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A CLADISTIC ANALYSIS OF CONIFERS: PRELIMINARY RESULTS

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A data matrix of 123 binary and multistate characters of 63 genera of conifers was constructed based on an extensive literature review and study of herbarium and living specimens. Subsequent cladistic analysis of this matrix strongly supports the monophyly of conifers; there is no reason to exclude the taxads. *Sciadopitys* should be considered as constituting a separate family, the Sciadopityaceae, which appears to be the sister group of the Cupressaceae-Taxodiaceae lineage. The Taxodiaceae and Cupressaceae together form a monophyletic group. The Cupressaceae form a monophyletic group within this lineage and can be divided into two groups, one of northern and the other of southern taxa. Within the Southern Hemisphere group, there are monophyletic groupings with separate Gondwanaland distributions. The remaining Taxodiaceae appear to be paraphyletic. The Taxaceae and Cephalotaxaceae also come out as sister taxa. The Pinaceae appear to be the sister group of the other living conifers. The placement of Araucariaceae and Podocarpaceae in relationship to the other living conifers is problematic.

Conifers have long been of interest to morphologists, anatomists, paleobotanists, and foresters. A cosmopolitan group, conifers include 60 to 63 genera and 500 to 600 species. Known from the fossil record from as far back as the Permian, conifers dominated the forest vegetation in the Mesozoic Era. They are the largest and most diverse group of living gymnosperms. To date, the monophyly of the conifers and the phylogenetic relationships of the families and genera have not been determined.

Most modern textbooks follow Pilger (1926) in dividing the group directly into seven families (Taxaceae Sprengel, Podocarpaceae Endl., Araucariaceae Strasburger, Cephalotaxaceae Nager, Pinaceae Lindley, Taxodiaceae Nager, and Cupressaceae S. F. Gray), but other classifications have also been proposed. Buchholz (1933) divided the Coniferae into two suborders: the Pinineae (in-

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cluding Pinaceae, Cupressaceae, Taxodiaceae, and Araucariaceae), with obvious cones, and the Taxineae (including Podocarpaceae, Taxaceae, and Cephalotaxaceae), without obvious cones. Sahni (1920) and Florin (1948b, 1951) elevated the Taxaceae to the Taxales, equal to all other conifers in ordinal rank. Keng (1973, 1975) has recently recognized eight families, elevating *Phyllocladus* Rich. (Podocarpaceae) to family rank. For a more complete review, see the excellent summaries by Florin (1955) and Turrill (1959).

The phylogenetic and evolutionary relationships among these families and genera have been widely debated. The lack of precise, explicit methodologies for assessing phylogenetic relationships has resulted in a diversity of views about conifer relationships. Historically, schemes of evolutionary relationships have been based primarily on assertions as to the usefulness of individual plant characters as phylogenetic markers.

With the introduction of cladistic theory as developed by Hennig (1950, 1966) and his followers, there has been a renewed interest in the study of higher-level taxonomic relationships in systematic biology. The purposes of this paper are to review the kinds of evidence used historically in assessing phylogenetic relationships among conifers; to construct a comprehensive character data matrix both to serve in the analysis and to provide the basis for further studies; to utilize cladistic methodology in the study of phylogenetic relationships of coniferous genera; to compare these results with previously held notions of relationships; and to suggest new areas of research needed to test my hypotheses of relationships among coniferous genera.

HISTORICAL CONCEPTS OF CONIFER SYSTEMATICS AND PHYLOGENY

The history of conifer studies shows somewhat closer relationship to the history of zoological systematics (at least in some groups) than to that of angiosperm systematics. The reasons for the similarity are precisely those that make conifers well suited for a cladistic analysis. First, gymnosperms, including conifers, have a clear fossil record compared to angiosperms (Florin, 1951; Stewart, 1983). Their remains are well preserved and have yielded a great deal of information. The relative antiquity of gymnosperms was realized very early. Brongniart (1849) recognized three principal plant groups—cryptogams, gymnosperms, and angiosperms—thought to follow one another in time and in a progression from “lower” to “higher” forms. Second, early anatomical and developmental studies of vegetative and reproductive structures have proved useful in elucidating relationships among conifers. Anatomical studies have also been employed in demonstrating relationships to other fossil and living groups of gymnosperms (Strasburger, 1872, 1878, 1879; Bertrand, 1879; Coulter, 1909; Buchholz, 1918, 1920, 1933, 1939, 1941; Jeffrey, 1926; Phillips, 1941; Greguss, 1955). Third, the small number of coniferous taxa, together with their economic and horticultural importance, has permitted botanists (e.g., Chamberlain, 1935; Sporne, 1965) to stress comparative biology more than species identification based on external morphology. Since the quantity is small, however, it is surprising that so few systematic revisions (for example, Shaw,

1914; De Laubenfels, 1969; Liu, 1971; and Liu & Su, 1983) have been completed.

Evolutionary hypotheses concerning conifers have been characterized by attempts to link extant groups in evolutionary time, very different relative importances attributed to characters, preconceived notions of the nature of evolution or evolutionary trends, and ideas regarding correlation of characters. The result has been confusion in determining phylogenetic relationships and classification.

LINKING EXTANT GROUPS IN EVOLUTIONARY TIME

A common problem, not unique to phylogenetic studies on conifers, has been the tendency to link extant groups in evolutionary time, an apparent holdover from the ancient *scala naturae* or "great chain of being" theme (Lovejoy, 1936). Living taxa, instead of characters, are viewed as either advanced or primitive. There are numerous examples in the systematics of both gymnosperms and conifers. For example, Eichler (1889) considered the Taxaceae advanced, while Penhallow (1907) considered them primitive. Other families and genera—Abietinae (= Pinaceae) (Jeffrey, 1917), Podocarpaceae (Sporne, 1965), and *Phyllocladus* (Core, 1955; Keng, 1973, 1975)—have been chosen as the most "primitive." Similarly, some groups such as the Taxodiaceae are considered relicts, while others such as the Cupressaceae are considered progressive (De Laubenfels, 1965). A few early morphologists saw the fallacy of lining up living taxa in this manner. Coulter (1909, p. 92) correctly remarked that "living forms . . . do not represent a series, but the ends of many series."

SPECIALIZATION OF RESEARCH

Gymnosperm biologists have often specialized in particular aspects of the plant body or life cycle. While many interesting studies have resulted from this approach, an unfortunate outcome has been systematic and phylogenetic speculation based on limited subsets of characters. Chamberlain (1935, p. 230) aptly stated that, "The grouping into families and the sequence of families and genera will depend upon each investigator. If he is an anatomist, anatomy will determine the grouping and sequence. . . . If the gametophytes are emphasized, there will be still another arrangement."

Examples of single-character analyses in conifer studies are common. The most frequently emphasized set of characters has involved the ovulate cone. For example, Čelakovský (*vide* Florin, 1955) assumed that the Pinaceae, Taxodiaceae, Cupressaceae, and Araucariaceae constitute a phylogenetic series based on increasing fusion of the bract and scale. The principal classification followed today is that of Pilger (1926); it is based primarily on the structure of the ovulate cone (although vegetative characters were also used).

The excessive attention paid to the ovulate cone structure is evident in the debate about the status of conifers without "evident" cones. Pilger's (1903) monograph on the Taxaceae included the conifers without (evident) cones; he later (1926) divided this group into the Taxaceae *sensu stricto*, the Cephalo-

taxaceae, and the Podocarpaceae. Sahni (1920) proposed an independent order, the Taxales, of equivalent rank with the Ginkgoales, the Cordianthales, and the Coniferales. Florin (1948b) also concluded that the taxads should be segregated from the rest of Pilger's families; he therefore placed them in the separate order Taxales. He maintained that the taxads are distinct from the conifers and traced their more immediate ancestry not to the Cordaitales but to the Devonian Psilophytales. His principal evidence was that both living and fossil members of the Taxales and the Psilophytales have a solitary ovule that is a direct continuation of the axis (uniaxial). Thus, the uniovulate strobilus of the Taxaceae was considered primitive rather than derived. Florin (1951) maintained that in the Podocarpaceae, in contrast, the uniovulate strobili are independently derived from taxa with multiovulate strobili. Others are reluctant to accept Florin's separation of the taxads from the rest of the conifers, at least at the ordinal rank. Chamberlain (1935) and Takhtajan (1953) have suggested that the uniovulate, uniaxial strobilus of taxads is derived from the multiovulate, biaxial cone. The argument becomes dangerously circular when the very character whose evolution is being discussed has been used as the principal line of evidence in forming the groups under discussion.

Other subsets of characters have been used to a lesser extent as the basis of phylogenetic and systematic speculation. Saxton (1913) and Moseley (1943) produced classifications based entirely on characters of the gametophyte and the embryo. Thomson and Sifton (1926) thought the Pinaceae to be the most highly evolved of conifers on the basis of the arrangement and structure of resin canals. Flory (1936) proposed a phylogeny using chromosome numbers. Praeger and colleagues (1976), relying on antigenic distances, suggested relationships among genera of Pinaceae.

Finally, as an extension of this approach, relationships of entire families of conifers are occasionally suggested based on characters found only in a few taxa. For example, the peltate, perisporangiate microsporophyll is often attributed to all Taxaceae (Stewart, 1983), although it is found only in *Taxus* L. and *Pseudotaxus* Cheng.

PRECONCEIVED NOTIONS OF HOW EVOLUTION WORKS

Interpretations of the evolution of conifers have been influenced by general notions of evolution. Florin (1951) made use of Zimmerman's (1930) telome theory to explain various aspects of the evolution of the ovulate cone of conifers. Jeffrey's (1917) three canons of comparative anatomy include the doctrine of conservative organs, which considered the leaf, reproductive axis, root, first annual ring of the stem, seedlings, and sporangia as "conservative." This idea was apparently borrowed from zoological embryology, in which it was thought that ancestral features, such as gill slits, are apt to persist in the earlier stages. Ideas about complexity have also influenced perceptions of relationships. Penhallow (1907) claimed that resin canals are more advanced than resin cells since they are more complex. Other preconceived theories can lead to just the opposite results. Jeffrey (1905) believed that resin canals disappear and are replaced by resin cells.

Another of Jeffrey's (1917) canons of comparative anatomy was the doctrine of reversion, in which wounding induces ancestral traits. The presence of resin canals after wounding was thus seen to be a reversion to a more primitive condition. Čelakovský (1890) also argued that teratological structures and wound tissues indicate evolutionary direction. Guédès and Dupuy (1974) observed hypertrophied, leaflike segments of ovulate cone scales and interpreted the ovules to be dorsal appendages ("leaves") of scale components. Chamberlain (1935) thought that the occasional abnormal occurrence of bisporangiate cones represent the ancestral state.

Botanists have long ranked characters according to preconceived notions of adaptive significance. Adaptive characters have generally been considered less useful at higher (less inclusive) taxonomic categories than at lower (more inclusive) ones (Stevens, 1980). Saxton (1913) thought that the stability of plant parts or organs is proportional to their distance from the surface of the plant and their proximity to, or connection with, the reproductive structures. Thus the external characters of the vegetative organs, such as shape and position of leaves—characters most susceptible to adaptive change—are less important than those of the reproductive structures (e.g., micro- and megagametophytes), embryology, and the internal anatomy of vegetative structures (such as the vascular system). Lawson (1907) similarly thought that various reproductive structures of conifers that are buried deep within the tissues of the sporophyte are less likely to be modified by external factors and more likely to preserve ancestral characters. Coulter (1909, p. 86) believed that gymnosperm leaves respond to "conditions of living" and so largely ignored them in his taxonomic studies. Holgar Erdtman (1963) emphasized the taxonomic importance of constituents excreted into dead conifer heartwood as metabolic end products since he believed they were not subject to external influence.

