Fossils and plant phylogeny[1]

Peter R. Crane,[2,5] Patrick Herendeen,[3] and Else Marie Friis[4]

[2]Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK; [3]Department of Biological Sciences, The George Washington University, Washington DC 20052 USA; [4]Department of Palaeobotany, Swedish Museum of Natural History, Box 50007, S-104 05 Stockholm, Sweden

Developing a detailed estimate of plant phylogeny is the key first step toward a more sophisticated and particularized understanding of plant evolution. At many levels in the hierarchy of plant life, it will be impossible to develop an adequate understanding of plant phylogeny without taking into account the additional diversity provided by fossil plants. This is especially the case for relatively deep divergences among extant lineages that have a long evolutionary history and in which much of the relevant diversity has been lost by extinction. In such circumstances, attempts to integrate data and interpretations from extant and fossil plants stand the best chance of success. For this to be possible, what will be required is meticulous and thorough descriptions of fossil material, thoughtful and rigorous analysis of characters, and careful comparison of extant and fossil taxa, as a basis for determining their systematic relationships.

Key words: angiosperms; fossils; paleobotany; phylogeny; spermatophytes; tracheophytes.

Most biological processes, such as reproduction or growth and development, can only be studied directly or manipulated experimentally using living organisms. Nevertheless, much of what we have inferred about the large-scale processes of plant evolution, and much of what we know about the plant diversity to which those processes gave rise, is based on preserved samples taken from living organisms. These samples, brought together in the collections of museums and herbaria around the world, are crucial to attempts to name, characterize, systematize, and understand the origin of the variety of plant life. They are also the starting point for any investigation of plant phylogeny. Preserved specimens are the essential samples and indispensable reference points on which knowledge of botanical diversity and large-scale processes of plant evolution are based.

Fossils, like herbarium specimens and leaf fragments kept in silica gel for DNA analysis, are the remains of once-living organisms gathered at a particular time and from a particular place. There is no essential difference between a dried specimen collected a decade ago and a fossil specimen entombed within rocks for millions of years. Neither is a perfect sample of a complex living organism, but combined with knowledge from other samples of plant diversity and supplemented by information from living plants, both can help answer questions about the form of the botanical tree of life and the processes by which it has come about.

Even relatively recently, paleontological data have been considered by some (e.g., Hughes, 1976, 1994) to be the final arbiters in any effort to understand plant phylogeny. We do not subscribe to this view. Recent advances in systematic theory have developed a more sophisticated perspective and have helped to clarify exactly what information fossils can and cannot deliver (e.g., Hill and Crane, 1982; Crane and Hill, 1987; Patterson, 1981; Doyle and Donoghue, 1987; Gauthier et al., 1988; Donoghue et al., 1989). The result is a straightforward and uncompromising view of paleontological data. In a cla-

distic context, neither fossils nor their stratigraphic position have any special role in inferring phylogeny, and although more complex models have been developed (see Fisher, 1994; Huelsenbeck, 1994), these have not been widely adopted. But fossils do provide additional information on the diversity of plants, which must be accounted for by any comprehensive understanding of plant phylogeny and evolution (e.g., Doyle and Donoghue, 1987). They also provide evidence on the timing of evolutionary events that is useful to develop and test ideas on how the variety of plant life may have arisen (e.g., Doyle and Donoghue, 1993; Crane et al., 1995).

In this paper, we discuss the contributions of paleobotanical data to understanding large-scale evolutionary patterns in the plant kingdom. We begin with a brief consideration of the nature of the paleobotanical record and the temporal information it provides. We then review three key areas of plant phylogeny with a particular focus on the contributions of paleobotanical data: the origin and diversification of vascular plants, the origin and diversification of seed plants, and the origin and diversification of flowering plants. The many other contributions of paleobotanical data, to areas of science as diverse as global environmental change, biostratigraphy, and paleogeography, are not considered in this paper.

FOSSIL PLANTS AND CHARACTERS FOR PHYLOGENETIC ANALYSIS

Fossil plants are generally more poorly known than their living counterparts. However, perhaps surprisingly, they are sometimes exquisitely well preserved. In many cases, they provide a level of structural detail that cannot be retrieved from living plants without significant investment of time and effort. For example, permineralized plant fossils from classic localities such as the Eocene Princeton Chert preserve near-perfect anatomical details of stems, fruits, and seeds (e.g., Cevallos-Ferriz and Stockey, 1991; Pigg and Stockey, 1996; Stockey et al., 1998). Equivalent information for the extant relatives of these plants is frequently not readily available. Similarly, the quality of preservation of morphological and anatomical details in charcoalified flowers from Cretaceous fossil floras may exceed that seen in standard herbarium specimens (e.g., Friis, 1990; Herendeen et al., 1994, 1995; Keller et al., 1996; Magallón-Puebla et al., 1997, 2001; Schönenber-

ger et al., 2001; Friis et al., 2003b). In both these cases, detailed comparison of fossil and extant material often requires extensive morphological and anatomical surveys of different organs from living plants. These, and many other examples, show that frequently it is not the quality of preservation of fossil material that limits comparison with extant taxa. Often it is simply that detailed comparative, morphological, and anatomical studies of the relevant living plants have not been done.

A much more significant problem, at least for most fossils of large and complex plants (e.g., shrubs or trees), is that the different organs derived from the same living plant rarely occur in attachment in fossil assemblages. Thus while the leaves, seeds, pollen grains, stems, and other parts of fossil plants can often be extremely well preserved, a central difficulty is determining which of these dispersed plant organs were produced by the same fossil species. Trying to understand which leaf "belongs to" which seed or pollen grain is not a straightforward undertaking.

Because attachment between different organs in the fossil record is the exception rather than the rule, attempts to reconstruct fossil plants generally lean heavily on a variety of indirect inferences (see for example the arguments used to reconstruct various fossil angiosperms; Dilcher and Crane, 1984; Magallón-Puebla et al., 1997; Manchester et al., 1999). Unless done extremely carefully, such inferences are potentially subject to significant error, with obvious consequences for evolutionary interpretations. This problem is especially severe in fossil assemblages that are composed mainly of different plant parts from extinct taxa that lack close living relatives. In such circumstances, where living counterparts are not available, comparisons with living taxa provide no clues to aid the process of reconstruction. Consequently, the connections among different organs of the same plant species can only be worked out from first principles, for example, by patterns of association within and among fossil localities (see for example, the extinct *Nordenskioldia* plant, Crane et al., 1991; Manchester et al., 1991), structural similarities (e.g., the treatment of the *Dicroidium fremouwensis* plant, Taylor, 1996), deductions based on a process of elimination (e.g., the treatment of extinct Bennettitales by Harris, 1932, 1969), or a combination of these approaches.

One result of the difficulty of reconstructing "whole fossil plants" from assemblages that consist mainly of isolated fossils of plant parts is that our understanding of many important groups of extinct plants is based frequently on a core of more or less reliably reconstructed "whole fossil plants" surrounded by a "halo" of other plant fossils that are not understood in equal detail. For example, Caytoniales are a key group of extinct Mesozoic seed plants. Based on occurrences of dispersed, isolated leaves assigned to *Sagenopteris*, this group appears to have been widespread in the Mesozoic. However, there are only a few convincingly reconstructed "*Caytonia* plants" (Thomas, 1925; Harris, 1932, 1964). Most of what we know about extinct groups like Caytoniales or Bennettitales (Table 1) is based on unconnected bits and pieces: mainly isolated leaves and reproductive structures. Improving this situation will be slow and labor intensive. Nevertheless, such work is crucial if we are to improve significantly the extinct diversity that we know for seed plants and other groups.

THE AGE OF PALEOBOTANICAL ASSEMBLAGES

For phylogenetic and evolutionary purposes, establishing the age of fossils is secondary to establishing their relationships with living and other fossil organisms. It is self-evident that it is of no value to know that a fossil is of a particular age unless it can also be linked to a previously recognized group of plants at some level.

In broad terms, establishing the age of fossil plants is not problematic. Decades of geological and paleontological research have established that the fossil record is strongly internally consistent, just as there is pattern and internal consistency in the distribution of character states among organisms. This is well corroborated by many millions of individual observations of plant and animal fossils, as well as by geological evidence from superposition, correlation, and large-scale stratigraphic and structural geological patterns. Our current understanding of the geological column is supported by a wealth of interlocking geological data. The large-scale patterns of geological succession are well known. This is not to say that current knowledge of geology is infallible and should not be subject to revision in light of information from biology or paleontology. But to overthrow a significant body of geological data, inferences from biology or paleontology will themselves need to be highly corroborated and unambiguous.

However, it is also the case that determining the age of fossil assemblages is generally most straightforward for marine deposits where correlation is possible over large distances. Long-distance correlation is more difficult in nonmarine situations (e.g., river deposits, lake basins). Unfortunately, plant fossils are more often preserved in these nonmarine, continental settings. In cases where overlying or underlying marine rocks are not present or where these or other kinds of "controls" are widely spaced, determining a precise age for a particular plant fossil assemblage may be problematic. In some situations, pollen transported into marine sediments may be helpful, or direct radiometric dating may be possible for rocks closely associated with fossil occurrences (for example, where there is volcanic ash or other volcanic deposits), but in many geologic settings such opportunities are not available.

