

Paleoecology of Late Paleozoic pteridosperms from tropical Euramerica¹

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DIMICHELE, W. A. (Department of Paleobiology, NMNH, Smithsonian Institution, Washington, DC 20560), T. L. PHILLIPS (Department of Plant Biology, University of Illinois, Urbana, IL 61801), AND H. W. PFEFFERKORN (Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, PA 19106). Paleoecology of Late Paleozoic pteridosperms from tropical Euramerica. *J. Torrey Bot. Soc.* 133: 83–118. 2006.—Late Paleozoic pteridosperms are a paraphyletic group of seed plants that were prominent elements of tropical ecosystems, primarily those of wetlands or the wetter portions of seasonally dry environments. Because the group is more a tradition-based, historical construct than a well circumscribed phylogenetic lineage, the wide variance in ecological roles and ecomorphological attributes should not be surprising. Pteridosperms can be the dominant canopy trees in local habitats, prominent understory trees, scrambling ground cover, thicket-formers, or liana-like plants and vines. Some species appear to have been weedy opportunists, although this ecological strategy seems to be a minor part of the wide spectrum of pteridosperm life habits. Most pteridosperms appear to have preferred wetter parts of the landscape, though not standing water, and relatively nutrient-rich settings (in comparison with groups such as tree ferns or lycopsids). Of the Paleozoic pteridosperms as traditionally circumscribed, only the peltasperms survived to become major elements in the Mesozoic. However, these plants may have been part of a derived seed-plant clade that also includes the corystosperms and cycads (see Hilton and Bateman, this volume), indicating that only the most derived of the Paleozoic pteridosperm lineages, those that appear to have evolved initially in extrabasinal settings, persisted into the Mesozoic.

Key words: Carboniferous, Devonian, paleoecology, Paleozoic, Permian, pteridosperms, seed ferns.

The pteridosperms (“seed ferns”) are an easy group to caricature but difficult to characterize. Phylogenetically diverse, and denizens of a wide range of terra firma habitats, the pteridosperms generally have been circumscribed by the possession of “fern-like”, compound fronds while also being the bearers of seeds. All are woody, but most not prominently so, the wood often appearing to be an evolutionary afterthought rather than the principal support tissue, except in a few clades. In addition, pteridosperms generally have monoaxial stems and sclerenchymatous

cortical regions. Many are vines or appear to have climbing plants at the root of their local branch of the phylogenetic tree. And large to super-sized seeds seem to have been prominent parts of the pteridosperm equation in some of the better known groups. Yet, there are clear exceptions to all of these attributes that make the group quite difficult to delineate ecologically. Just as there is no typical pteridosperm morphology (Galtier 1986), there likewise is no typical pteridosperm ecology, even though many of the putative clades within the ‘pteridosperms’ are ecologically rather uniform and narrowly distributed within the broader spectrum of ecological resource space.

Few Paleozoic pteridosperms persist into the Mesozoic, with the exception of the peltasperms. Of several lineages, the medullosans and lyginopterids may be considered the “classic” Paleozoic seed fern groups, both best known from the Pennsylvanian, in both adpression and petrification preservation. Other forms such as *Calistophyton*, the mariopterids, the peltasperms, and most of the latest Devonian and Mississippian seed-plant taxa are treated traditionally as

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pteridosperms largely because of their possession of some mixture of attributes, such as complex, frond-like leaves, sclerotic cortex, or radially symmetrical seeds. Unfortunately, the detailed relationships among these groups are rather poorly understood at the level of genera and species, even though a general phylogenetic architecture for the group does exist (Rothwell and Serbet 1992, 1994; Hilton and Bateman, this volume).

In this paper we review what is known or suspected of the ecology of the Paleozoic pteridosperms, focusing on the ecologies of the earliest forms, the autecologies of the broad diversity of Pennsylvanian-aged groups, the place of pteridosperms in the synecology of Pennsylvanian tropical wetlands, and finally the ecological patterns inferred for pteridosperms in the ensuing Permian seasonally dry tropical lowlands. The general message is that pteridosperms were diverse and ecologically heterogeneous, with a wide range of complex growth morphologies and roles in ecosystems of the time.

A note on geological terminology used in this paper: In order to date the events or fossil occurrences discussed herein, we will use the classical European Carboniferous stage names that are most appropriate for terrestrial deposits. These names, from youngest to oldest, are: Tournaisian, Viséan, Namurian, Westphalian, and Stephanian. We will refer to the Tournaisian as "early" Mississippian and the Viséan as "middle" Mississippian. The old, informal substages of the Namurian (A, B, C) also will be used, where Namurian A (= Serpukhovian) is latest Mississippian (Early Carboniferous) and the other two stages represent the earliest Pennsylvanian (Late Carboniferous). The use of the more numerous, formal substages of the Namurian would be cumbersome and imply a precision that is neither possible nor necessary in this review. We use Asselian, Sakmarian, Artinskian, and Kungurian for the Early Permian, and Guadalupian for the earliest stage of the Middle Permian.

Pteridosperm Phylogeny: Relevance to Ecology. The pteridosperms are a paraphyletic group as resolved by most phylogenetic analyses (Rothwell and Serbet 1994, Nixon et al. 1994, Doyle 1996, Hilton and Bateman, this volume). However, because these phylogenetic analyses focus mainly on a few representative members of a selected subset of seed-plant clades, they provide only a general sense of the relationships

among those groups traditionally identified as pteridosperms. Nonetheless, groups with shared morphological characteristics can be identified, often with confidence, even though the subsequent relationships among these "pteridosperm" groups are not well understood in many cases.

Phylogenetic pattern is relevant to ecological pattern because roles and environmental responses may be quite similar within clades and can be quite different from one clade to another. Clade membership seems to specify the basic ecological attributes of many families, genera and species. This is quite clear in Paleozoic ecosystems, especially those of the pre-Permian wetlands (DiMichele and Phillips 1996a) where species richness is low and several Linnean class-level groups, each characterized by a different basic body plan, dominate different ecological portions of landscapes. Such patterns have been identified even in modern systems (Prinz et al. 2001). For the late Paleozoic, the root of this extreme clade-by-environment ecological partitioning lies in the Middle to Late Devonian evolutionary radiation of basic plant body plans (DiMichele et al. 2001). The resulting pattern persisted until the Pennsylvanian, when global environmental changes began to disrupt the established dominance hierarchy, leading to the rise of dominance by a variety of seed-plant groups throughout the world (Gastaldo et al. 1996).

In the case of the pteridosperms, certain patterns of clade-by-ecology congruence are evident. Examples include the general liana-like habit of the members of the Pennsylvanian-Permian *Mariopteridaceae* (Krings et al. 2003b) and Pennsylvanian *Lyginopteridaceae* (Phillips 1981, Speck 1994, Gastaldo et al. 2004), the scrambling to liana-like habit of the members of the Mississippian *Calamopityaceae* (Galtier 1992), the tree architectures of the woody lyginopteroids of the Mississippian (Galtier 1992), and the gracile habit and opportunistic life history of the earliest seed plants (Rothwell and Scheckler 1988, Scheckler 1986b). Another instance is the vine/climber ancestry of the *Medullosales* (Dunn et al. 2003b), which manifests itself in the persistent polystelic anatomy of the group. Such anatomy can be found both in species with weak-stemmed, leaning, thicket-forming habit and in those forms with upright, monopodial tree habit (Pfefferkorn et al. 1984, Wnuk and Pfefferkorn 1984), some of which reached nearly 30 cm in diameter with massive secondary xylem and adherent large leaf bases (Cotta

1832). At a somewhat broader level, the peltasperms, although a highly diverse group of plants, appear to have preferred stream-side, periodically dry to quite dry substrates. The growth habits of peltasperms are not well understood, but the best known had rather slender axes and small fronds or leaves (Kerp 1988, Galtier and Broutin 1995, Barthel 2001).

It is possible that delineation of greater phylogenetic structure in the pteridosperms will permit the identification of more clade-level ecological specificity than now is recognized, based on the patterns that can be identified to date. Greater phylogenetic structure also will permit ecology to play a larger role in understanding evolutionary dynamics in this group.

The Earliest Pteridosperms. The earliest seed plant described as a “whole plant” is *Elkinsia polymorpha*, from rocks of mid-Late Devonian age. This plant has been characterized as a seed fern in the broad sense (Serbet and Rothwell 1992) and may be considered broadly representative, in terms of its ecology, of many early seed plants, part of an apparent radiation of this group in the Late Devonian. Some of these early forms, such as *Moresnetia zalesskyi* (Fairol-Demaret and Scheckler 1987), appear to have been reproductively and, perhaps, vegetatively similar to *E. polymorpha*, whereas others, such as *Aglosperma quadrapartita* (Hilton and Edwards 1996), have reproductive attributes that differ from the other known forms, such as non-cupulate seeds, suggesting an incompletely understood ecological breadth among these early plants. The earliest indication of seed-like habit precedes these better known seed plants by 20 million years; *Runcaria heinzelinii*, an integumented megasporangium surrounded by a cupule (Gerrienne et al. 2004), suggests the early appearance of wind delivery of male gametophytes to a non-integumented megasporangium (e.g., Bateman and DiMichele 1994a). Though lacking much of the reproductive sophistication of Late Devonian seeds, this organ significantly increases our appreciation of the ecological complexity of early terrestrial vegetation.

Elkinsia polymorpha was first described from seeds (Gillespie et al. 1981). It had hydrasperman reproduction (Rothwell 1986, Rothwell and Scheckler 1988), a pollination syndrome characterized by wind delivery of prepollen grains, open release of swimming sperm, specialized prepollen capture structures, and specialized prepollen isolation morphology within the ovule.

This was a precursor to the pollination-droplet capture and pollen-tube sperm delivery systems of later gymnosperms, first recognized in the Pennsylvanian (Rothwell 1981). Although hydrasperman prepollen capture mechanisms were evolutionarily primitive, these wind delivery systems provided early seed plants with the potential to escape the need for open-water sperm delivery. Thus, it gave them the potential to exploit environments in a new way, compared with their free-sporing heterosporous ancestors. Air-flow patterns around early seed-plant ovules and associated mechanisms of prepollen capture were studied by Niklas (1981a, b), who demonstrated that turbulent flow, produced by the cupules, increased prepollen-grain impacts in the area of the micropyle. He further demonstrated that younger, presumably more evolutionarily derived ovules had greater numbers of prepollen impacts. Ovules/seeds had open integuments, meaning that the integument consisted of lobes that were unfused at, and some distance back from, the apex (Gillespie et al. 1981). Consequently, it seems reasonable to assume (though an assumption it is) that the plants did not have a mechanism for seed dormancy.

Elkinsia polymorpha, based on the descriptions and reconstructions of Serbet and Rothwell (1992), was a plant of small, open, shrub-like stature that produced seed-bearing cupules in profusion on specialized branches dedicated to reproduction. Wind pollination permitted the plants to occupy primary successional areas as their principal habitat (Algeo and Scheckler 1998, Algeo et al. 2001). Such habitats initially appear to have been in lowland wetland settings. Scheckler (1986a, b) places these earliest seed plants in barren, prograding portions of small deltas, where they were succeeded rapidly by swamps populated by more aggressively growing spore-producing plants. He also suggested growth on levees in the lower delta plain, which, although wet, were subject to flood disturbance and may have been somewhat drier than the immediate stream sides or floodbasin/backswamp habitats. As far as currently understood, similar growth habits and ecological patterns appear to characterize other Late Devonian seed plants, most of which have similar cupuliferous reproductive systems bearing hydrasperman ovules/seeds (Rothwell and Scheckler 1988). In general, early seed plants appear to have been uncommon to rare elements of Late Devonian ecosystems. Algeo et al. (2001) noted that although seed plants diversified considerably during the

Late Devonian, they remained ecologically insignificant until the extinctions of the major forest forming progymnosperms at the end of the Devonian released ecological resource space.

From these beginnings as rare, opportunistic, early successional plants, pteridospermous seed plants rapidly began to diversify during the Mississippian as the archaeopterid progymnosperms disappeared and the seed habit permitted access to the vast, underexploited resource space of terra firma (Bateman and DiMichele 1994a). Despite the much lower overall species richness of the time, the ecosystems of the Late Devonian do not appear to have been any more “invasible” by evolutionarily advantaged new species than are many modern, relatively species-rich systems. This is particularly peculiar, given the supposed intrinsic superiority of the seed habit over other types of life histories in moisture-stressed environments, which are generally imagined to be greatly underpopulated at this time in Earth history. It is necessary to recall, however, that the seed is not the only trait needed to advance into areas of periodic moisture stress, where penetrating root systems and biochemical adaptations are equally important (e.g., Algeo et al. 2001). Strong incumbent advantage (physical space = resource occupation as described by Hubbell [2001], who emphasized that resource capture happens at the level of individual organisms, not species), in this case meaning occupation of resource and physical space by individual plants of pre-existing clades, also may have played a major role in keeping seed plants out of the vast majority of environments until extinctions released these areas for invasive colonization. There also are interesting parallels between the advent of seed plants and the advent of the angiosperms (Hickey and Doyle 1977)—both groups entered well populated ecosystems, possessing apparently unusually advantageous biological traits relative to the existing occupants. In each case they entered and initially diversified along stream margins in disturbed settings, only later rising to dominance in conjunction with extinctions of the earlier forms: perhaps passive replacement rather than competitive displacement, at least initially.

Pteridosperm Ecology in the Early to Middle Mississippian: the Emergence of Ecological Diversity. Pteridosperm species richness and the diversity of body plans increased enormously during the Mississippian—a time of veritable flowering of the group. Quite a lot is

known about the anatomical and morphological diversity of many of these plants, and credible whole plant concepts are emerging. In addition, the taxonomic implications of the anatomy and morphology have begun to crystallize.

MAJOR EVOLUTIONARY LINEAGES AND AUTECOLOGIES. According to Galtier (1992), the pteridosperms of the early and middle Mississippian can be grouped into three major clades based for the most part on common petiolar anatomies, all of which he tentatively considered to be members of the order Lyginopteridales.

