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THE IMPORTANCE OF FOSSILS IN PHYLOGENY RECONSTRUCTION

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INTRODUCTION

It is widely believed that fossils are of fundamental importance in reconstructing phylogeny (e.g. 24, 28). Simpson (52, p. 83), for example, argued that "fossils provide the soundest basis for evolutionary classification." Although phylogenies of many groups have been reconstructed using morphological or chemical characters of extant organisms alone, it is often noted that fossils would have been of great use in clarifying relationships and that conclusions are necessarily tenuous in their absence. Thus, Thorne (58, p. 85) commented

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in regard to angiosperms that "the best classification we can construct with present information is a poor semblance of what it should be if the fossil record were more complete."

This view of the importance of fossils has been criticized by phylogenetic systematists. Hennig (26) introduced a very general approach to the reconstruction of phylogeny—a method that could be applied to living organisms alone, to fossils, or to both. He recognized that fossils might be useful in assessing the direction of character evolution and could aid in detecting instances of convergence (e.g. through the discovery of plesiomorphic taxa lacking convergent characters of Recent groups). However, Hennig also stressed that fossils are generally less complete than living organisms and therefore should be less helpful in elucidating phylogenetic relationships. He (27) later developed the view that fossils, if considered at all, could be added to the "stem-groups" ("stem lineages" of Ax, 1) leading to Recent groups ("*groups" of Hennig; "crown-groups" of Jefferies, 29).

Subsequent discussion by cladists of the role of fossils in phylogeny reconstruction has tended to amplify the shortcomings noted by Hennig (e.g. 16, 30, 47). In particular, the view that phylogeny might be observed directly by paleontologists—that "the truth of evolution is there, in the rocks, waiting patiently to be revealed" (40, p. 40)—has been sharply criticized. As Nelson (39, p. 329) put it, the fossil record, like information on modern organisms, is "only data in search of interpretation." Likewise, the apparent preoccupation of paleontologists with identifying ancestors has come under attack: Ancestral higher taxa are paraphyletic, and ancestral species will generally be difficult to discover (e.g. 49, 59). Even the utility of the stratigraphic approach to character polarity has been criticized, primarily on the grounds that a spotty record might yield mistaken conclusions (13, 54; but see 14).

Patterson (43) made a different claim, namely that *in practice* fossils have little influence in establishing relationships among extant groups. Indeed, his evaluation of the bearing of fossils on pre-Darwinian classifications of a wide variety of organisms, or on more recent classifications based on molecular or cytological data, led him to conclude the "instances of fossils overturning theories of relationship based on Recent organisms are very rare, and may be nonexistent" (43, p. 218).

This view seems to have been widely accepted, at least among cladists. It is, for example, endorsed in Ax's textbook on phylogenetic systematics (1). Although Ax admits (1, p. 201) that "logically there can be no grounds whatever, in the theory of phylogenetic systematics, for treating extinct organisms differently from recent ones," he argues that fossils are so incomplete that cladograms should be based on Recent groups alone and that fossils (if any) should be added into appropriate stem lineages after the fact. This protocol is based on the assumption that "in general, adelphotaxon [sister group] relationships between the recent taxa . . . will not at all be changed by placing fossils in the stem lineages of these taxa" (1, p. 209), "nor by transferring the fossils from one stem lineage to another" (1, p. 223). Perhaps as a consequence of this outlook, cladists have tended to focus on problems associated with classifying fossils along with extant groups, especially on devising taxonomic conventions that minimize the proliferation of categorical ranks and attendant nomenclatural changes, such as the "plesion" concept (44; but see 4, 60) and the "annotated hierarchy" (59). Gauthier et al (21, 23) deal with this problem by abandoning categorical ranks for higher taxa altogether.

In view of the sweeping nature of Patterson's claim and the diversity of opinion regarding the importance of fossils, it is surprising that their role in phylogeny reconstruction has not been evaluated more rigorously. There have been several indirect explorations of the effects of addition or subtraction of taxa on establishing character polarities and phylogenetic relationships (e.g. 9, 17, 34, 37). These studies demonstrate that the addition of taxa can have an effect, and they help identify the circumstances under which this will occur (e.g. addition of outgroups closer to an ingroup can reverse a polarity assessment: 37). However, they do not address the effects of fossils in actual cases.

Recently, we conducted studies designed to test directly Patterson's claim that fossils will not overturn theories of relationship based on extant organisms. Doyle & Donoghue (12) assessed the importance of fossils in elucidating seed plant phylogeny, and Gauthier, Kluge & Rowe (22) examined the influence of fossils in establishing relationships among Recent groups of amniotes. Our aim here is to review these studies and to compare their results in the hope of extracting general conclusions regarding the importance of fossils. We have not attempted a complete review of the literature on fossils and phylogeny, nor have we considered all the ways in which fossils might provide phylogenetic information (e.g. stratigraphic distribution). Instead our concern is with the consequences of including (or ignoring) fossils as terminal taxa in numerical cladistic analyses, especially as regards topological relations among extant groups and theories of character evolution. These, we believe, are critical issues because they bear directly on the accuracy of phylogenetic hypotheses based solely on extant groups and, in turn, on theories that are contingent upon such phylogenies. Can we obtain a reasonably accurate picture of phylogenetic relationships based on extant organisms, or is there reason to be suspicious of results that fail to take into account extinct forms? Are fossils unlikely to change ideas on relationships of modern groups simply by virtue of their incompleteness, or can a consideration of incomplete samples substantially alter our understanding of phylogeny? And if fossils can make a difference, is it possible to identify circumstances in which we should be more or less concerned about their absence?

BACKGROUND ON RECENT STUDIES

The analyses of Doyle & Donoghue (12) and Gauthier et al (22) employed generally similar strategies. In both cases the effects of fossils were tested by means of computer experiments involving the addition and subtraction of taxa from data matrixes used in cladistic parsimony analyses. These experiments were designed to document both the influence of knowledge of fossil outgroups and the effects of including or excluding fossil ingroup taxa. Manipulations involving ingroup taxa were designed to identify how particular fossils or groups of fossils affected the outcome, and what combinations of characters were more or less likely to produce topological changes. In all cases, care was taken to recode characters and rescore taxa to reflect knowledge of only those groups actually included in the analysis. In other words, when fossils were omitted every effort was made to treat the remaining groups as if the excluded groups had never been discovered.

Amniotes

According to the traditional view of relationships among extant Amniota, birds are united with crocodiles and, in turn, with lepidosaurs, to the exclusion of mammals (plus extinct therapsids) and turtles (Figure 1, top). This implies that mammals and birds are independently derived from the paraphyletic "reptiles." In cladistic analyses involving fossil and Recent amniotes, Gauthier (19–21) supported the resolution of relationships shown in Figure 1 (middle).

The study of Gauthier et al (22) was prompted by the analysis of Gardiner (18), which was conducted without initially considering fossils. Using 37 characters of the extant groups, Gardiner (18) concluded that birds and mammals are directly united in a clade, for which he resurrected the pre-Darwinian name Haemothermia. In turn, he linked Crocodylia and Haemothermia in Thecodontia, and Thecodontia with Chelonia in Euamniota. This hypothesis is shown in Figure 1 (bottom). Further attention was drawn to Gardiner's proposal by Løvtrup (35), who supported the same relationships based on additional characters of extant groups.

Inasmuch as fossils are frequently cited as having played an important role in reaching the traditional view (e.g. 7), and Gauthier's hypothesis (19, 20) was strongly influenced by knowledge of fossil groups, Gauthier et al (22) viewed amniote phylogeny as an ideal case to test Patterson's proposition that fossils do not overturn hypotheses based on extant organisms. Existing phylogenetic hypotheses incorporating fossil data and/or those based solely on extant groups must be incorrect.