Therefore, the basis for establishing the age of particular fossil assemblages will vary, and it is in such details that the reliability of age determinations for fossil plant assemblages resides. For example, the age of many classic Tertiary paleobotanical localities in volcanic terrains is often well constrained by radiometric dates (e.g., Manchester, 1994, 2000), whereas the age of the classic Jurassic plant fossil assemblages of the Yorkshire coast is relatively well controlled based on the well-developed stratigraphy and overlying and underlying marine deposits (van Konijnenburg-van Cittert and Morgans, 1999). But the important early angiosperm assemblages on the Atlantic Coastal Plain of eastern North America and Portugal are much more difficult to date precisely (e.g., Brenner, 1963; Doyle and Hickey, 1976; Hickey and Doyle, 1977; Christopher, 1979; Doyle, 1992; Friis et al., 1999, 2000). Therefore, to a large extent, the age reported for any plant fossil assemblage is itself a hypothesis that is subject to test. In many cases, this hypothesis is highly corroborated by a large mass of paleontological and geological evidence, but in other cases, it may be weaker and based on less secure correlations of relatively few taxa over large distances. In most cases, the age of fossil plant assemblages in broad terms is clear (for example, at a level of tens of millions of years), but it is the precise age (millions of years) that is often much less certain. It is therefore important to understand the detailed evidence on which the age determination for a particular fossil assemblage is based.

TABLE 1. Fossil Bennettitales from the Middle Jurassic flora of Yorkshire (Harris, 1969) showing the different levels of knowledge of different "species" of fossil plants in one of the most intensively studied of all Jurassic fossil floras. Note that more than half of the species are known only from isolated leaves, others are known from two or more organs as listed. Information is available on leaves, pollen organs, and "gynoecia" for only five species.

Taxon	Comment
Bucklandia sp. A	Compressed stem
Bucklandia sp. B	Compressed stem
Zamites quinae	Isolated leaf
Otozamites thomasi	Isolated leaf
Otozamites leckenbyi	Isolated leaf
Otozamites venosus	Isolated leaf
Otozamites parallelus	Isolated leaf
Otozamites simpsoni	Isolated leaf
Otozamites anglica	Isolated leaf
Otozamites mimetes	Isolated leaf
Otozamites peuna	Isolated leaf
Otozamites tenuatus	Isolated leaf
Otozamites marginatus	Isolated leaf
Ptilophyllum hirsutum	Isolated leaf
Nilssoniopteris pristis	Isolated leaf
Anomozamites thomasi	Isolated leaf
Dictyozamites howelli	Isolated leaf
Pterophyllum fossum	Isolated leaf
Pterophyllum cycadites	Isolated leaf
Cycadolepis spheniscus	Scale leaf possibly associated with *Otozamites gramineus* leaves
Cycadolepis pelecus	Scale leaf possibly associated with *Otozamites falsus* leaves
Cycadolepis eriphorus	Scale leaf possibly associated with *Otozamites graphicus* or *Otozamites beani* leaves
Cycadolepis thysanota	Scale leaf possibly associated with *Otozamites graphicus* leaves
Cycadolepis hallei	Scale leaf possibly associated with *Pterophyllum thomasi* leaves
Williamsonia himas	Ovulate "flower" possibly associated with *Otozamites beani*
Bennetticarpus fragum	"Gynoecium" possibly associated with *Otozamites gramineus* leaves
Benneitticarpus litchi	"Gynoecium" possibly associated with *Otozamites gramineus* leaves
Weltrichia setosa	Pollen "flower" possibly associated with *Otozamites beani* leaves
Weltrichia spectabilis	Pollen "flower" possibly associated with *Otozamites gramineus* leaves
Bennetticarpus diodon	"Gynoecium" associated with *Cycadolepis stenopus* scale leaves and *Anomozamites nilssoni* leaves
Williamsoniella coronata	Bisexual "flower" associated with *Nilssoniopteris vittata* leaves
Williamsoniella papillosa	Bisexual "flower" associated with *Nilssoniopteris major* leaves
Williamsonia gigas	Ovulate "flower" associated with *Weltrichia sol* pollen "flower," *Zamites gigas* leaves, and *Bucklandia gigas* stems
Williamsonia leckenbyi	Ovulate "flower" associated with *Cycadolepis nitens* scale leaves, *Weltrichia pecten* pollen "flower," *Ptilophyllum pecten* leaves and *Bucklandia pustulosa* stems
Williamsonia hildae	Ovulate "flower" associated with *Cycadolepis hypene* scale leaves, *Weltrichia whitbiensis* pollen "flower," *Ptilophyllum pectinoides* leaves and *Bucklandia pustulosa* stems

COMPLETENESS OF THE PALEOBOTANICAL RECORD

The paleobotanical record preserves the fossil remains of only a minute fraction of all the plants that have ever existed. It is clearly incomplete, but this incompleteness is manifested in different ways (for example, spatially or temporally) that present different opportunities and problems (McKinney, 1991). The key to being able to use the paleobotanical record is to understand the nature of its incompleteness and whether or not it is adequate for the purposes for which it is being used. For example, certain kinds of plants, because of their biology and ecology, are more likely to be overrepresented or underrepresented in the paleobotanical record (e.g., see Herendeen and Crane, 1995 for comments on monocots, or Lidgard and Crane, 1990 for comments on different groups of seed plants). Similarly, different parts of the same plant also vary in the extent to which they are preserved. These and many other factors mean that different kinds of plants are represented in the fossil record to different extents. Therefore, the completeness of the record for different plants will vary con-

siderably from group to group, and the temporal ranges of different taxa will have different levels of error associated with them (e.g., Marshall, 1990).

In a phylogenetic context, it is also clear that the error bars for the ranges of fossil taxa in the same phylogenetic tree are not independent. If one node is fixed securely, then the others can only vary accordingly. As a result, the precise temporal scaling of a given phylogenetic tree is itself a complex interlocking hypothesis, with the age of different nodes established with different degrees of confidence. These in turn differentially constrain the potential age of other nodes within the tree of life. The situation is complex; nevertheless, almost 200 years of geological research has demonstrated that biostratigraphy works with rocks of different ages in many different places around the world. Furthermore, this biostratigraphic order is broadly consistent with the relative temporal sequence of the appearance of different groups or organisms that is predicted from independent estimates of phylogeny (e.g., Crane et al., 1995; Kenrick and Crane, 1997). This should give us confidence that well-corroborated patterns recognized in the fossil record are robust and likely to stand the test of time.

ORIGIN AND DIVERSIFICATION OF VASCULAR PLANTS

Progress—Over the last 50 years, enormous progress has been made with understanding the origin and diversification of vascular plants (e.g., Edwards, 1986; Edwards et al., 1995). Detailed paleobotanical studies have documented the structure of many key fossils (e.g., Li and Edwards, 1992), and careful comparative studies of living taxa have provided the essential framework in which studies of extinct taxa can be understood. The result has been an increasingly integrated understanding of the origin and diversification of tracheophytes (Fig. 1).

It is worthwhile tracing the development of the ideas that have brought us to our current understanding of tracheophyte phylogeny. A crucial step was the synthesis undertaken by Banks in the late 1960s and 1970s (e.g., Banks, 1975; see also Banks, 1992). This work effectively dismantled the earlier concept of the Psilophyta that had been established by Kidston and Lang (1917) and that subsequently had grown by accretion to accommodate a great variety of fossils from the Silurian and Devonian. Banks' key insight was that the Psilophyta had become increasingly unnatural and that within it, three clear groups could be recognized: Rhyniophytina, Zosterophyllophytina, and Trimerophytina. He also recognized the relationship between zosterophylls and extant lycopsids (Table 2).

Subsequent work showed that the rhyniophytes and trimerophytes were themselves of diverse relationships (Table 2). Zosterophylls were shown to be in large part monophyletic and the sister group to lycopsids. A small residue of zosterophyll species were of uncertain relationship to the lycopsids and core zosterophylls (Kenrick and Crane, 1997).

Other key components of the modification of Banks' scheme were the recognition of the polysporangiophyte clade and also the protracheophyte grade below the point of divergence of all extant lineages of vascular plants (crown group vascular plants), recognition of the euphyllophyte clade and extinct stem groups, and the proposal of a moniliform clade (ferns plus Psilotales and Equisetales and relevant fossils; Kenrick and Crane, 1997). Euphyllophytes were shown to be the sister group to zosterophylls plus lycopsids, whereas moniliforms were proposed as sister to lignophytes (Kenrick and Crane, 1997).

Clarification of phylogenetic patterns in and around the origin of vascular plants has provided the framework to develop initial evolutionary hypotheses on the evolution of many of the characteristic features of land plants. For example, current phylogenetic patterns indicate that the heteromorphic alternation of generations seen in all extant vascular plants arose by reduction of an isomorphic alternation of generations seen in extinct (but not extant) vascular and nonvascular plants at the protracheophyte grade (not to be confused with the isomorphic alternation of generations seen among some "green algae"). It also permitted development of new hypotheses for the origin of conducting cells, microphylls, and many other features (Crane and Kenrick, 1997; Kenrick and Crane, 1997).

Key persistent phylogenetic questions—Despite the progress made with understanding the origin and diversification of vascular plants, many important questions persist. For example, the exact relationships of hornworts, liverworts, and mosses to the polysporangiophyte clade remain controversial (based on different molecular data sets; Qiu and Lee, 2000; Shaw and Renzaglia, 2004), and this may have implications for understanding patterns of evolution among tracheophytes. Similarly, the concept of moniliforms, which was first proposed based on studies of fossils (Kenrick and Crane, 1997; but see Rothwell, 1999), has received support from studies of extant taxa (Pryer et al., 2001), but more detailed study is needed to understand exactly how these major lineages are interrelated. Many of the large number of fossils that seem to be relevant to this part of the vascular plant phylogeny also need to be understood in more detail, and their relationship to extant taxa and each other needs to be clarified. Resolving these and other uncertainties will be crucial to developing and testing hypotheses about the evolution of leaves, secondary xylem, and many other features.