The first group consists of the most primitive gymnosperms, such as *Elkinsia*, which have small narrow stems and gracile architecture. Rothwell and Erwin (1987) considered these forms to be similar to the progymnospermous group Aneurophytales, evidence that the seed plants were derived from this group of small progymnosperms rather than from large woody trees of the Archaeopteridales. *Elkinsia* is similar in its anatomy to several Mississippian genera, such as the anatomically preserved forms *Laceya*, *Triradioxylon*, and *Tristichia* (Galtier 1988), all of which have *Lyginopteris* (*Lyginorachis*)-like petiolar anatomy, *Sphenopteris*-type foliage, and gracile growth habit (e.g., Scott and Meyer Berthaud 1985).

A second group, closely related to these earlier forms is represented by *Calamopitys* and putatively related taxa, again known mainly anatomically, including *Diichnia*, *Triichnia*, *Galtiera*, *Bostonia*, and *Stenomyelon* (Galtier et al. 1993). These plants also have lyginopterid-like petiolar anatomy and comprise the family Calamopityaceae. Both groups 1 and 2 have secondary xylem, although it is limited in extent. In addition, for both these groups the tracheids of the metaxylem are considerably larger in diameter than those of the secondary xylem. In habit, as far as it is known, the plants of group 2 appear to be scrambling ground cover, possibly vines or liana-like plants (Fig. 1). This has been deduced from their stem architecture, wherein the internodal distance is relatively short in large diameter stems but becomes increasingly long in the smaller diameter stems, to the point that such small stems appear to have been incapable of self-support. Overall, this suggests an upright or corm-like basal portion with a more trailing or “semi-self supporting” upper part of the mature plant (Rowe et al. 1993), possibly with determinate growth (Hotton and Stein 1994). Fronds in these plants were relatively

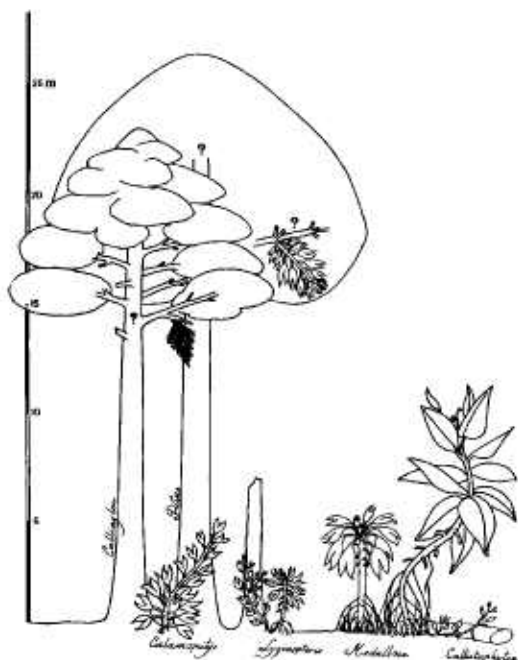


FIG. 1. Carboniferous pteridosperms and the progymnosperm *Callixylon-Archaeopteris*. Of particular note here are the reconstructed growth habits of *Calamopitys* (second from left) a small groundcover plant, and *Pitus* (third from left), a large tree. Note also *Lyginopteris*, also reconstructed with as a facultative climbing plant. Reprinted from Galtier (1986, Fig. 4) with permission.

large, up to 50 cm in length (Galtier 1974, Galtier et al. 1993).

The third group of Mississippian pteridosperm-like plants has larger, woody stems. Included are the genera *Eristophyton*, *Pitus*, and *Biliginea*, which Galtier (1986) has reconstructed as trees (Fig. 1). *Eristophyton* and *Biliginea* have been found in attachment to anatomically preserved petioles of the *Lyginorachis* type (Long 1987, Bateman and Rothwell 1990). Fronds, possibly attributable to the foliage genera *Rhacopteris* and *Spathulopteris*, and perhaps also *Sphenopteridium* or *Adiantites*, were borne densely on terminal shoots (Galtier and Scott 1994, Galtier et al. 1988). These fronds, about half a meter long, although larger than older forms (Long 1979a), may be considered relatively small in light of the large size of the parent trees. A biomechanical analysis of *Pitus dayi* (Speck and Rowe 1994), showed that the plants were certainly self-supporting and that they abscised their fronds. Although, like groups 1 and 2, these plants have lyginopterid-like petiolar anatomy, they also have thick secondary xylem,

and metaxylem tracheids smaller in diameter than those of the secondary xylem. Because of their larger size and thicker wood, Galtier and Scott (1990) considered group 3 pteridosperms to be longer-lived trees of forested landscapes, and thus more K-strategists (committing resources to vegetative tissues that will confer the ability to withstand environmental changes and to undergo repeated reproductive events) compared with the other groups of smaller stature. On the other hand, Bateman and Scott (1990) and Bateman (1991) identified a mixture of pteridosperms, including some of these larger forms, in volcanigenically disturbed habitats at the classic Oxroad Bay locality in Scotland, arguing for pteridospermalean scrub community that included *Eristophyton* and *Biliginea*, as well as the more gracile form, *Triradioxylon*. The larger pteridosperms were likely relatively deeply rooted, a morphological innovation supported by studies of fossil soils. Algeo et al. (2001) described several proximate changes in soil development, including the appearance of more abundant and widespread vertisols, indicating plant colonization of periodically moisture-limited habitats, and changes in the clay mineral content of soils, notably the increase in clays indicative of longer intervals of weathering (smectites and kaolinites). They speculate that the colonization of ever more physically stressful terra firma environments would have had major implications for global weathering cycles and, through that, had strong effects on atmospheric gaseous composition. Thus, the spread of plants, most likely pteridospermous seed plants as foundational elements, into the drier hinterlands is hypothesized to have profoundly affected global ecological patterns.

All of these pteridosperms or pteridosperm-like plants probably had hydrasperman reproductive biologies. All the well characterized reproductive organs from the Late Devonian and Mississippian are similar in their possession of this syndrome (Rothwell and Scott 1992). This includes wind delivery of prepollen, capture by a specialized lagenostome (a funnel-like structure that projects from the top of the megasporangium), and a pollen chamber that is closed by the ontogenetic development and upward growth of the female gametophyte following prepollen delivery. Integuments in these types of seeds often are composed of unfused lobes or, if fused, with very broad micropyles to accommodate the lagenostome (see the description in Rothwell and Scheckler 1988, p. 116). Such



FIG. 2. *Occloa*, a Mississippian-age lyginopterid pteridosperm forming ground cover in a coastal plain habitat. Reprinted from LePage and Pfefferkorn (2000, Fig. 1) with permission from the Paleontological Society.

seeds generally are small and can be produced in abundance. Additionally, many of the seeds are borne in cupules that themselves have lobes that are fused to varying degrees. The appearance of seed concentrations in sediments (e.g., Scott and Meyer-Berthaud 1985, Rothwell and Scott 1992) suggests that reproduction may have been periodic, probably seasonal. Generally small (≤ 5 mm in diameter), seed sizes do not suggest K-selected reproductive strategies (resource allocation to fewer larger seeds, increasing the investment in the success of each seed) to the same degree as seen in the development of larger stem sizes in the group 3 pteridosperms described above. The production of many small seeds, particularly if lacking dormancy, which seems likely given their open integumentary structure, continues to suggest the ability to invade and exploit disturbed landscapes. For example, *Eristophyton*, *Bilignea* and, in some cases, the other large-statured forms have been reported to be a significant component in volcanigenically influenced environments (e.g., Scott and Galtier 1988, Bateman and Scott 1990, Bateman 1991, Galtier et al. 1993). In some instances, these plant fossils are closely associated with fossil charcoal, an indication that the landscapes were repeatedly swept by wildfires (e.g., Scott et al. 1994).

Late Visean (late middle Mississippian) lyginopterid pteridosperms from the Paracan floral realm, a region between the south temperate Gondwanan and the tropical Euramerican floral realms (Iannuzzi and Pfefferkorn 2002), have been found to cover floodplains in monospecific stands (LePage and Pfefferkorn 2000) (Fig. 2). This pattern of distribution is associated with

numerous, small seeds (< 10 mm long) found in association with the vegetative remains, both of which point to opportunistic life histories (Erwin et al. 1994, Alleman et al. 1995). The similarity of such ecological patterns in the early and middle Mississippian tropics and paratropics indicates the broad generality of this autecological role for most early pteridosperms.

THE ROLE OF PTERIDOSPERMS IN EARLY AND MIDDLE MISSISSIPPIAN PLANT COMMUNITIES.

During the Mississippian, seed plants became dominant elements of both adpression and petrification, clastic substrate lowland (but not bone fide swamp) floras (Scheckler 1986a). In one of the few summaries of early pteridosperm ecology, Rothwell and Scheckler (1988) noted that the fossil floras from the early Mississippian are comparatively poorly known relative to those of the Late Devonian and middle through late Mississippian. Despite considerable increases in the empirical understanding of pteridosperm morphology and distribution since that time, the basic conclusions of these authors have proven robust. Early and middle Mississippian pteridosperms, in general, appear to have been most common in disturbed settings, including stream levees and drier parts of floodplains in North America, and in volcanogenic landscapes in western Europe. Of particular note is the quantitative study by Galtier et al. (1988) of the middle Tournaisian petrification flora (early Mississippian) from Montagne Noire, France. Three of four sampling sites were dominated by pteridosperms, particularly by the Calymopityaceae (group 2 above), at levels of 63–100% of the specimens recovered. These are largely ground cover plants, perhaps thicket forming. They are associated with small percentages of ferns and, at one site, with about 13% lycopsids. One site was dominated by the zygopterid fern, *Clepsydropsis*, with only minor amounts of pteridosperms, suggesting some degree of landscape heterogeneity. The flora is preserved in cherts interbedded with phosphatic nodules, indicating transport from the original environment of growth into standing water.

Scotland is perhaps the best known area for early and middle Mississippian (Tournaisian and Visean) terrestrial fossil deposits from Euramerica (see classic work of Long 1960a, b; 1961a, b, c; 1964, 1965, 1969, 1975, 1976, 1977a, b, c; 1979a, b). A few examples of these studies reveal the general patterns that have been found. Perhaps the best known of these sites is Oxroad

Bay of late Tournaisian age (Scott and Galtier 1988, Bateman and Scott 1990, Bateman 1991), which preserves a wide array of both petrification and compression plant fossils (Bateman and Rothwell 1990). A succession of environments has been identified, beginning with flood-plain deposits that include both small tree forms, such as *Eristophyton*, and pteridosperms with shrubby growth habit, such as *Stenomyelon*, some species of which are restricted to these wetter landscapes, which are the least disturbed of the environmental succession. The early fluvial environments are succeeded by a series of volcanigenically disturbed landscapes, in which pteridosperms are common and abundant, dominating some of the assemblages. Total species diversity in these landscapes was low, between 6–8 species on a reconstructed whole-plant basis, with pteridosperms accounting for half to nearly all the species at any one site, especially in the more heavily disturbed settings. Bateman (1991) noted that these pteridosperms formed a persistent scrub community consisting of the tree forms *Eristophyton* and *Bilignea*, and the gracile form, *Triradioxylon*. Low species richness, and the persistence and dominance of pteridosperms of several growth habits, suggest fairly wide ranging environmental tolerances and opportunistic life histories for a number of species. Scott and Meyer-Berthaud (1985) described another late Tournaisian volcanigenic landscape from Foulden in which fossil plants were preserved as both petrifications and compressions in two different beds. The gracile, primitive pteridosperm *Tristichia* dominates one of the beds in association with the seed *Stammnostoma*. The deposit appears to have been a standing water environment, possibly a lagoon, in which spirorhynchids could colonize locally transported plant material. In a deposit from the Castleton Bay locality in East Lothian, of approximately equivalent (late Tournaisian) age to that from Foulden, Scott and Galtier (1988) described plants in a wet floodplain deposit located between then-active volcanic vents. The plants were deposited in abandoned channels, after some transport, in small ponds where carbonate was precipitated, preserving the plants as petrifications. Included were spirorhynchid worms, ostracods, and fish bones, suggesting brackish water, possibly estuarine conditions. In this instance, the flora is dominated by the arborescent pteridosperm *Eristophyton*, but with a significant element of the small lycopsid “*Lepidodendron calamopsoides*” (not actually a *Lepidodendron*,

sensu stricto; possibly related to *Paralycopodites*; Bateman, personal communication), the calamopityacean ground cover pteridosperm, *Stenomyelon*, and some small ferns. When compared with other floras from approximately the same time interval and environmental conditions (Oxroad Bay—volcanigenic; Cove, Burnmouth, Foulden, Edrom—fluvio-lacustrine), Scott and Galtier (1988) echoed the conclusions of Rothwell and Scheckler (1988), arguing that pteridosperms, large and small, appear to have been particularly adapted to growth in disturbed environments. Some small lycopsids, such as *Oxroadia*, also appear to have been able to survive under disturbed conditions (Bateman 1992), as were many early ferns (Scott and Galtier 1985). “*Lepidodendron calamopsoides*,” in contrast, was not capable of survival under the conditions of heavy disturbance by repeated volcanism, which created ephemeral opportunistic settings.

These Tournaisian patterns continue into the Viséan. For example, Galtier et al. (1993) studied a flora from the Weaklaw site in East Lothian preserved in a volcanigenic sequence. The flora from this site, found in several ash beds, is uniformly pteridosperm dominated, but only by the large woody forms *Eristophyton* and *Pitus*, and the smaller tree or possible shrub, *Bilignea*. Also present are some compression foliage and the zygopterid *Diplolabis*. Several other volcanigenic sites of similar age are dominated by ferns and/or lycopsids. Yet other sites are dominated by pteridosperms, or a mixture of pteridosperms and ferns/lycopsids. Included are the Pettycur, East Kirkton, and Loch Humphrey Burn localities of Scotland, and the Esnost, and Roannais localities of France. Galtier et al. (1993) concluded from this analysis that there were two basic community types in these landscapes: those dominated by pteridospermous seed plants and those dominated by ferns and/or lycopsids.