CORRELATION OF CHARACTERS

The notion of correlation of characters has been common in conifer studies. Gaussen (1944, 1950) believed that the most recent species of a group are generally more evolved in all characters than were their ancestors. Stevens (1980) aptly pointed out that character states may occur in any combination: all primitive, all derived, or mixed.

A somewhat more reasonable class of correlations comprises functional ones. Sporne (1965) noted that the loss of the pollination drop is correlated with the loss of pollen wings. Coulter (1909) suggested that the position of the archegonium is related to the position of the pollen tube that reaches the embryo sac before the archegonial initials are evident.

Given such diverse views on how to classify organisms, the importance attributed to certain characters by some botanists, and how evolution is thought to proceed, it is little wonder that attempts at reconstructing phylogenetic relationships have been stuck in a morass of confusion, contradiction, uncertainty, and appeal to authority.

CLADISTIC THEORY

Several excellent discussions of cladistic methods now exist (e.g., Hennig, 1966; Hecht & Edwards, 1977; Wiley, 1981; Bremer, 1983). In a cladistic analysis, certain conditions are sought: the group being studied must be monophyletic, characters selected must be homologous (inherited from a common ancestor), there must be a known outgroup, and character states must be designated as either primitive or derived (Arnold, 1981). Hull (1967) and others have pointed out that there is not necessarily a precise order or progression in cladistic analysis. A systematist may work at several levels of analysis simultaneously.

Initially, a group being studied may not be known to be monophyletic. In this situation, a group may be selected based on previous taxonomic judgments or phenetic similarity.

Characters are recognized by similarity of structure in different organisms. Recently there has been considerable discussion about characters and homology (Sattler, 1984; Stevens, 1984; Tomlinson, 1984). During the first stages of phylogenetic reconstruction, it is not known if the characters are homologous in the cladistic sense (i.e., equivalent to apomorphies—see Patterson, 1982; Stevens, 1984). Homologies should, however, meet several criteria, including location, similarity, and connection of intermediate forms (Remane, 1952). Patterson (1982) recommended three tests of homology: similarity (topographic, ontogenetic, compositional), congruence (with other hypothesized homologies), and conjunction (two homologues cannot coexist in the same organism). Of these, the criterion of similarity is the first and thus the most important—the tests of congruence and conjunction can be applied only after an initial determination of the similarity of characters (Stevens, 1984).

Distinguishing between primitive and derived characters is one of the critical problems in phylogenetic reconstruction. Recently, attention has been devoted to the criteria by which this distinction is made (e.g., Crisci & Stuessy, 1980; Stevens, 1980; Watrous & Wheeler, 1981; Maddison *et al.*, 1984). Outgroup analysis based on parsimony is considered to be the most defensible criterion (Stevens, 1980). Wiley (1981, p. 139) defined the outgroup rule as follows: "Given two characters that are homologous and found within a single monophyletic group . . . the character found only within the monophyletic group is the apomorphic character." The underlying methodological principle of the outgroup rule is parsimony. The simplest hypothesis—the one that minimizes the number of parallelisms and convergences (homoplasy)—is preferred (Stevens, 1980; Farris *et al.*, 1982). This means that the preferred tree is congruent with the majority of apparent apomorphies. The use of parsimony does not mean that homoplasy is rare or uninteresting; it only seeks to minimize it.

MATERIALS AND METHODS

This study was based on a literature survey, an examination of herbarium specimens, and observations of living plants. The 63 genera of conifers used in the analysis were selected from the treatments of Dallimore and colleagues

(1966), Quinn (1970), and Silba (1984). I chose a set of characters using three criteria: a reasonable argument of similarity could be made supporting the homology of the different states of the character; character-state transformations could be determined on the basis of outgroup analysis; and character states could provide discrimination of families and genera (see APPENDIX, TABLE) (Rodman *et al.*, 1984). Characters or character states unique to individual genera (autapomorphies) were not included in the analysis. Morphological and anatomical information from all aspects of the life cycle, as well as chemical and chromosomal data, was utilized to avoid favoring certain subsets of characters.

A number of characters were not used for a variety of reasons, one of the most common being insufficient sampling. Quantitative characters showing apparently continuous variation or considerable overlap between possible states were avoided as much as possible (Almeida & Bisby, 1984; Hart, 1985). Characters showing considerable overlap between taxa were excluded. On some occasions when derived character states were rare and when the character was not recorded in many taxa, I assumed the primitive condition for missing characters (e.g., characters 75 and 76).

Different classifications of characters are often found in the literature. Thus Ueno's (1960) classification of pollen (character 61) based on extensive sampling using light microscopy differs somewhat from Reyre's (1968; character 62) system based on a more limited sampling using scanning electron microscopy. In this situation I have used Reyre's system but have included Ueno's in the TABLE for purposes of comparison.

Binary as well as multistate coding was used. The number 0 (primitive or plesiomorphic) was assigned to the character state found in one or all of the outgroups. With multistate coding, both unordered and ordered coding were used (APPENDIX, TABLE), depending upon whether or not there was justification for a transformation series. For example, leaves tetragonal in cross section (character 28) are found in the fossil conifer outgroups, and a variety of shapes are found among modern conifers (De Laubenfels, 1953); *a priori*, it is not possible to determine a transformation series of bifacially flattened, scalelike, or needlelike leaves. In certain situations it was possible to justify a transformation series. Thus, the presence of specialized winter bud scales (character 37) can be interpreted as having had intermediate steps in evolution.

The PAUP program used in the analysis allows for the coding of missing data ("9" in TABLE), treating them as equivalent to "all possible states." The missing states are filled in by the program according to what would be the most parsimonious character states, had they not been missing, and the tree length is then computed. Variable character states were also coded as "missing" (9).

A data matrix including 63 genera and 123 characters was assembled. Since current programs such as Swofford's PAUP cannot guarantee parsimony with such a large data matrix, the information was broken up into several smaller units. The first was a family-level analysis using eight representative genera: *Taxus* (Taxaceae), *Cephalotaxus* Sieb. & Zucc. ex Endl. (Cephalotaxaceae), *Araucaria* Juss. (Araucariaceae), *Podocarpus* L'Hér. ex Pers. (Podocarpaceae),

Data matrix for character states of conifers and outgroup gymnosperms listed in Appendix.*

[illegible]

*Plesiomorphic condition shown by 0, apomorphic states by 1-4, unknown and variable states by 9, character state not applicable by 8.

Pinus L. (Pinaceae), *Taxodium* Rich. (Taxodiaceae), *Cupressus* L. (Cupressaceae), and *Sciadopitys* Sieb. & Zucc. *Sciadopitys* was added to the list since it does not seem to share obvious synapomorphies with the Taxodiaceae, with which it is normally associated. In this analysis the characters chosen for the representative genera were consistent (with minor exceptions) within the family but varied across the families. This analysis was conducted using the branch-and-bound algorithm (Hendy & Penny, 1982). Next, a series of analyses of the separate families, such as Pinaceae, Podocarpaceae, and Taxaceae, or pairs of families, such as Taxodiaceae and Cupressaceae, was run. These analyses were conducted using the local-branch-swapping algorithm.

The selection of outgroups requires some discussion. The Lebachiaceae, *Cordaitea* Unger, *Ginkgo* L., and other gymnosperms were chosen as outgroups (see FIGURE 1). For many characters, only the living gymnosperms—*Ginkgo*, cycads, and the Gnetales—could be used as outgroups. Other characters were represented in the fossil record. Paleobotanists generally accept the family Lebachiaceae—which includes *Lebachia* Florin, *Ernestiodendron* Florin, and *Walchiostrobus* Florin—as the “stem” conifer group (Florin, 1951). It is, however, not certain that the “Lebachiaceae” represent a monophyletic group; C. N. Miller (pers. comm.) indicated that the family is paraphyletic and thus constitutes a series of outgroups. For some characters the various genera of “Lebachiaceae” were individually used as outgroups. On the other hand, the family Voltziaceae Florin—including *Pseudovoltzia* Florin, *Ullmannia* Göppert, and *Glyptolepis* Schimper—seems to comprise taxa intermediate between the Lebachiaceae and modern conifers (Stewart, 1983); these were not used as outgroups since they may be ingroups to conifers. The next outgroup chosen, *Cordaitea*, is generally acknowledged to be represented earlier in the fossil record than *Lebachia* and its relatives and is considered to share a common ancestor with them (Florin, 1951; Taylor, 1981; Stewart, 1983; Clement-Westerhof, 1984; Mapes & Rothwell, 1984). The position of *Ginkgo* and then cycads as the next most inclusive outgroups is supported by the work of Meyen (1984), Doyle and Donoghue (1986), and Crane (1985). Occasionally it was possible to use the initial cladogram of the families of conifers to determine polarity of particular characters (Watrous & Wheeler, 1981). Thus, the presence of inverted ovules in the Pinaceae, which seem to form a basal clade or functional outgroup (FIGURE 2), and in many members of the Lebachiaceae lent credibility to the polarity of this character. In determining the polarity of the characters generally, the algorithm developed by Maddison and colleagues (1984) was followed.

RESULTS

In this section I describe the results of attempts to analyze relationships 1) of conifers to other gymnosperms, 2) among families of conifers, and 3) among the genera of conifers within the different families. A complete resolution of the cladistic relationships among the genera and families of conifers requires more data. However, several hypotheses of phylogenetic relationships can be proposed with the information available.

