II. Paleobotany of Land Plants

By Paul Kenrick and Else Marie Friis

1. Introduction

The impact of paleobotanical data on land plant systematics is greatest for ancient cladogenic events, resulting in isolated extant groups of divergent morphology. Paleobotanical data are therefore ideally suited to addressing problems in land plant macrosystematics, an area of botanical research that has received considerable attention over the last 10 years. Macrosystematics deals with the recognition and definition of patterns of relationship among major groups of organisms. Current interest stems from important advances in systematic theory that began during the 1960s and have developed into the widely used "cladistic approach" (Nelson and Platnick 1981). Macrosystematic studies make use of data from a number of disciplines ranging from general comparative morphology to plant ultrastructure and biochemistry. Recently, the application of molecular biological techniques to systematic problems has generated a large and important new set of data. Because none of these sources of data produce unambiguous results, it is important to retain a critical multidisciplinary approach to macrosystematic problems. Furthermore, the prevalence of extinction in the history of land plants means that paleobotanical data contribute the only source of information on a huge range of forms, and many aspects of relationship, homology, and the history of terrestrial life can only be understood through the window provided by the fossil record.

This review summarizes important recent paleobotanical contributions to land plant systematics, focusing on the years 1992 to 1993. All major groups except angiosperms have been reviewed. Angiosperm phylogeny and floral evolution is an area of rapid expansion, and there is a considerable amount of new information on the structure and organization of early angiosperms and related anthophytes (Endress and Friis, 1994). These advances, together with new developments in the systematics and developmental morphology of extant groups, have resulted in an extensive revision of angiosperm classification. In order to give a more comprehensive account of the scientific progress in this area, anthophyte systematics and phylogeny will be treated in a separate chapter in the 1995 volume.

Several textbooks in paleobotany have been published during the past decade, and two new editions of earlier treatments appeared in 1993. *Paleobotany and the Evolution of Plants* by Stewar and Rothwell (1993) is an expanded sec-

ond edition of Stewart's textbook from 1983. *The Biology and Evolution of Fossil Plants* by Taylor and Taylor (1993) is based on Taylor's textbook from 1981 but is considerably expanded, including additional chapters on the structure and organization of vascular plants and on plant-animal interactions. Both books provide an excellent introduction to the fossil record. That of Stewart and Rothwell (1993) is aimed at undergraduates and has a particularly consistent form of presentation; Taylor and Taylor (1993) is aimed at upper-level undergraduate and graduate courses and is more encyclopedic. Both books are also invaluable reference sources for botanists and paleobotanists.

Information on stratigraphic occurrences of plants is essential to dating clades and charting temporal changes in floral diversity. A useful handbook treating the fossil record of plants and animals by Benton (1993) provides information on stratigraphic ranges of groups at the family level. The book includes four chapters devoted to the fossil record of plants: Bryophyta (Edwards 1993), Pteridophyta (Cleal 1993a), Gymnospermophyta (Cleal 1993b), and Magnoliophyta (Collinson et al. 1993). Short comments indicate whether a record is reliable or in need of further documentation.

2. Systematics

Recent developments in systematic theory have led to an important period of reevaluation, where the aim of many studies has been the reinterpretation of current knowledge from a new theoretical perspective. In botany, much recent work has focused on relationships among major groups of land plants. These studies have clarified many important aspects of relationship and homology and have brought the major systematic problems into sharper focus. Cladistic studies using paleobotanical data have addressed problems of relationship among major groups of seed plants. Classic early work adopted a synthetic approach that integrated paleobotanical and neobotanical data on comparative morphology (Crane 1985; Doyle and Donoghue 1986). Subsequent investigations have dealt with one or more seed plant groups in greater detail or reexamined the more general questions of relationship using updated morphological data or new molecular data sets. Recently, the role of paleobotanical data in seed plant macrosystematics has been examined in greater detail. Loconte and Stevenson (1990) analyzed relationships in extant seed plants based on comparative morphology and concluded that paleobotanical data are unnecessary to resolve relationships among *extant* groups. In response to this study, Doyle and Donoghue (1992) designed an explicit test of the effects of paleobotanical data and found that additional information from the fossil record did alter relationships and also had important implications for hypotheses of homology. Certain characters that appear to be homologous when viewed from a neobotanical perspective are best interpreted as convergences when fossils are considered. Although seed plant systematics can be addressed at the

neobotanical level, excluding the extensive, well-documented fossil record may lead to erroneous conclusions.

At the more general level of vascular plants and embryophytes, cladistic studies have focused mainly on neobotanical data (Mishler and Churchill 1984, 1985; Graham et al. 1991; Garbary et al. 1993). Integration of the large database on Paleozoic and Mesozoic fossils has begun, but no detailed cladistic synthesis has yet been published. Preliminary studies that include data from the early fossil record support vascular plant monophyly and an early divergence of lycopods from other tracheophytes (Kenrick and Crane 1991; Gensel 1992). The early fossil record is consistent with previous cladistic studies based on neobotanical evidence that support bryophyte paraphyly with a basal position for liverworts in embryophytes and a sister-group relationship between either mosses or hornworts and tracheophytes (Mishler and Churchill 1984, 1985; Fig. 1). The paraphyletic status of bryophytes has been challenged recently in a study based on male ga-
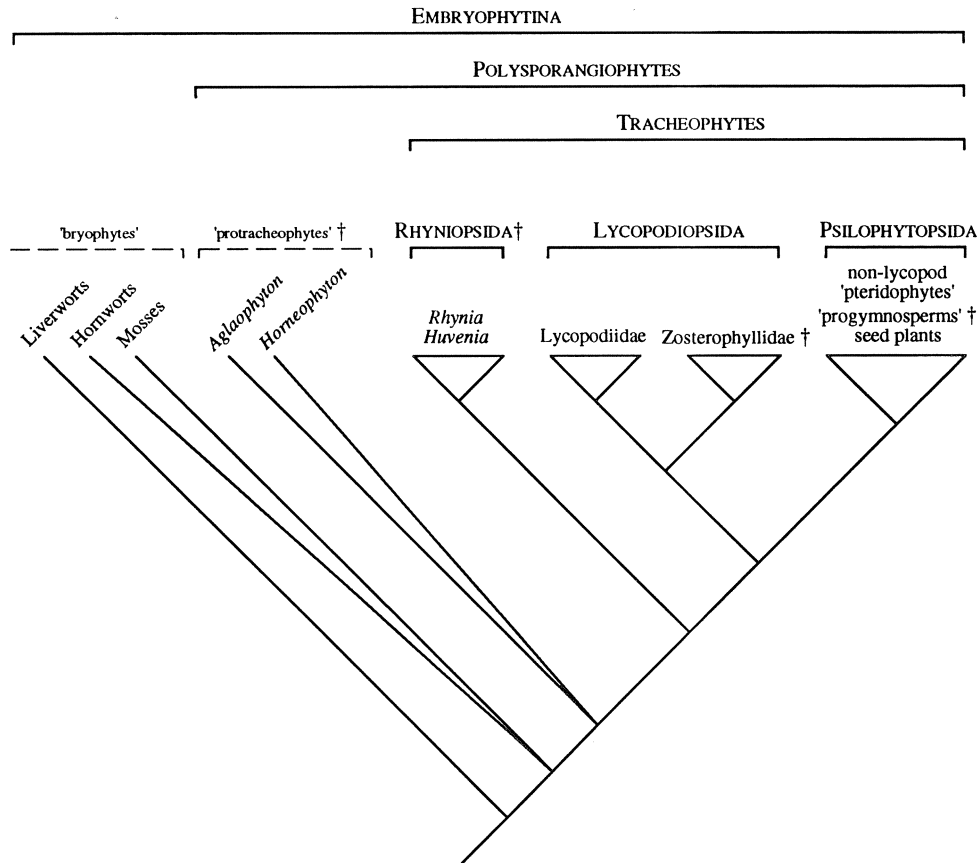
Fig. 1. Cladogram summarizing relationships among major basal land plant groups including some early fossils. † = extinct group. (Kenrick and Crane 1992)

