THE BOTANICAL REVIEW

Implications of Fossil Conifers for the Phylogenetic Relationships of Living Families

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I. Abstract

Fossils have played a central role in our understanding of the evolution of conifers. Interpretation of the seed cone as a compound strobilus and the homologies of the ovuliferous scales of modern conifers with the axillary dwarf shoot of Pennsylvanian forms are based on fossils. Similarly, early evolutionary trends involving the reduction, fusion, and planation of the fertile and sterile elements of the axillary dwarf shoot, leading to structures characteristic of modern families, are documented in Late Permian and Triassic conifers. However, a phylogeny elucidating the derivation of modern families from fossil forms based on shared derived features has been elusive.

The present cladistic treatment using 11 characters of ovulate cones and one of pollen grains suggests three phylogenetic groups of Late Paleozoic conifers, represented loosely by the Emporicaceae, Utrechtiaceae, and Majonicaceae of Mapes and Rothwell. The Taxaceae appears to have diverged from ancestors within the Utrechtiaceae, whereas the other modern families owe their origins to the Majonicaceae. The origin of the Taxodiaceae appears to have been biphyletic. *Taxodium*, *Cupressus* and *Sciadopitys* are strongly linked to *Dolmitia* of the Majonicaceae, but *Cryptomeria*, *Cunninghamia* and *Araucaria* are grouped together and diverge basal to the former taxa. *Pinus* branches from a position basal to the known genera of the Majonicaceae and all modern families except the Taxaceae. *Podocarpus* also diverges basal to *Majonica* but may share an ancestor with this genus; *Cepahalotaxus* diverges basal to the *Dolmitia-Pseudovoltzia* subclade but distal to *Majonica*. Similarly, the Cheirolepidiaceae originated from basal members of the Majonicaceae and shows no close phylogenetic relationship with any modern family. Except for a strong linkage between *Cycadocarpidium* and the *Araucaria-Cunninghamia* subclade, genera of the Voltziaceae appear to have branched more or less independently from within the Majonicaceae and show no strong affinity with modern conifers. Thus differences between modern conifer families are due mainly to their divergence from different Paleozoic ancestors.

II. Introduction

Most paleobotanists think that conifers either evolved from cordaites or share an ancestor with them (Clement-Westerhof, 1988). Within the conifer lineage, ancient forms exhibit vege-

tative structure fully comparable with living groups but have ovules borne in compound strobili homologous with those produced by cordaites. The variety of ovulate reproductive structures found in modern conifers arose through reduction in size and number of fertile and sterile appendages and through their fusion with one another and/or with the subtending bract or other similar modification. This is the generalization documented by the work of Rudolf Florin (1938–1945, 1951), and it is still valid today as a general explanation (Miller, 1982, 1988).

Just a decade ago our classification of fossil conifers, which also followed from Florin's work, lent itself quite well to the generalization. Conifers with strobiloid reproductive structures were treated in the Lebachiaceae, and transitional forms were classified in the Voltziaceae (Miller, 1977). Additional study of Florin's material and the description of new species of ancient and transitional forms (Clement-Westerhof, 1988; Mapes & Rothwell, 1984) has given good reason to reconsider that classification.

There has also been considerable work on the phylogenetic relationships of modern conifers. Hart's (1987) cladistic analysis used a broad array of morphological, anatomical, and chemical characters; other studies were based on differences in immunological responses (Price & Lowenstein, 1989) and on differences in DNA sequences in the chloroplast *rbc*L gene (Brunsfeld et al., 1994; Price et al., 1993). Affinities of modern taxa relative to one another are inferred from these studies, and important strides have been made in assessing the interrelationships of the Cupressaceae, Sciadopityaceae, and Taxodiaceae. However, there is only vague agreement on the relationships of the remaining families.

Phylogenetic studies that examine the relationships of both fossil and living conifers are more rare. Those of Miller (1982, 1988) were based on ovulate cone structure and were restricted in the number of characters used in the analyses. Nonetheless, it is clear that certain modern families, such as the Cupressaceae and the Taxodiaceae, show a closer phylogenetic relationship to fossil forms than to other living conifers (Miller, 1988: Fig. 10.1). New information, especially about Late Pennsylvanian and Early Permian conifers, permits a more detailed examination of the relationships of living conifers with fossil forms. The goal of this study is to reexamine the phylogenetic relationships between fossil and living conifers.

A. CONIFERS AND CONIFEROPHYTES

It is difficult to envisage a single feature that defines conifers. Living conifers tend to have needle- or scale-like leaves containing a single vascular strand, but we find similar leaves in microphyllous plants. The compound ovulate strobilus typical of conifers also occurs in the Gnetophyta. The bisaccate pollen of many conifers occurs as well in both Paleozoic and Mesozoic seed ferns, and the pycnoxylic wood typical of the group is also found in ginkgos and many fossil groups beginning with the progymnosperms.

Being able to distinguish conifers is important because two major groups of fossil plants are known that have coniferous vegetative structure but not compound ovulate strobili. They are coniferophytes, but we lack proof that they are actually conifers. These are the Buriadiaceae and Ferugliocladaceae.

The Buriadiaceae is a group of unusual plants from the Permian (Fig. 1) of the Southern Hemisphere. The leaves are needle-like, with bifurcate tips in some. In *Buriadia,* inverted ovules are randomly inserted between leaves (Pant, 1982; Pant & Nautiyal, 1967). In *Genoites* Feruglio (Cuneo, 1985), from the Permian of Argentina, leaves may or may not be bifurcate at the apex. Solitary ovules are borne axillary to a leaf, and these units are loosely clustered on the fertile branch. In *Walkomiella* (Feistmantel) Florin, from the Late Permian of Australia, ovules are associated with leaves in a strobiloid organ (White, 1981), but the strobi-
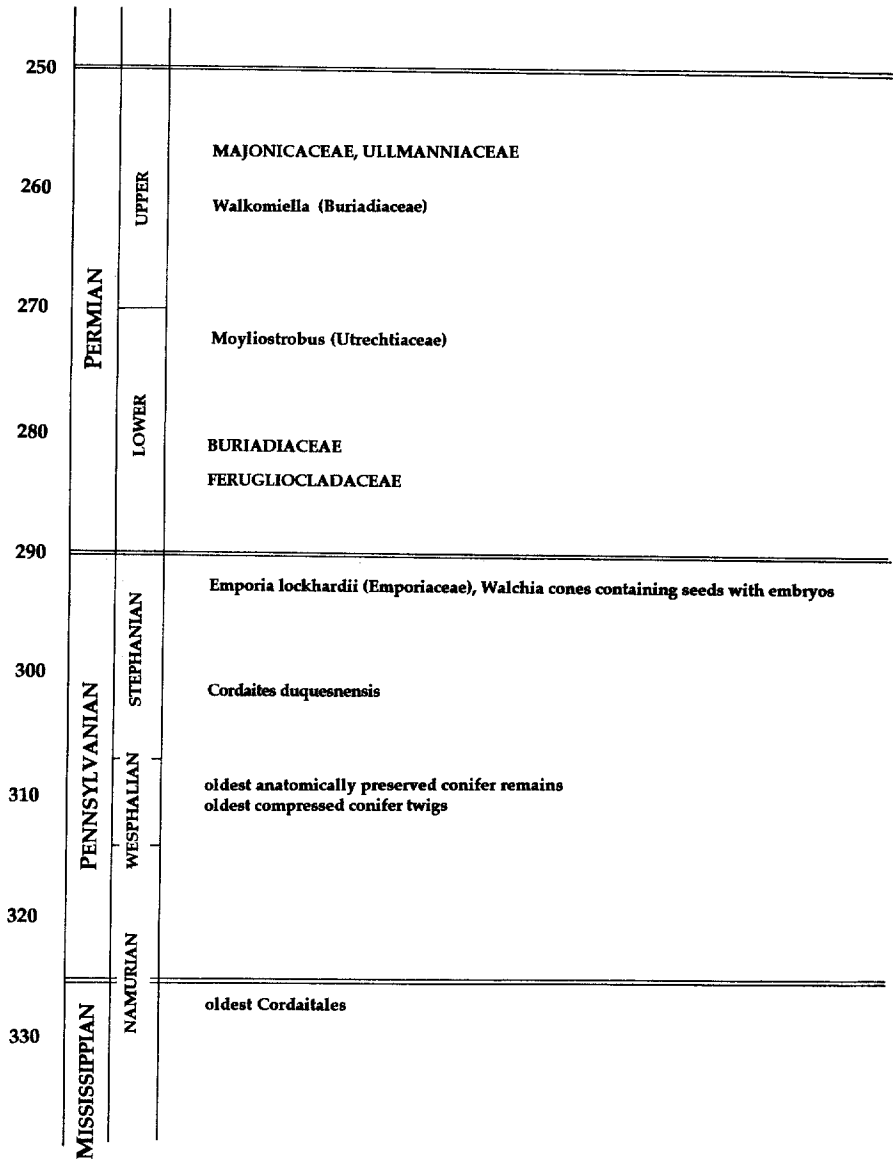
Fig. 1. Stratigraphic occurrence of early conifers and coniferophytes.

lus appears to be a simple rather than a compound. There is no evidence of ovuliferous scales subtended by bracts.

The Ferugliocladaceae (Archangelsky & Cuneo, 1987) includes plants from the Early Permian of Argentina (Fig. 1) in which needle-bearing twigs terminate in strobili consisting of

bracts, each with an axillary ovule. Ovules are erect and winged. Again, evidence of a compound ovulate strobilus is lacking.

These families are interesting, but it is not possible to include them in the present treatment because their ovule-bearing structures do not appear to be homologous with those of true conifers. There is no basis, then, for the evaluating the character states used in the present analyses.

B. HISTORICAL PERSPECTIVE

Prior to the onset of Florin's (1938–1945, 1951) investigations of cordaites and conifers, there were nearly a dozen different theories about the origin and homologies of the ovulate reproductive structures in conifers (Aase, 1915; Florin, 1954). Older ideas had conifers linked to groups as different as the lycopods and the cordaites. During the 1930s, 1940s, and 1950s Florin studied *Cordaianthus* and seed cones of numerous Paleozoic and Mesozoic conifers. He documented the nature of the bract and axillary fertile strobilus of the latter and illustrated variations in forms. He concluded that "The female cones of living conifers are directly connected with those of Mesozoic and Paleozoic types" (Florin, 1951: 375). His documentation was so thorough and convincing that the various other theories have been laid to rest (Florin, 1954).

Since Florin's time, there have been significant additions to our knowledge of ancient conifers. New forms have been discovered and described. Species known to Florin have been reinvestigated, sometimes based on new material, leading to refinements in our knowledge of these conifers. What is more, progymnosperms were discovered and defined and have become a leading candidate as coniferophyte ancestors.

Current views of the relationships were recently summarized by Clement-Westerhof (1988): The Florin view holds that ancient conifers of the Late Pennsylvanian and Early Permian assigned to the Lebachiaceae (*Lebachia, Ernesiodendron*, and *Walchia*) evolved from the Cordaitales and were transitional between them and Late Permian and Triassic conifers. Conifers with an evident ovuliferous scale could be derived from the *Lebachia* type and the Cephalotaxaceae from the *Ernestiodendron* type.

Some follow this idea fairly strictly but view the Lebachiaceae as closely related to the Cordaitales though not derived from it. Others disagree with Florin about the close phylogenetic relationship between the Lebachiacee and the Cordaitales. Beck (1981) thinks that both evolved from a common *Archaeopteris*-like ancestor. Pant and Nautiyal (1967) suggest Buriadiaceae-like ancestors for the Lebachiaceae. Some agree with Florin regarding the presumed ancestry of the Lebachiacae for younger conifers. Schweitzer (1963) derived the latter conifers from *Pseudovoltzia* and the Lebachiaceae from the Lycopsida.

C. NOMENCLATURE

The present work follows the classification of Mapes and Rothwell (1991) because it brings the nomenclature in line with the International Code (Table I). They, as well as Clement-Westerhof (1984), recognize that *Lebachia* is illegitimate. Mapes and Rothwell (1991) define a new genus *Emporia* and family Emporiaceae based on their *Lebachia lockhardii*. They further establish a new genus *Utrechtia* and family Utrechtiaceae based on *Lebachia piniformis*. Included in the latter family are *Utrechtia, Ortiseia, Moyliostrobus, Ernestiodendron*, and *Otovicia. Walchia* and *Walchiostrobus* are maintained as form genera and are thus not assigned to a family.

