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Fossils and seed plant phylogeny reanalyzed

JAMES A. DOYLE AND MICHAEL J. DONOGHUE

Doyle, James A. (Department of Botany, University of California, Davis, CA 95616) and Michael J. Donoghue (Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721). Fossils and seed plant phylogeny reanalyzed. *Brittonia* 44: 89–106. 1992.—In a cladistic analysis of Recent seed plants, Loconte and Stevenson (1990) obtained results that conflict with our 1986 analysis of both extant and fossil groups and argued that fossil data had led us to incorrect conclusions. To explore this result and the general influence of fossils on phylogeny reconstruction, we assembled new “Recent” and “Complete” (extant plus fossil) data sets incorporating new data, advances in treatment of characters, and those changes of Loconte and Stevenson that we consider valid. Our Recent analysis yields only one most parsimonious tree, that of Loconte and Stevenson, in which conifers are linked with Gnetales and angiosperms (anthophytes), rather than with *Ginkgo*, as in our earlier Recent and Complete analyses. However, the shortest trees derived from our Complete analysis show five arrangements of extant groups, including that of Loconte and Stevenson and our previous arrangements, suggesting that the result obtained from extant taxa alone may be misleading. This increased ambiguity occurs because features that appear to unite extant conifers and anthophytes are seen as convergences when fossil taxa are interpolated between them. All trees found in the Complete analysis lead to inferences on character evolution that conflict with those that would be drawn from Recent taxa alone (e.g., origin of anthophytes from plants with a “seed fern” morphology). These results imply that conclusions on many aspects of seed plant phylogeny are premature; new evidence, which is most likely to come from the fossil record, is needed to resolve the uncertainties.

Key words: angiosperms, cladistic analysis, fossil evidence, phylogeny, seed plants.

In a recent discussion of cladistic relationships of seed plants, Loconte and Stevenson (1990) criticized previous analyses by Crane (1985) and ourselves (Doyle & Donoghue, 1986) based on both extant and fossil taxa, and presented their own analysis based on extant taxa, which gave substantially different results. Rather than refuting our analysis, we suggest that these differences confirm and extend our views on the importance of fossils in reconstructing phylogeny and character evolution in ancient groups like seed plants and in judging the strength of conclusions reached. We first discuss differences in methodology, especially character analysis, arguing that some changes made by Loconte and Stevenson

are valid but not others. Next, we present a reanalysis of our own seed plant data set, with and without fossils, incorporating advances in numerical treatment of characters and understanding of taxa made since our previous studies, plus those revisions of Loconte and Stevenson that we accept. Finally, we compare the results of the two sorts of analyses to explore how fossils affect the results, and we evaluate the consequences of including or excluding fossil taxa in a broader context.

Background

In both Crane (1985) and Doyle and Donoghue (1986), seed plants formed a mono-

phyletic group linked with Devonian "progymnosperms," with lyginopterid "seed ferns" basal. Coniferopsids, including conifers, ginkgos, and Paleozoic cordaites, were nested within a "platysperm" clade including the Carboniferous seed fern *Callistophyton*, which had platyspermic seeds and saccate pollen. This clade also included Permian and Mesozoic seed ferns (*Peltaspermum*, glossopterids, corystosperms, *Caytonia*) and, nested among them, an "anthophyte" clade consisting of angiosperms, Gnetales, and fossil Bennettitales and *Pentoxylon*. In the many equally parsimonious trees of Doyle and Donoghue (1986), cycads were either positioned below the platysperms (by themselves or linked with the Paleozoic seed fern *Medullosa*) or nested among them (with or near *Peltaspermum*), resulting in two arrangements of extant taxa (Fig. 1a, b). These results imply that seed plants originally had fern-like pinnately compound leaves and sporophylls, and that the linear or dichotomous leaves and simple sporophylls of coniferopsids and Gnetales are derived.

In a subsequent paper (Doyle & Donoghue, 1987), we addressed the issue of the importance of fossils with a series of analyses beginning with our "Complete" (Recent plus fossil) data set, subtracting fossils and modifying character interpretations accordingly, and rereading various fossil taxa to evaluate their effects on the results, in keeping with the "experimental" approach developed in our previous study (Doyle & Donoghue, 1986). A similar analysis was conducted by Gauthier et al. (1988) on amniote vertebrates, and results of the two studies were synthesized by Donoghue et al. (1989). The study of Gauthier et al. differed from ours in beginning with a Recent data set and adding fossils, but if done carefully the two procedures should be equivalent.

In the amniote study of Gauthier et al. (1988), inclusion of fossils fundamentally altered cladogram topology, implying that mammals (plus fossil synapsids, or "mammal-like reptiles") are the sister group of other amniotes (turtles, lizards, crocodilians, "dinosaurs," and birds), whereas in the Recent analysis they were the sister group

of crocodilians and birds. In our seed plant study (Doyle & Donoghue, 1987), the effects of fossils on cladogram topology were less radical. The most parsimonious trees based on Recent taxa included one consistent with our Complete analysis (Fig. 1a), with cycads the sister group of angiosperms and Gnetales, plus a new tree with cycads the sister group of coniferopsids (Fig. 1c). However, fossils did have an important effect in strengthening key relationships and clarifying the course of character evolution. Thus trees with Gnetales linked with coniferopsids rather than angiosperms were only one step less parsimonious than the shortest trees with the Recent data set, but four steps less parsimonious with the Complete data set. With Recent taxa only, it is equally parsimonious to assume that either pinnate or linear-dichotomous leaves were ancestral in seed plants, as shown by the character distributions plotted in Figure 1a and c.

It might be argued that we were setting up a straw man when we compared our Complete analysis with an analysis that omitted fossils, but the study of Loconte and Stevenson (1990) shows that this is not so. They recommended that fossils be used only *a posteriori* when they clearly belong to stem lineages of modern taxa, as they assumed for medullosans and cycads (a questionable case, as discussed below). Their results do show some strong agreements with earlier analyses, particularly in indicating that Gnetales are a monophyletic group and the closest living relatives of angiosperms. However, the relationships of other groups and many implications for character evolution are different. In their single most parsimonious tree (Fig. 1d), cycads are the sister group of remaining seed plants, and coniferopsids are paraphyletic, with conifers the sister group of anthophytes. This arrangement recalls slightly less parsimonious trees found in experiments with our Complete data set (Doyle & Donoghue, 1986), in which anthophytes were nested within coniferopsids, though linked with ginkgos rather than conifers. Such "neo-Englerian" trees imply that the pinnately veined leaves and multiovulate carpels of angiosperms were derived from linear or dichot-