mete ultrastructure. Garbary et al. (1993) support monophyly of bryophytes, but their data also suggest controversially that bryophytes are nested within vascular plants and that lycopods are paraphyletic to all other embryophytes. These results are inconsistent with other aspects of morphology: lycopod monophyly is well supported by general neobotanical and paleobotanical morphological data (DiMichele and Skog 1992).

a) Embryophytes

The early fossil record of embryophytes (land plants) is dominated by a diverse range of microfossils including dispersed spores, cuticles, and other putative plant fragments (see reviews by Gensel et al. 1990; Gray and Shear 1992). Studies over the past 20 years indicate a probable mid-Ordovician origin for land plants documented by distinctive spores with an obligate tetrad morphology. Significant changes in spore morphology occurred rapidly around the mid-Silurian with the diversification of single trilete spores. These microfossil data indicate a marked alteration in composition of the terrestrial flora at this time (Gray 1991), but the meaning of this change in terms of major land plant groups is still unclear. The early microfossil record probably reflects a terrestrial flora at the bryophyte level of organization, but the systematic affinities of the spore producers are problematic because of the generalized spore morphology and the absence of associated macrofossils.

The earliest and most abundant macrofossil evidence of land plants comes from the Late Silurian and Early Devonian of northern Europe and North America (Edwards and Berry 1991). Information from these regions is particularly rich because of the historical development of paleobotany in research institutions in these areas. New early fossils from paleogeographically remote parts of China promise to redress this bias and are beginning to provide important comparative data. Cai et al. (1993) described an interesting Upper Silurian (Pridoli) compression fossil assemblage from northwest China. The assemblage includes probable basal tracheophytes or protracheophytes of slightly greater morphological complexity than those in contemporaneous northern European assemblages.

Recent discoveries of minute fossil sporophytes from Lower Devonian sediments of the Welsh Borderland, Britain, document a diversity of early land plants at the tracheophyte and "protracheophyte" (stem-group tracheophytes, Fig. 1) levels of organization. Many specimens are extremely well preserved, and remarkable cellular details of sporangia, epidermal structures, and internal anatomy have been observed (Fanning et al. 1992; Edwards et al. 1992). The fragmentary nature of this material makes more specific systematic assignments problematic.

In contrast to vascular plants, the early macrofossil record of "bryophytes" is poor (see recent review by Taylor and Taylor 1993). In many groups of liverworts, the poor fossil record has been attributed to the delicate nature of the

thallus (Krassilov and Schuster 1984), but taphonomic factors are unlikely to be important in other bryophyte groups, where collector bias and failure to recognize stem-group taxa probably also contribute to the poor early record (Kenrick 1994). Discovery of further Devonian taxa, in particular early relatives of mosses and hornworts, may prove decisive in clarifying relationships among basal embryophytes.

Well-documented observations on the gametophyte generation are extremely rare in the fossil record of vascular plants, but recent paleobotanical discoveries are beginning to clarify early stages in the evolution of this aspect of the plant life cycle. Exceptionally well-preserved Lower Devonian plants with intact gametangia have been described from the Rhynie Chert, Scotland, and these provide the first direct evidence of gametophytes and life cycles in early land plants (Remy et al. 1993). Life cycle reconstruction has been possible because the Rhynie Chert fossils are preserved in growth position, and linkage with associated sporophytes is achieved through anatomical comparisons. Observations on the Rhynie Chert have been extended to compression fossils at other Devonian localities. General features of the gametophyte generation in these early taxa include a simple, leafless, branched axial (as opposed to thalloid) morphology, terminal gametangia borne on an expanded disc-shaped or cup-shaped gametangiophore, and a level of anatomical differentiation comparable to associated tracheophyte or protracheophyte sporophytes (i.e., cuticle, stomates, and vascular tissues) (Remy et al. 1993). Cladistic analysis places taxa with isomorphic life cycles in basal tracheophytes and the tracheophyte stem-group, implying that the anisomorphic alternation of generations that characterizes extant vascular plants evolved from an isomorphic ancestral state. There is some corroborating evidence for gametophyte reduction in vascular plants in the complex gametophyte morphologies of extant Lycopodiaceae (Kenrick 1994).

b) Tracheophytes

Recent cladistic treatments of vascular plants recognize an early dichotomy between lycopods (Lycopodiopsida) and all other extant groups including *Equisetum*, "ferns", and seed plants (Psilophytopsida) (Kenrick and Crane 1991; Raubeson and Jansen 1992; Fig. 1). Relationships among basal members of the Psilophytopsida clade (nonlycopod vascular plants) are poorly understood, but this is an area in which the fossil record is currently making a significant contribution.

Recent paleobotanical studies on basal members of Psilophytopsida have emphasized the importance of the well-documented record of land plant soft tissues, which is unparalleled in any other group of organisms (Stein 1993). A number of important anatomical characters were identified and analyzed by Beck and Stein (1993) and Stein (1993) including xylem shape (deeply lobed), xylem development, protoxylem anatomy, appendage anatomy, presence of secondary

xylem, and root ontogeny. Many taxa in basal Psilophytopsida are characterized by a deeply lobed primary xylem, and within this group there are two distinctive types of stelar architecture. One group, "radiate protoxylem", is characterized by protoxylem distributions that radiate outwards from a central point along the arms of the primary xylem strand (e.g., *Pertica*, *Gothanophyton*, Stenokoleales, Aneurophytales, and basal seed plants) (Fig. 2). A second group, "permanent protoxylem", is characterized by mesarch protoxylem restricted to the tips of the lobes of the primary xylem. In this group, protoxylem also often contains parenchymatous inclusions (e.g., Iridopteridales, Cladoxylopsida: early groups related to Sphenopsids and "ferns") (Fig. 2). The Beck and Stein (1993) anatomical data support an *Equisetum*-fern clade that is sister group to lignophytes (seed plants plus extinct "progymnosperms"). Although primarily addressing relationships at a general level in Psilophytopsida, these observations are also relevant to basal seed plants. Beck and Stein (1993) confirm that most data are consistent with lignophyte monophyly, but they emphasize that there are few unequivocal characters supporting this clade. In particular, the bifacial cambium and other wood characteristics form a character complex with elements that may be more general in Psilophytopsida. Furthermore, the question of whether the protostelic condition observed in some early seed plants is plesiomorphic or autapomorphic has not yet been fully resolved. Further evaluation of lignophyte monophyly requires critical examination of the anatomy of closely related Paleozoic fossils. One such potentially relevant taxon is *Stenokoleos holmesii* from the Upper Devonian of New York. *S. holmesii* is a member of the Stenokoleaceae, a rather poorly understood group with significant anatomical similarities to early seed plants. Reproductive structures of Stenokoleaceae are unknown, but stem anatomy places the group within lignophytes and possibly early seed plants (Matten 1992).