A small window in the later Mississippian suggests that the flora described above continued to survive in disturbed, volcanigenic landscapes, which may, in fact, have constituted refugia in a world that was increasingly Pennsylvanian in aspect (evolutionary modernization of the plants with patterns of ecological partitioning more like that of the tropical wetland landscapes that would dominate peat-forming lowlands). Chalot-Prat and Galtier (1989) described a woody trunk fragment, tentatively attributed to *Eristophyton*, from Tazekka, Morocco, in rocks considerably younger than those of the Scottish or

French occurrences from which this genus is reported in abundance. The local sedimentary setting is complex and the cf. *Eristophyton* specimen is preserved in volcanogenic sediments distinct from, but associated with, floras dominated by lycopsids (*Lepidophloios*) in swamp deposits and calamitaleans (*Mesocalamites*) in clastic flood-basin sediments. This parallels patterns found in the Tournaisian-Visean where pteridosperms often were found interbedded with, but in different facies from, lycopsids, ferns, and sphenopsids. In this case, the lycopsid and calamite are of considerably more advanced aspect than those of the early Mississippian. In different sedimentary conditions, Gerrienne et al. (1999) described a flora from the late Mississippian of Belgium that contained *Eristophyton*-like wood in association with what are possibly the oldest records of *Arthropitys* calamitaleans and the marattialean tree fern *Psaronius*, clear harbingers of later Pennsylvanian wetland floras.

These changes in the composition of the dominant floras in Euramerica may have been driven by changes in continental positions, as Pangea accreted and formerly paratropical regions moved equatorward (Raymond 1985) from areas of strong seasonality to areas of less seasonal climate. However, they also may reflect the onset of the Carboniferous glacial interval, which would have produced strong polar high pressure cells and narrowed the atmospheric intertropical convergence zone, increasing rainfall at the equator and fundamentally changing tropical climatic dynamics (Cecil et al. 2003).

In summary, the data that have appeared since the publication of the review by Rothwell and Scheckler (1988) have expanded and confirmed their observations. The early pteridosperms, both in Devonian and early Mississippian tropical landscapes appear to have been opportunistic forms, centered ecologically in disturbed environments. This was especially true where the disturbances were floods, levee progradation, or volcanogenic events, which created opportunities for primary succession. The plants typically had rapid growth, early onset of reproduction, xerically adapted shoot morphologies, highly ramifying root systems, wind pollination, and production of large numbers of small, highly dispersible seeds. The ultimate evolutionary and ecological fate seems to have been extinction for the large tree forms but some appear to have been the evolutionary ancestors of the pteridosperms that were of importance in Pennsylvanian wetland landscapes.

The “Coal Swamp” Landscape. The floras associated with coal beds of Pennsylvanian age (late Namurian, Westphalian, and Stephanian) are among the best studied fossil floras. Well exposed in coal mines, plants have been studied for centuries and are known both as petrifications and adpressions. The mainly carbonate permineralizations of peat stages of coal, known as coal balls, have yielded unrivaled information on plant anatomy, development, and reproductive biology. However, with a few notable exceptions (e.g., Rothwell 1981), they have left much to be desired regarding whole-plant reconstructions or a clear picture of whole-plant (as opposed to organ-level) species-level taxonomic diversity. Quantitative studies of coal-ball floras have permitted large-scale analyses of community dynamics and responses of ecosystems to climate change (e.g., Phillips et al. 1985, DiMichele and Phillips 1996b). Adpressions, on the other hand, have revealed rare but significant insights into plant architecture (e.g., Bertrand and Corsin 1950, Laveine et al. 1977, 1997; Laveine and Duquesne 1998, Wnuk and Pfefferkorn 1984, Shute and Cleal 2002), *in situ* plant spacing and landscape structure (e.g., Gastaldo 1986, 1987), plant responses to glacial-interglacial climatic changes (e.g., Falcon-Lang 2003, 2004), and the complexities of taxonomic richness (e.g., Krings et al. 2003b). It has been difficult to reconcile or cross-correlate the petrification and adpression records; the differences in preservation frequently lead to different suites of characters, different traditions in the way the fossils are studied, and so forth.

The origins of the “coal-swamp” flora are uncertain. Was it assembled species-by-species from taxa that evolved elsewhere before entering the tropical lowlands, or did the flora evolve more as a unit that was assembled *in situ* from diversifying lineages as the glacial-interglacial rhythms of the latest Mississippian and Pennsylvanian began, taking the Earth from a warm to a cool global climate (Gastaldo et al. 1996)? The pteridosperm element of this flora may shed some light on the problem. Some of the pteridosperm lineages typical of peat-forming, wetland landscapes appear prior to the major development of such landscapes, in association with various elements of the earlier Mississippian floras.

EARLY APPEARANCES OF WETLAND, TROPICAL PTERIDOSPERMS. *Taxa and growth habits.* The two “classic” groups of Pennsylvanian-age pte-

ridosperm lineages are the orders Lyginopteridales and the Medullosales, each encompassing large taxonomic diversities. Each also appears to have its origins very early in, or before, the inferred onset of glacial conditions.

As noted in the discussion of earlier Mississippian pteridosperms, the matter of the morphological circumscription of the Lyginopteridales (Calamopityaceae, Lyginopteridaceae, perhaps others) and included families remains problematic (Meyer-Berthaud 1990). Nonetheless, plants with anatomical similarities to Pennsylvanian *Lyginopteris* have been described as early as the Viséan, from the classic Pettycur locality in Scotland (Bertram 1989). The family Lyginopteridaceae can be extended even further back into the Tournaisian if one is willing to accept the assignment of such taxa as *Laceya* or *Tristichia* to the Lyginopteridaceae (e.g., Dunn et al. 2003a). More certain records of the genus *Lyginopteris* place it as early as the upper Viséan, based on a suite of vegetative and reproductive organs described as *Lagenopteris bermudensisiformis* (Hartung 1938), and from the Namurian A, during the early phases of the onset of the late Paleozoic ice age, as compression foliage (Pattisky 1957, Pfefferkorn and Gillespie 1982), from anatomical preservation (*Lyginopteris royalii*: Tomescu et al. 2001), and as prepollen (*Schultzispora* sp.) in coal and organic shale beds (Peppers 1996, Eble and Greb 2004). Another member of the family, also described from Namurian A anatomical specimens, is *Trivenia arkansana* (Dunn et al. 2003a). Based on their anatomical features, both *L. royalii* and *T. arkansana* are interpreted as vines or scrambling ground cover. Another probable lyginopterid climber or scrambler, from the Mississippian/Namurian of Britain, was described as *Rhetinangium arberi* by Gordon (1912). This plant is preserved anatomically and has small diameter, woody stems with radially aligned sclerenchymatous bands in the cortex, massive leaf traces and petiole bases, and petiolar anatomy of the *Lyginorachis* type. The genus *Heterangium*, also assigned to the Lyginopteridaceae, and a member of Pennsylvanian peat-forming communities, has been described as early as the Viséan of Britain in anatomical preservation (Scott et al. 1984); like other lyginopterids, it is interpreted as a vine or scrambling plant based on small stem diameters and sclerenchymatous plates in the cortical tissues.

The order Medullosales also is first recognized as anatomically preserved specimens of

late Namurian A age from a wide geographical area (Taylor and Eggert 1967, Mapes and Rothwell 1980, Dunn et al. 2003b). The oldest well documented specimens attributable to *Medullosa* (*M. steinii*: Dunn et al. 2003b) have anatomical features consistent with vine/climber or scrambling habit. These include small stem diameters, spines on the bases of petioles that may have served as climber hooks, which are well documented in adpressions from the Pennsylvanian (Krings et al. 2003b), and a vascular system composed of cable-like, anastomosing, vascular strands. These features suggest a flexible stem that was incapable of self-support. The stelar architecture of medullosans has long been perplexing because of its “vine-like” structure, composed of distinct vascular bundles, each surrounded by a cylinder of secondary xylem, rather than a continuous band of wood surrounding the stele to the external side. In addition, the stems are rich in longitudinal fibrous bundles, which also confer flexibility in stem and leaf construction. It is difficult to have confidence that first stratigraphic occurrences are also the earliest/most primitive evolutionary states. Nonetheless, the early occurrence of such a vine or liana-like architecture in *Medullosa*, which also is a characteristic of most subsequent members of the Medullosales, presents the possibility that these were primitive features that were developmentally canalized and thus fundamental architectural elements. The later evolution of larger tree forms was only possible through modification of this ground plan, mainly through strengthening by adding features such as extensive secondary xylem or large quantities of sclerenchyma.

Quaestora amplexa is a small woody stem attributed to the medullosan evolutionary lineage (Mapes and Rothwell 1980). The plant is known only from small diameter specimens with a cruciate vascular system surrounded by secondary xylem, rather than the separate woody bundles typical of *Medullosa*. It may have been a small tree, possibly part of a subcanopy in early wetland ecosystems (Dunn 2004, Dunn et al. 2006). This plant is important because it suggests early ecological diversity in the Medullosales, something typical of this group during the Pennsylvanian.

Medullosan seeds also have been discovered in Namurian A deposits (Dunn et al. 2002b). Attributable to *Rhyncosperma quinnii*, these seeds have features that link them to triconocarpalean seeds, particularly the medullosan genus *Ste-*

phanospermum. *Rhyncosperma quinnii* is a moderate sized seed, reaching lengths of 22 mm, indicating that significant investment of energy in seeds was an early appearing trait in this group of plants, something that would reach much greater proportions in the Pennsylvanian wetlands.

Pteridosperms in early tropical wetland communities. The late Mississippian is a crucial time interval for the evolution of the later Carboniferous wetland biome, but remarkably little has been published about it from a synecological perspective. One of the few studies is that of Dunn (2004; Dunn et al. 2006), which considers the flora of the Fayetteville Formation of Arkansas of approximately Namurian A age. Three distinct plant communities have been recognized based on both adpression fossils, from terrestrial sandstone and mudstone, and petrification fossils, transported into marine black shale. One of these communities is dominated by lycopsid trees, one by pteridosperms, and one by opportunistic ferns. In the overall flora, consisting of 15 whole-plant species, pteridosperms, although not numerically dominant, are by far the most diverse group at the species level (10 species), with most of that diversity invested in ground cover and vines (7 species) rather than canopy trees (1 possible pteridosperm) or understory trees and shrubs (2 species). The canopy dominant has characteristics that would tie it more closely to earlier Mississippian "lyginopterids" than to later tropical wetland taxa. Similar patterns of distribution for the small pteridosperm trees, *Quaestora amplexa* and an undescribed "lyginopterid", were taken to suggest that these plants occupied the understory, also in such drier habitats. Possibly lyginopterid foliage, assigned to two different species of *Sphenopteris*, formed an abundant ground-cover component in each of two lycopsid dominated assemblages. Perhaps the most important findings from this study, relevant to this review, are that pteridosperms were diverse in their ecological roles early in the appearance of tropical wetland vegetation, and that they were mainly ground cover and vines, possibly shrubs, rather than major canopy trees. This would change during the Pennsylvanian as some pteridosperms broadened into the role of local canopy dominants.

Palynological analyses of coals and organic shales from the late Mississippian (Chesterian) of the U.S.A. (Eble and Greb 2004) have identified *Schultzispora rara*, the prepollen grain of

Lyginopteris, as a major floristic component in swampy habitats dominated by spores of the lycopsid tree *Lepidophloios*. *Schultzispora rara* remains a component of coal palynofloras though the Langsettian (Westphalian A), when *Lyginopteris* becomes extinct, and is frequently associated with lycopsid trees in coal-ball floras. Assuming the parent plant to be a vine or scrambling plant, based on the foliage and stem anatomy of later lyginopterids, it appears that there was a significant pteridospermous component of wetland vegetation early in the history of the tropical wetland biome.

PTERIDOSPERMS IN PENNSYLVANIAN-AGE WETLANDS. *Medullosans. Taxonomic Relationships.* The Medullosales is a complex group of plants with a variety of growth forms, frond architectures, and reproductive biologies. Organization of this variation within a well supported phylogenetic framework would be most welcome because it would permit a clearer evaluation of the relationship between ecological role and evolutionary relatedness. However, at present, there are few whole-plant reconstructions on which such relationship schemes can be based. One such attempt is that of Laveine (1997), who aligned medullosan taxonomic relationships on the basis of frond architecture and foliar morphology, and attempted to include what is known of the association between major types and taxa of dispersed organs. Laveine (1997) recognized three "family" level groups, which are outlined below. This summary permits some of the basic ecologically relevant aspects of the architecture of these plants to be summarized.

Neuraethopteridaceae includes the foliage genera *Alethopteris*, *Lonchopteris*, *Neuraethopteris*, *Cardioneuropteris*, and possibly *Neurocardiopteris*. *Lonchopteridium* is also a probable member of this group (Zodrow and Cleal 1998). These forms are expected to have a "bifurcate pinnate" frond architecture, in which the petiole is naked. These kinds of fronds can be very large, up to 7–8 m long and 4 m wide. Where known, these genera have *Aulacotheca-Whittleseya* pollen organs and *Trigonocarpus* seeds. *Alethopteris* is abundant in western Europe during the late Namurian and early Westphalian, can be abundant in the Stephanian, but is rare in the "Rotliegend/Autunian." It does not appear in China until the Stephanian, and then only occasionally. This clade may be the ancestral form for this entire group of plants. Based

on frond architecture, there is evidence that the earliest described medullosan foliage, “*Neuropteris*” *antecedens*, will likely prove to have a ‘bifurcate pinnate’ type frond. The same frond type is found in *Neurocardiopteris broilii*, a generic name that, according to Laveine (1997), has precedence for these early forms.

Parispermaceae include the foliage genera *Paripteris* and *Linopteris*. These forms have “pseudopinnate” compound fronds with two terminal pinnules on each pinna rachis (paripinnate condition). There are no pinnule lobations. Fronds are large and forked, with naked petioles and pinnules on rachises of all orders above the fork. They are associated with anatomically preserved stems of the *Sutcliffia*-type (Stidd et al. 1975) and have *Potonia* pollen organs and *Hexagonocarpus* seeds (for summary, see Laveine et al. 1993).