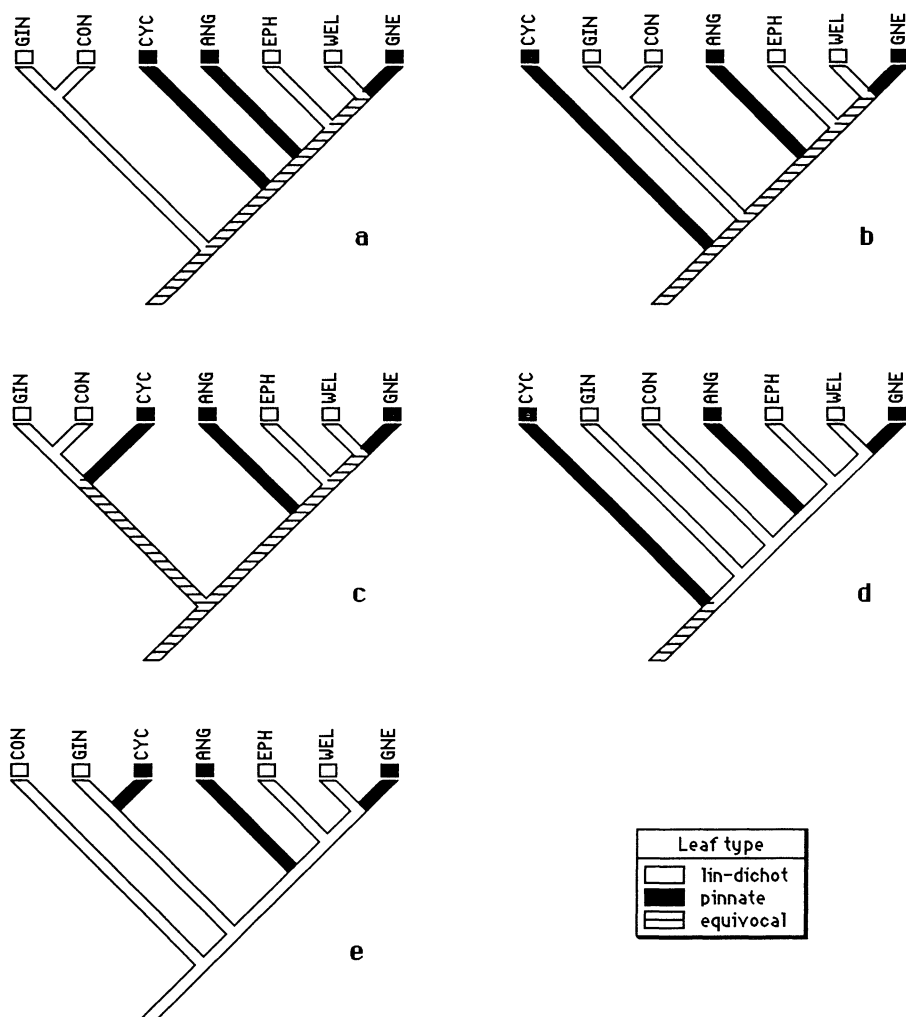


FIG. 1. Cladograms of Recent seed plants, showing distribution of the leaf character (shading). GIN: *Ginkgo*; CON: Coniferales; CYC: Cycadales; ANG: angiosperms; EPH: *Ephedra*; WEL: *Welwitschia*; GNE: *Gnetum*. Our previous analysis of Recent and fossil groups (Doyle & Donoghue, 1986) yielded arrangements A and B, while our previous analysis of Recent groups (Doyle & Donoghue, 1987) yielded arrangements A and C. The study of Loconte and Stevenson (1990) and our revised Recent analysis yielded tree D. Our revised analysis of Recent and fossil groups yielded all five arrangements, A-E.

omous leaves and uniovulate sporophylls, as in coniferopsids and Gnetales. In several cases, Loconte and Stevenson (1990) cited the same conflicts between the two sorts of analyses that we cited as evidence for the importance of fossils, but rather to claim that fossils are misleading. These comparisons suggest that we may have been incorrect in concluding that fossils have less effect on cladistic results in seed plants than in amniotes.

Character Analysis and Related Issues

In our opinion, some of the changes made by Loconte and Stevenson (1990) are necessary modifications of our analyses (Doyle & Donoghue, 1986, 1987), some are debatable but probably inconsequential, and some are serious errors. The latter tend to confirm our suspicion (Doyle & Donoghue, 1987, p. 91) that we may have been too

optimistic in treating some characters the same in our Recent analysis as we did in our Complete analysis, when a real investigator with no knowledge of fossils might have interpreted them differently. Presumably inconsequential disagreements are discussed in the Appendix; these include semantic conflicts, differences in treating conditions as separate characters or states of the same character, and recognition of additional states.

Loconte and Stevenson (1990) made two substantial changes in character analysis that we accept, at least when Recent groups only are considered. The first concerns axillary branching, which they scored as primitively lacking in cycads. In our Complete analysis, we scored cycads as unknown for this character, because there had been no modern developmental studies of branching in living members, and because some fossil cycads have a *Ginkgo*-like dimorphic shoot organization suggestive of axillary branching (*Nilssoniocladus*: Kimura & Sekido, 1975). Since the character then showed no informative variation among living seed plants, we eliminated it from our Recent data set. This argument no longer holds, because Stevenson (1988) has confirmed that extant cycads have apical dichotomous branching, like lycopsids and most ferns. The second change is the addition of a new character, seed germination, which contrasts cycads and *Ginkgo* (hypogeal) with conifers, Gnetales, and angiosperms (epigeal). This character seems functionally correlated with seed size, but this should not negate its value as long as seed size is not also included as a character.

Other changes follow from Loconte and Stevenson's (1990) splitting of cycads into Stangerineae and other groups, conifers into Taxaceae and other groups, and angiosperms into Calycanthales and other groups (Loconte & Stevenson, 1991). This led them quite validly to include new characters such as cycasin and coralloid roots in cycads, tiered proembryos in conifers, and companion cells and carpels in angiosperms. Their method of splitting these groups, however, is subject to debate. Thus cladistic analyses by Crane (1988) and Stevenson

(1990) concluded that *Cycas* is the sister group of other cycads. Taxaceae may not be the sister group of other conifers, but rather nested among them, based on similarities to Cephalotaxaceae in tracheid structure (tertiary thickenings), embryology, and pollen morphology. In our cladistic analysis of angiosperms (Donoghue & Doyle, 1989a), the basal group is Magnoliales rather than Calycanthales. Loconte and Stevenson also took advantage of the capacity of present algorithms to score taxa as polymorphic (uncertain), but this probably did not affect the results.

In some cases, the data set of Loconte and Stevenson (1990) differs from ours as a result of using ferns as the outgroup. In contrast, we used Devonian cladoxyloids, ferns, sphenopsids, and trimerophytes as outgroups in our Complete analysis (Doyle & Donoghue, 1986), which included progymnosperms as well as seed plants, and in our main Recent analysis ("conservative rooting") we assumed that seed plants are linked first with ferns and/or *Equisetum*, then with lycopsids (Doyle & Donoghue, 1987). The character most affected is leaf morphology, which Loconte and Stevenson inferred was primitively compound, but which we left unpolarized. When extant plants are considered, we see little evidence that ferns are closest to seed plants, except for the similarity between fern and cycad leaves, and this is weakened by the fact that conifer leaves are more like those of *Equisetum* and lycopsids.

Other problems are posed by Loconte and Stevenson's (1990) treatment of leaf morphology, which contrasts compound vs simple leaves and dichotomous vs pinnate venation as two characters. In our Complete analysis (Doyle & Donoghue, 1986), we recognized a different set of distinctions as states of a multistate character, and in our Recent analysis (Doyle & Donoghue, 1987) we simplified this to a binary character, pinnate vs linear or dichotomous leaf organization. The existence of fossil cycads with simple leaves (not only the contested Paleozoic *Taeniopteris*, but also Mesozoic *Macrotaeniopteris* and *Nilssonia*: Crane, 1988) calls into question Loconte and Stevenson's scoring of cy-

cads as having compound leaves (Doyle & Donoghue, 1986), but this might be reasonable considering extant forms only. However, even in terms of Recent groups, we question whether cycads should be compared with conifers and *Ginkgo* and contrasted with angiosperms in having dichotomous rather than pinnate venation, when this character applies to leaflets in cycads but to whole leaves in conifers and *Ginkgo*, and when the overall venation pattern of cycads resembles that of angiosperms in having veins issuing pinnately from a rachis or midrib.

