

Evolution of developmental potential and the multiple independent origins of leaves in Paleozoic vascular plants

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Abstract.—Four vascular plant lineages, the ferns, sphenopsids, progymnosperms, and seed plants, evolved laminated leaves in the Paleozoic. A principal coordinate analysis of 641 leaf species from North American and European floras ranging in age from Middle Devonian through the end of the Permian shows that the clades followed parallel trajectories of evolution: each clade exhibits rapid radiation of leaf morphologies from simple (and similar) forms in the Late Devonian/Early Carboniferous to diverse, differentiated leaf forms, with strong constraint on further diversification beginning in the mid Carboniferous. Similar morphospace trajectories have been documented in studies of morphological evolution in animals; however, plant fossils present unique opportunities for understanding the developmental processes that underlie such patterns. Detailed comparison of venation in Paleozoic leaves with that of modern leaves for which developmental mechanisms are known suggests developmental interpretations for the origination and early evolution of leaves. The parallel evolution of a marginal meristem by the modification of developmental mechanisms available in the common ancestor of all groups resulted in the pattern of leaf evolution repeated by each clade. Early steps of leaf evolution were followed by constraint on further diversification as the possible elaborations of marginal growth were exhausted. Hypotheses of development in Paleozoic leaves can be tested by the study of living plants with analogous leaf morphologies.

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Accepted: 15 August 2001

Introduction

Paleontology enjoys a rich tradition of research on the evolution of morphological diversity. Beginning with Raup's (1966) quantification of molluscan morphospace based on the geometry of coiled shells, paleontologists have used mathematical descriptions of shape (MacLeod 1999; Smith and Bunje 1999); continuous, quantitative measurements of distances among morphological points deemed homologous (Bookstein 1991); and discrete qualitative characterizations of morphology (Foote 1995) to illuminate the history of morphological diversity in invertebrates and skeltonized protists (see McGhee 1999 for review).

Developmental biology offers the prospect of understanding the genetic and physiological bases of morphology and, hence, of morphological evolution. To date, however, few attempts to integrate data from paleontology and developmental biology (reviewed in Shubin et al. 1997; Valentine et al. 1999; Knoll and Carroll 1999) have taken advantage of the possibilities afforded by morphometric analyses of the fossil record.

Vascular plants are particularly well suited for the integration of developmental biology and paleontology. The presence in plants of cell walls vastly increases the probability of anatomical preservation. Cell walls also prohibit cell migration, constraining the types of development that are possible in plants and facilitating the recovery of developmental pattern from fossils. (In structures such as the vascular cambium of seed plants, the tips of developing cells can grow intrusively between other cells, and cell contacts can be established between cell files on either side of a cambial initial that is lost. However, even in this special case of secondary growth, there is no actual cell migration; cambial ontogeny can still be traced readily in the cambium-derived wood [Barghoorn 1940]). This stands in marked contrast to animals, where ontogeny involves complex patterns of cell movement, changing cell contacts, and cell death.

Additional advantages arise because land plants essentially all make their living in the same way (Knoll and Niklas 1987; Niklas 1994). There are various specializations to deal with limitations of water, light, nutrients,

symbionts, and substrates, but, with the exception of a few parasites, all plants gather sunlight, water, and carbon dioxide in order to conduct photosynthesis. As a result, there is, in general, far less uncertainty about the interpretation of functional morphology in fossil plants than there is with fossil animals. This uniformity of life strategy, in conjunction with developmental constraints, also increases the likelihood of evolutionary convergence. Roots, secondary growth, and laminate leaves each evolved multiple times in different tracheophyte lineages. Such repeated instances of convergent evolution permit developmental comparison of multiple independent origins of morphologically and functionally similar structures.

This combination of developmental constraint, cellular preservation, and convergent evolution makes plants unusually attractive subjects for morphological analysis. Leaves are particularly advantageous for studies of morphological evolution. Leaf compressions are abundant in fluvial and lacustrine depositional systems, the leaf fossil record is well documented, and leaves are the one organ for which both overall morphology and details of vascularization are commonly available in the same specimen. Furthermore, laminate leaves are known to have evolved independently in several Paleozoic tracheophyte clades, and the degree of morphological convergence among these early leaves is high. Leaves produced by early pteridophyte and seed plant lineages were in some cases so similar to modern fern leaves that only in the early twentieth century did paleontologists recognize that some were borne by seed plants (reviewed in Scott 1909).

In this paper, we present a morphospace analysis of Paleozoic leaves and interpret the results in light of developmental processes inferred from preserved morphologies.

Patterns of Morphological Evolution in Paleozoic Leaves

During the later Devonian and Early Carboniferous, laminate leaves containing multiple veins evolved independently in seed plants, progymnosperms, ferns, and sphenopsids. The leaves of ferns, seed plants, and pro-

gymnosperms have traditionally been termed megaphylls and considered to be homologous. By definition (Gifford and Foster 1989), megaphylls are associated with leaf gaps in the stele of the supporting stem; they can be frondose or entire, and typically are laminate and contain more than one vein (unless secondarily reduced as in most conifers). Although widely applied, this megaphyll typology is an artifact of the depauperate living flora. Once fossils are included, no component of the megaphyll concept emerges as a synapomorphy uniting these lineages. In particular, the central tenet of associated leaf gaps is not relevant to the earliest fossil representatives of these lineages, all of which are protostelic (Taylor and Taylor 1993).

It is possible that some or all of these lineages inherited a lateral branch system with a broadly frondlike architecture from their common ancestor (Kenrick and Crane 1997). The likelihood of this is dependent on the phylogenetic placement of a few key taxa of ambiguous affinities. The traditional placement of the ferns and seed plants as sister taxa, with *Equisetum* as the closest outgroup, suggested that a frondose megaphyllous leaf was a synapomorphy shared by the ferns and the seed plants. However, the most recent phylogenetic work based on living plants places *Equisetum* and the Psilotales along with eusporangiate ferns as basal lineages in a clade containing all extant pteridophytes, save for lycopods (Pryer et al. 2001). Statements about last common ancestors, then, depend critically on how key Devonian plants without laminated leaves are added to this phylogeny.

Even if certain frond characteristics turn out to be synapomorphies of the clade that includes sphenophytes, ferns, progymnosperms, and seed plants, however, the terminal units on any fronds inherited from a common ancestor would have had little or no lamination. The earliest known leaves in each of the four clades are highly dissected structures composed of segments that were small, narrow, and with a single vein. In light of these fossils, our assessment of leaf evolution does not depend on any particular phylogenetic hypothesis.

A survey of the Paleozoic compression flora

of North America and Western and Central Europe was carried out to investigate patterns of morphological diversification in the early evolution of leaves within and among groups. Each species was described from a single primary source, although stratigraphic ranges and taxonomic affinities were modified using the full list of sources (see Appendix 1). Taxonomic affinity was assigned only to leaves with documented connection to either fertile structures or stems with diagnostic anatomical features. Association of leaves and fertile structures at the same localities was not considered sufficient for taxonomic assignment.

Morphological similarity of a species to other leaf species of known taxonomic affinity also was not considered. For example, many *Neuropteris* species are listed as having unknown affinities despite the fact that some *Neuropteris* species are known to have been borne by seed plants. An exception to this was made in the case of the gigantopterids. Seed plant identity has been documented only for Asian gigantopterid species, which are beyond the scope of this study, but the unique construction of gigantopterids warrants placement of the two gigantopterid species included from North American localities as seed plants. Fossils that could not be identified to the species level and taxa for which photos with identifiable venation were not available were excluded from the analysis. Of the resulting list of 641 taxa, 52 are seed plants, 144 are pteridophytes, and 445 are of unknown affinity (many of these are probably but not demonstrably seed plant remains). Among the pteridophytes, there are 15 progymnosperms, 33 sphenopsids, 19 leptosporangiate ferns, 27 marattialean ferns, 15 zygopterids, and 35 eusporangiate species of other or unknown affinities. See Appendix 3 for a list of species, their stratigraphic ranges, and their taxonomic affinities.

Taxa were coded for 63 unordered binary and multistate characters (see Appendix 2; a complete data matrix of character codings for each species is available from C. K. B.) describing individual pinnules rather than entire fronds and concerned primarily with venation and laminar structure rather than overall pinnule shape. Individual leaf species commonly

display considerable laminar variability, even between the pinnules within a single fossil frond. This variability was included in the character codings by the use of "variable" as a state for many characters (see Appendix 2 for examples). Coding for variability introduces two important, but potentially negative effects. First, it requires the use of characters that are inapplicable to large subsets of the taxa. Second, taxa based on few or incomplete fossil specimens can be miscoded because there is less opportunity for actual species variability to be demonstrated in available examples. Despite these complications, inclusion of variability is preferable to its exclusion, because variation is such a common aspect of plant morphology (e.g., Knauss and Gillespie 2001) and because range of variation is potentially informative about development.

A principal coordinate analysis was used to provide a more comprehensible summary of the information recorded in the study. The original matrix of character codings for the 641 taxa was used to create a 641 by 641 matrix of the pairwise dissimilarities of all species calculated as the number of character mismatches divided by the number of characters that are not missing or nonapplicable. (Dissimilarity matrix and related statistics were calculated using software provided by R. Lupia; further details of methodology described in Lupia 1999. Mathematica was used for the principal coordinates analysis and all other calculations.) This matrix was then transformed to move the centroid of the dissimilarity distribution to zero (Gower 1966). Eigenvalues and eigenvectors of the transformed dissimilarity matrix were determined, and the component values of each eigenvector were used to position each taxon with respect to a particular principal coordinate axis (Sneath and Sokal 1973). The magnitude of the eigenvalue corresponding to each eigenvector gives an indication of the relative contribution of that axis to the summary of information from the original data matrix. The first two principal coordinate axes were plotted as a representation of morphospace occupied through time (Figs. 1, 2). These axes contain about 51% of the information in the original distance matrix, as estimated from the sum of