Neurodopteridaceae of Laveine was split by Cleal and Shute (2003) into two families. The Neurodopteridaceae, *sensu stricto*, includes *Neuropteris*, *Reticulopteris*, *Odontopteris*, *Macroneuropteris*, and possibly *Neurocallipteris*, *Neurodopteris*, and *Barthelopteris*. The Cyclopteridaceae include *Laveineopteris*, *Margaripteris*, and *Calipteridium*. Laveine also included *Cardioneura*, *Cardiopteridium*, *Sphenoneuropteris* in his familial concept (see also Cleal and Shute 1995). The earliest occurrences of *Neuropteris* reliably reported date the genus to the Namurian A of the latest Mississippian (Purkyňová 1970) and appear attributable to *N. obliqua*. Plants of these two families have bifurcate, semi-pinnate fronds with pinnae (ultimate or bipinnate depending on the genus). In the Neurodopteridaceae *s.s.* large lateral pinnules are found below the main fork of the frond. As described by Cleal and Shute (2003) true cyclopterid pinnules occur in the Cyclopteridaceae. Intercalary ultimate pinnae may occur between insertions of bipinnate lateral pinnae. In each of the families, the apex of each major frond segment can have pinnules on the rachis and terminates with a single pinnule (imparipinnate). Fronds of *Macroneuropteris macrophylla* have been reconstructed from large partial specimens (Cleal et al. 1996). Some species of neuropterid genera have been shown to be attached unequivocally to stems with *Medullosa* anatomy (Beehler 1983).

Within this basic taxonomic configuration, information about medullosan species remains variously connected and disconnected with an increasing number of centers of attraction. In

some cases, for example, specific adpression taxa can be linked to anatomy and tied to growth habits and sedimentary environmental settings, which permits ecology to be understood, subject to reasoned speculation. In other instances there is only, say, foliage, linked partially or not at all to anatomy or whole-plant concepts. Or there is the vast information on seeds and their sizes, most of it not clearly linked to specific whole-plant concepts.

As part of this general set of background data, it can be determined that medullosans displayed a wide spectrum of growth forms. Clearly documented are climbing vines or liana-like morphologies, thicket-forming “leaning” tree forms that apparently were not self-supporting, and free-standing trees. However, for many taxa at the species level, the details of the growth habit, other than tree, vine, etc., remain unknown.

Tree forms. At the most general level, Pfefferkorn et al. (1984) and Wnuk and Pfefferkorn (1984) described stems from *in situ* deposits of middle and late Pennsylvanian age (Bolsvian/Westphalian C through Stephanian) from shales above and below coal beds in the U.S.A. and France. Two medullosan tree growth architectures were identified based on prostrate trunks with leaf bases (though not identifiable foliage) attached. One tree architecture consists of upright stems as much as 20 cm in diameter or more (based on these published papers and on subsequent personal field observations), probably less than 5 m in height, with closely spaced, densely packed fronds, about 10 per meter of stem length. The fronds appear to have recurved after death, possibly forming a “skirt” around the plant prior to rotting or breaking off; skirts are generally considered to be morphological mechanisms for shedding epiphytes and vines in modern plants such as palms or some tree ferns. Such trees appear to have been solitary with live fronds concentrated in a tuft near the plant apex (Fig. 3). The other growth form consisted of flexuose stems up to 13 cm in diameter and greater than 5 m in height, with widely spaced fronds, 3.0–4.5 cm in diameter at the base, which appear to have been shed regularly; there is no indication of a dense skirt of dead fronds (see also specimen illustrated by Demko and Gastaldo 1992) (Fig. 4). These latter trees appear to have formed thickets in which tall, but relatively small diameter; stems were able to support a mass of fronds by intertwining with adjacent stems; the authors report finding similar growth habits in modern tropical flowering plants. Pfeffer-

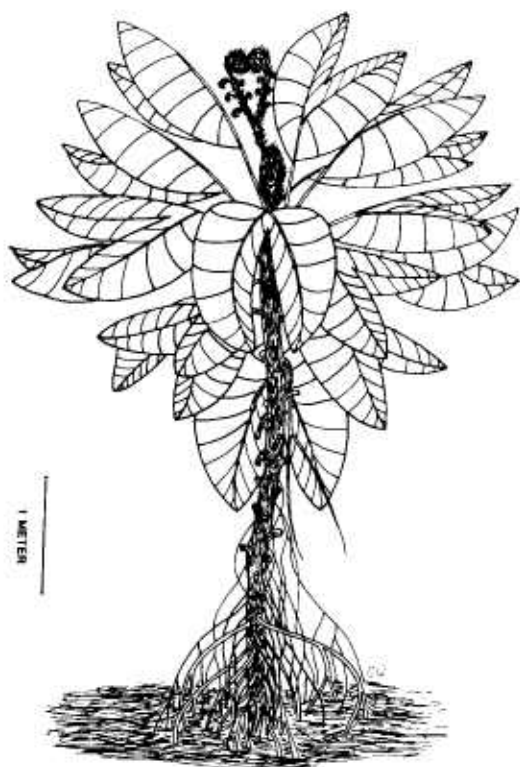


FIG. 3. Free-standing medullosan pteridosperm growth habit. Reprinted from Wnuk and Pfefferkorn (1984, Fig. 11) with permission from Elsevier.

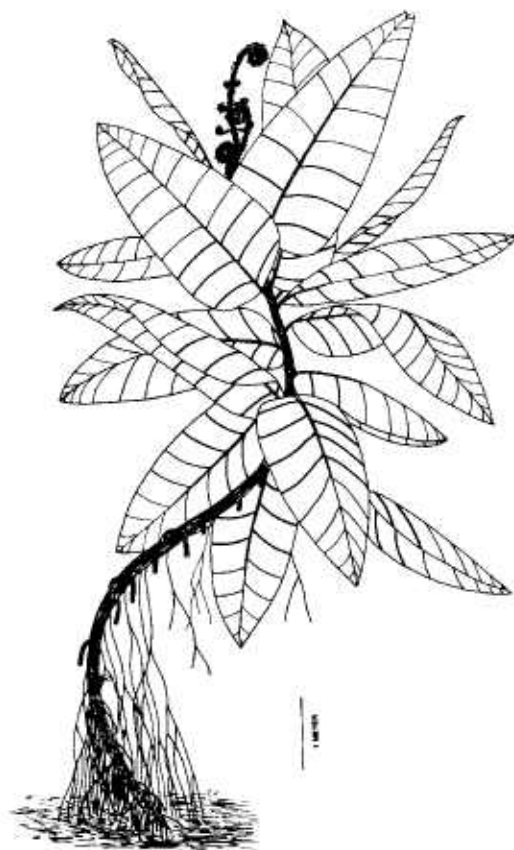


FIG. 4. Lax-stemmed medullosan pteridosperm growth habit. Reprinted from Wnuk and Pfefferkorn (1984, Fig. 10) with permission from Elsevier.

ferkorn et al. (1984) evaluated published reconstructions of medullosans, which show a wide range of variation in the interpretation of flexuose vs. upright habit (Fig. 5). Some of these reconstructions appear to be based on plants with dead or dying foliage or are unlikely for plants growing in natural stands of vegetation.

Adpressed foliage associated with these stems was attributed to two major groups of medullosan pteridosperms, the alethopterids and neuropterids. Wnuk and Pfefferkorn (1984), after examining the remaining segments of attached foliage, attributed *Alethopteris* sp. to flexuose stem morphologies; however, this assertion was disputed by Laveine (1997), who determined that the frond of *Alethopteris* and related genera has a different architecture than that described by Wnuk and Pfefferkorn (1984). Neuropterid forms could be less confidently assigned to architectural stem categories and were found in association with both flexuose and upright stem morphologies. The associated neuropterids, in the current taxonomic system (Cleal et al. 1990), can be assigned to species in three genera: *Ma-*

croneuropteris scheuchzeri, *Neuropteris ovata*, and *Laveineopteris rarinervis*.

Shute and Cleal (2002) reevaluated *Laveineopteris* specifically and suggested a growth habit for the plant that largely accorded with the findings of Wnuk and Pfefferkorn (1984) and Pfefferkorn et al. (1984) but showed some interesting ecological elaboration. Some neuropterids are associated with peculiar leaves termed "cyclopterids"—laminar, leaf-like organs generally placed near the base of fronds, along the petioles, or at the point of frond bifurcations. Shute and Cleal (2002) suggested that in *Laveineopteris* cyclopterids are actually leaves of pole-like juvenile plants growing in deep shade in the subcanopy. They argued that many of the undifferentiated smaller axes, attributed by Wnuk and Pfefferkorn (1984) to petiolar remains, are, in fact, such pole-like juvenile stems. Such stems would have borne cyclopterid foliage that left only cryptic scars where those cy-

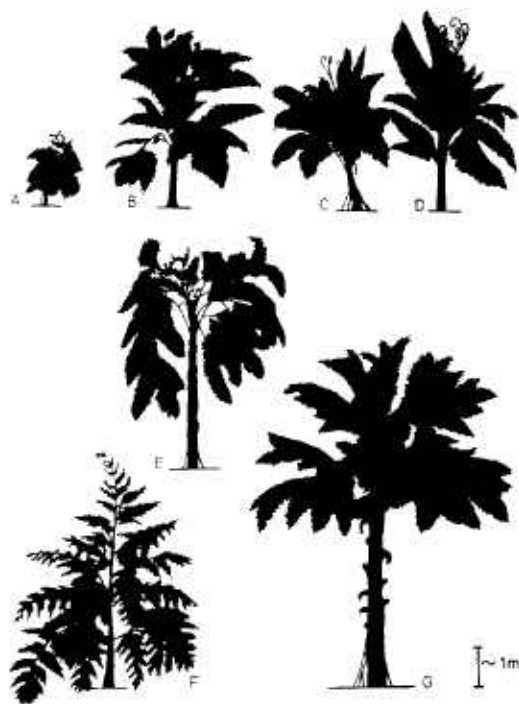


FIG. 5. Reconstructions of free-standing medullosan pteridosperms (A—Andrews, 1947; B, C, D—Bertrand and Corsin, 1950; E—Stewart and Delevoryas, 1956; F—Corsin in Buisine, 1961; G—Pfefferkorn et al., 1984). Reconstructions B, C, D, and G have the appearance of tropical plants. Reconstructions A and E show plant with drooping leaves that are either dead or dying. Reconstruction F is a growth form that is unlikely to occur in monocaulous tropical plants. Reprinted from Pfefferkorn et al. (1984, Fig. 1) with permission from the Delaware Valley Paleontological Society.

clopterid leaves abscissed. In their growth model, the typical laveineopterid foliage was produced once the trees reached the full sunlight of the canopy. They proposed that *Laveineopteris* species formed dense stands from which competing pteridosperms were excluded by the depth of understory shade. However, Krings et al. (2003b) considered *Laveineopteris* (*Neuropteris*) *rarinervis* to be a vine because fronds up to 80 cm long have been found on stems only 3 cm in diameter. Reihman and Schabillion (1978) found permineralized specimens of *L. rarinervis* to be mesomorphic with the capability to excrete water, favoring habitats of high soil moisture and limited evapotranspiration. This is in keeping with the interpretation of Shute and Cleal (2002) that this species specialized in low light conditions, possibly forming understory thickets. Shute and Cleal (2002) also noted that, in

contrast to other species of this genus, cyclopterids are found relatively rarely in association with *L. rarinervis*, which might be consistent with a liana-like or vine habit where long-lived shade leaves might be less important than in plants that spent much of their life in the understory (C. J. Cleal, personal communication, 2005). Perhaps all these sources of data and interpretation can be reconciled by imagining early growth as a small pole-like sapling with heteroblastic leaf development, bearing fronds only when reaching the canopy, there supported by intertwining with other individuals, forming a largely understory thicket.

The largest medullosans, based on stem diameters of permineralized specimens, have been reported from the Pennsylvanian-Permian transition in Germany and France. Sterzel (1918) reported stems of *Medullosa leuckartii* from Chemnitz, in the German Rotliegend, with diameters of up to 26 cm, bearing in helical phyllotaxis petioles up to 16 cm in diameter with massive secondary xylem. One fragmentary specimen was nearly two meters in length, suggesting considerable height. The stems were associated with adpressed foliage attributed to *Neurocallipteris planchardii* (moved from *Neuropteris* by Cleal et al. 1990) and *Neurodontopteris auriculata* (which Potonié 1893, segregated from *Neuropteris*, a determination reaffirmed by Kerp and Krings 2003). Stems of similar size were reported by Renault (1896) from the Autun Basin of France. These medullosans are qualitatively different in size and perhaps growth architecture from any known earlier. The authors' observations of coal-ball specimens from the middle and late Pennsylvanian also suggest that maximum medullosan stem sizes were greater in late Pennsylvanian peat-forming swamps and mires than earlier. Medullosans of the late Pennsylvanian and Early Permian thus may have elaborated on the stout tree morphology described by Wnuk and Pfefferkorn (1984) to reach even greater dimensions, probably achieving considerable heights and large frond sizes.

Vine and Liana-like Growth Habits. Some medullosans appear to have had scrambling or vine/liana-like growth morphologies. This has been described in *Medullosa steinii*, for example, the earliest described species of this genus from the Mississippian. Because it is based on anatomical preservation, this species is assigned to *Medullosa*. The adpressed foliage taxon to which this plant belongs is not clear (Dunn et al. 2003b). Climbing or scrambling medullosans

appear to have been most prominent in the late Pennsylvanian and earliest Permian although, by extrapolation of generic ranges and from anatomical studies (e.g., Scott 1899, Schopf 1939), also occurred in the earlier Pennsylvanian as well. Potential reasons for the increase in vines in the late Pennsylvanian are discussed later (see subsection entitled “Medullosans in the Landscape”).

Prominent among these scrambling and climbing forms are plants associated with the adpressed foliage *Odontopteris*, particularly the “small pinnuled” forms (Šimůnek and Cleal 2004), and *Lescuropteris* (Krings and Kerp 1997). Hamer and Rothwell (1988), following Baxter (1949), described the late Pennsylvanian, anatomically preserved *Medullosa endocentrica*, a plant with odontopterid-like foliage, as a vine or liana-like plant based on the apparent delayed development of the leaves (a pattern typical of vines), the absence of adventitious roots, slender stems with axillary branching, and long internodes. Fronds of the “small-pinnuled” group of *Odontopteris* are small, perhaps up to 1 m maximum length. Although growth habit is not known for certain, small tree form was suggested by Bertrand and Corsin (1950), based on similarity to neuropterids and on a stem specimen figured by Zeiller (1888), which Pfefferkorn et al. (1984) attributed to their “leaning” growth morphology. Šimůnek and Cleal (2004), on the other hand, argued that this stem is fully compatible with a scrambling plant, similar to *Calistophyton/Dicksonites pluckenettii* as reconstructed by Rothwell (1981) or by Galtier and Béthoux (2002). Šimůnek and Cleal (2004) made several interesting observations relevant to the species-level autecology of this group. Secretory ducts, for example, are present in the late Pennsylvanian and Early Permian *Odontopteris reichiana* and *O. nemejcii*, which may have helped repel piercing and sucking insects, but appear to be absent in the late Pennsylvanian *O. brardii* (Kerp and Krings 2003). They also note that hydathodes, structures that permit a plant to excrete excess water, appear to be present in *O. brardii*, based on specimens illustrated by Kerp and Krings (2003), but are absent in *O. reichiana* and *O. nemejcii*. Similarly, lower vein density in *O. nemejcii* than in *O. brardii* may be a further means of reducing water loss and an indication of growth under drier habitat conditions. *Odontopteris reichiana* and *O. nemejcii* may have occurred in environments with slightly more moisture stress than *O. brardii*, such as

intermontane basins in central Europe, which lacked marine influence and were possibly at higher altitudes than those of North America and western Europe. In these environments, *O. brardii* is the most commonly encountered species of this genus. Thus, there are both biogeographic patterns and associated habitat differences discernable in species of this genus.

