

## Patterns of segregation and convergence in the evolution of fern and seed plant leaf morphologies

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**Abstract.**—Global information on Paleozoic, Mesozoic, and extant non-angiosperm leaf morphologies has been gathered to investigate morphological diversity in leaves consistent with marginal growth and to identify likely departures from such development. Two patterns emerge from the principal coordinates analysis of this data set: (1) the loss of morphological diversity associated with marginal leaf growth among seed plants after sharing the complete Paleozoic range of such morphologies with ferns and (2) the repeated evolution of more complex, angiosperm-like leaf traits among both ferns and seed plants. With regard to the first pattern, morphological divergence of fern and seed plant leaf morphologies, indirectly recognized as part of the Paleophytic-Mesophytic transition, likely reflects reproductive and ecological divergence. The leaf-borne reproductive structures that are common to the ferns and Paleozoic seed plants may promote leaf morphological diversity, whereas the separation of vegetative and reproductive roles into distinct organs in later seed plant groups may have allowed greater functional specialization—and thereby morphological simplification—as the seed plants came to be dominated by groups originating in more arid environments. With regard to the second pattern, the environmental and ecological distribution of angiosperm-like leaf traits among fossil and extant plants suggests that these traits preferentially evolve in herbaceous to understory plants of warm, humid environments, thus supporting inferences concerning angiosperm origins based upon the ecophysiology of basal extant taxa.

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### Introduction

During the Late Devonian and Early Carboniferous, at least four vascular plant lineages (seed plants, progymnosperms, ferns, and sphenopsids) independently evolved laminate leaves and followed the same early sequence of morphological evolution. After this initial radiation, the ferns and seed plants shared nearly the complete morphological range found in Paleozoic leaves (Boyce and Knoll 2002). This repeated pattern of early evolution suggests a highly constrained radiation; however, this early history of morphological evolution contrasts strongly with the modern world dominated by angiosperms with leaf morphologies radically different from nearly all Paleozoic forms. Morphologies reminiscent of the Paleozoic do persist, but primarily only among ferns.

Living plants provide a developmental context for this evolutionary history. Marginal growth is found in fern laminae (Pray 1960,

1962; Zurakowski and Gifford 1988) that have one or two orders of veins with strictly marginal vein endings. A causal link between these morphological and developmental traits is consistent with current understanding of vascular differentiation along gradients of the hormone auxin produced in growing areas (e.g., Sachs 1991; Berleth et al. 2000). Alternatives to strictly marginal growth, including cell divisions dispersed throughout the leaf, are found in angiosperm leaves (Pray 1955; Poethig and Sussex 1985a,b; Hagemann and Gleissberg 1996; Dolan and Poethig 1998) that have many orders of veins and dispersed internal vein endings. These correlates have been used to interpret the fossil record of morphological evolution as reflecting the independent evolution of marginal meristematic growth in multiple lineages in the Paleozoic and the evolution of departures from strictly marginal leaf growth, notably in the angiosperm lineage, which dominates modern floras (Boyce and Knoll 2002).

Issues regarding this transition remain unresolved. First, the distinct morphological and developmental characteristics of angiosperm leaves have factored in several theories concerning the environmental and ecological origins of the group, but rarely have they been considered as part of the broader history of leaf evolution. Second, most morphologies related to strictly marginal growth are now associated only with ferns. This loss of seed plant morphological diversity may either simply reflect the depauperate nature of the extant gymnosperm flora—and thereby perhaps be tied to the rise of an alternative form of morphological diversity among angiosperms—or reflect an evolutionary trend independent of the decline in gymnosperm diversity.

### Analysis of Morphological Diversity in the Leaves of Fossil and Extant Plants

Leaf morphologies of extant plants and Paleozoic and Mesozoic fossils were surveyed at the generic level for 19 discrete characters describing the lamina and venation (see Appendices 1, 2, and 3 for character list, references, and morphological data and ranges). This data set consists of 281 fossil and 185 extant genera. Of the fossil genera, 107 are seed plants, 60 are ferns, seven are progymnosperms, four are sphenopsids, and 103 are of other or unknown affinities. Of the extant genera, 168 are ferns and 17 are seed plants. Occurrence data were assigned to geologic epoch or period, on the basis of durations stated in taxonomic descriptions and expanded by occurrence information reported from individual localities.

The data were summarized with a principal coordinates analysis (PCO). The pairwise comparison of all taxa was used to create a dissimilarity matrix, the eigenvectors of which form the axes of the PCO after Gower transformation of the matrix (Gower 1966) and multiplication of each eigenvector by its corresponding eigenvalue (for greater detail see Foote 1995; Lupia 1999; Boyce and Knoll 2002). PCO provides a method for visualizing large quantities of morphological information by geometrically summarizing as much of the variability between taxa as possible on a few

axes in the form of a morphospace. The first two PCO axes (Fig. 1) contain 55.7% of the information of the original data matrix, and the first three axes (Fig. 2) contain 74.1% as estimated by the sum of their eigenvalues divided by the sum of all eigenvalues (Foote 1995). PCO was supplemented by plotting of the average pairwise dissimilarity for all taxa and for several groups analyzed individually, as well as by plotting of the partitioned contributions of individual groups to the overall variance (Fig. 3). Partitioned variance is based on the squared Euclidean distances between the members of a group and the overall centroid for the 123 principal coordinate axes with positive eigenvalues (Foote 1993; Lupia 1999).

The character list was designed to *describe* the morphological diversity within leaves consistent with marginal growth and to *identify* leaves that suggest the evolution of departures from marginal growth. Hence, the large morphological diversity found within angiosperms would not be circumscribed with the current character list except as the evolution of an alternative to marginal growth. Proper investigation of morphological patterns within angiosperm-like leaves would require a large number of characters (e.g., Hickey 1974; Leaf Architecture Working Group 1999) that would not apply to and would obscure patterns within leaf forms consistent with marginal growth. Beyond an inadequate description of angiosperm morphological diversity with the current character list, including a large number of nearly identically coded angiosperm leaf genera to the current data set would overemphasize the narrow range of character states found within the angiosperms during the PCO analysis and hinder investigation of patterns within marginally organized leaves. (For further discussion of the sensitivities of such analyses, see McGhee 1999; Boyce and Knoll 2002.) The angiosperms have therefore been excluded. Similarly, linear leaves, such as those of the lycopods and many conifers and sphenopsids, would all be coded identically and were not included. The morphological codings that angiosperms and linear leaves would produce with this character set are approximated respectively by the Gnetales and

by *Czekanowskia* and several progymnosperms. All other leaf taxa with adequate description and preservational detail were included.

### Results

This global analysis demonstrates that the late Paleozoic maximum of morphological diversity documented previously (Boyce and Knoll 2002) among leaves consistent with marginal growth largely represents the morphological range of such leaves in later time as well (Figs. 1, 3). This morphological range is shared by the ferns and seed plants early in their history but is subsequently partitioned between the two groups, with the seed plants progressively losing much of this range after a Permian maximum (Figs. 1, 3). When not reduced to linear leaves, as in most conifers, leaves are less compound (a characteristic not included in the principal coordinates analysis); lamina attachment is often broad with multiple equivalent veins entering the leaf; venation is typically simplified to a single order without a midvein; and venation is parallel, typically open, and runs a straight course ending at the distal margin. These characteristics are found in Cordaitales, Ginkgoales, Cycadales, Bennettitales, and conifers including those with nonlinear leaves, as well as more poorly understood groups such as the *Czekanowskiales* and *Vojnovskyales*. Ferns rarely have exhibited the morphologies typical of post-Paleozoic seed plants, but otherwise they had occupied the morphological range of Paleozoic seed plants by the Triassic and they have maintained this morphological diversity through to the present.

Complex vascular characteristics that suggest departures from strictly marginal leaf growth have evolved repeatedly, and these venation patterns are found at low frequency at all times after their first appearance in the Permian gigantopterid seed plants (Fig. 4). Other seed plants to have independently evolved these leaf characteristics are the Triassic peltasperms, as well as the angiosperms and Gnetales with leaf macrofossil records that begin in the Cretaceous. These leaf traits occur in all three extant fern orders: in *Ophioglossum* of the Ophioglossales, in *Christensenia*

of the Marattiales, and in several filiclean groups (Fig. 5). Filicales include the Dipteridaceae (marking the Triassic first appearance of these characteristics among ferns) and at least four lineages in the large clade encompassing polypod and dryopterid ferns: Blechnaceae, Thelypteridaceae, Lomariopsidaceae/Dryopteroidae, and Polypodiaceae/Grammitidaceae. The last two lineages are large, heterogeneous groups in which internally directed veins likely evolved many times. Some of these characteristics also are found in fossils, such as the Triassic genus *Sanmiguelia* (Cornet 1986), of unknown or controversial affinity (Trivett and Pigg 1996).

### The Morphological Divergence of Ferns and Seed Plants

After the Paleozoic, the seed plants progressively lost leaf morphologies that persist among the ferns. This pattern corresponds, at least superficially, to extinction patterns within the two groups. Among lineages with a fossil record, 16 out of 24 filiclean families are extant, with only three lost since the Paleozoic, compared with only 4 of 19 non-angiosperm seed plant orders (compiled respectively from Collinson 1996; Taylor and Taylor 1993). Morphological patterns therefore might reflect the persistence of diverse morphologies among the ferns as a result of the persistence of basal lineages, versus progressive loss of seed plant morphological diversity as a consequence of the loss of higher-level groups. However, the evolution of leaf morphology is not sufficiently conservative for extinction to be the cause of these morphological patterns. Among extant ferns, the entire range of morphologies consistent with strictly marginal growth is covered by the genera of a variety of individual families (Fig. 2A). Furthermore, linking morphological diversity to extinction rates would not address the absence of ferns from the morphological range to which the seed plants became restricted (Figs. 1A, 2B).

