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The ecology of Paleozoic ferns

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Abstract

Ferns or fern-like plants have been important elements of terrestrial vegetation since the Late Devonian. *Rhacophyton*, a fern-like plant of the Late Devonian, appears to have been a colonizer of wet substrates, often forming large, nearly monotypic stands in peat-accumulating swamps. The earliest true ferns have been found in environments with high levels of disturbance, often fire, which suggest opportunistic, colonizing life histories, consistent with small, scrambling body plans. During the Early Carboniferous all major body plans and life histories of ferns appear, including scrambling ground cover, tree habit, and lianas. These ecological roles are distributed across several major lineages, including the Zygopteridales, Filicales, and Marattiales, plus some fern-like groups of uncertain affinity, and disappear and reappear independently within these groups. Until the Stephanian, the later part of the Late Carboniferous, ferns largely were confined to secondary ecological roles: colonists, understory vegetation, small vines. Beginning in the latter part of the Westphalian and expanding dramatically in the Stephanian, marattialean tree ferns became the dominant trees of tropical lowland, wetland forests. This dominance continued locally into the Permian in wetter parts of the landscape. The Paleozoic ferns suffered major extinctions at several times, beginning in the Late Carboniferous. By the Permian, new lineages were appearing, some of which would persist into and become dominant vegetational components during the Mesozoic. Among these lineages virtually all of the life histories and body plans that characterized Paleozoic ferns would reappear independently, plus some new kinds of organization and ecology, emphasizing the great evolutionary flexibility and responsiveness of fern-like construction and reproductive biology.

Keywords: ferns; Paleozoic; ecology; paleoecology; evolution

1. Introduction

Ferns are an ancient lineage of vascular plants. The first bone fide ferns appeared in the early Early Carboniferous, with fern-like plants occurring even earlier in the Late Devonian. As such, ferns are the last Class or body-plan clade of vascular plants to appear in the Devonian–Carboniferous radiation (DiMichele et al., 2001). Ferns are among the most recognizable groups to nonspecialists. In detail, however, the taxonomic circumscription of ferns is not such a simple task, especially during their early evolutionary history. Most of the characters shared by and considered to be uniquely characteristic of ferns are, in fact, primitive characteristics retained from their morphologically simple trimerophyte ancestors. Nearly all ferns are homosporous and free-spor-

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ing, with consequent independent and free-living sporophyte and gametophyte life history phases, and have only primary bodies composed of large, compound (megaphyllous) leaves with circinate vernation, foliar borne sporangia, and adventitious roots. Most ferns have siphonostelic stems that produce stelar gaps in association with leaf-trace production; late Paleozoic small ferns were largely protostelic and thus lacked leaf gaps. This kind of reproduction and structure has been referred to by Scheckler (1986b) as 'fern biology'. Many of the groups traditionally treated as ferns may be independent, Late Devonian derivatives of the trimerophytes (Galtier and Scott, 1985), sharing the basic characters of massive spore production, clonal reproduction, and large leaves with stem-like developmental aspects (Rothwell, 1999). As such, the concept of 'fern' is an organizational grade based on common morphological attributes.

In this essay, we consider the ecological history of Paleozoic ferns. In so doing, we have accepted the broad definition of 'fern biology' referred to above. The ferns have an extensive fossil record, which includes excellent examples of both anatomy and gross morphology. However, nearly all fossils are simply fragmentary remains, preserving only a portion of the plant body, often without clear connection between reproductive and vegetative organs. Furthermore, the rarity of such forms in adpression preservation suggests a strong preservational bias against small, surface-creeping growth habits, unless the plants formed extensive clones; coal balls are an exception because they preserve plants in situ. Structural preservation has played an inordinately important role in deciphering the biology of many fossil ferns, given its relative rarity, because it reveals subtle details of growth and reproduction. The fern fossil record, particularly from the Paleozoic and Mesozoic, shares a common taphonomic megabias with other fossil floras of these times – plants from basinal wetlands are by far the most likely to be preserved in the fossil record, screening from us much evolutionary innovation that may have taken place in the more demanding, environmentally extreme areas of the ancient extrabasinal lowlands and basin-margin uplands.

The ecology of fossil ferns can be elusive, especially at the species level. The bulk of the literature on fossil ferns is concerned with systematics and morphology, rather than the environmental context needed to infer many aspects of paleoecology. Ecology can be deduced from some aspects of functional morphology, although due caution must be exercised. An understanding of fern paleoecology is derived largely from floristic or diversity studies focused on a larger spectrum of plant groups (e.g., Scott, 1978; Pfefferkorn and Thomson, 1982; Lesnikowska, 1989; Pryor, 1993; Lyons et al., 1997). Studies of modern ferns include more information and, while most focus on systematics and morphology, provide more complete understanding of growth architecture and the timing of various growth and reproductive events. Ecological patterns also have been the explicit focus of some studies (e.g., Page, 1979) and appear as observations in many systematics papers. In addition, the modern record informs us of the complex chemical controls on many aspects of homosporous fern reproduction not accessible to studies of fossils.

Our examination will emphasize, for the most part, ecological patterns at the species level, with a focus on growth architecture, habitat preferences, and strategies permitting successful growth and reproduction. Where appropriate, we will consider the dynamics of fern-dominated communities. We will not consider the role of ferns in the biostratigraphy of Paleozoic terrestrial rocks, although they are important in this capacity (e.g., Zodrow and Cleal, 1985; Wagner and Winkler Prins, 1991; Cleal, 1997). There are several generalities that can be drawn from this review. Ferns have ventured into most ecological roles, from ground cover, to epiphytes, to forest trees, have grown in most kinds of habitats, from fire swept, to swampy, to xeric, and have exploited resources with a range of life-history strategies, from opportunists to resource accumulators. These roles have recurred throughout geological time, evolving independently in many different lineages. There are very few extinct fern ecologies, although there may be some when examined in terms of the scale at which a particular life form dominates the landscape.