Most macrofossil data on early vascular plants comes from Euramerican assemblages, but recent descriptions of Devonian fossils from China document
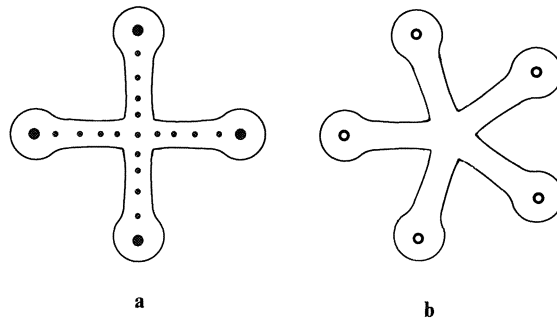
Fig. 2a,b. Diagrammatic representation of transverse section of xylem showing lobed morphologies common in early fossil members of Psilophytopsida (nonlycopod vascular plants). *Black circles* represent protoxylem positions; *black circles with white centers* represent protoxylem with parenchyma inclusions. **a** "Radiate protoxylem": protoxylem distributed along lobed arms of xylem strand. **b** "Permanent protoxylem": protoxylem confined to ends of xylem lobes

an interesting diversity of forms that provide important new comparative data. *Eophyllophyton bellum* (Hao and Beck 1993) documents the earliest evidence of planation in leaf-like appendages and provides the first evidence for G-type tracheids in the Psilophytopsida clade. The G-type tracheid is a distinctive wood cell that is widespread in early members of the Lycopodiopsida (Kenrick and Crane 1991). The documentation of this cell type in basal Psilophytopsida suggests that the G-type tracheid is probably ancestral for all crown group vascular plants.

Many early vascular plant fossils represent the remains of the distal portions of larger plants, and except under conditions of in situ preservation (e.g., coal measures) rooting structures are rarely observed attached. *Lorophyton goense* (Fairon-Demaret and Li 1993) is significant because it represents a rather complete small tree with roots and crown of branches. It is related to the Cladoxylopsida, an interesting early fossil group related to ferns.

c) Lycopods

Lycopods comprise a tiny fraction of extant land plant diversity but the group has a large and important fossil record. Lycopodiopsida (Fig. 1) first appear unequivocally in the Lower Devonian (Hueber 1992), where small herbaceous leafless taxa (Zosterophyllidae) dominate early plant assemblages and co-occur with other leafy forms (Lycopodiidae) that strongly resemble extant *Huperzia*. Lycopods flourished through the Devonian and, by the Lower Carboniferous, almost half of all known fossil plants are assignable to the group (Niklas et al. 1985). A diverse range of heterosporous arborescent forms dominated lowland peat-forming communities during the Carboniferous, and it is their remains that are largely responsible for the economically important coals of this age. Megafossil data suggest that lycopod diversity declined through the Upper Carboniferous and Mesozoic, but recent quantitative analysis of fossil megaspores suggests that diversity was greater in the Mesozoic than previously thought (Kovach and Batten 1993). The decline in lycopod megafossils is explained by extinction of the large swamp-dwelling arborescent forms and the diversification of herbaceous groups. Because of the important fossil record, lycopods continue to be the focus of much paleobotanical research, as reflected in a recent symposium organized by DiMichele and Skog (1992).

Recent cladistic treatments confirm a sister-group relationship between the extinct Zosterophyllidae and extant Lycopodiidae and support monophyly of both groups (Gensel 1992; Kenrick and Crane 1992). Cladistic studies suggest that the formerly enigmatic early fossil group Barinophytaceae is within the main Zosterophyllidae clade (Kenrick and Crane 1992). This conclusion indicates that some zosterophylls developed heterospory convergently with lycopods and increases knowledge of zosterophyll diversity in the Upper Devonian and Lower Carboniferous.

Although zosterophylls are abundant and widespread in many Early Devonian localities, the group has only recently been recognized in the most famous terrestrial Devonian lagerstätte, the Rhynie Chert (Lyon and Edwards 1991). Exceptionally well-preserved but highly fragmentary remains attributed to the group show certain cellular details of sporangial morphology and stem anatomy that have not been observed in other more common forms of petrifaction. *Trichopherophyton teuchansii* has the circinate vernation typical of the zosterophyll clade, but other features of stem anatomy suggest that it is a plesiomorphic member of the group.

Recent systematic studies of Lycopodiidae confirm monophyly of the heterosporous, ligulate group and a close relationship between Isoetaceae and arborescent Carboniferous forms (Bateman 1992; Bateman et al. 1992; Pigg 1992). A detailed systematic study focusing on extinct arborescent forms found that taxa with bisporangiate cones (i.e., *Paurodendron, Oxroadia, Anabathra, Chaloneria*) form a poorly resolved basal paraphyletic group subtending a clade characterized by monosporagiate cones (Fig. 3). The monosporangiate clade contains three well-defined families: Sigillariaceae, Lepidodendraceae, and the recently recognized Diaphorodendraceae (DiMichele and Bateman 1992). Progressive reduction of megaspore number per sporangium within this clade results in seed-like reproduction in Diaphorodendraceae and Lepidodendraceae. Despite their substantial size, the morphology of arborescent lycopods is relatively simple, and the bauplan can be reduced to a relatively small number of modular meristematic elements some of which appear to be essential (i.e., rhizomorphic root system, stem, cones) and others optional (i.e., lateral branches and crown branches). Based on systematic and morphological analyses, Bateman et al. (1992) suggest that arborescent lycopods are predisposed to nonadaptive saltational evolution through small changes in growth regulation early in ontogeny.