Kerp and Clement-Westerhof (1991) and Mapes and Rothwell (1991) agree on the makeup of the families Majonicaceae with *Majonica, Dolmitia*, and *Pseudovoltzia* and Ull-

Table I

Classification of ancient conifers treated in this report

Utrechtiaceae:	*Utrechtia* Mapes & Rothwell
	Ortiseia Florin
	Moyliostrobus Miller & Brown
	Ernestiodendron Florin
	Otovicia Kerp et al.
Emporiaceae:	*Emporia* Mapes & Rothwell
Majonicaceae:	*Majonica* Clement-Westerhof
	Dolmitia Clement-Westerhof
	Pseudovoltzia Florin
Ullmanniaceae:	*Ullmannia* Goeppert
Cheirolepidicaeae:	*Hirmeriella* Horhammer
Voltziaceae:	*Voltzia* Brongniart
	Aethophyllum Grauvogel-Stamm
	Cycadocarpidium Nathorst
	Glyptolepis Schimper
	Pararaucaria Wieland
	Schizolepis Braun
	Swedenborgia Nathorst
	Tricranolepis Roselt
Form Genus:	*Walchiostrobus* Florin

manniaceae with *Ullmannia*. Although Schweitzer (1996) recently proposed treating *Pseudovoltzia* as a synonym for *Voltzia*, the older classifications are followed here. His (1996) new species *V. hexagona*, the description of which became available too late to be included in the cladistic analyses, has a bract that is nearly twice as long as the axillary dwarf shoot, and the fertile and sterile elements are essentially free of one another and disposed around an axillary shoot axis rather than in a plane. Including this new species and *Pseudovoltzia liebeana* enlarges the circumscription of *Voltzia* to familial levels and should probably include *Telemachus* (Yao, Taylor & Taylor, 1993), and perhaps other genera as well. An alternative approach is to treat *Voltzia hexagona* in a separate genus that would probably be assignable to the Majonicaceae, along with *Pseudovoltzia, Dolmitia,* and *Majonica.*

D. OCCURRENCE OF CONIFERS IN GEOLOGICAL TIME

The earliest remains attributed to conifers occur in Westphalian B strata of England, which are about 310 million years old (Scott, 1974; Scott & Chaloner, 1983; Fig. 1). These fossils are fusinized leafy twigs that resemble those attributed to *Walchia* in younger strata. The material also includes information about stomatal structure that further supports the identification of these fossils as conifers. Anatomically preserved remains of conifer stems are known from Westphalian C strata of England, which are about 308 million years old (Galtier et al., 1992). They show well-preserved pith and primary and secondary xylem that clearly distinguish them from cordaitalean remains and leave little doubt that they represent conifers. The Late Pennsylvanian flora of Hamilton, Kansas, includes *Emporia* (Mapes & Rothwell, 1984) and at least three species of *Walchia* (Mapes & Rothwell, 1988). A seed cone containing seeds with embryos occurs in that assemblage, indicating that seed dormancy had evolved in conifers by that time (Mapes et al., 1989). Thus conifers were diverse and floristically important by the end of the Pennsylvanian.

Conifers exhibit increased diversification during the Permian. Several additional genera appear, and their ovulate reproductive structures show reduction and fusion of parts beyond that of the Late Pennsylvanian forms (Clement-Westerhof, 1988).

Modern families make their first appearance in the Triassic and all are in evidence by the Early Cretaceous (Miller, 1982). Mesozoic sediments also contain remains of numerous extinct conifers assigned to the Cheirolepidiaceae and Voltziaceae (Taylor & Taylor, 1993). A decade ago workers believed that living conifers evolved from these Mesozoic forms, especially the Voltziaceae. This follows from the order of appearance of the various taxa and their apparent intermediate cone construction between the Paleozoic Lebachiaceae and living families. As Thomas and Spicer (1987) point out, this view may be too simplistic in light of new discoveries, particularly the Majonicaceae (Clement-Westerhof, 1988; Kerp & Clement-Westerhof, 1991). An alternative view is that modern families may have evolved directly from Paleozoic ancestors. The present study examines this question through a series of cladistic analyses based mainly on ovulate cones.

III. Methodology

This study examines the cladistic relationships of 33 taxa of fossil and modern conifers. The analyses are based on 11 characters of the ovulate cone and one of pollen grains, using parsimony (Table II). These characters reflect broad trends in conifer cone evolution as summarized by Florin (1951). They are similar to those I have used earlier (Miller, 1988), but character states have been restructured to reflect current knowledge of the taxa, particularly of the more ancient forms (Clement-Westerhof, 1987, 1988; Kerp & Clement-Westerhof, 1991; Kerp et al., 1990; Mapes & Rothwell, 1991)

Analyses were conducted using PAUP version 3.1.1 (Swofford, 1993) on a Macintosh IIcx computer. Analyses are compartmentalized, so that the number of OTUs is equal to or less than the number of characters. To minimize polymorphic characters wherever possible, character-state evaluation is based on the generitype or a representative species rather than generalizing for a taxon or the concept of the taxon. This is especially true of fossil taxa. Accordingly, only 5 of the 408 cells in the data matrix (Table III) are polymorphic.

Although using only 12 characters has serious limitations on the number of taxa that can be included in any one analysis, it provides a reasonably informative database, in that the number of unknown states is kept to a minimum. Thirty-three of the 408 cells, or about 8%, are unknowns.

Searches for the shortest tree were first conducted using the random stepwise addition option and later with the branch and bound option once an idea of tree lengths was obtained. Finally, analyses involving 10 or fewer OTUs were examined using the exhaustive search option.

The genera were selected to represent the basal conifers, modern families, and a variety of possible intermediates among Mesozoic conifers. More of the latter could be included in a more comprehensive study. However, certain of those omitted are similar to those included, especially because the characters and states represent broad trends in cone modification. For example, except for somewhat greater fusion of elements of the ovuliferous scale, the variation in *Telemachus* Anderson (Yao, Taylor & Taylor, 1993) and *Florinostrobus* (Delevoryas & Hope, 1987) is represented by that in *Swedenborgia*, *Tricranolepis* and *Voltzia* for purposes of the cladistic analyses. *Glyptolepis* was omitted following publication of the study by Axsmith and Taylor (1997), which describes *G. richteri* and questions the accuracy of earlier descriptions. A clear understanding of seed-cone construction for at least one species is needed before characters for the genus can be scored accurately. Similarly, scoring for *Voltzia*

Table II
Characters and states

A. Axillary complex: 0 = free from bract; 1 = partially fused with bract; 2 = fused with bract obscuring identity.

B. Dwarf shoot complex: 0 = radially symmetrical; 1 = somewhat flattened; 2 = flattened.

C. Dwarf shoot axis: 0 = obvious; 1 = evident but obscured; 2 = not evident.

D. Appendages of dwarf shoot axis: 0 = free from one another; 1 = fused <½ their length; 2 = fused >½ their length; 3 = fused except for tips; 4 = completely fused & identity lost.

E. Ovules: 0 = erect; 1 = recurved.

F. Bract length: 0 = more or less as long as the axillary dwarf shoot; 1 = twice as long or longer than the axillary dwarf shoot; 2 = short or shorter than the axillary dwarf shoot.

G. Fertile scales per axillary dwarf shoot: 0 = >6; 1 = 4–6; 2 = 1–3.

H. Sterile appendages per axillary dwarf shoot: 0 = >10; 1 = 6–10; 2 = <6.

I. Bract vasculature: 0 = single vascular strand; 1 = >1 vascular strand.

J. Bract apex: 0 = acute; 1 = bifurcate.

K. Pollen type: 0 = prepollen; 1 = monosaccate; 2 = bisaccate; 3 = asaccate.

L. Appendage shape: 0 = narrow and needle-like; 1 = broad and scale-like.

is based on Schweitzer's (1963) publication. The Palissyaceae was not included because recent work (Parris, Drinnan & Cantrill, 1995) found that ovules are attached to sporophylls rather than ovuliferous scales, indicating that these fructifications are not those of conifers. Even though Schweitzer and Kirchner (1996) retain this family in the Coniferophyta, there remains too much uncertainty about the structure of the fructifications to include the family in this study.

Initially, interrelationships between basal conifers—that is, the Emporiaceae, Utrechtiaceae, and Majonicaceae—were examined using a series of analyses. First, genera of Emporiaceae and Utrechtiaceae, including three species of the form genus *Walchiostrobus*, were analyzed with *Cordaianthus duquesnensis* Rothwell as the outgroup, using the exhaustive search option. To confirm the resulting topology, the same analysis was conducted without *Walchiostrobus*, using the exhaustive search option both with and without a designated outgroup. Finally, both analyses were repeated including the three genera of the Majonicaceae with *Emporia* as the outgroup.

The relationships of higher conifers to basal groups were examined by analyzing each of the 21 genera representing the Ullmanniaceae, Voltziaceae, Cheirolepidiaceae, and seven families of modern conifers individually with the genera of the Majonicaceae and Utrechtiaceae including *Walchiostrobus*, using *Emporia* as the outgroup. The branch and bound option was used to search for the shortest trees. All but two of the genera were clearly linked with the Majonicaceae subclade. However, the lack of resolution of the relationships of most of the genera in the above analyses within that subclade prompted further examination.

The object of the study was to determine the involvement of higher fossil conifers in the evolution of modern forms from basal taxa. All but two genera of higher conifers are linked somehow to the three genera of the Majonicaceae. Thus each genus of higher fossil conifers was analyzed with the Majonicaceae and two groups of modern conifers. Group 1 consisted of three genera of the Majonicaceae, *Cryptomeria, Cunninghamia, Cupressus, Sciadopitys,* and *Taxodium,* using *Ernestiodendron* as the outgroup. Group 2 consisted of the three genera of

Table III
Data matrix[a]

	A	B	C	D	E	F	G	H	I	J	K	L
Cordaianthus duquesnensis[1]	0	0	0	0	0	0	0	0	0	0	0	0
Emporia lockardii[2]	0	1	0	0,1	1	0	2	0	0	1	0	0
Utrechtia floriniformis[3]	0	1	0	0	1	0	2	0	0	1	0	1
Ortesia jonkeri[4]	0	1	1	0,1	1	0	2	0	0	0	0	1
Moyliostrobus texanum[5,6]	0	1	1	0	1	0	2	0	0	0	?	1
Ernestiodendron filiciforme[4,7,8]	0	1	0	0	1	0	2	1	0	0	0	1
Otovicia leonardii[4]	0	1	1	0	1	0	2	0	0	1	0	1
Walchiostrobus gothanii[8]	0	1	1	1	1	0	2	1	0	?	?	1
Walchiostrobus meyenii[7,8]	0	1	1	1	1	0	1	2	0	1	?	1
Walchiostrobus florinii[7,8]	0	0	1	0	1	0	1	0	0	?	?	1
Majonia alpina[9]	0	2	2	1	1	0	2	2	0	0	2	1
Dolmitia cittertiae[9]	1	2	2	2	1	0	2	0	?	?	?	1
Pseudovoltzia liebeana[9,10]	1	2	2	2	1	0	2	2	0	0	?	1
Ullmannia bronnii[7,10]	0	2	2	4	1	0	2	2	0	0	2	?
Hirmeriella muensteri[11,12]	0	2	2	2	?	0	2	1	0	0	3	1
Voltziopsis africana[13,14]	0	2	1	2	1	0	1	2	0	1	?	1
Voltzia sp.[10]	0	2	2	2	1	0	2	2	0	0	?	1
Aethophyllum stipulare[15]	1	2	2	2	1	0	1	2	0	0	2	1
Schizolepis liasokeuperianus[16]	0	2	2	3	1	2	2	2	0	0	?	1
Cycadocarpidium pilosum[15]	1	2	2	2	1	1	2	2	1	0	?	1
Swedenborgia cryptomerioides[16]	1	2	2	2	1	2	1	2	1	0	?	1
Tricranolepis frischmannii[17]	?	2	2	2	1	?	2	2	?	?	?	1
Pararaucaria patagonica[18]	0	2	2	4	1	0	2	2	0	0	?	?
Pinus	0	2	2	4	1	0	2	0	0	0	2	?
Araucaria	1,2	2	2	4	1	1	2	2	1	0	3	?
Cryptomeria	1	2	2	2	0	0	2	2	1	0	3	1
Cunninghamia	2	2	2	3	1	1	2	2	1	0	3	1
Taxodium	2	2	2	4	0	0	2	0	0	0	3	?
Sciadopitys	1	2	2	4	1	0	0,1	0	0	0	3	?
Cephalotaxus	0	2	2	4	0	0	2	2	0	0	3	?
Podocarpus	0	2	2	4	1	0	2	2	0	0	2	?
Taxus	0	0	0	4	0	0	2	0	0	0	3	?
Cupressus	2	2	2	4	0	0	0	0	0	0	3	?

[a] See Table II for character states. Superscripted numbers following taxa refer to sources of information: 1, Rothwell, 1982; 2, Mapes & Rothwell, 1984, 1991; 3, Mapes & Rothwell, 1991; 4, Clement-Westerhof, 1984; 5, Miller & Brown, 1973; 6, Mapes, 1987; 7, Clement-Westerhof, 1988; 8, Kerp & Clement-Westerhof, 1991; 9, Clement-Westerhof, 1987; 10, Schweitzer, 1963; 11, Watson, 1988; 12, Jung, 1968; 13, Miller, 1977; 14, Townrow, 1967b; 15, Grauvogel-Stamm, 1978; 16, Harris, 1979; 17, Harris, 1935; 18, Roselt, 1958; 19, Axsmith & Taylor, 1997.

the Majonicaceae, *Araucaria, Cephalotaxus, Pinus,* and *Podocarpus,* with an outgroup made up of *Ernestiodendron* and *Moyliostrobus.* The exhaustive search option was used for each of these analyses.

Finally, genera of the Voltziaceae that in other analyses associated with the *Dolmitia–Pseudovoltzia* subclade were examined together with the latter two genera, using *Majonica* as the outgroup.