2. The early ferns

The earliest fern or fern-like plant is *Ellesmeris sphenopteroides* (Hill et al., 1997) from the Late Devonian (Frasnian) of the high Arctic. It is zygopterid-like with laminate pinnules; however, its ecology is not well understood. Better known ecologically is the related *Rhacophyton ceratangium*, known from the Late Devonian and earliest Early Carboniferous (Andrews and Phillips, 1968; Cornet et al., 1976). We do not include the Cladoxylales in this discussion because of the confusion this introduces regarding the nature of true ferns. *Rhacophyton* was a shrub or subtree that lacked laminate foliage but bore some determinate lateral branches that terminated in a dense mass of dichotomies, forming a light intercepting surface. Chaloner (1999) proposed that the development of such laminate foliage may be related to the global decline of CO_2 in the Late Devonian (Berner, 1998), favoring morphologies more conducive to CO_2 diffusion. *Rhacophyton* had typical fern biology: massive production of isospores, possibly clonal growth (Scheckler, 1986b), and frond-like branch systems as the major organs of the plant. *Rhacophyton* appears to have been the sole to overwhelmingly dominant plant in swampy, coastal lowland environments of the southeastern United States, where its organic remains formed thin coals. The plant was not confined to this habitat, however, but also was an element of low diversity, mixed communities on better drained substrates (Scheckler, 1986a,b). During the Late Devonian, species diversity in the subtropics, from which the plant is known, was low providing only a small number of taxa for landscape development, which possibly permitted a species to play a variety of ecological roles. This was a time of origin of the major body plans of vascular plants and the ecological centroids that would characterize these major groups during the Carboniferous when they were still being sorted out (DiMichele and Bateman, 1996; DiMichele et al., 2001).

A great variety of plants recognizable as ferns by their gross morphology made their first appearance in the Early Carboniferous. They belong to three major groups, the early filicaleans, the zygopterids, an extinct group, and the marattialeans. Almost all of these plants were homosporous, small, prostrate, clonal forms often described as 'sprawling' or 'rampant' (Phillips, 1974; Galtier and Holmes, 1982; Galtier and Phillips, 1996; Scott and Galtier, 1996), except the Marattiales. The known early marattialean stems indicate that they were arborescent forms (Goodlet, 1957; Remy and Remy, 1977; DiMichele and Phillips, 1977) of relatively small stature compared to later Carboniferous species. Upright, possibly small tree stature has been described for the Visean age *Australoclepsis australis*, made possible by a false stem made up of many smaller stems (Sahni, 1928). The small ferns appear to have occupied a wide range of physical conditions where they most often grew as opportunists in disturbed environments (Scott and Galtier, 1996). Many ferns, such as the filicalean *Botryopteris antiqua*, were common and cosmopolitan, and are well known from anatomical preservation in permineralized peats (Rex, 1986; Scott and Galtier, 1996). The zygopterid, *Clepsydropsis*, seems to have preferred alluvial and lagoonal settings where water tables were high but peat accumulation was minimal (Scott et al., 1984; Scott and Galtier, 1985). At the other extreme from these wetter sites, ferns of the later Early Carboniferous appear to have been well established in harsh environments, frequently disturbed and often fire-prone, where they are anatomically preserved as charcoal or occur in regular association with charcoal. Prominent in these settings were the zygopterids *Diplolabis* and *Metaclepsydropsis* (Scott and Rex, 1987; Rex and Scott, 1987). Many of these fire-prone habitats are associated with volcanic activity and the nature and quality of the substrates may have been very patchy. Scott and Galtier (1985) suggested such fire-swept environments were a major selective force in the early history of ferns, and helped hone opportunistic life histories. Certainly, ferns remain important colonizers of landscapes disturbed by fires and volcanic activity, and often are among the first plants to reappear in these kinds of habitats following catastrophic disturbance (Burnham and Spicer, 1986; Retallack, 1992). Within

Early Carboniferous, subtropical habitats, from which these patterns are known, fern abundances were highly variable, strongly suggesting patchy distributions. Similarly, the correlation between specific habitats and fern floras is weak because of the generally low abundance of ferns, although the most consistently high abundances and co-occurrences are with pteridosperms (seed ferns) in wet flood-plain environments (Scott et al., 1984).

3. Late Carboniferous and Permian ferns

3.1. Small ferns

3.1.1. Small-fern diversification

The small ferns underwent three major radiations (Rothwell, 1987). The first, near the Devonian–Lower Carboniferous boundary generated a number of families that did not survive the Paleozoic. The oldest families were in the Zygopteridales, with architecture, anatomy and reproductive organs distinct from those of the filicalean ferns. Most of the other forms are clearly identifiable as filicalean, including Botryopteridaceae, Psalixochlaenaceae, Anachoropteridaceae, and Tedeleaceae. A second filicalean radiation took place in the Permian, and generated a number of families that would rise to prominence in the Mesozoic, all apparently derived from the earlier filicalean forms. Many of the features of modern ferns, now considered advanced, evolved within the primitive filicalean families, and may have evolved more than once, independently in several of the lineages (Galtier and Phillips, 1996). It appears fairly certain that laminate foliage evolved independently in a number of fern groups, although the stem–leaf appendicular relationship is plesiomorphic (Phillips, 1974). As a consequence of the basic flexibility of their life history and simple growth architecture, Paleozoic ferns became members of plant communities in a broad array of habitats. Appreciation of this is somewhat limited by the nature of Lower Carboniferous exposures, but filicalean and zygopterid ferns from the Upper Carboniferous, clearly manifest a vast array of ecological roles.

3.1.2. Small-fern patterns of occurrence

Ferns are rare in local community analyses based on compression assemblages throughout the Permo-Carboniferous, representing clastic flood-basin habitats. In the Westphalian B of Yorkshire (Scott, 1977, 1978, 1979) the few filicalean species encountered occur at 1–10% cover in low diversity and only in flood-plain habitats, recognized as laminated mudstone with common rooted horizons; marattialean ferns are an insignificant part of lowland wetlands at this time. In flood-plains, rare ferns are found in monospecific stands, probably clones (Scott, 1978; Scott and Galtier, 1985). Community analyses of younger Westphalian D compression floras also reveal low filicalean fern diversities, similar to those found by Scott (Lamboy and Lesnikowska, 1988; DiMichele et al., 1991), although marattialean tree ferns are abundant.