Finally, Loconte and Stevenson (1990) added new characters that we do not accept. First, they split our character of motile sperm vs siphonogamy and nonmotile sperm into two: flagellated vs nonflagellated sperm, and haustorial vs penetrating pollen tube. These characters have the same distribution and seem functionally correlated, in that the penetrating pollen tube allows the sperm to be transferred as nonmotile cells. We therefore consider them redundant, as expressions of a single evolutionary change. Second, Loconte and Stevenson characterized leaf bases as simple (cycads), stipulate (*Ginkgo*, conifers, angiosperms), and sheathing (Gnetales). The distinction between the first two states is unclear, and sheathing bases are suspiciously correlated with opposite leaves in the taxa considered. Third, their character of long vs short cambial initials (Bailey, 1920) is closely correlated with presence and length of vessels (Bailey, 1944), and their scoring of angiosperms as having the derived state is doubtful because it probably arose within angiosperms. In the list of Bailey (1920), *Myristica* has cambial initials in the range of *Ginkgo* and conifers and more primitive scalariform vessel perforations than most other angiosperms.

Reanalysis of Recent and Complete Data Sets

Our reexamination of the importance of fossils is based on new versions of our Complete and Recent data sets, presented in the Appendix. Some of the modifications in

these data sets reflect new data or reinterpretation of characters, others the use of unordered multistate characters, which we previously reduced to binary characters or approximated with an "X-coding" system of binary characters (Doyle & Donoghue, 1986). We used the Macintosh version of PAUP (Swofford, 1990) to generate most parsimonious trees and a test version of MacClade (Maddison & Maddison, in press) to investigate alternative trees and character evolution. With the Recent data set, we used the branch-and-bound algorithm in PAUP, which guarantees finding all most parsimonious trees, but with the larger Complete data set we used a heuristic search algorithm (simple addition sequence, one tree held at each step, TBR branch swapping, MULTIPARS).

In our Complete analysis, for simplicity, we considered seed plants only, rather than progymnosperms plus seed plants. As we argued in Donoghue and Doyle (1989b), evidence that seed plants are monophyletic is probably stronger than we concluded from our previous analysis (cf. Rothwell & Scheckler, 1988). We polarized characters by a two-step outgroup procedure (Maddison et al., 1984). First, we determined ancestral states by outgroup comparison with the progymnosperms *Archaeopteris* and *Aneurophyton*, assumed to be the first and second outgroups to seed plants (Doyle & Donoghue, 1986). Second, we included the list of ancestral states in the matrix as a taxon (ANC), and we rooted the resulting network on the branch connecting this taxon to the seed plant taxa. This procedure is equivalent to explicit inclusion of two outgroups with known relationships to the ingroup (Maddison et al., 1984). "ANC" is not shown in the resulting trees. We used the same procedure in the Recent analysis, assuming that ferns and *Equisetum* form an unresolved trichotomy with seed plants and lycopsids are the next outgroup. We replaced "multiovulate" and "higher" lyginopterids with one taxon based primarily on the Late Devonian protostelic, multiovulate seed fern reconstructed by Rothwell and Erwin (1987) and Rothwell et al. (1989). Inclusion of this taxon and higher lyginop-

terids resulted in unresolved relationships at the base of the seed plants but did not affect relationships higher in the tree. We replaced *Medullosa* with a broader concept of medullosans, rescored as having a protostele (as in *Quaestora*: Mapes & Rothwell, 1980), a tetrahedral megaspore tetrad (Drinnan et al., 1990), and trilete pollen (as in *Pottonia*: Stidd, 1981).

The most important changes in character analysis are as follows; changes less likely to influence the results are described in the Appendix.

— In the Recent data set, we adopted Loconte and Stevenson's (1990) scoring of cycads as having apical branching, but in the Complete data set we continued to score cycads as unknown, because of the *Ginkgo*-like branching pattern of *Nilssoniocladus* (Kimura & Sekido, 1975).

— We removed characters from the Complete data set that express similarities in leaf and fertile appendage distribution in coniferopsids and the progymnosperm *Archaeopteris*, which might be automatic consequences of any shift to a coniferopsid habit and therefore tend to exaggerate the unity of coniferopsids (Doyle & Donoghue, 1986, p. 367).

— In the Recent data set, we recoded nodal anatomy as consisting of three unordered states. In the Complete data set, we split the multilacunar condition into two states, prompted by the observation of Pigg (1990) that the Triassic corystosperm *Dicroidium* has an arcuate arrangement of petiole bundles like that of cycads (omega pattern of Loconte & Stevenson, 1990), whereas medullosans have numerous scattered bundles. Furthermore, in cycads and corystosperms leaf traces depart from individual primary stem bundles, whereas in medullosans they depart from protoxylem points of a single mass or several broad arcs of primary xylem. The tri- and multilacunar nodes of angiosperms and *Gnetum* are more like the cycad type, so we scored them accordingly.

— To the character of presence or absence of mucilage canals, we added a third state, mucilage cavities. This is a prominent feature of *Ginkgo*, cordaites, *Callistophyton*, and corystosperms, and a potential inter-

mediate state in evolution of canals. We previously omitted this state because we did not wish to prejudge its relation to canals, but this is not a problem with unordered multistate characters.

— Whereas we previously treated micro- and megasporophyll morphology separately, we combined these characters in our Recent data set because they are completely correlated in extant groups and would best be considered redundant in the absence of fossils. Because micro- and megasporophyll characters are also strongly correlated in the Complete data set, we reduced them to one character there, but with a third state for the taxa where the correlation breaks down, namely Bennettitales and *Pentoxylon*, which have pinnate microsporophylls but simple megasporophylls (assuming that each ovule represents one reduced megasporophyll, a view that does need more research: Crane, 1985, 1988). We also eliminated the rather problematical distinction between pinnately compound and once-pinnate sporophylls.

— We rescored cycads as unknown for radiospermic vs platyspermic seeds, because seeds of *Cycas* are bilateral (Crane, 1988; Stevenson, 1990).

— We added a new character concerning structure of the seed coat (where this corresponds to the original seed plant integument, = inner integument of angiosperms and Gnetales): differentiated into sclerotesta and sarcotesta (cycads and *Ginkgo*) vs undifferentiated (conifers, angiosperms, and Gnetales). Medullosans, *Callistophyton*, and cordaites also have sclerotesta-sarcotesta differentiation, but more primitive lyginopterids and more advanced glossopterids, *Caytonia*, and Bennettitales do not.

— In the Complete data set, we split alveolar exine structure into spongy (progymnosperms, medullosans) and honeycomb-like (cycads, conifers, *Callistophyton*, and other saccate groups), which have been shown to develop differently (Taylor & Zavadra, 1986). We added a character expressing the distinction in saccus structure emphasized by Pedersen and Friis (1986), between eusaccate (conifers, cordaites, *Callistophyton*) and protosaccate (corystosperms, *Caytonia*).

—We added Loconte and Stevenson's (1990) character of hypogeal vs epigeal seed germination.

RESULTS

Unlike our previous Recent analysis (Doyle & Donoghue, 1987), which yielded one tree consistent with the Complete analysis (Fig. 1a) and one linking cycads with coniferopsids (Fig. 1c), our revised Recent analysis yields only one most parsimonious tree of 58 steps (Fig. 1d), which is the same tree obtained by Loconte and Stevenson (1990). Both topologies found previously are now two steps less parsimonious (60 steps). Branch-and-bound analysis shows that there are no trees of 59 steps. The new characters responsible for this result are mode of branching, seed coat structure, and seed germination. *Ginkgo* is united with coniferopsids and anthophytes on axillary branching and an existing character, coniferopsid primary xylem pitting (reversed in angiosperms). Conifers and anthophytes are united by loss of sclerotesta-sarcotesta differentiation, a shift from hypogeal to epigeal germination, and siphonogamy. The two-step difference between this tree and our previously preferred tree (Fig. 1a) is less than the four-step difference between the same two trees found by Loconte and Stevenson, because of elimination of their leaf organization, leaf base, and pollen tube characters.