The leaves of several early diversifying seed plant groups, such as the Medullosales and Lyginopteridales, are as morphologically diverse as those of the ferns, but later groups exhibit a much more restricted range of morphologies. DiMichele and Aronson (1992) em-

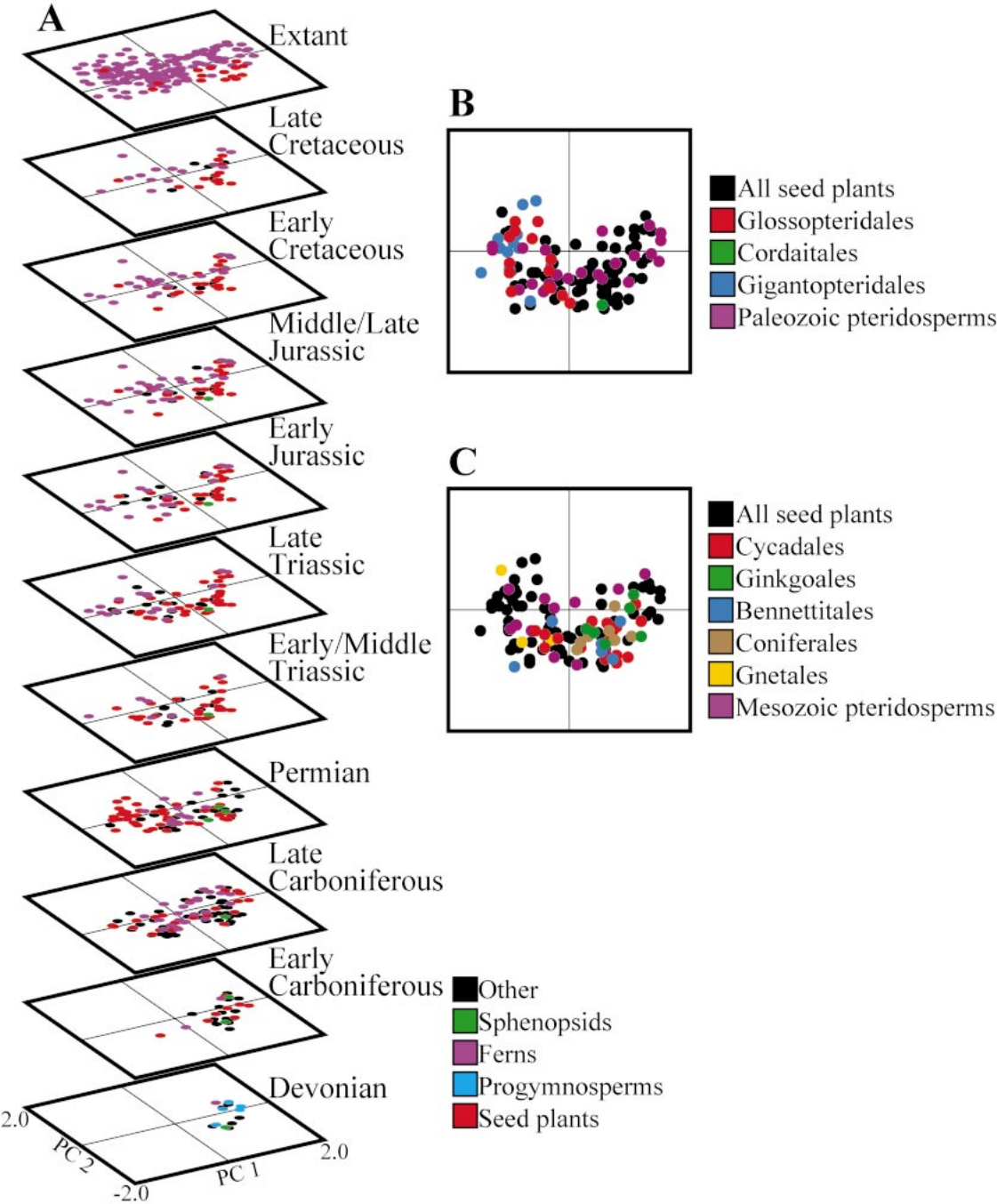


FIGURE 1. Principal coordinates analysis of global Paleozoic and Mesozoic fossils and extant fern and gymnosperm genera. Stratigraphic distribution of morphologies for all taxa (A) and phylogenetic distribution of morphologies for fossil and extant seed plants segregated based on Paleozoic or Mesozoic time of greatest diversity (B, C). “Ferns” includes Filicales, Marattiales, Ophioglossales, and Zygopteridales. “Paleozoic pteridosperms” includes Lyginopteridales, Medullosales, and Callistophytales. “Mesozoic pteridosperms” includes Peltaspermales, Corystospermales, and Caytoniales.

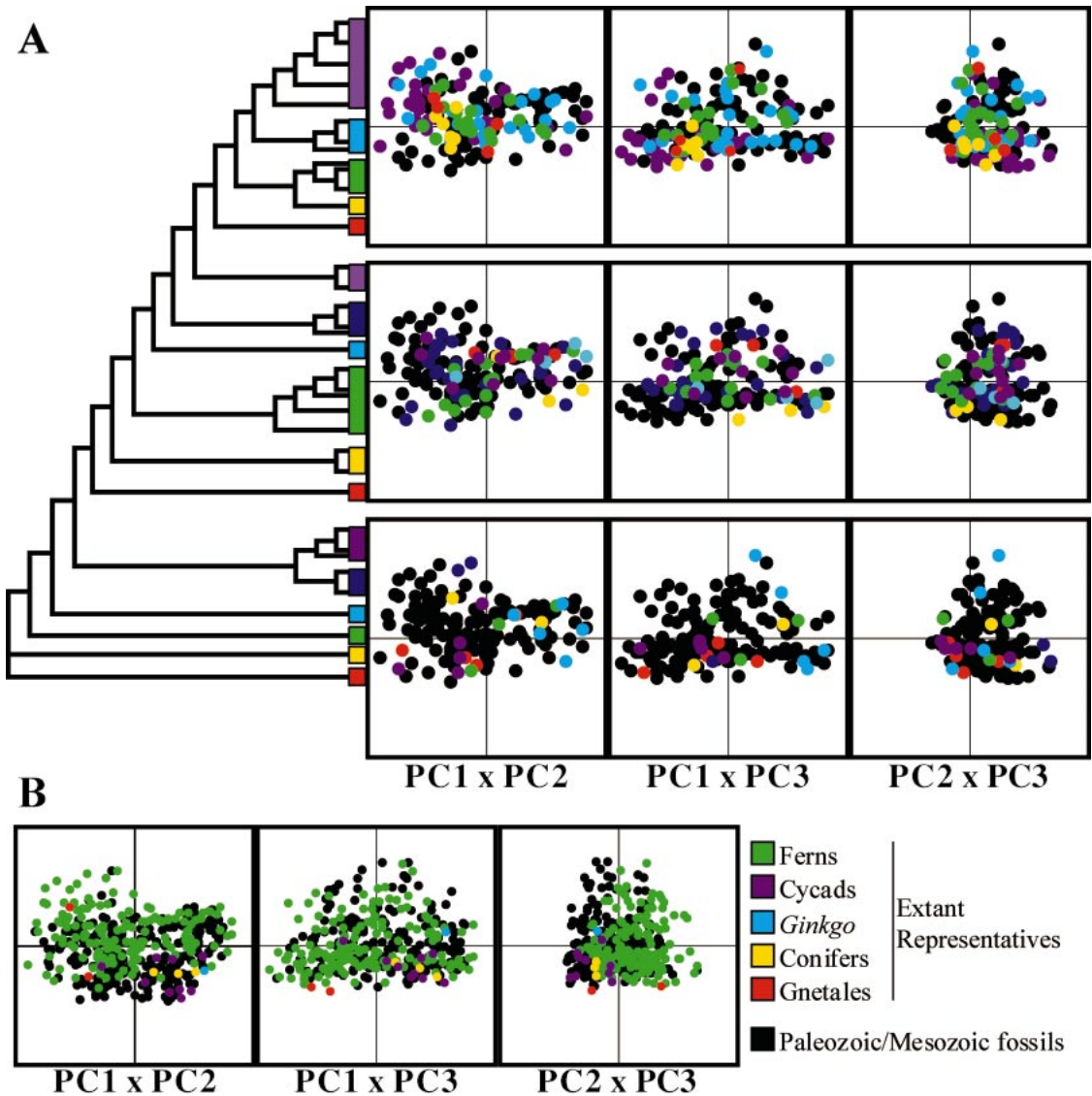


FIGURE 2. Phylogenetic distribution of morphologies among extant ferns (A), based on principal coordinates analysis of Figure 1 plotted against a black background of all extant fern genera and among all extant (B) plants plotted against a black background of all fossils included in the analysis. (Phylogeny based on Hasebe et al. 1994 and Pryer 1995. Taxon names available in Figure 5.)

phasized that drier environments foster the evolution of morphological novelty and documented that many higher-level groups originated in drier extrabasinal settings before later moving into basinal environments as wetlands contracted late in the Paleozoic. This “paleophytic/mesophytic” transition (reviewed in Knoll 1984) corresponds to the replacement seen here of seed plant groups with morphologically diverse fernlike leaves by those with a more restricted range of leaf ve-

nation patterns and morphologies. Therefore, dry, peripheral environments may well have fostered the evolution of the innovations in reproductive morphology that are given the most weight in establishing ordinal-level seed plant groups, but these environments appear to have fostered convergence in the evolution of leaf morphologies. This morphological convergence may well be adaptive in drier environments. The theoretically ideal morphology for maximizing water transport efficiency