In the larger data sets, only the most parsimonious cladograms—those with

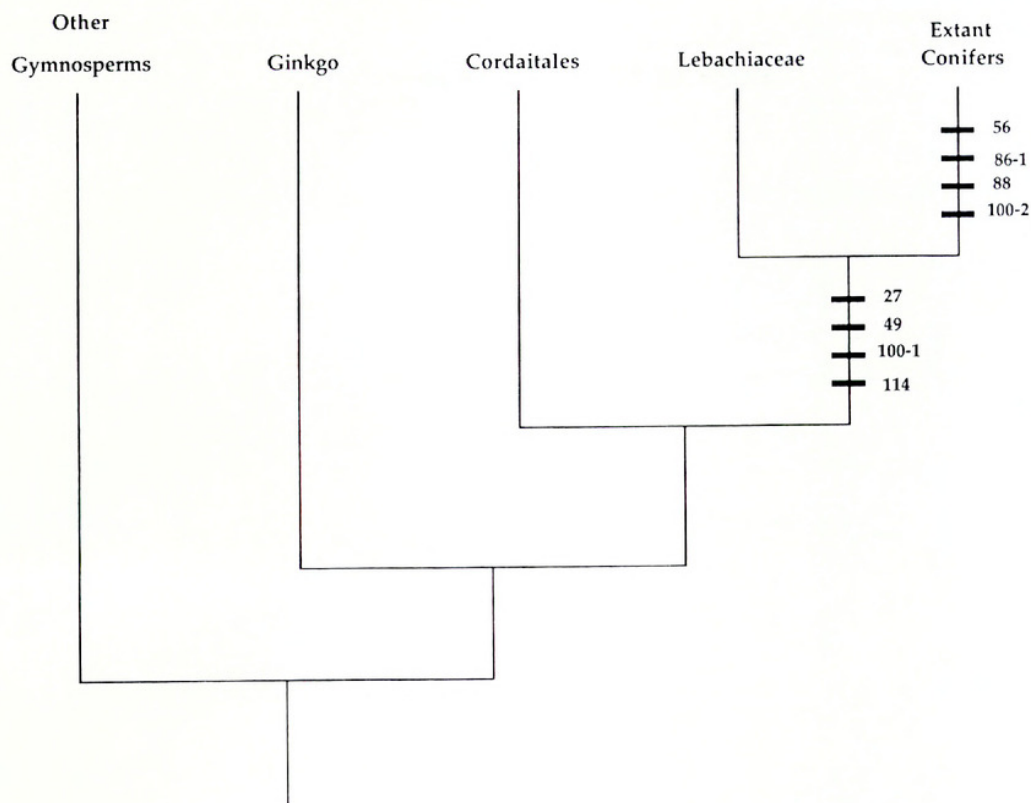


FIGURE 1. Hypothesized relationships of modern conifers to outgroups, including fossil and living gymnosperms, used as basis for polarization of character states. For some characters other taxa related to *Lebachia* used as outgroups intermediate between modern conifers and Cordaitales.

the fewest reversals, parallelisms, and convergences—are presented. The branch-and-bound algorithm, which generates the most parsimonious cladograms, can only work with smaller data sets. This algorithm was used solely in the family-level analyses and for the Taxaceae. The other data sets were analyzed using the local-branch-swapping algorithm, which unfortunately does not generate most parsimonious cladograms. A basis for comparing parsimony among cladograms is the consistency index, which is the minimum range of character-state changes in the data divided by the actual length of the tree—or the sum of character-state changes or patristic distances along all branches. Fractions close to unity indicate a tree with little homoplasy (Kluge & Farris, 1969).

MONOPHYLY OF CONIFERS AND PHYLOGENETIC RELATIONSHIPS WITH OTHER GYMNASPERMS

A manually generated cladistic hypothesis for the monophyly of living conifers and the relationships of these conifers with fossil and living gymnosperm outgroups is presented in FIGURE 1. The distinguishing characteristics that separate extant conifers from all other extant gymnosperms and angiosperms—and hence suggest monophyly—are embryological. There are at least two characters of importance. First, the number of free nuclear divisions in embryo-

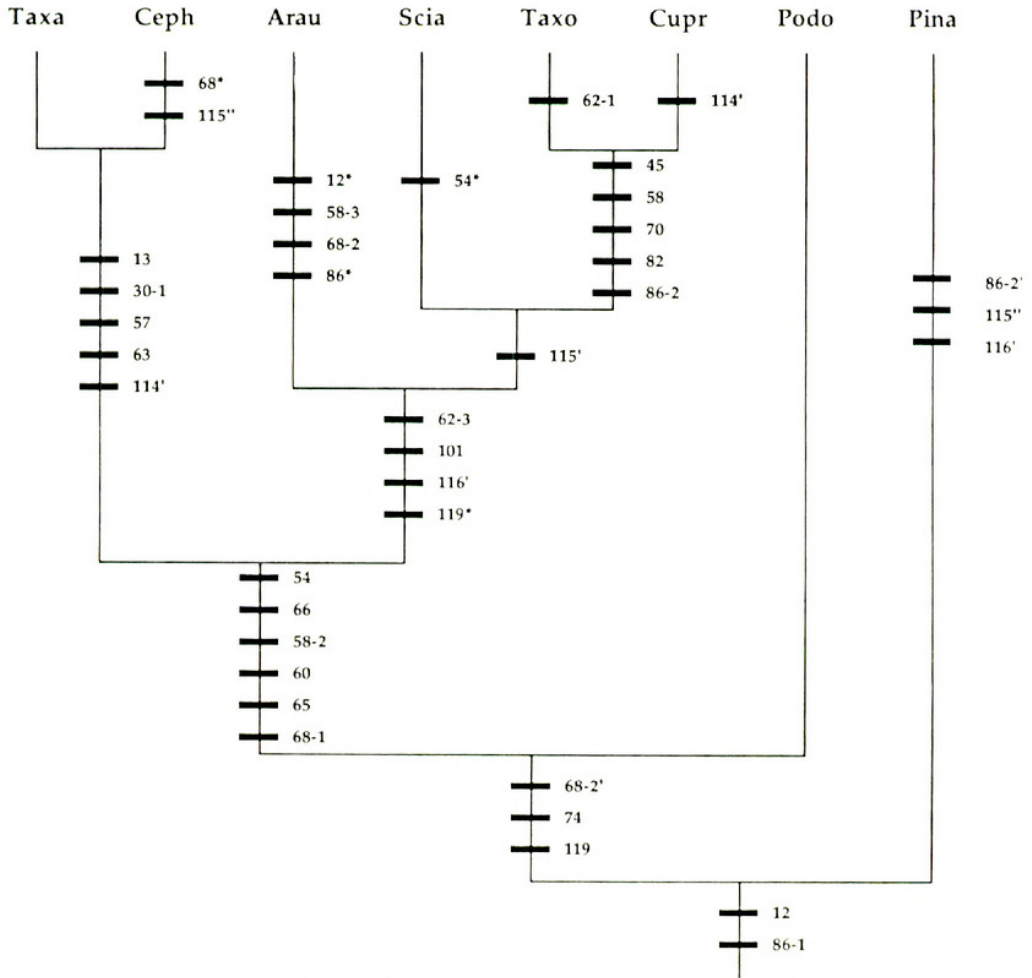


FIGURE 2. Hypothesized relationships between families of conifers, using representative genera. (Arau = *Araucaria* (Araucariaceae); Ceph = *Cephalotaxus* (Cephalotaxaceae); Cupr = *Cupressus* (Cupressaceae); Pina = *Pinus* (Pinaceae); Podo = *Podocarpus* (Podocarpaceae); Scia = *Sciadopitys*; Taxa = *Taxus* (Taxaceae); Taxo = Taxodiaceae; * = reversal; ' = one parallelism; '' = character evolved twice.)

genesis (character 86) is greatly reduced in living conifers (five or fewer) compared to *Ginkgo* and cycads (eight and ten, respectively). Second, the structure of the proembryo of conifers (character 88) is unique. In contrast to the proembryo of cycads and *Ginkgo*, which is characterized by an unstratified cell arrangement, that of conifers is stratified or tiered. The proembryo of *Gnetum* L. differs from them in having no free nuclear stage and no definite arrangement of cells, and in the elongation of each cell to form a suspensor (Johansen, 1950). In conifers the primary proembryo is the first cellular structure formed after the wall. It has two morphological units: an open tier and a lower primary embryonal cell group (Chowdhury, 1962; Dogra, 1978). This is characteristic of nearly all conifers, including the Araucariaceae (Haines & Prakash, 1980) and the Taxaceae (Chen & Wang, 1984). Since these characters are not known for the Cordaitales or the Lebachiaceae, they may be placed at one of three

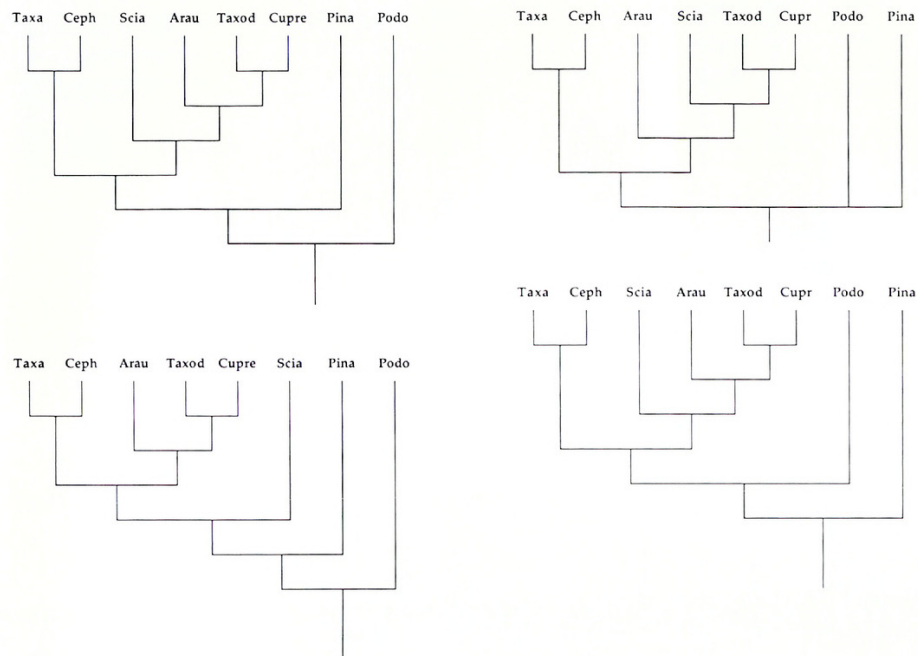


FIGURE 3. Hypothesized relationships of families, using representative genera; 4 cladograms involving 1 more step than in FIGURE 2.

nodes in the clades in FIGURE 1: extant conifers; extant conifers + Lebachiaceae; or extant conifers + Lebachiaceae + Cordaitales.

Other characters can be used to establish monophyly and outgroup relationships when fossil gymnosperms are used for comparison. Extant conifers can be distinguished from the fossil *Lebachia* by at least two characters. One is the cone scale (character 100-2), a highly modified fertile short shoot (Florin, 1951; Taylor, 1981; Stewart, 1983; Meyen, 1984; Crane, 1985). Crane (1985) stated that the ovulate fertile short shoot—or “scale”—of extant conifers differs from that of the Lebachiaceae in that the shoot apex is not differentiated and that there is no phyllotactic spiral in parts of the former. There is still considerable discussion as to exactly what it represents: for example, short shoot alone or short shoot plus sterile scale (Guédès & Dupuy, 1974; Jain, 1976). However, the exact nature of the structure does not affect my argument as long as part of the scale is a short shoot.

The second character is palynological. Pollen of modern conifers is characterized by distal germination, whereas that of the Lebachiaceae does not have a thin area on the distal surface, thus indicating proximal germination (Mapes & Rothwell, 1984). This character shows homoplasy; Millay and Taylor (1976) have shown that the shift from proximal to distal germination also occurred in the Callistophytaceae and the Cordaitales.

If *Cordaites* is considered as the outgroup to conifers (Doyle & Donoghue, 1986), a number of derived characters support monophyly of the Lebachiaceae + extant conifers. The pollen cones (character 49) of the Lebachiaceae and modern conifers are simple or uniaxial; those of *Cordaites* are compound. Conifer leaves—“microphylls” (character 27)—are rather small and usually single veined (except in the Araucariaceae and a few species of the Podocarpaceae); the leaves of the Cordaitales, *Ginkgo*, and the cycads are rather large and many veined. The Lebachiaceae (except a few species of genera such as *Ernestiodendron*) and extant conifers have bilaterally flattened ovulate short shoots (or scales); the Cordaitales have radially symmetrical fertile ovulate short shoots (Florin, 1951; Taylor, 1981; Rothwell, 1982; Stewart, 1983).