IV. Results

A. THE BASAL CONIFERS: EMPORIACEAE, UTRECHTIACEAE, MAJONICACEAE

Four analyses were conducted to determine whether there is a cladistic basis for the Emporiaceae, Utrechtiaceae, and Majonicaceae.

The first analysis treated *Cordaianthus duquesnensis* Rothwell (1982) as the outgroup and examined the relationships between species of the Emporiaceae and the Utrechtiaceae (Fig. 2). For the sake of this study, three species of the form genus *Walchiostrobus* were included. The exhaustive search option was used to search for the shortest trees.

A single tree of 16 steps resulted and shows *Emporia lockhardii* on a basal side branch. The five genera of the Utrechtiaceae occur on a distinct clade, and the three species of *Walchiostrobus* assort within the Utrechtiaceae. A basal bifurcation of the Utrechtiaceae clade yields *Utrechtia* on one branch, with all other taxa on the other. The latter subclade has a basal trichotomy, with *Otovicia* on one branch, *Walchiostrobus meyenii* and *W. florinii* as sister taxa on another branch, and a remaining branch including *Ortesia, Moyliostrobus, Ernestiodendron,* and *Walchiostrobus gothanii*. The latter two are sister taxa, whereas the former two diverge with the latter from a basal trichotomy.

Deleting the three genera of *Walchiostrobus* and using the exhaustive search option yields 21 equally parsimonious trees of 11 steps. The strict consensus when no outgroup is designated shows all OTUs branching from an unresolved basal polytomy. All of the 21 trees exhibit an unresolved basal polytomy. Thirteen show a trichotomy with *Cordaianthus, Emporia,* and a subclade consisting of the five genera of the Utrechtiaceae. Six have a trichotomy, with *Ernestiodendron* substituting for *Emporia* and with the latter included in the subclade with the remaining Utrechtiaceae. The remaining three trees have a basal polytomy, with *Emporia* grouping with certain genera of the Utrechtiaceae. In none of the trees does *Cordaianthus* occur as a sister taxon with *Emporia* or any genus of the Utrechtiaceae.

A second series of analyses was conducted to examine the relationship between the Majonicaceae and the Emporiaceae and Utrectiaceae. Initially, *Cordaianthus duquesnensis* was used as the outgroup. However, *Emporia* was substituted to reduce the number of OTUs after it became clear that the relationship between the latter genus and the Utrechtiaceae was unaffected by the addition of *Majonica, Dolmitia,* and *Pseudovoltzia,* the three genera of the Majonicaceae.

This results in 4 trees of 19 steps using the branch and bound option. The strict consensus shows the three genera of the Majonicaceae on a distinct clade branching from within the Utrechtiaceae (Fig. 3). Three of the equally parsimonious trees show the Majonicaceae sharing a node with *Walchiostrobus meyenii;* the fourth has the family branching from a basal polytomy, as in the strict consensus.

To confirm the relationship indicated above, an exhaustive search of the five genera of the Utrechtiaceae, excluding *Walchiostrobus,* and the three genera of the Majonicaceae, using *Emporia* as the outgroup, was conducted. This resulted in 50 trees of 15 steps. The strict consensus also shows the three genera of the Majonicaceae sharing an unresolved trichotomy that branches from within the Utrechtiaceae (Fig. 4).

B. RELATIONSHIPS OF OTHER CONIFERS WITH THE BASAL GROUPS

1. Basic Patterns

The following analyses are directed at examining the relationship of 20 additional fossil and modern taxa with these basal forms. Initial work indicates that all of these branch from the Utrechtiaceae and Majonicaceae and not the Emporiaceae. Thus the latter is treated as the outgroup. OTUs were added individually to determine their point of divergence. Two main patterns were evident. *Voltziopsis* and *Taxus* branch from different positions within the Utrechtiaceae. The remaining 18 OTUs are associated to one degree or another with the Majonicaceae clade.

Analyzing *Voltziopsis* with the basal conifers results in 5 equally parsimonious trees of 21 steps. Four of the five link *Voltziopsis* as a sister taxon with *Walchiostrobus meyenii* within the
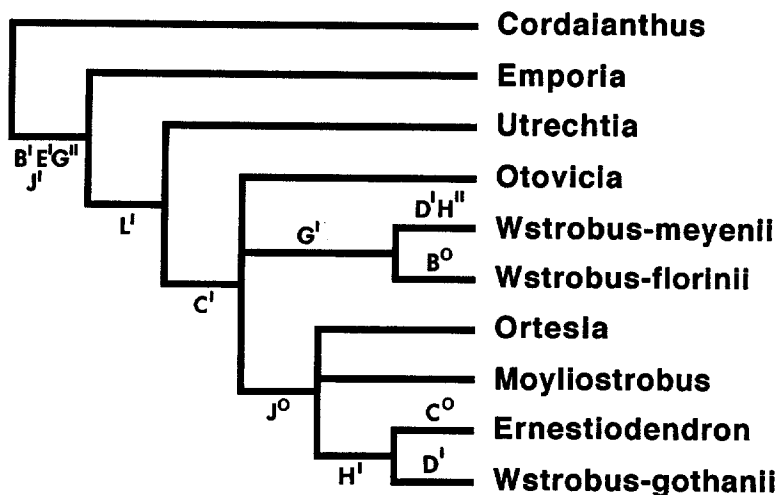
Fig. 2. Cladogram of the Emporiaceae and Utrechtiaceae including *Walchiostrobus,* using *Cordaianthus* as the outgroup, based on a branch and bound search, single shortest tree of 16 steps; CI = .750. X', X" = character X, state 1, 2, etc.; X° = character X, state 0, only indicated if attained via a reversal.
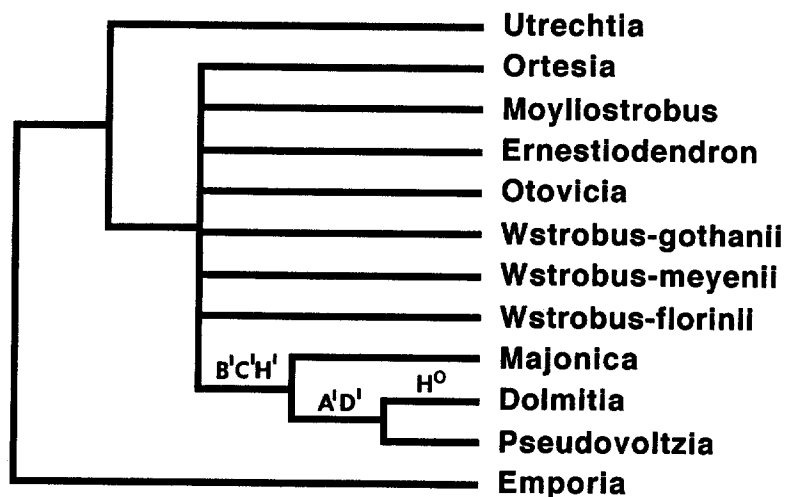
Fig. 3. Strict consensus cladogram of the Utrechtiaceae including *Walchiostrobus* and Majonicaceae, using *Emporia* as the outgroup, based on a branch and bound search yielding 4 trees of 19 steps; CI = .789.
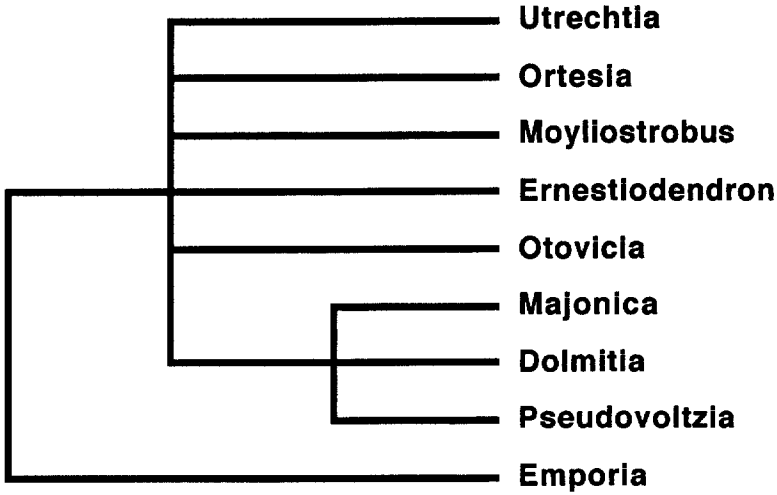
Fig. 4. Strict consensus cladogram of the Utrechtiaceae without *Walchiostrobus,* using *Emporia* as the outgroup, based on an exhaustive search yielding 50 trees of 15 steps; CI = .867.

Utrechtiaceae (Fig. 5). However, the branch bearing these two taxa shares a node with the Majonicaceae. The fifth tree shows *Voltziopsis* branching from the base of the Majonicaceae clade.

The 2 equally parsimonious trees of 23 steps show *Taxus* branching as a sister taxon with *Walchiostrobus florinii.* In one of these trees (Fig. 6) the pair is linked with *Moyliostrobus texanum;* in the other the pair branches from the basal polytomy of the Utrechtiaceae.

The remaining 18 taxa are associated to one degree or another with the Majonicaceae clade. When each OTU is analyzed with genera of the Utrechtiaceae and Majonicaceae, the strict consensus of the shortest trees show five different patterns of relationship (Fig. 7). In pattern 7A *Cupressus, Taxodium,* and *Sciadopitys* each occur as a sister taxon with *Dolmitia.* Pattern 7B shows *Voltzia* sharing a node with a subclade consisting of *Dolmitia* and *Pseudovoltzia.* In pattern 7C *Araucaria, Aethophyllum, Cycadocarpidium, Swedenborgia, Tricranolepis,* and *Cryptomeria* each branch from an unresolved trichotomy with *Dolmitia* and *Pseudovoltzia.* Pattern 7D shows *Podocarpus, Ullmannia, Hirmeriella, Schizolepis, Pararaucaria,* and *Cephalotaxus* each branching from an unresolved basal trichotomy of the Majonicaceae. Finally, in pattern 7E the *Pinus* and *Cunninghamia* each branches from an unresolved basal polytomy with other Majonicaceae.

These patterns reflect different degrees of resolution of the relationship of each OTU with the Majonicaceae. Patterns 7A and 7B are informative because all OTUs are resolved to bifurcations. Patterns 7C, 7D, and 7E, however, involve unresolved polytomies, and relationships are not as clear. Nonetheless, these patterns provide a basis for examining several different combinations of these taxa to further illuminate relationships.

2. Group 1 Conifers: Cupressaceae, Sciadopityaceae, Taxodiaceae

Cupressus, Sciadopitys, Taxodium, Cunninghamia, and *Cryptomeria,* all genera belonging to or closely related to the Taxodiaceae (Brunsfeld et al., 1994; Hart, 1987; Price &
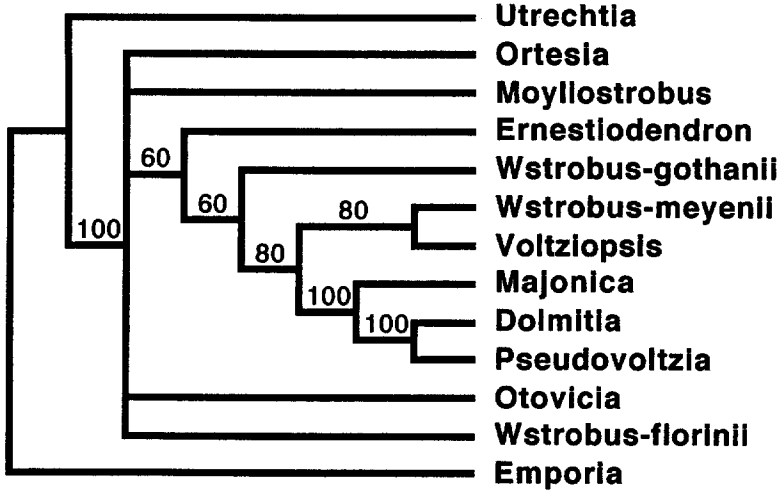
Fig. 5. Majority-rule consensus cladogram of *Voltziopsis* and the Utrechtiaceae including *Walchio-strobus,* using *Emporia* as the outgroup, based on a branch and bound search yielding 5 trees of 21 steps; CI = .714.
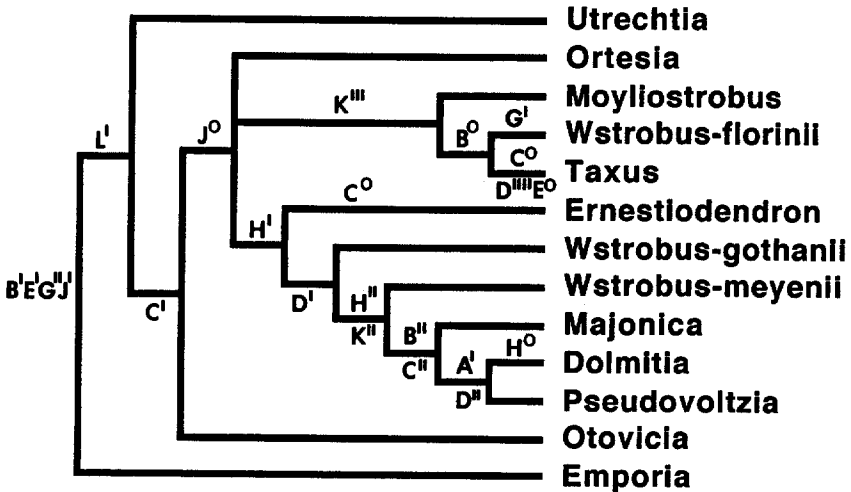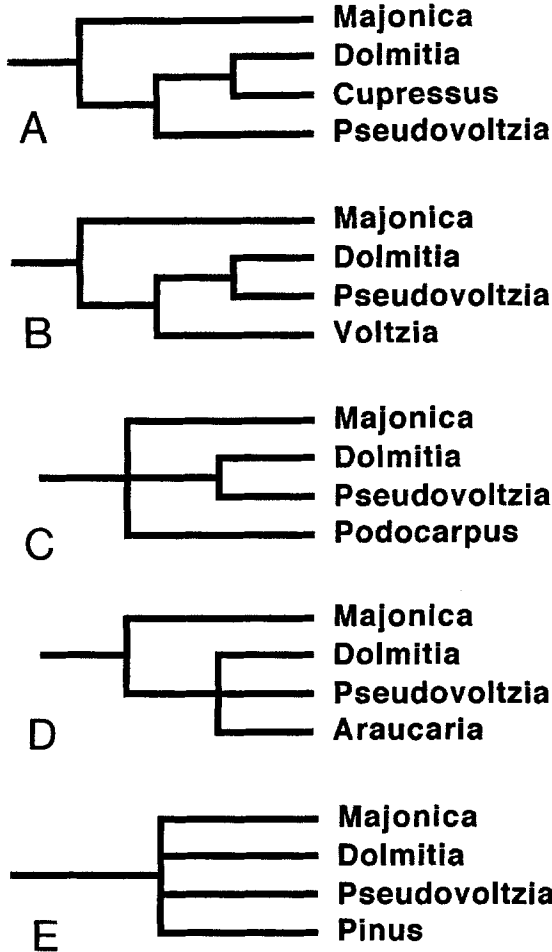