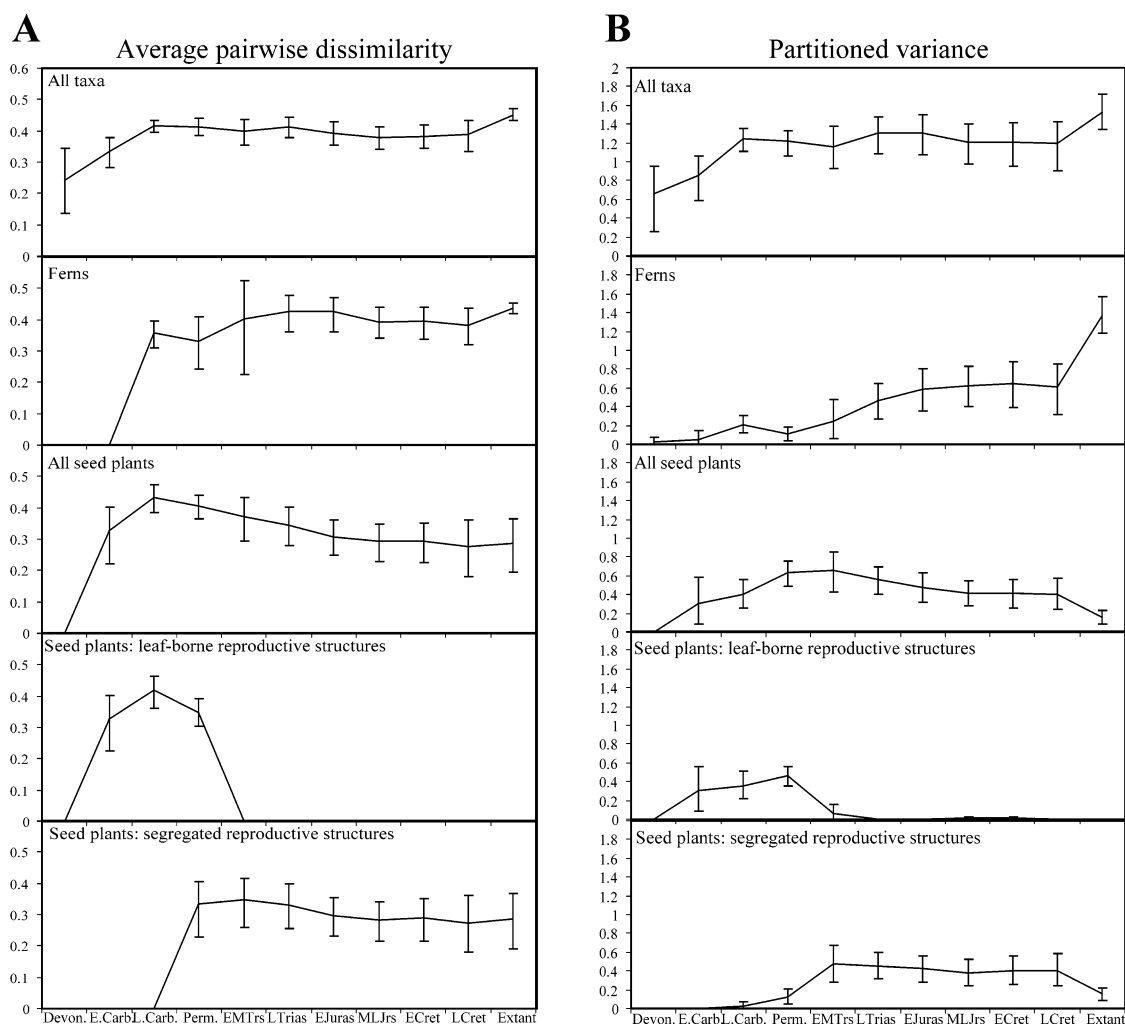


FIGURE 3. A, Pairwise dissimilarity for the entire data set and for individual groups analyzed separately. B, Contribution of different groups to the variance of the overall data set. Seed plant subgroups are not expected to be monophyletic. Jumps in variance values between the Late Cretaceous and the Recent reflects the larger number of taxa available in the living record and the fact that all living taxa can be assigned unambiguously to ferns or seed plants, whereas a large proportion of taxa are unassignable to either group in all other time intervals.

(Givnish 1979) is approached by these seed plant groups: a leaf with a single order of straight, unbranched veins radiating from the point of attachment.

The morphologically diverse leptosporangiate ferns, however, are also among the groups thought to have originated in drier, peripheral environments (Scott and Galtier 1985; DiMichele and Aronson 1992). The dual role fern leaves typically play in both photosynthesis and reproduction might lead to a larger range of morphologies than would be expected by selection for photosynthetic function

alone. The need for greater supply of water and photosynthate to specific areas of spore production rather than to a more homogeneous photosynthetic surface would likely result in different optimal vein patterns. Supporting the mass of reproductive structures may in some cases favor alternative vein patterns as well.

This conflict of optimizing for both photosynthetic and reproductive function might explain the overlap between the morphological range of the ferns and the Paleozoic pteridosperms, known in several cases to have borne

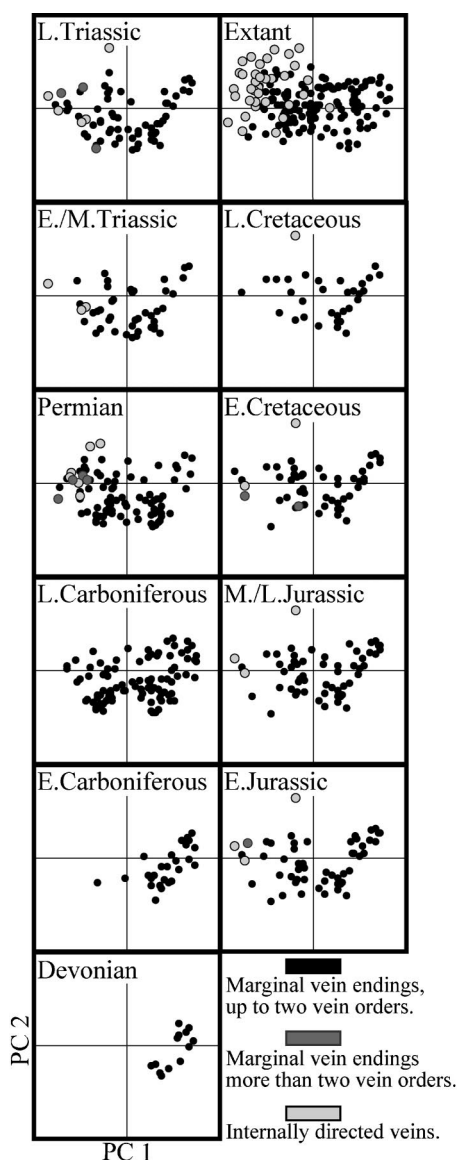


FIGURE 4. Stratigraphic distribution of basic venation characteristics in fossil and extant leaves plotted on principal coordinates analysis of Figure 1.

reproductive structures on the lamina of foliage leaves (medullosans [Halle 1929]; giganopterids [Li and Yao 1983]; glossopterids [Surange and Maheshwari 1970; Surange and Chandra 1972]; others [Delevoryas and Taylor 1969; Galtier and Béthoux 2002]). The morphological ranges of later seed plant groups would then be free to diverge from that previously shared with the ferns when the requirements of reproductive function were segregated into separate structures in later seed

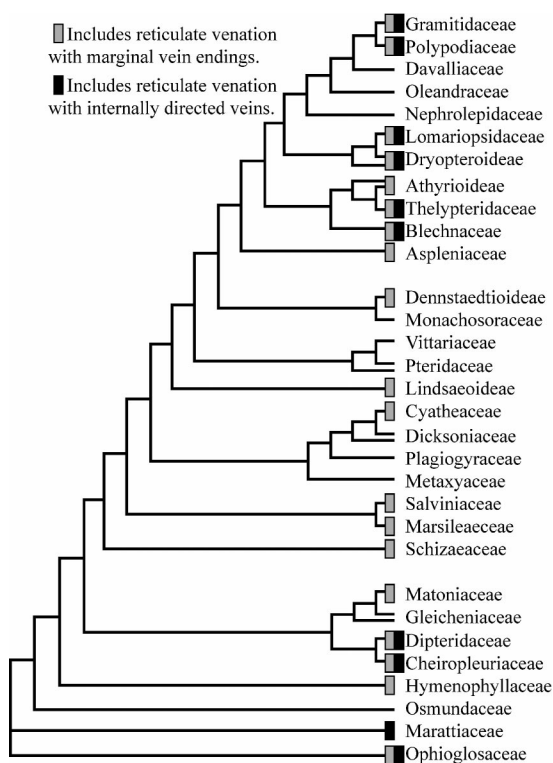


FIGURE 5. Phylogenetic distribution of venation characteristics among extant ferns. Fern families can be highly variable, and labeled taxa often include members that do not conform to the indicated morphological characteristics.

plants. This pattern is shown in full within fossils that have been interpreted as cycads: the earliest have seeds borne directly on leaves of taeniopterid morphologies (Mamay 1976; Gillespie and Pfefferkorn 1986; Axsmith et al. 2003), whereas Mesozoic cycads with reproductive organs segregated into independent structures tend towards leaf morphologies more typical of extant *Cycas* and *Zamiaceae* (e.g., Triassic *Leptocycas* [Delevoryas and Hope 1971]).

Some ferns do have morphologically distinct fertile and nonfertile leaves. This dimorphism often consists only of a less extensive lamina of the same morphology, but can involve complete loss of the lamina in entire fronds or portions thereof. However, the extent of dimorphism can be variable within individual genera and families and, even in the more extreme cases, fertile and vegetative leaves typically share the same frond architecture. These distinctions suggest that much less

developmental and genetic divergence between these forms is present than would be expected with any of the modifications between fertile and vegetative structures exhibited by extant seed plants.

If seed plant lineages with and without leaf-borne reproductive structures are considered separately, two distinct dynamics can be recognized in the overall seed plant pattern of gradual decline following a Paleozoic high in morphological disparity. First, seed plants with leaf-borne reproductive structures flourish in the Paleozoic before disappearing early in the Mesozoic. Second, seed plants with leaf-independent reproductive structures maintain a smaller, stable morphological range throughout their history through to the present (Fig. 3). The first appearance of this latter, more derived class is with the mid-Carboniferous Cordaitales, which had simple, strap-shaped leaves with a single order of parallel, open veins running to the distal margin that were remarkably different from the large, pinnately compound fronds with a diverse array of pinnule venation patterns that were borne by Carboniferous pteridosperms.

In living seed plants, peak reproductive and photosynthetic activity are typically temporally segregated, even in the Tropics (reviewed in Burnham 1993). Staggered schedules of vegetative and reproductive organ production confer potential advantages for both biotic and abiotic pollination syndromes (Fenner 1998; Sakai 2001), each of which has been inferred for different Paleozoic seed plants (Taylor and Millay 1979; Taylor 1988; Crepet 2001). Exploitation of such advantages would be precluded if seed and pollen organs are borne on leaves. Furthermore, direct hydraulic and energetic competition of photosynthetic and reproductive activities may have made Paleozoic pteridosperms more vulnerable to fluctuations in water supply. Segregation of these processes into independent organs may have been important for the occupation of drier and more seasonal habitats where many later seed plant groups appear to have originated.

Segregation of photosynthetic and reproductive functions would allow the specialization of leaves for hydraulic supply and the

morphologies typical of mesophytic foliage. However, several groups likely to have leaf-independent reproductive structures at least partially deviate from this pattern: the peltasperms, corystosperms, Caytoniales, and *Penetoxylon*. Although their architecture often is unknown, these plants, which maintain a more diverse array of leaf morphologies, tend to be smaller, subcanopy plants (Harris 1983; Bose et al. 1985) for which hydraulic specialization of the leaves may have been less important. Where either canopy dominance or drier, more open environments are likely in these groups, there is a trend towards more mesophyte-like morphologies, e.g., *Xylopteris* in the Corystosperms. Such partial approximations are also found among larger trees in lineages with leaf-borne reproductive structures, e.g., the glossopterids, and the largest Medullosan trunks in the earliest Permian (reviewed in Taylor and Taylor 1993) coincident with abundant *Odontopteris* foliage.

Evolutionary constraints are often evoked with regard to morphological limitations (reviewed in Wagner 2001), but the patterns discussed here suggest that such constraints can have unexpected outcomes. A single optimal form may exist for a particular function, but optimizing for multiple functions results in many coequal, suboptimal forms (Niklas 1994). The evolution of a narrow range of leaf morphologies may have been permissible in seed plants, owing to the segregation of reproductive and photosynthetic functions. The ferns have always had to balance reproductive and vegetative leaf functions and have always had a diverse range of leaf morphologies. In this case, any evolutionary constraints appear to have been acting upon the morphologically diverse group. Presumably, these later seed plants would be more morphologically diverse, rather than less, if all of morphology and anatomy were taken into account, instead of just leaves. However, the possibility of such counterintuitive relationships between evolutionary constraint and its expression in the fossil record of morphological diversity should be considered, because paleontologists must always work with such partial records, regardless of study organisms.