Lescuropteris genuina, one of two species in this genus, was found by Krings and Kerp (1997) to bear fronds about 60 cm long, small for a medullosan, but with terminal pinnules modified in some instances to form tendrils, similar to those found in some modern flowering plants, suggesting a climbing habit. These authors attributed Zeiller’s (1888) stem specimen (mentioned above) to *Lescuropteris genuina* based on the presence of an associated frond segment found with, but not in attachment to, the original stem specimen. This supports Šimůnek and Cleal’s (2004) architectural interpretation, although it results in assignment of the stem to a different, but related, genus.

A final medullosan with climbing growth architecture is *Blanziopteris praedentata*, described by Krings and Kerp (1999) based on material with small fronds and slender stems. It also appears to be broadly neuropterid in its affinities, based on forked frond morphology, pinnule venation, and pinnule attachment to rachises. *Blanziopteris praedentata* fronds are borne in subopposite pairs with one member of a pair highly modified such that pinnae end in pads that are interpreted as adhesive pads. Fronds are covered with a dense layer of hairs of different kinds. Some (of a type also found in *Odontopteris* and *Lescuropteris*) are bent apically and may have deterred insect predators. Others, with swollen bases and filaments of small cells, may have broken off when touched by animals such as arthropods, causing the release of repulsive chemicals (Krings et al. 2002).

Cormose stems. Not discussed in these considerations of growth habit is the possibility of medullosans with cormose stems and large fronds, emanating from near ground level. Such a growth form might be similar to that of modern *Nypa* palms or *Angiopteris evecta*. Unfortunately, such a growth form would be difficult to find preserved in the fossil record, especially considering the small number of reported adpressed stems with significant information on frond attachment. Yet, such a habit might be conceivable, especially for very large fronds of some species of *Alethopteris* and its relatives

(Laveine 1986, 1997). At present, there is no direct evidence for such a growth form.

Medullosan reproductive biology. Medullosans are characterized by large seeds, large pre-pollen grains, and generally low reproductive output, considering the general rarity of these organs in comparison to vegetative remains. In general, these features point to “K-selected” reproductive strategies. Based on analogy with extant plants that have large seeds and swimming sperm, such as *Ginkgo*, which has long time intervals between pollination and fertilization, even weedy medullosans may have been relatively slow to germinate and establish, when compared to modern weedy angiosperms. Plants with this type of reproduction would be expected to be long-lived, reproduction extending over many seasons, accompanied by low success rates when viewed relative to the lifetime of an individual plant. Alternatively, some medullosans may simply have reproduced infrequently, even if abundantly, similar to living cycads, as argued by Dimitrova et al. (*in press*). Medullosan seeds (e.g., Serbet and Rothwell 1995) and pollen organs (Millay and Taylor 1979) exhibit a wide range of sizes and degrees of complexity, which might be assumed to indicate ecological differences, perhaps in response to attack by arthropods or in relation to pollen dispersal and pollination (e.g., Taylor 1978, Taylor and Millay 1981), and in seed dispersal syndromes. Variation in seed sizes also may indicate differences in rapidity of germination and the allocation of resources to many vs. few seeds during any one episode of reproduction. However, lacking good correlations with each other or with parental plants and foliage types, it is difficult to do more than reason from the limited information such reproductive organs present. The structural diversity such organs encompass is consistent, however, with a wide spectrum of medullosan ecological roles, as inferred from other sources of information, some of which have been detailed herein.

Medullosan seeds and ecological implications: Medullosans had large seeds, which is part of their morphological and ecological mystique. The medullosan seed literature is large and detailed, leading to considerable knowledge about their female reproductive organs (see Crookall 1976, for a review of adpression forms, and Dunn et al. 2002a for a listing of permineralized taxa, which fall into 10 genera), all of which are built on the same basic structural plan, epitomized by *Trigonocarpus* (adpression) or *Pach-*

ytesta (petrification) (Hoskins and Cross 1946). Unfortunately, correlation of seeds with particular foliage species or stem anatomies is rather limited and many of the seeds form complexes that differ subtly, making fragmentary specimens difficult to differentiate to more than a species complex. Based mainly on evidence from adpression fossils, seeds appear to have been attached to fronds, in many cases replacing pinules within the architecture of the frond, or occurring along frond rachis segments. The largest seeds were gargantuan, reaching lengths of 7–11 cm in petrification (*Pachytesta incrassata*, *P. gigantea*, *P. noei*, *P. vera*; Taylor 1965) and 10–12 cm in adpressed forms (*Trigonocarpus*, authors’ observations and dimensions as summarized in Gastaldo and Matten 1978). Even the smaller medullosan seeds approximated a centimeter in length, which still makes them large by modern standards. Virtually all species had complex seed coats composed of multiple layers. The outer layer, or sarcotesta, typically was composed of large parenchymatous cells and may have been fleshy, in some instances containing resins or other intracellular secondary compounds. The middle layer of most medullosan seed coats, the sclerotesta, was typically sclerenchymatous, composed of stony cells. Within the seed was a large, multicellular gametophyte, which served as the energy reserve for the developing embryo, should one be present.

Given their large size, many of these seeds may have fallen close to the parental plants, which might account for the reports of thickets in several different medullosan species (e.g., Wnuk and Pfefferkorn 1984, Shute and Cleal 2002). More extensive dispersal of such large seeds most likely occurred by either animal vectors or water. Certainly, anyone who has collected extensively in the field occasionally has seen masses of small pteridospermous seeds, probably of lyginopterid origin, strewn across bedding surfaces in lake and lagoonal deposits or filling troughs in coarser sediments deposited in flowing water. Such small-seed accumulations imply periodic, probably seasonal, seed production and large reproductive output. In contrast, the larger medullosan seeds, although they rarely can be found in large accumulations, generally are found isolated or in small numbers and may have been produced somewhat more parsimoniously.

Clearly, seeds of all sizes were a potential energy source for animals. The well reinforced

sclerotestas of medullosans are similar to features of modern seeds designed to protect them from mechanical crushing or digestion by gut enzymes. And soft sarcotestas, it could be argued, served as attractants to herbivores, possibly vertebrates. But which ones? The evidence for Pennsylvanian herbivory is ambiguous (Hotton et al. 1997); animals such as *Edaphosaurus*, which has large, flat, tooth batteries, have been suggested as seed predators. Direct evidence is limited, however, and crushed seed remains have yet to be identified unequivocally in coprolites of any kind.

Medullosan pollen organs, prepollen grains, and pollination syndromes: The pollen organs of the medullosans, highly variable in morphological details but virtually all synangiate, have been well studied and elucidated (e.g., Millay and Taylor 1979) and, in some instances debated at length with regard to form and evolution (e.g., *Dolerotheca*: Dufek and Stidd 1981, Rothwell and Eggert 1986, Stidd 1990). In the medullosans these organs were foliar borne and distinctly individuated from pinnules. "Pollen" appears to have been, technically, prepollen; i.e., pollen tubes were haustorial and sperm were released directly, presumably freely into the pollen chamber. If modern *Ginkgo* and *Cycas* serve as accurate examples of this syndrome, sperm were likely flagellate. Furthermore, the time elapsed between pollination and fertilization may have been considerable, as in modern *Ginkgo* (Favre-Duchartre 1956, Royer et al. 2003).

Pollen/prepollen delivery systems in the pteridosperms appear, from data and inference, to have been diverse. The medullosan prepollen grains, largely attributable to *Monoletes*, were large, the longest dimension ranging from about 100 μm to over 500 μm (Taylor 1978). It seems impossible to imagine them being wind delivered, although forms have been reported with vestigial sacci (*Parasporites*: Dennis and Eggert 1978). Recent modeling studies (Schwendemann et al. 2005) indicate rapid settling dynamics for *Monoletes*, considerably different from known forms of wind-delivered gymnosperm pollen. Dispersal by arthropods, flying or otherwise, has been suggested, based on prepollen size alone (e.g., Taylor 1982). Coprolites filled with medullosan prepollen are known (Labandeira 2000) and sloppy eating arthropods, covered with unconsumed prepollen, may have been further attracted to the outer seed coats of the large medullosan seeds. Add to this the probability that at least some medullosans formed dense thickets,

environments in which large prepollen grains may not have had to travel far for pollination to be effective (C. J. Cleal, personal communication, 2005). Water pollination is another possibility (P. R. Crane, personal communication, 2005), given the large size of the seeds and prepollen grains, and the semi-aquatic habitats that many medullosans appear to have occupied.

Medullosan carbon allocation. *Medullosa*, *sensu lato*, may have been the most "expensive" plant in coal-swamp landscapes, in terms of whole-plant carbon allocation. In a study of late Pennsylvanian plants preserved in coal balls from one late Pennsylvanian coal bed (and thus subject to approximately the same depositional and diagenetic history), Baker and DiMichele (1997) compared *Medullosa*, *Sigillaria*, and *Psaronius* (but not cordaitalean woody plants) quantitatively in terms of carbon allocation. Unlike *Psaronius* and *Sigillaria*, in which different tissues and organs are very different in construction, *Medullosa* is uniformly rich in sclerotic tissue and resins, which greatly add to constructional cost. This is in keeping with large seeds and large fronds in this group, conforming with K-selected ecological strategies in many tree species.

Medullosans in the landscape. The study of Pennsylvanian tropical plant community paleoecology has a long history, given the numerous exposures of plant-bearing rocks during coal mining throughout western Europe. Reviewed by Scott (1977), much of the early work was closely tied to biostratigraphy (Davies 1929), although the development of quantitative approaches began in the mid-1900s (Dräger 1964, Pfefferkorn et al. 1975) and led to the development of generalities that have proven robust as the number of explicitly ecological analyses has increased. For pteridosperms, the following general patterns have emerged:

1. In the early and middle Pennsylvanian (Westphalian), medullosan pteridosperms are most abundant in the diversity of habitats that characterized clastic floodplain environments, from better drained levees and stream-sides to soggy soil areas. In such settings, most species appear to have been major colonists of non-swamp habitats, even if with wet soils, but only a few could tolerate areas of long-persistent standing water. Although anatomical evidence to support adaptation specifically to wetlands is limited, root systems of medullosans (Rothwell and Whiteside 1974) may have aerenchyma in the small

- rootlets, consistent with patterns in other plant groups from Pennsylvanian wetland systems. In addition, distributional evidence suggests that the group as a whole was centered in areas where mineral nutrients were readily available (e.g., Pfefferkorn and Thomson 1982, Lamboy and Lesnikowska 1988, DiMichele et al. 2005a, 2006). For example, certain medullosans are commonly abundant in organic-rich shales that probably formed as waterlogged mucks (e.g., when preserved in peat substrates, medullosan remains are commonly associated with mineral partings in the coal bed or with elevated levels of fossil charcoal: DiMichele and Phillips 1988).
2. At any local area in floodbasin settings, medullosans rarely were notably diverse. Rather, a few species proved to be widespread at any given time and in any given area. Numerous studies correlating lithofacies and plant distribution record a restricted spectrum of known species (e.g., Scott 1978, 1984; Gastaldo 1985, Wnuk and Pfefferkorn 1987, DiMichele and Nelson 1989, DiMichele et al. 1991, Demko and Gastaldo 1992, Willard et al. 1995, Pryor and Gastaldo 2000, Gastaldo et al. 2004, Falcon-Lang, *in press*). This may mean that only a few medullosan *species*, based on adpressed foliage, were dominant at any time. Most *species* were rare, either in terms of their biomass or in terms of the number of sites at which they occurred in detectable frequencies. However, in clastic soil habitats, the medullosans as a group had the highest recorded biomasses prior to the middle of the Westphalian D, after which they remained dominant but often shared that position with marattialean tree ferns (Pfefferkorn and Thomson 1982). Similar patterns of medullosan abundance and distribution appear to characterize coal-ball floras (Phillips et al. 1977, Phillips and DiMichele 1998).
 3. A subset of medullosan species, otherwise known from clastic adpression preservation, occurs in peat-substrate habitats where they are known anatomically from coal-ball petrifications. In other words, there are at this time no species that are known uniquely from peat substrates. However, the number of species reported from peats is quite small: *Neuropteris ovata*, *Macroneuropteris scheuchzeri*, *Laveineopteris rarineris*, *Alethopteris sullivantii*, *A. lesquereuxii*, *Linopteris* sp. *Lyginopteris* also known from fossil peats include *Lyginopteris hoeninghausii* and *Sphenopteris* spp. *Mariopteris*-like foliage has been reported as well. The narrowness of this subset may reflect, in large part, the difficulty of identifying foliage from the information most readily available in anatomical preservation, which may mask greater diversity.
 4. In late Pennsylvanian/Stephanian age tropical environments of Europe and North America, medullosan diversity appears to have decreased or remained steady following the regional extirpation of the dominant middle Pennsylvanian lycopsids (Phillips et al. 1974). Some medullosans, primarily *Macroneuropteris scheuchzeri*, have been recorded as dominant elements in clastic-rich organic mucks from the latest Pennsylvanian (Phillips et al. 1985, DiMichele et al., 2005a). However, for the most part, they continue to play a role as subdominant species at a landscape level.
 5. Pteridosperms are present as vines and ground cover throughout the Pennsylvanian (e.g., DiMichele and Phillips 1996b, Gastaldo et al. 2004). However, in the late Pennsylvanian/Stephanian, the abundance of vines increased significantly, both in terms of species numbers and biomass. This led Kerp and Krings (1998; see also Krings and Kerp 1999) to suggest that the advent of tree-fern dominance in the late Pennsylvanian/Stephanian in much of the tropics led to the closure of forest canopies and attendant light attenuation compared with forests of the middle Pennsylvanian/Westphalian, where open-canopied lycopsid forests were most common. This may have placed a premium on climbing growth forms, resulting in an increase in the abundance of climbers in late Pennsylvanian/Stephanian floras in general in Euramerican wetland habitats.
- Habitat segregation patterns among medullosans. Perhaps the most conspicuous pattern of habitat differentiation is that between the arborescent neuropterids and alethopterids. On average, compared with groups such as the lycopsids or sphenopsids, the alethopterids and the neuropterids probably were much alike ecologically, growing in high nutrient, woodland or forested environments (as opposed to standing water swamps or wet, aggradational, stream-lake side settings). However, within the narrower context of nutrient-rich, mineral substrate wetlands, these groups may have had different evo-