Areas for future research—There is still much to be learnt about those fossil plants relevant to the early diversification of vascular plants (e.g., Edwards, 1996), and further discoveries will provide an opportunity to confront current hypotheses (e.g., Kenrick and Crane, 1997; Rothwell, 1999) with new data. However, there is even more scope for increasing our current understanding of plants of the Middle and Late Devonian and Mississippian, which are related on the one hand to lignophytes and on the other to crown group moniliforms. In general, these plants are larger and more complex (especially in vegetative morphology and anatomy) than the small and relatively simple plants that predominate in the Silurian and Early Devonian, and as a result they are more difficult to characterize in detail. Nevertheless, a better knowledge of plants at this level will be crucial to an improved understanding of the diversification of crown group euphyllophytes (ferns, Psilotales, Equisetales, and seed plants).

It is also important to recognize that the Ordovician-Devonian radiation of embryophytes and vascular plants is of comparable importance to the "Cambrian explosion" in the evolution of Metazoa. The transition from an aquatic habit to a fully terrestrial existence had profound biochemical, physiological, developmental, anatomical, and morphological consequences (Bateman et al., 1998). It was during this phase of evolution that the basic characteristics of land plants were established. Subsequently, various subgroups became still more complex over the next 400 million years. Careful study of the evolutionary transitions inherent in current phylogenetic hypotheses is likely to be productive. In particular, the potential to integrate information on developmental patterns among extinct early land plants (preserved in the anatomy of permineralized material) with a modern understanding of development in extant relatives is especially appealing. Research that has modeled the relationship between the form of stelar tissues and patterns of branching (Stein, 1993; Hotton and Stein, 1994) or sought to understand how microphylls differ in their developmental genetics from megaphylls (J. Langdale, Oxford University, work in progress) points the way forward. Comparing patterns of development in extant plants with historical patterns may also be informative (e.g., Friedman and Cook, 2000). At the level of early land plant diversification, such work only makes sense in the broader comparative context provided by integrated studies of living and fossil plants.

ORIGIN AND DIVERSIFICATION OF SEED PLANTS

Progress—Although considerable effort has been devoted to understanding the origin and diversification of seed plants over the last 30 years (e.g., Doyle, 1978; Hill and Crane, 1982;
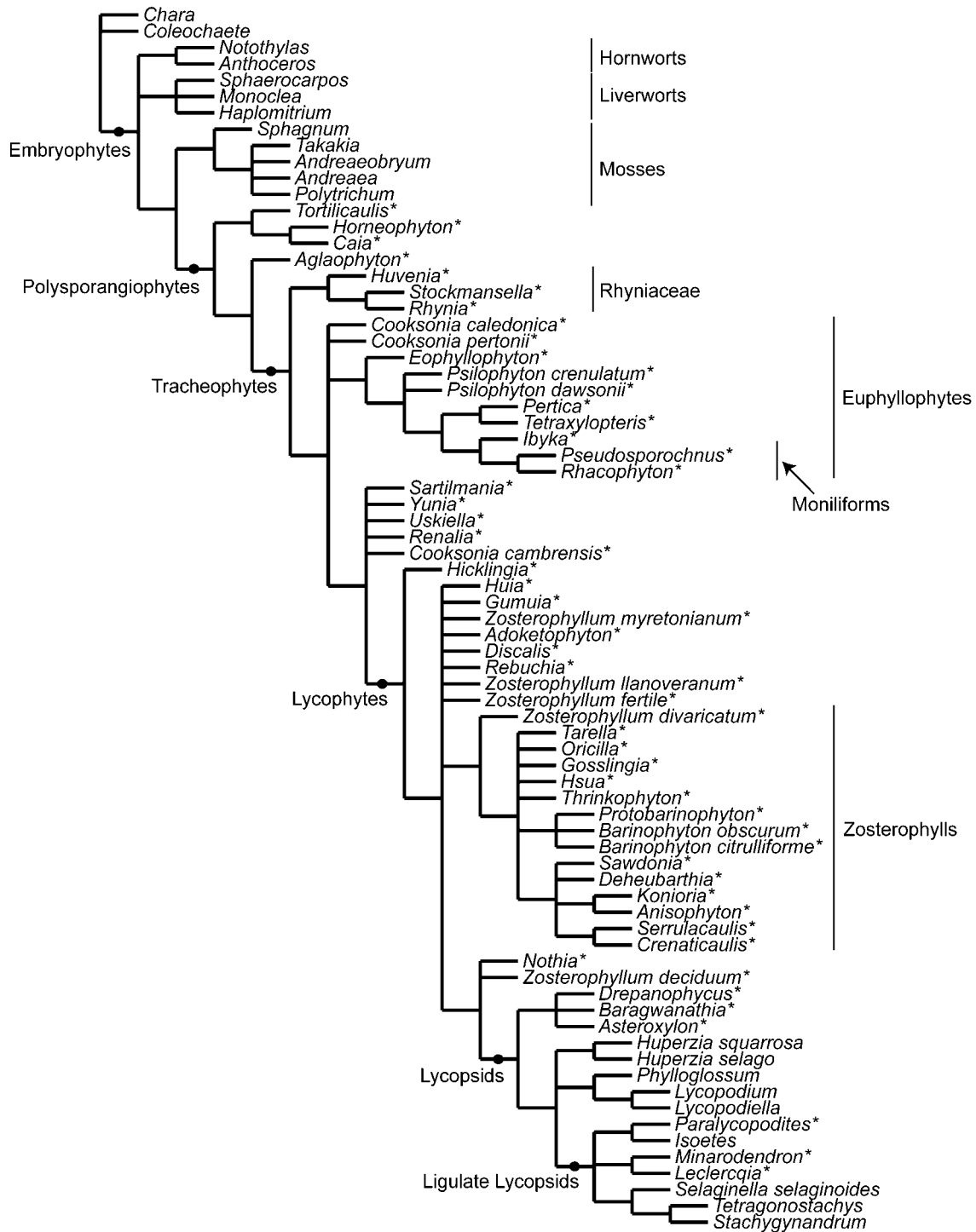
Fig. 1. Simplified cladogram showing relationships among extant hornworts, liverworts and lycophytes, and relevant fossil taxa. Note huge diversity of extinct taxa (indicated by *) interpolated among extant groups. Extant seed plants would be positioned as sister to *Tetraxylopteris* among euphyllophytes. Based on Kenrick and Crane (1997, figs. 3.35, 4.31, 5.25, and 6.18).

Crane, 1985; Doyle and Donoghue, 1986; Nixon et al., 1994; Rothwell and Serbet, 1994; Doyle, 1996, 1998; Chaw et al., 2000; Magallón and Sanderson, 2002; Soltis et al., 2002; Burleigh and Mathews, 2004), these efforts have yet to converge on a widely accepted hypothesis of relationships. Nevertheless, some progress has been made, particularly in terms of under-

standing the diversity of extinct seed plants. For example, 50 years ago, discussions of seed plant phylogeny were held back by the concept that the seed ferns (pteridosperms) were a natural evolutionary unit. A key advance was the recognition that "seed ferns" are not a meaningful group and should not be treated as such in phylogenetic discussions (e.g., Crane, 1985).

TABLE 2. Expanding knowledge of fossils of early plants and evolving ideas on their phylogenetic relationships. —= not known at the time of Kidston and Lang's (1917), circumscription of the Psilophyta. Note the accumulation of additional taxa after Kidston and Lang, then the reclassification by Banks (1975), followed by further resolution of relationships, especially of Rhyniophytina. The reevaluation of relationships includes the recognition of paraphyletic or polyphyletic genera (e.g., *Zosterophyllum*, *Cooksonia*; see Fig. 1) and the realization that some fossil genera are too inadequately known to be placed phylogenetically.

Taxon	Kidston and Lang (1917)	Banks (1975)	Current views on relationships (Kenrick and Crane, 1997)
Rhynia	Psilophyta	Rhyniophytina	*Rhynia gwynne-vaughanii* in Rhyniopsida, part of clade that is sister to all other tracheophytes; former *Rhynia major* transferred to *Aglaophyton* (nonvascular)
Horneophyton	Psilophyta	Rhyniophytina	Horneophytopsida, part of a clade at the protracheophyte grade that is sister to all tracheophytes plus *Aglaophyton*
Cooksonia	—	Rhyniophytina	Paraphyletic—of diverse relationships
Steganotheca	—	Rhyniophytina	Probably part of the *Cooksonia* complex
Salopella	—	Rhyniophytina	Incertae sedis
Dutoitea (= *Dutoitia*)	—	Rhyniophytina	Incertae sedis
Eogaspesiea	—	Rhyniophytina	Incertae sedis
Taeniocrada	—	Questionable Rhyniophytina	Polyphyletic, some taxa perhaps Rhyniopsida
Hicklingia	—	Questionable Rhyniophytina	Lycophytina, possible sister to Lycopsida, Zosterophyllopsida, and some stem lineage Lycophytina
Nothia	—	Questionable Rhyniophytina	Potential sister to Lycopsida (considered by Kidston and Lang as part of *Asteroxylon*)
Yarravia	—	Questionable Rhyniophytina	Incertae sedis
Hedeia	—	Questionable Rhyniophytina	Incertae sedis
Zosterophyllum	—	Zosterophyllophytina	Polyphyletic or paraphyletic; *Z. deciduum, Z. myretonianum* and other species outside Zosterophyllopsida, potential sister to Lycopsida
Rebuchia (= *Bucheria*)	—	Zosterophyllophytina	Probable Zosterophyllopsida, position unresolved with respect to certain groups on the zosterophyll stem lineage
Sawdonia	—	Zosterophyllophytina	Sawdoniaceae within Sawdoniales of the Zosterophyllopsida
Gosslingia	—	Zosterophyllophytina	Gosslingiaceae within Sawdoniales of the Zosterophyllopsida
Crenaticaulis	—	Zosterophyllophytina	Sawdoniaceae within Sawdoniales of the Zosterophyllopsida
Bathurstia	—	Zosterophyllophytina	Possible Zosterophyllopsida
Psilophyton	Psilophyta	Trimerophytina	Paraphyletic, stem lineages near base of Euphyllophytina
Trimerophyton	—	Trimerophytina	Probable Euphyllophytina
Pertica	—	Trimerophytina	Euphyllophytina, sister to lignophytes
Dawsonites	—	Trimerophytina	Incertae sedis
Hostimella (= *Hostinella*)	—	Trimerophytina	Incertae sedis
Psilodendrion	—	Trimerophytina	Incertae sedis
Sciadophyton	—	Incertae sedis	Gametophyte phase of some Rhyniopsida and perhaps other taxa
Barinophyton	—	Incertae sedis	Barinophytaceae, heterosporous genus in Sawdoniales of the Zosterophyllopsida