To avoid the criticism that a more complete analysis of modern groups than that performed by Gardiner (18) or Løvtrup (35) would yield results compat-

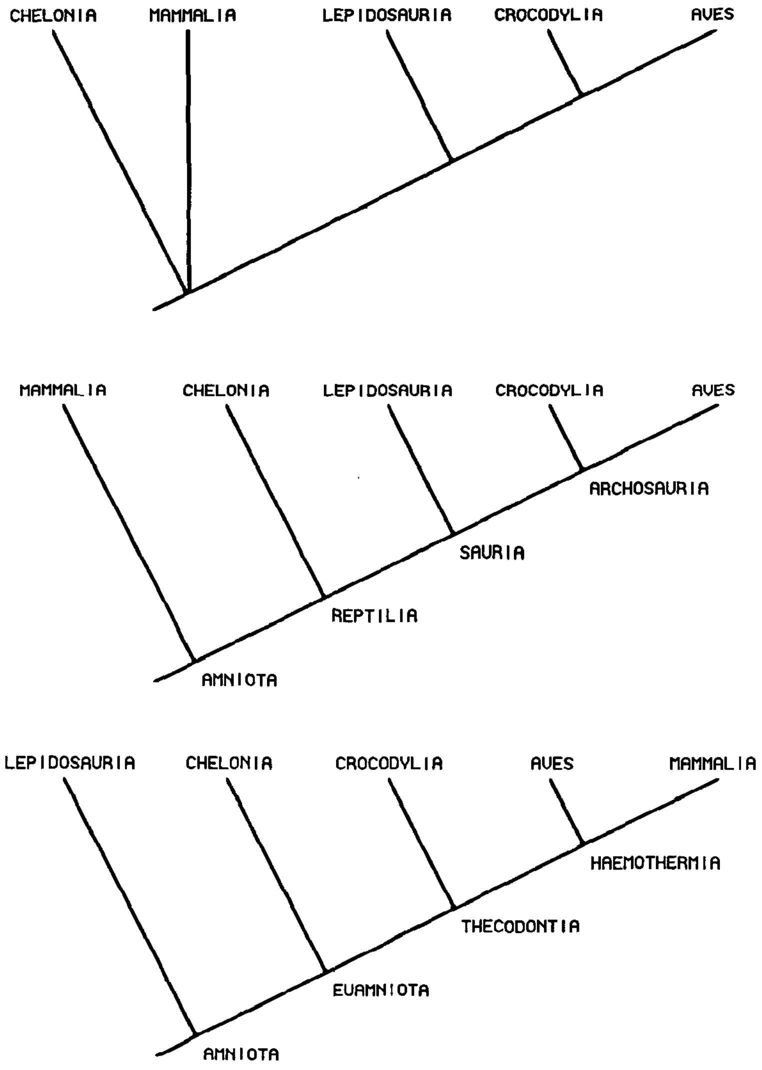

Figure 1 Competing hypotheses of relationships among major groups of Recent Amniota. Top: Traditional hypothesis; middle: Gauthier's hypothesis (19, 20); bottom: Gardiner's hypothesis (18).

ible with those based on both fossil and Recent groups, Gauthier et al (22) first reanalyzed cladistic relationships among extant amniotes. In this "Recent analysis" they took into account the characters assembled by Gardiner (18) and Løvtrup (35), reinterpreting some of these and adding many others. The resulting data set consisted of 109 characters (95 binary and 14 multistate) necessitating a minimum of 126 steps (state changes or synapomorphies); 45 of these steps concern fossilizable ("hard") attributes and 81 concern nonpreservable ("soft") anatomical features. Living lissamphibians and lungfish were considered the first and second outgroups, respectively, and fossil evidence was scrupulously avoided in character analysis and in scoring the extant groups.

Gauthier et al (22) then assembled a second data set in which 24 extinct taxa were added and fossil members of the 5 extant groups were taken into account. This "Complete analysis" was based on 274 characters (249 binary and 25 multistate) requiring a minimum of 303 steps, including the 81 steps in "soft" characters used in the Recent analysis and 222 steps in "hard" characters. The great increase in "hard" data primarily reflects the addition of characters that were excluded from the Recent analysis as autapomorphies of extant groups; when fossils are considered, many of these are seen to be synapomorphies uniting extant and extinct groups. The polarities of the soft characters in the Complete analysis were necessarily based on comparisons with extant outgroups, as in the Recent study. In contrast, the hard characters were polarized based on comparisons with extinct groups, such as diadectomorphs and seymouriamorphs, which are more closely related to amniotes than are lissamphibia and lungfishes (23).

Seed Plants

Doyle & Donoghue's (12) study was motivated by Patterson's (43) claim (based on discussions with paleobotanist C. R. Hill) that fossils have not had a significant impact on phylogenetic hypotheses based on Recent plants, a view that seemed at odds with the history of plant systematics. The starting point for Doyle & Donoghue's analysis was their own cladistic study of seed plants based on a data set of 7 extant and 13 extinct taxa scored for 48 characters (38 binary and 10 multistate), requiring a minimum of 62 steps (11). This contrasts with the amniote study, which was motivated by a prior analysis of extant groups alone.

The "Complete analysis" of Doyle & Donoghue (Figure 2) supports the view that seed plants are a monophyletic group, originally with fern-like leaves ("seed ferns"), nested within (derived from) "progymnosperms," a paraphyletic group represented by *Aneurophyton* and *Archaeopteris*. This contradicts the alternative hypothesis that seed plants are diphyletic, with coniferopsids (which have platyspermic, or bilateral, seeds) and "cycadopsids" (the remaining groups, with basically radiospermic, or radial, seeds) derived independently from "progymnosperms" (3). Specifically, the Complete analysis indicates that coniferopsids are nested within platyspermic "seed ferns" with saccate pollen grains (such as *Callistophyton;* 48). Furthermore, the angiosperms are united with Bennettitales, *Pentoxylon,* and Gnetales in an anthophyte clade, which is nested within the platyspermic, saccate clade. This hypothesis contrasts with the widespread view that angiosperms alone are related directly to *Caytonia* (10) or glossopterids (45), and that Gnetales are related to coniferopsids. The cycads are equally parsimoniously accommodated in several different positions: within the platyspermic clade (either linked with *Peltaspermum* or as the sister group of glossopterids, *Caytonia,* and anthophytes), as the the sister group of the entire platyspermic clade, or linked directly with *Medullosa* (see 11). Thus, the Complete analysis yields two arrangements of the extant seed plant taxa (See Figure 5a,b in the section on Summary of Results, Seed Plants).

Removal of fossil taxa ("Recent Analysis") resulted in a reduction in the

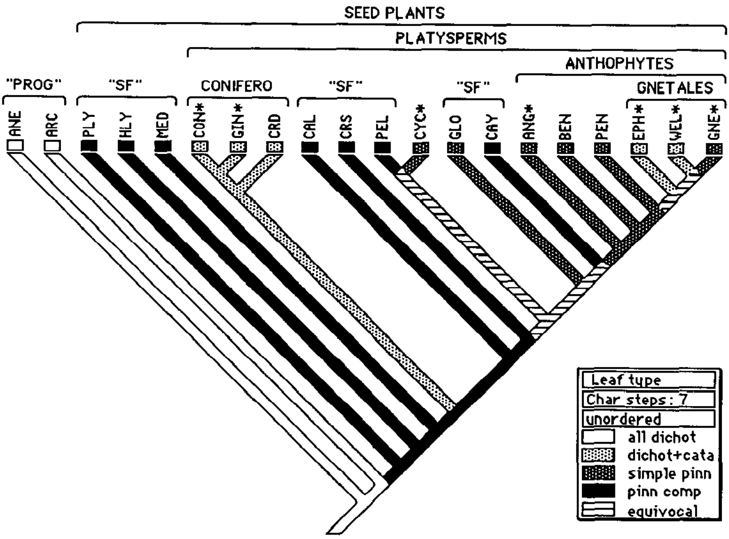

Figure 2 Representative most parsimonious cladogram of extinct and extant seed plants and "progymnosperms" (11), with evolution of leaf morphology indicated by shading. Names of terminal taxa, left to right: *Aneurophyton, Archaeopteris,* protostelic lyginopterids, "higher" lyginopterids, *Medullosa,* Coniferales, Ginkgoales, Cordaitales, *Callistophyton,* Corystospermaceae, Cycadales, *Peltaspermum,* Glossopteridales, *Caytonia,* angiosperms, Bennettitales, *Pentoxylon, Ephedra, Welwitschia, Gnetum.* "PROG", groups traditionally desginated "progymnosperms"; "SF", groups traditionally designated "seed ferns"; CONIFERO, coniferopsids. Extant taxa marked with *.

minimum number of steps from 62 to 40. Some characters were eliminated because they are invariant among extant groups (e.g. heterospory), while several multistate characters collapsed to binary characters (e.g. four leaf states were simplified to two, linear/dichotomous and pinnate). Similarly, some characters that vary independently when fossils are considered, such as reticulate venation and several vein orders, were combined because they are strictly correlated in extant groups and would probably be viewed as redundant in an analysis of extant groups alone. Several terminal taxa, particularly conifers, were rescored so as to eliminate information on fossils.