### The Repeated Evolution of Alternatives to Strictly Marginal Growth

Leaf venation with many orders, extensive reticulation, and vein endings dispersed throughout the leaf is often considered a hallmark of the angiosperms, and the presence of this syndrome, or a subset of its characteristics, has been used to argue angiosperm affinity for a variety of fossil plants (e.g., Surange 1966; Melville 1969; Asama 1985; Cornet 1986). These leaf characteristics have also been evoked as a part of several alternative hypotheses concerning the ancestral environment and ecology of the angiosperms. Recognizing the developmental novelty of angiosperm leaves in comparison to the ancestral marginal leaf growth, it has been suggested that these leaves represent a complete reinvention of a laminate leaf after passage through an evolutionary phase in which the lamina was lost through adaptation to an arid, or perhaps aquatic, environment (Doyle and Hickey 1976). It has also been argued that details of angiosperm leaves support an herbaceous origin for the group along mesic, frequently disturbed stream margins (Taylor and Hickey 1996). Other suggested advantages of different aspects of angiosperm leaf venation patterns, without necessarily making claims regarding angiosperm origins, include increased structural support of a large thin lamina (Givnish 1979), the maximization of photosynthetic rate with high light and nutrient availability (Bond 1989), a neotenic acceleration of the life cycle (Takhtajan 1976), and the ensuring of an adequate water supply under arid conditions (reviewed in Roth-Nebelsick et al. 2001). The obvious complication is that hypotheses concerning the site of angiosperm origination and the initial selective advantage of various aspects of angiosperm biology are poorly constrained because angiosperms now dominate most terrestrial environments. However, any patterns of ecological distribution among the unrelated groups that have convergently evolved angiosperm-like leaves may perhaps indicate the initial ecological conditions from which the angiosperms radiated.

Though less frequent than other morpho-

logical transitions, such as from open to reticulate venation, the evolution of leaves with internally directed veins and nonmarginal vein endings has occurred at least four times in the seed plants and seven times among ferns. Although these leaf morphologies are often distinctive and unlikely to be confused with those of angiosperms, they are all similar in suggesting departures from the strictly marginal laminar growth inferred to be the ancestral condition in both ferns and seed plants (Doyle and Hickey 1976; Wagner 1979; Boyce and Knoll 2002). The relatively frequent evolution of such characteristics suggests that they are not an adequate indication of angiospermous affinity for problematic fossils without other lines of evidence. Also, passage through a nonlaminar evolutionary stage may be likely for the Gnetales (Doyle and Hickey 1976) if linear-leaved *Ephedra* is basal within the group and if they are indeed closely related to or even nested within the conifers (Chaw et al. 1997, 2000; Winter et al. 1999; Bowe et al. 2000; Magallón and Sanderson 2002), but the frequent evolution of these leaf characteristics among the ferns indicates that such a scenario should not be considered necessary for the angiosperms.

Ferns represent the majority of independent evolutions of leaf morphologies that suggest departures from strictly marginal growth. The center of diversity of these lineages is in predominantly shaded areas of warm wet environments (compiled from Kramer and Green 1990), as is the case for ferns in general and the first appearance of many lineages within the Filicales (Skog 2001). The Triassic first occurrence of complex reticulation and internally directed veins within the ferns is in the dipterids, known from China (Li 1995), which was a series of equatorial islands with high rainfall at this time (Shangyou et al. 1990), and from northern (Harris 1926) and southern (Retallack 1977; Anderson and Anderson 1985) midlatitudes, which were warm, high-rainfall zones in hothouse climate regimes (Wing and Sues 1992; Ziegler et al. 2003). The pre-Cenozoic record of the clade including the dryopterid and polypod ferns is controversial (Collinson 1996), and neither *Ophioglossum* nor *Christensenia* has a fossil re-

cord, but the Cenozoic radiation of these lineages appears to be coincident with the rise of modern, angiosperm-dominated, tropical rain forests.

Fossil seed plant examples of the evolution of more angiosperm-like leaves largely correspond to the conditions described for ferns; they tend to be smaller plants in warm, at least seasonally wet environments, although not always likely to have been heavily shaded. Gigantopterid leaves are known from the Permian of China and the southwestern United States, although the two may not be closely related (Asama 1962, 1985). The diverse Chinese material allows reconstruction of the plant as a liana (Li and Taylor 1999) in a wet, tropical forest (Ziegler 1990), although such lycopod-dominated forests are likely to have had an open canopy (DiMichele and DeMaris 1987). North American gigantopterids are found in riparian environments that would have been the wettest areas in a landscape at least seasonally dry (DiMichele and Hook 1992). Triassic *Sanmiguelia* is found on levees in seasonally wet environments (Ash 1987). The peltasperms are thought to have been woody, because of the deciduous nature of their leaves and reproductive organs (Crane 1985). Complex vascular characteristics are found in a group of Triassic foliage taxa that have been related to the peltasperms by cuticular characteristics and interpreted as an understory component of conifer-dominated, wet, warm temperate forests of mid latitude Eurasia (Dobruskina 1975, 1995).

Morphological and ecological divergence within the living Gnetales hampers attempts to infer ancestral states for the group (Crane 1996). The living representatives with nonlinear leaves are *Gnetum*, a liana to small tree in tropical forests, and the desert plant *Welwitschia*. In the fossil record, *Drewria* from the Early Cretaceous Potomac Group of Virginia (Crane and Upchurch 1987) had a slender stem with no evidence of secondary growth or bud dormancy and the plant is reconstructed as an herbaceous to perhaps shrubby member of streamside, early-successional vegetation in a mesic environment. A diverse gnetalean assemblage, including broadleaf examples, that has recently been discovered in the Early Cre-

taceous of Brazil (Rydin et al. 2003) should provide a more robust understanding of the earlier history of the group.

The evidence presented here concerning the preferential ecology and environment of origin of angiosperm-like leaf traits in non-angiospermous plants is consistent with several lines of evidence from the early history of the angiosperms and their basal living members. The paucity of Early Cretaceous angiosperm wood relative to other angiosperm organs and to conifer wood suggests that the angiosperms were not initially large trees (Wing and Tiffney 1987). Recent molecular phylogenies have converged on a phylogeny of angiosperms (Mathews and Donoghue 1999; Qiu et al. 1999; Soltis et al. 1999; Barkman et al. 2000) with basal branches that consist of smaller woody plants of shaded, wet, tropical environments that are frequent sites of disturbance (Feild et al. 2003a,b). In this setting, the evolution of more angiosperm-like vein patterns may be involved in providing physical support (Givnish 1979) and equitable distribution of water (Zwieniecki et al. 2002) across the larger lamina common in shaded environments, perhaps also aiding in the exploitation of light flecks. The remarkable aspect of angiosperm leaves may not be so much their complex morphology, as such complexity has evolved repeatedly in smaller, understory plants in warm, humid environments, but rather the ability of angiosperms to export this complex morphology to so many other environments.

## Discussion

For the terrestrial biota, the Paleozoic has been described as a time of ecosystem assembly fundamentally different from later time (DiMichele and Hook 1992), an assessment broadly mirrored by the patterns described here. After the initial evolution of developmental mechanisms in Paleozoic plants, ecological and architectural specializations were partitioned in the post-Paleozoic, including the phylogenetic segregation of morphologies derived from marginal growth and the repeated evolution of departures from strictly marginal growth.

A great deal of developmental diversity is

found among plants with nonmarginal leaf growth (e.g., comparison of *Liriodendron* and *Quiina* in Foster 1952). For example, some fossil morphologies that are here lumped with diffuse growth, such as the giantopterids *Evolsonia* and *Gigantopteridium*, suggest a combination of marginal and internal growth in discrete intercalary zones. Because of this diversity, the repeated evolutions of alternatives to marginal growth are unlikely simply to replicate a fixed evolutionary sequence of morphologies, as was seen with the evolution of marginal growth during the Paleozoic (Boyce and Knoll 2002); however, a much more detailed analysis would be needed to determine whether regularities exist. The angiosperm leaves in the Cretaceous Potomac Group show a progression toward more highly organized venation and more-discrete differences between successive vein orders (Doyle and Hickey 1976), a pattern with which other groups can be compared. Despite any developmental diversity subsumed into the classification of alternatives to marginal growth, these leaves may be physiologically convergent. Vessels have been shown to play a key role in dicot leaf hydraulic function and in the equitable distribution of water across the broad laminar surface (Zwieniecki et al. 2002); this role is consistent with the two other known evolutions of vessels among the seed plants being in the only examples of alternatives to marginal leaf growth for which anatomy is available, the Gnetales and giantopterids (Boyce in press).

In the same way that the enormous radiation of angiosperms has obscured the environment and ecology of their origin, the angiosperm radiation has likely obscured a variety of patterns concerning the former ecological distributions of other plant lineages (Wing and Sues 1992) and of leaf morphologies derived from strictly marginal growth. Future locality-based investigations may reveal more detailed patterns of morphological occupation in pre-angiosperm floras, including latitudinal and ecotype gradients as well as further segregation than has been shown here between plants of different overall habit. Furthermore, the nearly complete overlap of living fern and gymnosperm leaf morphologies

with those of fossils (Fig. 2B) suggests that many hypotheses concerning developmental and physiological implications of different leaf morphologies seen in the fossil record can be tested with study of living analogues.

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#### Appendix 1

Characters used for description of leaf morphologies. Inapplicable or missing characters were coded as “?”.

1. Lamina lobed: 0 yes; 1 no; 2 variable.
2. Veins per laminar segment: 0 one; 1 more than one; 2 variable.
3. Vein paths: 0 divergent or parallel; 1 convergent; 2 variable.
4. Venation: 0 open; 1 always includes reticulation; 2 variable.
5. Marginal vein closure: 0 no; 1 yes; 2 variable.
6. Endings: 0 all equally marginal; 1 also internally directed; 2 variable.
7. Marginal endings: 0 along some margins; 1 along all margins; 2 variable.
8. Internal endings: 0 all marginally directed, but unevenly truncated; 1 internally directed.
9. Midvein: 0 no; 1 yes; 2 variable.
10. Vein orders (except any midvein): maximum number.

11. Lamina attachment: 0 narrow (can include both sessile and petiolate); 1 broad; 2 variable.
12. Number of entering veins: 0 one; 1 multiple; 2 variable.
13. Multiple entering veins: 0 multiple equivalent; 1 multiple not equivalent; 2 both.
14. Vein paths: 0 regular; 1 irregular; 2 both.
15. Vein paths: 0 not parallel; 1 extensively parallel.
16. Vein paths: 0 no arching; 1 arching concave up; 2 arching concave down; 3 both.
17. Lamina shape: 0 regular; 1 irregular; 2 variable.
18. Vein branching: 0 no; 1 yes.
19. Vein branching: 0 evenly distributed; 1 uneven arm to arm; 2 origin to edge; 3 both.