The low diversity of small ferns in community analyses of compression floras may be reflective of several factors. Of most importance is the apparent patchy distribution of small ferns, which, combined with small biomass and the lack of organ abscission in most species, severely restricts the input of tissues and organs to environments of burial. Also important is the sampling scale, generally quite restricted in most analyses of local communities. Limited sample size and coverage is mitigated in fossil assemblages to some extent; plant remains of compression floras were generally transported from the environment of growth to the environment of deposition, even if only a short distance. Thus, intrahabitat transport of debris can reduce the impact of restricted sampling by homogenization of the flora, to some extent, but only for those plants that shed leaves and other parts. Overall, therefore, the interaction of sampling scale and preservational bias tends to reduce apparent fern abundance and local, intracommunity species richness.

In contrast to analyses carried out at small spatial scales on essentially local floras is the allochthonous Mazon Creek flora of Westphalian D age. The Mazon Creek flora, which is collected from brackish to marine shales, is drawn from a large terrestrial source area, and therefore is not a picture of community diversity, but rather of the diversity in the regional species pool. In addition, Mazon Creek may be the most heavily collected and best known Pennsylvanian age flora from western Euramerica. According to the analysis of Pfefferkorn (1979), ferns are the most diverse group of plants in this flora, comprising 37 of the 96 described 'whole plant' species. Twelve of these species are marattialean ferns, which had become diverse and abundant by the late Westphalian D, and the remaining 25 are small ferns, known mainly from their reproductive organs. This contrast suggests that small ferns were diverse at the regional spatial scale, but perhaps quite patchy and localized in their distributions within a region, rarely forming an abundant grass-like ground cover over broad areas.

Studies of peat-substrate floras, preserved in coal balls, provide a more compelling picture of small-fern ecology. Because coal balls are permineralized peat stages of coal, they capture both tree litter and groundcover on the floor of the swamp or mire. In some of the oldest Upper Carboniferous coal-ball floras, from the Westphalian A of Britain and western Europe, ferns are a common component. The Bouxharmont Seam of Belgium (Holmes and Fairon-Demaret, 1984), for example, is rich in ferns; 17 species have been identified, occurring on a frequency rather than biomass basis in 25% of the 500 coal balls examined, ranking behind arborescent lycopsids and sphenopsids, and above pteridosperms. Nearly all these ferns are groundcover or facultative climbers/sprawlers. Quantitative analyses of coal balls from the Union and Bouxharmont seams (Phillips et al., 1985) indicate that small ferns were minor biomass contributors, despite their species diversity, accounting for less than 10% of total peat biomass. A similar pattern is found in coal beds throughout the Pennsylvanian of North America and Europe. Small-fern diversity in the coal-ball analyses of the Westphalian D coals of the United States is nine species that, on average, account for less than 2% of the biomass in any given coal seam (Phillips et al., 1985).

3.1.3. *Small-fern growth habits and ecologies*

Small ferns of the late Paleozoic had evolved a remarkable array of growth architectures, paralleling those seen in modern ferns. These growth forms are summarized by Galtier and Holmes (1982). They fall into four basic categories. (1) Species with upright growth habits, often unbranched. Included are some zygopterids, most species of *Tubicaulis* (an anachoropterid), some species of *Ankyropteris* (*A. hendricksii*, Read, 1938) of the Tedeleaceae, and the three species of *Grammatopteris* (Sahni, 1932; Tidwell and Rozefelds, 1990). (2) Rampant forms without a clear relationship between phyllotaxy and stem dichotomy. Included are a number of zygopterids, including the early ferns *Diplolabis* and *Metaclepsydropsis*, as well as *Zygopteris*, *Psalixochlaena*, and *Botryopteris*. (3) Forms with axillary branching included *Psalixochlaena*, *Ankyropteris*, and some species of the anachoropterid *Tubicaulis*. (4) Forms with cauline units originating from buds on fronds included many species of *Botryopteris*, *Anachoropteris*, and *Psalixochlaena*.

These different growth architectures permitted small ferns to acquire a variety of growth habits and occupy a wide range of ecological roles. Most species likely formed surface creeping ground cover, especially those with rampant habit or with axillary branching. This includes most species of the Zygopteridaceae, a family extending from the Late Devonian into the Permian, including the genera *Clepsydropsis*, *Metaclepsydropsis*, *Diplolabis*, *Zygopteris*, and *Nemejcopteris* (Dennis, 1974; Phillips, 1974; Barthel, 1968) (Fig. 1). Many species of *Botryopteris* and *Anachoropteris* may have been much like modern 'walking ferns' that produce stem buds on fronds enabling them to spread rapidly across open substrates (Phillips, 1974; Trivett and Rothwell, 1988). In the case of *Psalixochlaena*, its prostrate stem may have been subterranean, given that it can occur in excellent preservation (Holmes, 1977) in otherwise heavily rotted root peats, suggesting penetration of the substrate. Assemblages of small ferns, minimally fragmented and apparently in place, can be found commonly in coal balls (Plate I, 1), occupying what appear to be exposure surfaces in the peat (Phillips, 1974). Such assemblages often are mixed and their commoness indicates a convergent cross-species ecological strategy among the rampant forms, aimed at exploitation


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of open areas, possibly after some kind of disturbance.

Upright habit permitted the evolution of small trees or shrubs. This habit has been suggested for *Zygopteris primaria* (Sahni, 1931a). Tidwell and Rozefelds (1990) suggest that some *Grammatopteris* species may have been upright.