Changes in the Complete analysis are more complex, with at least 93 equally parsimonious trees. The general result of Doyle and Donoghue (1986) concerning angiosperms remains unchanged: anthophytes are nested among platyspermic seed ferns, specifically corystosperms, glossopterids, and *Caytonia*, and angiosperms are basal in anthophytes. However, relationships of other platysperms are destabilized. Most notably, coniferopsids are equivocal as a monophyletic group. Ginkgos are found in three positions: associated with conifers and cordaites (e.g., Fig. 2a); in a clade with *Peltaspermum* (cf. Meyen, 1984) and cycads, located between conifers plus cordaites and corystosperms; or with cycads,

Peltaspermum, and *Callistophyton*, variously arranged as a paraphyletic group below other platysperms (e.g., Fig. 2b). Cycads are never linked with medullosans, but in some trees they are the sister group of platysperms (Fig. 2b), and in others cycads, *Callistophyton*, and *Peltaspermum* are on the line leading to coniferopsids.

As a result of these variations, trees derived from the Complete analysis show five arrangements of extant groups (Fig. 1). These include all three arrangements found in our previous Complete and Recent analyses (Doyle & Donoghue, 1986, 1987; Fig. 1a–c), plus one in which conifers are basal and cycads are linked with *Ginkgo* (Fig. 1e) and the Loconte and Stevenson (1990) arrangement (Figs. 1d, 2b). Apparently, the seed germination character increases the relative parsimony of the Loconte and Stevenson tree, with epigeal germination becoming a synapomorphy of conifers and anthophytes. However, addition of fossils weakens the support for this arrangement by implying that other supposed homologies of conifers and anthophytes (especially Gnetales) are convergences, namely linear-dichotomous leaves, coniferopsid primary xylem pitting, simple sporophylls, lack of sclerotesta-sarcotesta differentiation, and siphonogamy, since fossils without these features are interpolated between conifers and anthophytes.

In summary, these results are generally similar to those found in our previous study of the effects of fossils (Doyle & Donoghue, 1987), but with significant differences. Previously, our Recent and Complete analyses were equally ambiguous: both resulted in two most parsimonious trees of extant groups, and one of these (Fig. 1a) was found with both analyses. This time, the Recent analysis supports a single tree, that of Loconte and Stevenson (1990; Fig. 1d), but the Complete analysis is ambiguous, because fossils imply that characters supporting the Recent result are homoplastic. As before, the greatest effect of fossils is on the understanding of character evolution. Thus the Loconte and Stevenson topology favors a neo-englerian scenario for evolution of leaves and sporophylls when Recent groups

alone are considered (compare the distribution of the leaf character in Fig. 1d), as implied by Loconte and Stevenson's use of the term "Cladospermae" for *Ginkgo*, conifers, and anthophytes. However, this is not so in trees with the same arrangement of Recent groups when fossils are included, because platyspermic seed ferns with pinnately compound or simple-pinnate leaves are interpolated between conifers and anthophytes (Fig. 2b). Instead, as with the other trees (Fig. 2a), a scenario is favored in which a seed fern morphology was ancestral in seed plants and there were parallel trends to linear-dichotomous leaves and simple sporophylls in *Ginkgo*, conifers, and Gnetales.

Specific Effects of Fossils

The significance of fossils can be understood in greater depth by considering specific examples of their effects on inferences concerning phylogenetic relationships and/or character evolution.

APICAL BRANCHING AND THE BASAL POSITION OF CYCADS

One of the characters favoring the basal position of cycads in Loconte and Stevenson (1990) and our Recent analysis is apical branching. However, the Complete analysis implies that this condition is a reversal. Even when cycads are the sister group of platysperms (Fig. 2b), they are firmly situated above groups with axillary branching, namely Carboniferous lyginopterids (probably located between DSF and MED) and medullosans (Galtier & Holmes, 1982; Hamer & Rothwell, 1988). This inference is still stronger in the many trees in which cycads are nested among platysperms (Fig. 2a). Discovery of a *Ginkgo*-like branching pattern in fossil cycads (Kimura & Sekido, 1975) also raises the likelihood that the apical branching of extant cycads is derived.

Ironically, recent data refute the one use of fossils admitted by Loconte and Stevenson (1990), the assumption that medullosans are related to cycads. In Doyle and Donoghue (1986), derived features of cycads but not medullosans were endarch pri-

mary xylem, abaxial microsporangia, and a sulcus. These features are at home among platysperms, but they must originate extra times or undergo reversals if cycads are linked with medullosans. To these may now be added the corystosperm-like nodal anatomy of cycads (Pigg, 1990) and the protostelic stem anatomy (Mapes & Rothwell, 1980), trilete pollen (Stidd, 1981), tetrahedral megaspore tetrad (Drinnan et al., 1990), and spongy exine structure (Taylor & Zavadra, 1986) of some or all medullosans.

Our results leave unresolved whether radiospermic seeds in cycads are secondarily derived from platyspermic or homologous with the radiospermic seeds of medullosans and lyginopterids, as argued by Loconte and Stevenson (1990). With cycads scored as unknown, the hypothesis that radiospermy is derived is favored when cycads are nested among platysperms (Fig. 2a), but its status is equivocal when cycads are basal (Fig. 2b).

Whether one accepts trees with cycads basal or nested in platysperms, our results do not conflict with the conventional view, reaffirmed by Loconte and Stevenson (1990), that cycads are the most archaic living seed plants, as measured by number of retained ancestral states or overall similarity to the original seed fern morphology. However, we do not agree that compound leaves, ptyxis, and pubescence are homologous in cycads and ferns, as assumed by Loconte and Stevenson (1990) and Bremer (1985), because our results imply that Paleozoic seed ferns and progymnosperms lacking these features are interpolated between the two groups.

SACCATE POLLEN

Loconte and Stevenson (1990) concluded that saccate pollen is a conifer autapomorphy, since it occurs today only in conifers and is absent in several families, including Taxaceae, which they assumed is the sister group of other conifers. In contrast, the preferred tree of Doyle and Donoghue (1986) indicated that sacs were basic in the platysperm clade (which contains all extant seed plants) but were lost in *Ginkgo*, cycads plus *Peltaspermum*, and anthophytes. This followed from the fact that conifers were nest-