Fig. 6. Cladogram of *Taxus,* the Utrechtiaceae including *Walchiostrobus,* and the Majonicaceae, using *Emporia* as the outgroup, one of two equally parsimonious trees of 23 steps, based on a branch and bound search; CI = .783. X′, X″ = character X, state 1, 2, etc.; X° = character X, state 0, only indicated if attained via a reversal.

Fig. 7. Strict consensus cladograms showing the five patterns that result when each genus of the modern and higher fossil conifers is analyzed with the Utrechtiaceae including *Walchiostrobus* and the Majonicaceae, using *Emporia* as the outgroup. **A.** *Cupressus,* as well as *Sciadopitys* and *Taxodium.* **B.** *Voltzia.* **C.** *Araucaria,* as well as *Aethophyllum, Cryptomeria, Cycadocarpidium, Swedenborgia,* and *Tricranolepis.* **D.** *Podocarpus,* as well as *Cephalotaxus, Hirmeriella, Pararaucaria, Schizolepis* and *Ullmannia.* **E.** *Pinus* and *Cunninghamia.*

Lowenstein, 1989), were analyzed with the three genera of the Majonicaceae, using *Ernestio-dendron* as the outgroup. An exhaustive search produced 2 equally parsimonious trees of 20 steps. The strict consensus (Fig. 8) shows *Taxodium* and *Cupressus* as sister taxa linked with *Sciadopitys* and with this subclade sharing a node with *Dolmitia*. *Cryptomeria* and *Cunninghamia* appear as sister taxa, and they branch from an unresolved trichotomy that also bears *Pseudovoltzia* and the *Dolmitia* subclade.

Using *Moyliostrobus* as the outgroup yields trees one step shorter than the above but with less resolution of the taxa. A strict consensus of the 17 equally parsimonious trees retains pair-
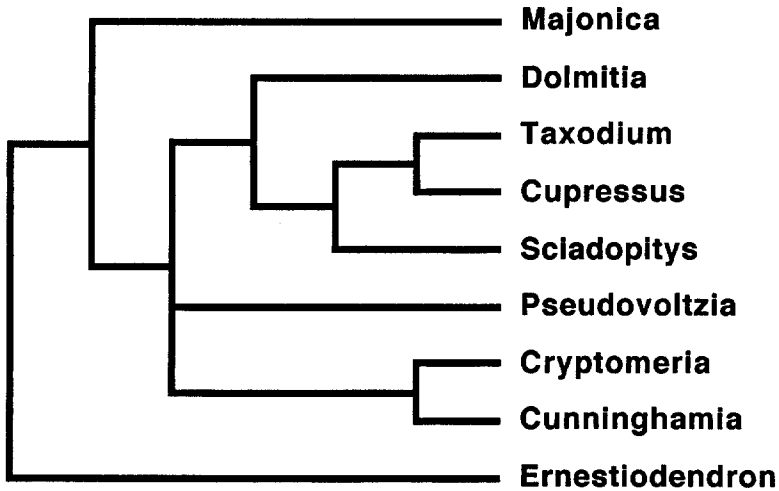
Fig. 8. Strict consensus cladogram showing group 1 conifers with *Ernestiodendron* as the outgroup, based on an exhaustive search yielding 2 trees of 20 steps; CI = .850.

ing of *Cryptomeria* and *Cunninghamia* and of *Cupressus* and *Taxodium* as sister genera. However, these subclades branch, with all other OTUs, from a massive basal polytomy. *Sciadopitys* is associated with the *Cupressus-Taxodium* subclade in 10 of the 17 equally parsimonious trees, arises from an unresolved polytomy with the latter subclade in four trees, and is associated with a different clade in three trees.

When *Araucaria* is added to the above OTUs using *Ernestiodendron* as the outgroup, 5 equally parsimonious trees of 22 steps result. The strict consensus of these trees (Fig. 9) shows *Araucaria* paired with *Cunninghamia* as sister taxa and *Cupressus* and *Taxodium* linked as sister taxa. These two pairs, *Dolmitia, Pseudovoltzia, Cryptomeria,* and *Sciadopitys,* each branch from an unresolved polytomy. The subclade in turn diverges from an unresolved trichotomy that also bears *Majonica* and the outgroup.

When *Cephalotaxus* is added to an exhaustive analysis of group 1 conifers, 61 equally parsimonious trees of 22 steps result. The strict consensus shows all taxa except the outgroup branching from a massive basal polytomy (Fig. 10). *Cephalotaxus* occurs in five alternative positions. Sixteen of the trees show this genus on a subclade associated with *Cupressus* and *Taxodium,* and in 15 additional trees that subclade also involves *Sciadopitys.* Twelve trees have *Cephalotaxus* at the base of a subclade consisting of *Dolmitia, Pseudovoltzia,* and the group 1 conifers. In ten trees *Cephalotaxus* branches from a basal polytomy, and in seven trees it occurs as a sister genus with *Majonica.*

Analyzing *Pinus* with group 1 conifers yields 10 trees of 21 steps. The strict consensus shows *Pinus* branching from a basal polytomy of the Majonicaceae subclade (Fig. 11). In four of the equally parsimonious trees *Pinus* shares a node with *Majonica.* In three trees the genus branches from a basal polytomy, and in three other trees it diverges from the base of a subclade consisting of *Dolmitia, Pseudovoltzia,* and the group 1 conifers.

Adding *Podocarpus* to the analysis of group 1 conifers results in 34 trees of 21 steps (Fig. 12). The strict consensus tree is uninformative in having all taxa branching from a mas-

Majonica
Dolmitia
Pseudovoltzia
Araucaria
Cunninghamia
Cryptomeria
Taxodium
Cupressus
Sciadopitys
Ernestiodendron

Fig. 9. Strict consensus cladogram showing *Araucaria* with group 1 conifers, using *Ernestiodendron* as the outgroup, based on an exhaustive search yielding 5 trees of 22 steps; CI = .818.

Majonica
Dolmitia
Pseudovoltzia
Cryptomeria
Cunninghamia
Taxodium
Sciadopitys
Cephalotaxus
Cupressus
Ernestiodendron

Fig. 10. Strict consensus cladogram showing *Cephalotaxus* with group 1 conifers, using *Ernestiodendron* as the outgroup, based on an exhaustive search yielding 61 trees of 22 steps; CI = .773.

Fig. 11. Strict consensus cladogram showing *Pinus* with group 1 conifers, using *Ernestiodendron* as the outgroup, based on an exhaustive search yielding 10 trees of 21 steps; CI = .810.
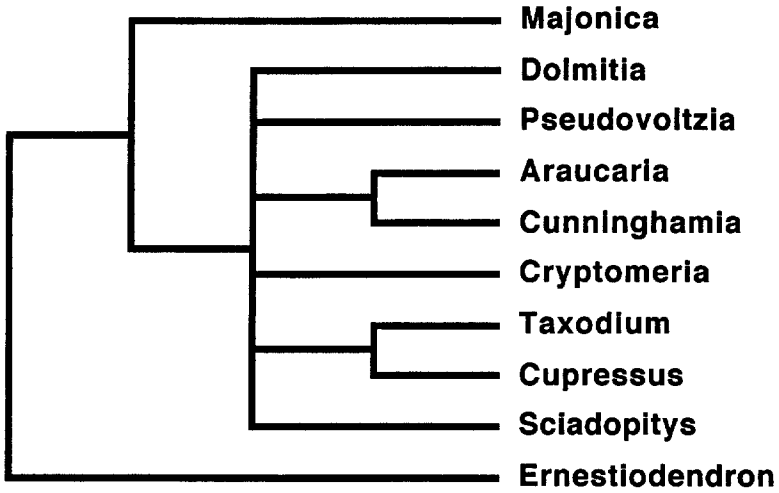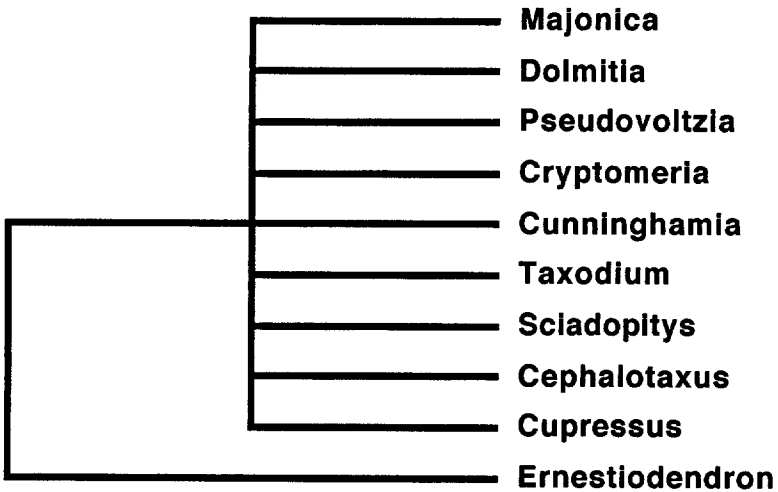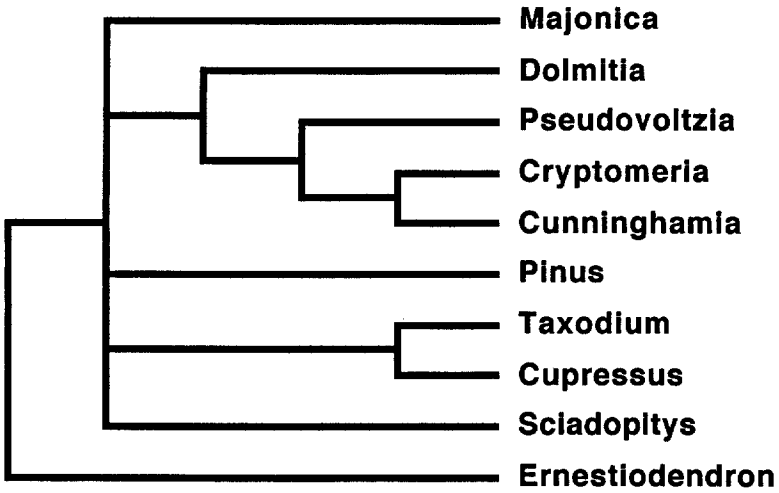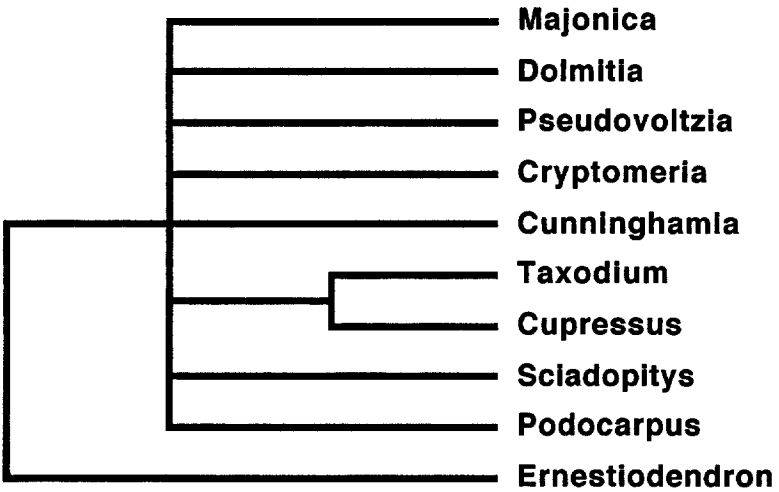

Fig. 12. Strict consensus cladogram showing *Podocarpus* with group 1 conifers, using *Ernestiodendron* as the outgroup, based on an exhaustive search yielding 34 trees of 21 steps; CI = .810.

sive basal polytomy. However, three alternative positions are evident within the equally par-
simonious trees. In 11 trees *Podocarpus* branches from a basal polytomy; in 11 other trees it
branches from the base of subclade that also bears *Dolmitia, Pseudovoltzia,* and the group 1
taxa; and in 12 trees *Podocarpus* is a sister genus with *Majonica.*

3. Group 2 Conifers: Araucariaceae, Cephalotaxaceae, Pinaceae, Podocarpaceae

Four modern taxa representing the Araucariaceae, Cephalotaxaceae, Pinaceae, and Podo-
carpaceae were analyzed by the exhaustive search option with the Majonicaceae, using *Ernes-
tiodendron* and *Moyliostrobus* together as the outgroup. The latter three modern taxa are not
linked with group 1 conifers. The Araucariaceae is included in group 2 because its linkage
with group 1 *Cunninghamia* and *Cryptomeria* of is inconsistent with phylogenetic studies of
modern conifers (Brunsfeld et al., 1994; Hart, 1987; Price & Lowenstein, 1989). A single
shortest tree results (Fig. 13). It is 16 steps long and shows *Araucaria, Cephalotaxus,* and *Po-
docarpus* branching from within the Majonicaceae but *Pinus* diverging basal to this family.