Climbing habit has been suggested for many species. A liana growth form has been suggested for an *Anachoropteris* species, based on coal balls of Late Pennsylvanian age (Trivett and Rothwell, 1988). This species has latent croziers that have been found to replace basal pinnae on fronds otherwise fully developed. Facultative climbing habit has been suggested for *Ankyropteris brongnartii* (Stenzel, 1889; Sahni, 1935; Mickle, 1980, 1984; Rößler, 2000), of the Tedeleaceae (Fig. 1) and for *Botryopteris cratis* (Phillips, 1974; Millay and Taylor, 1980) of the Botryopteridaceae based on their occurrences both as prostrate stems and embedded in root mantles of *Psaronius* (Plate I, 2, 3) from a number of Late Carboniferous and Permian localities.

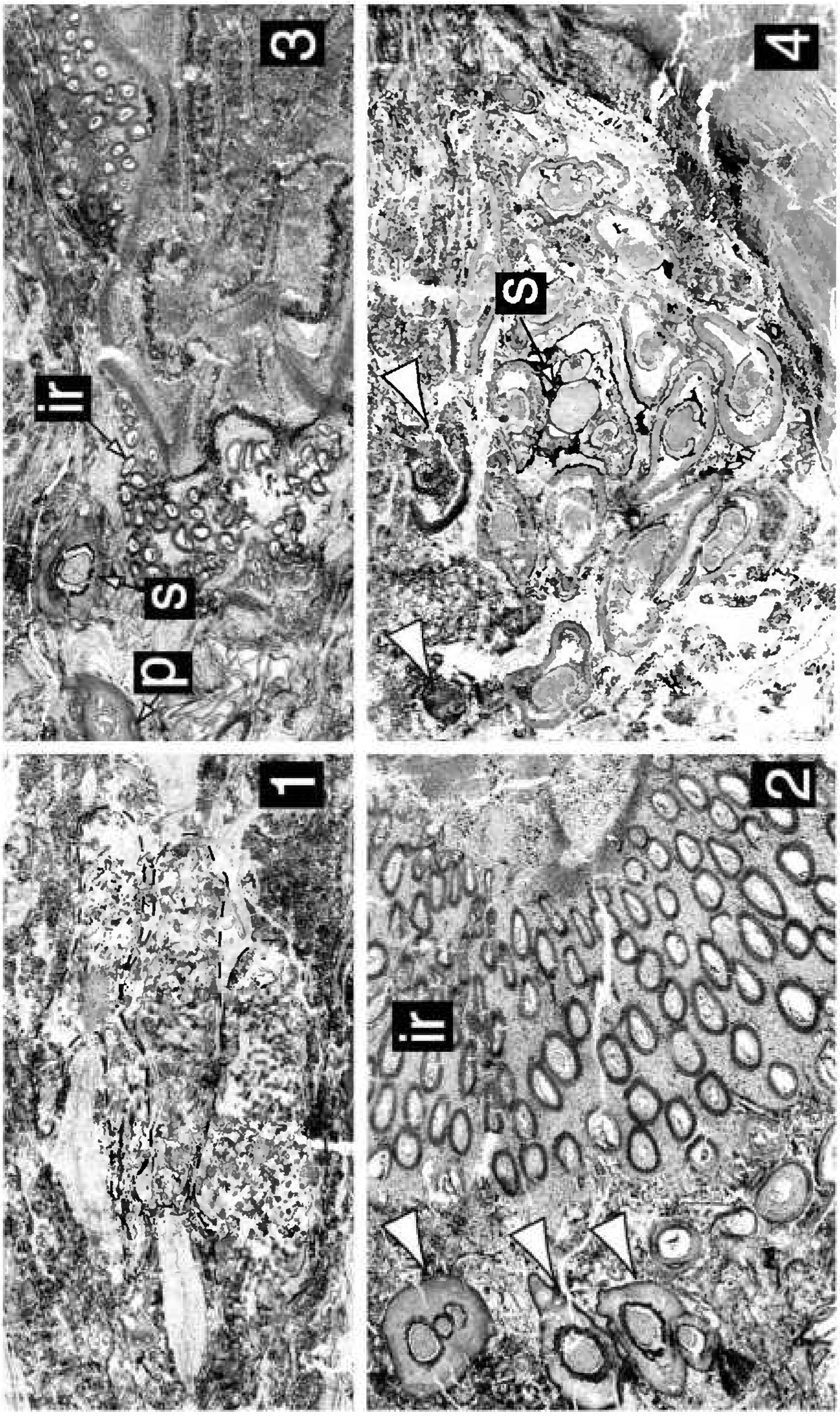
Epiphytic ferns may have been common, but this habit is possibly the most difficult to document. An epiphytic habit has been suggested for *Botryopteris forensis* (Rothwell, 1991). This plant was first suggested as an epiphyte by Mamay and Andrews (1950) based on its growth architecture and association with *Psaronius* root mantles (Fig. 1). Association of small-fern stems of the genus *Tubicaulis* with tree-fern root mantles has led several other authors to suggest an epiphytic habit for *T. berthieri* (Bertrand, 1909; Bertrand and Bertrand, 1911) and *Tubicaulis* sp. (Sahni, 1931b, 1935; Rößler, 2000) of Permian age, and for the Pennsylvanian species *T. scandens* (Mamay, 1952), which, as its name indicates, had long internodes and a slender stem. Rößler (2000) has found a close association of *Anachoropteris* foliage with *Tubicaulis* stems in Permian material from Chemnitz embedded within *Psaronius* root mantles, an organ association known for some other, non-epiphytic, species of *Tubicaulis*. Rößler (2000) also has identified a small stem attributable to *Grammatopteris* (Kidston and Gwynne-Vaughan, 1907; Beck, 1920; Miller, 1971), embedded with the root mantles of Permian-aged *Psaronius* stems; this association suggests a growth habit quite different from that for other species of this genus, which, as noted above, may have been small tree ferns (Tidwell and Rozefelds, 1990).

3.1.4. The association of small ferns with fire

Small-fern debris in coal balls is commonly preserved as charcoal (Plate I, 4). In such instances, the remains of stems, foliage, reproductive organs and roots often are fragmentary and not clearly associated with a diagnostic site of growth. In keeping with other ancient and modern observations, filicalean and zygopterid ferns of the late Paleozoic appear to have grown in habitats that were periodically disturbed, and fire is and was one of the major disturbance agents in those habitats.