The individual elements lumped into the traditional seed fern concept are of diverse relationships. The concept of seed ferns is at best paraphyletic and more likely polyphyletic. The information available for different seed plant groups has also expanded dramatically. Callistophytes, corystosperms, and glossopterids are all groups for which important new information has become available, including important studies of permineralized material (e.g., Rothwell, 1981; Taylor and Taylor, 1992; Yao et al., 1995; Taylor, 1996; Axsmith et al., 2000; Klavins et al., 2002).

A further advance in terms of phylogeny has been the recognition that there are two grades of organization that have combinations of features that are unknown among extant taxa (Fig. 2). The first comprises early diverging lignophytes below the seed plant clade. The second comprises seed plant lineages that differentiated below the point at which the five extant groups diverge (crown group seed plants).

Since the breakthrough by Beck (1960) that resulted in the concept of the progymnosperms, it has become widely accepted that there is a grade of organization characterized by plants that produce secondary xylem and phloem but that reproduce like ''pteridophytes'' through the dispersal of free spores. Among extant plants, there is a one-to-one correspondence (except for some losses of secondary growth) between the production of secondary xylem and phloem, and reproduction by seeds. Among pteridophytes, only in some Ophioglossales is there any indication of secondary xylem and phloem in the form of a eustele. However, among extinct taxa, the correlation between seed plant reproduction and production of large woody stems breaks down. This important advance was made possible initially by a single fossil specimen that showed a connection between the wood of *Callixylon* and the leafy branch system of *Archaeopteris* (Beck, 1960).

It is also significant that almost all phylogenetic analyses of seed plants that include extinct and extant taxa have recognized hydraspermans, ''lyginopterids,'' and medullosans as the seed plant lineages that were established prior to the divergence of extant seed plant groups. These stem lineages apparently retained sporelike pollen (prepollen, microspores) with proximal germination. They also retained tetrahedral megaspores with a trilete mark. All extant seed plants have pollen with (primitively) distal germination and a linear tetrad of megaspores, which precludes the development of megaspores with a trilete mark. It thus seems likely that the early stem
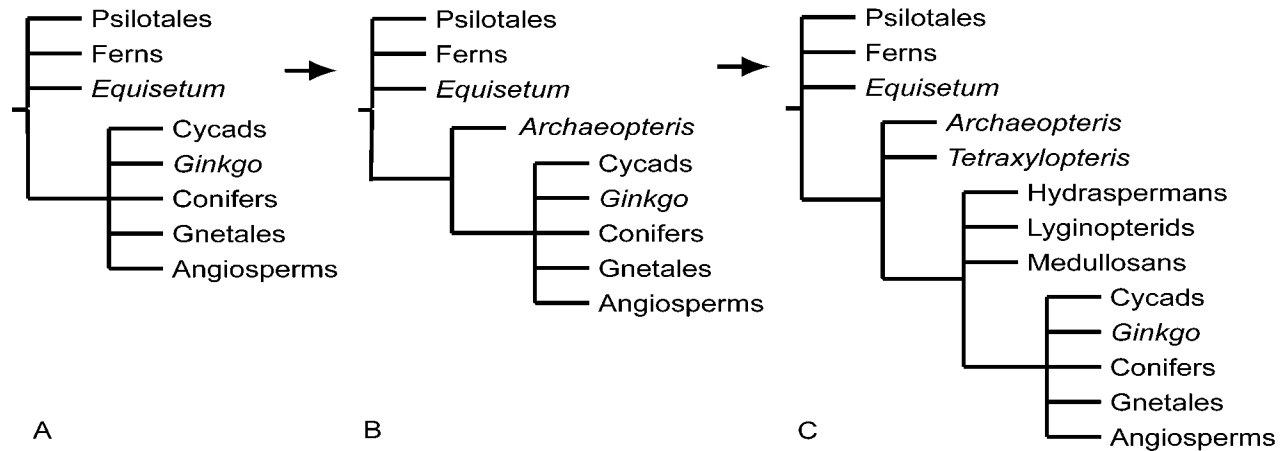
Fig. 2. Simplified cladogram showing interpolation of fossils among extant euphyllophytes. A. Extant taxa. B. Incorporation of *Archaeopteris* following recognition of "progymnosperms" by Beck (1960). C. Recognition of additional "progymnosperm" diversity and early "pteridophyte-like" seed plants.

lineages of seed plants had a reproductive biology much more like that of pteridophytes than living seed plants.

Another area of seed plant phylogeny in which there is emerging (but not universal) agreement concerns the monophyly of the five extant groups. *Ginkgo* is in any case monotypic, and as far as we are aware, no one has seriously questioned the monophyly of cycads. But at various points in the past, there have been suggestions that conifers, Gnetales, and angiosperms may be polyphyletic or paraphyletic.

There is now strong consensus based on both molecular and morphological data that angiosperms are monophyletic. Previous speculations of angiosperm polyphyly (e.g., Meeuse, 1961, 1966; Hughes, 1976) have fallen by the wayside. Indeed, angiosperms appear to be one of the best-supported major groups among plants as a whole. There seems little doubt that all extant angiosperms are more closely related to each other than they are to any extant or currently known fossil "gymnosperm."

Similarly with Gnetales, previous implications of polyphyly (Eames, 1952) are no longer supported, and phylogenetic studies that supported paraphyly as a possibility (Nixon et al., 1994) now seem aberrant in the context of other studies. There also seems to be a broad consensus that *Gnetum* and *Welwitschia* are together sister to *Ephedra*. The rapid recent expansion in the known fossil record of Gnetales is also remarkable (Crane and Upchurch, 1987; Krassilov and Bugdaeva, 1988; Crane, 1996; Guo and Wu, 2000; Rydin et al., 2003) and indicates that we still have much to learn about this group, which we now know was once much more diverse.

With regard to conifers, the situation is more complex. Since the earliest phylogenetic studies of seed plants (e.g., Crane, 1985), it has been recognized that conifers are a difficult group to define based on morphological features. There have been two kinds of challenges to the conclusion that conifers are monophyletic: one based on morphological data and incorporating fossils; the other based solely on evidence from comparative studies of DNA sequences.

The challenge to standard concepts of conifer monophyly based on morphological data comes from analyses by Rothwell and Serbet (1994) in which extant conifers and early fossil conifers (e.g., *Lebachia*) are widely separated in phylogenetic analyses that incorporate extant and fossil taxa. In broad terms, this result comes about (in the context of one particular

selection of taxa and scoring of characters) because *Lebachia* associates with strong support with cordaites, whereas extant conifers (which remain monophyletic in these studies) are placed elsewhere. Such patterns, and contrary results obtained by others (e.g., Doyle, 1996), emphasize the need for more detailed integrated research on conifer phylogeny, and even raise the possibility that the long-accepted relationship between conifers and cordaites established by Florin (e.g., 1939, 1951) may be worthy of reexamination using modern techniques.

The challenge to conifer monophyly based on molecular data comes from several analyses in which Gnetales are placed within conifers, which therefore become paraphyletic (the so-called "gnepine" hypothesis, e.g., Hansen et al., 1999; Qiu et al., 1999; Bowe et al., 2000; Chaw et al., 2000; Donoghue and Doyle, 2000; Soltis et al., 2002; Burleigh and Mathews, 2004). Analyses by Rydin et al. (2002) and Magallón and Sanderson (2002) indicated that the gnepine hypothesis was not strongly supported, but Burleigh and Mathews (2004) recovered well supported gnepine trees in analyses of combined data from 13 loci using parsimony (when fastest evolving sites are excluded) and maximum likelihood.

Key persistent phylogenetic questions—In many respects, our understanding of phylogenetic relationships among extant and fossil seed plants is much less satisfactory than for phylogenetic patterns among early-diverging tracheophytes or among major groups of angiosperms. Indeed, from a state of relative consensus that was reached in the late 1980s and early 1990s around the anthophyte hypothesis, the current situation is much more uncertain. Under the anthophyte hypothesis, angiosperms were grouped with Gnetales among extant taxa (and to Bennettitales, *Pentoxylon*, and sometimes *Caytonia* among fossils). Under this interpretation, extant "gymnosperms" are paraphyletic. In contrast, recent analyses of molecular data have proposed various alternative patterns of relationships among extant taxa. In some of these analyses, Gnetales are nested within conifers (discussed earlier), and according to several different sets of results, the four groups of extant gymnosperms form a monophyletic group sister to flowering plants (e.g., Bowe et al., 2000; Chaw et al., 2000; Magallón and Sanderson, 2002; Soltis et al., 2002; Burleigh and Mathews, 2004).