When *Cryptomeria* is analyzed with group 2 conifers, 8 trees at 18 steps result. In the strict
consensus diagram (Fig. 14) the genus is linked with *Araucaria, Dolmitia,* and *Pseudovoltzia*
in an unresolved polytomy. The alternative positions among the equally parsimonious trees
show the same linkage to one degree or another with these same OTUs. *Cunninghamia* ap-
pears as a sister taxon with *Araucaria* in each of the eight equally parsimonious trees (18
steps) when it is analyzed with group 2 OTUs (Fig. 15). Both *Cupressus* and *Taxodium* show a
single shortest tree of 19 steps when analyzed with group 2 taxa (Figs. 16 & 18), and both are
linked as sister taxa with *Cephalotaxus* in their trees (((((*Cupressus* or *Taxodium, Cephalo-
taxus*)((*Dolmitia, Pseudovoltzia*) *Araucaria*) *Majonica, Podocarpus*) *Pinus*) outgroup). Fi-
nally, the analysis of *Sciadopitys* with group 2 conifers results in 4 trees of 19 steps (Fig. 17).
The genus is linked in different ways on a subclade consisting of *Pseudovoltzia, Dolmitia,* and
Araucaria and occurs as a sister genus with *Dolmitia* in two of these trees.

4. Higher Fossil Conifers

The ten remaining genera of ancient conifers representing the Cheirolepidiaceae, Ullman-
niaceae, and Voltziaceae (Mapes & Rothwell, 1991; Miller, 1977) were analyzed first with
group 1, consisting of the Majonicaceae, Taxodiaceae, Sciadopityaceae, and Cupressaceae,
using *Ernestiodendron* as the outgroup, and then with group 2, consisting of the Majoni-
caceae plus *Pinus, Araucaria, Podocarpus,* and *Cephalotaxus,* using both *Ernestiodendron*
and *Moyliostrobus* as the outgroup. The exhaustive search option was used throughout.

a. Aethophyllum

Aethophyllum, when treated with group 1 OTUs, results in 3 trees of 21 steps. In the strict
consensus tree this genus branches from within the *Pseudovoltzia* subclade from a polytomy
involving the latter genus, the sister taxa *Cryptomeria* and *Cunninghamia,* and a subclade
consisting of *Taxodium* and *Cupressus* as sister taxa sharing a node with *Sciadopitys,* which
in turn shares a node with *Dolmitia* ((*Aethophyllum, Pseudovoltzia* (*Cryptomeria, Cunning-
hamia*) (((*Taxodium, Cupressus*) *Sciadopitys*) *Dommitia*) outgroup). Two trees show *Aetho-
phyllum* at the base of the *Pseudovoltzia* subclade basal to the latter genus; one shows it
sharing an unresolved trichotomy with *Pseudovoltzia* and the *Dolmitia* subclade. In all three it
is distal to *Majonica.*
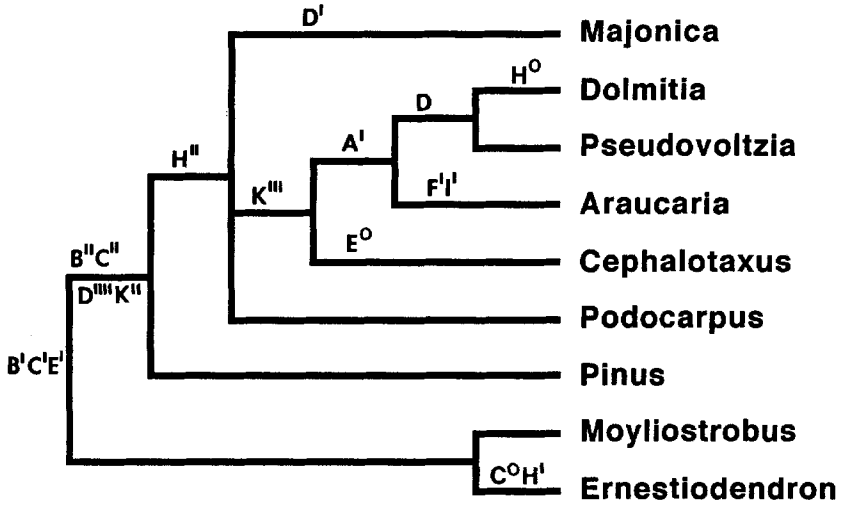
Fig. 13. Cladogram showing group 2 conifers with an outgroup consisting of *Ernestiodendron* and *Moyliostrobus*; single shortest tree of 16 steps; CI = .938. X′, X″ = character X, state 1, 2, etc.; X° = character X, state 0, only indicated if attained via a reversal.
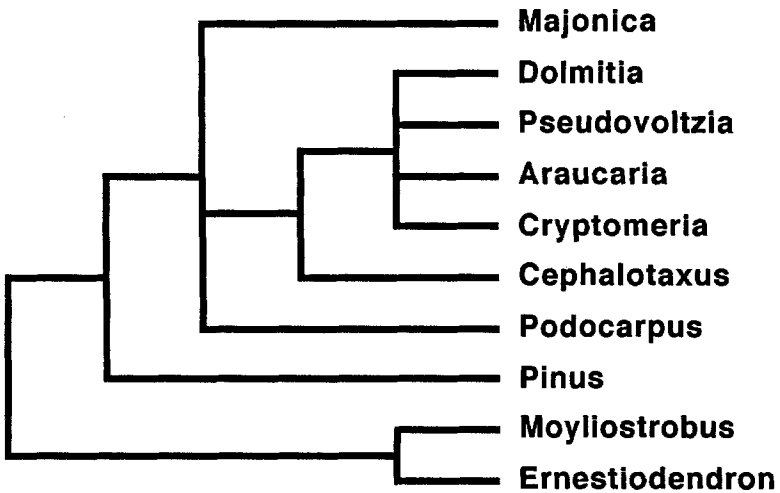
Fig. 14. Strict consensus cladogram showing *Cryptomeria* with group 2 conifers, using an outgroup consisting of *Ernestiodendron* and *Moyliostrobus,* based on an exhaustive search yielding 8 trees of 18 steps; CI = .833.
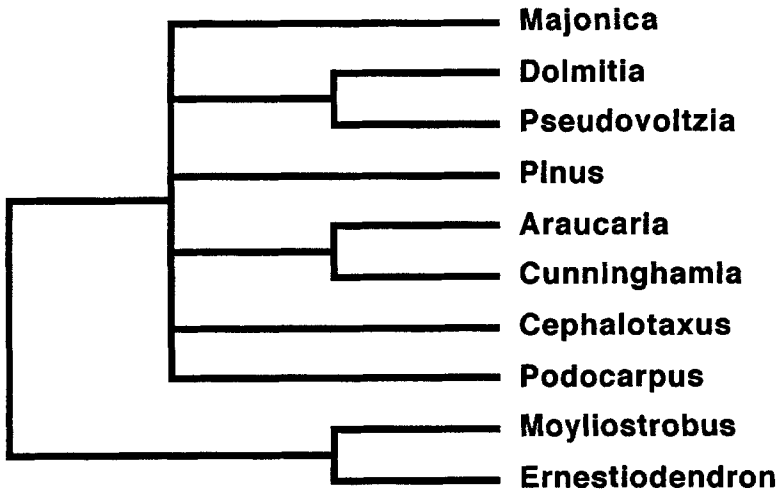
Fig. 15. Strict consensus cladogram showing *Cunninghamia* with group 2 conifers, using an outgroup consisting of *Ernestiodendron* and *Moyliostrobus,* based on an exhaustive search yielding 8 trees of 18 steps; CI = .944.
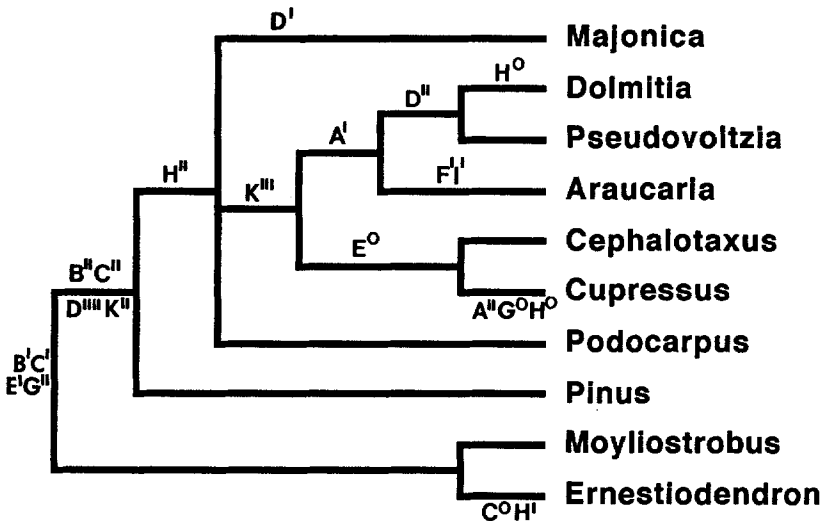
Fig. 16. Cladogram of *Cupressus* with group 2 conifers, using an outgroup consisting of *Ernestioden-dron* and *Moyliostrobus,* based on an exhaustive search; single shortest tree of 19 steps; CI = .895. X', X″ = character X, state 1, 2, etc.; X° = character X, state 0, only indicated if attained via a reversal.

Fig. 17. Strict consensus cladogram of *Sciadopitys* with group 2 conifers, using an outgroup consisting of *Ernestiodendron* and *Moyliostrobus*, based on an exhaustive search yielding 4 trees of 19 steps; CI = .895.

Fig. 18. Cladogram of *Taxodium* with group 2 conifers, using an outgroup consisting of *Ernestiodendron* and *Moyliostrobus*, based on an exhaustive search; single shortest tree of 19 steps; CI = .889. X', X" = character X, state 1, 2, etc.; X° = character X, state 0, only indicated if attained via a reversal.
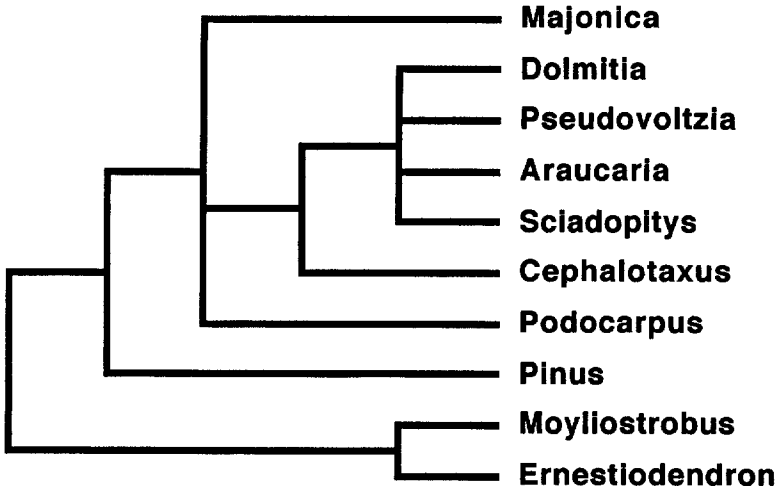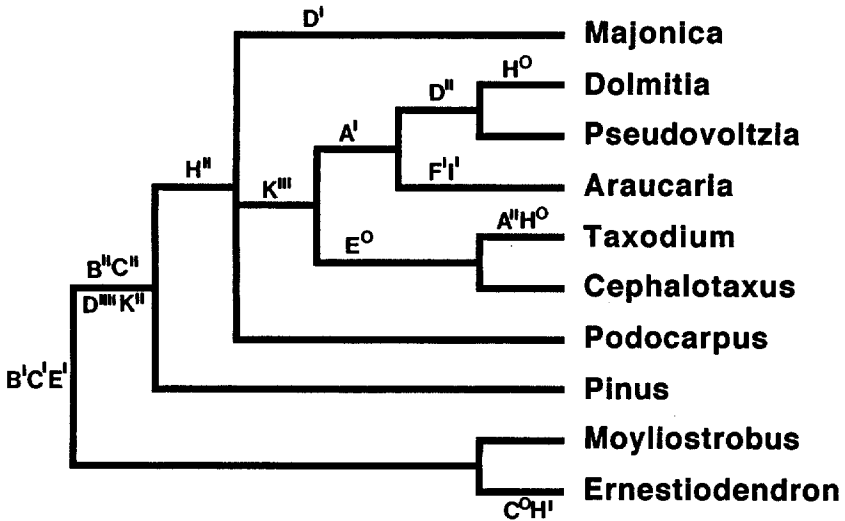
When analyzed with group 2, *Aethophyllum* yields 10 trees of 18 steps. The strict consensus tree ((*Aethophyllum, Pseudovoltzia, Dolmitia*) *Pinus, Podocarpus, Cephalotaxus, Majonica*) outgroup) shows *Aethophyllum* on an unresolved trichotomy with *Pseudovoltzia* and *Dolmitia*. This subclade branches from an unresolved basal polytomy with all other ingroup taxa; there are no other subclades. In 5 of the 10 equally parsimonious trees *Aethophyllum* branches from an unresolved trichotomy as in the strict consensus; in four trees it is a sister genus with *Pseudovoltzia,* and in one it is a sister genus with *Dolmitia.*