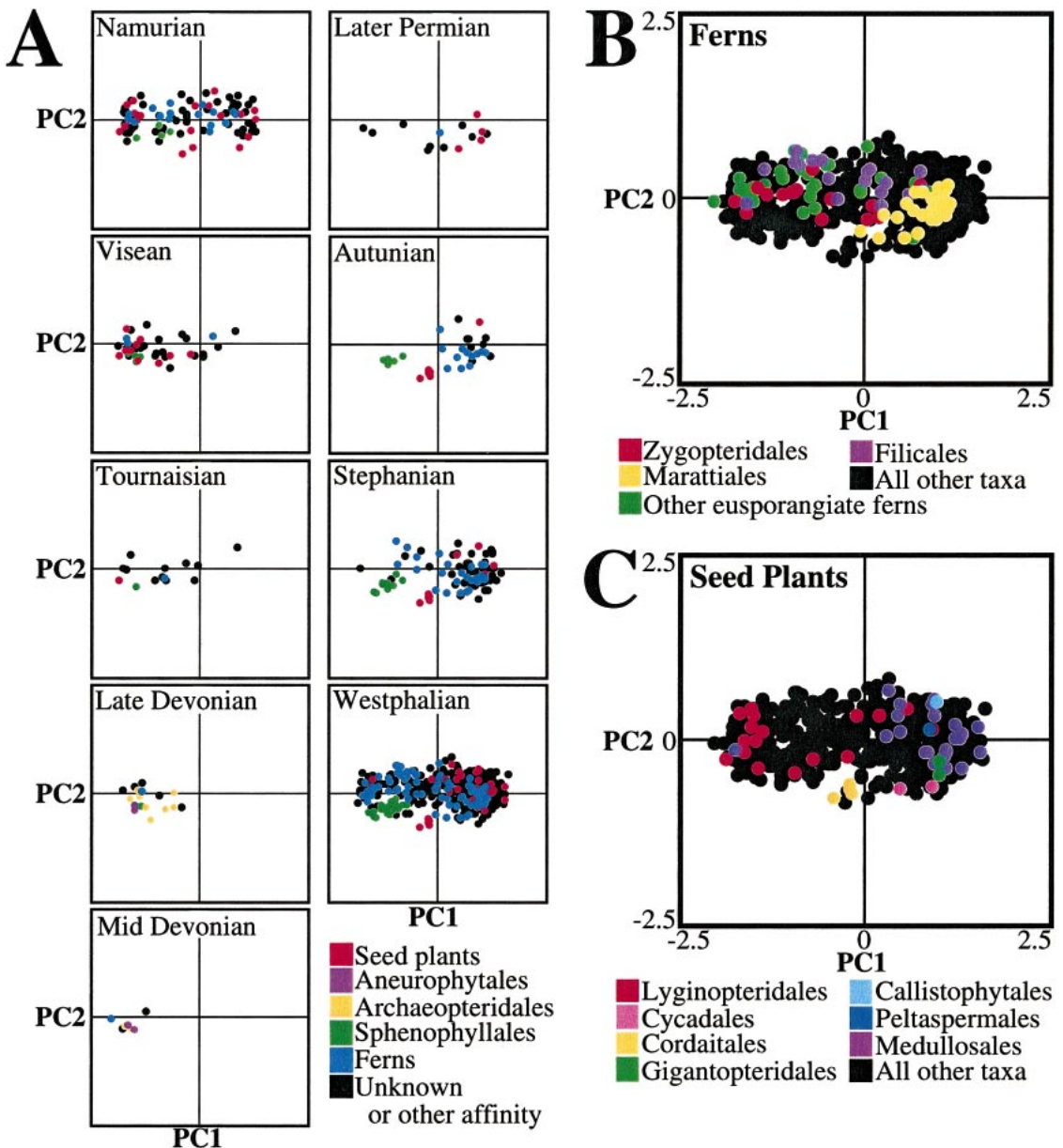


FIGURE 1. Principal coordinate analysis morphospace of Paleozoic leaf compression fossils, plotted by stratigraphic interval (A); and showing the placement of taxa within important groups of ferns (B) and seed plants (C).

the two corresponding eigenvalues divided by the sum of all eigenvalues of the transformed distance matrix (Foote 1995).

The taxa span the time interval from Middle Devonian until the end of the Permian. The Devonian through Early Permian (Autunian) is divided into intervals averaging approximately 15 million years and ranging from 8 to 21 million years in duration. The later Permian

is not well represented for two reasons: (1) there are fewer productive localities within the geographic area covered, and (2) poor preservation and coriaceous habit commonly obscure venation pattern in specimens that are available (Kerp 2000).

Principal coordinate analyses provide a convenient method for visualizing large quantities of morphological information by geo-

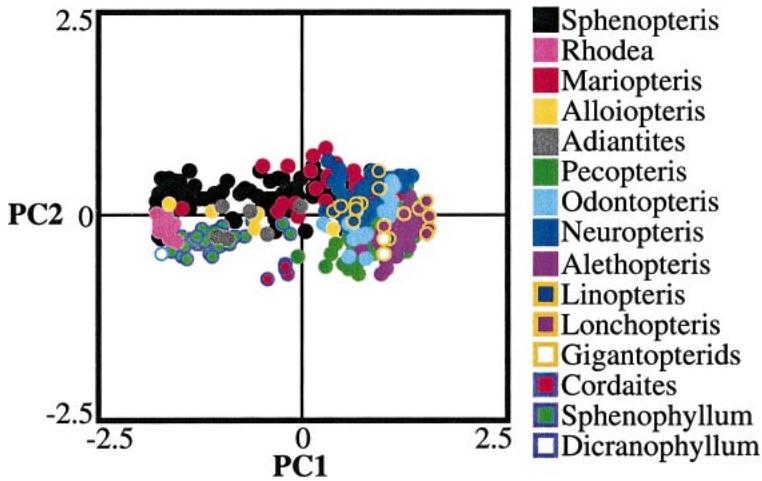


FIGURE 2. Location within the morphospace of important form genera and other morphologically distinctive groups.

metrically summarizing as much of the variability between taxa as possible on a few axes in the form of a morphospace. However, because such an analysis is entirely dependent upon the overall composition of the data set, it can be highly influenced by taxonomic and morphological decisions. In particular, the gigantopterids bore the most complex and morphologically distinctive leaves of any plants in the Paleozoic, but there was no possibility of their leaves having coordinates distinct from other taxa on axes 1 and 2 because gigantopterids represented only about 0.3% of the included species and the characters that distinguish them were invariant among all other taxa. Placement of the diverse morphologies of the Devonian and Carboniferous leaves is, however, more amenable to morphological in-

terpretation (Figs. 1, 2), and the overall pattern of diversification seen in the 50% of the information summarized in the two-dimensional morphospace plot represents well the data set as a whole (Fig. 3).

Three interesting patterns emerge from the resulting Paleozoic leaf morphospace (Fig. 1). First, the areas of initial morphospace occupation in the Devonian and Early Carboniferous remain occupied in the later record, but the taxonomic affinities of the plants exhibiting these leaf morphologies change over time. Second, ferns, seed plants, progymnosperms, and sphenopsids all share the same initial location in morphospace, diverging only with subsequent evolution. This suggests that the independent origins of leaves were based on modifications of a common underlying developmental system. Third, diversity and disparity (total occupied morphospace) initially increase in tandem, but after the Namurian, further increases in taxonomic diversity do not change the range of morphologies occupied, suggesting that the limits of a biologically constrained system had been reached. Early leaf evolution thus appears to be constrained at both ends of the radiation, first by initial architectures and later by the limits of leaf morphological variation.

Developmental Interpretations of Morphological Patterns

Insights from living organisms have long been applied to paleontological studies of

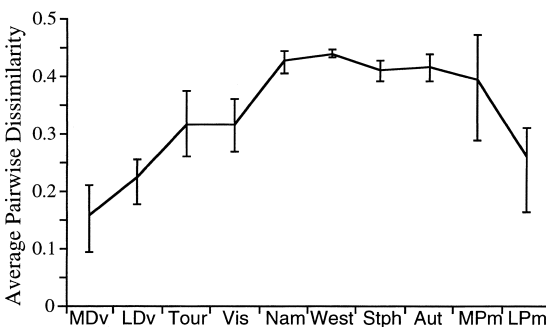


FIGURE 3. Average pairwise dissimilarity between species for each interval with 95% confidence intervals based upon 1000 bootstrap resampling runs.

plant function. Examples include biomechanical modeling of extinct species based on characteristics of living tissues (Roth and Mosbrugger 1996; Niklas 1997a,b; examples in Bateman et al. 1998) and estimates of past carbon dioxide levels based on stomatal indices derived from present-day plants (McElwain et al. 1999). In similar ways, paleobotanical studies of morphological evolution can benefit from advances in plant developmental biology. For example, following earlier suggestions (Scheckler 1976, 1978; Wight 1987), Stein (1993) modeled stem vasculature as a function of auxin diffusion from the stem apex and lateral primordia, successfully reproducing the observed stelar morphologies of some Devonian plant axes.

An understanding of leaf development in living plants may similarly inform our understanding of early leaf evolution. Comparative biology suggests that mechanisms of meristematic growth will likely impose constraints on leaf development and, hence, potential leaf morphologies. For this reason, fossil leaves may provide an indirect record of leaf meristematic capability through time. The study of leaf evolution has traditionally relied upon interpretation of frond architecture and the positional identity of laminar subunits of the frond. These traits are important for whole-plant reconstruction and for systematics, but they cannot illuminate the developmental capacity of the foliar meristems of these plants. The emphasis here is on the meristematic potential present in early leaf-bearing plants, using comparisons with living plants to constrain models of lamina development and evolution. Rather than considering *positional* homology and evolution, the focus is upon *meristematic* homology and evolution (Stein 1998).

Development can be considered in terms of two related processes: (1) growth, including cell division and the differentiation of individual cells, and (2) the patterning of differentiated cells to form functional tissues (Wolpert 1971; Sachs 1991). The leaves of extant plants display a number of different growth mechanisms. Anatomical studies of morphologically diverse ferns indicate leaf growth by meristems located at the margin of the developing

organ (Pray 1960, 1962; Zurkowski and Gifford 1988; White and Turner 1995; Korn 1998). Marginal meristems consist of a peripheral row of dividing initials, which are the ultimate source of all cells in the leaf. Additional submarginal cell divisions are necessary both for cell differentiation and for building up the thickness of the developing leaf. The marginal meristem remains active until general pinnule morphology and the location of all procambium has been determined (Pray 1962). In contrast, angiosperm leaves grow diffusely, with meristematic activity throughout the developing leaf. Clonal analysis experiments corroborate anatomical work (Pray 1955) and SEM studies (Hagemann and Gleissberg 1996) in demonstrating that the marginal cells of an angiosperm leaf play almost no role in leaf growth (*Nicotiana tabacum* [Poethig and Sussex 1985a,b]) or, at least, play no greater a role than other parts of the leaf (*Gossypium barbadense* [Dolan and Poethig 1998]).

Marginal and diffuse growth are not necessarily mutually exclusive mechanisms; more likely, they represent end-members of a large and complex continuum. Although the few fern leaves for which development has been studied in detail possessed marginal meristems, others are likely to possess more varied and complex mechanisms of growth (such as those described as having "dilatatory" leaf growth by Wagner [1979]). Furthermore, there is much variety in what is here summarized as internal, as opposed to marginal, growth (Foster 1952; Hagemann and Gleissberg 1996). Although continuing research is needed to explore the complete developmental diversity of leaves in living plants, what matters for an initial assessment of Paleozoic plants is that their leaves could grow exclusively by means of a marginal meristem or could include extensive internal growth.

Although differing mechanisms of leaf growth exist, vascular patterning is broadly similar across all tracheophytes. Vascular plants all have a flux of auxins from distal meristems in the shoot system toward more proximal tissues. Auxin transport is accomplished by the pumping of auxin into cells from all sides and the preferential pumping of auxin out of cells proximally down the stem

(Gälweiler et al. 1998; Steinmann et al. 1999; Berleth et al. 2000). Physiological studies have demonstrated the importance of auxins both for overall stelar patterning (Ma and Steeves 1992) and for finer scales of differentiation, including the establishment of cell polarity and the continuity of vascular strands (Sachs 1981). Sachs (1981, 1991) has hypothesized that the differentiation of individual vascular strands is based upon the distal to proximal flux of auxin, which determines cell polarity and induces the development of procambial characteristics in the files of cells through which it flows. These procambial characteristics increase the cells' capacity to transport auxin, further increasing flux through the cell file and, in consequence, decreasing fluxes through adjacent cell files. In this way, the widths of procambial strands can be limited without the necessary action of a second, inhibitory hormone.