In these experiments character polarities were determined using several outgroup arrangements. Three "rootings" were based on extant outgroups only: a "conservative" rooting with ferns and/or sphenopsids as the first outgroup(s) and lycopsids more distantly related, and two "fern" rootings meant to reflect the older view that seed plants are derived from "ferns" (31; 5). Two other arrangements, involving "progymnosperms" and early "seed ferns," tested the effects of including more distant and closer fossil outgroups.

SUMMARY OF RESULTS

Amniotes

The analysis of Recent amniote taxa conducted by Gauthier et al (22) yielded the result shown in Figure 3. This cladogram is not identical to that obtained by Gardiner (18; Figure 1, bottom); crocodiles, rather than mammals, are the sister group of birds, and Haemothermia is therefore not supported. Surprisingly, however, mammals are the sister group of the crocodile-bird clade, which means that many features generally interpreted as convergent in mammals and birds (such as homeothermy) can be interpreted as homologous, as in Gardiner's tree (assuming they were lost in crocodiles). Two of Gardiner's clades that conflict directly with traditional views *are* confirmed by this analysis, namely Euamniota and Thecodontia. Given the Recent data set,

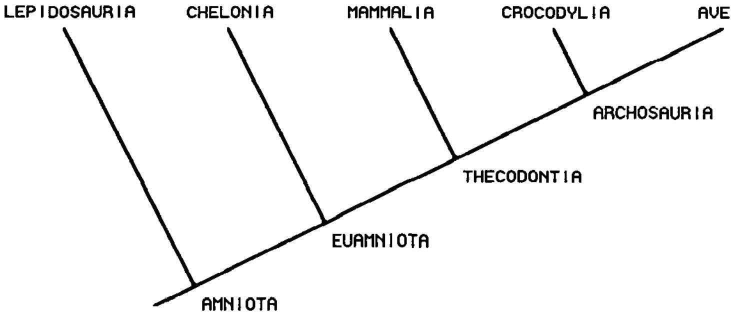

Figure 3 Amniote phylogeny based exclusively on evidence available from extant forms (22).

Gauthier's hypothesis (Figure 1, middle) is 8 steps less parsimonious than the Recent tree (Figure 3), requiring 183 steps. Gardiner's hypothesis (Figure 1, bottom) is even less parsimonious, requiring 11 more steps than the Recent tree.

The Complete analysis, including both Recent and fossil taxa, resulted in the tree shown in Figure 4. This result is consistent with the traditional view (Figure 1, top), and it corresponds precisely with Gauthier's hypothesis for extant groups (Figure 1, middle). It differs radically, however, from Gardiner's hypothesis (Figure 1, bottom), and it is inconsistent with the Recent hypothesis (Figure 3) in reversing the position of mammals and lepidosaurs.

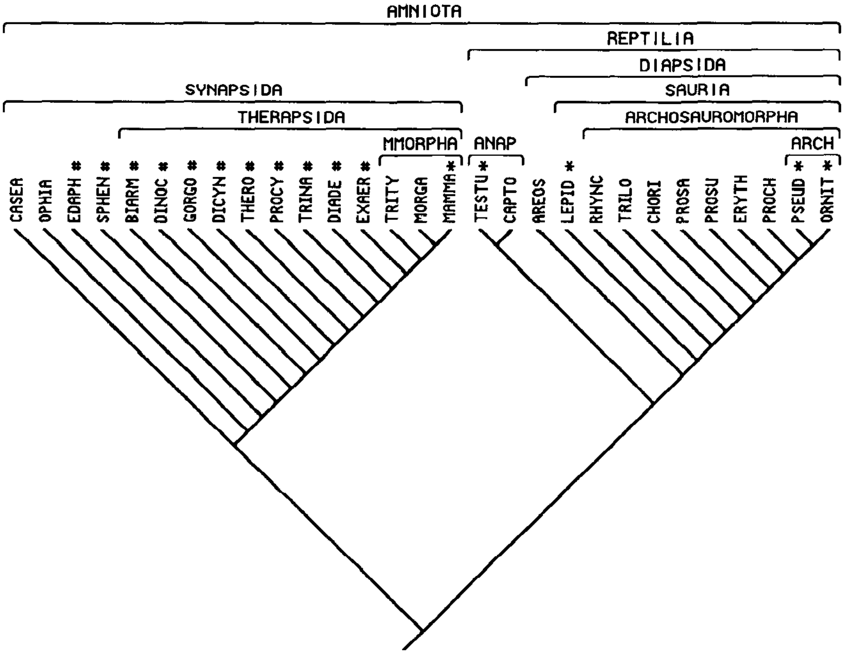

Figure 4 Amniote phylogeny based on evidence from extinct and extant forms (22). Names of terminal taxa, left to right: *Casea, Ophiacodon, Edaphosaurus,* Sphenacodontinae, Biarmosuchia, Dinocephalia, Gorgonopsia, Dicynodontia, Therocephalia, *Procynosuchus, Thrinaxodon, Diademodon, Exaeretodon,* Tritylodontidae, Morganucodontidae, Mammalia, Testudines (extant Chelonia plus extinct outgroups), Captorhinidae, Araeoscelidia, Lepidosauromorpha (extant Lepidosauria plus extinct outgroups), Rhynchosauria, *Trilophosaurus,* Choristodera, Protorosauria, Proterosuchidae, Erythrosuchidae, Proterochampsidae, Pseudosuchia (Crocodylia plus extinct outgroups), Ornithosuchia (Aves plus extinct outgroups, i.e. "dinosaurs"). MMORPHA, Mammaliamorpha; ANAP, Anapsida; ARCH, Archosauria. Extant taxa marked with *; crucial synapsid fossils marked with # (see text).

These results therefore refute Patterson's (43) assertion that fossils will not overturn relationships based upon extant groups alone. Inferred phylogenetic relationships among major groups of extant amniotes are dramatically altered by including fossil taxa in the analysis. In this case, topological relationships more consistent with traditional views are obtained by adding fossils.

Gauthier et al (22) explored the reasons for the change in relationships with a series of computer experiments designed to isolate the fossil taxa responsible. To test the effects of fossil outgroups, they deleted all 24 extinct taxa from the ingroup, but retained polarity assessments for the "hard" characters based on fossil outgroups. The resulting cladogram of extant taxa matched the Recent hypothesis in uniting mammals with archosaurs, indicating that fossil outgroups, and the polarity assessments they provide, are not sufficient to cause the change in the position of mammals seen in the Complete analysis.

If the addition of ingroup fossils is responsible for altering relationships, which groups are especially important in doing so? To answer this question Gauthier et al (22) first excluded all fossil reptiles (anapsids and diapsids, including birds) from the analysis of the Complete data set, and then all synapsid fossils. This coarse-grained analysis revealed that only the removal of the synapsid fossils yielded Thecodontia (mammals plus archosaurs), indicating that it is the inclusion of these extinct groups that forces the change in the position of extant mammals.

In order to identify the pivotal taxa, Gauthier et al (22) conducted fine-grained inclusion/exclusion experiments on synapsids. Fossil synapsid taxa were first added sequentially to the analysis, from those most distantly to those most closely related to mammals (based on Figure 4), and then in the reverse order. Finally, the effect of each fossil synapsid taxon was assessed by adding it individually. These tests identified a broad range of crucial synapsid fossils (those inserted above *Ophiacodon* and below Tritylodontidae in Figure 4), the inclusion of any one of which is sufficient to recover the cladogram of extant groups implied by the Complete analysis, and without which mammals and archosaurs appear as sister groups.

In contrast, addition of the earliest and/or the latest synapsid groups did not alter the Recent tree; mammals remained the sister group of crocodiles plus birds. The Complete analysis suggests an explanation. Living mammals and archosaurs independently acquired numerous modifications of the girdles, limbs, and vertebral column that facilitated an erect posture and narrow-tracked gait, which enabled them to breathe while running. Indeed, 80% of the characters they share are related to the locomotor system even though only 40% of the characters in the Complete data set pertain to the postcranial skeleton. The earliest synapsids, such as *Casea, Varanops,* and *Ophiacodon,* possess few of the diagnostic characters of living mammals and none of those uniting mammals with archosaurs. When only these synapsids are added to the analysis, they attach near the base of the tree rather than with mammals. Evidently, the few synapomorphic resemblances between early synapsids and mammals are overwhelmed by the larger number of locomotor characters shared by mammals and archosaurs. The latest fossil synapsids, tritylodonts and morganucodontids, have no effect for a different reason. They possess most of the hard characters that distinguish mammals from other extant amniotes, and all of the locomotor specializations that mammals share with archosaurs. Furthermore, like mammals, they are so highly modified that several synapomorphies of early synapsids are either reversed or are not present in a recognizable form in the absence of earlier groups with transitional states.