Disproportionate fusain preservation, by itself, should not be taken to indicate growth in fire-prone habitats, however. Given that most small filicaleans and zygopterids did not readily disintegrate into separate, easily transportable organs, that they were often ground cover, sheltered from destructive winds, and that their populations were patchy in time and space, preservation of plants should have been much rarer than was characteristic of canopy trees. This observation is supported by modern actualistic studies (Scheihing, 1980), wherein ground cover was found to be disproportionately rare following major storm events that created substantial fresh debris. Fire, on the other hand, will kill and fragment these small, clonal plants. Charcoal is light,

Fig. 1. Late Pennsylvanian (Stephanian) tropical coal-swamp scene in a *Psaronius* tree-fern-dominated area with exposed peat, some charred debris, and abundant fern ground cover, especially in light gaps. Setting based on coal-ball observations in the Calhoun Coal, Berryville, Illinois. At right: *Ankyropteris brongnartii* climbing on the outer root mantle of *Psaronius blicklei* tree-fern trunk. At trunk base, *Botryopteris forensis* with some globose fertile pinnae on otherwise laminate fronds. At left: large stand of *Zygopteris berryvillensis* with erect fronds and perpendicular pinnae. Lower left: charred *Tubicaulis* rhizome.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highly transportable, and resistant to degradation. Consequently, the common fusinization of small ferns may simply reflect a strong taphonomic bias in the nature of litter input into the potential fossil record – if burned and fusinized the likelihood of preservation and detection increases significantly.

3.2. *Marattialean tree ferns*

3.2.1. *Marattialean diversification*

The evolutionary history of the Marattiales has been reviewed by several authors in the past quarter century (Stidd, 1974; Hill and Camus, 1986; Millay, 1997). In broad terms, the group does not appear until the Namurian, in the latest Early Carboniferous (Goodlet, 1957; Remy and Remy, 1977; Gerrienne et al., 1999). The geographical origin appears to be tropical and Euramerican, based on the first occurrences and the pattern of later global radiation in the Stephanian. The nearest relatives or likely ancestors are unclear. Marattialean ferns have typical fern biology – megaphyllous leaves, siphonostelic stems, adventitous roots only, homosporous reproduction, abaxially foliar borne sporangia, and prolific production of isospores. The Marattiales are eusporangiate, however, and do not seem to be allied closely with other common Paleozoic ferns. The phylogenetic linkages between the dominant Paleozoic forms and those typical of the Mesozoic, persisting until today, are not agreed upon either. Both Stidd (1974) and Delevoryas et al. (1992) suggest descent of the two groups from common, largely unrecognized Paleozoic ancestors, rather than one from the other; *Radstockia* is posited as a likely member of the ancestral plexus and may have been an element of extrabasinal floras, occurring as it does rarely in the Mazon Creek flora and in other clastic adpression assemblages. In contrast, Hill (1987) argues that there are sufficient similarities in a number of Paleozoic species to indicate derivation of the extant lineages from late Paleozoic precursors.

On the basis of adpression foliage and both adpressed and structurally preserved reproductive structures, marattialean species diversity literally exploded during the Stephanian (Late Pennsylvanian) (Boureau and Doubinger, 1975; Millay, 1997). Prior to that time, tree ferns were an increasingly important part of tropical floras, beginning their quantitative rise to prominence in the wetlands during the Westphalian B, based on the spore record and during the early Westphalian D, based on the record of macrofossils (Pfefferkorn and Thomson, 1982; Phillips et al., 1985). By the late Westphalian D, a majority of adpression floras, likely from wet flood-plain habitats, were dominated by marattialean tree ferns (Pfefferkorn and Thomson, 1982); in contemporaneous peat swamps, tree ferns had become common, and dominated some local assemblages within these edaphically restricted environments (Phillips and DiMichele, 1981; DiMichele and Phillips, 1988). However, they remained at about 10–20% of the peat biomass when averaged across the peat-swamp landscape (whole seam basis). Near the Westphalian–Stephanian (approximately equals the Middle–Late Pennsylvanian) boundary, dramatic changes in tropical vegetation occurred, es-

Plate I.

1. Transverse cut through peat revealing a *Zygopteris* horizon with three rhizomes (circled by dotted lines) crossing each other. 1.8×. University of Illinois Coal Ball Specimen 38896, Herrin (No. 6) Coal, Middle Pennsylvanian, Shawneetown, Illinois.
2. Cross section of part of the upper stem of *Psaronius* (upper right) with inner root mantle (ir) and three adjacent shoots of *Ankyropteris* alongside the trunk (arrowheads). 2×. University of Illinois Coal Ball Specimen 7406B, Herrin (No. 6) Coal, Middle Pennsylvanian, Sahara Coal Company Mine No. 6, Illinois.
3. Cross section of about half of a *Psaronius* trunk with irregular inner root mantle (ir) and adjacent *Ankyropteris* stem (s) and petiole (p). 1.8×. University of Illinois Coal Ball 22686B,
4. Cross section of *Tubicaulis* stem (s) with petioles distally exhibiting *Anachoropteris involuta*-type xylary configurations. The in situ specimen terminates in upper levels in charred remains (arrowheads), consistent with loss in ground fire. Long arrow points to stele of stem. 2.1×. University of Illinois Coal Ball 524762, Middle Pennsylvanian, Urbandale Mine, Iowa.