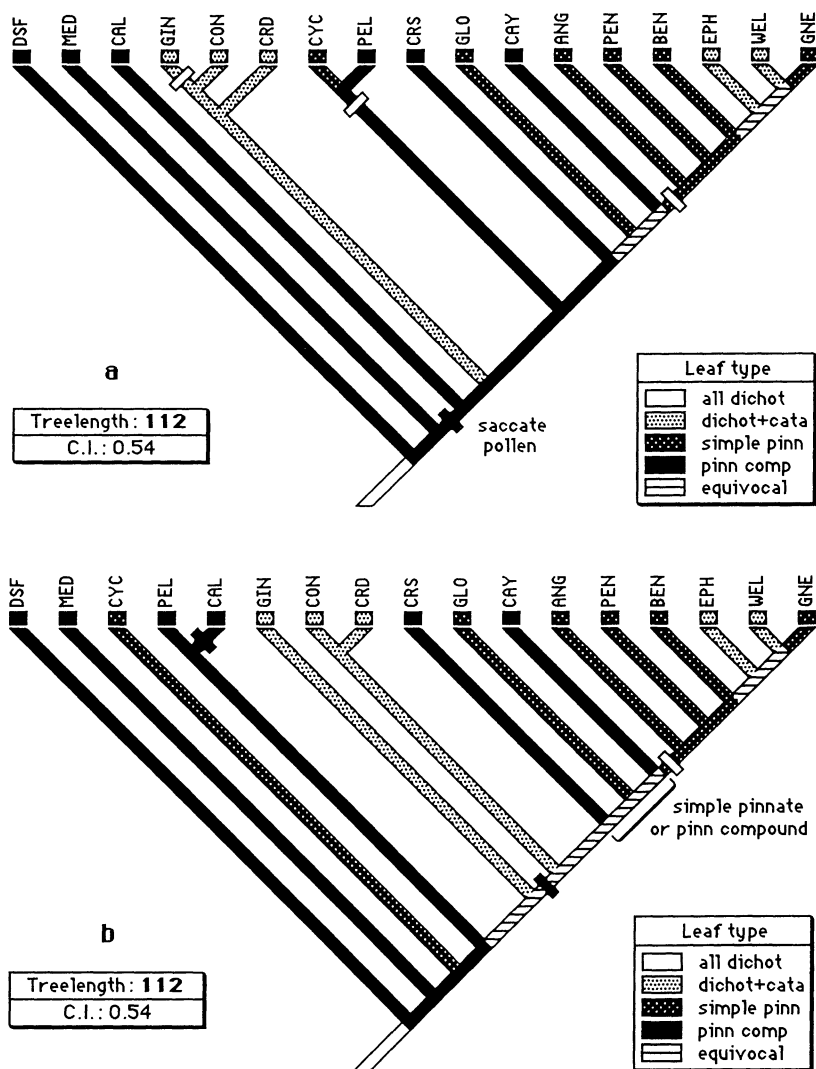


FIG. 2. Representative most parsimonious cladograms found in analysis of the revised Complete data set, showing distribution of the leaf character (shading) and the pollen character (solid bars: origin of sacs; open bars: loss of sacs). DSF: Devonian protostelic "seed fern" (Rothwell & Erwin, 1987; Rothwell et al., 1989); MED: Medullosaceae; CAL: *Callistophyton*; GIN: Ginkgoales; CON: Coniferales; CRD: Cordaitales; CYC: Cycadales; PEL: *Peltaspermum*; CRS: Corystospermaceae; GLO: Glossopteridales; CAY: Caytoniaceae; ANG: angiosperms; PEN: *Pentoxylon*; BEN: Bennettitales; EPH: *Ephedra*; WEL: *Welwitschia*; GNE: *Gnetum*.

ed among Paleozoic and Mesozoic groups with saccate pollen—cordaites, *Callistophyton*, corystosperms, glossopterids, and *Caytonia*. In addition, the oldest and most plesiomorphic Paleozoic conifers have saccate pollen (Florin, 1951; Kerp et al., 1990; Mapes & Rothwell, 1984), which led us to score the group as saccate. *Peltaspermum* is not saccate, but saccate pollen does occur

in apparently related Permian "peltasperms" (e.g., *Autunia*, formerly *Callipteris*; Kerp, 1988; Meyen, 1984). In this light, the absence of sacs in modern conifers appears to be another reversal. This example was used by Doyle and Donoghue (1987) to illustrate how fossils can affect ideas on character evolution even when they do not affect cladogram topology.

In most trees of Doyle and Donoghue (1986), saccate pollen is basic for platysperms, but, as illustrated by Doyle (1988), this is not true of all shortest trees, some of which place cycads below saccate platysperms (with or without *Medullosa*), or higher, such that saccate pollen arises independently in "lower" and "higher" platysperms. These two scenarios hold for the trees obtained with our revised data set (e.g., Fig. 2a, b). However, even when saccate pollen is not basic for platysperms as a whole, it occurs in one or both of the first two outgroups of conifers, which is at least consistent with our assumption that conifers are basically saccate.

Similar considerations apply to another feature that Loconte and Stevenson (1990) concluded is a conifer autapomorphy, one-trace nodes. Our results imply that this condition is homologous with the original one-trace condition of progymnosperms and primitive seed ferns, even in trees with the Loconte and Stevenson topology of extant groups (Fig. 2b).

SIPHONOGAMY AND THE CONIFER-ANTHOPHYTE CONNECTION

Loconte and Stevenson (1990) considered siphonogamy a synapomorphy of conifers and anthophytes, but Doyle and Donoghue (1986) plotted it as a synapomorphy of anthophytes, while recognizing that it could have arisen one or two nodes lower among Mesozoic seed ferns, where conditions are unknown. This conclusion depends both on tree topology and on interpretation of fossils. Under a rigorous assumption that only extant groups can be scored for this character, our inference that siphonogamy arose twice still holds for trees such as Figure 2a, where zooidogamous cycads and *Ginkgo* are interpolated between conifers and anthophytes, but not for trees with the Loconte and Stevenson arrangement of extant groups (Fig. 2b). However, we also scored conifers and cordaites as zooidogamous in our previous and present Complete analyses, based on presence of a proximal aperture and absence of a sulcus in cordaites (Millay & Taylor, 1976) and primitive Paleozoic conifers (reaffirmed by

Kerp et al., 1990), on the assumption that a sulcus is a prerequisite for a pollen tube and in turn for siphonogamy. This interpretation is admittedly somewhat speculative, but if correct it implies that siphonogamy arose twice even in trees with the Loconte and Stevenson arrangement (Fig. 2b).

FLOWERS AS A SYNAPOMORPHY OF ANTHOPHYTES

We did not include flowers as a character in our data set, but we concluded *a posteriori* that they may be an additional synapomorphy of the anthophytes, all of which have strongly aggregated and modified sporophylls (Doyle & Donoghue, 1986). This inference was criticized by Loconte and Stevenson (1990) on the grounds that all extant seed plants show aggregation of sporophylls. This is another case where fossils modify scenarios of character evolution based on living forms, because the extant taxa are nested among fossil groups with sporophylls that show no sign of being aggregated into flowers. For anthophytes, the relevant outgroups are *Caytonia*, glossopterids, and corystosperms. These groups imply that there was a shift to sporophyll aggregation in the common ancestor of anthophytes, independent of that in other extant seed plants.

Although definition of the flower is admittedly somewhat arbitrary, we see no advantage in defining it on presence of a carpel, as advocated by Loconte and Stevenson (1990). If our results are correct, a strobilus directly homologous with the angiosperm flower, with closely aggregated sporophylls and possibly a perianth, originated independently of the strobili of other seed plants but well before the origin of the carpel. This is a conclusion of potentially great biological significance that is highlighted by extending the concept of the flower to anthophytes as a whole and separating it from the concept of the carpel.

Loconte and Stevenson (1990) also rejected our more speculative suggestion that anthophyte flowers were originally bisexual (Doyle & Donoghue, 1986). This idea has become less defensible as a result of Crane's (1988) cladistic analysis of Bennettitales,

which implies that bisexual flowers are derived within that group. However, the presence of a reduced ovule in male flowers of *Welwitschia* and occasional microsporophylls in female flowers of *Ephedra* (Crane, 1985) cautions that bisexual flowers may have once existed in anthophyte taxa where they do not occur today.

OTHER CHARACTERS OF GNETALES

Loconte and Stevenson (1990) concluded that coniferophyte primary xylem pitting is a symplesiomorphy of coniferopsids and Gnetales, but this is not so if glossopterids are interpolated between coniferopsids and anthophytes and Bennettitales between angiosperms and Gnetales, since these fossil taxa have normal primary xylem. They criticized our suggestion that double fertilization (independent of endosperm formation) is a synapomorphy of anthophytes, on the grounds that occurrences in *Ephedra* are teratisms, but Friedman (1990) has shown that this is a regular feature.