Seed Plants

In the case of seed plants, topological relations among extant groups are not radically altered by the subtraction of fossils as they are in amniotes. When extant taxa are analyzed using polarities derived from the conservative extant outgroup arrangement (see above), two most parsimonious cladograms are obtained. One of these (Figure 5a) corresponds to one of the two arrangements of extant groups derived from the Complete data set (Figure 5a,b). The second (Figure 5c) is incompatible with either result of the Complete

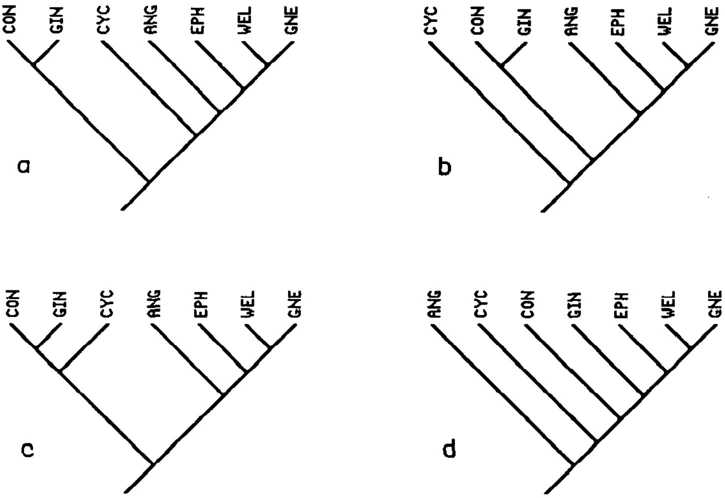

Figure 5 Alternative relationships of extant groups of seed plants. a, b: most parsimonious trees derived from the Complete analysis (Recent plus fossil taxa); c: additional most parsimonious tree obtained from the Recent analysis; d: additional most parsimonious tree obtained from the Recent analysis with the "extreme fern" rooting (see text).

analysis, because cycads are united with the conifer-ginkgo clade. Both trees, however, support the unity of the coniferopsids and of the Gnetales, as well as the link between angiosperms and Gnetales seen in the Complete analysis.

A primary effect of ignoring fossils is that some relationships that are substantially less parsimonious in the Complete analysis become more parsimonious. An important example concerns the position of Gnetales. Based on the Recent data set, there is one tree with Gnetales nested in coniferopsids that is only one step longer than the best trees (Figure 5d), whereas with the Complete data set the shortest trees of this type are four steps longer than the best trees. Thus, in the Recent analysis the position of Gnetales is more tenuous in the sense that it might be altered by the addition or reinterpretation of a single character. It appears, then, that fossil seed plants somehow solidify relationships among extant groups.

Even more significant are the effects of fossils on hypotheses of character evolution. For example, the Complete analysis implies that pinnately compound leaves are ancestral in seed plants, and that linear-dichotomous leaves were derived independently in coniferopsids and in Gnetales (Figure 2). This conclusion is not based on outgroup information, because the primitive condition was assumed to be a third state (dichotomous leaves without cataphylls/scale leaves), and states within seed plants were not ordered. Instead, it is based on a posteriori character optimization (mapping), reflecting the arrangement of a series of Paleozoic "seed ferns" with pinnately compound leaves at the base of the seed plant tree. In contrast, in the Recent analysis leaf evolution is highly ambiguous (Figure 6). Under the conservative rooting, in which the ancestral condition is equivocal due to varia-

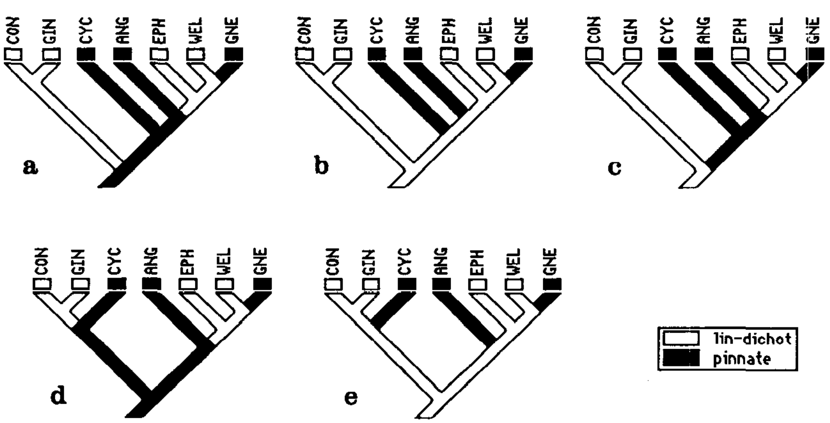

Figure 6 Alternative equally parsimonious hypotheses on the evolution of leaf morphology in seed plants based on extant forms only.

tion among outgroups, a variety of equally parsimonious ways exist to map the leaf character on the ingroup tree, including arrangements in which linear leaves are ancestral and pinnate leaves derived (Figure 6b, c, e).

Pollen and vessels illustrate other effects of fossils on the interpretation of character evolution. Based on the Complete data set, saccate pollen grains are basic in the large platyspermic clade, which includes all extant groups; this condition is retained in conifers and lost in ginkgos, cycads, and anthophytes. However, when only extant groups are considered, saccate pollen appears to be an autapomorphy of conifers. Vessels can be interpreted as homologous in angiosperms and Gnetales in the Recent analysis, whereas the Complete analysis implies that they arose independently, because vesselless fossil groups (Bennettitales and *Pentoxylon*) are interpolated between the extant anthophytes.

The "extreme fern" rooting, which assumes that seed plants are nested within "ferns" (cf 31), yielded the same two topologies found with the conservative rooting, plus the very different alternative mentioned above, with angiosperms basal (Figure 5d). Under this arrangement, the scalariform secondary xylem pitting, flat stomates, and cellular embryogeny of angiosperms appear to be primitive retentions rather than reversals, as inferred from the Complete analysis. With both fern rootings, leaf evolution is interpreted as it is in the Complete analysis, with pinnate leaves ancestral (e.g. Figure 6a, d). However, this "correct" result is obtained for the wrong reason, namely by interpreting the "megaphylls" of ferns as homologous with seed plant leaves (see also 5), whereas they are best interpreted as independently derived when fossil outgroups are considered.

Rooting the Recent cladograms by reference to Paleozoic "seed ferns" might be expected to give results most similar to the Complete analysis, as these outgroups are closer to extant seed plants than are any others. However, the most parsimonious topologies obtained are positively at odds with the Complete analysis; the connection between cycads and coniferopsids (Figure 5c) and a new tree with *Gnetum* basal in Gnetales are preferred. This result suggests that ingroup fossils may be necessary to obtain the "correct" topology. At the same time, these trees yield interpretations of character evolution that agree with the Complete analysis; for example, pinnate leaves and manoxylic wood are viewed as ancestral.

The most informative experiments concerning ingroup fossils were those designed to test the bearing of the Bennettitales and *Caytonia* on the position of angiosperms and Gnetales. The Complete analysis suggests that Bennettitales (and similar fossil genus *Pentoxylon*) are important in linking angiosperms and Gnetales: They share several apomorphies with Gnetales (e.g. single, erect ovules) but retain some primitive states apparently lost in Gnetales (e.g. pinnate leaves). In keeping with this assessment, when Bennettitales and *Pentoxylon* are removed, trees that link angiosperms directly with *Caytonia* and nest Gnetales within coniferopsids become only one step less parsimonious than the shortest trees, rather than four steps less. Similarly, when Bennettitales are added to the Recent data set, trees with Gnetales nested in coniferopsids become three steps less parsimonious than the shortest trees, rather than only one. When *Caytonia* alone is added to the Recent analysis, it links directly with angiosperms, and Gnetales are either linked with angiosperms plus *Caytonia* or nested in coniferopsids. This result implies that if Bennettitales were unknown, angiosperms would be united with *Caytonia* and their association with Gnetales would be ambiguous, presumably because several features shared by *Caytonia* and angiosperms are lost in Gnetales (e.g. megasporophylls with several reflexed cupules/bitegmic ovules). In these trees, the outer integument of angiosperms is seen as homologous with the cupule of *Caytonia,* but there is no reason to suspect that Gnetales ever had a cupule, as inferred from the Complete analysis. Addition of *both* Bennettitales and *Caytonia* is needed to obtain the "correct" topological arrangement and to recover the inferred evolution of the cupule and other characters.