lutionary and ecological centroids. Consider the study of Arens (1993), for example. She examined the palynofloras above and below 10 fusain (fossil charcoal) horizons, presumably the remains of wildfires, in the Westphalian B Joggins section of Nova Scotia. *Monoletes*, a prepollen grain produced by medullosan pteridosperms, was abundant only in sediments immediately above the fire horizons. In these cases, the medullosans were part of post-disturbance, colonizing vegetation, presumably in open, unshaded habitats. Comparing the known anatomical and morphological features of *Macroneuropteris scheuchzeri* and *Alethopteris* spp. with extant tropical pioneer trees, she found strong congruence, but also one marked difference—the large size of the seeds typical of the Pennsylvanian medullosans. Anecdotal observations in the field, however, have led many authors to speculate about the differences between *Alethopteris* and neuropterids, concluding that these lineages occupied different kinds of physical settings. Wnuk and Pfefferkorn (1984), for example, noted a separation of dominance of these two genera in the Westphalian D-aged Bernice Basin of Pennsylvania. They suggested that *Alethopteris* was generally the more xeromorphic of the two genera based on anatomical construction (Franks 1963, Reihman and Schabillion 1976). Working with late Pennsylvanian age coal-ball floras, Mickle and Rothwell (1982) found that either *Macroneuropteris-Neuropteris* or *Alethopteris* tended to be dominant in coal balls but not occur together in equal frequency. Unpublished data from the late Pennsylvanian of Texas corroborate these observations. *Macroneuropteris scheuchzeri* and *Alethopteris zeilleri* both may occur in shales associated with organic accumulations, but *M. scheuchzeri* is widespread, abundant, and mainly restricted to organic-rich beds, whereas *A. zeilleri* is abundant only locally and tends to occur in less organic-rich accumulations. Co-occurrence within deposits is minimal. Cuticular studies of *A. zeilleri* from several Stephanian/late Pennsylvanian areas of Western Europe reveal cuticles with upper surface hairs and stomata restricted to the lower surfaces of pinnules. On the basis of such cuticular data, Kerp and Barthel (1993) interpret this plant as mesophytic, growing on the margin of organic accumulating areas. Thus, although these two species may have overlapped within the overall species pool, there appears to be an average difference in their ecological centroids.

Cleal and Shute (1995) and Shute and Cleal

(2002) also argued for niche segregation among genera of the neuropterids, particularly *Neuropteris* s.s. and *Laveinopteris*, based on species abundances and patterns of turnover through geological time. They first found that species of *Neuropteris* s.s. and species of *Laveinopteris* do not appear to have been in competition for resources. The former genus, in which they identified 20 species, apparently favored open habitats where seeds could germinate in full sun, giving it a broad range of potential habitats. *Laveinopteris*, on the other hand, formed dense thickets where its seeds would have to germinate in relatively deep shade—more a “niche specialist”, in their terms, and in keeping with the identification of hydathodes in some species of this genus.

Such findings can be extended to the species level. Wnuk and Pfefferkorn (1984) note that *Macroneuropteris scheuchzeri* was likely a xeromorphic species (Schabillion and Reihman 1985), consistent with Arens (1993) inferences, and suggest that there were significant ecological differences among neuropterids. However, xeromorphy does not necessarily mean the lack of water in the environment. On the contrary, such plants may have grown in habitats with very wet substrates, presenting a different kind of physical stress; *M. scheuchzeri*, for example, had hydathodes (Schabillion and Reihman 1985), suggesting excessive water. Data from the latest Pennsylvanian of Texas corroborate this inference. Such data indicate that *M. scheuchzeri*, at this time and place, appears to have preferred and nearly monodominated organic shales that probably were mucks, formed in clastic swamps with low oxygenation. *Neuropteris ovata*, in comparison, at the same time and place (late Pennsylvanian, north-central Texas) is rarely found in organic shales, occurring in clayier lenses in association with *Pecopteris*, possibly bordering sluggish channels, or in more oxidizing channel deposits, uncommonly occurring in nearly monospecific assemblages in which *N. ovata* appears to have been the only tree present. *Neurodontopteris auriculata* is also an element of this same species pool, but occurs yet more rarely, its association extending into assemblages that include conifers and *Sphenopteridium* (sensu Mamay 1992, a probable seed plant characteristic of moisture-stressed habitats of the Mississippian, rediscovered by Mamay in late Pennsylvanian and Early Permian seasonally dry floodplain floras) both xeromorphic groups, suggesting that *N. auriculata* was the medullosan

most tolerant of moisture stress, at least in these landscapes.

At much larger scales of analysis, patterns of medullosan diversity and species turnover can reveal broad trends in ecological tolerance. Cleal and Shute (1995) is an exemplar of such a study. After extensive reassessment of neuropterid taxonomy and stratigraphic distribution, they were able to use the refined systematic database to examine diversity patterns and possible paleoecological controls on diversity. Looking mainly at species from Western Europe, Cleal and Shute found that neuropterids show marked correlated changes in diversity corresponding to inferred broad-scale climatic changes in the Pennsylvanian tropical lowlands (Phillips and Peppers 1984, Gastaldo et al. 1996, Cleal et al. 1999). Species of *Neuropteris* s.s., in particular, were restricted to the wetter intervals. With the initial onset of long-term drier tropical conditions, neuropterids with flexuous veins begin to appear, ultimately leading phylogenetically to forms with reticulate venation (*Reticulopteris*). Similarly, in *Laveineopteris* there is a change in the predominant species at the points of climatic transition, although the most common late middle Pennsylvanian species, *L. rarinervis*, shows no response to such inferred changes in climate. *Macroneuropteris*, a genus with only four reported species, only two of which are well known, also seems robust to macroclimatic changes, possibly because the entire species group had similar ecological tolerances. The genus *Paripteris*, which Laveine (1997) assigns to the Perispermaceae, also undergoes a marked change in species representation at the initial onset of widespread climatic changes at the early-middle Pennsylvanian transition; the newly appearing species go extinct with the presumed return of wetter conditions in the later part of the middle Pennsylvanian, giving rise to a reticulate veined form, *Linopteris* (the foliage of the stem genus, *Sutcliffia*), which is common through the climatic changes of the middle-late Pennsylvanian boundary and into the late Pennsylvanian (Stephanian). Finally, the species of *Neuraethopteris* appear to have been strongly confined to wetter conditions and disappeared with the onset of climatic drying.

In light of these patterns, Cleal and Shute (1995) also noted that “climate” per se may not be the sole arbiter of such diversity trends. Correctly, it seems to us, they note that climate will interact with topographic factors, exacerbating the effects of landscape heterogeneity. It might

be speculated that changes in regional patterns of moisture distribution, particularly drying, could have affected the ability of populations to maintain both critical size and spatial continuity, which may be the key to many of the species extinctions. Species that survive and transgress times of major environmental change, *L. rarinervis* and *M. scheuchzeri* for example, are strongly associated with organic accumulating, swampy conditions, and occur both in wet clastic substrate and wet peat substrate habitats. These broad, catholic distributions in wetlands may have buffered them against the regional wetting and drying trends in the later middle Pennsylvanian. Similar patterns are found in the survival patterns of tree ferns and other wetland plants from the Carboniferous into the Permian, where the “Carboniferous” taxa survive well into the Early Permian in “wetspots” within the drier landscape (Kerp 1996, 2000; DiMichele et al., 2006).

Inferring medullosan environments of growth. Although primarily plants of wetlands, medullosans also appear to have grown in habitats with some seasonal water limitation. Linking morphology to physiology is often ambiguous, however, and the determination of ancient habitats of growth should be made with caution from morphology alone. For example, reticulate venation has been suggested to enhance physiological functioning under water-limited conditions, and appears in parallel in several groups of medullosans. Yet, sedimentology and other aspects of anatomy conflict with this generalization for some species. For example, the reticulate-veined *Reticulopteris muensteri* also has hydathode-like structures (Reihman and Schabillion 1978), anatomical modifications of leaf vein endings that permit water to be exuded without transpiration. Hydathodes occur in plants that grow under conditions of high soil moisture and low transpiration and, thus, help to keep water moving through the plant. Zodrow and Cleal (1993) argued that the reticulate venation of *R. muensteri* places it ecologically in slightly drier parts of floodplains. However, Willard et al. (1995) identified pinnules with venation similar to *R. muensteri* in dark organic shales immediately above the Springfield Coal bed, Westphalian D of Indiana, interpreted as standing-water clastic swamps, and suggesting growth of this species in water saturated soils. Phillips and DiMichele (1998) identified (incorrectly as *Reticulopteris*) *Linopteris* in a thin coal, also above the Springfield Coal bed, in association with the

uncommon petrified medullosan stem *Sutcliffia*, raising the possibility that reticulate veins are not necessarily a sign of serious water limitation in these plants either. On the other hand, the reticulate-veined *Barthleopteris germarii* lacks hydathodes and has cuticular morphology (papillate stomata and glandular trichomes) that led Krings and Kerp (1998) to place it in periodically water-limited environments.

As an aside, reticulate veins also have been a source of taxonomic confusion, only recently clarified by cuticular analysis. *Reticulopteris muensteri*, for example, is the only species of the genus and, through cuticular analysis, shows clear affinities with *Neuropteris* of the *N. genuina* lineage (Zodrow and Cleal 1993). *Barthleopteris germarii*, originally described as a species of *Reticulopteris*, has cuticular morphology that places it closest to *Neurocallipteris* (Zodrow and Cleal 1993).

Hydathodes have been described in a number of different pteridosperms, including *Laveineopteris rarineris* (Oestry-Stidd 1979), *Macroneuropteris scheuchzeri* (Schabillon and Reihman 1985), *Lescuropteris genuina* (Krings and Kerp 1997), *Mariopteris occidentalis* (Krings et al. 2001), as well as *Reticulopteris muensteri*. These structures do not appear to be unambiguous indicators of high soil moisture, however, and need to be interpreted in light of plant habit and likely conditions of growth. *Lescuropteris genuina* and *M. occidentalis*, for example, are interpreted as climbers, plants that generally grow under conditions of high insolation and thus water stress. Hydathodes in *M. scheuchzeri* are consistent with its growth in swampy settings, especially in the later Pennsylvanian where it has been identified as a dominant element in organic shales and coals of the latest Pennsylvanian in Texas (Phillips et al. 1985, DiMichele, unpublished data). Yet, Schabillon and Reihman (1985) argued, in apparent contradiction with their recognition of hydathodes in the species, that *M. scheuchzeri* had xeromorphic leaf anatomy. *Macroneuropteris scheuchzeri* has a long stratigraphic history and may have varied considerably in its habitat preferences during that time. There do appear to have been changes in size, in the density of leaf hairs, diminishing over time, and in the shape of the pinule base. Perhaps this "species" is, in fact, a complex of closely related species not easily differentiable from leaf morphology alone (Darrah 1969).

Growth habits and ecology of the Pennsylvanian Lyginopteridaceae. Early Westphalian coal-ball specimens of *Lyginopteris* helped provide the concept of the "seed fern." Oliver and Scott (1904), using permineralized specimens, demonstrated the common taxonomic affinities of the seed *Lagenostoma lomaxii*, the stem *Lyginodendron*, and foliage of this plant, which, in adpression, had been attributed to the forked and highly divided, "fern-like" fronds *Lyginopteris* (*Sphenopteris*) *hoeninghausii*. Other genera referred to this family include the following plants all largely circumscribed on the basis of anatomical preservation: *Rhetinangium arberi*, *Heterangium* spp., *Schopfiastrum decussatum*, and *Microspermopteris aphylla*. All are believed to bear small fronds (up to 1 m in length, but perhaps ≤ 30 cm in some species: Gastaldo 1988) with finely dissected foliage of the *Eusphenopteris* or *Lyginopteris* type, bear small seeds (≤ 5 mm), have various configurations of sclerenchymatous plates of small diameter in the cortical tissues, and monostelic stems. These plants are frequently preserved as charcoal in coal-ball permineralizations, far more frequently than would be expected given their generally small biomass in coal-ball assemblages.

Lyginopteris, the basis of the Lyginopteridaceae, is considered to have been a facultative climber (Fig. 1), based on a wide range of evidence. The plant may have been one of the more robust Carboniferous plants with such habit, its stem commonly reaching 3.0–4.5 cm in diameter but bearing relatively small fronds. Biomechanical analysis suggests that the stem was not self-supporting (Speck 1994), which is consistent with the generally low abundance but wide occurrence of the plant. Its habit was probably shrub-like to scrambling where trees were lacking, perhaps forming thickets (Gastaldo et al. 2004). Because of the distinctive anatomy and morphology of the stems and fronds, *Lyginopteris* fossils are identifiable in both adpression and permineralized modes. In the classic study of Oliver and Scott (1904), *Lyginopteris oldhamia* was correlated with *Lyginopteris* (*Sphenopteris*) *hoeninghausii* partially on the basis of distinctive capitate secretory glands on the stem, frond, and seed cupule. These glands both aided in recognition of the whole plant assemblage and raised questions about the gland functions as animal deterrents, attractants, or satiation substitutes (Phillips 1981, Krings et al. 2003a).