Based on the apparent conflict between current molecular analyses that only sample extant taxa and analyses that are based on structural features and sample extant and fossil taxa, it would be easy to argue in support of one or other of these contrasting views. However, it may be more productive to recognize that both sets of results have inherent strengths and limitations. Seeking to identify the strengths, and dedicating efforts to minimize the limitations, would seem to be a sensible way forward.

Current morphological data sets incorporate only a "compromise" selection of fossil plants based on taxa that are relatively well understood (i.e., well preserved and at least partially reconstructed) and that maximize the possibilities for comparison with extant taxa, albeit solely based on morphological and anatomical characteristics. Successive analyses have also sought to increase the list of characters to maximize phylogenetic resolution (compare Crane, 1985, with Doyle, 1996). However, to the extent that these efforts result in weak interpretations of homology, it may be that this is not the most productive approach (Nixon, 1996).

In the current seemingly confusing situation, it may be more helpful to strive for more limited, but more secure, resolution by focusing solely on those characters in the morphological–anatomical analyses that have been investigated in detail, and for which homology statements are most reliable. This will require the exercise of judgment, but similar judgments are inherent in the construction of any data matrix based on the structural characteristics of plants.

Such an approach might also generate more initial discussion of the characters themselves rather than the resulting phylogenetic hypotheses. For example, even among extant seed plants, it is uncertain exactly how best to compare the seed-bearing structures of Gnetales, conifers, and angiosperms. The situation is still more problematic for extinct groups such as *Caytonia*, corystosperms, glossopterids, and Bennettitales. Previous cladistic analyses of relationships have made various attempts to compare these structures, but if the hypotheses of homology are weak, then the estimates of relationships based on those comparisons will also be weak. A smaller set of characters for which homologies are more secure may have given more useful results. Exactly which characters are included in a morphological analysis and exactly how they are scored makes a big difference (see also Scotland et al., 2003). It may also be valuable to increase the sampling of fossil taxa and to focus on specific fossil species (see Kenrick and Crane, 1997), rather than restricting the paleobotanical sampling and using "composite" fossil taxa (see also Nixon, 1996). Achieving the right balance in the selection and scoring of both characters and taxa will require both broad knowledge and good judgment.

However, the problems are not restricted to morphological data sets. Molecular analyses also have their own problems (e.g., Qiu and Palmer, 1999), and we do not subscribe to the view that morphological studies are only useful in the context of a hypothesis based on molecular data (compare Scotland et al., 2003). And in molecular studies, just as in morphology, there is a difficult cost-benefit trade-off between the competing priorities of maximizing sampling (albeit among only extant taxa) and maximizing characters (amount of sequence data). Again, it may be helpful to look for a new approach, for example by considering other kinds of changes in the genome (as opposed to just sequence data) as well as seemingly clear-cut morphological characters. For example, two apparently
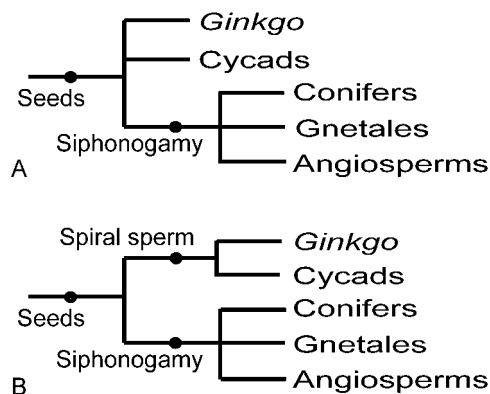

Fig. 3. Simplified cladograms showing resolution of relationships among extant seed plants. A. Occurrence of siphonogamy conflicts with monophyletic gymnosperms indicated by recent molecular studies, unless siphonogamy can be shown to have originated more than once. B. Distinctive spiral sperm with many hundreds of flagellae in a spiral groove is unlike the condition in any moniliform and potentially unites *Ginkgo* and cycads, unless this was the basic condition among crown-group seed plants that was lost in siphonogamous taxa.

clear features of the reproductive biology of extant taxa (siphonogamy and the distinctive sperm type of cycads and *Ginkgo*) indicate a pattern of relationships (Fig. 3) that combines elements of both the morphological and molecular results. It rejects gymnosperm monophyly but resolves conifers and Gnetales as part of a clade with angiosperms. Arguments that suggest multiple origins of siphonogamy or that interpret the distinctive sperm structure of *Ginkgo* and cycads as plesiomorphic for seeds plants as a whole, should not be glossed over, but they do require more explicit and more critical discussion than they have received so far.

Areas for future research—With respect to the evolution of seed plants, it will be difficult to move on to the detailed consideration of specific evolutionary questions until there is greatly improved clarity about the major patterns of phylogenetic relationships. Paleobotanically, one key priority must be to know our current fossil plants better. Improving the information available for fossil plants of which we already have some knowledge will be just as important as discovering new fossil taxa.

Another key priority should be improved synthesis of the existing paleobotanical record. The information on many interesting and potentially phylogenetically informative fossil plants remains scattered and poorly collated. There is considerable scope for renewed attempts at synthesis that build on earlier, but now outdated, efforts (e.g., Crane, 1985, 1988) and draw together the existing information in a standardized way that facilitates comparative analyses (see for example Hilton et al., 2003).

ORIGIN AND DIVERSIFICATION OF FLOWERING PLANTS

Progress—Forty years ago, studies of the fossil record of flowering plants largely focused on floras of Tertiary age with the prime motivation of inferring the nature of ancient climates or habitats. In the 1960s and 1970s, however, first through applications of palynology (e.g., Doyle, 1969; Muller, 1970; Hughes et al., 1979; Hughes, 1994), and then through increas-
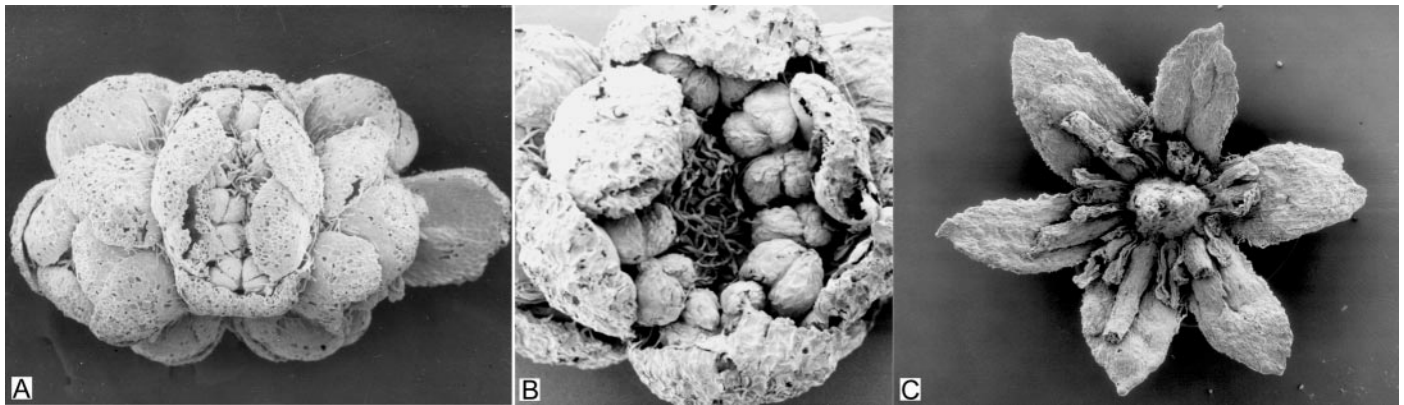
Fig. 4. Examples of fossil charcoalified flowers from the Late Cretaceous (late Santonian) Allon locality in central Georgia demonstrating exceptional three-dimensional morphological and anatomical preservation. A, B. *Protofagacea allonensis* (Herendeen et al., 1995). A. Dichasium of staminate flowers (×50). B. Close-up of staminate flower just prior to anthesis (×100). C. *Antiquacupula sulcata* (Sims et al., 1998). Staminate flower with vestigial gynoecium and bases of 12 filaments alternating with elongate nectary lobes (×20).

ingly careful comparisons of angiosperm megafossils with their extant relatives (e.g., Dilcher, 1974), the potential of paleobotanical data to contribute to ideas of angiosperm evolution gradually became more widely appreciated. Especially influential were studies of fossil angiosperm pollen from the Early Cretaceous of southern England (Hughes, 1976) and reinvestigations of the classic mid-Cretaceous floras of the Atlantic Coastal Plain and Eocene floras of the Mississippi Embayment.

In southern England, Hughes and collaborators documented the increasing diversity and abundance of angiosperm pollen through Early Cretaceous Wealden and overlying sediments. On the Atlantic Coastal Plain, Doyle and Hickey (Doyle, 1969; Doyle and Hickey, 1976; Hickey and Doyle, 1977) demonstrated a coordinated pattern of increasing diversity, abundance, and "advancement" of angiosperm leaves and pollen. In the Mississippi Embayment, Dilcher and collaborators carefully compared well-preserved fossil leaves, fruits, and flowers from the Eocene of Kentucky and Tennessee (Dilcher et al., 1976) with their extant relatives and discovered new character combinations not seen in extant taxa. Hickey and Wolfe (1975) showed that the leaves of extant and fossil angiosperms could be compared in detail using previously unrecognized characters of venation, serrations, and other features.