The studies of vascular patterning and the auxin canalization hypothesis reviewed in the preceding paragraph are based principally on stems—molecular and biochemical studies of leaves are largely limited to investigations of vascular cell differentiation in *Zinnia* tissue cultures. Nonetheless, several considerations justify the assumption that leaves and stems follow similar mechanisms of vascular patterning and differentiation: The canalization hypothesis is the only hypothesis that has been documented in any part of the plant and it is consistent with all available information from leaves. Leaf primordia are known to be important sources of auxin (Ma and Steeves 1992; Stein 1993), and the disruption of leaf vascular patterning by auxin transport inhibitors (Sieburth 1999; Mattsson et al. 1999) and by mutations that disrupt auxin transport (Carland and McHale 1996) has been documented. (Leaf development is, of course, also influenced by auxin-independent factors [Carland et al. 1999]). The documentation of vascular patterning mechanisms in leaves remains an important research goal, and emerging techniques (Caruso et al. 1995; Moctezuma and Feldman 1999) suggest that new insights are on the horizon.

The growth and patterning mechanisms exhibited by living plants can be used to con-

strain hypotheses about developmental mechanisms present during the early evolution of leaves. The role of auxin fluxes from active meristems in the patterning of vascular tissue appears to be conserved throughout tracheophytes. We assume, therefore, that it applies to Paleozoic leaves. This assumption, in turn, provides a means of generating hypotheses about leaf growth in extinct plants. If the leaves of Paleozoic plants grew exclusively by marginal meristems, venation should be oriented toward leaf margins with all veins ending marginally, as observed in the living ferns for which marginal growth has been documented. If the leaf development included extensive internal, nonmarginal growth, venation would not be expected to have uniform orientation and vein endings should be dispersed throughout the lamina.

All Devonian and Carboniferous leaves, regardless of phylogenetic affinity, have exclusively marginal vein endings (Figs. 4, 5). This suggests that each origin of laminated leaves relied on marginal meristems. The only Paleozoic leaves with extensive internal vein endings were those of the late Early to Late Permian gigantopterid seed plants. In their case, internal tertiary veins are oriented toward one another and meet in discrete areas between the marginally ending secondary veins. This suggests a two-stage process in which marginal growth was followed by internal growth at discrete intercalary meristems. There is no evidence of true diffuse growth until the Mesozoic.

The early leaves of each lineage likely grew by means of marginal meristems, but our understanding of those meristems can be further refined. In some living ferns, a direct correspondence has been found between specific marginal initials and the cell types to which they give rise (parenchyma, or parenchyma and vasculature [Pray 1960, 1962; Zurakowski and Gifford 1988]). Other work with different ferns has found marginal meristems of uniform composition; in these plants, vascular patterning responds to marginal signals, but without reference to specific marginal initial cells (Korn 1998). Tissue patterning based on discrete ground meristem and procambial marginal initials would be expected to result

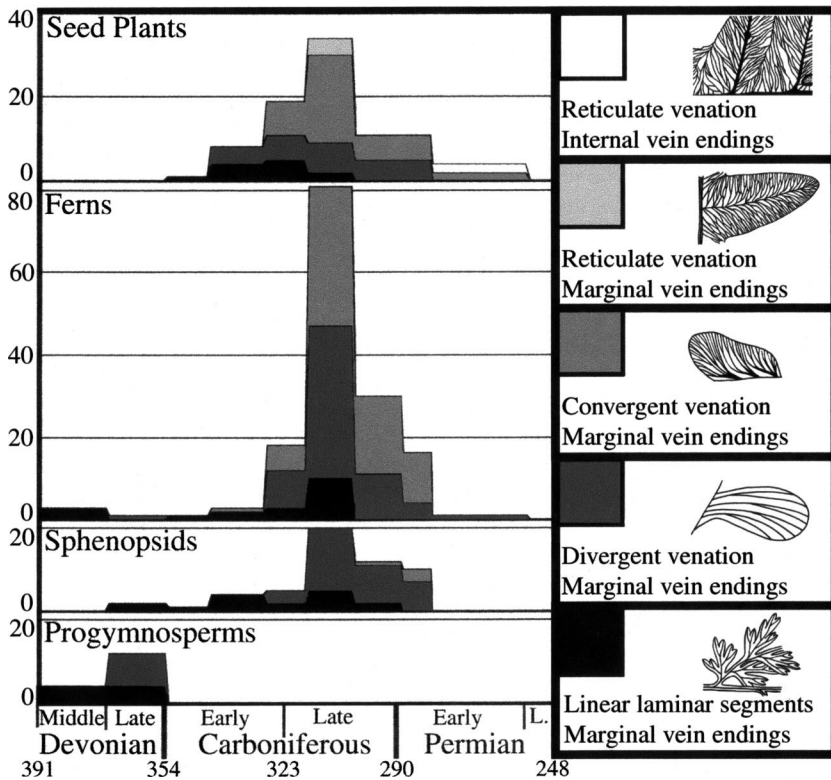


FIGURE 4. Abundances of venation types among Paleozoic leaves of known phylogenetic affinity (leaf venation images modified from Boureau and Doubinger 1975, except top image from Beck and Labandeira 1998).

in leaves with divergent venation, because the marginal initials corresponding to any two adjacent veins can only maintain their distance or grow farther apart as growth continues. Extra submarginal growth can distort the vein paths into convergence (Pray 1960), but in any event, a meristem of distinct initial types could never account for reticulately veined leaves.

Because marginal-meristem types place constraints on resulting leaf morphologies, we can draw inferences about meristem types from fossils with preserved venation. If the marginal meristems of Paleozoic leaves had distinct vasculature and parenchyma initials, divergent venation should dominate the early record. If the marginal meristems were homogenous, vein convergence and reticulation would be expected to be relatively common.

As shown in Figure 4, divergent venation was the first pattern to appear in each lamina-evolving clade. Progymnosperms show only divergent venation. Among seed plants and

ferns, convergent venation first occurred in the Visean, and it did not occur among Sphenopsids until the Stephanian. Reticulate venation appeared in the Westphalian, but only in seed plants and leaves commonly presumed to have been borne by seed plants. (Ferns evolved reticulate venation during the Mesozoic Era.) The predominance of divergent venation in early leaves across all phylogenetic groups suggests that each group convergently evolved a marginal meristem with discrete initial types and only later diverged into other development types, including modified forms of marginal meristems with discrete initial types and homogenous marginal meristems.

Leaf evolution in each clade followed the same sequence of morphologies. Paleozoic seed plants first evolved dichotomizing, finely lobed leaves with a single vein per laminar segment, and only later evolved laminar multiveined leaves with divergent venation, followed by convergent venation, followed by re-

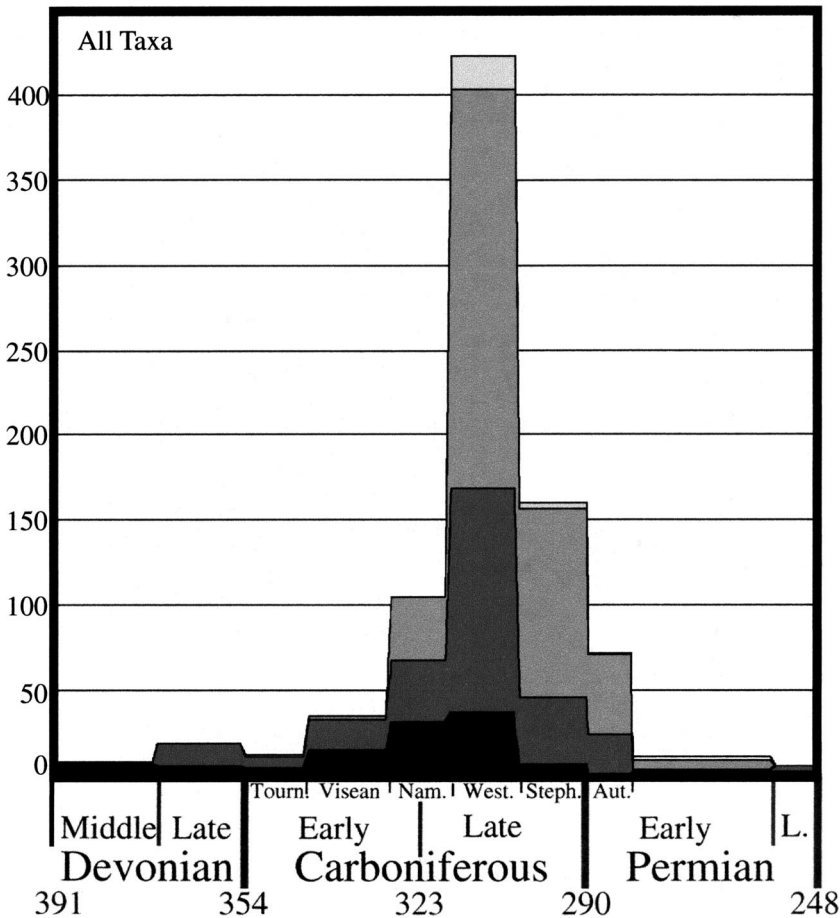


FIGURE 5. Abundances of venation types among all Paleozoic leaf species included in the analysis. Coding of venation types as in Figure 4.

ticulation. The other clades followed the same sequence to a varying extent. It is proposed that this repeated pattern reflects the limited number of ways that plants can form laminate photosynthetic surfaces. The range of morphological possibilities is further constrained by the common ancestry of the groups in question: evolution works by the modification of preexisting structures and developmental pathways, and the available underlying pathways common to the four clades and ultimately derived from a shared ancestor was stem development. Stems are indeterminate, cylindrical structures that grow from a discrete apical meristem, providing the source of an auxin gradient involved in vascular patterning. We hypothesize that stepwise modification of the growth and patterning employed in this ancestral, axial system produced marginal mer-

istems and laminate leaves in each lineage (Table 1).

Just as the early steps of marginal meristem evolution were constrained by the scope of developmental possibility, the ultimate range of possible leaf morphologies must have been constrained by available developmental mechanisms. Early leaves consisting of linear, dichotomizing segments had limited potential for morphological variability: they could be three-dimensional or planar; dichotomies could be equally distributed, concentrated distally, or concentrated proximally; and the relative strengths of the two arms of a dichotomy could be altered (Fig. 6). Each of these modifications had been explored by the Late Devonian.

The possibilities of marginal growth are also limited. Simple marginal growth with

TABLE 1. Hypothesized sequence of developmental evolution and time of first occurrence of each innovation by lineage.

Growth	Patterning	First occurrence
Indeterminate Axial growth	Venation oriented along hormone gradient from subset of meristematic cells	Ancestral stem architecture Present throughout Devonian
Determinate Axial growth		Several originations or present in common ancestor Present by Middle Devonian
Determinate Marginal growth		Progymnosperms: Late Devonian Sphenophylls: Middle Carboniferous Ferns: Late Dev./Early Carb. Seed Plants: Early Carboniferous
Determinate Modified marginal growth		Progymnosperms: Never Sphenophylls: Latest Carboniferous Ferns: Middle Carboniferous Seed Plants: Middle Carboniferous
Determinate Marginal & intercalary growth	Venation oriented along hormone gradient from all meristematic cells	Progymnosperms: Never Sphenophylls: Never Ferns: Mesozoic Seed Plants: Late Carboniferous
Determinate Diffuse growth		Progymnosperms: Never Sphenophylls: Never Ferns: Mesozoic Seed Plants: Mesozoic

point initiation will result in a fan-shaped leaf with vein endings along the distal margin, the only margin along which a marginal meristem would have been active. This system can be modified by symmetric or asymmetric alteration of the rate of growth parallel and/or perpendicular to the marginal meristem or by variation in the duration of growing time along the meristem (Fig. 7). Other possible modifications include the development of a midvein, and broad rather than point initiation of lamina growth. A rigorous documentation of possible leaf forms in terms of a theoretical morphospace (McGhee 1999) based on developmental mechanisms is needed, but it is fair to state that, even though the various possible combinations of these modifications continued to be shuffled within individual lineages, all specified variables had been explored by the Namurian. The lack of further increase in overall morphological disparity after the Namurian, despite further increase in taxonomic diversity, likely reflects limitations on possible elaborations of marginal growth.