b. *Cycadocarpidium*

Cycadocarpidium, when analyzed with group 1 taxa, produces 2 trees of 20 steps. The two show the same topology ((((*Cycadocarpidium, Cunninghamia*) *Cryptomeria*)(((*Taxodium, Cupressus*) *Sciadopitys*) *Dolmitia*) *Pseudovoltzia*) *Majonica,* outgroup). *Cycadocarpidium* is a sister taxon with *Cunninghamia,* and these two genera share a node with *Cryptomeria.* This latter subclade branches from an unresolved trichotomy that also contains *Pseudovoltzia* and the *Dolmitia* subclade. The trichotomy is attached to a basal trichotomy that bears the outgroup and *Majonica.* The two trees show exactly the same topology.

When treated with group 2 taxa, *Cycadocarpidium* yields 3 trees of 17 steps. The strict consensus ((((((*Cycadocarpidium, Araucaria*) *Dolmitia, Pseudovoltzia*) *Cephalotaxus*) *Majonica, Podocarpus*) *Pinus*) outgroup) shows it paired with *Araucaria,* and the two branch from an unresolved trichotomy with *Dolmitia* and *Pseudovoltzia.* The latter subclade shares a node with *Cephalotaxus.* This subclade branches from an unresolved trichotomy with *Majonica* and *Podocarpus.* This latter subclade shares a basal node with *Pinus.* Alternative positions have to do with how *Dolmitia, Psuedovoltzia, Araucaria,* and *Cephalotaxus* assort on their subclade.

Because both *Araucaria* and *Cycadocarpidium* appear as sister taxa with *Cunninghamia* when each is analyzed individually with group 1 taxa, the two were included together in an analysis. This resulted in 4 trees of 22 steps. The strict consensus (Fig. 19) shows *Araucaria, Cunninghamia,* and *Cycadocarpidium* sharing an unresolved trichotomy. In two of the equally parsimonious trees *Araucaria* and *Cunninghamia* are sister genera, with *Cycadocarpidium* sharing a node with the pair; and in the other two trees the three genera branch from an unresolved trichotomy as in the strict consensus.

c. *Hirmeriella*

Analyzing *Hirmeriella,* representing the Cheirolepidiaceae, with group 1 conifers using the exhaustive search option results in a single tree of 20 steps (Fig. 20). *Hirmeriella* branches from a basal dichotomy sharing a node with all group 1 OTUs.

When *Hirmeriella* is analyzed with group 2 taxa, 17 trees of 18 steps result. The strict consensus tree shows all taxa of the ingroup arising from a massive basal polytomy. Among the 17 equally parsimonious trees, *Hirmeriella* occurs basal to all group 2 taxa in eight trees. In one it is a sister taxon with *Dolmitia;* in four it shares a node with the latter genus and its sister genus *Pseudovoltzia.* In the remaining five trees *Hirmeriella* occurs within the group 2 subclade but is not linked with particular OTUs.

d. *Pararaucaria*

Pararaucaria, when treated with group 1 taxa, yields 34 trees of 21 steps. The genus arises from massive basal polytomy in the strict consensus tree. The only pairing is *Taxodium* and
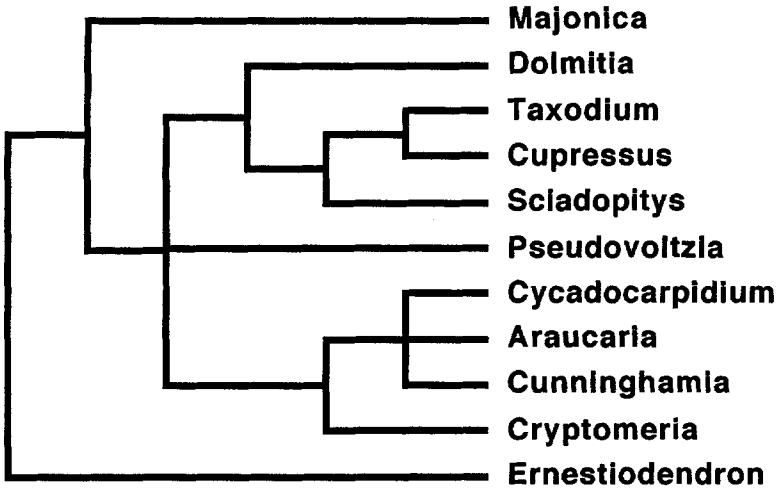
Fig. 19. Strict consensus cladogram showing *Araucaria* and *Cycadocarpidium* with group 1 conifers, using *Ernestiodendron* as the outgroup, based on an exhaustive search yielding 4 trees of 22 steps; CI = .818.

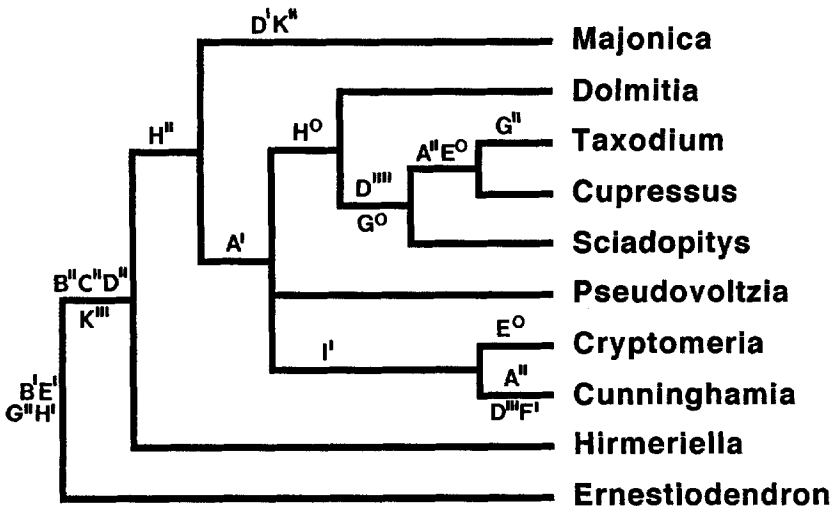**Fig. 20.** Cladogram showing *Hirmeriella* with group 1 conifers, using *Ernestiodendron* as the outgroup, based on an exhaustive search; single shortest tree of 20 steps; CI = 850. X′, X″ = character X, state 1, 2, etc.; X° = character X, state 0, only indicated if attained via a reversal.

Cupressus; all other OTUs branch independently from the polytomy. Within the 34 trees *Pararaucaria* occurs in three alternative positions: in 11 trees it branches from a massive basal polytomy, as in the strict consensus; in 12 trees it is paired with *Majonica*; and in 11 trees it branches from the base of the *Dolmitia-Pseudovoltzia* subclade.

Analyzing *Pararaucaria* with group 2 results in 3 trees of 16 steps. In the strict consensus tree (((((*Dolmitia, Pseudovoltzia*) *Araucaria*) *Pararaucaria, Cephalotaxus, Podocarpus*) *Pinus*) outgroup) *Dolmitia* and *Pseudovoltzia* are sister taxa. The pair shares a node with Araucariaceae, and this subclade branches from a basal polytomy from which branch *Pararaucaria* and the other ingroup taxa. The polytomy shares a node with *Pinus*. One of the equally parsimonious trees has the *Cephalotaxus* subclade of the strict consensus sharing a node with *Pararaucaria*; one is like the strict consensus; and in the third *Cephalotaxus, Pararaucaria*, and the *Araucaria* subclade of the strict consensus branch from an unresolved trichotomy.

e. *Schizolepis*

Analyzing *Schizolepis* with group 1 taxa produces 29 trees of 22 steps. In the strict consensus tree *Schizolepis* branches from a massive unresolved basal polytomy. The only subclade in this tree is a pairing of *Taxodium* and *Cupressus*. A variety of alternative positions occur among the 29 equally parsimonious trees. In nine trees *Schizolepis* branches from a basal polytomy. In seven the genus occurs as a sister taxon with *Majonica*, in two with *Cunninghamia*, and in one it shares a trichotomy with these two genera. *Schizolepis* shares a node with the sister taxa *Cupressus* and *Taxodium* in six trees, and in four other trees the genus occurs at the base of a subclade consisting of all group 1 genera except *Majonica*.

Schizolepis, when analyzed with group 2, results in 4 trees of 18 steps. The strict consensus tree (((((*Dolmitia, Pseudovoltzia*) *Araucaria*) *Cephalotaxus, Podocarpus*) *Pinus*) outgroup) shows *Pinus* on one branch of a basal dichotomy, with the rest of ingroup on the other branch. *Dolmitia* and *Pseudovoltzia* are sister taxa, and the two paired with *Araucaria*. Each of the remaining ingroup taxa branches individually from polytomy with the latter subclade. One of the four equally parsimonious trees has *Schizolepis* branching from a polytomy, as in the strict consensus tree; in another the genus branches from a trichotomy with *Cephalotaxus* and a subclade made up of *Araucaria, Dolmitia,* and *Pseudovoltzia*; and in a third tree *Schizolepis* occurs at the base of a subclade consisting of the latter three taxa and *Cephalotaxus*. In the fourth tree *Schizolepis* is a sister taxon of *Majonica*.

f. *Swedenborgia*

Analyzing *Swedenborgia* with group 1 taxa yields 4 trees of 22 steps. The strict consensus tree ((*Swedenborgia, Cryptomeria, Cunninghamia*) *Pseudovoltzia* ((*Cupressus, Taxodium*) *Sciadopitys*) *Dolmitia*) *Majonica*, outgroup) shows *Swedenborgia* linked in an unresolved trichotomy with *Cryptomeria* and *Cunninghamia*. The latter subclade is attached via an unresolved trichotomy with *Pseudovoltzia* and the *Dolmitia* subclade. This trichotomy is attached to a basal trichotomy that also bears the outgroup and *Majonica*. In two of the four trees *Swedenborgia* is a sister taxon with *Cunninghamia*; in the other two it is part of the trichotomy, as in the strict consensus. In two of the trees the intermediate trichotomy is resolved with *Pseudovoltzia* at the base sharing a node with a dichotomy leading to the *Cryptomeria* subclade and the *Dolmitia* subclade.

Analyzing *Swedenborgia* with group 2 conifers results in 8 trees of 19 steps. The strict consensus links this genus with *Dolmitia, Pseudovoltzia,* and *Araucaria* in an unresolved polytomy. Three of the eight equally parsimonious trees show *Swedenborgia* as a sister genus with *Araucaria;* two show it as a sister genus with *Dolmitia;* and in two trees *Swedenborgia* branches from an unresolved trichotomy with the two latter genera. In the remaining two trees *Swedenborgia* shares a node with *Dolmitia* and *Pseudovoltzia,* which occur as sister taxa.

g. *Tricranolepis*

Tricranolepis, when analyzed with group 1 taxa, yields 16 trees of 20 steps. *Tricranolepis* branches in the strict consensus from a massive basal unresolved polytomy; the only subclade is the *Dolmitia* subclade (*Dolmitia* (*Sciadopitys* (*Cupressus, Taxodium*))). All other taxa branch independently from the polytomy. Twelve of the trees show a basal trichotomy with the outgroup, *Majonica,* and the *Pseudovoltzia* subclade (*Pseudovoltzia* (*Dolmitia* (*Sciadopitys* (*Cupressus, Taxodium*)))). The latter has a basal polytomy from which branch *Tricranolepis, Pseudovoltzia,* the *Dolmitia* subclade, and the *Cunninghamia* subclade. Alternative positions are a pairing with *Majonica* in two trees and linkage with *Cryptomeria* and *Cunninghamia* in one way or another in 6 of the 16 trees.