## Appendix 2

Sources used to compile leaf morphological characters as indicated in Appendix 3 and to determine stratigraphic ranges and systematic affinities.

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## Appendix 3

Phylogenetic affinity, literature sources, and stratigraphic range for all taxa included in the analysis. Affinity of fossil ferns, seed plants, progymnosperms, and sphenopsids identified to the ordinal level; living ferns assigned to families. An affinity of "Other" indicates unknown affinity, known affinity to a group not discussed here, or a form-genus of multiple affinities. Abbreviations: C, Carboniferous; D, Devonian; E, Early; J, Jurassic; K, Cretaceous; L, Late; M, Middle; P, Permian; Tr, Triassic.

Genus	References	Affinity	Range	Characters: 1-10	11-19
Abropteris	22	Other	L.Tr	1111001?11	111100012
Acithea	12	Fern-Marattiales	L.C-P	2110001?11	10?013013
Acrangiophyllum	12	Other	L.C	0100000?11	10?000113
Acrophorous	21	Fern-Dryopteridaceae	Extant	0100000?01	00?000111
Acrostichum	21, 35	Fern-Pteridaceae	Extant	111100?11	00?011010
Adiantites	12	Other	E.-L.C	2100000?01	20?011013
Adiantopteris	11	Fern-Filicales	M.J-L.K	2100000?01	00?010212
Adiantum	21, 35	Fern-Pteridaceae	Extant	2122000?21	00?201213
Aenigmopteris	21	Fern-Dryopteridaceae	Extant	0100000?11	00?000111
Agathis	21	Seed-Coniferales	Extant	1100000?01	00?012012
Aipteris	11	Seed-Gigantopteridales	P	011101?113	00?210110
Albertia	22	Seed-Coniferales	E./M.Tr	1110000?01	???010012
Alethopteris	12	Seed-Medullosales	L.C-P	2110001?11	121211013
Allantodiopsis	11, 34	Fern-Filicales	L.K	1110001?11	00?010?12
Alloiopteris	12	Other	L.C	2210002?21	20?013213
Alsophila	21, 35	Fern-Cyatheaceae	Extant	2120002?11	10?013012
Alsophilites	11	Fern-Filicales	M.J-E.K	1100000?01	10?000010
Aneimites	12	Other	E.C	21?00???01	00?????01?
Anemia	21, 35	Fern-Schizaeaceae	Extant	2122000?21	2??000210
Anemia	11, 33, 34	Fern-Filicales	E.-L.K	0110000?11	120000210
Anetium	21, 35	Fern-Vittariaceae	Extant	1111001?11	00?100010
Angaridium	11	Other	P	0000000?01	00?000111
Angaropteridium	22	Other	E.C-P	0110000?01	0??011011
Angiopteris	21	Fern-Marattiaceae	Extant	111000?11	00?011012
Anisopteris	12	Seed-Lyginopteridales	E.-L.C	2200000?01	00?012213
Anogramma	21, 35	Fern-Pteridaceae	Extant	0200000?01	00?000110
Anomozamites	37	Seed-Bennettitales	L.Tr-L.K	1110000?01	110010012
Antrophyum	21, 35	Fern-Vittariaceae	Extant	1112000?11	00?101010
Arachniodes	21	Fern-Dryopteridaceae	Extant	0100000?21	20?000111
Araiostegia	21	Fern-Davalliaceae	Extant	0100000?01	00?000111
Aranetzia	11	Other	P	0100000?01	0??00011?
Araucaria	21	Seed-Coniferales	Extant	1200000?01	00?0100?2
Arberia	1	Seed-Glossopteridales	P	1111001?11	00?201010
Archaeopteridium	12	Seed-Lyginopteridales	E.-L.C	2100000?01	112000013
Archaeopteris	12	Progym.-Archaeopterid.	D	2200000?01	00?010213
Archangelskya	11	Other	E.J	01?0000?01	00?00011?
Arthropteris	21, 35	Fern-Oleandraceae	Extant	0110000?11	00?000010
Asiopteris	22	Other	P	2110001?11	111000111
Asplenium	21, 35	Fern-Aspleniaceae	Extant	2222002?21	20?210212
Asterotheca	12, 1	Fern-Marattiales	L.C-L.J	2110001?11	10?011013
Astralopteris	34	Fern-Filicales	E.K	1111001?12	22?210010
Atalopteris	21, 35	Fern-Dryopteridaceae	Extant	1100001?11	20?010010
Athyrium	21, 35	Fern-Dryopteridaceae	Extant	0100000?21	20?010112
Autunia	12	Seed-Peltaspermales	L.C-P	2110001?21	122000010
Baiera	33, 37	Seed-Ginkgoales	L.Tr-L.K	0100000?01	0??000112
Belemnopteris	33	Seed-Glossopteridales	P	1111001?11	00?100010

## Appendix 3. Continued.

Genus	References	Affinity	Range	Characters: 1-10	11-19
Benlightfootia	1	Other	P	0100000?01	00?011111
Bernouillia	11	Fern	L.Tr	1110002?11	20?103113
Bicoempleopteridum	11	Seed-Gigantopteridales	P	1111001?13	2??21001?
Bicoempleopteris	3, 11	Seed-Gigantopteridales	P	0111001?13	00?210012
Blechnum	21, 35	Fern-Blechnaceae	Extant	1112202?11	20?010012
Blotiella	21, 35	Fern-Dennstaedtiaceae	Extant	2111101?11	10?100010
Bolbitis	21, 35	Fern-Lomariopsidaceae	Extant	211202?113	00?203210
Bommeria	21, 35	Fern-Pteridaceae	Extant	0112001?11	111100010
Botrychiopsis	1	Other	L.C-P	0110001?11	11101111?
Botrychium	21, 35	Fern-Ophioglossaceae	Extant	2100000?21	10?000111
Bowenia	20, 21	Seed-Cycadales	Extant	1100000?01	00?010010
Boweria	12	Fern-Filicales	L.C	0200000?21	00?000211
Brainea	21	Fern-Blechnaceae	Extant	1111000?11	00?100012
Burgersia	1	Other	E./M.Tr	0110000?11	00?010010
Calamophyton	12	Other	D	0000000?01	00?0?0010
Callipteridium	12	Other	L.C-P	1110001?21	122211013
Calochlaena	21	Fern-Dicksoniaceae	Extant	0100000?11	00?000112
Camptosorus	11	Fern-Filicales	L.Tr	01110????12	1??000010
Camptosorus	21, 35	Fern-Aspleniaceae	Extant	111100??11	00?101010
Campyloneurum	21, 35	Fern-Polypodiaceae	Extant	111101?113	00?210010
Cardiopteridium	12	Other	E.-L.C	1100000?01	00?011011
Cardiopteris	12	Other	E.-L.C	1100000?01	11001101?
Cathaysiopteris	11, 22, 33	Seed-Gigantopteridales	P	111101?112	00?011012
Cephalomanes	21	Fern-Hymenophyllaceae	Extant	0000000?01	00?0???11?
Ceratopteris	21, 35	Fern-Pteridaceae	Extant	21110????11	0??100112
Ceratozamia	20, 21	Seed-Cycadales	Extant	1100?00?01	1100100??
Cheilanthes	21, 35	Fern-Pteridaceae	Extant	2122202?21	20?000210
Cheiropleuria	21	Fern-Cheiropleuriaceae	Extant	211101?104	00?100210
Chigua	20, 21	Seed-Cycadales	Extant	1100000?11	00?01001?
Christensia	21	Fern-Marattiaceae	Extant	111101?112	0??21001?
Cibotium	21, 35	Fern-Dicksoniaceae	Extant	2100000?11	20?000210
Cladophlebis	1	Fern-Filicales	E.Tr-L.K	2110001?11	221211212
Clathropteris	11, 19, 34, 37	Fern-Filicales	L.Tr-L.J	011101?113	111210010
Cnemidaria	21, 35	Fern-Cyatheaceae	Extant	1112001?12	10?013012
Colysis	21	Fern-Polypodiaceae	Extant	111101?112	22110001?
Comia	22	Other	P	011?000?01	11001101?
Compsopteris	11, 22	Other	P-L.Tr	1110001?11	111011012
Conchophyllum	22	Other	L.C	0100000?01	110000112
Coniogramme	21	Fern-Pteridaceae	Extant	111200??11	00?010012
Coniopteris	11, 19, 37	Fern-Filicales	E.Tr-L.K	0200000?21	00?000111
Cordaites	12	Seed-Cordaitales	L.C-P	1100000?02	112010022
Cornopteris	21	Fern-Dryopteridaceae	Extant	1110001?11	10?00221?
Corynepteris	12	Fern-Zygopteridales	L.C-P	2210002?21	20?011213
Crepidomanes	21	Fern-Hymenophyllaceae	Extant	0000000?01	00?000110
Crossopteris	11	Other	L.C	2110001?11	221101210
Crossotheca	12	Other	L.C	2210002?21	20?001213
Cryptogramma	21, 35	Fern-Pteridaceae	Extant	2110000?11	00?000212
Ctenis	37	Seed-Cycadales	L.Tr-L.K	1111000?01	110010010
Ctenitis	21, 35	Fern-Dryopteridaceae	Extant	2120002?11	121012210
Ctenozamites	19, 37	Other	L.Tr-E.K	1110001?01	110000010