Loconte and Stevenson (1990) questioned our implication that pinnately organized leaves could be homologous in angiosperms and *Gnetum*, on the grounds that vein reticulations develop dichotomously in *Gnetum* but monopodially in angiosperms. However, this confuses the pinnate pattern of major venation with the presence of reticulations, which we consider separate characters. Our trees imply that the pinnate venation of angiosperms and *Gnetum* could equally well be convergent, and we suspect that this hypothesis will be favored when Cretaceous Gnetales with parallel venation (Crane & Upchurch, 1987) are added to the analysis. As for reticulations, the developmental distinction made by Loconte and Stevenson is weakened by the fact that finer veins have been shown to develop dichotomously in one angiosperm, *Aucuba* (Pray, 1963), and this is suspected in other angiosperms with "low rank" venation (Doyle & Hickey, 1976). However, we agree that reticulations are not homologous in angiosperms and *Gnetum*, because our results interpolate taxa with open venation (Bennettitales, *Pentoxylon*, *Ephedra*) between the two groups.

Discussion

We wish to emphasize that our disagreements with Loconte and Stevenson (1990) concern attitudes toward phylogenetic analysis as much as results. In our original study (Doyle & Donoghue, 1986), we not only presented the several most parsimonious trees obtained, but we also used an experimental approach to test the strength of various results and to point out weak points for future investigation, and we concluded that some results were robust but others much weaker. Our revised analysis confirms this view. Significantly, our main agreements with Loconte and Stevenson concern two of the conclusions that seemed strongest (monophyly of Gnetales, relationship of angiosperms and Gnetales), whereas the conflicts involve weaker conclusions. We believe it is premature to present one cladogram and codify it in a definitive-appearing formal classification, as done by Loconte and Stevenson. This has the unfortunate effect of engendering a false sense of security, when what is needed most at this point is an active search for new data to clarify a problematical situation.

As a result of our revised analyses, the situation in seed plants now seems somewhat more like that found in amniotes by Gauthier et al. (1988) than it seemed previously. Unlike the seed plant analyses, the Recent and Complete amniote analyses gave markedly different trees. However, the seed plant and amniote results are similar in that both Recent analyses give trees in which two advanced groups (mammals and archosaurs, conifers and anthophytes; Fig. 1d) are linked by features that the Complete analyses indicate are convergences (in the seed plant case, linear-dichotomous leaves, coniferopsid primary xylem, simple sporophylls, lack of sarcotesta, and siphonogamy). To us, these results mean that fossil data call into question the one most parsimonious tree based on Recent seed plants—much of the apparent support for this tree is illusory.

An additional reason to question the Recent tree is the fact that the main character still supporting it in the Complete analysis, epigeal seed germination, is one of three

characters (along with lack of a sarcotesta and siphonogamy) that may be functionally correlated with reduction in seed size. These characters have the same distribution in the Recent data set, but evidence on germination is lacking in fossils. As we have seen, at least lack of a sarcotesta and siphonogamy appear to be convergent based on fossil data. If these three characters are functionally correlated, their individual weight as potential conifer-anthophyte synapomorphies may be less than it would be if they were functionally independent.

It is worth considering evolutionary explanations for the less striking differences between results of the Complete and Recent analyses in seed plants than in amniotes, building on Donoghue et al. (1989). In amniotes, Gauthier et al. (1988) argued that many of the inferred convergences that link mammals and archosaurs in the Recent analysis are functionally related to more rapid and sustained locomotion. Similarly, the inferred convergences between conifers and anthophytes, which were the most diverse and "progressive" Mesozoic plant groups, represent advances over cycads, ginkgos, and Paleozoic seed ferns in both vegetative and reproductive features, most of which may be functionally related to widespread Mesozoic aridity and/or seed protection. Perhaps, because of the lower degree of morphological integration (i.e., modular construction) in seed plants, the pressures for convergence simply affected fewer structures than they did in amniotes.

Another difference between the two groups is that basal relationships seem more poorly resolved in seed plants than in amniotes, even when fossils are included. If valid, this difference may reflect very early divergence of amniotes into two distinct lines, synapsids and diapsids, whereas Late Carboniferous and Permian platysperms radiated rapidly into a large number of poorly differentiated lines. As a result, the few synapomorphies between seed plant lines may have been more easily obscured by later convergences.

This leads us back to the central question: which results should we believe, those based on data sets with fossils or without them?

Doyle and Donoghue (1987), Gauthier et al. (1988), and Donoghue et al. (1989) used conflicts between the two sorts of analyses as evidence that fossils are needed to obtain the correct story. In contrast, Loconte and Stevenson (1990) used them explicitly as evidence that our inferences on seed plant evolution (Doyle & Donoghue, 1986) were incorrect. What basis is there for this conclusion?

One argument for relegating fossils to a secondary role is that they have no effect on cladistic results anyway, but this was not pursued by Loconte and Stevenson (1990). Our results refute this view at least for character evolution, and Gauthier et al. (1988) showed that it is incorrect for cladogram topology. The main reason for believing that fossils have no effect is that they are too incomplete. However, as shown by Donoghue et al. (1989), some fossils are so well reconstructed that they have as many phylogenetically informative characters as living organisms, especially considering loss of information due to specialization in extant forms. Even when fossils are more poorly known, they may reveal character combinations that significantly alter cladistic results.

Loconte and Stevenson (1990) did argue that fossils may be misleading because they bias in favor of accelerated rather than delayed transformation: i.e., one origin of a feature followed by its loss (reversal) rather than multiple origins (parallelism). However, although addition of fossils may be expected to raise the inferred level of homoplasy, like addition of any new taxa (Sanderson & Donoghue, 1989), we see no reason to assume that this homoplasy should take the form of reversal rather than parallelism. In fact, the opposite may be true.

In their critique, Loconte and Stevenson (1990) focused on the paracytic (syndetocheilic) stomates of angiosperms, Bennetitales, *Welwitschia*, and *Gnetum*, which we plotted on our cladogram as originating in the common ancestor of anthophytes and being lost in *Pentoxylon* and *Ephedra* (Doyle & Donoghue, 1986). As they showed, it is equally parsimonious to assume that paracytic stomates evolved more than once on

the Recent seed plant tree. However, the same is also true for our tree that included fossils (cf. Doyle & Donoghue, 1986, p. 356). When (but only when) reversal and parallelism were equally parsimonious, we preferred reversal in some cases (e.g., with complex structures, where we found it easier to imagine several losses than several origins) and parallelism in others (e.g., reductions). However, these criteria had nothing to do with fossils, and we adopted them more for convenience than out of philosophical commitment.

In contrast, Loconte and Stevenson (1990) implied that parallelism should actually be preferred over reversal when both are equally parsimonious. As support, they cited the observation of Cronquist (1968, 1988) that many putative examples of homology are actually parallelisms, and the inferred parallelisms between angiosperms and Gnetales. Based on the effects of adding fossils to the seed plant and amniote data sets, we also suggested that parallelism may be more common than reversal, and we speculated that this may reflect progressive trends in the evolution of the earth's biota (Donoghue et al., 1989; Doyle & Donoghue, 1987). However, such examples do not establish a general law that can be used to favor parallelism in new cases, and they do not imply that fossils are particularly misleading.

Loconte and Stevenson's (1990) primary reason for preferring results based on Recent plants was not an argument at all, but rather the fact that Hennig (1966) and Ax (1987) said that phylogenies should first be reconstructed using extant groups, and fossils should be incorporated *a posteriori*. In contrast, we recommend *a priori* inclusion of fossil taxa simply because they are additional groups that provide potentially relevant data. When faced with a choice between a course of action based on authority and one based on taking into account more data, we have no difficulty in making a decision. To this may be added the fact that there has been much recent theoretical concern over the importance of an adequate sampling of taxa in cladistic analyses, especially when taxa are separated by many character changes (so-called "long branch-

es": Felsenstein, 1978), as they are in seed plants. Furthermore, at least some fossils are likely to be more plesiomorphic than their extant relatives and may therefore have a large effect on the position of specialized lines (Donoghue et al., 1989).