One of the most complete reconstructions of an early rhizomorphic lycopod is the pseudoherbaceous *Oxroadia*. Reconstructions of two species are based on a rich assortment of well-preserved material from lowermost Carboniferous (Upper Tournasian) limestone horizons in Scotland (Bateman 1992). *Oxroadia* is clearly a rhizomorphic lycopod because of its shoot-like rooting system with secondary growth. It is a plesiomorphic member of this clade (Fig. 3) and has an unusual growth form resulting from early dichotomy of the main stem followed by repeated branching of a prostrate cone-bearing crown. The woody anatomy, growth form and systematic position of *Oxroadia* suggest that this unusual pseudoherbaceous habit may have evolved through saltation from a tree-like ancestor involving a highly precocious dichotomy of the apical meristem giving an abbreviated stem and a much smaller plant (Bateman 1992).

d) Ferns

Relationships among Marattiales, Ophioglossales, leptosporangiate ferns, and other major Paleozoic clades of Psilophytopsida including sphenopsids and seed
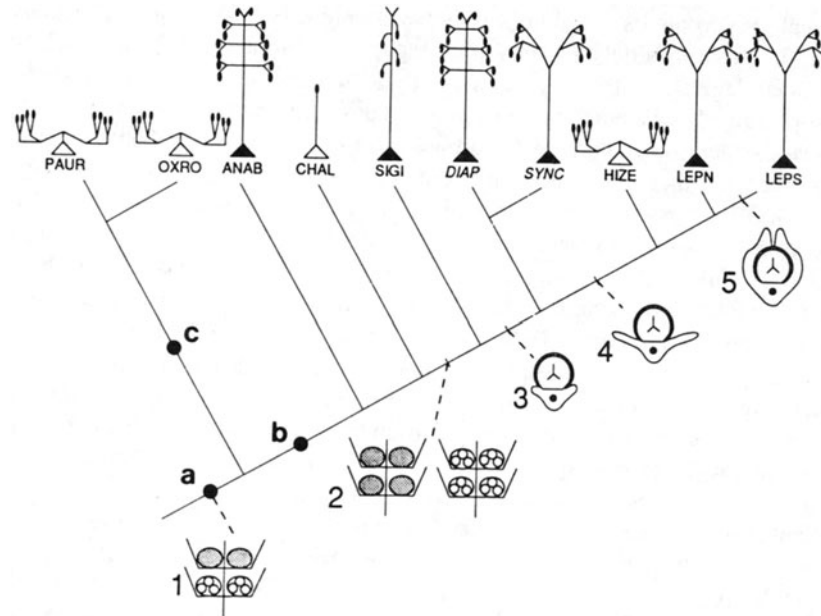
Fig. 3. Cladogram summarizing relationships among extinct arboreous rhizomorphic Lycopodiopsida. Reproductive innovations: *1* bisexual cone; *2* segregation of megasporangia and microsporangia into separate cones; *3* reduction to single functional megaspore; *4* lateral expansion of megasporophyll; *5* enclosure of megasporangium by megasporophyll. Growth habit (not to scale) illustrated on **upper part** of cladogram: *Paurodendron* (*PAUR*); *Oxroadia* (*OXRO*); *Anabathra* (*ANAB*); *Chaloneria* (*CHAL*); *Sigillaria* (*SIGI*); *Diaphorodendron* (*DIAP*); *Synchysidendron* (*SYNC*); *Hizemodendron* (*HIZE*); *Lepidodendron* (*LEPN*); *Lepidophloios* (*LEPS*). (Bateman 1992)

plants are still poorly understood. Cladistic treatments at the macrosystematic level have focused on extant taxa and are preliminary (e.g., Bremer 1985; Bremer et al. 1987). No cladistic study based on extant groups has yet exhausted the general data of comparative morphology. Furthermore, problems of homology recognition among extant taxa are exacerbated because many of the major cladogenic events occurred in the Devonian, and there has been significant subsequent morphological divergence. Over the last 30 years there has been a growing realization that many Carboniferous ferns assigned to the extinct Coenopteridales actually represent ancient members of the Filicales (Rothwell 1991). Further clarification of relationships and homologies at this systematice level requires a synthetic approach modeled on recent macrosystematic studies of seed plants.

Marattiales and leptosporangiate ferns have an extensive Late Paleozoic and Mesozoic fossil record. The history of marattialean ferns extends back to the Lower Carboniferous, where pinnules bearing distinctive abaxial exannulate synangia are the commonest form of fossil evidence. Late Carboniferous and Permian marattialean ferns were diverse and form the focus of many studies, including

description of new taxa (Wan and Basinger 1992; Gao and Thomas 1993) and reevaluations of previously described material. *Grandeuryella* is a permineralized marattialean fossils from the Late Carboniferous and Early Permian of France. The presence of synangiate organs rather than clusters of free sporangia in specimens originally described by Renault in 1883 demonstrates a greater similarity to modern *Angiopteris* than had previously been supposed (Lesnikowska and Galtier 1991, 1992). Cladistic analysis suggests that most Late Palaeozoic fossils are stem-group taxa and that the marattialean crown group first appears in the Mesozoic (Hill and Camus 1986). Most late Paleozoic stem-group fossils are extinct by the Early Mesozoic, but *Scolecopteris antarctica*, recently described from the early Middle Triassic of Antarctica, represents one of the longest surviving examples (Delevoryas et al. 1992).

Taxa assignable to the Osmundales first appear unequivocally in the Permian and are commonly preserved as permineralized stems. Recent descriptions include late Permian taxa from China (Li 1993), Mesozoic taxa from Australasia (Tidwell 1991; Tidwell et al. 1991; Tidwell and Pigg 1993), and Cenozoic taxa from Spitsbergen (Kvaček and Manum 1993).

Leptosporangiate ferns underwent their main diversification during the Mesozoic, and the history of the group is documented by numerous dispersed spores and abundant macrofossils. Van Konijnenburg-van Cittert discussed the evolutionary history of Matoniaceae (van Konijnenburg-van Cittert 1993) and Schizaeaceae (van Konijnenburg-van Cittert 1991, 1992a) based on a study of in situ spores from both extant and extinct taxa. The Matoniaceae, now restricted to the Malaysian Archipelago, were widespread during the Jurassic and Early Cretaceous in both Southern and Northern Hemispheres. Spores of Matoniaceae may be separated into three groups, with those of modern genus *Phanerosorus* being the most derived (van Konijnenburg-van Cittert 1993). The Schizaeaceae are now mainly a Southern Hemisphere family, but the group was a common element in Northern Hemisphere floras during the late Mesozoic. van Konijnenburg-van Cittert (1992a) suggests that forms with heavily ornamented, trilete spores developed earlier than other forms. The oldest unequivocal schizaeaceous remains are *Lygodium*-like fossils from the Jurassic and Early Cretaceous. *Anemia*-like and *Mohria*-like plants are recorded from the Early Cretaceous. A more comprehensive analysis of relationships among extant and extinct species of *Anemia* and species of the extinct genera *Ruffordia* and *Pelletixia* showed that *Anemia* section *Coptophyllum* is paraphyletic (Skog 1992). The inclusion of fossil taxa further provided information on the timing of divergence.