## Appendix 3. Continued.

Genus	References	Affinity	Range	Characters: 1-10	11-19
Culcita	21, 35	Fern-Dicksoniaceae	Extant	0200000?01	00?000111
Cyathea	21, 35	Fern-Cyatheaceae	Extant	1112001?11	10?010012
Cycas	20, 21	Seed-Cycadales	Extant	1000000?01	00?0?000?
Cyclodium	21	Fern-Dryopteridaceae	Extant	2112001?11	20?002010
Cyclopeltis	21, 35	Fern-Dryopteridaceae	Extant	111001?011	00?000011
Cyclosorus	21	Fern-Thelypteridaceae	Extant	2112002?12	20?012013
Cystodium	21	Fern-Dicksoniaceae	Extant	2110000?11	010000012
Czekanowskia	33, 34, 37	Seed-Czekanowskiales	E.Tr-L.K	000000??01	00?0?0110
Dactylotheca	12	Fern-Zygopteridales	L.C	1100001?11	10?010012
Danaea	21, 35	Fern-Marattiaceae	Extant	1110201?11	00?010012
Danaeopsis	11, 15, 16	Fern-Marattiales	L.Tr-E.J	1110001?11	111011012
Davallia	21	Fern-Davalliaceae	Extant	2220000?21	00?010212
Dennstaedtia	21, 35	Fern-Dennstaedtiaceae	Extant	2120000?21	20?000111
Deparia	21	Fern-Dryopteridaceae	Extant	1110002?11	10?002010
Desmiophyllum	23, 33	Other	E.Tr-E.K	1110000?01	010010012
Desmopteris	12	Other	L.C	1110001?11	1??011012
Dichophyllites	12	Sphen.-Equisetales	E.C	0000000?01	00?0?0110
Dicksonia	21, 35	Fern-Dicksoniaceae	Extant	2110001?21	10?000210
Dicksonia	11, 33, 37	Fern-Filicales	M.J-L.K	1120001?21	10?000211
Dicksonites	12	Seed-Callistophytales	L.C-P	2110001?11	10?001010
Dicranoglossum	21, 35	Fern-Polypodiaceae	Extant	011220??11	0??200112
Dicranophyllum	12	Seed-Ginkgoales	L.C	2000000?01	00?0?0022
Dicranopteris	21, 35	Fern-Gleicheniaceae	Extant	1110001?11	1??010013
Dicroidiopsis	11	Other	E.Tr-E.J	2120000?01	120000211
Dicroidium	1, 11, 33	Seed-Corystospermales	E.Tr-E.J	1110001?21	112011212
Dictymia	21	Fern-Polypodiaceae	Extant	111102?111	???100?12
Dictyodroma	21	Fern-Dryopteridaceae	Extant	011101?011	20?100012
Dictyophyllum	17	Fern-Filicales	E.Tr-E.K	111101?113	111100010
Dictyozamites	1	Seed-Bennettitales	E.J-E.K	1111001?01	110211012
Didymochlaena	21, 35	Fern-Dryopteridaceae	Extant	1110020001	00?001011
Dinophyton	5	Seed	L.Tr	1111000?01	01001000?
Dioon	20, 21	Seed-Cycadales	Extant	1100200?01	110010012
Diplaziopsis	21	Fern-Dryopteridaceae	Extant	111100??11	00?100012
Diplazium	21, 35	Fern-Dryopteridaceae	Extant	2122002?11	20?012213
Diploptemna	12	Seed-Lyginopteridales	E.-L.C	0200000?21	20?000113
Dipteris	21	Fern-Dipteridaceae	Extant	011101?103	00?100211
Discopteris	12	Fern-Filicales	L.C	2110002?21	20?013213
Dizuegotheca	11	Fern	P	1100001?11	10?01000?
Doleropteris	12	Other	L.C	1100000?01	00?011010
Doodia	21	Fern-Blechnaceae	Extant	2111001?11	111100?12
Doratophyllum	22, 33	Other	L.Tr-E.K	2110000?01	110010012
Doryopteris	21, 35	Fern-Pteridaceae	Extant	211220??11	222200210
Drepanozamites	22	Seed-Cycadales	L.Tr	1100000?01	00?010013
Drewria	14	Seed-Gnetales	E.K	1111000?03	110010010
Drynaria	21	Fern-Polypodiaceae	Extant	1111021113	1??210010
Dryopolystichum	21	Fern-Dryopteridaceae	Extant	1110000?11	10?000010
Dryopteris	21, 35	Fern-Dryopteridaceae	Extant	2110000?11	20?010012
Eboracia	11, 37	Fern-Filicales	M.J-E.K	2110001?11	111000111
Eddya	12	Progym.-Archaeopterid.	D	1100000?01	010010010
Edyndella	16	Seed-Peltaspermales	E.-L.Tr	1100000?01	10?011012

## Appendix 3. Continued.

Genus	References	Affinity	Range	Characters: 1-10	11-19
Elaphoglossum	21, 35	Fern-Lomariopsidaceae	Extant	222220??11	00?200212
Ellesmeris	12	Fern-Zygopteridales	D	0100000?01	00?000111
Empleopteridum	11, 22	Seed-Gigantopteridales	P	2111001?21	111100212
Empleopteris	3, 11, 22	Seed-Gigantopteridales	L.C-P	1111001?11	111100010
Encephalartos	20, 21	Seed-Cycadales	Extant	2121100?01	110010012
Enigmophyton	12	Other	D	0100000?01	???011110
Eremopteris	12	Other	L.C	2100000?01	210011212
Eretmonia	24, 32	Seed-Glossopteridales	P	1122000?01	110210012
Eretmophyllum	11, 37	Seed-Ginkgoales	E.J-E.K	1110000?01	00?010012
Eriosorus	21, 35	Fern-Pteridaceae	Extant	2200000?01	00?001111
Estcourtia	1	Seed-Glossopteridales	P	1111000?11	00?100010
Eupecopteris	12	Other	L.C	1110001?22	10?211013
Eusphenopteris	12	Seed-Lyginopteridales	E.-L.C	2110000?21	222013213
Evolsonia	12, 33	Seed-Gigantopteridales	P	111101??14	00?010010
Flabellofolium	1	Other	D-P	1100000?01	0??01101?
Fortopteris	12	Other	L.C	2110002111	121011010
Gangamopteris	33	Seed-Glossopteridales	P	111100??01	???011010
Genselia	12	Other	E.C	2100000?01	00?010210
Gigantonoclea	3, 11, 22, 33	Seed-Gigantopteridales	P	0111021112	00?210012
Gigantopteridium	12	Seed-Gigantopteridales	P	011101?113	?11010010
Gigantopteris	22, 33	Seed-Gigantopteridales	P	111101?113	00?210010
Ginkgo	21	Seed-Ginkgoales	Extant	2100000?01	010011211
Ginkgoites	1, 37	Seed-Ginkgoales	E.Tr-L.K	0120000?01	00?010213
Ginkgophyllum	1, 33	Other	L.C-P	1100000?01	00?01101?
Ginkgophyton	12	Other	L.C	2100000?01	?10010210
Gleichenia	21, 35	Fern-Gleicheniaceae	Extant	1110001?11	10?010010
Gleichenites	11	Fern-Filicales	L.Tr-L.K	1100000?01	10?000111
Glenopteris	11	Other	P	1110001?11	111011010
Glossopteris	1, 33	Seed-Glossopteridales	L.C-M.Tr	1111202?11	00?211010
Gnetum	21	Seed-Gnetales	Extant	111101?114	000100010
Goeppertella	11, 22	Fern-Filicales	L.Tr-E.J	2111001?12	1??10001?
Gonatosorus	11	Fern-Filicales	M.J-L.K	2110001?11	121103210
Gondomaria	11	Other	L.C	1110001?11	111010012
Goniophlebium	21	Fern-Polypodiaceae	Extant	?11101?112	???100?12
Grambastia	12	Fern-Filicales	L.C	1100000?11	20?012012
Grammitis	21, 35	Fern-Grammitidaceae	Extant	2112021121	2??101010
Gymnocarpium	21, 35	Fern-Dryopteridaceae	Extant	2100001?21	10?00221?
Gymnogrammitis	21	Fern-Davalliaceae	Extant	0000000?01	00?0??111
Hamatophyton	22	Other	D-E.C	0000000?01	00?0?0?10
Hausmannia	2	Fern-Filicales	L.Tr-L.K	011101?104	00?100210
Hecistopteris	21, 35	Fern-Vittariaceae	Extant	0200000?01	00?000110
Hemidictyum	21, 35	Fern-Dryopteridaceae	Extant	111110??11	00?210012
Hemionitis	21, 35	Fern-Pteridaceae	Extant	0112001?11	00?210012
Hirsutum	1	Seed-Glossopteridales	P	1111000?11	00?011012
Histiopteris	21, 35	Fern-Dennstaedtiaceae	Extant	2111101?11	10?100210
Holodictyum	21, 35	Fern-Aspleniaceae	Extant	1111001?11	00?100010
Hsiangchiphyllum	22	Other	E.J	1100000?01	110010012
Hyenia	12	Other	D	0000000?01	00?0?0110
Hymenophyllites	12	Fern-Filicales	L.C	0100000?21	00?000211
Hymenophyllum	21, 35	Fern-Hymenophyllaceae	Extant	2222000?21	20?010211

## Appendix 3. Continued.

Genus	References	Affinity	Range	Characters: 1-10	11-19
Hymenotheca	12	Other	L.C	2200001?01	20?000213
Hypodematium	21	Fern-Dryopteridaceae	Extant	0100000?11	20?012111
Hypoderris	21, 35	Fern-Dryopteridaceae	Extant	211101?113	00?100010
Hypolepis	21, 35	Fern-Dennstaedtiaceae	Extant	2110002?11	10?000210
Imparipteris	12	Seed-Medullosales	L.C-P	2110002?21	222211013
Isiolopteris	11	Other	P	2110000?01	10?000011
Jacutopteris	11	Fern-Filicales	E.K	1110001?11	111001011
Jamesonia	21, 35	Fern-Pteridaceae	Extant	2120000?01	20?001110
Jarenga	11	Other	M./L.J	0100000?11	00?000111
Jidopteris	11	Other	P	1111001?11	121102012
Johnstonia	11	Seed-Corystospermales	E.Tr-E.J	0100000?11	010000111
Karinopteris	12	Seed-Lyginopteridales	L.C	2110002?21	221211213
Katasiopteris	11	Other	P-M.Tr	1110002?11	20?001013
Kenderlykia	11	Other	E.J	011100??11	11110001?
Klukia	11, 37	Fern-Filicales	M.J-E.K	2110001?11	10?00001?
Konnoa	11	Seed-Gigantopteridales	P	1110001?11	111011012
Kugartenia	11	Other	L.Tr-E.J	0110001?11	10?000112
Kylikipteris	11, 18, 33	Fern-Filicales	M./L.J	0110001?11	10?000111
Lacopteris	18	Fern-Filicales	L.Tr	1112021011	10?203013
Lanceolatus	1	Seed-Glossopteridales	P	1111001?11	00?211012
Langcamia	11	Other	L.Tr	1111001?11	111100010
Lastreopsis	21, 35	Fern-Dryopteridaceae	Extant	2220002?21	20?212211
Laveineopteris	12	Seed-Medullosales	L.C	2110000?11	221011011
Lemmaphyllum	21	Fern-Polypodiaceae	Extant	111101?112	00?100010
Lepeophyllum	22	Other	P	1100000?01	11001101?
Lepidopteris	1, 16, 33	Seed-Peltaspermales	P-L.Tr	2120002?11	111000113
Lepidozamia	20, 21	Seed-Cycadales	Extant	1100?00?01	1100100??
Leptochilus	21	Fern-Polypodiaceae	Extant	111101?111	00?100010
Leptopteris	21	Fern-Osmundaceae	Extant	0200000?21	20?000210
Leslya	12	Seed-Cycadales	L.C-P	1110002?11	10?011012
Leucostegia	21	Fern-Davalliaceae	Extant	0110000?11	00?000110
Lidgettonia	1	Seed-Glossopteridales	P	1111001?11	00?211010
Liknopetalon	1	Other	P	1100000?01	01001101?
Lindleycladus	37	Seed-Coniferales	M.J-E.K	1110000?01	110010012
Lindsaea	21, 35	Fern-Dennstaedtiaceae	Extant	2200200?01	00?003211
Linguifolium	9, 28, 29	Other	E.Tr-E.J	1110001?11	00?010010
Linopteris	12	Seed-Medullosales	L.C-P	2111002?21	222201013
Lithostegia	21	Fern-Dryopteridaceae	Extant	0000000?01	00?0?0?011
Llavea	21, 35	Fern-Pteridaceae	Extant	1110000?11	00?001012
Lobifolia	2, 11	Fern-Filicales	E.Tr-E.K	2110002?11	20?100010
Lomagramma	21, 35	Fern-Lomariopsidaceae	Extant	1111000?11	00?100012
Lomariopsis	21, 35	Fern-Lomariopsidaceae	Extant	1110000?11	00?010012
Lonchitis	21, 35	Fern-Dennstaed.	Extant	1112001?21	10?000010
Lonchopteridium	12	Seed-Medullosales	L.C	1111001?11	111100010
Lonchopteris	12	Seed-Medullosales	L.C	1111001?11	111200010
Loxogramme	21, 35	Fern-Polypodiaceae	Extant	1111021111	00?100012
Lyginopteris	12	Seed-Lyginopteridales	L.C	2210002?21	20?001211
Lygodium	21, 35	Fern-Schizaeaceae	Extant	2112000?11	00?201213
Lygodium	11, 34	Fern-Filicales	L.K	2110000?11	00?200010
Macroneuropteris	12	Seed-Medullosales	L.C	2110002?21	220211010