Lyginopteris was an important plant in both peat-forming habitats and in clastic wetland en-

vironments in the late Mississippian and early Pennsylvanian of Europe, where it is most common in clastic environments associated with marine bands (e.g., Evans et al. 2003). It was long thought not to be present in American floras. However, it was reported and figured in compressions by Gillespie and Pfefferkorn (1979) and Blake et al. (2002), and anatomical studies have found it and closely related forms to be present as early as the Upper Mississippian/lower Namurian A, in deposits from Arkansas (Tomescu et al. 2001, Dunn et al. 2003a). It also occurs in coal-ball deposits from a Westphalian A (Langsettian) coal of Alabama (Winston and Phillips 1991). Gastaldo et al. (2004) found *Lyginopteris hoeninghausii* to be very abundant to dominant locally in an *in situ*, spatially preserved, drowned, swamp forest of early Pennsylvanian age in Alabama. As with others, these authors inferred *Lyginopteris* to be a climber or ground cover, probably a thicket-forming plant, widespread but most abundant in areas where the sparseness of trees suggested high light availability, paralleling the abundance of vines and ground cover in modern forests.

Lyginopteris is a more common and abundant component of Westphalian A/Langsettian adpression floras, representing the wide array of floodbasin habitats, than it is in peat-forming environments, represented by coal balls. The coal-ball distribution of *Lyginopteris oldhamia* is quite variable among the coal-ball collections from England and Belgium, being most abundant at the famous Shore locality in the Lancashire coal field but much less conspicuous at other heavily collected sites in the same coal bed (Phillips et al. 1985). In the American coal-ball deposit from Alabama (Winston and Phillips 1991) *Lyginopteris* is common but not particularly abundant, accounting for about 1.5% of the total peat biomass. The plant may be most abundant in ecotonal areas where nutrient levels were higher than in subenvironments with long periods of standing water. For example, Phillips (1981) noted the highest abundance of *Lyginopteris* (9% of biomass) in the Katharina seam of the Ruhr, where the lycopsid *Paralycopodites brevifolius* was abundant. This was the highest reported stratigraphic occurrence of *Lyginopteris* in coal balls.

Patteisky (1957) developed a detailed biostratigraphic zonation for *Lyginopteris* from goniatite zones from the Visean up into the Westphalian B in Western Europe. The sudden extinction of *Lyginopteris* across all Euramerica

near the Westphalian A-B boundary suggests some kind of complex ecological cause, possibly the conjunction of several things, for demise of such a cosmopolitan genus.

Schopfiastrum decussatum (Rothwell and Taylor 1972, Stidd and Phillips 1973) is very likely a climber. It consists of small diameter (3 cm or less), woody stems that bear relatively large petioles, inferred from their diameters in permineralized specimens, with some similarities to *Mariopteris* according to Stidd and Phillips (1973). The fronds are borne alternately and distichously. The stem cortex contains radially elongated, longitudinal sclerenchyma bundles, giving the stem strength but flexibility, typical of plants with climbing habit. *Schopfiastrum decussatum* is known from the middle Pennsylvanian of North America. The plant is almost identical anatomically and in general foliage morphology to *Rhetinangium arberi*, which was described from the Namurian of Britain (Gordon 1912). However, the latter plant bears its fronds helically rather than in a decussate manner.

Microspermopteris is a small lyginopterid pteridosperm that spans most of the Westphalian (lower and middle Pennsylvanian). It is known exclusively from coal balls (Pigg et al. 1986). Anatomically, the plant is most similar to *Heterangium*. However, the maximum known stem diameters are only about 1 cm and stems have proven to be highly sinuous. The frond of the plant appears to bear foliage most similar in form to the genus *Sphenopteris*, but with a uniform internal histology, lacking differentiation into palisade and spongy mesophyll. Scattered resinous cells may be present within the laminate portions of the foliage. Fronds do not fork, which is unusual in the lyginopterids. Overall, the growth habit appears to be that of a gracile vine or scrambling ground cover. Pigg et al. (1986) suggest that the small seeds *Conostoma villosum*, which have conspicuous integumentary flanges and trichomes, similar to such features found on *Microspermopteris* stems, may belong to these stems. Lack of attached reproductive organs, or regular association with any particular seeds or pollen organs, suggests infrequent reproduction, possibly confined to specialized environmental conditions. The plant may have mainly spread by vegetative propagation, typical of a vine or scrambler.

Heterangium is another of the small, probable climbing or scrambling lyginopterids known exclusively from anatomical, coal-ball preservation. Numerous species have been described

(Pigg et al. 1987), the oldest from the mid-Mississippian. Plants are often found preserved as fossil charcoal, suggesting that these species, much like other small climbers or ground cover, occupied environments frequently swept by fires. *Sphenopteris obtusiloba* has been described as the foliage of *Heterangium americanum* (Shadle and Stidd 1975) and *Rhodeopteridium* (as *Rhodea*) has been reported from a Mississippian species of *Heterangium* (Jennings 1976).

The Mariopteridaceae: climbing and thicket-forming habit. The Mariopteridaceae is a putative family of pteridosperms all of which appear to have had climbing habits (Krings et al. 2003b). Plants of this group are known from adpression preservation and have not been well documented anatomically, although *Mariopteris* has been reported as the foliage of the vine-like *Schopfiastrum* (Stidd and Phillips 1973), consistent with the inferred habits of these plants. Included are the genera *Mariopteris*, *Karinopteris*, *Pseudomariopteris*, and *Helenopteris*. The strong morphological similarities among these plants indicate close phylogenetic relationships and their climbing habit can be seen as an example of phylogenetic/historical constraints on ecology. The species that have been identified as climbers use small hooks on the ends of lateral pinnae or the undersides of fronds to attach themselves to each other or to other plants, creating thickets or climbing on the organs of other plants. Most of the species exhibiting these features are geographically and/or stratigraphically restricted in their distributions. One species, *Pseudomariopteris busquetii*, has been found to bear small, platyspermic seeds on the underside of fronds, which is similar to the disposition of seeds in the scrambling plant *Dicksonites* (*Callistophyton*). This suggests a relationship of the Mariopteriaceae and the Callistophytaceae, in the Callistophytales (Krings et al. 2001), assuming that the mariopterids actually are related as a monophyletic group.

Mariopteris is the largest genus of the family. Species in the genus initially were identified as having simple "spine-like prolongations" of the lateral pinnae (Boersma 1972), which, under closer scrutiny, have proven to bear small spines or hooks that facilitate attachment to other plants. For example, *M. occidentalis*, which is known mainly from the eastern and midwestern United States, reached its zenith of abundance during the middle Pennsylvanian in Oklahoma.

It is interpreted as a climber (Krings et al. 2001) based on small hooks on the lower/abaxial sides of the pinnae, a pattern that differs from all other known mariopteroids, which have climber hooks on apical extensions of the pinnae. The extensive distribution of these hooks probably means the plant climbed in dense vegetation or on delicate foliage, given the large number of small, widely dispersed hooks. In Oklahoma, *M. occidentalis* tends to occur alone in abundance on rock slabs and is not so common in mixed assemblages (DiMichele et al. 1991). It is possible that it formed thickets. Vein endings are thickened and may have functioned as hydathodes to help facilitate water flow in young fronds. These are very common in scrambling/climbing pteridosperms. This species also has low stomatal density, small stomatal apertures, and sunken guard cells, which also indicate water stress, typical of a vine (Krings et al. 2001). The widespread, middle Pennsylvanian species *Mariopteris muricata* was shown by Barthel (1962) to have numerous hairs on the upper surface of its leaf laminae, which could be considered to be in keeping with a xeromorphic, climbing or thicket-forming habit for members of this clade.

There are two species in the genus *Pseudomariopteris*, both of which appear to have been climbers or thicket formers, based on the presence of climber hooks (Fig. 6). *Pseudomariopteris busquetii* is known from the late Stephanian of France, the upper Rotliegend of Germany, and the latest Pennsylvanian/earliest Permian of north-central Texas, a restricted stratigraphic range overall. Krings et al. (2001) determined that the plant had a climbing habit based on stems 1.0–1.5 cm in diameter bearing forked fronds 15–30 cm in length. Such narrow stems and relatively large fronds suggest that the plants were not self-supporting. Support came from climber hooks borne on apical extensions of pinna axes. In addition to, or perhaps more likely than, climbing, plants of this species, as with most of the mariopterids, appear to have formed dense thickets in which the plants were mutually supporting. This interpretation is further borne out by observations of patchy dense accumulations of *Pseudomariopteris busquetii* in late Stephanian equivalent deposits from north-central Texas. In these deposits, *P. busquetii* is far and away the dominant species, raising questions of how such large, local biomass could be derived from climbing plants (climbing on what?). *Pseudomariopteris cordato-ovata* has small fronds with paired climber hooks at the

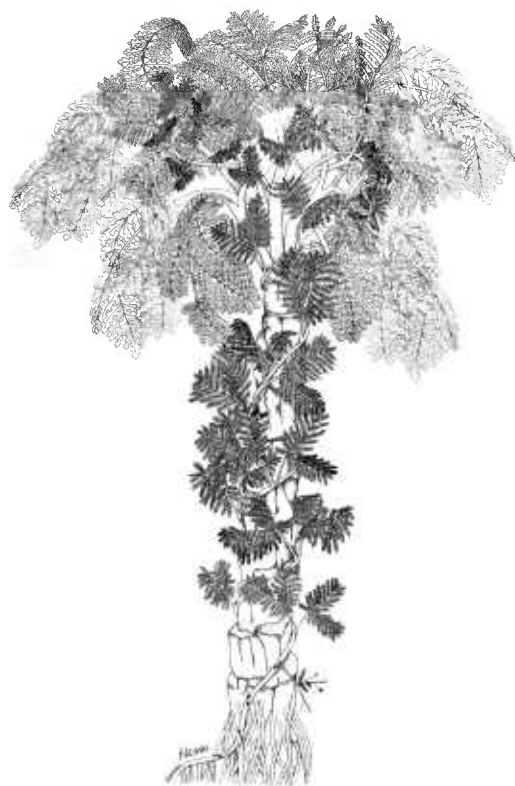


FIG. 6. *Pseudomariopteris busquetii*, a climbing or thicket forming plant, reconstructed here as climbing a medullosan pteridosperm with free-standing growth habit. Reprinted from Krings et al. (2001, Fig. 12) with permission from the Botanical Society of America.

end of spine-like prolongations of pinnae, and, thus, also appears to be a climber or thicket-former, like *P. busquetii* (Krings and Kerp 2000).

Krings and Kerp (2000) segregated the genus *Helenopteris* from *Pseudomariopteris*. Although the single species, *H. paleau* has not been found to have climber hooks, it has been interpreted as a climber/thicket-former on the basis of small stems bearing fronds with a maximum length of 20 cm, and on its clear phylogenetic affinity to other members of the mariopterid clade. The species has a restricted geographic distribution, found for certain only in the late Stephanian of central France.

Karinopteris follows the morphological and distributional patterns found in other members of the mariopterid group. Schultka (1995) reported *Karinopteris acuta* from the Namurian B of Germany, which is a very early occurrence of mariopterid climbing plants. The species appears to be a climber with many hooklets borne

on club-shaped tips of larger hooks. DiMichele et al. (1984) described a *Karinopteris* species from the Indiana “paper” coal that had small bifurcate fronds, perhaps as much as 25 cm in length, with robust hooks borne on the abaxial sides of pinna prolongations. Kerp and Barthel (1993) reexamined cuticles of this plant and determined that it was highly xeromorphic. Upper leaf surfaces were found to be hairy with thick cuticle and lacking in stomata, which were restricted to thinly cutinized lower leaf surfaces where they were likely sunken and overarched by papillae. The remains of these plants occur in dense accumulations in restricted deposits—the plant locally dominates the flora of the Indiana paper coal, which, again, might indicate formation of dense thickets in which the plants were hooked onto one another for support. The undescribed species appears to be both stratigraphically and geographically restricted.

A report of climber hooks in a plant described as *Eremopteris lincolniana* by White (1943; discussed in Krings et al. 2003b—likely not an *Eremopteris* according to C. J. Cleal, personal communication) suggests that this mode of climbing evolved in other lineages. The possibility of mariopteroid affinity for this plant also should be considered, given the unusual nature of the climber-hook morphology and its strong expression among this phylogenetically related group of plants (Gastaldo and Boersma 1983a, b).

Krings et al. (2003b) noted that this kind of climbing or thicket-forming habit, one facilitated by the presence of small numbers of small hooks, is most common today among angiosperm vines and lianas of medium to small stature that grow in areas of dense vegetational cover. A parallel ecomorphological syndrome was described for several adpression species of the small sphenopsid *Sphenophyllum* by Batenburg (1982), which bore hooks at the end of leaves and appear to have formed dense thickets. In either instance, pteridosperm or sphenophyll, the possibility has been raised of much denser ground cover on Pennsylvanian-age landscapes, particularly those of flood-basins with wet mineral soils, than is traditionally shown in reconstructions. Large areas of such landscapes may have been occupied by dense monospecific stands of plants with facultative thicket-forming to climbing growth habits—Paleozoic kudzu, paralleling the recent explosion of that plant throughout much of the southern United States



FIG. 7. *Callistophyton* sp., a scrambling ground-cover plant. Reprinted from Rothwell (1981, Fig. 1) with permission from Elsevier.

after its introduction from Asia for soil erosion control.

The ecology of *Callistophyton*. *Callistophyton* is the anatomically preserved equivalent of the addressed genus *Dicksonites*. Thanks to detailed anatomical studies, organs of the plant have been correlated and one of the best “whole plant” concepts of any Pennsylvanian plant has been developed (Rothwell 1981). Recently, Galtier and Béthoux (2002) have further refined understanding of the growth habit. There are two anatomically circumscribed species of *Callistophyton*, *C. boysettii*, from the middle Pennsylvanian and latest Pennsylvanian-earliest Permian of North America and Europe, and *C. poroxylodes* from the late Pennsylvanian of North America. In both instances, the plants have a scrambling to climbing habit and could form dense stands (Galtier and Béthoux 2002) (Fig. 1, 7). They bore bifurcate fronds to which the seeds, known as *Callospermation* in petrification, were attached abaxially to pinnules (Langiaux 1986). Seeds were on the smaller end of the pteridosperm range, 4–5 mm in length, which is still rather large when compared with many modern flowering plants. The seeds were borne in great abundance (Grand'Eury 1905). Bisaccate pollen, attributed to *Vesicaspora*, was produced in foliar borne synangia. It was delivered by wind to the ovules and captured by a pollination droplet. The male gametes were delivered to the eggs via a pollen tube, making this the earliest known occurrence of modern seed-

plant sperm delivery (Rothwell 1972). The overall aspect of this plant is one of an opportunist: wind pollination followed by the production of many, highly dispersible, small seeds, patchy, often dense occurrence within wetland landscapes, and frequent preservation as charcoal, as if growing in areas prone to fires. Species of the genus appear focused on the colonization of available physical space and thus the garnering of light and mineral resources by space expropriation.