Ovule orientation (character 114) is a difficult character to employ because it is variable in some groups. The ovule is erect in *Ginkgo*, the cycads, *Ephedra* L., and *Gnetum*. The most recent interpretation for the Voltziales is that most have inverted ovules (Clement-Westerhof, 1984; Mapes & Rothwell, 1984).

Crane (1985) also suggested resin canals as a synapomorphy for *Lebachia* and extant conifers. Resin canals do occur in nearly all conifers and taxads, although in many different plant parts (i.e., xylem, roots, leaves, seed coats); this may suggest different origins (homoplasy). Mucilage canals have been described for *Ginkgo* and may be similar to resin canals in conifers. Studies of resin-duct development and resin chemistry may help our understanding of these characters.

FAMILY-LEVEL ANALYSIS

In this analysis the characters chosen for the representative genera were consistent (with minor exceptions) within the family but varied across the

The placement of *Sciadopitys*, the Podocarpaceae, and the Araucariaceae is variable.

PINACEAE. Ten genera and 48 characters were used in the cladistic analysis of the Pinaceae (results shown in FIGURE 4). The consistency index is .600. Members of this family are distinguished by seven synapomorphies restricted to them: 6 (phloem fibers absent), 41 (leaf transfusion-tissue tracheids all around vascular bundle), 43 (biflavonoids absent), 69 (sperm cells without cell walls), 74 (ventral-canal cells without walls (nuclei only)), 78 (megaspore membrane thin at micropylar end), and 89 (proembryo four-tiered). Several other characters (e.g., resin ducts, character 19), initially scored as derived within the Pinaceae, are derived at the family level but show subsequent loss in different lineages. There were numerous other synapomorphies (e.g., character 39) showing homoplasy within conifers that are evidently derived at the family level.

PODOCARPACEAE. Fifteen genera and 24 characters were used in the analysis of the Podocarpaceae (results presented in FIGURE 5). The consistency index is .500, rather low. Only two unique synapomorphies seem to unite the Podocarpaceae: the binucleate embryonal cell of the proembryo (90), and the epimatium (105, but missing in two taxa). Additional apomorphies are found in other conifers (28-2; 119) or are only found in most Podocarpaceae (e.g., 48); the algorithm has interpreted them as being derived at the family level but subsequently lost within the family.

TAXODIACEAE-CUPRESSACEAE. Thirty-one genera and 53 characters of the Cupressaceae and the Taxodiaceae (including *Sciadopitys*) were analyzed (see FIGURES 6 and 7). The consistency index is .544. *Sciadopitys* is even more clearly separated from the Taxodiaceae-Cupressaceae than the family-level analysis indicated, with 12 synapomorphies separating them. It can be seen that the Taxodiaceae, even exclusive of *Sciadopitys*, are paraphyletic. There are several monophyletic groupings within the Taxodiaceae, including *Sequoia* Endl. and *Sequoiadendron* Buchholz; *Metasequoia* Miki, *Taxodium*, and *Glyptostrobus* Endl.; and *Taiwania* Hayata, *Cryptomeria* D. Don, and *Cunninghamia* R. Br. ex Rich.

Several synapomorphies define the Cupressaceae as a monophyletic group within the Taxodiaceae (see FIGURE 6). Within the Cupressaceae, there is division of northern and southern taxa (FIGURE 7). The analysis indicates that northern Cupressaceae are paraphyletic although there are several monophyletic groupings, including *Microbiota* Komarov and *Platyclusus* Spach, *Thuja* L. and *Thujopsis* Sieb. & Zucc., *Fokienia* A. Henry & H. Thomas and *Calocedrus* Kurz, and *Juniperus* L., *Chamaecyparis* Spach, and *Cupressus*. However, it should be remembered that these hypotheses of relationships are tenuous since few characters were utilized in the analysis. The southern taxa, including the African *Tetraclinis* Masters, form a monophyletic group. This group divides into an unresolved quadrachotomy: *Diselma* J. D. Hooker, *Fitzroya* J. D. Hooker, and *Pilgerodendron* Florin; *Austrocedrus* Florin & Boutelje, *Libocedrus* Endl., and *Papuacedrus* L.; *Neocallitropsis* Florin; and *Widdringtonia* Endl., *Callitris* Vent., and *Actinostrobus* Miq.

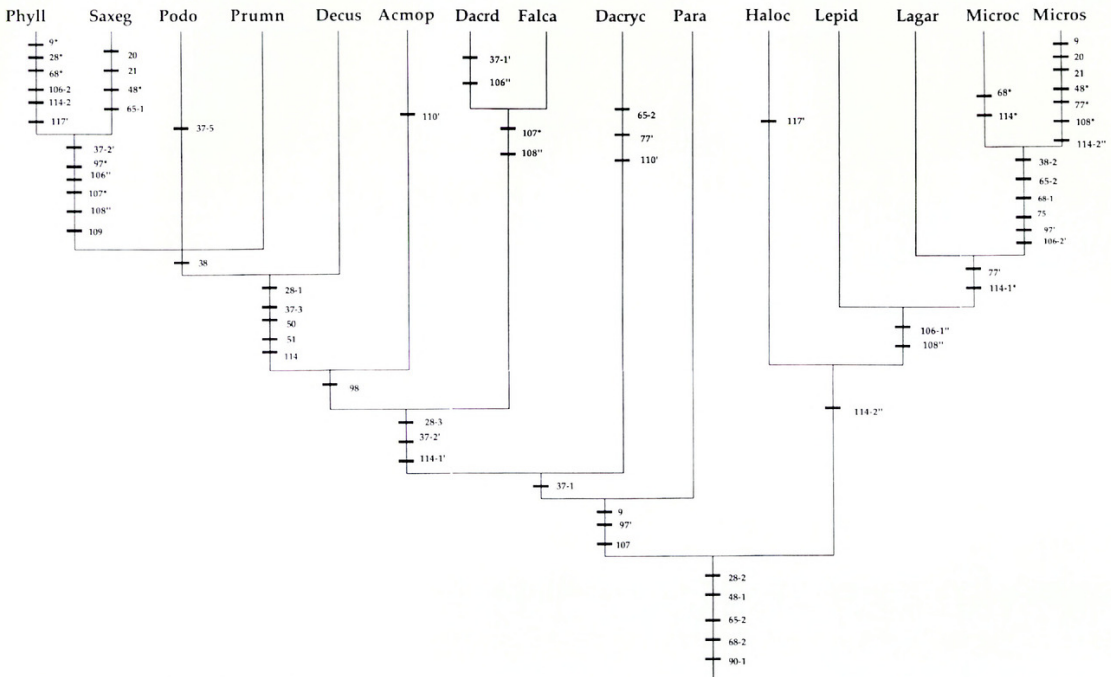


FIGURE 5. Cladistic relationships of Podocarpaceae. (Acrop = *Acropyle*; Dacryc = *Dacrycarpus*; Dacrd = *Dacrydium*; Decus = *Decussocarpus*; Falca = *Falcatifolium*; Haloc = *Halocarpus*; Lagar = *Lagarostrobos*; Lepid = *Lepidothamnus*; Microc = *Microcachrys*; Micros = *Microstrobos*; Para = *Parasitaxus*; Phyll = *Phyllocladus*; Podo = *Podocarpus*; Prumn = *Prumnopitys*; Saxeg = *Saxegothaea*; * = reversal; ' = one parallelism; " = character evolved twice.)

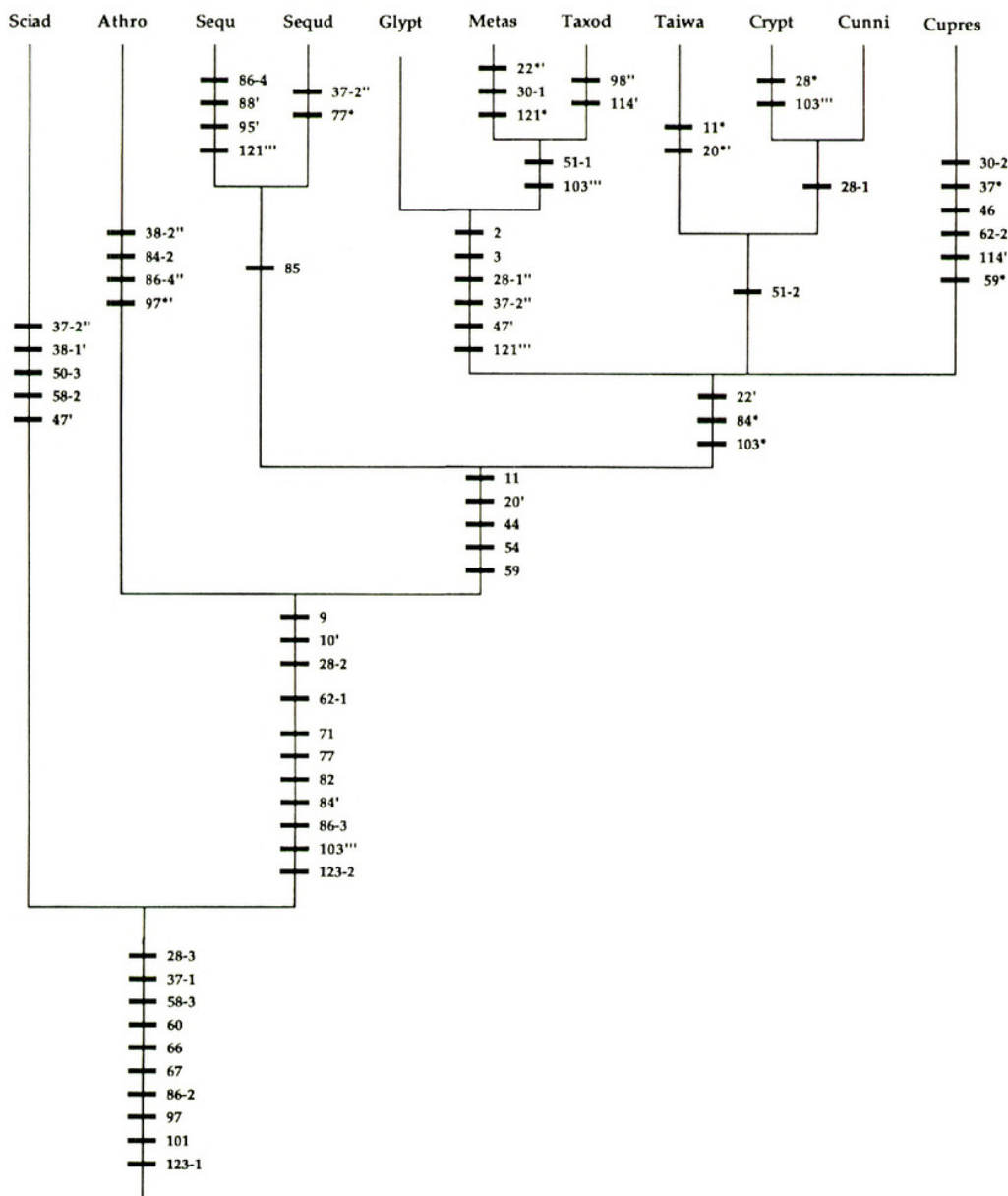


FIGURE 6. Cladistic relationships of Taxodiaceae and Cupressaceae. (Athro = *Athrotaxis*; Crypt = *Cryptomeria*; Cunni = *Cunninghamia*; Cupres = Cupressaceae; Glypt = *Glyptostrobus*; Metas = *Metasequoia*; Sciad = *Sciadopitys*; Sequ = *Sequoia*; Sequd = *Sequoiadendron*; Taiwa = *Taiwania*; Taxod = *Taxodium*; * = reversal; ' = one parallelism; '' = character evolved twice; ''' = character evolved three times.)