## Appendix 3. Continued.

Genus	References	Affinity	Range	Characters: 1-10	11-19
Macrosphenopteris	12	Other	L.C	?1000???11	???011?10
Macrothelypteris	21	Fern-Thelypteridaceae	Extant	0110001?11	10?000010
Macrozamia	20, 21	Seed-Cycadales	Extant	2100?00?01	1100100??
Madygenia	11, 33	Seed-Peltaspermals	E./M.Tr	1110001?11	11100101?
Marattia	11, 37	Fern-Marattiales	E.J-L.K	1110001?11	00?010?12
Marattia	21, 35	Fern-Marattiaceae	Extant	0100000?11	00?000010
Marcouia	6	Other	L.Tr	2111001?11	111210112
Margaritopteris	12	Other	L.C	0100001?11	00?001211
Marginariopsis	21, 35	Fern-Polypodiaceae	Extant	111101?112	???100012
Mariopteris	12	Other	L.C	2210002?21	222213213
Marsilea	21, 35	Fern-Marsileaceae	Extant	0111200?01	0??000010
Matonia	34, 37	Fern-Filicales	M.J-L.K	1110001?11	10?000010
Matonia	21	Fern-Matoniaceae	Extant	1112021111	11121001?
Matonidium	11, 18	Fern-Filicales	M.J-E.K	1112001?11	10?000010
Matteuccia	21, 35	Fern-Dryopteridaceae	Extant	2120001?11	20?012212
Megalopteris	12	Other	L.C	1110001?11	111011012
Merianopteris	11	Fern	L.Tr	1110001?11	111003011
Metaxya	21, 35	Fern-Metaxyaceae	Extant	1110000?11	00?010012
Metreophyllum	1	Other	P	1110000?01	00?010012
Mexiglossa	27	Other	L.Tr-L.J	1111001?11	00?010010
Microcycas	20, 21	Seed-Cycadales	Extant	1100?00?01	1100100??
Microgramma	21, 35	Fern-Polypodiaceae	Extant	1112021112	00?200012
Microlepia	21, 35	Fern-Dennstaedtiaceae	Extant	2110000?11	00?000212
Microsorium	21	Fern-Polypodiaceae	Extant	111101?113	00?100012
Mixoneura	12	Other	L.C	2110000?21	212011011
Monachosorum	21	Fern-Monachosoraceae	Extant	2100000?21	00?010111
Monogramme	21	Fern-Vittariaceae	Extant	1000000?01	00?0?00?
Myriotheca	12	Other	L.C	0100001?11	00?001013
Nageia	21	Seed-Coniferales	Extant	1110000?01	00?013012
Nemejcopteris	12	Fern-Zygopteridales	L.C-P	1100001?11	10?010010
Nephelea	21, 35	Fern-Cyatheaceae	Extant	2120001?21	10?00001?
Nephopteris	21, 35	Fern-Pteridaceae	Extant	0100000?01	00?001010
Nephrolepis	21, 35	Fern-Nephrolepidaceae	Extant	1110200?11	00?001010
Nephropsis	22	Seed-Vojnovskyales	P	1100000?01	110010012
Neuralethopteris	12	Seed-Medullosales	L.C	1110002?11	221011013
Neurocallis	21, 35	Fern-Pteridaceae	Extant	111100?11	00?101012
Neurodium	21, 35	Fern-Polypodiaceae	Extant	111101?112	00?100010
Neuropteris	12	Seed-Medullosales	E.C-P	2112002?21	222211013
Nilsonia	1, 19, 33	Seed-Cycadales	P-L.K	2100000?11	22001020?
Nilssoniopteris	37	Seed-Bennettitales	L.Tr-E.K	1110001?11	00?01001?
Nipaniophyllum	10	Seed-Pentoxylales	E.-L.J	1110001?11	00?010012
Niphidium	21, 35	Fern-Polypodiaceae	Extant	111101?113	00?210010
Noeggerathia	12, 22	Other	L.C-P	1100000?01	210012012
Noeggerathiopsis	1, 22	Seed	P	1100000?01	110011012
Notholaena	21, 35	Fern-Pteridaceae	Extant	211000?11	20?101211
Nothorhacopteris	12	Other	L.C-P	2100000?01	???001210
Octotheca	11	Fern	L.C	1110001?11	10?001011
Odontopteris	12	Other	L.C-P	1110002?21	112213013
Odontosoria	21, 35	Fern-Dennstaedtiaceae	Extant	0200200?01	00?000110
Odontosorites	11	Fern-Filicales	E.-L.J	0120000?00	10?000111

## Appendix 3. Continued.

Genus	References	Affinity	Range	Characters: 1-10	11-19
Oenotrichia	21	Fern-Dennstaedtiaceae	Extant	0100000?21	00?000110
Oleandra	21, 35	Fern-Oleandraceae	Extant	1112000?11	00?010012
Olfersia	21	Fern-Dryopteridaceae	Extant	1110100?11	00?010012
Oligocarpia	12	Fern-Filicales	L.C-P	2110002?11	20?000211
Onoclea	21, 35	Fern-Dryopteridaceae	Extant	2111001?01	20?100212
Onocleopsis	21, 35	Fern-Dryopteridaceae	Extant	111100???11	211100012
Onychiopsis	1, 11	Fern-Filicales	M.J-L.K	0200000?01	20?000111
Ophioglossum	21, 35	Fern-Ophioglossaceae	Extant	111101?101	0??100210
Orthotheca	12	Fern-Marattiales	L.C	1110001?11	121010013
Osmunda	21, 35	Fern-Osmundaceae	Extant	1110002?11	20?011013
Otozamites	27, 37	Seed-Bennettitales	L.Tr-L.K	1100000?01	110010012
Ottokaria	1	Seed-Glossopteridales	P	1111001?11	110011010
Ovopteris	12	Other	L.C-P	1110001?11	10?001010
Pachypteris	11, 19, 33, 37	Seed-Corystospermales	E.Tr-E.K	2110001?11	111000210
Paesia	21, 35	Fern-Dennstaedtiaceae	Extant	1110100?11	00?000111
Palaeovittaria	1, 26, 33	Seed-Glossopteridales	P-M.Tr	1102001?01	110011010
Palaeoweichselia	12	Other	L.C	1111001?11	121001012
Paleopteridium	12	Other	L.C	2110000?01	20?010011
Palibiniopteris	11	Other	E.K	0110001?11	111000112
Palmatopteris	12	Seed-Lyginopteridales	L.C	0200000?01	20?001113
Paracalathiops	12	Seed-Medullosales	L.C	0000000?01	00?0?0111
Paracycas	37	Seed-Cycadales	E.-L.J	1000000?01	00?00000?
Paratingia	22	Other	P	1100000?01	???010012
Paripteris	12	Seed-Medullosales	L.C	1110000?21	00?011010
Pecluma	21	Fern-Polypodiaceae	Extant	1112021111	10?002010
Pecopteridium	12	Other	L.C	1110001?21	122211013
Pecopteris	12	Fern-Marattiales	L.C-P	2210001?21	221213023
Pekinopteris	11	Other	L.Tr	0111000?11	00?100010
Pellaea	21, 35	Fern-Pteridaceae	Extant	211220???11	00?201210
Pelourdea	8	Seed	L.Tr	1111000?01	1100100??
Peranema	21	Fern-Dryopteridaceae	Extant	0100000?11	10?000110
Phanerosorus	21	Fern-Matoniaceae	Extant	0112020011	00?00001?
Phasmatocycas	12	Seed-Cycadales	P	1110001?11	10?010013
Phegopteris	21	Fern-Thelypteridaceae	Extant	1120001?11	10?002010
Phlebopteris	11, 34, 37	Fern-Filicales	L.Tr-L.K	1111021011	121100012
Phoenicopsis	22	Seed-Ginkgoales	E.Tr-L.K	1100000?01	???010012
Phymatosorus	21	Fern-Polypodiaceae	Extant	?11101?112	???100?10
Piazopteris	11	Fern-Filicales	E.-L.J	1111001?11	111210012
Pilularia	21, 35	Fern-Marsileaceae	Extant	0000000?01	00?0??00?
Pityrogramma	21, 35	Fern-Pteridaceae	Extant	2220002?21	210011211
Plagiogyria	21, 35	Fern-Plagiogyriaceae	Extant	1110001?11	221010012
Plagiozamites	12	Other	L.C-P	1100000?02	110010022
Platyserium	21, 35	Fern-Polypodiaceae	Extant	0111020103	1??100110
Pleocnemia	21	Fern-Dryopteridaceae	Extant	1111021111	10?200012
Pleopeltis	21, 35	Fern-Polypodiaceae	Extant	2111021112	20?100210
Plumatopteris	12	Other	E.C	2100000?21	112010012
Plumsteadia	1	Seed-Glossopteridales	P	1111001?11	00?000012
Podozamites	1, 34	Seed-Coniferales	P-L.K	1100000?01	00?010012
Polybotrya	21, 35	Fern-Dryopteridaceae	Extant	2112000?11	20?013212
Polymorphopteris	12	Other	L.C	1110001?11	121211011