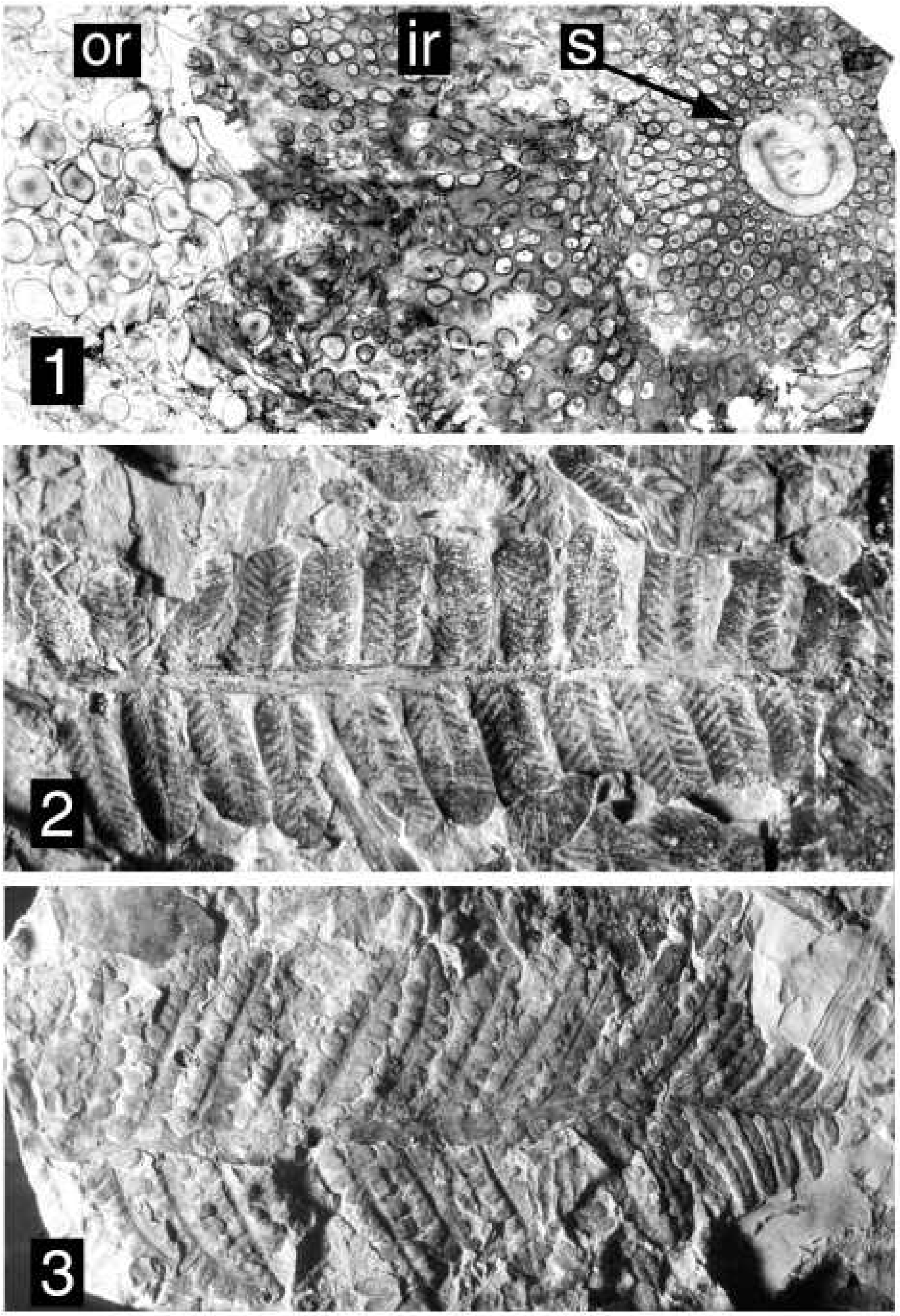

Plate II.

1. Cross section of stem of *Psaronius blicklei* with small distelic stem (s), thick inner root mantle (ir) and part of the outer root mantle (or) of large free roots. 0.4×. USNM Specimen 458422, Calhoun Coal, Upper Pennsylvanian, Berryville, Illinois.
2. Coalified compression specimen of *Pecopteris* cf. *cyathea*, foliage of *Psaronius*. 2.5×. Upper Pennsylvanian, Texas, USNM Locality Number 39997.
3. Coalified compression of *Pecopteris puertollanensis*, foliage of *Psaronius*. 1.4×. Upper Pennsylvanian, Texas, USNM Locality Number 39992.

pecially in the western parts of Euramerica, thought to be induced by major changes in climate (Phillips et al., 1974; Phillips and Peppers, 1984; Frakes et al., 1992; DiMichele and Phillips, 1996). Following these disruptions, tree ferns rose to prominence, quantitatively dominating many lowland, wetland habitats and also diversifying greatly. The exact number of species is difficult to determine, despite the many described forms. The genus *Pecopteris* appears to taxonomically oversplit, possibly enormously, but in a complex way reflecting fragmentary preservation, complex intrafrond morphological differences, and regional taxonomic differences, both real and resulting from historically different practices in different parts of the world.

3.2.2. *Marattialean growth habits*

The classic image of a Paleozoic marattialean fern is the reconstruction in Morgan (1959), which has been widely reproduced: a straight-growing, arboreous plant several to perhaps 10 m or more in height, its primary stem mantled by adventitious roots, topped by a crown of large, graceful, compound fronds. The largest reported basal diameter is 1 m or more (Willard and Phillips, 1993) from Late Pennsylvanian deposits of Illinois in the USA. In Permian deposits of Chemnitz in Germany, Rößler (1995) estimates stem diameters up to 1.5 m when a correction is made for preservational distortion. The stems of these plants are classified as *Psaronius*, if preserved anatomically (Plate II, 1), a name that has come to be used as shorthand for the entire plant, or as several other genera if preserved as adpression fossils (*Megaphyton*, *Caulopteris*, *Artisophyton*, depending on arrangement and nature of leaf scars, Pfefferkorn, 1976); foliage is generally of the *Pecopteris*-type (Plate II, 2, 3), and, if fertile, most often bears radially symmetrical synangia classified as *Scolecopteris* or several other genera (Millay, 1979). This was the typical marattialean growth form of the late Middle Pennsylvanian and Late Pennsylvanian tropical lowlands. It persisted through the Permian (e.g., Rößler, 2000) and into the Triassic, where it was finally replaced by forms typical of modern groups (Delevoryas et al., 1992), with bilaterally symmetrical synangia, foreshortened stems, and no root mantle.