The macrofossil record of Marsileales is poor, but the group is thought to extend back into the Early Cretaceous based on megaspores of *Molaspora* (Collinson 1991). This hypothesis has recently been confirmed by the first description of unequivocal megafossils of *Marsilea* from the Mesozoic (mid-Cretaceous) (Skog and Dilcher 1992, 1994). These fossil data document a nearly complete plant with roots, rhizome, leaflets, and possible sporocarps, showing morphology and habit that is almost identical to extant *Marsilea*. Megaspores characteristic of extant Salviniales occur in the earliest Tertiary, and other similar

forms can also be traced to the early Cretaceous (Collinson 1991). The Tertiary megafossil record is better than for Marsiliales, but the earliest megafossils resembling extant *Salvinia* and *Azolla* have recently been described from the late Cretaceous Deccan Intertrappean beds, India (Nambudiri and Chitaley 1991).

e) Sphenopsids

Sphenopsid diversity is greatest in Lower Carboniferous coal-swamp floras, where the group comprises both arborescent and herbaceous taxa. Species numbers declined through the Upper Carboniferous to relatively low levels that have persisted to the present day, where the group is represented by the small but widespread genus *Equisetum*. Relationships among sphenopsids including Archaeocalamitaceae, Calamitaceae and Equisetaceae, and putative Devonian presphenopsids such as *Arachnoxylon*, *Calamophyton*, *Cladoxylon*, *Hyenia*, *Ibyka*, and *Pseudosporochnus* have been widely discussed (Stein et al. 1984). Archaeocalamitaceae are the earliest unequivocal sphenopsids and form an important link between Calamitaceae, Equisetaceae, and putative Devonian ancestors. Recent descriptions of permineralized Archaeocalamitaceae strobili and vegetative axes from the Lower Carboniferous of Scotland have clarified certain aspects of sporangium morphology and demonstrate that at least some members of this group were heterosporous (Bateman 1991). Preliminary cladistic analysis of relationships among the three families supports the plesiomorphic position of Archaeocalamitaceae with sphenopsids and suggests that both heterospory and secondary xylem may have been lost in *Equisetum*. A considerable extension of the stratigraphic range of Archaeocalamitaceae from Upper Carboniferous (Namurian) to mid-Lower Permian (Artinskian) has recently been reported (Mamay and Bateman 1991). The appearance of *Archaeocalamites lazarii* some 55 Ma after the last recorded occurrence of the group in the Carboniferous is probably the greatest known paleobotanical stratigraphic hiatus.

f) Early Seed Plants

The early fossil record of seed plants has attracted considerable attention over the last few years with the discovery and characterization of several important taxa from Upper Devonian sediments (Rothwell and Scott 1992; Rothwell and Serbet 1992; Stewart and Rothwell 1993; Taylor and Taylor 1993; Erwin et al. 1994). Most early seed plants are characterized by fern-like leaves bearing ovules and pollen-producing structures on relatively slender stems with small amounts of primary vasculature and manoxylic secondary wood. The earliest taxa have hydrasperman reproduction, which has been interpreted as the plesiomorphic condition for all seed plants (Rothwell 1986). Hydrasperman reproduction refers to the

special structures and processes involved in pollen capture, fertilization, and sub-sequent dispersal of fertilized ovules in early seed plants. One of the most distinc-tive features of plants with hydrasperman reproduction is the elaborate structure that develops from the distal portion of the ovule nucellus and which functions in pollen capture and fertilization (Stewart and Rothwell 1993). Evidence from the early fossil record currently supports seed plant monophyly (Rothwell and Scott 1992; Rothwell and Serbet 1992; Serbet and Rothwell 1992), but lack of resolution in the relationships of basal seed plants (Doyle and Donoghue 1992), character conflicts involving vegetative morphology and anatomy (Galtier 1992), and uncertainties concerning important aspects of morphology in other potentially closely related Upper Paleozoic groups (Galtier 1992; Beck and Stein 1993) point to continued uncertainty over many aspects of relationship and homology.

Most information on Upper Devonian seed plants comes from isolated ovules, permineralized plant fragments or larger but nonpermineralized compression fos-sils. While these data have considerable interest, it is widely recognized that further clarification of the early stages of seed plant phylogeny requires more complete reconstructions involving anatomical and morphological characteriza-tion of vegetative and fertile parts. A series of important recent studies have focused on reconstructing one of the earliest seed plants, *Elkinsia polymorpha*, in some detail (Rothwell et al. 1989; Serbet and Rothwell 1992; Rothwell and Serbet 1992). *E. polymorpha* has helically arranged dimorphic fronds. Fertile fronds branch dichotomously and bear terminal ovulate cupules (hydrasperman type) or pollen organs comprising six to eight partially fused, radially arranged sporangia. Vegetative fronds are planar, have up to four orders of branching, and bear pinnate laterals that terminate in pinnules of sphenopterid type. Stem anatomy comprises a three-ribbed protostele, secondary xylem in larger axes, and a prominent sclrenchymatous cortex. Fronds have two C-shaped xylem strands. The reconstruction of *E. polymorpha* represents an important step in under-standing early seed plant morphology, and this taxon will figure prominently in ongoing phylogenetic studies on the origin of seed plants.

Current understanding of early seed plant morphology is based on megafossils from North America and Europe. Ovulate and associated microsporangiate struc-tures have been described recently from the Late Carboniferous of Peru (Erwin et al. 1994). *Oclloa cesariana* has hydrasperman reproduction and is interesting because the ovules are terminal but not borne in a cupule, as with most other early seed plants. Because many aspects of morphology and anatomy are still unknown, the systematic position of *O. cesariana* is equivocal. It is not yet pos-sible to determine whether the absence of a cupule is a retained plesiomorphic feature or a loss.

Late Paleozoic seed ferns including taxa such as medullosans, lyginopterids, and *Callistophyton* have played an important role in understanding relationships in seed plants and have figured prominently in several recent cladistic treatments (see literature cited in Doyle and Donoghue 1992). Cladistic studies have brought the systematic problems in basal seed plants into sharper focus, but relationships among these groups and extant cycads, *Ginkgo*, conifers, and anthophytes are

still the subject of much debate. Co-occurring with these taxa is a diverse range of less well known but important fossil material that is likely to contribute information critical to further clarification of relationships and homologies. Recent research has focused on Calamopityaceae, an abundant but rather poorly understood group of Lower Carboniferous plants that share generalized features of several Paleozoic seed ferns. Calamopityaceae are known mainly from fragments of stem anatomy, and one of the major challenges is reconstructing stem, branch, and leaf architecture. A major revision of the group is currently in progress (Beck et al. 1992; Galtier 1992; Galtier and Beck 1992; Galtier et al. 1993; Stein and Beck 1992).

g) Cycads

Studies based on extant plants indicate that cycads are sister group to all other seed plants (Loconte and Stevenson 1990; Doyle and Donoghue 1992). The systematic position of the group is less clear in more comprehensive analyses that include well-known fossils, in particular "pteridosperms" and "progymnosperms". Phylogenetically informative cycad reproductive material is rare in the fossil record, and while the abundant leaf record provides important information on quantitative diversification and geographic distributions of the group, it has had little impact on cycad systematics. An interesting rediscovery of the cycadalean ovule *Cycadeocarpus columbianus* was recently reported from the Middle Jurassic of Queen Charlotte Island, British Columbia, Canada (Chaloner and Hemsley 1992). The ovules are permineralized and excellently preserved with pollen grains inside the micropyle. Pollen is of general *Cycadopites* type and monocolpate. Associated with the ovules are leaf petioles and leaflets with cycad anatomy. The large size of the ovules combined with the radiosymmetrical organization of the ovule wall clearly indicate a cycadalean affinity and distinguish them from the platyspermic ovules of ginkgos.