Discussion

The stratigraphic distributions of individual characters may provide crude tools for investigating the evolution of leaf development, but the results are compelling. Internal vein endings are not present for the first 100 million years of leaf evolution; convergent venation is absent for the first 50 million years. The morphological constraints apparent in early leaves strongly suggest specific mechanisms of development. Although multiveined leaves evolved independently at least four times, the close similarities of early leaves in all groups suggest parallel evolution by modification of common developmental mechanisms inherited from ancestors whose photosynthetic organs consisted of apically growing, bifurcating axial systems.

The evolution of laminated leaves may be related to the evolution of vascular systems competent to support high levels of evapotranspiration and other aspects of whole-plant function in increasingly stratified later Devo-

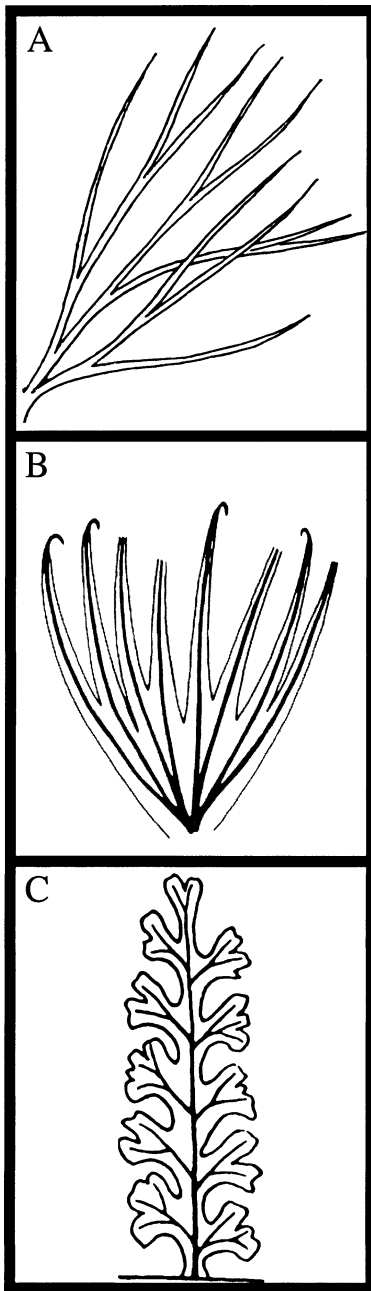


FIGURE 6. Axially organized leaves with dichotomies. A, Evenly distributed. B, Proximally concentrated. C, Distally concentrated and with unequal strength between the two arms of the dichotomies. (Leaf images modified from Remy and Remy 1977 [A, C] and Batenburg 1977 [B].)

nian and Early Carboniferous communities. It has also been proposed that appearance of laminate leaves was causally linked to a drop in atmospheric CO_2 concentration through the

Devonian (Beerling et al. 2001). Changing environmental conditions may well have removed a physiological barrier to the evolution of leaf lamination. Nonetheless, the staggered timing of lamina evolution among clades—in the Devonian, multiveined, laminate leaves occurred primarily in the Archaeopterid progymnosperms—suggests that both intrinsic and extrinsic factors are necessary to explain the observed patterns of leaf evolution.

After an initial period of parallel evolution, leaf morphologies within and among the groups diverged; however, by Namurian times the limitations of marginal meristematic development had been reached and further increases in taxonomic diversity did not increase morphological disparity. Innovations in frond architecture, leaf anatomy, and biochemistry continued to evolve, but the possibilities of marginal pinnule growth had been explored.

The use of vascular patterning as a proxy for developmental mechanism can illuminate other patterns of developmental evolution and convergence, including the evolution of diffuse leaf growth in post-Paleozoic time. Angiosperms radiated initially in the Cretaceous Period. One of the hallmarks of angiosperm morphology, at least among dicots, is highly reticulate leaf venation with multiple vein orders and freely ending internal veinlets in the vascular aureoles (Esau 1953; Gifford and Foster 1989). On the basis of available experimental evidence (Foster 1952; Pray 1955; Poethig and Sussex 1985a,b; Hagemann and Gleissberg 1996; Dolan and Poethig 1998), this pattern is interpreted as an indication of diffuse leaf growth. Venation patterns suggestive of diffuse leaf growth, however, are not limited to the angiosperms. Species in two other groups that radiated in the Cretaceous and early Tertiary, the Gnetales and the fern clade that includes the polypods and dryopterids, also possess leaves of this type. As in the Paleozoic, Mesozoic innovations in leaf development were convergent. The simultaneously radiating angiosperms, gnetaleans, and polypods were the only groups to evolve this type of leaf, aside from a small leptosporangiate fern clade that includes *Dipteris* (fossil record dating to the Late Triassic [Collinson 1996]),

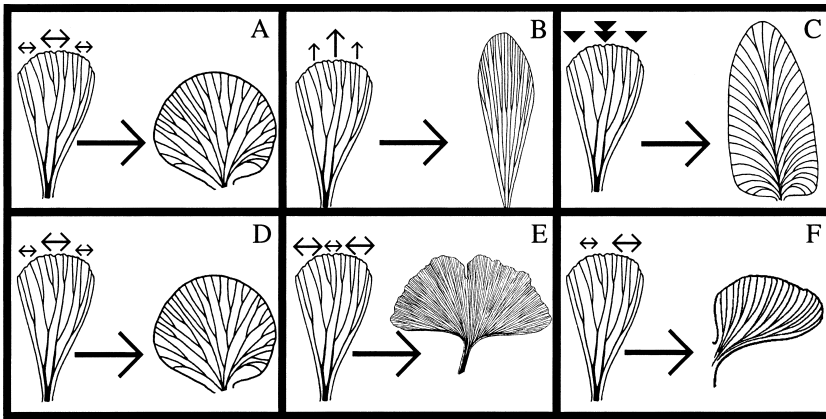


FIGURE 7. Possible modifications of marginal growth and hypothesized morphological consequences. Simple marginal growth from a point-initiation site will result in a fan-shaped leaf with all veins running to the distal margin along which all growth occurred. Variables include the following: rate of growth parallel to the margin (A), rate of growth perpendicular to the margin (B), and the duration of marginal growth (C). Each class of modification may be symmetric favoring the median areas of the meristem (D), symmetric favoring the peripheral areas of the meristem (E), or asymmetric (F). Modifications can also exist in varying degrees of strength and combination (leaf images modified from Abbott 1958 [A-F], Andrews 1961 [F], Boureau and Doubinger 1975 [B, C], Arnott 1959 [E], and Cleal and Thomas 1994 [A, D]).

the eusporangiate ferns *Ophioglossum* (order Ophioglossales represented in record only by Cenozoic specimens of another genus [Rothwell and Stockey 1989]) and *Christensenia* (order Marattiales has an extensive Paleozoic and later fossil record, but there are no known fossils of this genus), and a few Mesozoic specimens of unknown affinities (examples in Trivett and Pigg 1996).

Diffuse leaf growth may well provide structural or physiological advantages to vascular plants. For example, the pattern of highly reticulate venations, many vein orders, and internally ending veinlets that we associate with diffuse growth should provide redundancy of water transport and increased structural support for the typically larger laminae of angiosperms (Givnish 1979; Roth-Nebelsick et al. 2001). The capacity for developmental flexibility that this growth requires may also be advantageous. In addition to any particular functional value, convergent leaf form in these three groups might reflect initial radiations in similar environments. The center of diversity for polypod ferns is in the Tropics. Most basal angiosperm lineages (Feild et al. 2000) and *Gnetum* are also tropical understory plants. The convergent evolution of leaf development in these groups could reflect radiation in trop-

ical understory environments with low light levels and high humidity.

The developmental hypotheses advanced in this paper are testable. Although living *Sphenophyllum* will never be available for direct scrutiny, the logic of using adult morphology as a proxy for developmental processes can be tested because the same arguments can be used to make developmental predictions about other laminar organs available for study in living plants. These include not only the leaves of unstudied ferns, angiosperms, cycads, *Ginkgo*, araucarian conifers, and Gnetales, but also additional organs such as laminate floral parts and winged seeds. Venation patterns in these organs can differ substantially from those of leaves borne on the same plant. We predict that differing venation patterns will be found to reflect developmental mechanisms similar to those documented for leaves.

Acknowledgments

We thank R. Lupia for providing software to create the dissimilarity matrix (available at <http://geosci.uchicago.edu/paleo/csource>); B. Craft for programming assistance; W. Stein and N. Sinha for thoughtful reviews; and T. Feild, M. Foote, M. Hoolbrook, E. Kellogg, E.

Kramer, R. Lupia, C. Marshall, R. Moran, and M. Thompson for helpful discussions. Research leading to this paper was supported in part by a National Science Foundation predoctoral fellowship and by the NASA Astrobiology Institute.

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Appendix 1

Sources used to compile morphological characters of Paleozoic leaf species and to determine their stratigraphic ranges and systematic affinities.

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Appendix 2

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

1. Lamina: 0, three-dimensional; 1, planar.
2. Lamina: 0, lobed; 1, not lobed; 2, variable.
3. Entire lamina: 0, simple; 1, sinuous margin; 2, variable.
4. Margin: 0, smooth; 1, margin responds to each vein ending; 2, variable.
5. Location of maximum width: 0, proximal; 1, central; 2, distal; 3, variable.
6. Maximum width: 0, singular; 1, maintained; 2, variable (for characters 5 and 6, linear or lobed = ?).
7. Attachment: 0, narrow; 1, broad; 2, variable.
8. Narrow attachment type: 0, not stalked; 1, stalked; 2, variable.
9. Insertion: 0, perpendicular to somewhat angled (>60°); 1, severely angled (<60°); 2, variable; 3, skew (*Sphenophyllum*; *Cordaites*).

10. Attachment proximal: 0, straight; 1, constricted; 2, decurrent; 3, variable.

11. Attachment distal: 0, straight; 1, constricted; 2, decurrent; 3, variable.

12. Shape of pinnule body: 0, symmetric; 1, not symmetric; 2, variable.

13. Not-symmetric pinnules are: 0, falcate or otherwise regular but asymmetric; 1, irregular; 2, variable.

14. Lamina (or lobe) tip: 0, regular; 1, irregular edge; 2, variable (linear, lobed leaves are 1).

15. Regular lamina tip: 0, acute; 1, rounded; 2, variably rounded or acute; 3, wedge.

16. Wedge leaf distal margin: 0, curved; 1, straight; 2, acute; 3, irregular; 4, variable.

17. Maximum number of veins in laminar segment: 0, one; 1, more than one; 2, variable.

18. Branching of veins within lamina: 0, absent; 1, present; 2, variable.

19. Number of distinct vein orders besides any midvein present: number.

20. Relations of vein orders: 0, strictly hierarchical; 1, not; 2, variable (= ? if no midvein).

21. Minimum number of branchings from base or midvein to margin: number (from midvein = 1).

22. Maximum number of branchings from base or midvein to margin: number.

23. Branching of laterals: 0, just dichotomous; 1, also subdichotomous; 2, also pinnate.

24. Location of vein branching along proximal-distal axis: 0, only dispersed; 1, restricted at vein level; 2, restricted at whole lamina level; 3, restriction at both vein and whole lamina level (restrictions in linear leaves are considered at whole lamina level = 2).