TAXACEAE. Five genera and 16 characters were used in the analysis (see FIGURE 8); the consistency index is .857. This family can be recognized at least by the uniaxial or "simple" seed "cone" (99). Characters such as the aril (117) are also found in other families.

ARAUCARIACEAE. This family comprises only two genera (*Agathis* Salisb. and *Araucaria*) and as such does not require a phylogenetic analysis. It is defined by at least ten apomorphies (FIGURE 8).

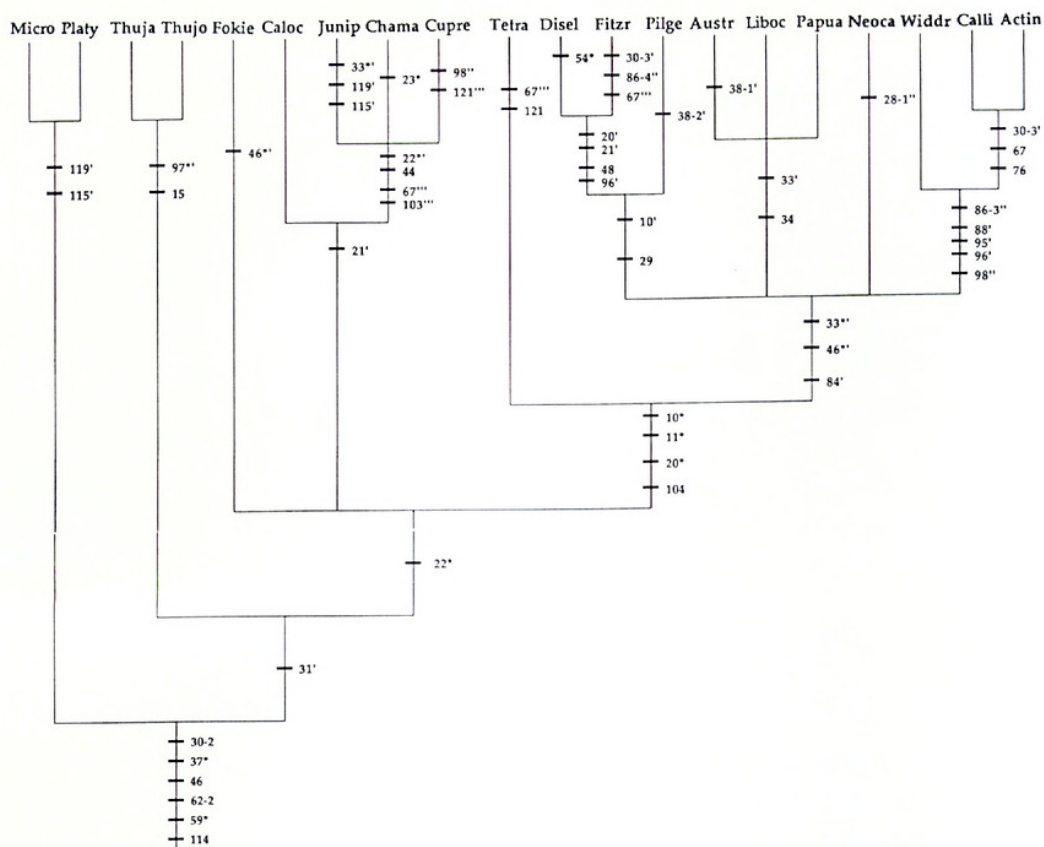


FIGURE 7. Cladistic relationships of Cupressaceae. (Actin = *Actinostrobus*; Austr = *Austrocedrus*; Calli = *Callitris*; Caloc = *Calocedrus*; Chama = *Chamaecyparis*; Cupre = *Cupressus*; Disel = *Diselma*; Fitzr = *Fitzroya*; Fokie = *Fokienia*; Junip = *Juniperus*; Liboc = *Libocedrus*; Micro = *Microbiota*; Neoca = *Neocallitropsis*; Papua = *Papuacedrus*; Pilge = *Pilgerodendron*; Platy = *Platycladus*; Tetra = *Tetraclinis*; Thujo = *Thujopsis*; Widdr = *Widdringtonia*; * = reversal; ' = one parallelism; '' = character evolved twice; ''' = character evolved three times.)

DISCUSSION

This cladistic analysis of conifers provides explicit criteria for establishing phylogenetic relationships and classifications based on multiple character sets, facilitates the understanding of the evolution of characters, illustrates the distinction between character-state polarity and taxonomic polarity, is helpful in understanding evolution and biogeography of the group, demonstrates the usefulness of fossil gymnosperms as outgroups, and focuses attention to gaps in knowledge requiring further research.

CLASSIFICATION

The classification of conifers, especially with regard to their relationships with taxads and other taxa lacking "evident" cones, has been much discussed. The results of this analysis strongly support the monophyly of conifers and taxads. Traditional approaches to conifer systematics (e.g., Sinnott, 1913; Aase, 1915; Thomson, 1940; Florin, 1951; C. N. Miller, 1976, 1982, 1985) have

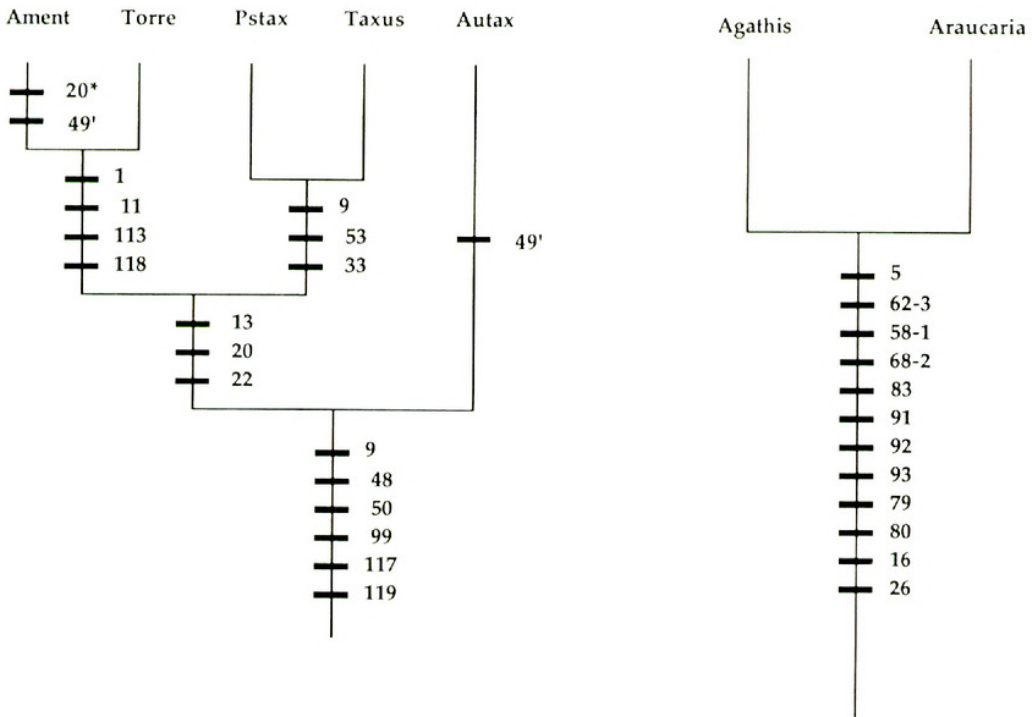


FIGURE 8. Cladistic relationships of Taxaceae (left) and Araucariaceae (right). (Ament = *Amentotaxus*; Autax = *Austrotaxus*; Pstax = *Pseudotaxus*; Torre = *Torreya*; * = reversal; ' = one parallelism.)

tended to emphasize ovulate cone structure. This study has uncovered embryological, palynological, and anatomical features that also provide bases for the recognition of conifers as a monophyletic group (see FIGURES 1, 2).

The placement of the Taxaceae has been controversial in the past (see, for example, Chamberlain, 1935; Florin, 1948b, 1951; Takhtajan, 1953; Sporne, 1965). The simple, uniaxial cone—in contrast to the biaxial one found in all other conifers—is unique to this family, and Florin (1948b, 1951) championed the separation of the Taxaceae from the rest of the conifers based on this character alone. He found a similar cone in the Jurassic *Paleotaxus jurassica* Florin and concluded that, since this structure is old and thus primitive, the Taxaceae should therefore be elevated to the rank of Taxales, coordinate with the Coniferales. In this cladistic analysis the taxads clearly fall out as a sister group to the Cephalotaxaceae, well within the rest of the conifer families (see FIGURE 2), all of which have biaxial cones. Embryologically, the Taxaceae have patterns of development similar to those of other conifers—a reduced number of divisions in embryogenesis and a tiered proembryo. In this analysis the most parsimonious explanation of the distribution of character states suggests that the uniaxial ovulate cone is derived from a compound, biaxial one. Florin's reason for elevating the Taxaceae is apparently unjustified: although uniaxial cones apparently similar to those of *Taxus* are found in the Jurassic, numerous earlier gymnosperms had biaxial cones.

A close relationship between the Taxodiaceae and the Cupressaceae has been recognized (e.g., Saxton, 1913; Eckenwalder, 1976; Stewart, 1983), although

an isolated position for *Sciadopitys* (which is placed in the Taxodiaceae) has also been suggested (Velenovský, 1905; Seward, 1919; Florin, 1922; Hayata, 1932; Eckenwalder, 1976; Schlarbaum & Tsuchiya, 1985). The results from this cladistic analysis support these general conclusions since the monophyly of the Taxodiaceae (minus *Sciadopitys*) + Cupressaceae is supported by many characters (see FIGURE 6). However, the Taxodiaceae as currently recognized are not monophyletic but paraphyletic; the Cupressaceae form a monophyletic grouping *within* that family. Thus, if one chooses to recognize the Cupressaceae as presently circumscribed at the family rank, then the Taxodiaceae cannot be recognized, and many clades within the current Taxodiaceae will have to be elevated to family ranking. A possible solution is to recognize the entire Taxodiaceae-Cupressaceae clade as the Cupressaceae, which has nomenclatural priority (Eckenwalder, 1976).