Extant cycads have a relict distribution, but the group was a ubiquitous and cosmopolitan element of Mesozoic vegetation. During the late Mesozoic and Tertiary, the importance of cycads declined through loss of diversity and contraction of geographic range. A recent study of leaves assigned to *Eostangeria ruzinciniana* from Romania indicates that cycads survived in Europe at least to the end of the Miocene, probably in vegetation adapted to subxeric conditions (Palamarev and Usunova 1992). *Eostangeria ruzinciniana* was originally assigned to the fern genus *Angiopteris*, but was transferred to cycads based on epidermal characters of the leaflets. Extinct cycads assigned to the genus *Pterostoma* from high latitude floras in the Tertiary of Australia and New Zealand provide further evidence for a greater diversity and wider distributions in the Southern Hemisphere (Pole 1992; Rowett 1992; Hill and Pole 1994). *Pterostoma* was widespread particularly in Early Tertiary floras and became extinct by the Late Tertiary.

h) Pteridosperms

Pteridosperms are a heterogenous group of fossils comprising a grade of organization characterized by plants with ovules and pollen producing organs borne either on leaves, as in many Paleozoic taxa, or on simple or branched axes, as in many Mesozoic taxa. A study of medullosan pteridosperms from China has revealed significant new details on leaf morphology and reproductive organization in two widespread Paleozoic genera, *Paripteris* and *Linopteris*. Most significant is probably the discovery that the microsporangiate organ (*Potoniea*) associated with *Paripteris* is borne on planate, dicotomously branched axes in a dense spiral arrangement forming a large compound structure (Laveine et al. 1993). This arrangement is very different from that in other medullosans and may be of importance in future phylogenetic studies.

Permineralized fossils discovered during the past few years in silicified Permian and Triassic peats from Antarctica constitute one of the most important sources of information on structure and organization in Gondwanan pteridosperms. Anatomically preserved leaves of *Glossopteris* from the Permian and of *Dicroidium* from the Triassic were reported in Progress in Botany, Volume 53, and several new publications on this silicified material have appeared recently. One step towards a more comprehensive understanding of the *Glossopteris* plant is the discovery of silicified axes with leaves attached from the Transantarctic Mountains (Pigg and Taylor 1993). This is the first direct link between anatomically preserved leaves and axes for *Glossopteris*. In compression material leaf arrangement sometimes appears to be whorled, but the permineralized specimens clearly show a spiral arrangement of densely crowded leaves.

The recent discovery of permineralized ovulate structures is one of the most significant findings in the Antarctic *Glossopteris* flora (Taylor and Taylor 1993). Although reproductive structures of *Glossopteris* are extremely common in Late Paleozoic Gondwanan floras, most are impression fossils and their organization is poorly understood. Lack of critical information on the ovulate structure has caused problems in scoring reproductive characters in glossopterids, resulting in weakly supported hypotheses of relationship. Taylor and Taylor (1993) were able to document that in these Antarctic glossopterids ovules were borne adaxially on laminate structures that completely matched *Glossopteris* leaves previously described from the same locality. Taylor and Taylor (1993) figured one ovulate structure with several ovules, but they also noted that uni-ovulate structures were recovered from the same horizon. A further addition to our knowledge of the *Glossopteris* plant comes from a silicified Permian peat in East Antarctica. This peat has yielded well-preserved glossopterid roots (*Vertebraria*) with evidence for stages in root ontogeny (Neish et al. 1993).

Several new descriptions of glossopterid plants from other Gondwanan regions are based on impression and compression fossils (e.g., Chandra and Singh 1992; Maheshwari and Tewari 1992; Srivastava 1991; Mcloughlin 1994a,b). Although

these fossils generally do not provide any new information of phylogenetic importance, they document the abundance of glossopterids in Late Paleozoic Gondwanan floras. They also demonstrate problems in specific delimitation for the huge number of species described from the various areas.

Permineralized Triassic floras from Antarctica are providing important new information on corystosperms. It has long been debated whether the microsporangiate organs were compound microsporophylls or branch systems. Discovery of anatomically preserved material from Antarctica clearly demonstrates that at least some corystosperms had helical arrangements of microsporangiate units (Yao et al. 1992). This material is beautifully preserved and also provides details on in situ pollen morphology (eusaccate) and ultrastructure (Osborn and Taylor 1993). Microsporangiate units are associated with abundant leaves of *Dicroidium* described in detail earlier (see Progress in Botany, Vol. 53). New findings of small stems with leaf bases attached show anatomical similarities to these *Dicroidium* leaves and provide the first direct evidence for a link between *Dicroidium* leaves and *Rhexoxylon* stems (Meyer-Berthaud et al. 1992, 1993).

Another significant discovery in the Mesozoic floras of Antarctica is the microsporangiate organ of *Caytonanthus* (*Caytonia* plant). This is the first report of *Caytonia* from a Gondwanan flora (Rees 1993). The material comes from the classic Hope Bay and Botany Bay floras, northern Graham Land, Antarctica. It is interesting that *Caytonanthus* in Antarctica is associated with the *Caytonia* leaf, *Sagenopteris*, as it is in many Northern Hemisphere floras. The occurrence of the *Caytonia* plant in Gondwana is consistent with the close relationship between *Caytonia* and the glossopterids inferred from several phylogenetic analyses (e.g., Nixon et al. 1994).

A new microsporangiate structure, *Brenneria potomacensis*, containing pollen grains of the *Decussosporites* type has recently been discovered from Early Cretaceous strata of eastern North America (Pedersen et al. 1993). *Brenneria* is believed to be related to other Mesozoic pteridosperms but also shares some similarities with conifers. *B. potomacensis* consists of a central axis bearing microsporangiate units in a helical arrangement similar to several other pteridosperms (*Antevsia, Harrisiothecium*: Friis and Pedersen unpubl.; *Pteruchus*: Yao et al. 1992; Kirchner and Müller 1992). Microsporangiate units bear two laterally fused sporangia and are in this respect simpler than other pteridosperms. Pollen grains are striate and disaccate with infilling of sacci resembling *Caytonanthus, Harrisiothecium* and some glossopterids. Associated dispersed seeds have been linked to *Brenneria* on the basis of in situ *Decussosporites* pollen. At present, too many critical features of the *Brenneria* plant are missing to allow a more detailed analysis of relationship (Pedersen et al. 1993).

i) Ginkgos

The phylogenetic position of Ginkgoales is one of several unresolved questions in seed plant systematics. Meyen (1987) grouped the Ginkgoales in its own class,