25. Vein level restriction of branching favors: 0, distal; 1, center; 2, proximal; 3, variable.

26. Lamina level restriction of branching favors: 0, distal; 1, center; 2, proximal; 3, variable.

27. Location of vein branching from origin to edge: 0, only dispersed; 1, restricted; 2, variable.

28. Location of vein branching from origin to edge favors: 0, origin; 1, edge; 2, variable.

29. Vein paths: 0, only divergent; 1, convergence present; 2, variable.

30. Vein convergence: 0, only passive; 1, strict; 2, variable.

31. Location of convergence: 0, dispersed; 1, restricted; 2, variable.

32. Location of convergence restricted to: 0, vein origin; 1, lamina edge; 2, variable.

33. Vein reticulations: 0, no; 1, irregular; 2, regular.

34. Minimum number of reticulations from base or midvein to margin: number.

35. Maximum number of reticulations from base or midvein to margin: number.

36. Location of reticulations: 0, dispersed; 1, restricted to origin; 2, restricted to edge.

37. Vein orders with reticulation: 0, only most distal; 1, more than most distal.

38. Enclosed space: 0, elongate perpendicular to margin; 1, elongate parallel to margin; 2, isodiametric; 3, irregular; 4, variable.

39. Lamina innervated from rachis: 0, once; 1, more than once; 2, variable.

40. Multiple lamina innervations: 0, all equivalent; 1, unequal strength; 2, variable.

41. Lamina innervations from base: 0, evenly spaced; 1, unevenly; 2, variable (centered single vein = 0).

42. Lamina innervations from midvein: 0, evenly spaced; 1, unevenly; 2, variable.

43. Innervation of lamina from base: 0, straight; 1, angled; 2, branches immediately; 3, irregular (with respect to main axis of lamina, a vein following the angled insertion of the lamina would be scored as straight).

44. Innervation of lamina from midvein: 0, straight; 1, angled; 2, branches immediately; 3, irregular.

45. Midvein: 0, no; 1, yes; 2, variable.

46. Midvein: 0, weak, not straight; 1, strong; 2, variable.

47. Midvein: 0, included in lamina; 1, distinct from lamina; 2, variable.

48. Midvein length: 0, as long as lamina; 1, closer to distal than other margins; 2, reaches all margins equally; 3, farther from distal; 4 variable.

49. Midvein of uniform thickness: 0, no; 1, yes; 2, variable.

50. Angle of midvein (or other innervation) insertion: 0, same as pinnule; 1, different; 2, variable.

51. "midvein" branches: 0, to both sides; 1, just 1, side; 2, variable.

52. Path of laterals to margin: 0, parallel; 1, not parallel; 2, variable (if linear =?).

53. Lateral vein paths: 0, straight; 1, curved; 2, variable but regular; 3, irregular paths.

54. Concavity of vein curvature: 0, concave up (distal); 1, concave down (proximal); 2, variable.

55. Location of vein endings: 0, all veins equally reach margin (or marginal vein); 1, some internal endings; 2, only internal endings; 3, no free endings.

56. Direction of vein paths: 0, only toward a margin; 1, internally directly veins (perpendicular to or independent of margin).

57. Marginal vein: 0, absent; 1, present.

58. Vein endings: 0, just on distal edge; 1, all margins but expanded base; 2, all margins; 3, variable.

59. Vein density: 0, uniform; 1, increases; or 2, decreases toward margin; 3, irregular.

60. Veins within a lamina lobe: 0, always include all of the connected veins distal to the last shared dichotomy (i.e., always forming a monophyletic group of veins); 1, not always the case (i.e., also paraphyletic vein groupings within lobes).

61. Lobing: 0, about each vein; 1, vein groups; 2, both types present.

62. Angle of marginal intersection of veins: 0, $\sim 90^\circ$; 1, angled; 2, variable but consistent; 3, irregular.

63. Vein endings where present: 0, evenly spaced; 1, uneven but predictable; 2, irregular; 3, variable type (if linear or lobed about each vein, then 62 and 63 =?).

Appendix 3

Phylogenetic affinity, primary literature reference, and stratigraphic range for all taxa included in the analysis.