The earliest marattialeans appear to have differed considerably from this growth form, based on the limited evidence at hand (Pfefferkorn, 1976; Remy and Remy, 1977; DiMichele and Phillips, 1977). These forms, which occur from the latest Mississippian into the Early Pennsylvanian, are anatomically much simpler than later forms, with monocyclic dictyosteles instead of the polycyclic dictyosteles of younger forms. Although arborescent, given the lengths and dimensions of the stems, they appear to have had very limited root mantle development. Fronds were borne distichously, meaning that in compression, the stems would be classified as *Megaphyton*, and due to the lack of associated *Pecopteris* remains, may have been of some other, perhaps sphenopterid form. Given the totality of the evidence, Millay (1997) suggested that these early forms should be placed in a distinct genus rather than in *Psaronius*.

Stems with polycyclic organization, probably of tree habit, are known from the Westphalian A (Early Pennsylvanian equivalent) of England (Scott, 1920), and correspond to the rise in importance of *Pecopteris* and *Scolecopteris*. Lesnikowska (1989), in a detailed study of the morphology of marattialeans in coal-ball deposits, determined that a number of Middle Pennsylvanian marattialeans were of considerably smaller stature than that portrayed in Morgan (1959), generally with small diameter stems and thin root mantles. She even described one species that lacked a root mantle altogether and had a sprawling growth form. Mickle (1984) hinted at the existence of a similar growth form in the Late Pennsylvanian, based on a single petrified specimen completely lacking a root mantle, but could not unequivocally rule out the possibility of it being a developmentally young plant. Climbing and epiphytic growth habits have not been suggested for any Paleozoic marattialeans.

3.2.3. *Paleozoic marattialean ecology*

Early marattialeans, those with 'monocyclic', simple stem anatomy, frequently are preserved as sandstone casts, bearing little morphological or contextual evidence of ecological preference. The form of preservation suggests growth near streams in wet habitats. Possibly the best documented of these early forms, in terms of its ecology, is *Psaronius simplicicaulis* from the Early Pennsylvanian of Illinois (DiMichele and Phillips, 1977). This plant evidently was a tree fern of small stature. Its remains occur in dark, pyritic, organic shales that represent the final phases of clastic, mud fill in narrow, steep-sided channels cut into limestone bedrock. Most of the channel fill is light gray siltstone bearing a distinctive 'extrabasinal' flora (Leary, 1981), probably representative of plants growing along the margins of the channels while water was actively flowing. The tree ferns occur in association with lycopsid trees in what seems to have been a stagnant-water, swamp assemblage that formed as channels were cut off or drowned. Thus, the earliest known forms seem to be associated with wet habitats, but possibly within broader, seasonally dry or well-drained landscapes.

Marattialeans are notably rare in clastic adpression assemblages from the Westphalian A and B (Early and early Middle Pennsylvanian) (e.g., Scott, 1977, 1978). In the Westphalian C and D (Middle Pennsylvanian) they colonized the wet lowlands, primarily in clastic-substrate environments, becoming important components of adpression floras, rising to biomass dominance in many (Pfefferkorn and Thomson, 1982). The subtleties of physical control on these plants are not particularly clear, due to transport and fragmentary preservation. Stephanian tree ferns occupied a wide range of flood-basin habitats from moderately well-drained soils to swampy sites, continuing the expansion in diversity and ecological dominance that started in the late Middle Pennsylvanian. Most of the described adpression species of *Pecopteris* (or its segregate genera, *Lobatopteris* and *Polymorphopteris*) are from the Stephanian. The ecologies of these individual species are, for the most part, unknown. What can be said is that many species of Stephanian tree-fern foliage can co-occur at a single, environmentally homogeneous collecting site, that species richness tends to be higher in non-swamp flood-basin deposits, those that may have been more aerated or periodically dry, than in stagnant-water swamps (DiMichele and Mamay, 1996; Barthel and Weiss, 1997), and that maximal tree size was attained during the Stephanian and Early Permian based on in situ stumps and the diameters of permineralized stems (e.g., Cross, 1952; Mickle, 1984; Lesnikowska, 1989; Rößler, 2000). Personal observations suggest that there are species differences in habitat preferences of many pecopterid species, something also alluded to by Mickle (1984); these have yet to be documented in detail.

The expansion of tree ferns into peat substrate floras was gradual and by the late Middle Pennsylvanian, such ferns were an important and widespread component of these habitats (Phillips et al., 1985). Quantitative study of coal-ball floras has revealed some important aspects of tree-fern ecology in peat swamps. The following points are taken from data and discussion in Phillips and DiMichele (1981) and DiMichele and Phillips (1988), Willard (1993) and Phillips and DiMichele (1998), studies of late Middle Pennsylvanian coals. Tree ferns appear to have been excluded during the Middle Pennsylvanian from the wettest habitats in peat swamps, those inferred to have long periods of standing water, dominated by species of the lycopsid tree *Lepidophloios*, which generally lack all vestiges of ground cover as well. This is not surprising, considering the free living, terrestrial gametophyte phase of the marattialean life history. They are components of virtually all other assemblages, at about 10–20% of aerial biomass on average, varying independently of the dominant elements. Most species of these late Middle Pennsylvanian tree ferns appear to have been opportunists, exploiting disturbance. Individual species do not have diagnostically specific distributions with regard to habitat markers such as charcoal, clastic partings, or clastic enrichment of the coal, markers that do correlate strongly with species from other taxonomic groups, such as lycopsids and pteridosperms. In general, early Middle Pennsylvanian tree ferns in coal swamps were of relatively small stature compared to those that would dominate Late Pennsylvanian swamps. Lesnikowska (1989) compiled data on organ diameters and discovered that only in the latest coals of the Middle Pennsylvanian do root diameters appear that rival those found in the Late Pennsylvanian.