Treating *Tricranolepis* with group 2 taxa results in a single tree of 16 steps. *Tricranolepis* is linked with *Dolmitia* and *Pseudovoltzia* in an unresolved trichotomy. This group shares a node with *Araucaria,* which in turn is linked with *Cephalotaxus.* This subclade branches from an unresolved trichotomy with *Majonica* and *Podocarpus.* The latter subclade is paired with *Pinus.*

h. *Voltzia*

When *Voltzia* is analyzed with group 1, 6 trees of 20 steps result. In the strict consensus tree the genus branches from a basal polytomy with the outgroup, *Majonica,* and the *Pseudovoltzia* subclade ((((*Cupressus, Taxodium*) *Sciadopitys*) *Dolmitia*) *Pseudovoltzia*). Two trees show *Voltzia* as a sister taxon with *Majonica,* and two trees show it at the base of the *Pseudovoltzia* subclade basal to the latter genus.

Voltzia, analyzed with group 2, results in 14 trees of 17 steps. The strict consensus tree shows *Voltzia* branching from a basal polytomy of the Majonicaceae with all other ingroup taxa except *Pinus,* which is basal to this subclade. In one of the equally parsimonious trees *Voltzia* occurs as a sister genus with *Majonica.* In another *Voltzia* branches from an unresolved trichotomy with the latter genus and the sister taxa *Dolmitia* and *Pseudovoltzia.* A third tree shows *Voltzia* diverging from an unresolved polytomy that also bears *Podocarpus, Majonica,* and a subclade made up of *Dolmitia, Pseudovoltzia, Araucaria,* and *Cephalotaxus.* In all other trees the genus is a member of the latter subclade. Five of these trees show *Voltzia* sharing a node with *Dolmitia* and *Pseudovoltzia,* which occur as sister taxa; the remaining six trees place the genus in every other possible position within this subclade.

i. *Ullmannia*

Analyzing *Ullmannia* with group 1 results in 34 trees of 21 steps. In the strict consensus tree *Ullmannia* branches from a basal polytomy with all other OTUs. The equally parsimonious trees display only three alternative positions. In eleven trees *Ullmannia* branches from a

basal polytomy. Twelve trees show *Ullmannia* as a sister genus with *Majonica.* The remaining eleven trees have *Ullmannia* at the base of a subclade that includes all group 1 taxa except *Majonica.*

The analysis of *Ullmannia* with group 2 results in 1 tree of 16 steps. *Ullmannia* branches from the basal polytomy of the Majonicaceae, along with *Majonica, Podocarpus,* and a clade with *Dolmitia, Pseudovoltzia, Cephalotaxus,* and *Araucaria.*

V. Discussion

A. CHARACTERS

The characters and states used in the present study are similar to those used in my earlier report (Miller, 1988). Both sets reflect broad trends in the modification of the highly strobiloid conifer cone of certain ancient conifers summarized by Florin (1951). During early evolution in conifers, different modifications occurred at different times in different lineages. For example, there was an early reduction in number of ovules per fertile dwarf shoot to as few as one in *Utrechtia.* Fusion of separate sterile elements of the fertile dwarf shoot is complete in *Ullmannia* by the Late Permian. Reduction of the ovuliferous scale relative to the bract is evident by the Middle Triassic in *Cycadocarpidium.* Thus these and other modifications (Tables I and II) are translated into character-state transitions for use in phylogenetic inference.

The main differences between the characters and states used in my 1988 study and those in the present work recognize subsequently published information. This research on ancient conifers (Clement-Westerhof, 1988; Kerp & Clement-Westerhof, 1991; Kerp et al., 1989, 1990; Mapes & Rothwell, 1991) has greatly expanded our understanding of ovulate cone construction in basal members of the conifer clade, and any new studies using phylogenetic inference must take this information into account.

B. EMPHASIS ON OVULATE CONES IN PHYLOGENETIC INFERENCE

There are both good reasons to emphasize characters based on ovulate cones when studying phylogeny in conifers and limitations inherent in doing so. One of the main reasons for using ovulate cones is that they tend to be more distinctive of a taxon than other organs. Except for the Taxodiaceae and Cupressaceae, in which there is considerable variation from genus to genus, modern families are clearly distinguished by their seed cone structure. Similarly, with few exceptions the main taxa of fossil conifers are also distinguished by their seed cones.

On the other hand, variation in pollen grain construction is relatively limited. In this study, four states are recognized (Table II). These are general conditions; and although more specific pollen features occur in conifers, they would amount to autapomorphies for individual taxa included in the study if structured as character states.

Similarly, secondary xylem construction is limited in its variability. Some modern families can be recognized by their wood construction; others cannot. Similarly, a number of fossil conifers are known by their seed cones, but we have no knowledge of their secondary xylem construction.

The same can be said for leaf morphology. De Laubenfels (1953) recognized only four types of foliage in his survey of modern conifers, and more than one of these types may be produced by certain conifers during their lifetime. Many of the conifers included in the present study, particularly the more ancient forms, display Type 1 foliage. This kind of foliage (Fig. 1) apparently also represents the oldest known in conifers (Galtier et al., 1992; Scott,

1974; Scott & Chaloner, 1983), probably represents the plesiomorphic condition for the group, and thus has no value in determining phylogenetic relationships within conifers.

Additional characters may be determined from leaf epidermal tissues, directly for living conifers or interpreted from cuticle when it is preserved in fossil forms. This may be useful in basal conifers and modern forms, but leaf epidermal structure is unknown in most of the Voltziaceae. Furthermore, although outgroup comparison can be used to infer the plesiomorphic condition, transitional states leading to modern families are as yet undetermined.

Using characters based on these vegetative features may be productive in restricted data sets but leads to scoring many cells in a data matrix as unknowns. For purposes of this study this was regarded as a serious limitation, and the decision was made to focus on broad characters of the ovulate cone and pollen grain to minimize unknown character states.

The main limitation in excluding characters from vegetative organs is the small number of characters on which analyses are based. Ideally, the number of OTUs that can be analyzed without generating homoplasy is one more than the number of characters. Thus study of the 34 OTUs in the data matrix must be compartmentalized to a maximum of 13 or fewer taxa in each analysis. Although this process may seem unwieldy, it permits wide use of the exhaustive search option with the likelihood of finding the shortest trees.

C. OUTGROUP SELECTION

Cordaianthus duquesnensis Rothwell (1982), which represents ovulate cones of the *C. dumusum* plant (Trivett & Rothwell, 1991), was selected as the outgroup for the initial analysis of basal conifers for several reasons. There is general agreement in current cladistic studies that cordaites somehow share an ancestor with conifers, although the details of this relationship are still a matter of some conjecture (Clement-Westerhof, 1988; Nixon et al., 1994; Rothwell & Serbet, 1994). In certain of these and other studies *Ginkgo* is used as the outgroup for the conifer clade (Hart, 1987), appearing as either unresolved or between cordaites and conifers in other studies (Crane, 1985, 1988; Doyle & Donoghue, 1986). However, the present work is based primarily on ovulate cones, and homologies between the ovulate fructification of *Ginkgo* and that of conifers is too poorly understood to define character states. On the other hand, organ correspondence between cordaites and conifers is well understood (Florin, 1951), and homologies can be assessed with reasonable accuracy.

Although certain remains from Namurian B sediments may represent cordaites (Rothwell, 1988, 1995, pers. comm.), the oldest unequivocal cordaite remains come from Late Pennsylvanian Westphalian A sediments (Trivett & Rothwell, 1991); conifers are first in evidence in Westphalian B sediments (Fig. 1). Remains of *Cordaianthus duquesnensis* come from sediments of the Conemaugh group, which is equivalent to the Stephanian division in Europe (Rothwell, 1982). This makes *C. duquesnensis* one of the oldest cordaites for which information about ovulate reproductive structures is relatively complete. The oldest known conifers are only slightly older, ten million years or less. Thus comparing basal conifers with a relatively basal cordaite allows determination of character-state polarity while minimizing the risk of parallelisms and/or reversals that might have occurred had a younger outgroup taxon been used.

Most importantly, information about the construction of the ovulate reproductive structures in *Cordaianthus duquesnensis* is based on permineralized material and is as complete as we have for the basal conifers and for most cordaites.

Choice of an appropriate outgroup for subsequent analyses is based on divergence patterns expressed in earlier cladograms. Specifically, once the initial analysis (Fig. 2) established that *Emporia* was basal to all genera of the Utrechtiaceae, this genus was used as the outgroup in

analyzing relationships between the Utrechtiaceae and the Majonicaceae (Fig. 3). Similarly, cladistic relationships in the latter analysis (Fig. 3) were the basis for selecting genera of the Utrechtiaceae as outgroups in determining relationships of higher conifers and genera of the Majonicaceae. Thus, other than the selection of *Cordaianthus duquesnensis* as the initial outgroup, choice of later outgroups was based on prior cladistic analyses.

D. RELATIONSHIPS OF BASAL CONIFERS

1. Emporiaceae and Utrechtiaceae

Both *Emporia* and *Cordaianthus duquesnensis* appear basal to the Utrechtiaceae (Fig. 2). However, *Utrechtia* also appears basal to other genera included in the Utrechtiaceae. Transitions in four characters distinguish *Cordaianthus duquesnensis* from the remaining taxa, whereas a single transition supports the branch to *Utrechtia,* with the subclades of the Utrechtiaceae being also supported by single transitions. A transition in Dwarf Shoot Axis (character C) from "obvious" to "evident but obscured" forms the synapomorphy that distinguishes all other members of the Utrechtiaceae from *Utrechtia*. The large number of transitions between *Cordaianthus duquesnensis* and the remaining taxa indicates that *Emporia* is more of a "conifer" than a "cordaite," as was suggested by Rothwell and Serbet (1994), and the same is true of *Utrechtia*. Thus *Emporia* is a closer sister group for the Utrechtiaceae and Majonicaceae than is *Cordaianthus duquesnensis*. In none of the equally parsimonious trees is *Emporia* or *Utrechtia* linked as a sister taxon with *Cordaianthus*.

The organization of the genera of the Utrechtiaceae in the cladogram of this family and the Emporiaceae (Fig. 2) shows that further subdivision of the Utrechtiaceae may be in order.

2. Majonicaceae

It is clear from the analyses that *Majonica, Dolmitia,* and *Pseudovoltzia* form a distinct clade (Fig. 3) which in all cases branches from within the Utrechtiaceae. Alternative positions show the Majonicaceae clade sharing an unresolved polytomy with other genera of the Utrechtiaceae and sharing an ancestor with *Walchiostrobus meyenii*. Synapomorphies that distinguish the Majonicaceae clade are a somewhat flattened dwarf shoot complex (character B) and an evident but obscured dwarf shoot axis (character C), which occur in all four equally parsimonious trees. An additional synapomorphy of having 6 to 10 sterile appendages per axillary dwarf shoot (character H) occurs in one of these trees.

In all four equally parsimonious trees *Dolmitia* and *Pseudovoltzia* appear as sister taxa, and this pair shares a node with *Majonica* (Fig. 3). Synapomorphies in an axillary complex that is partially fused with the bract (character A) and appendages of the dwarf shoot axis that are fused less than one-half their length (character D) define the *Dolmitia-Pseudovoltzia* subclade, whereas a reversal in sterile appendages per axillary dwarf shoot (character H) in the former genus distinguishes it from the latter.

E. PHYLOGENETIC RELATIONSHIPS OF EXTANT CONIFER FAMILIES

1. Taxaceae

The two equally parsimonious trees that result when *Taxus* is analyzed with the Emporiaceae, Utrechtiaceae, and Majonicaceae show this genus as a sister taxon with *Walchiostrobus florinii,* with the latter branching from within the Utrechtiaceae (Fig. 6). Thus there are no

grounds for inferring a relationship between *Taxus* and the Majonicaceae. It is premature to regard *Walchiostrobus florini* as an ancestor of the Taxaceae, but we can infer divergence of this family from ancestors within the Utrechtiaceae.

In my earlier treatment *Taxus* was in a basal position among conifers (Miller, 1988: Fig. 10.1), but both Hart (1987) and Price et al. (1993) found the genus to have a sister-group relationship with *Cephalotaxus* and both grouped with Taxodiaceae, Cupressaceae, Sciadopityaceae, and Araucariaceae. If the latter relationships are borne out by further work, it may provide a reason to reconsider my interpretation of the ovulate fructification (Miller, 1988) and the scoring of character states (Table III). Another approach would be to use characters based on other organs of fossil and modern material.

Taxus is the only genus of living conifers included in this study to show derivation from the Utrechtiaceae, and the relationship underscores the distinctiveness of this taxon. Florin (1948, 1958) argued that *Taxus* and its related genera *Amentotaxus, Austrotaxus, Pseudotaxus,* and *Torreya* differed significantly from other conifers and should be segregated in their own class, mainly because the ovule is terminal on a shoot in this group and lateral in other living conifers. Even though Florin's classification is seldom followed today, many still recognize the uniqueness of these conifers by treating them as a separate order. Their derivation from an ancestral source different than other modern conifers provides a phylogenetic basis for this distinctiveness.