Ginkgoopsida, together with a number of extinct plants traditionally classified as pteridosperms. Alternatively, several cladistic analyses indicate that Ginkgoales may be more closely related to conifers and cordaits (e.g., Doyle and Donoghue 1992; Nixon et al. 1994). However, in these analyses only the extant species *Ginkgo biloba* was included. It has long been clear from the study of fossil leaves that variation within the group was considerable, particularly in the Mesozoic. New studies, mainly on Chinese material, now provide evidence for considerable variation in the organization of reproducture structures, and this material may eventually help in clarifying the phylogenetic position of the group. Two ovulate structures described by Zhou were reported earlier (Progress in Botany, Vol.50 1989) and one new ovulate structure, *Yimaia recurva*, was described recently (Zhou and Zhang 1992). This fossil is particularly interesting because it has been possible to link ovulate branches with leafy branches and pollen. The female branch of *Yimaia* comprises eight to nine densely spaced, sessile and orthotropous ovules. In contrast to *Ginkgo*, the ovules are not borne in a cupule. *Yimaia* is associated with leafy branches of *Baiera hallei*. Pollen grains have been observed adhering to both ovules and leaves. Zhou (1993) has added further ultrastructural details of the megaspore membrane in *Yimaia* and the fossil *Ginkgo yimaensis*. This study also includes a detailed analysis of developmental stages in the megaspore membrane of extant *Ginkgo biloba.*

   Further details on epidermal characters have also emerged from cuticular studies of fossil *Ginkgo* leaves from the Late Jurassic and Early Cretaceous of Mongolia (Sun 1993; Zhao et al. 1993). A preliminary phylogenetic analysis of Ginkgoales based on living and fossil material by Zhou (1991) used Cordaites and early conifers as outgroups. This analysis does not address questions of relationships to other nonginkgoalean seed plants but may be a useful basis for further macrosystematic studies.

   The Mesozoic *Czekanowskia* group is sometimes classified with Ginkgoales, but the systematic status of the group is equivocal because reproductive organs are poorly understood. *Czekanowskia* is a very conspicuous element in many Mesozoic floras of Eurasia. In a recent monograph, Samylina and Kirtchkova (1991) provide a detailed survey of the genus. This study includes the description of 62 species of *Czekanowskia* from the former USSR, and most of these are new. The paper is written in Russian, but descriptions are documented by numerous line drawings and good quality SEM micrographs as well as transmitted light micrographs of epidermal details. A key is provided for all species, and there are a number of tables and maps to illustrate geographic and stratigraphic distributional patterns. Several of these maps and tables were published later in a shorter paper in English that summarizes the characters and history of the genus (Samylina and Kirtchkova 1993).

   A variety of large *Gingko*-like, flabelliform leaves from the Late Paleozoic are sometimes collectively referred to the highly heterogenous Palaeophyllales. Some leaves may be classified with the Ginkgoales, while the position of other taxa is uncertain. A new taxon, *Velizia inconstans*, related to this morphological complex has been described from the Late Paleozoic of Argentina (Césari and Hünicken 1992). This material is significant because it includes leaves and re-

productive structures attached to shoots. Although preservation does not permit detailed reconstruction of the plant, it is clearly distinct from the Ginkgoales in organization of vegetative and reproductive organs. The leaves of *Velizia* show morphological resemblance to leaves of *Rhipidopsis*. Interestingly, Maheshwari and Bajpai (1992) reported new specimens of *Rhipidopsis* from the Permian Gondwana flora of the Rajmahal Basin, India, which also showed attachment of the shoot, documenting a spiral phyllotaxis and the apparent absence of short shoots as observed in *Velizia*.

j) Cordaitopsids and Coniferopsids

During the past few years considerable progress has been made towards a better understanding of Palaeozoic coniferopsids. The discovery of new material together with reinvestigation of critical key fossils has identified a much wider diversity of early coniferopsids than previously known, and reinterpretations of ovulate structures in members of the extinct order Voltziales indicate that classification and evolutionary models may have to be modified. Reinvestigation of the fossil *Walchiostrobus* (Kerp and Clement-Westerhof 1991) has shown that the ovulate dwarf shoot had three ovules rather than one, as originally described by Florin (1940). Furthermore, ovules are adaxially attached as in other Walchiaceae. This has some phylogenetic implications since a derivation of ovulate cones such as *Pseudovoltzia* with abaxially attached ovules from *Walchiostrobus* is not as straightforward as anticipated in classical phylogenetic hypotheses (Kerp and Clement-Westerhof 1991).

New findings of cheirolepidiaceous conifers provide further knowledge of structure and diversity in this enigmatic family (Clement-Westerhof and van Konijnenburg-van Cittert 1991; Raubeson and Gensel 1991; Srinivasan 1992; Thévenard 1993). Well-preserved ovuliferous material of *Hirmeriella* from the Early Jurassic of Germany was described by Clement-Westerhof and van Konijnenburg-van Cittert (1991) and forms the basis for a detailed discussion of ovuliferous structures in the Cheirolepidiaceae and a reevaluation of previous interpretations of cone structure in the family. Comparisons among the various taxa are visualized with instructive line drawing, and characters are documented in tabular form. The authors conclude the *Hirmeriella* possesses the most primitive characters within the family, while *Frenelopsis* may be regarded as a derived form. They also suggest that the Cheirolepidiaceae are derived from the Paleozoic volzialean family Majonicaceae (Clement-Westerhof and van Konijnenburg-van Cittert 1991).

A rich assemblage of fossil conifers has been described from calcium carbonate nodules in the Late Cretaceous of Hokkaido, Japan (Nishida 1991). Preservation is excellent and reveals a wealth of systematically important details. Recent descriptions include a sciadopityaceous seed cone assigned to a new form genus

Sciadopityostrobus (Saiki 1992), a taxodiaceous seed cone also assigned to a new form genus *Mikasastrobus* (Saiki and Kimura 1993), an arauracarian seed cone (Stockey et al. 1992), and leafy branches of *Brachiophyllum* (Ohana and Kimura 1993). The araucarian seed cone from Hokkaido has well-preserved seeds with embryos, and the fossil can be assigned to modern *Araucaria* based on well-documented features of seed anatomy. This is the first record of *Araucaria* cones in Asia, and this discovery extends the Northern Hemisphere stratigraphic record of *Araucaria* into the Late Cretaceous. New descriptions of Early Cretaceous arauracarian fossils from other parts of the world include leaves and pollen cones from Spain (Barale 1992) and a rich assemblage of leaves from Australia (Cantrill 1992). The Spanish leaves and pollen cones were assigned to the same species based on epidermal features. The material shares features of *Agathis* as well as *Araucaria* and was placed in the form genus *Dammarites* (Barale 1992). The Australian material includes six new species of leaf fossils referable to *Araucaria*. Based on epidermal features, Cantrill (1992) was able to separate these into three groups, one group comparable to modern members of section *Eutacta*, one group comparable to section *Columbea*, and one group (with one species) showing characters of both *Eutacta* and *Columbea*.