## Appendix 3. Continued.

Genus	References	Affinity	Range	Characters: 1-10	11-19
Polypodium	21, 35	Fern-Polypodiaceae	Extant	2112021211	2??210213
Polyspermophyllum	33	Seed	P	1000000?01	00?000110
Polystichum	21, 35	Fern-Dryopteridaceae	Extant	1100000?21	20?002111
Proteokalon	12	Progym.-Aneurophyt.	D	0000000?01	00?0?0010
Protoblechnum	4, 11	Other	L.C-L.Tr	2110001?11	111011012
Protophyllocladus	34	Seed-Coniferales	L.K	1000000?11	00?010110
Prynadaeopteris	11	Fern	L.C-P	0100000?11	10?000111
Pseudadiantites	12, 22	Other	L.C-P	2100000?01	220011011
Pseudoctenis	1, 19, 33, 37	Seed-Cycadales	E.Tr-L.K	1100000?01	110010012
Pseudocycas	37	Other	M.J-L.K	1000000?01	00?00000?
Pseudomariopteris	12	Other	L.C	1110001?11	10?000111
Pseudosporochnus	12	Other	D	0000000?01	00?0?0110
Pseudotenis	12	Other	P	1100000?01	110010012
Pteridium	21, 35	Fern-Dennstaedtiaceae	Extant	1110001?11	111000010
Pteridrys	21	Fern-Dryopteridaceae	Extant	111001?011	111000012
Pteris	21, 35	Fern-Pteridaceae	Extant	1112201?11	121210012
Pterophyllum	22, 37	Seed-Bennettitales	P-L.K	1100000?01	11001000?
Pterozonium	21, 35	Fern-Pteridaceae	Extant	1120000?21	00?011012
Ptilophyllum	37	Seed-Bennettitales	L.Tr-L.K	1100000?01	110010010
Ptilozamites	16	Seed-Peltaspermales	E.-L.Tr	1110000?01	110011012
Ptychocarpus	12	Fern-Marattiales	L.C-P	2110001?12	10?002010
Pyrrosia	21	Fern-Polypodiaceae	Extant	111101?113	00?210010
Rajahia	11	Fern-Marattiales	P	1120001?11	121010012
Regnellidium	21, 35	Fern-Marsileaceae	Extant	0100200?01	0??01001?
Rellimia	12	Progym.-Aneurophyt.	D	0000000?01	00?0?0110
Renaultia	12	Other	L.C	2200000?21	20?003213
Reticaletopteris	22	Other	L.C	2111001?11	111100011
Rhabdotaenia	25	Seed-Glossopteridales	P	1110001?11	00?010010
Rhachiphyllum	12, 33	Other	L.C-P	2110001?11	112011012
Rhacopteris	12	Other	E.-L.C	2210000?01	020010213
Rhaphidopteris	11	Other	L.Tr-L.J	0000000?01	00?000111
Rhodea	12	Other	E.-L.C	0000000?01	00?0?0113
Rhodeopteridium	22	Other	E.-L.C	0000000?01	00?000111
Rigbya	1	Seed-Glossopteridales	P	1111001?11	00?100012
Rufloiria	11	Seed	M.J-E.K	0100001?01	10?000011
Rumohra	21, 35	Fern-Dryopteridaceae	Extant	2100000?21	20?002211
Saccoloma	21, 35	Fern-Dennstaedtiaceae	Extant	2120002?11	10?010210
Saccoloma	34	Fern-Filicales	L.K	1111000?11	00?100012
Sachalinia	11	Other	L.K	0110000?21	20?001211
Sagenopteris	19, 33, 37	Seed-Caytoniales	L.Tr-L.K	1111001?11	00?101010
Salpichlaena	21, 35	Fern-Blechnaceae	Extant	1112001?11	00?010012
Sanmiguelia	13	Seed	L.Tr	1111000?04	110213012
Schaffneria	21, 35	Fern-Aspleniaceae	Extant	1111000?01	00?011012
Schizaea	21, 35	Fern-Schizaeaceae	Extant	0100000?01	00?000211
Schizaeopsis	11	Fern-Filicales	E.K	0100000?01	00?01011?
Schizoneura	1	Sphen.-Equisetales	P-L.J	1110000?01	11001000?
Scleroglossum	21	Fern-Grammitidaceae	Extant	1000000?01	00?0?0?00?
Scoresbya	11	Fern-Filicales	E.J	0111001?11	221210010
Scutum	1, 31	Seed-Glossopteridales	P	1111001?11	00?211012
Scytophyllum	11	Seed-Peltaspermales	E.-L.Tr	211001?112	211211113

## Appendix 3. Continued.

Genus	References	Affinity	Range	Characters: 1-10	11-19
Selenocarpus	11	Fern-Filicales	E.-L.J	1110001?11	10?010012
Selliguea	21	Fern-Polypodiaceae	Extant	111101?113	00?21001?
Senftenbergia	12	Fern-Filicales	E.C-P	2110001?21	20?013013
Serpyllopsis	21	Fern-Hymenophyllaceae	Extant	1000000?01	00?0?00?
Siberiella	11	Other	L.C	0200000?11	20?000110
Sinoctenis	22	Seed-Bennettitales	E./M.Tr	1110000?01	110010012
Sinozamites	22	Seed-Bennettitales	L.Tr	0100000?01	00?010012
Solanopteris	21, 35	Fern-Polypodiaceae	Extant	011101?112	00?100112
Spathulopteris	12	Seed-Lyginopteridales	E.C	2100000?01	00?010213
Sphaerocionium	21	Fern-Hymenophyllaceae	Extant	0000000?01	00?0???11?
Sphaeropteris	21, 35	Fern-Cyatheaceae	Extant	2112001?11	20?000012
Sphenobaiera	1, 33, 37	Seed-Ginkgoales	P-L.K	2110000?01	1??010212
Sphenocallipteris	12, 33	Other	P	0000000?01	00?0?0112
Sphenocyclopteridium	12	Other	D	0100000?01	0??001110
Sphenophyllum	12, 1	Sphen.-Sphenophyllales	D-P	2210000?01	220211223
Sphenopteridium	12	Seed-Lyginopteridales	E.-L.C	2210000?01	220011113
Sphenopteris	12, 1	Other	D-L.K	2210002?21	222013223
Sphenozamites	22	Seed-Cycadales	L.Tr-L.J	1100000?01	010010012
Stachypteris	11, 18	Fern-Filicales	E.J-E.K	0200000?01	00?000111
Stangeria	20, 21	Seed-Cycadales	Extant	1110001?11	221010010
Stenochlaena	21	Fern-Blechnaceae	Extant	1111001?11	00?010012
Stenopteris	37	Seed	L.Tr-L.J	0200000?01	10?000111
Sticherus	21	Fern-Gleicheniaceae	Extant	1110001?11	10?000012
Stigmatopteris	21, 35	Fern-Dryopteridaceae	Extant	1102021111	10?00201?
Sturia	12	Fern-Filicales	L.C	0200000?11	00?000211
Supaia	12	Other	P	1110001?11	111011012
Svalbardia	12	Progym.-Archaeopterid.	D	0200000?01	00?010211
Syngamma	21	Fern-Pteridaceae	Extant	111220???11	020011012
Taeniopteridium	16	Other	E.-L.Tr	1211001?11	00?011012
Taeniopteris	12, 1	Other	L.C-L.K	1110001?11	20?011013
Taenitis	21	Fern-Pteridaceae	Extant	111100???11	020100012
Tapeinidium	21	Fern-Dennstaedtiaceae	Extant	0100200?21	00?000011
Tectaria	21, 35	Fern-Dryopteridaceae	Extant	2112021113	221100212
Telangium	12	Seed-Lyginopteridales	E.C	0200000?01	00?010112
Tetraxylopteris	12	Progym.-Aneurophyt.	D	0000000?01	00?0?0210
Thainguayopteris	11	Fern-Marattiales	L.Tr	1110001?11	111001011
Thelypteris	21, 35	Fern-Thelypteridaceae	Extant	1110001?11	10?000010
Thyrsopteris	21, 35	Fern-Dicksoniaceae	Extant	0200000?01	00?000111
Tingia	22	Other	L.C-P	1100000?01	110010012
Todea	21	Fern-Osmundaceae	Extant	1120000?11	00?000010
Todites	2, 11, 37	Fern-Filicales	E.Tr-E.K	1110002?11	20?200213
Tongchuanophyllum	22	Seed	E./M.Tr	0111001?11	11110001?
Trachypteris	21, 35	Fern-Pteridaceae	Extant	0111001?11	2??100212
Trichipteris	21, 35	Fern-Cyatheaceae	Extant	2110001?11	10?010012
Trichomanes	21, 35	Fern-Hymenophyllaceae	Extant	2222002?21	221002211
Trichopitys	33	Seed	P	0000000?01	00?000110
Tricoemlecopteris	3, 11	Seed-Gigantopteridales	P	11110????14	00?210010
Triloboxylon	12	Progym.-Aneurophyt.	D	0000000?01	00?0?0010
Triphylopteris	12	Other	E.C	2100000?01	00?011213
Tristachya	12	Sphen.-Sphenophyllales	P	1100000?01	00?010013

## Appendix 3. Continued.

Genus	References	Affinity	Range	Characters: 1-10 11-19	
Tuarella	2, 11	Fern-Filicales	M./L.J	1110000?01	10?100111
Tungussopteris	11	Other	E./M.Tr	2110000?11	111003111
Tyrmia	22	Seed-Bennettitales	E.-L.J	1100000?01	11001000?
Uralophyllum	16	Other	E.-L.Tr	21?0002?21	210011012
Urnatopteris	12	Other	L.C	0200000?21	00?010013
Validopteris	12	Other	L.C-P	2112001?11	221211111
Vittaephyllum	16	Seed-Peltaspermales	E.-L.Tr	011001?113	111210013
Vittaria	21, 35	Fern-Vittariaceae	Extant	1112101?11	???210010
Welwitschia	21	Seed-Gnetales	Extant	111101?103	110010010
Wingatea	34	Fern-Filicales	L.Tr	0000000?01	00?000111
Woodsia	21, 35	Fern-Dryopteridaceae	Extant	0100002?11	10?000210
Woodwardia	21, 35	Fern-Blechnaceae	Extant	2111001?11	10?103012
Xihuphyllum	22	Other	D	?100000?01	110010?1?
Xylopteris	28, 29	Seed-Corystospermales	E.Tr-E.K	0000000?01	00?000110
Yabeiaella	23, 33	Seed-Bennettitales	E.-L.Tr	1112101?11	???010012
Zamia	20, 21	Seed-Cycadales	Extant	1100200?01	210010013
Zamiopteris	22	Seed	P-M.Tr	1100000?01	11001001?
Zamites	1, 37	Seed-Bennettitales	L.Tr-E.K	1100000?01	110010010
Zeilleria	12	Other	E.-L.C	2200000?21	20?000213
Zeilleropteris	33	Seed-Gigantopteridales	P	011101?112	00?000011