ADDED TAXA AND TOPOLOGICAL CHANGE

Our studies demonstrate that the inclusion of fossils in cladistic analyses can substantially alter inferred relationships among extant groups and/or ideas on character evolution. Although changes in cladogram topology have the most profound effects, because these automatically influence character optimization, changes in ideas on character evolution will probably be the most common consequence of including fossils. Clearly, both kinds of change can dramatically affect biogeographic and macroevolutionary scenarios that are based upon phylogenies (e.g. 11, 13). In this section we consider general factors that bear on whether and how additional taxa result in topological changes, in the hopes of identifying circumstances in which knowledge of fossils in particular is likely to be critical.

Gaps and Fossils

Effects of fossils are most likely if there are large "gaps" in a cladogram—clades separated from others by branches bearing numerous apomorphies. Such gaps suggest the existence of organisms with combinations of characters not found among extant groups, assuming that gaps are not due to saltation. In most cases, "long branches" are probably not solely the result of anagenetic change within a single ancestral lineage; instead, a series of species or entire clades probably attach to the long branch. The converse also probably holds in most cases; that is, it is less likely that there are distinctive new taxa associated with short branches. This observation highlights the importance of considering autapomorphies of terminal taxa in assessing the possible impact of additional taxa. Such characters are often removed from cladistic analyses, since they are consistent with all possible trees and are therefore phylogenetically uninformative at the level under consideration. When this is done, any character changes on a branch leading directly to a terminal taxon are necessarily homoplastic, that is, reversals or states that arise independently elsewhere on the tree (32). However, the additional nonhomoplastic apomorphies are also important in suggesting the existence of missing taxa that might change the position of the terminal taxon.

The addition of taxa to long branches can change cladogram topology, as when closer outgroups change ingroup polarity assessments (37). However, new taxa may be of considerable interest even when topological relations are not altered. Such taxa help establish the sequence of character changes, which may be critical in choosing among alternative evolutionary explanations (8); for example, the origin of the flower before angiospermy (11). Inclusion of such groups also might lead to changes in character optimization. Thus, a character initially hypothesized to be homologous in two taxa might appear to be homoplastic with the insertion of taxa between them (e.g. the case discussed above of vessels in angiosperms and Gnetales). Indeed, the discovery of homoplasy is a very general outcome of increasing the number of taxa considered in cladistic studies (50).

The special importance of fossils in this context results from what appears to be a widespread evolutionary pattern, and from the present state of exploration of the Earth's biota (12). Major groups of organisms, whose origin and relationships we are often especially concerned to explain, are almost by definition distinguished from all other groups by complex suites of traits whose order of assembly we would like to untangle. Within amniotes, for example, modern mammals and birds are each marked by a large number of derived traits, as are angiosperms and Gnetales within seed plants. One possible reason for this pattern is that early "experimental models" tend to be replaced by derivative clades unless the former become highly specialized (autapomorphic) themselves. In any case, at least in relatively conspicuous and well-studied groups such as amniotes and seed plants, it is likely that most large gaps will be filled through the discovery of fossil rather than living organisms. For this reason, if for no other, fossils are likely to have a disproportionate impact on our understanding of the origin and radiation of major groups.

Causes of Topological Change

Added taxa are most likely to have an important influence when two or more trees are equally or almost equally parsimonious. When there is limited character support for some relationships and/or high levels of homoplasy, a clade whose placement in the tree is tenuous may change position if added taxa favor a different topology.

New taxa with certain combinations of characters are unlikely to alter cladistic relationships. In general, taxa that do not introduce character conflict will simply be inserted along previously established lines. Gauthier et al (22) provided a hypothetical example involving three taxa (A, B, C), with one putative synapomorphy supporting (AB)C and another supporting A(BC). The addition of a taxon possessing the synapomorphy of AB or that of BC will not help choose between the two hypotheses—both remain equally parsimonious. Likewise, addition of what Gauthier et al (22) called an "apomorphic sister group"—possessing a synapomorphy of one clade (say AB) and a second character uniting it with one of the included terminal taxa (say A)—does not allow a choice between the competing trees.

In some cases an additional taxon can favor one of the alternative cladograms by revealing something new about the characters used initially—information necessitating a change in character coding. For example, a new organism might exhibit a new state that is best interpreted as an intermediate condition in an ordered transformation series, or between autapomorphies that were previously excluded from the analysis. In either case, the net result is an increase in the number of presumed transformations and the addition to the matrix of a new derived state that might influence the choice among trees. Thus, the addition of a taxon with a state intermediate between the ancestral condition and the derived state that unites A and B in the example discussed above would lead to a preference for (AB)C; A(BC) would now entail an extra step. Fossils may be of special importance in this regard, since they may show intermediate states more often than extant organisms, especially if groups with more primitive conditions tend to be displaced by more derived groups. For example, Carboniferous seed plants add the pinnately compound leaf type to the analysis, from which the linear and simple pinnate leaves of extant forms were derived (Figure 2).

The most profound topological changes will result from the addition of taxa with combinations of characters that necessarily introduce character conflict (cf 9). A simple case is illustrated by Gauthier et al (22), again with reference to the hypothetical example introduced above. They show that the addition of a "plesiomorphic sister group" allows a clear choice between trees, where the added taxon is united with one of the terminal taxa (say A) by the derived state of a new character, but possesses the ancestral condition of every other character in the data set. Under these circumstances the tree A(BC) is now preferred over (AB)C.

Although the outcome of adding plesiomorphic sister taxa is clear, the general cause of this effect is more subtle than it might seem. Consider the case illustrated in Figure 7, in which five taxa (A-E) have been scored for five characters whose distributions are evident on the most parsimonious cladogram of five steps (Figure 7a; contrast 7b). The addition of a sixth taxon, X, with primitive states of characters 1–3 but the derived states of characters 4 and 5 (previously interpreted as autapomorphies of C), requires at least seven steps. The extra steps can be accounted for by reversals in characters 1 and 2 in X if the relative position of C is not changed (Figure 7c). However, the presence of ancestral states in X suggests the possibility of moving the CX clade to the base of the cladogram. The resulting tree (Figure 7d) also entails seven steps overall, but the homoplasy is accounted for by the independent acquisition of characters 1 and 2 in C and within the ABDE clade.

Inasmuch as inserting the CX clade in two different positions entails the same amount of homoplasy, how could the addition of a taxon like X ever favor a new topology for A-E? It seems that once enough character conflict is introduced that the number of reversals equals the number of convergences (as in our example), any additional conflict introduced by X can always be accounted for either by an origin and a loss or by two origins. That is, beyond a critical minimum the number of character conflicts introduced is not by itself a decisive factor. Character conflicts simply have the effect of neutralizing characters that formerly unequivocally united C with DE, such as character 2, which now undergoes two steps with C in either position.

This observation indicates that topological change must be a function of other characters in the data set. In particular, the preferred topology will depend on how many characters favor nesting C within ABDE, versus the number that support ABDE to the exclusion of CX. If there are more of the

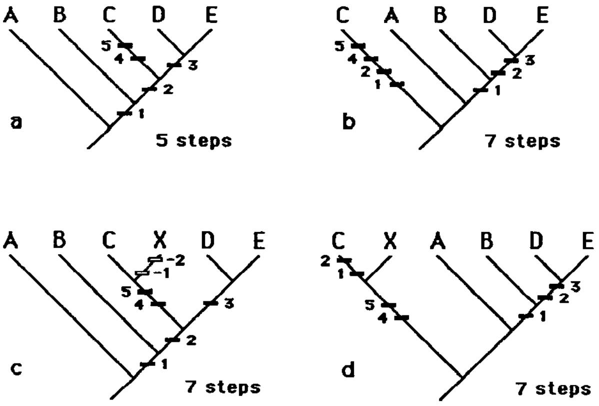

Figure 7 Hypothetical example illustrating the effect of adding a "plesiomorphic sister group" (X) of taxon C (see text).

latter, then the basal position of CX (Figure 7d) will be preferred. This point is illustrated by the addition of a sixth character to our hypothetical analysis (Figure 8)—a trait shared by A, B, D, and E, which is most parsimoniously interpreted as arising at the base of the tree and reversing in C (Figure 8a, contrast 8b). Now the addition of X, again with ancestral states for all characters except 4 and 5, requires nine steps if CX remains nested within ABDE (Figure 8c), but only eight steps if CX is excised and inserted as the sister group of ABDE (Figure 8d). The former arrangement requires a reversal in character 6 in CX, while the latter does not. The crucial difference between this case and the case illustrated in Figure 7 is that here there is a character that might unequivocally unite ABDE, which without taxon X is best interpreted as undergoing a reversal in C. The addition of X, as long as it shares enough apomorphies with C to ensure that the two are linked, means that character 2 no longer unequivocally supports uniting C with DE, thus allowing the possibility of placing CX elsewhere. And placing CX at the base of the tree eliminates the need to postulate a reversal in character 6.