The monophyly of the Pinaceae is well established (see FIGURE 4), with at least ten unique synapomorphies. Within the Pinaceae, grouping of genera is uncertain, as has been suggested by previous workers (e.g., Van Tieghem, 1869; Jeffrey, 1905; Pilger, 1926; Gaussen, 1966), who have each emphasized different characters in suggesting relationships. Van Tieghem (1869), for example, divided the family into two groups, those with short shoots and those without them. My results do not support his division of the family. In my analysis short shoots have evolved three times: in the lineage giving rise to *Pinus*, *Cathaya* Chun & Kuang, and *Larix* Link; in *Cedrus* Trew; and in *Pseudolarix* Gordon. Inspection of the morphology of the short shoots suggests differences between them (Thomson, 1914). Those of *Cedrus*, *Larix*, and *Pseudolarix* are persistent, and the leaves fall separately on an annual basis or in the second to fifth year. In *Pinus* the short shoots are deciduous as an entire unit in the second to twentieth (rarely to the forty-fifth) year, they produce a fixed number of needles in a single season, and they are axillary to a scale. In the other genera of Pinaceae, the needles are not fixed in number, and the short shoots are not deciduous or axillary to a scale. In *Cathaya* the short shoots are poorly developed. However, even acknowledging the differences between short shoots within the Pinaceae does not tell if they represent the same character or separately evolved, nonhomologous ones. Phylogenetic hypotheses can assist in answering such questions: this analysis suggests that short shoots have evolved three different times and so may not be homologous, yet that the morphological variation noted by Thomson (1914) may not be relevant in suggesting different evolutionary origins. Alternatively, if the information given by Thomson is used to record the character, short shoots may have evolved at least four times! Barnard (1926) claimed that some shoot dimorphism is common in conifers—another suggestion that short shoots are a weak phylogenetic character.

The grouping of the Pinaceae into two lineages is based on a few characters: the presence of resin ducts in the seeds (character 120) and of cleavage polyembryony (97) supports monophyly of *Abies* Miller, *Pseudolarix*, *Keteleeria* Carrière, *Cedrus*, and *Tsuga* Carrière; resin ducts in the secondary wood (17) and leaves with endodermis having thickened Casparian strips (39) support monophyly of *Cathaya*, *Pinus*, *Larix*, *Pseudotsuga* Carrière, and *Picea* Dietr.

Singh (1978) listed embryological characters of the Podocarpaceae in addition

to those used in this analysis; for example, densely staining cytoplasm surrounding the archegonium (character 81). This character, however, needs further investigation to verify its use as a character state. De Laubenfels (1962) suggested that the presence of two cotyledons, each with two vascular bundles, is a feature unique to the Podocarpaceae. However, the use of this character does not stand up to cladistic reasoning. The fact that members of the outgroup comprising *Ginkgo*, the cycads, and the Gnetales have two cotyledons—and those of *Ginkgo* have two vascular bundles—might suggest that this is a primitive character within the Podocarpaceae. The morphological heterogeneity of the Podocarpaceae is underscored by the variation in chromosome numbers, which is extreme when compared to that within other conifer families (Sax & Sax, 1933; Hair & Beuzenberg, 1958; Khoshoo, 1961; Mehra, 1968). Given the high levels of homoplasy, the groupings of genera within the Podocarpaceae (FIGURE 5) must thus be very tentative, and additional research is clearly needed to confirm them.

Although the Podocarpaceae are usually considered a natural group, Keng (1973, 1974, 1975) has elevated *Phyllocladus* to family ranking, suggesting that the phylloclade of *Phyllocladus* was a very ancient structure that linked conifers with progymnosperms. For this to be the case, *Phyllocladus* would have to fall out not only as separate from the rest of the Podocarpaceae, but also as splitting off first in the family-level analysis. This is clearly not the case (see FIGURES 2 (Podocarpaceae), 5). *Phyllocladus* is not only a terminal taxon within the Podocarpaceae, but the Podocarpaceae in which it belongs split off after the basal Pinaceae (FIGURE 2; compare FIGURE 3).

How does one evaluate a cladogram? A significant quantity of homoplasy (the amount of parallelisms, convergence, and reversals in character states) seriously weakens cladistic hypotheses. One measure of homoplasy is the consistency index, which is the minimum range of character-state changes in the data divided by the actual length of the tree—or the sum of character-state or patristic changes along all branches. Fractions close to unity indicate a cladogram with little homoplasy (Kluge & Farris, 1969). In this study it varied from .500 to .857, a modestly good figure compared to that in some studies (for example, .40 in Rodman *et al.*, 1984). There may be several factors—both artificial and real—that explain the relatively low levels of homoplasy in this study. Comparing homoplasy indices among different taxonomic groups may lead to divergent values due to different sizes of data matrices. The greater the number of taxa and characters, the greater the amount of homoplasy. Thus, the consistency index for the Cupressaceae-Taxodiaceae analysis, with 31 taxa and 53 characters, was .544, while that for the Taxaceae analysis, with 5 taxa and 15 characters, was .857.

There may also be biological reasons why the homoplasy values are comparatively low in this study. In groups like conifers, in which great gaps exist between taxa due to extinction, character states may be comparatively distinctive, while in some more recent angiosperm groups characters may show nearly continuous variation, with character-state delimitation correspondingly uncertain.

Phylogenetic analyses using multiple sets of characters taken from all aspects

of the plant demonstrate the value of not relying on any particular subset of characters, such as cone structure. We also see, not surprisingly, the importance of looking beyond the readily visible morphological features. Many of the phylogenetically useful characters are anatomical, embryological, palynological, or chemical. For example, apomorphies for the Pinaceae include p-type plastids, absence of biflavonoids, arrangement of transfusion-tissue tracheids, absence of phloem fibers, lack of cell walls in ventral-canal nuclei, thinning at the micropylar end of the megaspore membrane, and four-tiered proembryo. But the converse position—that gross morphological characters are not useful as phylogenetic markers—cannot be maintained. Saxton (1913) and Eckenwalder (1976) downplayed the value of decussate phyllotaxy that characterize Cupressaceae, but for different reasons. Saxton (1913) believed that external morphological characters respond to “conditions of living” and are therefore poor indicators of phylogeny. Although there is some merit in what Saxton says, a case can be made for the functional nature of just about any structure. It is best to exclude notions of adaptation and/or function from phylogenetic analysis, at least in the initial stages. This is not to say that phylogenies based on characters that seem adaptive should not be questioned.

Eckenwalder (1976) dismissed decussate phyllotaxy as not being a useful character for the Cupressaceae since it reportedly occurs elsewhere. However, there are two problems with this position. First, some of Eckenwalder's examples of decussate phyllotaxy are not really decussate, but bijugate or spiral opposite—e.g., *Metasequoia* and the Taxaceae (Morley, 1948; De Laubenfels, 1953; Greguss, 1955). Second, while perfectly decussate leaves have indeed evolved elsewhere (e.g., in the Cheirolepidiaceae Takht. (Alvin, 1982) and in *Microcachrys tetragona* J. D. Hooker), the usefulness of this character, although perhaps weakened, cannot be altogether discounted.

UNDERSTANDING THE EVOLUTION OF PARTICULAR CHARACTERS

Cladograms facilitate the understanding of the evolution of particular characters. Florin (1951) argued for a separation of conifers and taxads based on the single terminal ovule of the latter, which he claimed did not evolve by reduction from a bract and ovuliferous short-shoot system. The results of this cladistic analysis suggests, on the contrary, that the ovule structure of the taxads evolved from the biaxial cone of the conifers. Indeed, Harris (1976) suggested a possible scenario. An example is the peltate, perisporangiate microsporophyll of some Taxaceae (*Taxus*, *Pseudotaxus*), which has been likened to the sporangiophore of the Cordaitales (Dupler, 1919). Outgroup analysis indicates that this unique taxad microsporophyll is derived from the bisporangiate, hyposporangiate microsporophyll of other conifers.

“PRIMITIVE” CHARACTERS VS. “PRIMITIVE” TAXA

The cladistic results illustrate what to many is a contradiction: the presence of both specialized and generalized (or primitive) traits within particular taxa, or heterobathmy (Stevens, 1986). As mentioned above, much early discussion centered on which of the modern groups of conifers is the most primitive. In

cladistic reasoning, living taxa are not viewed as primitive or advanced; only individual characters are advanced or primitive with respect to their condition in related taxa. Cladograms themselves simply represent the sequence of divergence of lineages. Thus the occurrence of so many derived characters in an apparently basal clade such as the Pinaceae may seem to be a contradiction, but it is not unexpected. The cladistic interpretation of the relative age of the Pinaceae is not inconsistent with the fossil record, which indicates that the group is very old (C. N. Miller, 1976, 1982; Meyen, 1984).

BIOGEOGRAPHY

The distribution of conifers—both fossil and extant—has long been of interest to biogeographers. Conifers have been divided into northern and southern “groups.” Florin (1940, 1963) found that the southern conifer floras were different from the northern ones as early as the late Carboniferous and Permian periods.

Li (1953b) discussed the high diversity of extant conifers in the Pacific Basin and showed that in both Northern and Southern hemispheres, the majority of relict, endemic, or disjunct genera are concentrated in moist, mountainous regions with warm temperatures bordering the eastern and western parts of the Pacific.

In accounting for the distribution of conifers, biogeographers have drawn upon various explanations: migration and dispersal from centers of origin, extinction, and continental drift (Florin, 1963).

Seeking centers of origin was a common endeavor for conifer biogeographers, as it was for other specialists. Brown (1869) concluded that each genus had arisen out of the center in which the greatest number of species is found. Conifers were commonly believed to have originated in northern polar regions. Koch (1927) suggested a European origin for them.

In explaining the disjunct distribution patterns of conifers, biogeographers generally have suggested that long-distance dispersal has not been as frequent as in angiosperms. This is expected, given the relatively large size of most conifer seeds. However, the fleshy propagules of many conifers (e.g., Podocarpaceae, Taxaceae, *Juniperus*) are likely candidates for long-distance dispersal, since birds are known to eat them (Givnish, 1980). Land bridges and connections have been hypothesized to get conifers from one continent to another. Florin (1963) postulated that the migration of conifers has occurred in or along mountain belts during the Paleozoic, Mesozoic, and Cenozoic eras. Continental drift has often been employed to explain conifer distribution, especially in the Southern Hemisphere (Florin, 1963; Aubréville, 1973; Page & Clifford, 1981).

Whatever cause for these distribution patterns of conifers one chooses, the explanation will be influenced—if not determined—by cladistic relationships. As an example, consider some of the southern Cupressaceae (FIGURE 7). Several groups show Gondwanaland distributions: *Pilgerodendron*, *Fitzroya* (both South America), and *Diselma* (Tasmania); *Austrocedrus* (South America), *Libocedrus* (New Zealand, New Caledonia), and *Papuacedrus* (New Guinea); and *Callitris*, *Actinostrobus* (both Australia), and *Widdringtonia* (southern Africa). Of these,

the first two groupings are somewhat tenuous since they are supported by few characters, but the clade of *Widdringtonia*, *Callitris*, and *Actinostrobus* is supported by several. A likely explanation is that the common ancestor of these genera inhabited Gondwanaland, and with subsequent continental drift these lineages became recognizable. Florin (1963) contended that the conifers divided very early into northern and southern groups. The Araucariaceae, the Podocarpaceae, *Athrotaxis* D. Don, *Paranocladus* Florin, *Walkomiella* Florin, and *Buriadia* A. C. Stewart & B. Sahni constituted the southern group, while the rest of the conifers constituted the northern one. My cladistic analysis does not support the contention that modern evolutionary distributions reflect that early distribution of two groups. It does suggest multiple Gondwanaland distributions—two in the Taxodiaceae-Cupressaceae clade and one in the Taxaceae. Many conifer groups (e.g., *Araucarites* C. Presl, *Athrotaxites* Unger, and *Podocarpus*, *fide* Krassilov, 1974) had both northern and southern distributions, relative to the Tethys Sea, in the Mesozoic. Extinction, perhaps due to changing climates, may also account for some of the disjunctions, especially in the Northern Hemisphere.