A new species of *Pinus* (subsection *Oocarpae*), closely related to modern Californian closed pines, has been described from well-preserved permineralized material in a Miocene chert, Washington State, USA (Miller 1992). The material comprises permineralized pinaceous leaves, dwarf shoots, pollen, and seed cones. Reconstruction of the whole plant based on organ associations was possible because only one type of each organ was present in the locality and the material had not been transported. Closed cone pines have also been reported from younger deposits in California (Axelrod and Cota 1993). Another new pinaceous cone was described from the Miocene of Idaho, USA, by Mente and Brack-Hanes (1992). This material is preserved as compression fossils and information is restricted mainly to morphological features and epidermal details. A comparison between the fossil material and modern Pinaceae is presented in tabular form and illustrates that the fossil has a mosaic of features found in several extant taxa. For this reason, Mente and Brack-Hanes (1992) were unable to place the material in any of the modern genera and referred it to the form genus *Pityostrobus*. The fossil history of Pinaceae was briefly summarized by Mente and Brack-Hanes (1992), and a more detail account of phylogenetic and spacial patterns in the radiation of the genus *Pinus* was given by Millar (1993) with special emphasis on events during the Eocene.

A recent study by Ferguson (1992) provides important new information on the fossil history of the taxaceous genus *Amentotaxus*. The work includes a detailed survey of the extant species focusing on characters that may be useful in identifying fossil material. Ferguson (1992) concluded that *Amentotaxus* is basal in the Taxaceae, which is consistent with the long fossil record dating from the Palaeocene. The genus shows great morphological stability for the first 55 million years, but considerable evolutionary change took place during the Quaternary. Recent morphological evolution was attributed to geological changes occurring in eastern Asia during the last few million years (Ferguson 1992).

k) Anthophytes

Under this heading we include angiosperms and closely related gymnospermous seed plants such as the Gnetales and the extinct order Bennettitales, in addition to several unassigned forms recognized as possible anthophytes during the past few years (see Progress in Botany, Vol. 54). A recent study by van Konijnenburg-van Cittert (1992b) has added a significant new member to the anthophytes group by documenting pollen of *Ephedripites* in situ in the Liassic microsporangiate organ *Piroconites*. *Piroconites* consists of numerous densely packed and three-loculed synangia borne on one surface of a larger bract-like structure (*Bernettia*). The individual synangium shows some resemblance to the synangia of extant *Welwitschia*, but the dense clustering is unlike anything known in members of the Gnetales. A comparable clustering of synangia is reported for the microsporangiate structure *Erdtmanitheca*, which has *Eucommiidites* pollen in situ. *Erdtmanitheca* is also considered to be related to anthophytes and especially close to the Gnetales (Pedersen et al. 1989). *Piroconites*, however, differs from *Erdtmanitheca* in its planate organization.

A monograph of Bennettitales from the English Wealden documents the vast diversity of this group in the Early Cretaceous (Watson and Sincock 1992). The work includes well-documented and well-illustrated descriptions of about 50 taxa of leaves, flowers, bracts, and stems. More than half of the species described are new.

Structure, homology and relationship within anthophytes are currently widely debated and many studies have been published over the last few years. These studies include classical morphological and anatomical investigations of fossil and living material, molecular investigations of extant taxa and theoretical computer-based analyses. A more comprehensive account of progress in this area will be given in Progress in Botany, Volume 57.

3. Discussion

Paleobotanical data play an important role in elucidating relationships among major groups of land plants. Much land plant diversity is extinct, and many extant groups represent the last vestiges of once diverse and important Paleozoic and Mesozoic clades. Recent advances in systematic theory have brought the role of paleobotanical data into sharper focus by highlighting the importance of the fossil record for understanding relationships and homology, particularly at higher systematic levels. Much recent work has focused on reinterpreting current knowledge from the new theoretical perspective offered by cladistic analysis. Early studies focused on seed plants and were characterized by their synthetic approach that integrated paleobotanical and neobotanical comparative data. This approach

is currently being extended to lycopods and other "pteridophyte" groups with an extensive and well-documented fossil record. Cladistic analysis has helped to clarify important macrosystematic problems and to identify those areas where an empirical approach is likely to have greatest impact. The most interesting new data are likely to come through detailed reconstructions of plants in the stem groups and basal crown groups of major clades such as angiosperms, seed plants, leptosporangiate ferns, tracheophytes and, in particular, mosses, hornworts, and liverworts.

Systematic studies provide the essential framework for interpreting other paleobotanical and neobotanical patterns of land plant diversity. In this chapter, we have focused on the systematic phylogenetic aspects of paleobotanical research, but information from fossil plants has much wider applications in areas such as stratigraphy, paleoecology, paleoclimatology, paleogeography, biogeography, and historical aspects of species diversity. The synthesis of data from these diverse disciplines provides an overall picture of life history over time. A recent synthesis has been published in a multiauthor volume edited by Behrensmeyer et al (1992) which discusses the evolution of Phanerozoic terrestrial ecosystems focusing on the taphonomy and paleoecology of land-based faunas and floras. *Terrestrial Ecosystems Through Time* reconstructs the general components of past communities and deals with general patterns of change over long time periods from a broad historical perspective. Geographical, ecological, climatological, and stratigraphic aspects of the Paleozoic fossil record have recently been analyzed in a book edited by Cleal (1991).

The origins of modern diversity have attracted much attention recently, and the problem has been approached from a number of different perspectives. Recent trends in books such as Ricklefs and Schluter (1993) have been towards an integration of data from the fossil record with modern biogeographic and ecological analysis. This approach acknowledges the importance of historical processes, understood through systematics, biogeography, and paleontology, and ecological processes, such as interactions among extant populations, in the origin and maintenance of species diversity. The origin of modern distributions and community structure were treated in a book by Tallis (1991), focusing mainly on the late Cenozoic. Much recent analysis and synthesis deals with general trends and large-scale pattern, but other studies have focused on narrower, more specific issues. Details of community structure such as the historical development of plant-animal interactions have also attracted attention, and recent approaches have been summarized in a Royal Society Symposium (Chaloner et al. 1991). More specific biological questions recently addressed using paleobotanical data include the origins of polyploidy in angiosperms using variations in stomatal guard cell size as a measure of total DNA content (Masterson 1994). Measures of carbon isotope abundances in fossil material are also providing data on the origins of major photosynthetic pathways (Cerling et al. 1993; Bocherens et al. 1994; Morgan et al. 1994).

Reconstructing climatic change through the Cenozoic has attracted much attention recently and is of great potential importance to understanding modern

climates and predicting the effects of future climatic changes. Data on the temporal and geographic distributions of temperature-sensitive groups of plants and animals are critical to testing computer-based climate models for the Cenozoic (Spicer and Corfield 1992; Taylor et al. 1992; Wing and Greenwood 1993). Analyses of isotope abundances may also prove to be useful in tracing changes in major atmospheric components through time. Changes in stomatal densities are currently being tested as potential indicators of historical changes in atmospheric carbon dioxide concentrations (Beerling and Chaloner 1992; Beerling et al. 1992; Van der Burgh et al. 1993).

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Dr. Paul Kenrick
Prof. Else Marie Friis
Department of Palaeobotany
Swedish Museum of Natural History
Box 50007
S-104 05 Stockholm
Sweden