A plesiomorphic sister group such as X may also bring about a change in topology if it has the ancestral state of a character with the derived state in B, D, and E (such as character 1 or 6 in Figure 8), but for which C is so highly autapomorphic that its state must be scored as unknown. Here, there will be an extra step (a reversal) in the character if CX remains nested within ABDE, but not if CX is basal.

The effects of adding more than one taxon along a particular branch can also be explored. If the additional taxa are best united as a clade, the general effect will be similar to adding a single taxon, although character conflicts

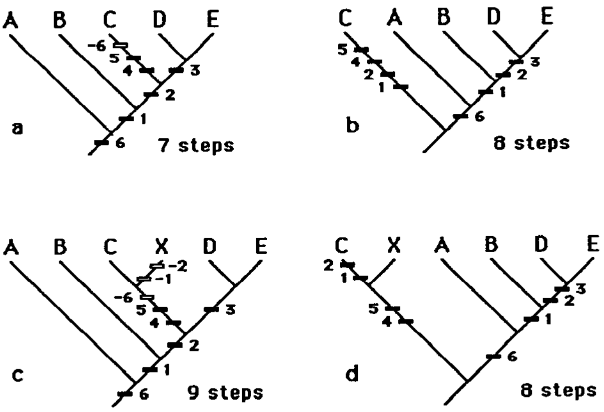

Figure 8 Hypothetical example as in Figure 7, but with an additional character (6) with the derived state in A, B, D, and E and the ancestral state in C and X (see text).

within this new clade might have some influence on the overall topology. The most profound changes occur when the new taxa are best arranged along an existing branch in a pectinate (comb-like) fashion. If all the added taxa are plesiomorphic in a number of characters, a maximum number of reversals will be required (if the position of the entire clade is to be maintained). A pectinate arrangement also can have the most powerful effect on the inferred sequence of character evolution.

This exercise suggests another reason why fossil taxa in particular may substantially alter cladogram topology. "Plesiomorphic sister taxa" are more likely to have a significant impact than apomorphic groups by introducing character conflicts of the type described, and as Gauthier et al (22) argued, early fossil members of a group are likely to be more plesiomorphic than modern members. They are often representatives of "truncated" early lines that, by virtue of not having undergone any further evolution, preserve character combinations that were later modified in the origin of extant groups.

AMNIOTES AND SEED PLANTS REVISITED

Analysis of extant groups of both amniotes and seed plants gives ample reason to suspect the existence of fossil taxa that might cause topological changes. First, in both groups there are several conspicuously "long" branches, notably mammals, birds, Gnetales, and angiosperms, which are marked by numerous homoplastic changes plus autapomorphies not included in the analyses. Second, the overall level of homoplasy is high in both Recent analyses. The most parsimonious cladogram of Recent amniotes yields a consistency index (CI) of 0.67, a value substantially below the average CI for five taxa (ca. 0.80; 50). In the case of Recent seed plants the CI was 0.68, again below the expectation for seven taxa (ca. 0.76). In view of these similarities, what is it that accounts for the observation that the addition of fossils dramatically changes inferred cladistic relationships among extant amniotes but not among seed plants?

As noted above, it is the addition of synapsid fossils to the amniote data set that changes the position of mammals. These fossils have characters linking them with extant mammals but are otherwise characterized by the ancestral states for amniotes; that is, they lack the derived traits of turtles, lepidosaurs, crocodiles, and birds. Fossil synapsids, then, are superb examples of "plesiomorphic sister groups," as discussed in the preceding section.

A critical factor in this case is that many of the characters that affect the topology are new to the data set. First, addition of any of the crucial fossil synapsids introduces many new characters linking them with mammals—characters analogous to 4 and 5 in Figures 7 and 8, which were formerly interpreted as autapomorphies of mammals and therefore excluded from the

Recent analysis. Second, fossil synapsids introduce many characters for which they have the plesiomorphic state. These were not included in the Recent analysis because the mammal state is so highly modified that it could not be interpreted as either ancestral or derived relative to the state in Recent reptiles. With the addition of synapsid fossils, the mammal condition (scored as unknown in the Complete analysis) can be seen to have arisen from the fossil synapsid state, which is ancestral for amniotes as a whole. Characters of this sort function like character 6 in Figure 8, but with C initially scored as unknown. Once they are firmly linked with mammals, fossil synapsids introduce so much character conflict that the synapsid clade (including mammals) is no longer securely nested within amniotes. Reversals are required in the fossil synapsid if the synapsid clade remains connected to archosaurs, and convergences are entailed in mammals and archosaurs (especially birds) if the synapsid clade is moved to the base of the tree. This effect is presumably all the more powerful when several extinct synapsids are added at once, since these take up a pectinate arrangement relative to mammals (see above).

In the end, the reason why the basal position of the synapsid clade is more parsimonious is that, with the new characters and character conflict introduced by fossil synapsids, there are more characters that unite the Reptilia (including Recent turtles, lepidosaurs, crocodiles, and birds) than unite the synapsid clade directly with archosaurs. The cause of this result is the same as that illustrated in Figure 8, where mammals correspond to taxon C, fossil synapsids to taxon X, and archosaurs to D and E.

Two factors can be viewed in retrospect as signs that the position of mammals in the Recent analysis was likely to change with the addition of fossils. First, there are at least nine reversals along the mammal line in the Recent analysis. In contrast, there are no reversals in turtles and lepidosaurs, one in crocodiles, and two in birds. The significance of the characters for which mammals are reversed is that they do not support the union of mammals with archosaurs. If mammals were a basal clade in amniotes, these characters would not have to reverse; instead their derived state would simply unite the reptiles, like character 6 in Figure 8. It happens, however, that enough primarily locomotor advances are shared by mammals and archosaurs, and especially birds, to overwhelm the reptile characters—it is eight steps more parsimonious to nest mammals within amniotes even though this entails so many reversals in mammals. The addition of fossil synapsids effectively neutralizes some of the characters that link mammals and archosaurs, thereby shifting the balance to a basal position of the synapsid clade and uniting the reptiles.

Second, it is noteworthy that the lepidosaurs are marked by seven convergent characters in the Recent analysis, conspicuously more than turtles, crocodiles, and birds (with two convergences each) and mammals (with only one). Furthermore, four of the lepidosaur convergences are with archosaurs. This anticipates the shift in position of lepidosaurs that occurs when fossil synapsids are added, after which only a single step is required to account for the distribution of each of these four characters.

In retrospect, several features of the seed plant data set help explain why fossils do not have such radical effects on inferred relationships as they do in the case of amniotes. Extant seed plants do resemble extant amniotes in including two highly apomorphic branches, angiosperms and Gnetales, which are linked based on Recent data. There is also a radically different alternative tree (somewhat analogous to the Recent tree of amniotes), with Gnetales nested in coniferopsids and angiosperms basal (Figure 5d), which is only one step less parsimonious. However, in seed plants the addition of fossils, especially Bennettitales and *Pentoxylon,* does not weaken but instead strengthens the relationship between angiosperms and Gnetales, thereby confirming the convergent origin of linear leaves, reduced sporophylls, and pycnoxylic wood features in coniferopsids and Gnetales. The convergence between Gnetales and coniferopsids is analogous to that between mammals and archosaurs, but it is not extensive enough to overwhelm the evidence of relationship between angiosperms and Gnetales, even when only Recent groups are considered.

Most importantly, no extant seed plant group shows as many reversals as mammals do in the Recent analysis of amniotes. The closest approach is seen in several fern-like features of angiosperms, such as flat stomates, scalariform pitting, and cellular embryogeny, some of which have been used to argue that angiosperms could have been derived from only the most primitive "seed ferns" (57). Given only Recent taxa, these features are almost sufficient to shift the balance to the tree with angiosperms basal and Gnetales nested in coniferopsids (Figure 5d). However, in seed plants there are no fossils analogous to fossil synapsids that favor a basal position for angiosperms. In fact, better understanding of Paleozoic "progymnosperms" and "seed ferns" refutes the concept that the angiosperm conditions are ancestral (2, 10, 11). Instead, the fossil record provides forms that reinforce the position of angiosperms among more advanced, platyspermic groups—primarily *Caytonia,* Bennettitales, and *Pentoxylon*.