ROLE OF FOSSILS

Many botanists (e.g., Stevens, 1980, 1984) and some zoologists (e.g., Patterson, 1982) are reluctant to use fossils in polarizing character states. Stevens (1980, p. 342) stated "...the imperfections of the fossil record cast doubt on this method of giving evolutionary polarity to a morphocline." However, the relevance of fossils depends upon the group being studied (Crane & Manchester, 1982). It may also depend upon the level of grouping in which a systematist is interested: for example, fossils may be of importance in assessing relationships of conifers to other gymnosperms, or among genera of conifers, but less useful for species of *Podocarpus*.

The use of fossils in phylogenetic reconstruction may be questioned somewhat differently: are fossils automatically to be considered ancestors, are they merely another organism, or are they special outgroups, to be given special consideration? The answer to the first query should be obvious. Despite repeated claims by paleontologists to have discovered *the* "ancestor" for particular groups, it is extremely doubtful that ancestors for many groups will ever be determined with any certainty.

The answer to the second will be determined by the quality and quantity of the characters shown by the fossils. Fossils may help greatly in the understanding of characters. Thus Florin (1951) was perfectly justified in discussing the evolution of cone scales in modern coniferous taxa from short shoots of fossils, because these characters are well represented in the fossil record.

Should fossil outgroups be given special status—that is, greater importance than living outgroups? Here there can be no easy solution. *A priori*, fossil outgroups cannot be given special status over living outgroups. However, it all depends on the group being studied. Well-represented fossil groups may be weighted more than isolated living outgroups, or vice versa. Fossil representatives have been crucial in the phylogenetic analysis of conifers. The use of

fossil groups like the Lebachiaceae, the Cordaitales, and others puts the cladistic analysis of living conifers on a much firmer footing than if only other living gymnosperms were employed for outgroup comparison.

Fossils also tell us something of past distributions. The relictual nature of many genera of conifers is borne out in studies such as Chaney's (1951). *Sequoia*, for example, once had a far greater distribution than it does now. Florin (1940, 1963) used fossil evidence to plot former distributions of conifers on a global basis. This type of information would never be known from the study of living taxa.

Despite these manifest benefits of the fossil record, numerous characters are not readily observable from fossils. Many paleobotanists will be dependent upon the more enriched data sets available only from living plants.

NEW RESEARCH

This study has attempted to demonstrate the potential of cladistic analysis in phylogenetic reconstruction; Hennig's work (e.g., 1950, 1966) is now taking root in systematic botany. While much of the current direction in cladistics is methodological, the basis of phylogenetic hypotheses and evolutionary scenarios is careful research on the organisms—their characters and character states. This analysis was possible only because of the careful work of the classical morphologists—biologists who were greatly motivated by discovering patterns of evolution (e.g., Thomson, 1905, 1940; Coulter, 1909; Coulter & Chamberlain, 1917; Buchholz, 1918, 1920, 1933, 1939, 1941; Chamberlain, 1935). Since the purpose of this study was to bring together and critically analyze current information, future research utilizing new techniques is needed to confirm (or modify) some of the preliminary conclusions presented above.

This future work must develop in two directions. First, new and more complete information is needed. Anatomical analyses have already proven useful in elucidating phylogenetic relationships, and character analyses using new techniques should be given priority. Especially needed are more studies of reproductive biology—such as microgametophyte and megagametophyte development, embryology, and palynology—which have already contributed many characters useful in understanding the phylogeny of conifers (Thomson, 1905; Buchholz, 1941; Lurzer, 1956; J. Doyle, 1957; Ueno, 1960; Chowdhury, 1962; Dogra, 1966, 1978; Pettitt, 1966, 1977; Singh, 1978; Haines & Prakash, 1980). In particular, studies are needed of the poorly understood tropical and south-temperate genera in the Podocarpaceae, Cupressaceae, and Araucariaceae, but many northern taxa, especially those in groups that are not economically important, also need investigation. A fresh look at characters studied decades ago, such as the megaspore membrane (Thomson, 1905), is necessary. New anatomical techniques such as ultrathin sectioning and scanning and transmission electron microscopy can contribute much to character discovery and analysis and ultimately to phylogenetic reconstruction. We can also look for important results from biochemical and molecular research (Praeger *et al.*, 1976; Praeger & Wilson, 1978; Cronin & Sarich, 1980; Sibley & Ahlquist, 1984), but the use of this approach is not without criticism with respect to inherent assumptions

of the constancy of molecular evolution ("molecular clock") and to whether these kinds of data are amenable to tree construction (Farris *et al.*, 1982; Farris, 1985).

Second, once the information is collected, character states must be analyzed very carefully before they are incorporated into cladistic analyses. There is substantial character variation in any group of organisms that is not suitable for cladistic analysis due to continuous variation or incomplete surveys. As mentioned above, careful attention must be given to the recognition of character states. Polarization of character states may be impossible due to their unknown status in outgroups. After construction of a cladogram, a second stage of character evaluation may be necessary in the weighting of functionally correlated characters.

Assumptions of computer programs also need to be addressed. The underlying assumption of Swofford's PAUP program used in this analysis is unrestricted parsimony. Characters may be lost, regained, and perhaps lost again. Unlimited reversals, especially of complicated characters, may be unlikely in evolution. We might look to the next generation of computer programs to address this problem.

Third, new paleobotanical information is needed. Much of the past digging has been conducted near major research institutions in northern regions. It is not surprising that most fossil conifers—such as *Lebachia*—are northern in distribution. No doubt there are as-yet-undiscovered fossils in southern regions that will cast light on early conifer evolution. Eventually, fossil and modern taxa will be included in the same analysis.

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APPENDIX. Character states used in the phylogenetic analysis of coniferous taxa.*

BRANCHING AND GROWTH PATTERNS. 1, Higher-order branches spiral / opposite (Morley, 1948; Dallimore *et al.*, 1966). 2, Short shoots absent / present (Barnard, 1926; Doak, 1935; Morley, 1948; Stebbins, 1948; Dallimore *et al.*, 1966). 3, Branches not annually deciduous / annually deciduous (Morley, 1948; Stebbins, 1948; Eckenwalder, 1976).

ANATOMY. 4, Sieve-element plastids starch accumulating / protein accumulating (Behnke, 1974).

STEM ANATOMY. 5, Stem tip without / with tunica corpus (Johnson, 1951; Griffith, 1952; Jackman, 1960; Pillai, 1963; Sporne, 1965; Pillai & Pillai, 1974). 6, Phloem fibers present / absent (Esau, 1969).

WOOD ANATOMY. 7, Phloem-fiber sclereids absent / present (Lotova, 1975). 8, Phloem mucilage absent / present (Lotova, 1975). 9, Xylem parenchyma absent / present (Bailey, 1909; Phillips, 1941; Greguss, 1955; Sporne, 1965; Tegner, 1965, 1967; H. J. Miller, 1973; Chu & Sun, 1981). 10, End or transverse walls of wood parenchyma (as seen in tangential section) smooth / nodular or pitted (Peirce, 1936, 1937; Phillips, 1941; Boultje, 1955). 11, Horizontal walls of wood parenchyma (as seen in radial section) smooth / nodular or pitted (Greguss, 1955). 12, Bordered pits of tracheids alternate, multiseriate, hexagonal in outline / uniseriate (Phillips, 1941; Florin, 1951; Greguss, 1955; Sporne, 1965; Stewart, 1983). 13, Spiral thickenings on longitudinal tracheid walls (early wood) absent / present (Compton, 1922; Phillips, 1941; Greguss, 1955, 1972; Stewart, 1983). 14, Spiral thickenings on transverse tracheid walls absent / present (Greguss, 1972; Hu & Wang, 1984). 15, Bordered pits with / without torus (Bauch *et al.*, 1972). 16, Crassulae

*The descriptor to the left of the slash (/) indicates the primitive condition, the one to the right the derived condition. For multistate characters a slash (/) is used for ordered characters, a vertical line (|) for unordered ones.

(bars of Sanio) present / absent (Jeffrey, 1905; Gerry, 1916; Hale, 1923; Chamberlain, 1935; Phillips, 1941). 17, Resin ducts in secondary wood absent / present (Jeffrey, 1905; Chamberlain, 1935; Jain, 1975; Taylor, 1981; Hu & Wang, 1984). 18, Traumatic resin ducts absent / present (Bailey, 1909; Phillips, 1941). 19, Resin ducts in rays present / absent (Patton, 1927; Phillips, 1941; Hu & Wang, 1984). 20, Horizontal walls of wood rays smooth / thickened, nodular or with simple pits (Bannan, 1934; Phillips, 1941; Boutelje, 1955; Greguss, 1955). 21, Tangential walls of wood rays smooth / thickened, nodular (Greguss, 1955). 22, Indentations on horizontal walls of ray parenchyma absent / present (Phillips, 1941; Kaeiser, 1954; Greguss, 1955). 23, Ray tracheids absent / present (Holden, 1913; Phillips, 1941). 24, Ray tracheids smooth walled / dentate (Phillips, 1941). 25, Cross-field pits cupressoid or taxoid (round) / piciform (narrow slits) (Phillips, 1941). 26, Tracheids not resinous / resinous (Patton, 1927; Pool, 1929).

LEAVES. 27, Leaves large / small. 28, Leaves falcate in profile and tetragonal in cross section / (1) linear or lanceolate and bifacially flattened | (2) scalelike | (3) bilaterally flattened | (4) needlelike | (5) double (fused?) (De Laubenfels, 1953). 29, Leaves single, spread out on branch / (1) in fascicles, spirally arranged on short shoots | (2) helically arranged on short shoots (Thomson, 1914). 30, Leaf phyllotaxy spiral / (1) spiral opposite (bijugate) | (2) decussate | (3) ternate (3-whorled) (De Laubenfels, 1953). 31, Seedling phyllotaxy whorled / opposite (De Laubenfels, 1953, 1965). 32, Leaf attachment decurrent / (1) with stalklike constrictions | (2) with shield-shaped attachment (De Laubenfels, 1953; Liu, 1971). 33, Mature foliage leaves monomorphic / dimorphic (facial and lateral leaves) (De Laubenfels, 1953). 34, Lateral margins of lateral leaves (in flattened branches with dimorphic leaves) free / fused. 35, Leaf bases distinctly decurrent / fused (De Laubenfels, 1953). 36, Leaves persistent / annually deciduous (Dallimore *et al.*, 1966). 37, Apical meristems without modified leaves / (1) shorter leaves interrupting growth / (2) scale leaves / (3) winter buds, tips free / (4) winter buds, scales overlapping (Florin, 1951; De Laubenfels, 1953). 38, Leaves amphistomatic / (1) hypostomatic | (2) epistomatic (Florin, 1951; Florin & Boutelje, 1954). 39, Leaves with endodermis (vascular sheath) not having / having thickened Casparian strips (Yao & Hu, 1982). 40, Mesophyll parenchyma smooth / plicate (Kausik & Bhattacharya, 1977; Yao & Hu, 1982; Han, 1984). 41, Tracheids of leaf transfusion tissue lateral to the vascular bundle / all around vascular bundle (mostly on abaxial side) (Griffith, 1971; Kausik, 1976; Kausik & Bhattacharya, 1977; Hu & Yao, 1981). 42, Vascular bundles of leaf 1 / (1) 2 / (2) more than 2 (Chamberlain, 1935; Kausik & Bhattacharya, 1977; Stewart, 1983).