Taken together, these advances stimulated further interest in angiosperm paleobotany, which today is a well-established and flourishing subdiscipline. In the Tertiary, a continuing emphasis is on careful comparisons of fossil angiosperms with extant taxa, sometimes supplemented by reconstructions based on similarities in structure or patterns of co-occurrence (e.g., Manchester, 1987, 1994, 2000). In the Cretaceous, there is increased emphasis on the study of fossil flowers (e.g., Friis, 1983, 1984, 1990; Dilcher and Crane, 1984; Herendeen et al., 1995; Gandolfo et al., 1998a, b; Magallón et al., 2001; Friis et al., 2003a).

A further important development has been the discovery and study of small, exquisitely preserved, mummified, or charcoalified fossil flowers from the Cretaceous (Fig. 4). These studies were pioneered by Friis (e.g., Friis and Skarby, 1981, 1982; Friis, 1983) based on bulk sieving of material from the Campanian-Santonian of Åsen, southern Sweden (see also Knobloch and Mai, 1986), but have since been extended to the classic Potomac Group localities of eastern North America

(e.g., Friis et al., 1988, 1997a; Crane and Herendeen, 1996), other later Cretaceous localities on the Atlantic Coastal Plain (e.g., Gandolfo et al., 1998a, b; Herendeen et al., 1999), the classic Cretaceous localities in Portugal (e.g., Friis et al., 1992, 1999), and fossil assemblages in Asia (e.g., Frumin and Friis, 1995; Takahashi et al., 1999, 2001, 2003) and Antarctica (Eklund, 2003; Eklund et al., 2004a). The discovery and study of this material has revolutionized our knowledge of angiosperm diversity during the Cretaceous. It has also provided valuable information on the parent plants of fossil angiosperm pollen grains that were previously only known as dispersed (e.g., Normapolles pollen now known in situ within flowers, e.g., Friis, 1983; Sims et al., 1999; Schönenberger et al., 2001; Friis et al., 2003b).

The result of the explosion of work on angiosperm fossils, and especially on ancient angiosperm flowers, over the last several decades is a greatly expanded availability of high quality and systematically useful information on fossil angiosperms from the Cretaceous and Early Tertiary. In several cases, for example Juglandaceae (Manchester, 1987, 1989) and Betulaceae (e.g., Crane, 1981; Manchester and Crane, 1987; Crane, 1989; Manchester and Chen, 1998; Fig. 5), the available fossil material has greatly improved knowledge of the true diversity of extant families. Similarly, fossil floral material has established the presence during the Cretaceous of many different families (and even genera) of extant angiosperms (Magallón-Puebla et al., 1999). In other cases, fossils that are well understood in structural terms are clearly not referable to any family of extant angiosperms (e.g., Friis, 1990; Friis et al., 1997a).

So far, the recently expanded Cretaceous and Tertiary fossil record of angiosperms has not changed our understanding of relationships among angiosperm genera, families, or other groups. However, it has expanded knowledge of the diversity within certain groups of angiosperms and provided important information on their likely age. It is the rapidly improving understanding of angiosperm phylogeny, based almost entirely on molecular data, that is establishing the structure of angiosperm relationships (e.g., APG II, 2003), whereas angiosperm fossils help calibrate the age of individual units in this framework. Significantly, the overall temporal pattern in the fossil record is broadly consistent with the chronology implicit in the molecular results (Crane et al., 1995; Doyle, 2001).
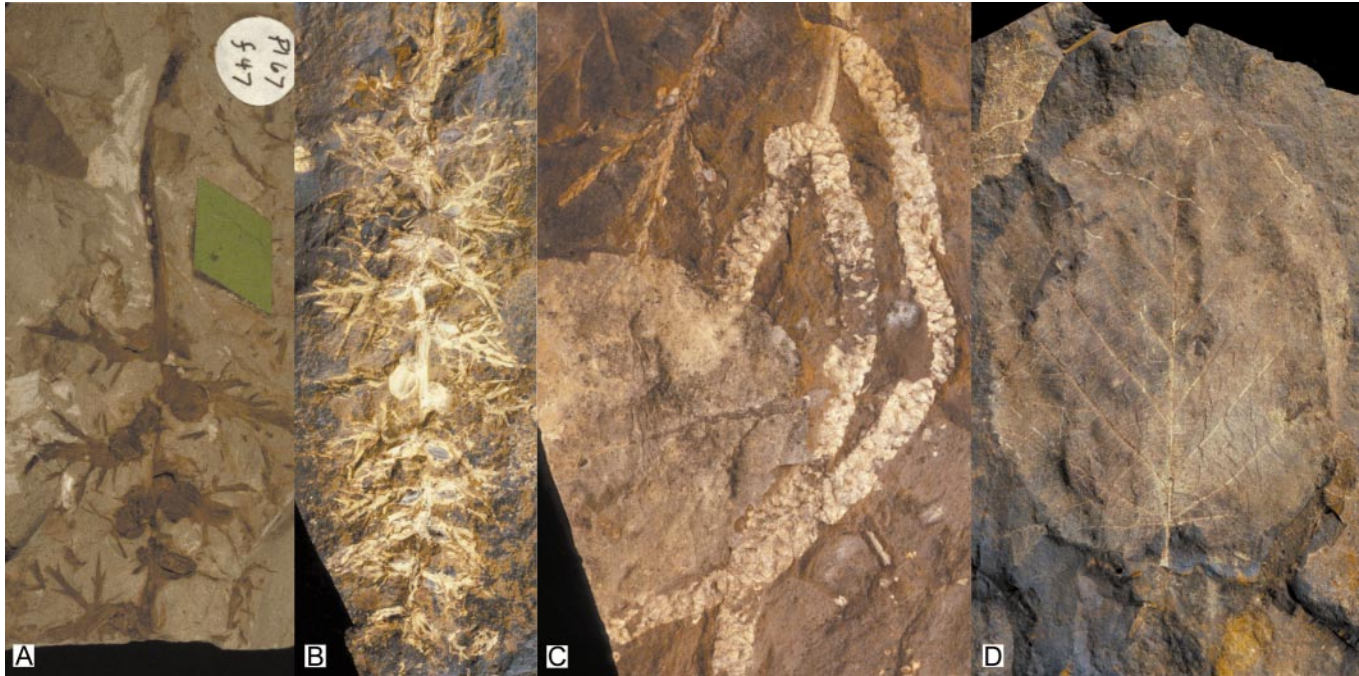
Fig. 5. Fossil fruits, staminate catkins, and leaves of *Palaeocarpinus* (Coryleae, Betulaceae) from the Paleocene of North America. A. Fossil infructescence from the Fort Union Formation, near Riverton, Wyoming (see also Brown, 1962, p. 67, fig. 47) (×1.2). B. Fossil infructescence of *Palaeocarpinus* from the Almont locality, North Dakota (×1). C. Probable staminate catkin of *Palaeocarpinus* from the Almont locality, North Dakota (×0.8). D. Probable leaf of *Palaeocarpinus* from the Almont locality, North Dakota (×0.8).

Key persistent phylogenetic questions—Despite rapid and remarkable progress with understanding the relationships among different groups of angiosperms based on molecular data, significant questions still remain at many levels. Among the apparently later-diversifying groups (e.g., genera of Asteraceae or Lamiaceae), it seems unlikely that paleobotany will contribute significantly to understanding extinct diversity and thus to phylogenetic issues. At intermediate levels in the angiosperm hierarchy, paleobotany is likely to be more informative, and it has already significantly expanded knowledge of the diversity of some families and helped calibrate the timing of evolutionary events (e.g., Juglandaceae, Betulaceae). There is every reason to suspect that continued studies of well-preserved Late Cretaceous and Early Tertiary material will continue to contribute in this way. However, it is at the base of the angiosperm tree that paleobotany is likely to prove most useful in terms of expanding the data available from extant plants.

In many analyses of extant taxa based on molecular data Amborellaceae, Nymphaeaceae, and Austrobaileyales are successive sisters to all other angiosperms, with the position of Chloranthaceae and Ceratophyllaceae uncertain with respect to three major clades, eudicots, magnoliids, and monocots (Qiu et al., 1999; Soltis and Soltis, 2004). Amborellaceae, Nymphaeaceae, and Austrobaileyales, and magnoliids are systematically depauperate (of 28 families recognized by APG II [2003] in these clades, 23 have less than 10 genera, and 13 have less than 10 species). In only a few families (Annonaceae, Lauraceae, Piperaceae) are there more than a few hundred extant species, and in many cases, these reflect the presence of relatively large genera that in many respects are structurally stereotyped (e.g., *Piper*). In paleobotanical assemblages from the Barremian-Aptian (Early Cretaceous) phase of an-

giosperm evolution, it is fossils similar to Amborellaceae, Nymphaeaceae, Austrobaileyales, and Chloranthaceae, perhaps with a few early representatives of monocots and magnoliids, that dominate rich plant fossil assemblages, both in terms of diversity and abundance (Pedersen et al., 1991; Friis et al., 1997b, 1999). Eudicots are sparse at this level, and "core eudicots" (Magallón et al., 1999) are not yet represented. In rare cases, some of these very early fossils may even be sister to or within modern genera (e.g., *Hedyosmum–Asteropollis* plant, Chloranthaceae; Eklund et al., 2004b), but more usually these fossils cannot be assigned to extant taxa (at least at the level of families or below; Friis et al., 1999). They show unusual combinations of features that are no longer represented among extant taxa. Continuing studies of these fossil plants from the Cretaceous will significantly expand our current understanding of diversity among early angiosperms. What remains to be determined is the extent to which the extant sample of Amborellaceae, Nymphaeaceae, Austrobaileyales, Chloranthaceae, and magnoliids, left to us by the vagaries of history, is truly representative of total diversity at this level of angiosperm evolution.