Prospectively, these comparisons between the two analyses suggest that those working on Recent organisms alone should be especially suspicious of groups like mammals that show numerous apparent reversals. These are liable to change position with the addition of fossils, such that their reversals are replaced by convergences. There are, perhaps, reasons why convergences may be more common than reversals: There may be strong parallel pressures on different groups due to progressive change in the physical or biotic environment, or certain directions of change may almost always enhance efficiency. The locomotor trends shared by mammals and archosaurs are an especially plausible example, since improved locomotion should be advantageous for both parties in any coevolutionary "race" between predators and prey. In seed plants, convergent evolution of reduced leaves and pycnoxylic wood features in coniferopsids and Gnetales could be examples, possibly related to climatic change in low-latitude areas, from wet in the Carboniferous to semi-arid in the Permian and early Mesozoic, due to a shift from zonal to monsoonal global atmospheric circulation (42).

It might be argued that although fossils overturned Recent relationships in amniotes, this may be a highly unusual case, possibly even unique. Perhaps, in most cases, the effects of adding fossils will be more like those seen in seed plants. We believe that this view is unwarranted, especially since parallel trends like those seen in mammals and archosaurs may well be common. For example, Panchen & Smithson (41) have refuted the claim (47) that lungfish are the sister group of tetrapods by arguing that the addition of fossils shows that the presumed synapomorphies of the Recent groups actually arose convergently. In seed plants, we note that parallel trends in Gnetales and coniferopsids were almost sufficient to change the results of the Recent analysis: If only one or two more characters had been affected, the link between angiosperms and Gnetales might have been overwhelmed. Different results might also have been obtained if one or two more groups had become extinct (*Ginkgo* and *Welwitschia* are already monotypic). In fact, reanalysis of the Recent seed plant data set with *Gnetum* removed yielded both trees linking Gnetales with coniferopsids and trees linking Gnetales with angiosperms. Apparently, removal of *Gnetum* eliminates conflict in leaf characters within Gnetales, such that *Ephedra* and *Welwitschia* can be unambiguously united with coniferopsids by possession of linear leaves.

INCOMPLETENESS AND INFORMATIVENESS

The primary reason for believing that fossils are relatively powerless in assessing phylogenetic relationships is that they are incomplete, often providing only a small fraction of the information that can be obtained from living organisms. However, our studies demonstrate that missing information is by no means limited to fossils. In extant groups missing information is caused by evolutionary modification that renders the homology of traits uninterpretable, rather than by nonpreservation. That evolution itself can lead to the loss of phylogenetic information is seldom acknowledged, although this can have profound consequences for phylogenetic analysis. For example, the relation of the quadratojugal to adjacent bones in modern turtles and mammals is unknown simply because the quadratojugal is missing in these groups. Likewise, the angular bone in mammals would be uninterpretable without information provided by extinct synapsids, which imply that it is homologous with the ectotympanic bone. It is unclear which of the two basic configurations of the occiput found in early amniotes is present in mammals, because the evolution of large brains induced profound changes in occipital morphology. Indeed, the occipital region, which provides several characters that are important in reconstructing early tetrapod phylogeny, has been highly modified in all extant tetrapods (20a).

To assess the importance of the two sources of missing data in amniotes, we computed the amount due to nonpreservation (scored ? in 22) and that due to divergence (scored N), which were treated identically by the parsimony algorithm used. As expected, incompleteness as a function of nonpreservation is limited to fossils, whereas missing information due to divergence is found in both extinct and extant groups (Figures 9 and 10). Of the total of 411 instances of missing information on "hard" parts in Gauthier et al (22), only 79 cases are the result of nonpreservation; the remaining 332 are due to divergence. In this skeletal data set, the extant taxa are missing an average of 23 characters, whereas fossil taxa average only 12 missing characters, of which only 3 are due to nonpreservation. Surprisingly, extant turtles and mammals are less complete than Paleozoic and Mesozoic fossils, missing 40 and 43 characters, respectively, due entirely to divergence (Figure 9).

Of course, amniote fossils also lack all of the 67 "soft" characters (22). However, this loss of information is not as severe as it may seem, as can be seen by comparing extant mammals with the Carboniferous caseoid clade, the sister group of all other synapsids in the Complete analysis (Figure 10). Overall, caseoids are missing 71 of the 274 characters (26%), whereas Recent mammals are missing 43 (15%). It is remarkable that living organisms, with all systems intact and available for study, preserve only 11% more of the data relevant to amniote relationships than do fossils that are 300 million years old. Moreover, of the characters preserved in mammals and caseoids, a larger percentage of the characters of mammals are homoplastic, judging by the Complete analysis.

In contrast to amniotes, where soft anatomy is very rarely recovered in fossils, almost all systems in plants are potentially fossilizable owing to the presence of resistant cell walls; these systems include gametophytes and other delicate phases of the reproductive cycle in plants preserved in Carboniferous coal balls. More missing information on extinct groups is due to the lack of association of parts (e.g. leaves, stems, reproductive structures) than to inherent nonpreservability. As in amniotes, there are instances of missing data in Recent groups due to evolutionary divergence. For example, the ovule symmetry of angiosperms (whether radio- or platyspermic) must be scored as unknown because the ovules are so reduced that they lack vasculature, the main indicator of symmetry (11).

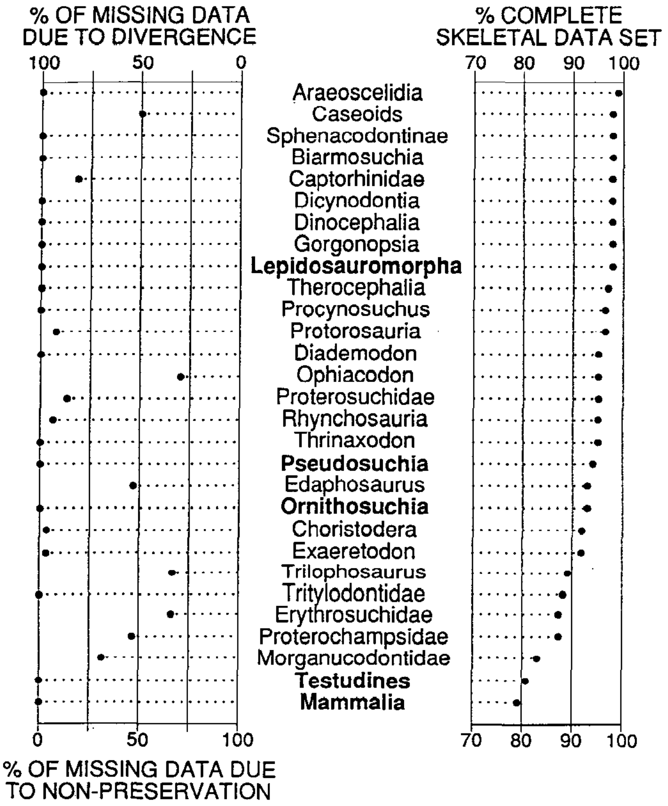

Figure 9 Completeness of skeletal character information in extant (bold) and extinct amniotes (right), and the proportion of missing skeletal data due to nonpreservation and to evolutionary divergence (left).