During the transition from the Middle to the Late Pennsylvanian, extinctions of lycopsid trees began, spreading from west to east across the Euramerican–Cathaysian tropics (Phillips et al., 1985). This extinction wave did not reach the rain forest areas of Cathaysia, where typically Middle Pennsylvanian vegetation persisted into the Late Permian (Guo, 1990). The disruption of swamp vegetation was accompanied by extinction of nearly two-thirds of the species, including most of the trees (DiMichele and Phillips, 1996). In the resulting Late Pennsylvanian coal swamps, tree ferns appeared as the dominant elements, including trees of large stature, but representing an almost complete turnover in tree-fern species (Lesnikowska, 1989). In Late Pennsylvanian coal swamps of the Illinois Basin, marattialean tree ferns account for 60% to over 80% of peat biomass (Phillips et al., 1985). More detailed ecological analyses of these swamp assemblages (Pryor, 1993; Willard and Phillips, 1993; DiMichele and Phillips, 1996) suggest that tree ferns occurred in most mire subhabitats, dominating many, especially on thick peats with little mineral matter. Edaphic variation in the swamps appears in the distribution of subdominant elements such as medullosans, cordaites, and sigillarian lycopsids. Pryor (1993) and Grady and Eble (1990) have described patterns of species succession, corresponding to changes in the amount of mineral matter and evidence of peat decay. In general, plants other than tree ferns dominate those assemblages associated with the base of the coal bed or with mineral bands in the coal, tree ferns rising to importance in the thicker parts of the seam.

The era of marattialean importance lasted well over 10 Myr, beginning in earnest at the end of the Middle Pennsylvanian and continuing into the Permian. For most of this time marattialean tree ferns were part of floras that would be categorized broadly as 'wetland', rich in pteridosperms and lycopsids, associated with organic-rich deposits of various sorts, and generally connected evolutionarily to the floras of the Carboniferous tropical lowlands (Fig. 1).

During the Permo-Carboniferous transition new floras began to appear that were dominated by a variety of xeromorphic seed plants, such as conifers and callipterids. These new floras shared few species with those of the primordial tropical wetlands and gradually became predominant in the tropical lowlands as climatic seasonality increased (Knoll, 1984; Broutin et al., 1990; DiMichele and Aronson, 1992). The marattialean tree ferns were one of the few groups with species in tropical wetlands that also were locally abundant in the newly emerging lowland vegetation, which appears to have grown under seasonally dry conditions. Studies of the floral transition in north-central Texas (DiMichele and Mamay, 1996) indicate that tree ferns were persistent elements in the newly appearing vegetation, probably in wetter areas, but in association with conifers and other plants that would dominate the Permian landscapes. They persist, and even dominate sites on occasion (Mamay, 1968) well into the later part of the Early Permian in the western US, ultimately disappearing as conditions become very dry in that part of the world. Their ability to make this ecological jump from one dominant flora to the other may reflect their fundamentally opportunistic life histories and flexible body plans, the same characteristics that contributed to their ascendency following the Middle–Late Pennsylvanian extinctions. Such a life history predisposes the plants to the formation of ecologically evolutionary isolates and encourages speciation in the course of opportunistic resource exploitation.

4. Discussion

The Paleozoic fern radiation gave rise not only to most of the major taxonomic groups, but also saw the evolution of nearly all the basic body plans ever to appear within this clade. Importantly, however, these growth habits evolved across the full spectrum of the existing groups. Trees appeared in both the Marattiales and Zygopteridales, epiphytes, vines and sprawling ground cover in the Filicales and Zygopteridales, and upright shrubby plants and subtrees in the

Marattiales and Filicales. Among the filicalean groups, the variety of anatomy and architectures was greater than that seen after the Paleozoic, when a second major radiation of this group took place (Rothwell, 1987).

Virtually all the Paleozoic groups were replaced in the Mesozoic, when the Filicales rose to prominence. In this instance we are including the Osmundaceae in the Filicales. Filicaleans included many species with surface ground cover growth habits, many of which have persisted until today. Modern tree ferns are entirely filicalean in affinities. And, false stems can be found in modern *Hemitelia* as well as in the fossil filicalean *Tempskya* (Andrews and Kern, 1947). Filicaleans also are epiphytes and vines. In addition, aquatic ferns of the Hydropteridales, a group of filicalean affinity, appeared in the Mesozoic, adding a new dimension to fern ecology (Rothwell and Stockey, 1994). Thus, many of the life habits found in Paleozoic ferns re-evolved in the Mesozoic, although on a narrower phylogenetic base than earlier.

Within the confines of the diversity of body plans, Paleozoic ferns occupied a wide range of habitats and played many ecological roles. Early forms included both opportunists, capable of exploiting disturbed and possibly burnt-over landscapes (Scott and Galtier, 1985), and more typical ground cover in a variety of settings. By the end of the Middle Pennsylvanian, tree ferns had become important dominants in wetlands (Phillips and Peppers, 1984), forming what may have been the most extensive fern-dominated landscapes of the Phanerozoic. A remaining question is the role of ferns as ground cover. Clearly, there are places today where fern thickets can cover broad areas. However, the evidence available from Paleozoic rocks does not reveal extensive stands of ferns analogous to the grasslands of today. Such a ground cover role has been postulated for Mesozoic filicaleans (Coe et al., 1987; Wing and Tiffney, 1987), based on inferences about dinosaur feeding habits rather than direct evidence.

In conclusion, fern biology, in its morphological simplicity, appears to have permitted the ferns to remain evolutionarily flexible, by not placing strong constraints on the direction of evolution. As a consequence, many groups of ferns diversified not only at the level of species but in terms of life habits. The more complex architectures, such as trees with false trunks, lianas, and aquatic ferns, are not diverse and never have been, regardless of the clade in which the habit evolved. The evolutionary, and hence ecological, strength of the ferns has been the long persistence of ground cover forms with minimal morphological specialization, providing a pool of ancestors from which more derived growth habits could evolve and specialize ecologically. This potential appears to remain in the group at large and may be the major explanation for their continued diversity.

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