In view of the small number of steps separating very different trees, we reiterate that strong conclusions about seed plant phylogeny would be premature, except that both angiosperms and Gnetales are monophyletic and more closely related to each other than they are to other extant groups. The uncertainties are underlined by studies of ribosomal RNA (Hamby & Zimmer, 1992; Zimmer et al., 1989), which contradict both our results and those of Loconte and Stevenson (1990) in linking conifers with cycads. In our opinion, this ambiguity is not merely a sign of lack of progress, but an important result in itself, which has to be recognized and faced at the present stage of development of the field. These conflicts are unlikely to be resolved without new evidence. Molecular studies are an obvious source of new evidence in extant plants. However, molecular sequence data have intrinsic problems that are especially severe when dealing with rapid radiations that occurred long ago, like the radiation of seed plants: the tendency for spurious attraction of long branches (Felsenstein, 1978; Lake, 1987; Wheeler, 1990), and the possibility that molecular synapomorphies marking major clades are either erased by later evolution in rapidly evolving sequences or too infrequent in slowly evolving ones (Donoghue et al., 1989; Donoghue & Sanderson, 1992). In such cases, decisive new data may come only from fossils—discovery of new groups, or new information on characters of known groups.

We do not mean to imply that fossils are always needed to obtain valid phylogenetic results. When enough intermediate taxa are still extant and branch lengths are short, fossils may well be superfluous. *A posteriori* consideration may be the only practical way to make use of highly fragmentary fossils, such as dispersed pollen grains (Doyle & Hotton, 1991). However, we believe that students of groups such as vascular plants,

vertebrates, or arthropods would be ill-advised to undertake higher-level cladistic analyses without *a priori* consideration of their many well-documented fossil members. And for the foreseeable future, students of presumably ancient groups with no fossil record may have to live with the unpleasant possibility that even apparently well-supported cladistic results are actually incorrect. It is our hope that this discussion will stimulate a search for critical new data on fossil seed plants, especially evidence on basic conditions in the cycad and ginkgo lines and anatomical and reproductive characters of platyspermic seed ferns.

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Appendix

DATA MATRICES

	1	2	3	4
ANC	0?00?00??700000000?700?0000?00?7000?0000?00?7???			
DSF	?70300000?000000 10?0000?0 100 10000?000?7000?000?7??			
MED	100300000?00 1000 12?00 10?0 100 11 10 1?000?0000?0?0?7??			
CAL	1003 100?0? 100000 11?00 100 110021100?1110 10?00?70?7??			
CRD	100 1?0000? 1100000 1?200 10?000 12 110?700 10 10?000?0?7??			
CON	100 1?00000 10 100002020 10? 100?20 10000 110 10 100000001			
GIN	100 1?00000 113 1000 1020 10?70002 11000 110? 10 100000000			
CRS	?70300000?2020000 1?00201 10002? 1?70 11110?12?7?7?7??			
PEL	?7?3 100?0?7?			
CYC	?702?00000 112000 12000 10? 1000? 110 10 110? 10 100000000			
GLO	1002? 10?0? 1?70000?700?00000020 100 111? 11?0?7?0?7??			
CAY	1003? 10 10?7?			
BEN	1002?000 1? 1100 1012? 1030 10 10?0 110? 110?20 11?70?0?7?			
PEN	1002?0000?2?30 1010? 1030 10?7020 100 11 10?20? 1?7?7?7??			
EPH	1111?0000 1113 10 110 12 111?0 11120 11002 10?21 110 100001			
HEL	1111? 110 10 113 10 112 12 111?0 11120 1100 110?21 11111111			
GNE	1112? 1101 11112 1? 110 12111?0? 110 11002?0?2?7? 11111111			
ANG	1002? 11111 1120 1? 10 10020 1? 100?0?7?0 1110?20 1?7? 100 101			

	1	2	3	4
ANC	0?0?-0-100--00?0?70?7??-??70?7?-??7?-?-??-00000 10?			
CYC	0?00-0-000--1000 1200000-1000?0-0 100-0-00-00000000			
GIN	100 1-0-000--2 1000 10 1000-1000 10-0000-0-00-00000000			
CON	100 1-0-000--0 100020 1000-1000? 11-0000-1-00-00 10000 1			
EPH	1111-0-001--2 10 110 11101-0 11111-1001-0-11-10 10000 1			
HEL	1111-1-010--2 10 112 11101-0 11111-1000-0-11-11111111			
GNE	1110-1-011--1? 110 11101-0? 1101-1001-0-1? 11111111			
ANG	1000-1-111--10 1? 10 100 10-? 100?1-00 10-0-10-1? 100 101			

Top: Complete data set; bottom: Recent data set, with characters omitted indicated by dashes. ANC: ancestral states, based on outgroup comparison with *Archaeopteris* and *Aneurophyton* in the Complete data set, and with ferns and *Equisetum* (forming an unresolved trichotomy with seed plants) and lycopsids (the next outgroup) in the Recent

data set; DSF: Devonian protostelic "seed fern" of Rothwell and Erwin (1987) and Rothwell et al. (1989); MED: Medullosaceae; CAL: *Callistophyton*; GIN: Ginkgoales; CON: Coniferales; CRD: Cordaitales; CYC: Cycadales; PEL: *Peltaspermum*; CRS: Corytospermaceae; GLO: Glossopteridales; CAY: Caytoniaceae; ANG: angiosperms; PEN: *Pentoxylon*; BEN: Bennettitales; EPH: *Ephedra*; WEL: *Welwitschia*; GNE: *Gnetum*.

Characters

Where character states are defined differently in the Complete and Recent analyses, the definitions used in the Complete analysis are indicated first, then those used in the Recent analysis.

1. Branching (0) apical, (1) axillary. Polarity in the Recent data set is based on ferns and lycopsids; the monopodial but non-axillary branching of *Equisetum* is presumably an autapomorphy.

2. Axillary buds (0) single, (1) multiple. As a consequence of scoring cycads as apical or unknown for branching, we rescored them as unknown for this character, and we rescored the ancestral state as unknown rather than single, because the outgroups lack axillary buds.

3. Phyllotaxy (0) spiral, (1) opposite or whorled.

4. Leaves (0) all dichotomous, (1) linear or dichotomous plus cataphylls, (2) simple pinnate plus cataphylls, (3) pinnately compound plus cataphylls; Recent: (0) pinnately organized, (1) linear or dichotomous.

5. Rachis (0) bifurcate, (1) simple.

6. Laminar venation (0) one, (1) reticulate.

7. Laminar vein orders (0) open, (1) two or more.

8. Guard cell poles (0) raised, (1) level with aperture.

9. Stomates (0) haplocheilic, (1) some or all syndetocheilic.

10. Apical meristem (0) without tunica, (1) with tunica. Loconte and Stevenson (1990) rejected our character "apical meristem with differentiation of tunica and corpus," which links angiosperms and Gne-

tales, as "a composite character of the apomorphic tunica and plesiomorphic corpus." We were trying to contrast the apomorphic state where both a tunica and a corpus are present with the plesiomorphic state where a tunica is absent. Whether meristems of the latter type have a corpus is a semantic issue; the distinction between the two meristem types remains.

11. Stele (0) protostele, (1) eustele with external secondary xylem only, (2) eustele with internal secondary xylem.

12. Primary xylem (0) mesarch, (1) endarch.

13. Nodes with (0) one leaf trace, (1) more than two traces derived from a solid mass or arcs of primary xylem, scattered in petiole, (2) more than two traces derived from individual primary xylem bundles, arcuate in petiole, (3) two traces from two adjacent primary bundles; Recent: (0) one trace, (1) more than two traces, (2) two traces.

14. Primary xylem (0) with scalariform pitting in the metaxylem, (1) with no scalariform pitting (coniferopsid type).

15. Secondary xylem (0) with circular bordered pitting or perforations only, (1) with at least some scalariform pitting or perforations. Cycads are scored as circular bordered because occurrences of scalariform pitting (*Zamia*, *Stangeria*) seem derived within the group (Crane, 1988; Stevenson, 1990).