Genus	Species	Affinity	Ref.	Range
Acitheca	adaensis	Marattialean	51	Westphalian
Acitheca	longifolia	Marattialean	18	Westphalian
Acitheca	polymorpha	Marattialean	42	Westphalian–Autunian
Acrangiophyllum	pendulatum	Eusporangiate	49	Namurian
Adiantites	adiantoides	?	42	Westphalian
Adiantites	antiquus	?	42	Tournaisian–Namurian
Adiantites	bondi	?	42	Westphalian
Adiantites	eremopteroides	?	66	Namurian
Adiantites	tenellus	?	42	Westphalian
Adiantites	tenuifolius	?	42	Visean–Namurian
Alethopteris	ambigua	?	70	Westphalian–Stephanian
Alethopteris	anglica	?	70	Westphalian
Alethopteris	antiqua	?	67	Namurian
Alethopteris	arberi	?	70	Westphalian
Alethopteris	barruelensis	?	70	Stephanian
Alethopteris	bertrandi	?	14	Westphalian
Alethopteris	bohémica	Medullosan	70	Stephanian
Alethopteris	calva	?	70	Stephanian
Alethopteris	corsini	?	14	Westphalian
Alethopteris	davreuxi	Medullosan	19	Westphalian
Alethopteris	decurrens	Medullosan	19	Westphalian
Alethopteris	densinervosa	?	70	Westphalian
Alethopteris	distantinervosa	?	70	Westphalian
Alethopteris	edwardsi	?	66	Namurian
Alethopteris	grandini	Medullosan	19	Westphalian–Stephanian
Alethopteris	grandinioides	?	70	Westphalian–Stephanian
Alethopteris	hermeteti	?	14	Westphalian
Alethopteris	integra	?	19	Westphalian
Alethopteris	intermedia	?	66	Namurian
Alethopteris	kanisi	?	70	Westphalian–Stephanian
Alethopteris	lancifolia	?	13	Westphalian
Alethopteris	leonensis	?	70	Stephanian
Alethopteris	lesquereuxi	?	70	Stephanian
Alethopteris	lonchitica	Medullosan	19	Namurian–Westphalian
Alethopteris	magna	?	70	Stephanian
Alethopteris	michauxi	?	14	Westphalian
Alethopteris	minuta	?	70	Westphalian–Autunian
Alethopteris	missouriensis	?	70	Westphalian–Stephanian
Alethopteris	nemejci	?	70	Westphalian
Alethopteris	nevesi	?	70	Westphalian
Alethopteris	palentina	?	70	Westphalian–Stephanian
Alethopteris	pennsylvanica	?	70	Stephanian
Alethopteris	pontica	?	19	Westphalian
Alethopteris	pseudoboheémica	?	70	Stephanian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Alethopteris	quadrata	?	70	Westphalian
Alethopteris	rarenervosa	?	13	Westphalian
Alethopteris	riosensis	?	70	Westphalian
Alethopteris	robusta	?	70	Westphalian
Alethopteris	rubescens	Medullosan	19	Westphalian
Alethopteris	scalariformis	?	8	Westphalian
Alethopteris	serli	Medullosan	19	Westphalian–Stephanian
Alethopteris	subdavreuxi	?	20	Westphalian
Alethopteris	subelegans	?	56	Stephanian–Autunian
Alethopteris	tectensis	?	66	Namurian
Alethopteris	valida	Medullosan	19	Namurian–Westphalian
Alethopteris	westphalensis	Medullosan	70	Westphalian
Alloiopteris	crenulata	?	3	Westphalian
Alloiopteris	cupuliformis	?	23	Namurian
Alloiopteris	gracillima	?	47	Namurian
Alloiopteris	inversa	?	3	Westphalian
Alloiopteris	palatina	?	3	Westphalian
Alloiopteris	radstockensis	?	42	Westphalian
Alloiopteris	serrula	?	42	Westphalian
Aneimites	acadica	?	55	Tournaisian
Anisopteris	circularis	?	71	Visean
Anisopteris	inaequilatera	?	42	Tournaisian–Namurian
Anisopteris	lindsaeiformis	Lyginopterid	42	Visean
Anisopteris	machaneki	?	71	Visean
Anisopteris	petiolata	?	42	Visean
Archaeopteridium	tschermaki	Lyginopterid	42	Visean–Namurian
Archaeopteris	fissilis	Archaeopterid	4	U. Devonian
Archaeopteris	haliana	Archaeopterid	54	U. Devonian
Archaeopteris	hibernica	Archaeopterid	5	U. Devonian
Archaeopteris	latifolia	Archaeopterid	5	U. Devonian
Archaeopteris	macilentia	Archaeopterid	15	U. Devonian
Archaeopteris	obtusa	Archaeopterid	4	U. Devonian
Archaeopteris	roemeriana	Archaeopterid	57	U. Devonian
Archaeopteris	sphenophyllifolia	Archaeopterid	61	U. Devonian
Asterotheca	abbreviata	Marattialelean	30	Westphalian–Stephanian
Asterotheca	arborescens	Marattialelean	42	Westphalian–Autunian
Asterotheca	Candolleana	Marattialelean	42	Westphalian–Autunian
Asterotheca	crenulata	Marattialelean	42	Westphalian
Asterotheca	cyathea	Marattialelean	42	Westphalian–Autunian
Asterotheca	daubreei	Marattialelean	42	Westphalian–Stephanian
Asterotheca	hemitelioides	Marattialelean	42	Westphalian–Autunian
Asterotheca	herdii	Marattialelean	8	Westphalian
Asterotheca	hucheti	Marattiales	18	Westphalian
Asterotheca	lamurensis	Marattialelean	42	Westphalian–Autunian
Asterotheca	lepidorachis	Marattialelean	42	Westphalian–Autunian
Asterotheca	lobulata	Marattialelean	22	Westphalian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Asterotheca	longiphylla	Marattialean	18	Westphalian
Asterotheca	micromiltoni	Marattialean	18	Westphalian–Stephanian
Asterotheca	miltoni	Marattialean	42	Westphalian
Asterotheca	opulenta	Marattialean	18	Westphalian–Stephanian
Asterotheca	oreinervosa	Marattialean	18	Westphalian
Asterotheca	oreopteridia	Marattialean	42	Westphalian–Autunian
Asterotheca	platoni	Marattialean	18	Westphalian–Autunian
Asterotheca	potonie	Marattialean	56	Autunian
Asterotheca	saraefolia	Marattialean	18	Westphalian–Stephanian
Autunia	conferta	Peltasperm	27	Stephanian–M. Permian
Boweria	minor	Filicalean	42	Westphalian
Boweria	schatzlaensis	Filicalean	42	Westphalian
Calamophyton	primaevum	Hyenialean	62	M. Devonian
Callipteridium	armasi	?	71	Westphalian–Stephanian
Callipteridium	costei	?	46	Stephanian
Callipteridium	devillei	?	46	Westphalian
Callipteridium	gigas	?	30	Stephanian
Callipteridium	ibericum	?	69	Stephanian
Callipteridium	jongmansi	?	46	Westphalian–Stephanian
Callipteridium	pteridium	?	69	Stephanian–Autunian
Callipteridium	rochei	?	27	Stephanian–Autunian
Callipteridium	striatum	?	46	Stephanian
Callipteridium	sullivanti	?	70	Westphalian–Stephanian
Callipteridium	trigonum	?	56	Stephanian
Callipteridium	zeilleri	?	46	Stephanian–Autunian
Cardiopteridium	nanum	?	19	Tournaisian–Visean
Cardiopteridium	spetsbergense	?	56	Tournaisian–Namurian
Cardiopteridium	waldenburgense	?	56	Namurian
Cardiopteris	frondosa	?	56	Visean–Namurian
Cardiopteris	polymorpha	?	36	Visean
Cordaites	angulosostriatus	Cordaitalean	19	Westphalian–Autunian
Cordaites	borassifolius	Cordaitalean	19	Westphalian–Autunian
Cordaites	microstachys	Cordaitalean	19	Westphalian–Autunian
Cordaites	palmaeformis	Cordaitalean	19	Namurian–Autunian
Cordaites	principalis	Cordaitalean	19	Namurian–Autunian
Corynepteris	angustissima	Zygopterid	23	Namurian–Stephanian
Corynepteris	coralloides	Zygopterid	42	Westphalian
Corynepteris	cristata	Zygopterid	3	Westphalian
Corynepteris	erosa	Zygopterid	23	Westphalian–Stephanian
Corynepteris	essinghi	Zygopterid	23	Westphalian
Corynepteris	magnifica	Zygopterid	3	Westphalian
Corynepteris	pecopteroides	Zygopterid	3	Westphalian–Autunian
Corynepteris	quercifolia	Zygopterid	3	Namurian–Westphalian
Corynepteris	saraepontana	Zygopterid	3	Stephanian
Corynepteris	similis	Zygopterid	3	Namurian–Westphalian
Corynepteris	sternbergi	Zygopterid	42	Namurian–Westphalian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Corynepteris	tenuissima	Zygoterid	42	Westphalian
Crossothea	boulayi	Eusporangiate	23	Westphalian
Crossothea	bourozi	Eusporangiate	23	Westphalian
Crossothea	communis	Eusporangiate	42	Westphalian
Crossothea	pinnatifida	Eusporangiate	42	Westphalian
Crossothea	schatzlarensis	Eusporangiate	42	Namurian–Westphalian
Dactylothea	sturi	Zygoterid	42	Namurian
Desmopteris	longifolia	?	19	Westphalian
Dichophyllites	pachystachya	Sphenopsid	12	Visean
Dicksonites	pluckeneti	Callistophyte	42	Westphalian–Autunian
Dicranophyllum	richiri	?	66	Namurian
Diplotmema	adiantoides	Lyginopterid	36	Visean–Namurian
Diplotmema	arnoldi	?	68	Westphalian
Diplotmema	coemansi	?	42	Westphalian
Diplotmema	coutissense	?	66	Namurian
Diplotmema	dissectum	Lyginopterid	42	Visean
Diplotmema	dixi	?	66	Namurian
Diplotmema	duponti	?	42	Westphalian
Diplotmema	furcatum	?	42	Namurian–Westphalian
Diplotmema	geniculatum	?	42	Westphalian
Diplotmema	lineare	?	66	Namurian
Diplotmema	patentissimum	Lyginopterid	42	Tournaisian–Namurian
Diplotmema	schatzlarensis	?	42	Westphalian
Diplotmema	sturi	?	42	Westphalian
Diplotmema	zobeli	?	42	Westphalian
Diplotmema	bermudensiforme	Lyginopterid	42	Visean–Namurian
Discopteris	bertrandi	Filicalean	23	Westphalian
Discopteris	karwinensis	Filicalean	2	Namurian–Westphalian
Discopteris	opulenta	Filicalean	23	Westphalian
Discopteris	wagneri	Filicalean	2	Westphalian–Stephanian
Doleropteris	pseudopeltata	?	19	Westphalian
Doleropteris	sewardii	?	19	Westphalian
Eddyia	sullivanensis	Archaeopterid	7	U. Devonian
Ellesmeris	sphenopteroides	Zygoterid	38	U. Devonian
Enigmophyton	superbum	?	33	M. Devonian
Eremopteris	artemisiaeefolia	?	42	Westphalian
Eupecopteris	cisti	?	42	Westphalian
Eupecopteris	fletti	?	42	Westphalian
Eupecopteris	pteroides	?	42	Westphalian
Evolsonia	texana	Gigantopterid	50	M. Permian
Genselia	compacta	?	43	Tournaisian
Gigantopteridium	americanum	Gigantopterid	13	M. Permian
Ginkgoites	lodevensis	?	27	Autunian
Ginkgophyton	delvali	?	66	Namurian–Westphalian
Gondomaria	alethifolia	?	13	Stephanian
Grambastia	goldenbergi	Filicalean	57	Westphalian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Hyenia	sphenophylloides	Hyenialean	39	M. Devonian
Hymenophyllites	bronni	Filicalean	42	Westphalian
Hymenophyllites	quadridactylites	Filicalean	23	Westphalian–Stephanian
Hymenotheca	acuta	?	42	Westphalian
Hymenotheca	broadheadi	?	8	Westphalian
Hymenotheca	dathei	?	55	Westphalian
Leslya	cheimarosa	Cycadalean	47	Namurian
Leslya	eckardti	?	57	U. Permian
Leslya	weilerbachensis	?	57	Westphalian
Linopteris	elongata	?	71	Westphalian–Stephanian
Linopteris	germari	?	44	Stephanian–Autunian
Linopteris	munsteri	Medullosan	19	Westphalian
Linopteris	neuropteroides	?	19	Westphalian
Linopteris	obliqua	?	19	Westphalian
Linopteris	palentina	?	71	Westphalian–Stephanian
Linopteris	regniezi	?	45	Westphalian
Linopteris	subbrongiarti	Medullosan	57	Westphalian
Linopteris	weigeli	?	56	Westphalian
Lonchopteridium	laxereticulosum	?	13	Westphalian
Lonchopteris	alethopteroides	?	13	Westphalian
Lonchopteris	bricei	Medullosan	19	Westphalian
Lonchopteris	chandresrisi	?	56	Westphalian
Lonchopteris	eschweileriana	?	19	Westphalian
Lonchopteris	legrandi	?	14	Westphalian
Lonchopteris	monomakhoffi	?	14	Westphalian
Lonchopteris	petiti	?	14	Westphalian
Lonchopteris	rugosa	Medullosan	19	Westphalian
Lyginopteris	baeumleri	Lyginopterid	42	Namurian–Westphalian
Lyginopteris	hoeninghausi	Lyginopterid	42	Namurian–Westphalian
Macrosphenopteris	lindsaeoides	?	42	Westphalian
Margaritopteris	coemansi	?	29	Westphalian
Mariopteris	acuta	Lyginopterid	42	Namurian–Westphalian
Mariopteris	andraeana	?	24	Westphalian
Mariopteris	bellanii	?	17	Westphalian
Mariopteris	bourozi	?	24	Westphalian
Mariopteris	busqueti	?	30	Stephanian
Mariopteris	carnosa	?	24	Westphalian
Mariopteris	corsini	?	71	Westphalian–Stephanian
Mariopteris	daviesi	?	42	Westphalian
Mariopteris	daviesoides	?	66	Namurian
Mariopteris	demoncourti	?	42	Westphalian
Mariopteris	eremopteroides	?	55	Namurian
Mariopteris	guillaumei	?	17	Westphalian
Mariopteris	hirsuta	?	24	Westphalian
Mariopteris	hirta	?	42	Westphalian
Mariopteris	jacquoti	?	42	Westphalian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Mariopteris	latifolia	?	24	Westphalian
Mariopteris	leharlei	?	17	Westphalian
Mariopteris	lobatifolia	?	24	Westphalian
Mariopteris	microsauveri	?	24	Westphalian
Mariopteris	mosana	?	24	Namurian
Mariopteris	muricata	?	42	Westphalian
Mariopteris	nervosa	?	42	Namurian–Westphalian
Mariopteris	nobilis	?	42	Westphalian
Mariopteris	obovata	?	42	Westphalian
Mariopteris	opulenta	?	24	Westphalian
Mariopteris	plumosa	?	42	Westphalian
Mariopteris	pottsvillea	?	35	Namurian
Mariopteris	robusta	?	24	Westphalian
Mariopteris	roussini	?	24	Westphalian
Mariopteris	sarana	?	17	Westphalian
Mariopteris	sauveuri	?	42	Westphalian
Mariopteris	siviardii	?	17	Westphalian
Mariopteris	soubeirani	?	42	Westphalian
Mariopteris	warnantensis	?	67	Namurian
Mariopteris	wittieri	?	17	Westphalian
Megalopteris	fasciculata	?	47	Namurian
Megalopteris	ovata	?	47	Namurian
Mixoneura	deflinei	?	10	Westphalian
Mixoneura	voutersi	?	10	Westphalian
Myriotheca	monomakhoffi	Eusporangiate	23	Westphalian
Nemejcopteris	feminaeformis	Zygoterid	57	Stephanian–M. Permian
Neuralethopteris	jongmansii	Medullosan	16	Westphalian
Neuralethopteris	larischi	?	70	Namurian–Westphalian
Neuralethopteris	rectinervis	Medullosan	70	Westphalian
Neuralethopteris	schlehani	Medullosan	70	Namurian–Westphalian
Neuralethopteris	schlehanoides	?	66	Namurian
Neuropteris	aculeata	?	8	Westphalian
Neuropteris	antecedens	?	19	Visean–Namurian
Neuropteris	antiqua	?	32	Tournaisian
Neuropteris	arberi	?	19	Westphalian
Neuropteris	beveridgei	?	19	Westphalian
Neuropteris	blissi	?	19	Westphalian
Neuropteris	bourozii	?	45	Westphalian
Neuropteris	britannica	?	56	Westphalian
Neuropteris	chalardi	?	45	Westphalian
Neuropteris	condrusiana	?	67	Namurian
Neuropteris	cordata	?	56	Stephanian–M. Permian
Neuropteris	desorii	?	25	Stephanian
Neuropteris	duprei	?	45	Westphalian
Neuropteris	dussartii	?	16	Westphalian
Neuropteris	formosa	?	19	Westphalian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Neuropteris	ghayei	?	45	Westphalian
Neuropteris	gigantea	Medullosan	56	Namurian–Westphalian
Neuropteris	grangeri	?	19	Westphalian
Neuropteris	hemingwayi	?	19	Westphalian
Neuropteris	heterophylla	Medullosan	19	Westphalian
Neuropteris	hollandica	?	19	Westphalian
Neuropteris	jacksoni	?	25	Westphalian
Neuropteris	jongmansi	?	19	Westphalian
Neuropteris	jugosa	?	19	Westphalian
Neuropteris	lanarkiana	?	19	Westphalian
Neuropteris	linguaeolia	Medullosan	57	Westphalian
Neuropteris	linguaenova	?	10	Westphalian
Neuropteris	loshii	Medullosan	16	Westphalian
Neuropteris	macrophylla	?	19	Westphalian
Neuropteris	maltbyensis	?	19	Westphalian
Neuropteris	mathieui	?	66	Namurian
Neuropteris	missouriensis	?	19	Westphalian
Neuropteris	moorii	?	35	Autunian
Neuropteris	morini	?	45	Westphalian
Neuropteris	nikolausi	?	10	Westphalian