Whatever the source or amount of missing information, it is important to recognize that completeness and informativeness are not strictly coupled. Taxa that can be scored for every character are not necessarily especially relevant in answering specific phylogenetic questions, whereas taxa that are rather poorly known may nevertheless reveal combinations of characters that are critical in establishing relationships. This is at least partly a function of the level of generality of the problem under consideration. Although the limited fossil information available on many taxa within angiosperms or birds may have very little impact on our understanding of their relationships, fossils may be critical in assessing relationships among major groups of seed plants or amniotes, because they reveal character combinations quite unlike those in any extant groups. If organs are preserved that show such characters, they

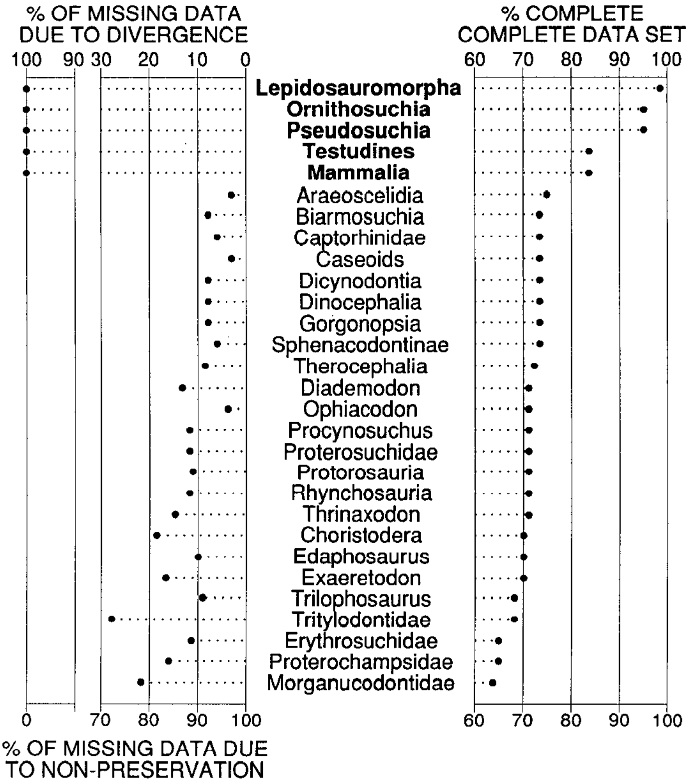

Figure 10 Completeness of total character information in extant (bold) and extinct amniotes (right), and the proportion of missing data due to nonpreservation and to evolutionary divergence (left).

may have a significant effect even if other organs are unknown. The Mesozoic seed plant *Caytonia* provides a good example: Although its stem anatomy is unknown and it therefore has a high proportion of characters missing due to nonpreservation (32%), it plays a vital role as a link between anthophytes and "lower" groups by preserving features such as platyspermic seeds and saccate, alveolar pollen, combined with anthrophyte advances such as cupules and features of seed anatomy.

Inasmuch as fossils can preserve relatively unmodified conditions of the major lines in a radiation, they may be more informative about the relationships among these lines than are highly derived modern groups, even if the latter are much more complete. Indeed, experimental removal of extant groups from the amniote analysis did not alter the relationships of the remaining groups (22). Extant turtles provide a particularly striking example, being distinguished by a set of highly divergent traits that are useless in placing the group among amniotes. Extinct captorhinids clarify the ancestral condition from which the highly modified traits of extant turtles evolved, and this is critical in determining their phylogenetic relationships. Bennettitales and *Pentoxylon* play a similar role in elucidating basic conditions in the clade including Gnetales. These observations emphasize that simply having survived to the Recent does not guarantee that a taxon will provide more relevant character information.

FOSSILS, MOLECULES, AND MORPHOLOGY

The view that phylogenetic relationships among extant groups should be determined first, and that fossils should be added after the fact, effectively assumes that fossils will not influence the placement of the extant groups in relation to one another. The studies reviewed here demonstrate that this view is unfounded. In fact, our results imply that in some cases the old view that the true phylogeny cannot be obtained without fossils is correct. Therefore, rather than setting fossils aside at the outset of a cladistic analysis, we suggest that every effort be made to incorporate them from the beginning.

Controversy over the treatment of fossils may be considered an example of a general issue that has arisen several times in the development of phylogenetic systematics, concerning sequential versus simultaneous analysis. This is well illustrated by disputes over the best way to assess the position of the root of a tree. It has been suggested, for example, that a network should first be constructed for the ingroup taxa and that outgroups should be attached afterward to root the network ("Lundberg rooting": 36, 38). However, this sequential form of analysis, which initially ignores the outgroups, can yield globally unparsimonious results (9, 37): It can blind one to a more parsimonious solution that might have been discovered if the outgroups and their characters had been taken into account from the outset of the analysis. Other examples concern the omission of characters, as in character compatibility analysis, where trees are constructed based only on the largest set (clique) of mutually compatible characters. Characters in smaller cliques can be added subsequently to help resolve unresolved portions of the tree (55), but they are not allowed to influence the primary structure of the tree, as they would be if all of the data were analyzed simultaneously.

A similar problem arises when one type of data is given priority over other types, as though the latter could not or should not be allowed to influence the outcome of an analysis. The most obvious example concerns recent claims that trees should first be constructed on the basis of molecular data alone and that the evolution of morphological characters should then be evaluated by reference to these trees (25, 51, 56). Curiously, the reverse argument, that molecular evolution should be evaluated by reference to trees based on morphology, has not been made, although the principle that trees should not be based on characters whose evolution one wishes to evaluate would appear to apply in both directions. This outlook seems to assume that molecular data are less likely to be misleading than are morphological characters, because the latter are more subject to convergence, and/or because there are so many more molecular characters that these would simply outweigh the morphological data.

Even if it were accepted that molecular data always provide an accurate picture of the relationships among extant taxa, it is important to note that simply mapping morphological characters onto cladograms of extant groups could give a misleading picture of character evolution, since fossil taxa may have a significant effect on character optimization. In particular, a morphological character viewed as homologous based on a molecular analysis of Recent taxa might be more parsimoniously interpreted as having evolved independently when fossil taxa are intercalated. As noted above, the seed plant study provides several examples of this effect, such as the derivation of seed plants from forms with fern-like leaves, or the independent evolution of vessels in angiosperms and Gnetales. Likewise, fossil amniotes show that several characters associated with the ear evolved separately in crocodiles and birds (22). An accurate picture of morphological evolution requires that all relevant taxa be incorporated in the analysis, whether these happen to be extant or extinct.

In any case, the expectation that molecular data alone can (or eventually will) provide an accurate and unambiguous account of phylogenetic relationships among extant groups may be overly optimistic. Many molecular studies are plagued by levels of homoplasy comparable to those seen in morphological analyses (when adjustments are made for the number of taxa and for autapomorphies; 50), and they often yield several to many equally or almost equally parsimonious trees (6, 61). Despite the much larger number of molecular characters potentially available, the addition of even a few morphological characters to such an analysis might be decisive in choosing among a set of trees. And in some cases it is possible to assemble very large sets of potentially informative morphological characters; for example, 972 characters were used in analyzing tetrapod phylogeny (20a).

Furthermore, contingencies of evolutionary history may put molecular data at a disadvantage under some circumstances. The most difficult cases are perhaps those in which a group radiated very rapidly at some time in the distant past. In such cases one would like to focus attention on a molecule that evolved quickly enough during the radiation to generate synapomorphies that mark early branches in the tree. However, if subsequent evolution proceeded at anything like the same rate, the extant representatives of these ancient branches will be highly divergent. In view of the limited number of possible states of molecular characters (e.g. four nucleotides), these long branches may lose considerable phylogenetic information by virtue of subsequent changes at the same sites (15, 33); in effect, evolution might become an "information destroying" process (53, p. 3). In contrast, any molecule that evolved slowly through the critical period of radiation would fail to resolve relationships of major lines. These problems could be overcome if one could identify a molecule that evolved rapidly early in the radiation but then stopped evolving (or at least slowed dramatically), so that information on the early branching events would be faithfully retained. If molecular evolution is clock-like, such molecules do not exist, and if molecular evolution is not clock-like, it may be difficult to identify molecules that have changed rate in an appropriate way.

In contrast, it has long been appreciated that rates of change in morphological characters are not uniform, and a feature whose evolution happened to coincide with the origin of an early branch may be retained in a more or less unmodified form in all of the descendants of that line. Indeed, this retention is the expected outcome of increased "burden" due to the evolution of functionally and developmentally dependent characters (8, 46). Furthermore, fossils may show morphological characters of early representatives of lines, prior to any further evolutionary modification. Some extant organisms might provide similar information, but as we have noted most surviving representatives of early branches are likely to be highly modified (e.g. turtles, cycads). At least with fossils one can be certain that there has been no further evolutionary change since the time of burial. By virtue of their relatively unmodified characters, fossils may provide a clearer picture of phylogeny than could be obtained using only highly modified extant organisms.

In view of these observations we suggest that all of the available evidence—on both Recent and fossil organisms—be taken into consideration in assessing phylogenetic relationships (cf 32). Setting data aside at the outset runs the risk of obtaining results that are globally unparsimonious. Even taxa that are incompletely known, whether extinct or extant, can exert a significant influence on the outcome of cladistic analyses. Moreover, completeness and relevance to particular phylogenetic questions are not necessarily coupled. Fossils may be especially relevant in sorting out ancient radiations, by preserving information on early branching events and rendering interpretable the highly divergent morphological attributes of extant groups.

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