CHEMISTRY. 43, Biflavonoids present / absent (Hegnauer, 1962; Harborne, 1967). 44, Nootkatin absent / present (H. Erdtman, 1963; H. Erdtman & Norin, 1966). 45, Hinokininflavone absent / present (H. Erdtman, 1963; Harborne, 1967). 46, Tropolones absent / present (H. Erdtman, 1963; H. Erdtman & Norin, 1966). 47, Leaf wax estolid / nonestolid (Hegnauer, 1962).

SEX DISTRIBUTION. 48, Plants monoecious / dioecious (Chamberlain, 1935; Florin, 1948b; Li, 1952; Greguss, 1955; Singh, 1961; Dallimore *et al.*, 1966; Ntima, 1968; Givnish, 1980).

MICROSPORANGIATE STROBILUS. 49, Microsporangiate strobili compound / simple (Stewart, 1983). 50, Microsporangiate strobili terminal / axillary. 51, Microsporangiate strobili single at ends of leafy shoots / (1) grouped in clusters | (2) grouped in racemes or panicles. 52, Microsporophylls spiral / decussate (whorled). 53, Microsporophylls open (laminar), hypostorangiate / peltate, perisporangiate (Thomson, 1905; Dupler, 1919; Chamberlain, 1935; Ueno, 1960; Wilde, 1975). 54, Microsporangia 2 / more than 2 (Saxton, 1934; Chamberlain, 1935; Florin, 1951; Ueno, 1960). 55, Microsporangial dehiscence longitudinal / (1) oblique / (2) transverse (Liu, 1971).

MICROGAMETOPHYTE. 56, Prepollen / pollen (Mapes & Rothwell, 1984). 57, Pollen-tetrad formation simultaneous (tetrahedral) / successive (bilateral) (Ueno, 1960). 58, Pollen

with shallow functional germination furrow / (1) with harmomegathus | (2) with functionless germ furrow | (3) with pore (Wodehouse, 1935; Ueno, 1960; G. Erdtman, 1965). 59, Pollen without / with papilla germination (Elliot, 1950; Takeuchi, 1953; Ueno, 1960; Ho & Sziklai, 1973). 60, Pollen grains with comfit perine absent / present (Ueno, 1960). 61, Pollen sexine tegillate / (1) rough corrugate | (2) granular | (3) roughened (Wodehouse, 1935; Ueno, 1960). 62, Pollen-sexine ultrastructure simple or absent / (1) compound / (2) double / (3) roughened (Wodehouse, 1935; Ueno, 1960; Reyre, 1968). 63, Pollen without / with annular thickenings (Ueno, 1960). 64, Pollen without / with triradial streaks (Ueno, 1960). 65, Pollen winged (monosaccate: bilateral or bisaccate) / (1) wingless | (2) with 3 or more wings (Wodehouse, 1935; Cranwell, 1940; Buchholz & Gray, 1948; Florin, 1951; Ueno, 1960; Bharadwaj, 1963; Sporne, 1965; Millay & Taylor, 1974; Singh, 1978). 66, Pollen intine thin / thick (Ueno, 1960; Singh, 1961; Liu & Su, 1983). 67, Pollen multi- or binucleate / uninucleate at pollination (Singh & Chatterjee, 1963; Vasil & Sahni, 1964). 68, Pollen grains containing 1 or 2 / (1) 0 | (2) many prothallial cells (Chamberlain, 1935; Wodehouse, 1935; Elliot, 1950; Ueno, 1960; Sterling, 1963; Konar & Oberoi, 1969; Millay & Eggert, 1974; Singh, 1978). 69, Sperm nuclei with / without cell walls (Chamberlain, 1935; Singh, 1978). 70, Sperm cells unequal / equal (Burlingame, 1915; Ueno, 1960; Sterling, 1963; Owens & Molder, 1975; Wang, Chen, & Hu, 1979).

MEGAGAMETOPHYTE AND EMBRYO. 71, Pollination drop present / absent (J. Doyle, 1945; Dogra, 1964; Singh, 1978). 72, Pollen germination on nucellus / on scales (Dogra, 1964; Singh, 1978). 73, Micropyle symmetrical / asymmetric (J. Doyle & O'Leary, 1935a, 1935b; J. Doyle & Kane, 1943; Looby & Doyle, 1944; J. Doyle, 1945; Dogra, 1964; Singh, 1978). 74, Ventral-canal cell with distinct cell wall / with no wall, but having nuclei (Lawson, 1907; Chamberlain, 1935; Owens & Molder, 1975). 75, Alveoli open on area adjacent to central vacuole / closed by cell walls (Lawson, 1923). 76, Megagametophyte without / with layer of peripheral cells (Saxton, 1913; Maheshwari & Singh, 1967; Singh, 1978). 77, Megaspore membrane thick, double / thin (Thomson, 1905; Lawson, 1907; Quinn, 1966; Owens & Molder, 1975; Stidd & Cosentino, 1976; Singh, 1978). 78, Megaspore membrane of uniform thickness / thin at micropylar end (Thomson, 1905). 79, Megaspore membrane suberized / not suberized (Thomson, 1905). 80, Tapetum primary / secondary (Thomson, 1905; Saxton, 1913; Singh, 1978). 81, Archegonia not surrounded / surrounded by densely cytoplasmic tissue (Singh, 1978). 82, Archegonia separate / grouped together to form complexes (Lawson, 1907; Chamberlain, 1935; Maheshwari & Singh, 1967; Owens & Molder, 1975, 1980; Singh, 1978; Wang, Lee, & Chen, 1980). 83, Archegonia separated by vegetative cells / arranged in ring (Eames, 1913; Eckenwalder, 1976). 84, Archegonia apical (at micropylar end) / (1) lateral (at middle of gametophyte) | (2) lateral (at chalazal end of gametophyte) (Saxton, 1913; Moseley, 1943; Florin, 1951; Maheshwari & Singh, 1967; Konar & Oberoi, 1969; Foster & Gifford, 1974; Singh, 1978). 85, Archegonial jacket present / absent (Singh, 1978). 86, Proembryo with free nuclear divisions many / (1) 5 or 4 / (2) 3 / (3) 2 / (4) 0 (Eames, 1913; J. Doyle & Saxton, 1933; J. Doyle, 1954; Chowdhury, 1962; Sporne, 1965; Chen & Wang, 1984). 87, Proembryo with secondary / primary type of wall formation (Dogra, 1966). 88, Proembryo nontiered / (1) with upper, suspensor, and embryonal tiers / (2) nontiered (reduced) (Moseley, 1943; Chowdhury, 1962; Foster & Gifford, 1974; Dogra, 1978; Haines & Prakash, 1980). 89, Proembryo 3- / 4-tiered (Dogra, 1978; Singh, 1978). 90, Proembryo with embryonal cells uninucleate / binucleate (Saxton, 1913; J. Doyle & Looby, 1939; Buchholz, 1941; Elliot, 1950; Brownlie, 1953; J. Doyle, 1954; Chowdhury, 1962; Quinn, 1964, 1966, 1970). 91, Proembryo basal / central (Haines & Prakash, 1980). 92, Proembryo with irregular shape / with spherical shape of free nuclear embryo and curved planes of upper, suspensor, and embryonal tiers of cellular phase (Haines & Prakash, 1980). 93, Proembryo with development of primary suspensor from suspensor / from upper tier (Dogra, 1978). 94, Suspensor anchorage of proembryo not within / within archegonium (Haines & Prakash, 1980). 95, Prosuspensor present / absent (Baird, 1937, 1953; Johansen, 1950). 96, Proembryo not completely filling / completely filling arche-

gonium (Moseley, 1943). 97, Polyembryony simple / cleavage (J. Doyle, 1957; J. Doyle & Brennan, 1971, 1972; Singh, 1978).

OVULATE STROBILUS. 98, Cone terminal on leafy branches / axillary on short, leafy shoots (Saxton, 1913; Moseley, 1943; Florin, 1951; Dallimore *et al.*, 1966; Quinn, 1970). 99, Ovulate strobilus compound / simple (Dupler, 1920; Li, 1952; Sporne, 1965). 100, Ovulate strobilus short shoots radially symmetrical / (1) bilaterally flattened / (2) "scales" (Taylor, 1981; Mapes & Rothwell, 1984; Meyen, 1984). 101, Bract-scale complex free / fused (Sporne, 1965). 102, Cone bract not keeled / keeled (C. N. Miller, 1985). 103, Cone scales flat / peltate (Chamberlain, 1935; Li, 1953a; Sporne, 1965; Foster & Gifford, 1974). 104, Cone scales imbricate, thin / valvate, thickened (Li, 1953a). 105, Cone scales woody / modified into an epimatium (Sinnott, 1913). 106, Epimatium fully covering seeds / (1) half covering seeds / (2) lacking (Sinnott, 1913; Herzfeld, 1914; Aase, 1915; Chamberlain, 1935; Florin, 1951, 1958). 107, Epimatium not fused / fused to seed coat (Quinn, 1982). 108, Bracts not fleshy / fleshy (De Laubenfels, 1969; Quinn, 1982). 109, Bracts free / fused (De Laubenfels, 1969; Quinn, 1982). 110, Receptacle not warty / warty (De Laubenfels, 1969). 111, Cone scales persistent / deciduous (Chamberlain, 1935; Liu, 1971). 112, Cones pendulous / upright at maturity (Liu, 1971). 113, Uniaxial seeds arranged singly on primary shoots of unlimited / limited growth (Florin, 1948a, 1948b, 1954).

OVULES AND SEEDS. 114, Ovules inverted / (1) semi-erect / (2) erect (Stebbins, 1948; Stewart, 1983; Clement-Westerhof, 1984; Mapes & Rothwell, 1984; Miller, 1985). 115, Number of ovules per cone scale: 1 / 2 or more (Clement-Westerhof, 1984). 116, Seed storage product: starch / oils (Hegnauer, 1962). 117, Seed without / with aril (Florin, 1951, 1958; Sporne, 1965; Foster & Gifford, 1974; Quinn, 1982). 118, Aril not developed by intercalary growth, not fused to seed / partly developed by intercalary growth, fused to seed coat (Florin, 1948a, 1948b). 119, Seeds winged / not winged (Taylor & Stewart, 1964; De Laubenfels, 1965; Dallimore *et al.*, 1966; Singh, 1978; Rothwell, 1982). 120, Resin ducts in seed coat absent / present (Price, pers. comm.). 121, Number of cotyledons: 2 / more than 2 (Hill & De Fraigne, 1906, 1908, 1909a, 1909b; Buchholz, 1920; Butts & Buchholz, 1940; De Laubenfels, 1962). 122, Seeds maturing in 2 / 1 year(s) (Singh, 1978).

CYTOLOGY. 123, Chromosome number: 12 / (1) 10 | (2) 11 (Sax & Sax, 1933; Flory, 1936; Mehra & Khoshoo, 1956).



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