A particularly important question that may be elucidated by a combination of neobotanical and paleobotanical studies concerns the position of Chloranthaceae. Current phylogenetic analyses place this family in an uncertain position with respect to magnoliids, eudicots, and monocotyledons (e.g., Doyle and Endress, 2000). Paleobotanical studies show that the family, and forms similar to it, are well represented in some of the earliest known assemblages of angiosperm fossils (Crane et al., 1989; Pedersen et al., 1991; Herendeen et al., 1993; Eklund et al., 1997, 2004b).

It may be that the prominence of Chloranthaceae in the early phases of angiosperm evolution is overestimated as a result of

biases of representation and recognition in the fossil record. However, it is also possible that the extant family is merely part of a broader group that was once much more diverse and prominent during the early phases of angiosperm evolution. Understanding this extinct diversity may be helpful in resolving relationships among early diverging groups of angiosperms. A better understanding of the enigmatic floral construction of Choranthaceae may also be significant in understanding the evolution of angiosperm flowers (Doyle et al., 2003).

A final set of persistent questions relating to angiosperm evolution concerns the origin of the group itself. Resolving this issue will require resolving phylogenetic relationships among the major groups of extant and extinct seed plants (Crane, 1985). More specifically, experience based on the recognition of the protracheophyte and progymnosperm grades indicates that we might expect to recognize stem group angiosperms. More provocatively, experience also indicates that we may have already described such ''proangiosperms,'' but have failed to recognize them for what they really are. *Aglaophyton*, the best known protracheophyte, was first described by Kidston and Lang in 1917 (as *Rynia major*), but its true significance was only realized much later (Edwards, 1986; see also Kenrick and Crane, 1997). Similarly, both *Callixylon* and *Archaeopteris* had been known and characterized in detail long before ''progymnosperms'' were recognized by Beck (1960).

Archaefructus is a recent candidate ''proangiosperm'' (Sun et al., 2002), but alternative interpretations place it within the angiosperm crown group (Friis et al., 2003a). Other candidate proangiosperms will undoubtedly be proposed in the future. They will stand or fall, based on the detail in which they are understood and, therefore, on the detail with which they can be compared to angiosperms and other seed plants.

Areas for future research—A key priority for future research with angiosperm fossils, in addition to the ongoing discovery and characterization of systematically informative material, is the continued integration of fossil taxa into morphology-based phylogenetic analyses of extant taxa. With a few notable exceptions (e.g., Crane and Manchester, 1982; Keller et al., 1996; Magallón-Puebla et al., 1996; Crepet and Nixon, 1998a; Schönenberger and Friis, 2001; Doyle et al., 2003; Eklund et al., 2004b), this has not yet become standard practice, in large part because structural data comparable to that obtainable from fossil material is rarely readily available. This situation reflects a fundamental problem in angiosperm phylogenetics. Our ability to acquire both genetic sequence data and high quality paleobotanical data has ''run ahead'' of ''traditional'' comparative studies of extant taxa based on morphological, anatomical, and other features. As a result, there have been insufficient tests of DNA-based phylogenetic hypotheses and too few analyses that combine morphological and molecular data. There is a clear ongoing need for careful comparative, morphological, and anatomical studies of extant taxa.

DISCUSSION

Over the last 50 years, the discovery, description, and analysis of fossil plants has greatly enhanced our understanding of large-scale patterns of plant evolution, including the origin and diversification of major groups. Progress in understanding the origin and diversification of vascular plants has been especially striking. More remains to be done in terms of understanding the relationships among living and fossil seed plants, but even here some progress has been made. The next steps need to focus on new approaches to the analysis and synthesis of the available paleobotanical data. Directed efforts to better understand the structure of certain key groups of fossil plants will also be required.

For studies of the origin and diversification of flowering plants, the major patterns based on phylogenetic analyses of molecular data are now well established, and they are broadly consistent with paleobotanical data. The opportunity now is for further integration of neobotanical and paleobotanical data, especially at the Amborellaceae, Nymphaeaceae, Austrobaileyales, and Chloranthaceae level, to flesh out in detail the earliest phases of angiosperm diversification.

Key modes of progress—Reflecting on what has been accomplished in terms of palaeobotanical contributions to plant phylogeny over the last 50 years, it is clear that progress has come about in many ways, but especially by parallel efforts on three fronts: (i) continued efforts to expand the known diversity of plants through the discovery and description of informative fossil material (including the reconstruction of fossil plants); (ii) attempts to analyze the relationships of fossil plants to their living relatives using cladistic methods; and (iii) the progressive disassembly of paraphyletic groups.

The recent expansion of paleobotanical knowledge has been dramatic. New information continues to accumulate, and a vast amount of potentially informative material exists that has not yet been studied in detail (e.g., from the Triassic Molteno formation of South Africa, Anderson and Anderson, 2003; Permian Angara floras of Russia, Meyen, 1987). There have been some remarkable discoveries of new localities that have yielded impressive amounts of important new data on key fossil plants. For example, the discovery of permineralized Permian and Triassic peats from Antarctica has generated a wealth of new information on late Paleozoic and early Mesozoic plants (e.g., Taylor, 1996), whereas extensive fieldwork in Europe and North America has yielded many new localities with well-preserved angiosperm reproductive structures (e.g., Crane and Herendeen, 1996; Crepet and Nixon, 1998a, b). New discoveries from the Jehol biota of China are also of great interest (Sun et al., 1998, 2002; Zhou et al., 2003). The application of new collecting techniques has also produced informative material from localities that in the past would have been regarded as unproductive for anything other than pollen and spores (e.g., in the Potomac Group and the Lower Cretaceous of Portugal). The technique has also been applied to Silurian and Devonian sediments with surprising results (e.g., Edwards, 1996).

It is also notable that reinvestigations of classic fossil floras have also been exceptionally informative. For example, renewed study of the Rhynie Chert (e.g., Remy and Remy, 1980; Lyon and Edwards, 1991; Remy et al., 1993) has yielded spectacular new information on gametophytes and life cycles of early land plants and helped clarify the vascular/nonvascular status of sporophytes. Similarly, reinvestigation of classic localities in the Potomac Group of eastern North America, first described in the nineteenth century, revealed a coordinated pattern of angiosperm leaf and pollen evolution (Doyle, 1969; Doyle and Hickey, 1976; Hickey and Doyle, 1977) and then yielded a previously unsuspected diversity of angiosperm reproductive structures (Crane et al., 1989; Drinnan et al., 1990,

1991; Pedersen et al., 1991; Crane and Herendeen, 1996; Herendeen et al., 1999).

In these and other cases, an important factor has been the application of new paleobotanical techniques. In the Rhynie Chert, Remy and collaborators combined traditional studies of thin sections with new "wafering" approaches, whereas in the Potomac Group it was first the application of palynology to classic leaf floras and then the discovery and study of angiosperm reproductive structures using bulk sieving techniques (combined with scanning electron microscopy to study minute charcoalified and mummified material). These experiences indicate that the information retrievable from classic localities is not exhausted. New approaches and techniques are likely to produce much unsuspected and important additional information.

The quality of the paleobotanical data available for phylogenetic and evolutionary purposes has also been improved by painstaking efforts to reconstruct "whole" fossil plants from their dispersed and isolated individual fossil organs. This approach has been crucial in expanding the information available for extinct taxa and therefore in providing a more complete basis for comparisons both with extant and other fossil plants. In many cases, reconstructions of fossil angiosperms from the Cretaceous and Early Tertiary (e.g., Dilcher and Crane, 1984; Manchester et al., 1999) have highlighted important combinations of characters that are no longer represented among extant plants.

Among non-angiosperm taxa, reconstructions of fossil plants have also been important in recognizing novel character combinations that have called into question the homogeneity of previously recognized groups. For example, it was the reconstruction of a fossil seed plant with fernlike leaves (Oliver and Scott, 1904) that led to the recognition of the pteridosperms, and it was Rothwell's (1975, 1980) classic reconstruction of *Callistophyton* that was especially influential in documenting the heterogeneity of seed ferns and thereby undermining the utility of the pteridosperm concept for evolutionary purposes.

A special case of efforts to reconstruct fossil plants has been the considerable progress in identifying the parent plants of fossil pollen grains that were previously only known as dispersed entities. For example, the inferred relationship between *Asteropollis* and *Hedyosmum*, first suggested based on palynological similarities (e.g., Walker and Walker, 1984), has been confirmed by recognition of *Asteropollis* grains on the apices of unequivocal fossil *Hedyosmum*-like fruits and also in *Hedyosmum*-like stamens (Friis et al., 1997b). Similarly, much has been learnt about the parent plant of dispersed *Eucommiidites* pollen (originally misinterpreted as an angiosperm pollen grain) through its discovery in situ within pollen organs and also inside the micropyles of dispersed seeds (Pedersen et al., 1989; Friis and Pedersen, 1996; Kvacek and Pacltová, 2001). All these studies have significantly expanded the information available for plants that were otherwise only known from dispersed pollen and provide a more secure basis for a better understanding of interrelationships.

The accumulation of new and high quality fossil data has been the core preoccupation of paleobotany since its inception, but over the last three decades a key development has been increased emphasis on analyzing the relationships of fossil plants using implicit or explicit cladistic techniques. This reflects increased recognition that from the standpoint of evolutionary studies paleobotany cannot be viewed as a separate subdiscipline: fossil plants can only be understood in comparison to their living relatives. For example, Banks's (1975) incorporation of lycopsids into his treatment of Devonian fossil plants was crucial to the recognition and widespread acceptance of two main lines of vascular plant evolution. Similarly, critical comparisons of fossil angiosperms with extant taxa (e.g., Dilcher, 1973, 1974; Dilcher et al., 1976) documented inadequacies in earlier approaches and opened the possibility of recognizing extinct taxa among angiosperm fossils, thereby greatly increasing the potential value of such paleobotanical research.

