)* 2: 63–67.
- Kim, K., S. S. Whang, and B. Y. Sun. 1993. Tracheid structure in aerial system of several ophioglossaceous plants. *Korean Journal of Botany* 36: 337–343.

- Li, R., D. Zhang, and H. Zhang. 1999. Scanning electron microscope observations on the vessels of ferns: *Adiantum*, *Matteuccia*, and *Osmunda* from Heilongjiang province, China. *International Journal of Plant Sciences* 160: 595–602.
- Löve, A., D. Löve, and R. E. G. Pichi Sermolli. 1977. *Cytotaxonomical atlas of the Pteridophyta*. Vaduz: Cramer.
- Mahlberg, P. G. 1993. Laticifers: an historical perspective. *Botanical Review* 59: 1–23.
- Moteete, A., J. G. Duckett, and A. J. Russell. 1996. Mycorrhizas in the ferns of Lesotho. Pp. 621–631 in *Pteridology in perspective*, eds. J. M. Camus, M. Gibby, and R. J. Johns. Kew: Royal Botanic Gardens.
- Page, C. N. 1972. An interpretation of the morphology and evolution of the cone and shoot of *Equisetum*. *Botanical Journal of the Linnean Society* 65: 359–397.
- Payne, W. W. and K. M. Peterson. 1973. Observations on the hypodermis of ferns. *American Fern Journal* 63: 34–42.
- Peterson, R. L. 1971. Induction of a periderm-like tissue in excised roots of the fern *Ophioglossum petiolatum*. *Annals of Botany* 35: 165-167.
- Roth, I. 1963. Histogenese der Luftspresse und Bildung der "dichotomen" Verzweigungen von *Psilotum nudum*. *Advancing Frontiers in Plant Science* 7: 157-180.
- Rouffa, A. 1978. On phenotypic expression, morphogenetic pattern and synangium evolution in *Psilotum*. *American Journal of Botany* 65: 692–713.
- Sakakibara, K., T. Nishiyama, M. Kato, and M. Hasebe. 2001. Isolation of homeodomain-leucine zipper genes from the moss *Physomitrella patens* and the

- evolution of homeodomain-leucine zipper genes in plants. *Molecular Biology and Evolution* 18: 491–502.
- Schmid, E., F. Oberwinkler, and L. D. Gómez. 1996. Light and electron microscopy of a host-endophyte interaction in the roots of some epiphytic ferns from Costa Rica. *Canadian Journal of Botany* 72: 955–962.
- Schmidt, M. 2000. Phytochrome in Gymnospermen: Genfamilien, Evolution und Expression in *Pinus sylvestris* L. PhD. thesis. Köln (Germany): University of Cologne.
- Schneider, E. L. and S. Carlquist. 1999. SEM studies on vessels in ferns. 13. *Nephrolepis*. *American Fern Journal* 89: 171–177.
- Schneider, E. L. and S. Carlquist. 2000. SEM studies on vessels in ferns. 17. Psilotaceae. *American Journal of Botany* 87: 176–181.
- Sheffield, E. and P. R. Bell. 1987. Current studies of the pteridophyte life cycle. *Botanical Review* 53: 442–490.
- Shindo, S., M. Ito, K. Ueda, M. Kato, and M. Hasebe. 1999. Characterization of MADS genes in the gymnosperm *Gnetum parvifolium* and its implication on the evolution of reproductive organs in seed plants. *Evolution and Development* 1: 180–190.
- Siegert, A. 1964. Morphologische, entwicklungsgeschichtliche und systematische Studien an *Psilotum triquetrum* Sw. I. Erstarkung und primäres Dickenwachstum. *Beiträge zur Biologie der Pflanzen* 40: 121–157.
- Siegert, A. 1965. Morphologische, entwicklungsgeschichtliche und systematische Studien an *Psilotum triquetrum* Sw. II. Die Verzweigung (mit einer allgemeinen