Neuropteris	obliqua	Medullosan	19	Namurian–Westphalian
Neuropteris	osmundae	?	19	Westphalian–Stephanian
Neuropteris	ovata	?	19	Westphalian–Autunian
Neuropteris	parvifolia	?	36	Westphalian
Neuropteris	planchardi	?	56	Stephanian–Autunian
Neuropteris	pocahontas	?	55	Namurian
Neuropteris	praedentata	?	30	Westphalian–Stephanian
Neuropteris	pseudoblissi	?	19	Westphalian–Autunian
Neuropteris	pseudogigantea	?	56	Westphalian
Neuropteris	pseudoimpar	?	66	Namurian
Neuropteris	rarinervis	?	19	Westphalian
Neuropteris	rytonia	?	19	Westphalian
Neuropteris	sarana	?	10	Westphalian–Stephanian
Neuropteris	scheuchzeri	Medullosan	19	Westphalian–Stephanian
Neuropteris	semireticulata	?	57	Westphalian
Neuropteris	simoni	?	10	Westphalian
Neuropteris	squarrosaeformis	?	19	Westphalian
Neuropteris	subauriculata	?	56	Westphalian
Neuropteris	subplicata	?	19	Westphalian
Neuropteris	subsessilis	?	67	Namurian
Neuropteris	tenuifolia	?	19	Westphalian
Neuropteris	thompsonii	?	25	Westphalian
Neuropteris	thymifolia	?	19	Westphalian
Neuropteris	triangularis	?	10	Westphalian
Neuropteris	waltoni	?	66	Namurian
Neuropteris	willieri	?	45	Westphalian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Noeggerathia	chalarzii	?	16	Westphalian
Noeggerathia	foliosa	?	56	Westphalian
Odontopteris	aequalis	?	35	Westphalian
Odontopteris	alpina	?	57	Westphalian–Stephanian
Odontopteris	barroisi	?	10	Westphalian
Odontopteris	brardii	?	29	Westphalian–Autunian
Odontopteris	cantabrica	?	29	Westphalian–Stephanian
Odontopteris	dufrenoyi	?	29	Autunian
Odontopteris	genuina	?	57	Westphalian–Stephanian
Odontopteris	gimmi	?	56	Stephanian–Autunian
Odontopteris	glossoides	?	29	Westphalian
Odontopteris	leptoneura	?	29	Westphalian
Odontopteris	lingulata	?	56	Autunian
Odontopteris	macrophylla	?	29	Westphalian
Odontopteris	minor	?	27	Stephanian–Autunian
Odontopteris	obtusa	?	29	Westphalian–Autunian
Odontopteris	osmundaeformis	?	56	Stephanian–Autunian
Odontopteris	peyerimhoffi	?	10	Westphalian
Odontopteris	reichiana	?	10	Westphalian–Stephanian
Odontopteris	schlotheimi	?	29	Stephanian
Odontopteris	subcrenulata	?	57	Stephanian
Oligocarpia	brongniartii	Filicalean	42	Westphalian
Oligocarpia	gutbieri	Filicalean	42	Westphalian–Stephanian
Oligocarpia	leptophylla	Filicalean	30	Stephanian–Autunian
Oligocarpia	missouriensis	Filicalean	8	Westphalian
Orthotheca	saraepontana	Marattialean	18	Westphalian–Stephanian
Orthotheca	trevirani	Marattialean	18	Westphalian–Stephanian
Ovopteris	pecopteroides	?	42	Westphalian–Autunian
Palaeoweichselia	defrancei	?	25	Westphalian
Paleopteridium	reussi	?	42	Namurian–Westphalian
Paleopteridium	sessilis	?	57	Westphalian
Palmatopteris	alata	Lyginopterid	42	Westphalian
Palmatopteris	furcata	Lyginopterid	36	Namurian–Westphalian
Palmatopteris	sarana	?	3	Westphalian
Palmatopteris	wellesweileri	?	3	Westphalian
Paracalathiops	stachei	Medullosan	57	Namurian
Pecopteridium	cuvellettei	?	11	Westphalian
Pecopteridium	devillei	?	11	Westphalian
Pecopteridium	jongmansi	?	11	Westphalian
Pecopteridium	lerati	?	14	Westphalian
Pecopteridium	magnum	?	27	Stephanian
Pecopteridium	vermeleni	?	14	Westphalian
Pecopteris	acadica	?	9	Westphalian
Pecopteris	acuta	?	18	Westphalian–Stephanian
Pecopteris	affinis	?	18	Westphalian–Stephanian
Pecopteris	alloiophylla	?	28	Westphalian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Pecopteris	ambigua	?	18	Westphalian
Pecopteris	ameromi	?	69	Stephanian
Pecopteris	armasi	?	42	Westphalian
Pecopteris	aspidoides	?	42	Westphalian
Pecopteris	asymmetra	?	28	Westphalian
Pecopteris	bidoni	?	18	Westphalian
Pecopteris	bioti	?	42	Westphalian–Stephanian
Pecopteris	bourozi	?	22	Westphalian
Pecopteris	brachyphylla	?	28	Westphalian
Pecopteris	bredovi	?	18	Westphalian–Autunian
Pecopteris	brieni	?	69	Stephanian
Pecopteris	bucklandi	?	42	Westphalian
Pecopteris	camptophylla	?	28	Westphalian
Pecopteris	cantabrica	?	69	Stephanian
Pecopteris	clarkii	?	8	Westphalian
Pecopteris	clintoni	?	18	Westphalian–Stephanian
Pecopteris	corsini	?	70	Stephanian
Pecopteris	densifolia	?	18	Westphalian–M. Permian
Pecopteris	densinervosa	?	30	Stephanian
Pecopteris	engyphylla	?	28	Westphalian
Pecopteris	entemna	?	28	Westphalian
Pecopteris	epimeca	?	28	Westphalian
Pecopteris	folschwillerensis	Eusporangiate	18	Westphalian
Pecopteris	gothani	?	37	Westphalian–Stephanian
Pecopteris	integra	?	42	Westphalian–Stephanian
Pecopteris	intermedia	?	22	Westphalian
Pecopteris	jongmansii	?	13	Stephanian–Autunian
Pecopteris	josteni	?	28	Westphalian
Pecopteris	koenigi	?	18	Westphalian–Stephanian
Pecopteris	houvensis	?	18	Westphalian
Pecopteris	labachensis	?	28	Stephanian
Pecopteris	loxoneura	?	28	Westphalian
Pecopteris	macronervosa	?	18	Stephanian
Pecopteris	major	?	13	Stephanian
Pecopteris	martinezi	?	13	Stephanian
Pecopteris	melendezi	?	13	Stephanian
Pecopteris	microphylla	?	18	Westphalian–Stephanian
Pecopteris	monyi	?	27	Westphalian–Stephanian
Pecopteris	obliquenervis	?	18	Westphalian
Pecopteris	ocejensis	?	71	Westphalian–Stephanian
Pecopteris	oligoneura	?	28	Westphalian
Pecopteris	pachyneura	?	28	Westphalian
Pecopteris	paleacea	?	18	Westphalian–Stephanian
Pecopteris	pectinata	Eusporangiate	18	Westphalian–Stephanian
Pecopteris	pinnatifida	Eusporangiate	56	Stephanian–Autunian
Pecopteris	platyphylla	?	28	Westphalian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Pecopteris	polita	?	18	Westphalian
Pecopteris	precyathea	?	22	Westphalian
Pecopteris	prepolymorpha	?	22	Westphalian
Pecopteris	pseudobucklandi	?	56	Stephanian
Pecopteris	pseudointegra	?	69	Stephanian
Pecopteris	pseudoreopteridia	?	13	Stephanian–Autunian
Pecopteris	punctata	?	18	Westphalian
Pecopteris	pynconeura	?	28	Westphalian
Pecopteris	raconensis	?	71	Westphalian–Stephanian
Pecopteris	rarinervosa	?	18	Stephanian
Pecopteris	rotundifolia	?	18	Stephanian
Pecopteris	simoni	?	22	Westphalian
Pecopteris	sitteri	?	69	Westphalian
Pecopteris	stievenardi	?	22	Westphalian
Pecopteris	subelegans	?	30	Stephanian–Autunian
Pecopteris	subvictoriae	?	69	Stephanian
Pecopteris	tenuinervis	?	18	Westphalian
Pecopteris	tenuinervosa	?	18	Westphalian–Stephanian
Pecopteris	thuringiaca	?	56	Autunian
Pecopteris	vedrinei	?	22	Namurian–Westphalian
Pecopteris	vera	?	31	Westphalian
Pecopteris	vetteri	?	28	Westphalian
Pecopteris	viannai	?	30	Stephanian–Autunian
Pecopteris	victoriae	?	18	Westphalian–Stephanian
Pecopteris	villaverdensis	?	69	Westphalian
Pecopteris	villosa	?	18	Westphalian
Pecopteris	waltoni	?	18	Westphalian–Stephanian
Pecopteris	wongi	?	18	Stephanian
Phasmatocycas	kansana	Cycadalean	34	M. Permian
Plagiozamites	belli	?	63	U. Permian
Plagiozamites	planchardi	?	57	Stephanian–Autunian
Plumatopteris	elegans	?	42	Visean
Proteokalon	petryi	Aneurophyte	6	Tournaisian
Pseudodiantites	sessilis	?	66	Namurian
Pseudosporochnus	chlupaci	Eusporangiate	53	M. Devonian
Pseudotenis	midddridgensis	?	63	U. Permian
Pterophyllum	blechnoides	?	57	Autunian
Ptychocarpus	unitus	Marattialean	42	Westphalian–Autunian
Rellimia	thomsonii	Aneurophyte	48	M. Devonian
Renaultia	acutiloba	Eusporangiate	23	Westphalian
Renaultia	bella	Eusporangiate	2	Westphalian
Renaultia	chaerophylloides	Eusporangiate	23	Westphalian–Stephanian
Renaultia	crepini	Eusporangiate	42	Westphalian
Renaultia	footneri	Eusporangiate	42	Westphalian
Renaultia	gracilis	Eusporangiate	42	Namurian–Westphalian
Renaultia	hemingwayi	Eusporangiate	42	Westphalian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Renaultia	launoiti	Eusporangiate	66	Namurian
Renaultia	laurenti	Eusporangiate	42	Westphalian
Renaultia	rotundifolia	Eusporangiate	42	Westphalian
Renaultia	schatzlarensis	Eusporangiate	2	Namurian–Westphalian
Renaultia	schwerini	Eusporangiate	23	Namurian–Westphalian
Rhachiphyllum	schenkii	?	41	Stephanian–Autunian
Rhacopteris	dichotoma	?	42	Visean
Rhacopteris	dubia	?	42	Westphalian
Rhacopteris	elegans	?	36	Westphalian
Rhacopteris	latifolia	?	55	Tournaisian
Rhacopteris	transitionis	?	42	Visean–Namurian
Rhodea	conradi	?	66	Namurian
Rhodea	eltringhami	?	42	Westphalian
Rhodea	fluitans	?	21	Visean
Rhodea	gigantea	?	42	Visean
Rhodea	launoiti	?	66	Namurian
Rhodea	leckwijcki	?	66	Namurian
Rhodea	marlierei	?	66	Namurian
Rhodea	nematophylla	?	21	Visean
Rhodea	patentissimoides	?	66	Namurian
Rhodea	pilosa	?	21	Visean
Rhodea	rigida	?	67	Namurian
Rhodea	robusta	?	67	Namurian
Rhodea	subpetiolata	?	42	Westphalian
Rhodea	vespertina	?	35	Tournaisian
Senftenbergia	aspera	Filicalean	57	Visean–Westphalian
Senftenbergia	pennaeformis	Filicalean	57	Namurian–Westphalian
Senftenbergia	plumosa	Filicalean	57	Namurian–Westphalian
Senftenbergia	plumosa-dentata	Filicalean	42	Namurian–Autunian
Senftenbergia	volkmanni	Filicalean	42	Westphalian
Spathulopteris	obovata	Lyginopterid	42	Visean
Sphenocallipteris	raymondi	?	27	Autunian
Sphenocyclopteridium	belgicum	?	65	U. Devonian
Sphenophyllum	angustifolium	Sphenopsid	19	Westphalian–Autunian
Sphenophyllum	arkansanum	Sphenopsid	1	Namurian
Sphenophyllum	costae	Sphenopsid	73	Westphalian–Autunian
Sphenophyllum	cuneifolium	Sphenopsid	1	Namurian–Stephanian
Sphenophyllum	emarginatum	Sphenopsid	1	Westphalian–Autunian
Sphenophyllum	fasciculatum	Sphenopsid	1	Westphalian
Sphenophyllum	geigense	Sphenopsid	12	Visean
Sphenophyllum	gilmorei	Sphenopsid	1	Autunian
Sphenophyllum	incisum	Sphenopsid	12	Stephanian
Sphenophyllum	involutum	Sphenopsid	12	U. Devonian
Sphenophyllum	laurae	Sphenopsid	66	Namurian–Westphalian
Sphenophyllum	lescurianum	Sphenopsid	1	Westphalian
Sphenophyllum	longifolium	Sphenopsid	1	Westphalian–Stephanian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Sphenophyllum	majus	Sphenopsid	1	Westphalian
Sphenophyllum	myriophyllum	Sphenopsid	19	Westphalian–Stephanian
Sphenophyllum	oblongifolium	Sphenopsid	1	Westphalian–Autunian
Sphenophyllum	obovatum	Sphenopsid	1	Autunian
Sphenophyllum	orbiculare	Sphenopsid	12	Westphalian
Sphenophyllum	pachycaule	Sphenopsid	12	Visean
Sphenophyllum	saarensis	Sphenopsid	12	Westphalian
Sphenophyllum	saxonicum	Sphenopsid	6	Westphalian
Sphenophyllum	subtenerrimum	Sphenopsid	12	U. Devonian
Sphenophyllum	tenerrimum	Sphenopsid	1	Tournaisian–Namurian
Sphenophyllum	tenue	Sphenopsid	1	Namurian–Westphalian
Sphenophyllum	tenuifolium	Sphenopsid	1	Stephanian–Autunian
Sphenophyllum	tenuissimum	Sphenopsid	19	Westphalian
Sphenophyllum	thonii	Sphenopsid	1	Stephanian–Autunian
Sphenophyllum	trichomatosum	Sphenopsid	19	Westphalian–Stephanian
Sphenophyllum	verticillatum	Sphenopsid	1	Westphalian–Autunian
Sphenophyllum	wingfieldense	Sphenopsid	19	Westphalian
Sphenophyllum	zwickaviense	Sphenopsid	73	Westphalian
Sphenopteridium	dissectum	Lyginopterid	42	Visean–Namurian
Sphenopteridium	macconochiei	?	42	Visean
Sphenopteridium	pachyrrhachis	?	42	Tournaisian–Visean
Sphenopteridium	speciosum	?	42	Visean
Sphenopteris	arberi	?	42	Westphalian
Sphenopteris	aureli	?	23	Westphalian
Sphenopteris	bertrandi	?	26	Namurian
Sphenopteris	beyschlagii	?	2	Stephanian
Sphenopteris	biturica	?	30	Stephanian
Sphenopteris	cantiana	?	42	Westphalian
Sphenopteris	corifolia	?	42	Westphalian
Sphenopteris	crenatodentata	?	8	Westphalian
Sphenopteris	delavali	?	42	Westphalian
Sphenopteris	dentaefolia	?	23	Westphalian
Sphenopteris	devians	?	23	Namurian–Westphalian
Sphenopteris	dichotoma	?	63	U. Permian
Sphenopteris	digitata	?	2	Westphalian–Stephanian
Sphenopteris	dilatata	?	42	Westphalian
Sphenopteris	dimorpha	?	2	Westphalian–Stephanian
Sphenopteris	dissymetrica	?	2	Westphalian
Sphenopteris	dixonii	?	42	Westphalian
Sphenopteris	douvillei	?	23	Westphalian
Sphenopteris	durbanensis	?	2	Stephanian
Sphenopteris	flabellifolia	?	42	Westphalian
Sphenopteris	flaccida	?	65	U. Devonian
Sphenopteris	flexuosissima	?	42	Westphalian
Sphenopteris	foliolata	?	42	Visean–Namurian
Sphenopteris	formosa	?	42	Westphalian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Sphenopteris	fossorum	?	2	Westphalian–Stephanian
Sphenopteris	fragilis	Lyginopterid	42	Namurian
Sphenopteris	fredericqui	?	67	Namurian
Sphenopteris	goniopteroides	?	2	Westphalian–Stephanian
Sphenopteris	gutbieriana	?	2	Westphalian
Sphenopteris	hansae	?	23	Westphalian
Sphenopteris	hollandica	?	66	Namurian–Westphalian
Sphenopteris	jongmansi	?	26	Namurian
Sphenopteris	kayi	?	42	Westphalian
Sphenopteris	kevretensis	?	66	Namurian
Sphenopteris	kilimli	?	42	Westphalian
Sphenopteris	kukukiana	?	57	M. Permian–U. Permian
Sphenopteris	laciniosa	?	2	Westphalian
Sphenopteris	lanarkiana	?	42	Westphalian
Sphenopteris	latinervis	?	23	Westphalian
Sphenopteris	macilenta	?	42	Westphalian
Sphenopteris	macroductylites	?	2	Westphalian
Sphenopteris	magdalenae	?	69	Stephanian
Sphenopteris	magnifica	?	23	Westphalian
Sphenopteris	maillieuxi	?	65	U. Devonian
Sphenopteris	matheti	?	30	Stephanian
Sphenopteris	mendescoreae	?	30	Stephanian
Sphenopteris	microcyclos	?	23	Westphalian
Sphenopteris	microscopica	?	23	Westphalian
Sphenopteris	minutisecta	?	2	Stephanian–Autunian
Sphenopteris	mira	?	42	Namurian
Sphenopteris	morrowensis	?	47	Namurian
Sphenopteris	mourloni	?	65	U. Devonian
Sphenopteris	moyseyi	?	42	Westphalian
Sphenopteris	neuropteroides	?	42	Westphalian
Sphenopteris	nummularia	?	42	Westphalian
Sphenopteris	obtusdentata	?	23	Westphalian
Sphenopteris	obtusiloba	Lyginopterid	42	Namurian–Westphalian
Sphenopteris	ocquierensis	?	67	Namurian
Sphenopteris	ornithopus	?	66	Namurian
Sphenopteris	ovalis	?	56	Westphalian
Sphenopteris	ovatifolia	?	42	Westphalian
Sphenopteris	oxydonta	?	2	Namurian–Westphalian
Sphenopteris	polyphylla	?	42	Westphalian
Sphenopteris	pseudofurcata	?	42	Westphalian
Sphenopteris	pseudomarrati	?	23	Westphalian
Sphenopteris	purvesi	?	66	Namurian
Sphenopteris	quadriloba	?	42	Westphalian
Sphenopteris	rejectifolia	?	67	Namurian
Sphenopteris	rutaefolia	?	23	Westphalian–Stephanian
Sphenopteris	sauveuri	?	42	Westphalian