The extent of extant-fossil comparisons has increased dramatically in the last two decades at all levels from vascular plants (e.g., Kenrick and Crane, 1997) to seed plants (e.g., Zhou et al., 2003) and angiosperms (e.g., Schönenberger et al., 2001). This is a positive trend that has already produced new insights and shows the way for future paleobotanical research. Even seemingly "extinct groups" can be compared with extant taxa at some level, and this will be important if they are to be integrated into the tree of life.

A third key mode of progress has been the gradual disassembly of polyphyletic and paraphyletic groups, as has also been the case with studies of extant taxa. Important paleobotanical examples include rejection of the seed fern concept (e.g., Crane, 1985), dismantling Psilophytales (e.g., Banks, 1975), and disassembly of Rhyniophytes and some of the genera therein (e.g., Kenrick and Crane, 1997; Table 3). Much progress with plant phylogenetics in recent years reduces to this. Because many of these polyphyletic and paraphyletic groups have themselves been the creation of paleobotany, it could be argued that this merely reflects the cleaning up of problems created by paleobotanists in the past. However, such iterative advances have greatly enhanced our understanding of extant taxa and their place in the broader context of plant phylogeny and evolution (Figs. 1, 2). They also help us understand how the characteristic features of extant taxa may have arisen. Recognition of fossil plants as stem relatives of extant taxa helps establish the order in which particular characters have been acquired. For example, recognition of progymnosperms indicates that the bifacial cambium was acquired prior to the seed habit in the seed plant lineage (Fig. 6A), and the recognition of protracheophytes (Kenrick and Crane, 1997) supports the hypothesis that a branched sporophyte evolved prior to the origin of typical tracheids (Fig. 6B).

Challenges for the future—The capacity of paleobotany to influence our understanding of phylogenetic patterns in the tree of life depends on the quantity and quality of the information that it provides, as well as the extent to which these data expand knowledge of plant diversity.

The amount of paleobotanical information available depends to a large extent on the geographic and stratigraphic "spread" of paleobotanical sampling, and this can always be improved. For example, there is a clear need for paleobotanical exploration outside Laurasia in the Silurian–Devonian. Similarly, in the Cretaceous it will be important to explore low paleolatitudes (e.g., Africa, Brazil, China). Exploratory fieldwork is slow and often relatively high risk, but it must ultimately occur if geographic sampling of the available paleobotanical data is to be broadened.

The ability to compare extant and fossil material depends on the availability of comparable information for extant and fossil taxa. On the paleobotanical side, the amount of infor-

TABLE 3.   Paraphyletic and polyphyletic groups in land plant diversification modified from Kenrick and Crane (1997, table 7.4). Classification after Kenrick and Crane (1997).

Taxon	Phylogenetic status and relationships
Bryophytes	Probably paraphyletic to vascular plants (Tracheophyta); comprises three monophyletic groups: Marchantiopsida, Anthocerotopsida, and Bryopsida
Protracheophytes	Paraphyletic to Tracheophyta; comprises extinct, nonvascular polysporangiophytes, such as *Aglaophyton major* and *Horneophyton lignieri* and some nonvascular *Cooksonia*-like fossils
Psilophytes	Paraphyletic or polyphyletic assemblage of extinct basal polysporangiophytes (Polysporangiomorpha) comprises taxa in the tracheophyte stem group, such as *Aglaophyton*, as well as taxa that are within Zosterophyllopsida and Euphyllophytina, such as *Sawdonia* or *Psilophyton*, respectively (see Table 2).
Rhyniophytina sensu Banks (rhyniophytes)	Paraphyletic (possibly polyphyletic) to eutracheophytes; much disagreement over scope and definition
Zosterophyllophytina sensu Banks ("zosterophylls")	Paraphyletic to Lycopsida; comprises Zosterophyllopsida and basal Lycophytina
Trimerophytina sensu Banks ("trimerophytes")	Paraphyletic to Moniliformopses and Radiatopses; comprises taxa such as *Psilophyton* and *Pertica*
Pteridophytes	Paraphyletic to seed plants (Spermatophytata); comprises nonseed plant tracheophytes
Progymnosperms	Paraphyletic to seed plants (Spermatophytata); comprises woody seed-plant stem lineage plants, such as *Tetraxylopteris* and *Archaeopteris*
Pteridosperms	Paraphyletic or polyphyletic assemblage of extinct Paleozoic and Mesozoic seed plants (Spermatophytata); comprises seed-plant stem lineages, such as hydraspermans and medullosans, as well as taxa that are more closely related to extant seed plants, such as *Callistophyton, Caytonia*, glossopterids, etc.
Gymnosperms	Paraphyletic to angiosperms (Magnolidra); comprises all non-angiosperm seed plants

mation available is limited by preservation. Localities with exceptional preservation are therefore disproportionately important. On the neobotanical side, the amount of information available is limited more by accidents of history in terms of what features may have been studied in which taxa. The detailed and comprehensive studies of extant taxa that are necessary for full comparison with fossil taxa have not often been done. This problem is exacerbated by the fact that comparative molecular studies have quickly overtaken comparative morphological studies. Thus, from some perspectives, there is little incentive to develop morphological data sets for extant taxa or, indeed, to train practitioners with the necessary skills. However, detailed morphological studies of extant plants are fundamental. They are needed to test and supplement analyses based on molecular data and to facilitate the integration of paleobotanical information. Truly integrated studies that incorporate morphological data from fossils and living plants

and combine these data with information from molecular analyses are still relatively rare. But they are necessary if all the available evidence is to be brought to bear on key phylogenetic problems.

CONCLUSIONS

Elucidating the botanical tree of life is the crucial first step to developing a robust and detailed understanding of plant evolution. For many years, we have had general ideas about how some of the key innovations in plant evolution must have come about, but moving to a more sophisticated understanding will require a much more specific level of insight. For example, we know that the origin of the seed must be linked to heterospory and involve reduction of the number of megaspores in a megasporangium to one and retention of that megaspore in the megasporangium. But to move beyond this kind of generality, we need much better knowledge of the plants involved. A great variety of other structural and biological changes must have accompanied the transition from homospory to seed plant reproduction (see for example, Bateman and DiMichele, 1994). Without the additional diversity provided by fossil plants, it will be impossible to develop a deeper and more particularized understanding. Our knowledge of the processes involved will be incomplete, and many of the key issues will inevitably be overlooked.

A key challenge for the future will be dealing with the problem of missing data on the true diversity of life over evolutionary time. We are trapped in a paradox. Extant taxa can, in principle, be studied in enormous detail, for example, down to the totality of their genetic sequences. But on some branches of the botanical tree of life, the living sample of all the diversity that has ever existed is very poor. This sample can be expanded by paleobotanical data, but under such circumstances the selection of characters is limited and the possibilities for full phylogenetic resolution are reduced. Therefore, in many cases, it will be possible to have good sampling of characters but only for relatively few of the relevant taxa. Equally, we can achieve better sampling of the relevant taxa but only for a few characters. Unfortunately, around the divergence of
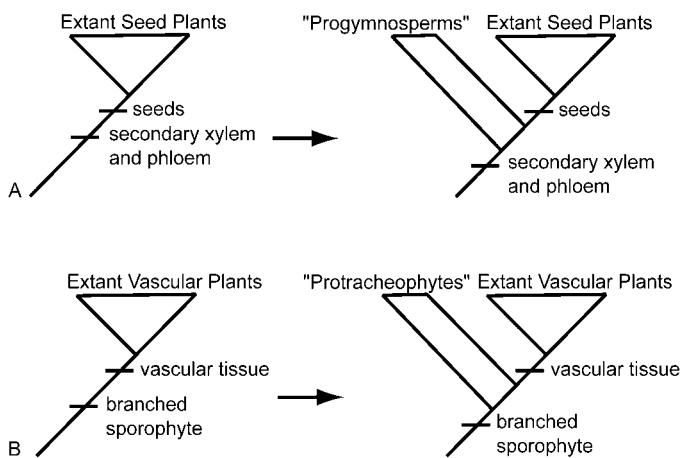

Fig. 6.   Recognition of stem relatives of major clades of land plants. A. Recognition of fossil "progymnosperms" establishes the likely sequence of appearance of characters that are correlated among extant taxa. B. Recognition of fossil "protracheophytes" establishes the likely sequence of appearance of characters at the "bryophyte"–vascular plant transition.

the deep major branches in the tree of life, we will not achieve good sampling of both taxa and characters.

In the future, we can expect paleobotany to contribute as it has in the past by expanding our knowledge of plant diversity and thereby documenting new combinations of characters not seen among extant taxa. The discovery of new localities, the application of new techniques of study, and the reexamination of classic localities will all play their part.

There may be areas on the tree where it is possible to have both good sampling of taxa and characters, for example, in recently diversified groups where most of the total diversity is still extant, but this is not the case for lineages that have long evolutionary history and where the tree has been extensively pruned of diversity by extinction. In these circumstances, attempts to integrate data and interpretations from extant and fossil plants as closely as possible in a collaborative and creative way, combined with thoughtful interpretation of the results, stand the best chance of success. For that to be possible, there is no substitute for thorough descriptions of fossil material, rigorous analysis of characters, and careful comparison of extant and fossil taxa as a basis for determining their systematic interrelationships.

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