16. Vessels (0) absent, (1) present.

Instead of the two preceding characters, Loconte and Stevenson (1990) recognized one character with three states, imperforate (pitted), foraminate (as in vessels of Gnetales), and scalariform (as in angiosperms). This is consistent with our formulation if only Recent taxa are considered, but it entails some loss of information if one includes fossil Bennettitales and *Pentoxylon*, which have scalariform pitting but no vessels.

17. Rays (0) uniseriate or biseriate, (1) at least some multiseriate.

18. Cortical secretory structures (0) absent, (1) cavities, (2) canals. Loconte and Stevenson (1990) divided secretory tissues into mucilage (cycads, *Ginkgo*, *Welwitschia*,

Gnetum), resin canals (conifers), oil cells (angiosperms), and absent (*Ephedra*), but because all but the first state are restricted to single taxa, this character would have no effect on topology.

19. Lignin with (0) no Mäule reaction, (1) Mäule reaction.

20. (0) Micro- and megasporophylls pinnate, (1) microsporophylls pinnate, megasporophylls simple, (2) micro- and megasporophylls simple; Recent: sporophylls (0) pinnate, (1) simple.

21. Ovule position (0) appendicular, (1) terminal.

22. Cupule (0) radial, lobed, (1) absent, (2) anatropous, (3) orthotropous unlobed; Recent: (0) absent, (1) present. Loconte and Stevenson (1990) treated ovule orientation and integument number (=presence or absence of a cupule, under our interpretation) as two characters. These characters could be questioned as redundant in terms of extant groups, because anatropous and bitegmatic ovules are both restricted to angiosperms, but this should not affect the results.

23. Outer integument derived from two appendages (0) absent, (1) present.

24. Ovules per anatropous cupule or potential homolog (0) several, (1) one.

25. Microsporangia (0) terminal, marginal, or adaxial, (1) abaxial. Because microsporangia are abaxial in *Ginkgo* but terminal in some fossil Ginkgoales (*Baiera*), we scored Ginkgoales as unknown in our previous Complete analysis, but we failed to rescore *Ginkgo* as abaxial in our previous Recent analysis. We have corrected this oversight in the present study. We note that Loconte and Stevenson (1990) were mistaken in stating that we attributed no fossil taxa to the stem lineage of Ginkgoales; we explicitly included *Baiera* and *Karkeniania*.

26. Microsporangia (0) free, (1) fused at least basally.

27. Microsporophylls (0) spirally arranged, (1) whorled.

28. Strobili (0) lacking or simple, (1) compound. We previously defined this character as "compound male and female strobili" and scored all groups lacking strobili as unknown ("not applicable"), including cycads, because *Cycas* has megasporophylls not borne in strobili. However, we have redefined the ancestral state to include groups without strobili, on the assumption that evolution of compound strobili was always preceded by evolution of simple strobili. We have also rescored conifers, which have compound female but simple male strobili, as unknown rather than primitive. Based on Paleozoic conifers, we assumed that conifers originally had simple male strobili, and that aggregation of the female strobili occurred independently from the aggregation of both male and female strobili in cordaites and Gnetales. However, this scenario seems equivocal on fossil evidence, and it is even less clear in extant seed plants, because some species of *Podocarpus* have compound male strobili.

29. Seeds (0) absent, (1) radiospermic, (2) platyspermic; Recent: (0) radiospermic, (1) platyspermic.

30. Integument (0) simple, (1) with sclerotesta and sarcotesta.

31. Megasporangium with (0) lagenostome, (1) simple pollen chamber.

32. Micropyle (0) normal, (1) tubular.

33. Nucellus (0) not vascularized, (1) vascularized.

34. Nucellar cuticle (0) thin, (1) thick.

35. Pollen with (0) tetrad scar, (1) sulcus, (2) no aperture; Recent: (0) sulcus, (1) no aperture.

36. Pollen symmetry (0) radial, (1) bilateral. Previously we scored the reduced, spherical pollen of *Gnetum* as radial, but it is better interpreted as autapomorphic in having neither radial nor bilateral but rather global symmetry. We have therefore rescored *Gnetum* as unknown in the Complete data set and deleted the character from the Recent data set, where all taxa except *Gnetum* have bilateral symmetry.

37. Pollen (0) non- or sub-saccate, (1) saccate.

38. Saccus structure (0) eusaccate, (1) protosaccate.

39. Exine structure (0) spongy alveolar, (1) honeycomb alveolar, (2) granular; Recent: (0) alveolar, (1) granular.

40. Exine striations (0) absent, (1) present. We rescored *Gnetum* as unknown for this character, on the grounds that its tectal

layer is so reduced that any striations in its ancestors would have been lost during reduction.

41. Megaspore tetrad (0) tetrahedral, (1) linear.

42. Megaspore wall (0) thick, (1) thin or absent.

43. Microgametophyte with (0) more than four nuclei, (1) four nuclei.

44. Sperm transfer (0) zooidogamous, (1) siphonogamous.

45. Megagametophyte (0) monosporic, (1) tetrasporic.

46. Egg (0) cellular, (1) free-nuclear.

47. Early embryogenesis (0) free-nuclear, (1) cellular.

48. Embryo (0) without feeder, (1) with feeder.

49. Seed germination (0) hypogeal, (1) epigeal.

BOOK REVIEW

The Key to the Vascular Flora of the Northeastern United States and Southeastern Canada. By Floyd Swink. Plantsmen's Publications, Box 1, Flossmoor, IL 60422. ISBN not given. 1991. 546 pp. \$21.95 (paper) plus \$3 shipping and handling.

This book is a "fieldguide" key, intended to complement *Gray's Manual of Botany* (8th edition). The nomenclature is that of *Gray's Manual* and the range covered is purported to be that covered by *Gray's Manual* (though in fact this book does not cover the whole range of *Gray's Manual*, e.g., it omits the Gaspé Peninsula).

After the short introduction there is a list of families in Englerian order, a key to the families, and alphabetically arranged keys to genera and species. An appendix lists species not treated in the keys and there is a glossary.

The concept and some of the keys to species are useful. Unfortunately, the book has many problems. To begin with it was poorly edited. For instance, the title on the copyright page is given as "*KEY TO THE FLORA OF THE CHICAGO REGION*," which it is assuredly not, and in the introduction a bibliography is referred to several times yet I can find no bibliography.

The keys, the heart of this book, leave much to be desired. They are botanically incorrect, poorly constructed, and difficult to read. I shall cite just a few of the many problems with the keys. The very first cou-

plet (p. 1, couplet A) separates Ferns and Fern Allies from Gymnosperms and Angiosperms based on the presence or absence of stamens, pistils, and true seeds. Since when do Gymnosperms have stamens or pistils? In the Key to Families there are over a hundred leads that read "Plants without the above combination of characters" and there are many more examples throughout the rest of the book. Furthermore, the leads often have the more variable characters first and more stable characters later. Lastly, the leads are run together without line breaks between and, in many cases, without letters signifying the start of a new lead. I lost my place many times trying the keys.

I feel that the exclusion from the keys of rare and local species makes this work much less useful than the author might think. Professional botanists, government agencies, environmentalists, and many amateurs will find this work useless for much, or all, of their work. The presence of a list at the back of the book with the excluded species is a help. But it would have been better to list the excluded species of a particular genus with the key to species of that genus, so that one could see at a glance which species are missing and where they occur.

Although the price of the book is reasonable, the concept is good, and some of the keys useful, I cannot recommend this work because of the many errors and omissions. — STEVEN E. CLEMANTS, Brooklyn Botanic Garden, 1000 Washington Ave., Brooklyn, NY 11225-1099.