- Erörterung des Begriffes "Dichotomie"). *Beitrage zur Biologie der Pflanzen* 41: 209–230.
- Siegert, A. 1967. Morphologische, entwicklungsgeschichtliche und systematische Studien an *Psilotum triquetrum* Sw. III. Das Blatt aus der Sicht der Homologien. *Beitrage zur Biologie der Pflanzen* 43: 285–328.
- Siegert, A. 1969. Morphologische, entwicklungsgeschichtliche und systematische Studien an *Psilotum triquetrum* Sw. IV. Die Bildungsabweichungen der Sporophylle. *Beitrage zur Biologie der Pflanzen* 46: 45–71.
- Siegert, A. 1970. Morphologische, entwicklungsgeschichtliche und systematische Studien an *Psilotum triquetrum* Sw. IV. Die Bildungsabweichungen der Sporophylle. *Beitrage zur Biologie der Pflanzen* 46: 435–459.
- Siegert, A. 1973. Morphologische, entwicklungsgeschichtliche und systematische Studien an *Psilotum triquetrum* Sw. IV. Die Bildungsabweichungen der Sporophylle. *Beitrage zur Biologie der Pflanzen* 49: 291–319.
- Stein, D. B., D. S. Conant, M. E. Ahgearn, E. T. Jordan, S. A. Kirch, M. Hasebe, K. Iwatsuki, M. K. Tan, and J. A. Thomson. 1992. Structural rearrangements of the chloroplast genome provide an important phylogenetic link in ferns. *Proceedings of the National Academy of Sciences USA* 89: 1856–1860.
- Sztein, A. E., J. D. Cohen, I. G. de la Fuente, and T. J. Cooke. 1999. Auxin metabolism in mosses and liverworts. *American Journal of Botany* 86: 1544–1555.
- Svensson, M. E., H. Johannesson, and P. Engström. 2000. The MAMB1 gene from the clubmoss, *Lycopodium annotinum*, is a divergent MADS-box gene, expressed specifically in sporogenic structures. *Gene* 253: 31–43.

- Stützel, T. and A. Jädicke. 2000. Verzweigung bei Schachtelhalmen. *Feddes Repertorium* 111: 15–22.
- Taylor, T. N. 1981. *Paleobotany: An Introduction to Fossil Plant Biology*. New York: McGraw-Hill.
- Taylor, T. N. and E. L. Taylor. 1993. *The biology and evolution of fossil plants*. New Jersey: Prentice Hall.
- Taylor, W. A. 1994. Recognition and characterization of inner exospore wall layers in modern and fossil lycosids - the mesospore. *Grana* 33: 44–48.
- Theissen, G., A. Becker, A. Di Rosa, A. Kanno, J. T. Kim, T. Muenster, K.-U. Winter, and H. Saedler. 2000. A short history of MADS-box genes in plants. *Plant Molecular Biology* 42: 115–149.
- Vangerow, S., T. Teerkorn, and V. Knoop. 1999. Phylogenetic information in the mitochondrial *nad5* gene of pteridophytes: RNA editing and intron sequences. *Plant Biology* 1: 235–243.
- Wagner, W. H., Jr. 1978. Venuloid idioblasts in *Pteris* and their systematic implications. *Acta Phytotaxonomica et Geobotanica* 29: 33–40.
- Wagner, W. H., Jr. and D. M. Johnson. 1983. Trophopods, a commonly overlooked storage structure of potential systematic value in ferns. *Taxon* 32: 268–269.
- White, R. A. 1961. Vessels in roots of *Marsilea*. *Science* 133: 1073–1074.
- Winter, K.-U., A. Becker, T. Münster, J. T. Kim, H. Saedler, and G. Theissen. 1999. MADS-box genes reveal that gnetophytes are more closely related to conifers than to flowering plants. *Proceedings of the National Academy of Sciences USA* 96: 7342–7347.

Wilson, K. A. 1959. Sporangia of fern genera allied with *Polypodium* and *Vittaria*.

Contributions from the Gray Herbarium 185: 97–127.