Appendix 3. Continued.

Genus	Species	Affinity	Ref.	Range
Sphenopteris	schillingsi	?	42	Namurian–Westphalian
Sphenopteris	seussi	?	58	M. Permian–U. Permian
Sphenopteris	sewardi	?	42	Westphalian
Sphenopteris	souichi	?	23	Westphalian
Sphenopteris	spiniformis	?	42	Westphalian
Sphenopteris	spinosa	?	42	Westphalian
Sphenopteris	spinulosa	?	42	Westphalian
Sphenopteris	stipulata	?	42	Westphalian
Sphenopteris	stonehousei	?	42	Westphalian
Sphenopteris	straeleni	?	66	Namurian
Sphenopteris	striata	Lyginopterid	2	Westphalian
Sphenopteris	trifoliata	?	42	Westphalian
Sphenopteris	trigonophylla	?	42	Westphalian
Sphenopteris	vernoni	?	42	Westphalian
Sphenopteris	villeti	?	23	Westphalian
Sphenopteris	walteri	?	42	Westphalian
Sphenopteris	weissi	?	2	Stephanian–Autunian
Sphenopteris	westphalica	?	42	Westphalian
Sphenopteris	woodwardi	?	42	Westphalian
Sphenopteris	filiformis	?	42	Tournaisian
Sturia	amoena	Filicalean	23	Westphalian
Supaia	thinnfeldioides	?	72	M. Permian
Svalbardia	banksii	Archaeopterid	52	M. Devonian
Svalbardia	polymorpha	Archaeopterid	4	U. Devonian
Taeniopteris	angelica	?	72	M. Permian
Taeniopteris	jejunata	?	57	Stephanian–Autunian
Taeniopteris	multinervis	?	57	Stephanian–Autunian
Taeniopteris	tenuis	?	30	Stephanian
Telangium	affine	Lyginopterid	42	Visean
Telangium	bifidum	Lyginopterid	42	Visean
Tetraxylopteris	schmidtii	Aneurophyte	59	M. Devonian–U. Devonian
Triloboxylon	ashlandicum	Aneurophyte	59	U. Devonian
Triphyllopteris	gothani	?	21	Visean
Triphyllopteris	rhombifolia	?	21	Visean
Triphyllopteris	uberis	Eusporangiate	64	Tournaisian
Tristachya (Lilpopia)	crockensis	Sphenopsid	57	Autunian
Urnatopteris	herbacea	Eusporangiate	23	Westphalian
Urnatopteris	tenella	Eusporangiate	42	Westphalian
Zeilleria	avoldensis	Eusporangiate	42	Namurian–Westphalian
Zeilleria	damesi	Eusporangiate	57	Westphalian
Zeilleria	delicatula	Eusporangiate	42	Westphalian
Zeilleria	frenzli	Eusporangiate	23	Westphalian
Zeilleria	hymenophylloides	Eusporangiate	42	Westphalian
Zeilleria	moravica	Eusporangiate	42	Visean–Namurian
Zeilleria	tenuiplanata	Eusporangiate	21	Visean