Johnhallia, a possible relative of *Callistophyton*. *Johnhallia lacunosa* is a small pteridosperm (Stidd and Phillips 1982) similar in anatomical form to *Callistophyton* but differing sufficiently that the authors considered its relationships ambiguous and possibly distant. Stems are small (about 1 cm in diameter) and bear small fronds—the petiole bases are 2.5 mm in diameter. Foliage is delicate without internal cellular division into palisade and spongy mesophyll; it appears to be of the *Rhodeopteridium*/*Diplothemum*/*Palmatopteris* type, which is nearly non-laminate in form. Growth habit is not known. *Johnhallia lacunosa* is quite rare, although it may have been confused with *Callistophyton* and so under-reported. As with many of the small pteridosperms known from anatomical preservation in coal balls, specimens are often preserved as charcoal.

Peltasperms in Permian landscapes. The peltasperms are a group of pteridospermous plants that were thought to be largely Mesozoic in distribution until Kerp (1982) determined that the widespread and well known callipterids were associated with peltaspermous-type reproductive organs. Since that time, it has become increasingly appreciated that this was a diverse group with complex morphologies, widely distributed primarily in the Early Permian tropics and in the latest Early through Late Permian in the temperate regions (Naugolnykh and Kerp 1996, Naugolnykh 1999). These plants are known exclusively from foliar and reproductive adpressions. It can be supposed from the shapes, sizes, and epidermal features of the known organs that the plants assumed a variety of growth forms. At present, however, the growth habits of these plants are effectively unknown.

The peltasperms consist of several major plant groups: the callipterids (probably many undescribed forms, the best known being *Autunia* and *Rhachiphyllum*), the comioids (*Comia* and pos-

sibly one or more undescribed genera), the supaioids (*Supaia*, *Glenopteris*, *Compsopteris*, *Protoblechnum*, *Brongniartites*), and probably (and perhaps most controversially) the ‘American’ gigantopterids (as opposed to the forms described from the Cathaysian areas, sometimes under the same generic names) (*Gigantopteridium*, “*Cathaysiopteris*”, “*Zeilleropteris*”, *Evolsonia*, *Delnortea*, and *Lonesomia*). The taxonomy of these plants has been summarized in papers by several authors (Kerp 1988, Kerp and Haubold 1988, Naugolnykh 1999, Kerp et al. 2001, Krings et al. 2005, DiMichele et al. 2006).

Members of all these plant groups are abundant in the American southwest (Arizona, Kansas, New Mexico, Oklahoma, Texas), which may serve as a model for the basic aspects of their paleoecology; similar patterns have been identified in Europe (Kerp and Fichter 1985). In these environments, the fossils can be closely associated with depositional environments (Read and Mamay 1964, Nelson et al. 2001, Mack et al. 2002, 2003) and with associated indicators of paleoclimate, such as paleosols and geochemical estimates of temperature (White 1929, Mack et al. 1991, Tabor and Montañez 2004, 2005). Indicators of depositional environments place the plants mostly in streamside environments, with preservation occurring in small lakes, crevasse splays, or slack-water deposits in bars of actively flowing channels. Associated indicators of local climate consistently point to seasonality, often with the possibility of severe drought at times, indicated by calcic vertic paleosols, caliche paleosols, molds of evaporate crystals in plant-bearing mudstones, and associated evidence of strongly seasonal flow and surface exposure of deposits in plant-bearing channels and crevasse splays. Recent studies on paleotemperature patterns in the Early Permian of Texas and Oklahoma (Tabor and Montañez 2005), suggest that significant increases, of at least 10° C accompanied a shift from dominance of basinal wetlands by “Pennsylvanian” floras, rich in medullosan pteridosperms and marattialean tree ferns, to “Permian” floras, rich in peltasperms and conifers.

Detailed studies of European callipterids have found distinct environmental preferences for some species (Kerp 1988). *Autunia conferta*, for example, is commonly found in environments that are drier or better drained and only exceptionally in swampy deposits, such as dark organic shales. Morphological features of this species support this environmental inference (Kerp

1996). On the other hand, *Rhachiphyllum schenkii* (Kerp 1988) occurs in association with *Calamites gigas* on floodplains (Barthel 1976, Barthel and Roessler 1994, 1996). Other species appear to have been more strongly confined to better drained substrates.

Unfortunately, it has not been possible to make clear distinctions among most of the major peltasperm lineages as regards particular environmental tolerances or ecological centroids, which would be related to growth habits as well as intrinsic physiological differences. The callipterids are the most widespread of this group of plants. The full range of species diversity in this group has yet to be fully understood and the pattern of broad geographic and environmental occurrence seems to reflect several species and genera (Kerp and Haubold 1988) with slightly different environmental tolerances. The American gigantopterids, on the other hand, are relatively rare, occurring generally in low abundance, even if widely distributed. Furthermore, the dominant genera of this clade have only limited spatio-temporal overlap, suggesting possible environmental differences or replacements in time-space through background extinction and evolution. The comioids illustrate a pattern similar to the gigantopterids—there are at least three forms in the southwestern U.S.A. that are complementary in space and time.

Some of the more peculiar patterns of occurrence are to be found among the supaioids. For example, in the Abo Formation of New Mexico, deposits have been found that are uniformly monotypically dominated by *Supaia thinnfeldioides* through several meters of crevasse-splay sandstones, suggesting large areas of seasonally flooded forests occupied nearly entirely by one species of peltasperm. Yet, in other parts of the southwest, such deposits have not been seen, and *Supaia*, in general, does seem to be concentrated in its ecological dominance to the farthest western parts of the Early Permian tropical region. The distinct spatial distribution in North America of such plants as *Supaia* and *Glenopteris*, proposed by Read and Mamay (1964), has not proven to be as robust as originally proposed, particularly for *Supaia*, which more recently has been reported from the Permian in widely separated parts of the world (e.g., Wang 1997). However, when viewed globally, there are centers of distribution of these plants, at least as their taxonomy is presently understood. *Protoblechnum*, for example, is best known from China (Halle 1927, Sun et al. 1999), whereas

Naugolnykh (1999) has argued that *Compsopteris* is restricted to the Angaran floral realm, and *Glenopteris* (Sellards 1900) is largely confined to Kansas, with some questionable occurrences in surrounding states (Krings et al. 2005). These genera are quite similar in many aspects of their morphology and taxonomic refinements are needed to work out the biogeographic patterns. Such refinements may reveal that apparent regional differences are, in fact, a consequence of poorly understood taxonomy.

In summary, the peltasperms appear to have escaped restriction to wetland environments and to have undergone a significant morphological radiation in seasonally dry environments during the Early Permian. The initial phases of this radiation appear to have begun in the late Pennsylvanian, based on reports of callipterids from that time (Remy 1975 and Remy et al. 1980, reported "*Callipteris*" *flabellifera* from the Stanton Limestone of Kansas, which is considered to be late Pennsylvanian in age on the basis of marine fossils), interestingly in association with primitive conifers. The tolerance of seasonal drought may have been a key factor in permitting elements of this group to move into, and become ecologically significant components of, higher latitude, temperate environments subject to light and temperature seasonality. Many of the important genera were first described from high-latitude Late Permian assemblages and only later were discovered to be abundant in Early Permian tropical habitats.

Pteridosperms, Ecology and Evolution.

The evolution of innovation in pteridosperms follows a pattern that has become increasingly apparent in studies of the relationship between Paleozoic terrestrial plants and what, for lack of a better descriptor, might be termed "landscape position." It appears that speciation, particularly of a magnitude that leads to major new body plans, what has been termed "saltational" evolution (Bateman and DiMichele 1994b), is most likely to occur in environments that are resource undersaturated. In such settings, there are opportunities for survival of radically new forms because of reduced incumbent advantage (Valentine 1980, Gilinsky and Bambach 1987)—if plants are already present in such settings, it is probable that resources remain for exploitation by new innovations. Even though it might be expected that survival of novel morphologies will be low in any kind of environment, due to anything from exceedingly slow increases in

population size, developmental instabilities, random walk to extinction in small founder populations, etc., the potential for survival may be orders of magnitude higher, even if still quite low, in such "empty" habitats. Once a radiation takes place on some body-plan theme, resource saturation is expected to increase and the potential for the survival of innovations will decrease significantly (Valentine 1980).

Early land plants appear to have accrued morphological complexity only gradually, radiating extensively once some critical level of complexity and associated developmental control was attained (Knoll et al. 1984, DiMichele and Bateman 1996). Once major morphological changes were possible, however, plants began a morphological radiation in the Middle Devonian that led to the emplacement of all major body plans by the end of the Devonian or perhaps into the earliest Mississippian (DiMichele et al. 2001). During this radiation, major clades partitioned the terrestrial habitat, with the seed plants and the ferns becoming most prominent in terra firma settings. Of the Late Devonian through Permian seed plants, as demonstrated by the phylogenetic analysis of Hilton and Bateman (this volume), nearly all can be considered part of the paraphyletic pteridosperm ("seed fern") clade, especially during the Mississippian.

The signature pattern for evolution of new pteridosperm families and genera is the appearance of new forms in disturbed and extrabasinal areas. During the early Mississippian (Tournaisian) for example, pteridosperms are both abundant and diverse elements in highly disturbed landscapes where preservation was made possible, perhaps, only because of associated volcanism, giving us a look at vegetation types we might not ordinarily see (e.g., Scott et al. 1984, Galtier et al. 1988, Bateman and Scott 1990, Bateman 1991). Early ferns follow a similar pattern, appearing in highly disturbed environments (Scott and Galtier 1985), thus settings with constant areas of resources available to species with opportunistic life histories. Equally interesting is the appearance of larger, somewhat more "K-selected" tree pteridosperms at this same time, appearing as isolated pieces of wood potentially transported from more remote, extrabasinal settings (Galtier 1992). Evidence of deeply rooted paleosols as early as the Late Devonian (Algeo et al. 2001) also suggests that some lineages were evolving the potential to escape from the heavily populated wet lowland habitats, so abundantly preserved in the terrestrial fossil record.

By the Pennsylvanian, the record of pteridosperms was mostly that of lowland wetlands. We can only speculate about the origin of the diverse groups of pteridosperms that populated these environments because extrabasinal floras are rare. It is possible that many, such as the medullosans, originated in what were initially resource undersaturated habitats during the late Mississippian, or by exploitation of life roles that permitted resources to be exploited in novel ways, such as through the evolution of climbing habit, which appears to be ancestral in this group (Dunn et al. 2003b). Subsequent evolution reflects the carving up of portions of the lowland wetlands, which were the environments in which the model pteridosperms, the medullosans and lyginopterids, reached their zenith.

There is, however, evidence that evolution continued in seasonally dry, physically stressful marginal areas and that such areas also may have harbored elements of much older pteridosperm lineages, serving as refugia, as the tropical areas became increasingly suitable for plants tolerant of moist climates. Consider, for example, the genus *Sphenopteridium*, which has been attributed to some of the larger early arborescent pteridosperms. Characteristic of the Mississippian, it occurs then in plant associations that evidence seasonal climates and moisture deficits. This genus appears to jump over most of the fossil record of the Pennsylvanian tropics, to reappear late in the Pennsylvanian in isolated assemblages, and continue into the Early Permian as a component of floras rich in conifers and peltasperms, typical of warm, seasonally moisture-limited environments (Mamay 1992).

The transition between the Pennsylvanian and Permian, in the tropical realm, is an extended one. The intercalation of floras typical of ever to mostly wet climates with those of seasonally dry climates begins in a small way as far back as the late Middle Pennsylvanian, and is detectable through such robust plants as conifers, whose foliage could survive transport and thus give evidence of their presence in the hinterlands long before they appeared in the lowlands as part of autochthonous or parautochthonous assemblages (Lyons and Darrah 1989). Although floras typical of on-average wetter and drier climatic regimes are intercalated during the late Pennsylvanian, and even into the earliest Permian, they exchange few species, and then primarily those of streamside wet habitats, such as sphenopsids and opportunistic/weedy tree ferns

(Broutin et al. 1990, DiMichele and Aronson 1992).

With the advent of seasonal climate regimes in the western tropical belt during the latest Pennsylvanian and Early Permian, the flora underwent dramatic changes. However, the plants that dominated the newly appearing landscapes did not occur as gradual invaders, displacing the Pennsylvanian elements from increasingly restricted wet sites. Rather, the change was one of wholesale biome replacement—plants track climate in groups, reflecting the discontinuities in climatic conditions (Ziegler 1990). As a result, a new flora became emplaced in the depositional basins of the tropics, one rich in such pteridosperm groups as peltasperms, which harbored enormous diversity. The peltasperms are among many lineages thought to have been exclusively Mesozoic in distribution, but which have since been discovered to have Permian ancestry (Kerp 1988). This pattern, now found for a number of lineages, suggests that considerable body-plan level macroevolution was taking place in remote, extrabasinal areas (Broutin et al. 1986, Kerp 1996, 2000; DiMichele et al. 2001), where resource underutilization may well have been the key to evolutionary opportunity. It is the taxa that evolved in these remote areas, and that appeared “fully formed” when climatic conditions changed and allowed them to occupy the lowlands, that persisted into the Mesozoic to become significant elements of those floras.

Although the pteridosperms are good indicators of this basic spatial evolutionary model, it does appear to be generalizable to seed plants, and probably ferns. The patterns become more muddled in the later Mesozoic as the diversity of land floras explodes with the advent of the angiosperms. Thus, these ancient lineages, in the less diverse world of the Paleozoic, may be among the clearest indicators of some of the basic relationships between plant evolution and the physical environment.

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