2. Araucariaceae, Cupressaceae, Sciadopityaceae, Taxodiaceae

The fully resolved subclade formed by *Taxodium, Cupressus,* and *Sciadopitys* (Fig. 8) and its branching from the same node as *Dolmitia* further support the relationship obtained when each of these genera is analyzed independently with the basal conifers (Fig. 7A). Linkage of *Cupressus* and *Taxodium* as sister taxa is consistent with the close relationship between these taxa at the family level proposed by Eckenwalder (1976) and is further supported by recent work on modern conifers by Hart (1987), using a broad based cladistic study of modern conifers, by Price and Lowenstein (1989), using antisera and more recently using DNA sequences from the *rbc*L gene in plastids (Price et al., 1993), by similar work by Brunsfeld et al. (1994), and by my earlier work that included fossils (Miller, 1982, 1988)

The relationship of *Cupressus* and *Taxodium* with *Dolmitia* is somewhat equivocal. This pair of modern genera shifts to an unresolved basal polytomy of the Majonicaceae when *Araucaria* (Fig. 9), *Pinus* (Fig. 11), or *Podocarpus* (Fig. 12) are added to the analysis. Yet, in most trees of group 1 conifers, *Cupressus* and *Taxodium* are linked with *Dolmitia*.

Branching of *Sciadopitys* from a node basal to these two taxa is also consistent with work by the above authors, who give grounds for treating the latter genus in its own family. Further support for this treatment comes from alternative positions of *Sciadopitys* in 7 of the 17 equally parsimonious trees when *Moyliostrobus* is used as the outgroup, either diverging from an unresolved polytomy or associated with other Majonicaceae and Taxodiaceae. Moreover, when *Sciadopitys* is analyzed with group 2 conifers, it is linked strongly in an unresolved polytomy with *Dolmitia, Pseudovoltzia,* and *Araucaria.* There is no pairing with other group 2 conifers in any of the trees.

Casting some doubt on a hypothesis of close relationship of *Sciadopitys* with *Cupressus* and *Taxodium* is the shifting of the former genus to unresolved positions when it is analyzed with *Araucaria, Cephalotaxus, Pinus,* or *Podocarpus* (Figs. 9–12). Indeed, Brunsfeld et al. (1994) found *Sciadopitys* to be a sister genus of *Podocarpus.* Thus, if *Taxodium* and *Cupressus* are to be combined in the same family, whether to include *Sciadopitys* remains unresolved.

Most current authors regard *Sciadopitys* as closely related to the Taxodiaceae and Cupressaceae yet different enough to be classified in a separate family (Hart, 1987; Price & Lowenstein, 1989). The Sciadopityaceae shares a node with the sister taxa Cupressaceae and Taxodiaceae in Hart's (1987) shortest trees.

The combination of *Cryptomeria* and *Cunninghamia* as sister taxa and their branching (Fig. 8) from a position basal to the *Dolmitia-Sciadopitys-Cupressus-Taxodium* subclade suggests that the Taxodiaceae may have had a biphyletic origin, because the different genera appear to have originated from different Paleozoic ancestors within the Majonicaceae. There is more variation in ovulate cone structure in the Taxodiaceae than in any other modern family, and a hypothesis of a bi- or polyphyletic origin of these genera is consistent with these differences. These results are also reflected in Hart's (1987) tree treating the genera of the Taxodiaceae, which shows *Taxodium*, the Cupressaceae, and *Cunninghamia-Cryptomeria* on three different subclades branching from an unresolved trichotomy.

The Araucariaceae is also linked with *Cunninghamia*. *Araucaria* appears as a sister taxon with *Cunninghamia* when analyzed alone with this group (Fig. 9), and *Cryptomeria* shifts to an unresolved basal polytomy of the Majonicaceae. *Araucaria* also appears in an unresolved trichotomy with *Cunninghamia* and *Cycadocarpidium* when the latter is included in the analysis (Fig. 19), and the three share a node with *Cryptomeria*. The synapomorphy these three taxa have is a bract-scale complex in which the bract is large and contains many vascular strands and the scale is relatively small. *Athrotaxis* and *Taiwania*, though not included in this study, also have similar bract-scale complexes and must be considered members of the same phylogenetic group. Either this type of bract-scale complex evolved several times in different lineages, or these taxa share an ancestor that had this feature. The Araucariaceae is closely associated with the Taxodiaceae, Cupressaceae, and Sciadopityaceae in Hart's (1987) cladograms, but studies based on immunology and DNA sequences do not agree (Brunsfeld et al., 1994; Price & Lowenstein, 1989); and my earlier work that included fossils (Miller, 1982, 1988) is also inconsistent with the present results.

Cycadocarpidium, usually treated as a member of the Voltziaceae (Miller, 1977), also appears to be part of this lineage (Fig. 19). The genus includes nearly two dozen species from the Middle and Late Triassic from a wide variety of Northern Hemisphere localities (Grauvogel-Stamm, 1978). In some of the species the bract, though containing numerous vascular strands, is no longer than the ovuliferous scale (Grauvogel-Stamm, 1978). In other species the bract is ten times as long as the ovuliferous scale. Such variation may reflect the evolution of this type of bract-scale complex during the Triassic.

Remains attributable to the Araucariaceae are known from the Late Triassic (Bock, 1954), and *Araucaria* has been documented from the Jurassic (Calder, 1953; Stockey, 1975, 1978, 1982). This timing is consistent with the divergence of the family from an ancestor within *Cycadocarpidium* or the divergence of both taxa from a common ancestor during the Early Triassic or Late Permian.

The *Cunninghamia* lineage represented by *Elatides* also dates from the Jurassic (Harris, 1943; Schweitzer & Kirchner, 1996) and is well represented by the latter genus as well as *Cunninghamiostrobus* in the Cretaceous (Harris, 1953; Miller, 1975, 1990; Ogura, 1930; Ohana & Kimura, 1995). The *Athrotaxis* lineage, though not necessarily the genus itself, may also have been well established by the Early Cretaceous (Miller & LaPasha, 1983). Thus the divergence of this lineage from *Cycadocarpidium*, from early araucarian conifers, or from a common ancestor with either of these two groups is consistent with their respective geologic ages.

3. Cephalotaxaceae

This family appears to diverge from the base of the *Dolmitia-Pseudovoltzia* subclade of the Majonicaceae (Fig. 13). When analyzed with basal conifers, *Cephalotaxus* branches from a basal trichotomy that also bears *Majonica* and the *Dolmitia-Pseudovoltzia* subclade (Fig. 7D). It also branches from an unresolved basal polytomy of the Majonicaceae when analyzed with group 1 conifers (Fig. 10). These analyses, then, fail to resolve its relationships. Better resolution results from the analysis with group 2 conifers (Fig. 13), in which its point of divergence is distal to *Majonica*, *Pinus*, and *Podocarpus* and basal to *Araucaria*, *Dolmitia*, and *Pseudovoltzia* (Fig. 13).

Florin (1951) and Schweitzer (1963) thought that the Cephalotaxaceae evolved from ancestors more like *Ernestiodendron* than *Utrechtia* (formerly *Lebachia*), because the ovuliferous scale in *Cephalotaxus* seems to consist of fertile elements only. However, work on the construction of ovulate cones in *Cephalotaxus* (Singh, 1961) revealed a ridge of sterile tissue between the ovules. The present analyses give no indication of a close relationship with *Ernestiodendron* and point to derivation from the Majonicaceae instead.

Modern work on conifer phylogeny shows no close agreement on a hypothesis of relationships of the Cephalotaxaceae. Hart's (1987) cladistic analysis shows this family as a sister group with the Taxaceae in his shortest trees. The Cephalotaxaceae appears as a sister group with the Araucariaceae in the tree summarizing the immunological studies of Price and Lowenstein (1989), which did not include the Taxaceae, and it is a sister group with the Podocarpaceae in my 1988 study. Work by Brunsfeld et al. (1994) based on DNA sequences in the *rbcL* gene shows the closest agreement with the present analyses, in that *Cephalotaxus* appears basal to genera of the Cupressaceae and Taxodiaceae and distal to the Podocarpaceae and Pinaceae.

4. Pinaceae

The Pinaceae appears well divergent from other modern families branching from a basal position within the Majonicaceae subclade. It diverges from a basal polytomy of the Majonicaceae when analyzed with basal conifers (Fig. 7E) and branches from a position basal to the three genera of the Majonicaceae, *Araucaria*, *Cephalotaxus*, and *Podocarpus* in the analysis of group 2 conifers (Fig. 13). Connection of *Pinus* to an unresolved basal polytomy of the Majonicaceae subclade when analyzed with group 1 conifers is consistent with the former trees.

This basal position of the Pinaceae agrees with current phylogenetic analyses of living conifers. Hart's (1987) cladistic analysis of modern conifers found that the Pinaceae diverged basal to all other modern conifers in his shortest tree, with the Podocarpaceae branching next. In the four trees that are one step longer, the Podocarpaceae branches basal to all other conifers in two, the Pinaceae in one, and both of these families plus a subclade of the other modern families form an unresolved trichotomy in a fourth tree (Hart, 1987). Recent work using DNA sequences from the chloroplast *rbcL* gene (Price et al., 1993) indicates that the Pinaceae is an isolated group, well removed from other modern families. Similar work by Brunsfeld et al. (1994) using *Pseudotsuga* to represent the Pinaceae found the latter branching from a basal trichotomy, along with the outgroup *Araucaria* and a subclade including all other conifers, and the family is linked as a sister group with the Araucariaceae in my 1988 study. Price and Lowenstein (1989), using immunological distance based on antisera, found *Pinus* on a subclade diverging basal to the sister taxa Araucariaceae and *Cephalotaxus* and distal to *Podocarpus*. This subclade shares a node with another involving the Cupressaceae and Taxodiaceae.

Early arguments about whether the Pinaceae is more primitive than the Araucariaceae or vice versa are resolved with the understanding that neither family served as an ancestor for the other and that both diverged from different ancestors within the Majonicaceae clade. The Pinaceae appears to be cladistically more basal within the Majonicaceae, and a hypothesis of a close phylogenetic relationship of the Araucariaceae with the more distal *Cunninghamia* and *Cycadocarpidium* is inferred from the present cladistic analyses. Yet the Pinaceae is not known for certain before the Early Cretaceous, whereas the Araucariaceae is well documented in the Middle Jurassic.

The Late Triassic *Compsostrobus* (Delevoryas & Hope, 1987) may be an early pinaceous conifer. Its early Mesozoic occurrence bridges the gap between Permian ancestors and the earliest unequivocal remains of the family in the Early Cretaceous. The morphology of its bract-scale complexes is consistent with those of certain modern Pinaceae, although having a bract that is almost twice as long as the scale presents a problem. Speculatively, however, this may represent the plesiomorphic condition in the family. Some indication of the vasculature of the bract and ovuliferous scale is required to resolve the question.

5. Podocarpaceae

The Podocarpaceae also appears to have diverged from basal Majonicaceae and may share an ancestor with *Majonica*. *Podocarpus* is a sister genus with *Majonica* in one-third of the equally parsimonious trees when analyzed with group 1 conifers and shares with the latter genus an unresolved trichotomy when analyzed both with basal conifers (Fig. 7D) and with group 2 taxa (Fig. 13). In none of the trees is there evidence of linkage with another modern family.

Phylogenetic work on modern conifers (Hart, 1987; Price & Lowenstein, 1989) agrees fairly well with the present analyses, showing that the Podocarpaceae diverges basal to most other modern conifers. In Hart's (1987) most parsimonious tree the Pinaceae is the most basal group to diverge from the clade, with the Podocarpaceae branching next. This pattern occurs as well in one of the four equally parsimonious trees that are one step longer. In two of the latter the Podocarpaceae is basal to the Pinaceae, and in one both diverge from an unresolved trichotomy with other conifers. Similarly, *Podocarpus* is basal in the subclade including *Pinus*, *Cephalotaxus*, and the Araucariaceae in work based on immunological distance by Price and Lowenstein (1989), and analyses based on *rbc*L sequences (Brunsfeld et al., 1994) have *Podocarpus* in a relatively basal position but distal to the Pinaceae. The *rbc*L studies of Price et al. (1993) place the Podocarpaceae in the clade with conifers other than the Pinaceae, and this is in keeping with 11 of the 34 equally parsimonious trees when *Podocarpus* is analyzed with group 1 conifers. My 1988 study links the Podocarpaceae and Cephalotaxaceae, but there is no agreement with other work, including the present results.

The Podocarpaceae is known from the basal Triassic onward (Townrow, 1967a), and its early appearance is in keeping with a Middle-to-Late Permian divergence from basal Majonicaceae.

F. PHYLOGENETIC RELATIONSHIPS OF THE CHEIROLEPIDIACEAE, ULLMANNIANCEAE, AND VOLTZIACEAE

1. Cheirolepidiaceae

The Cheirolepidiaceae represented here by *Hirmeriella* has been thought to be related to the Araucariaceae, Taxodiaceae, and Cupressaceae because fossil foliage now assigned to

this extinct group was originally treated in these three modern families (Watson, 1988). However, *Hirmeriella* has no close relationship with any modern family. It branches from a position basal to all of the Araucariaceae, Cupressaceae, Sciadopityaceae, and Taxodiaceae included in this study (Fig. 20), and its position with other modern conifers and the Majonicaceae is not resolved. Thus, although it is associated with the Majonicaceae clade (Fig. 7D), the Cheirolepidiaceae does not appear to be closely related to any of the modern conifer families and may share an ancestor with the three known genera of the Majonicaceae.

Other studies that include *Hirmeriella* place the latter at the base of a group that includes the Pinaceae and Araucariaceae (Miller, 1982: Fig. 4), at the base of a group including all modern families except the Cephalotaxaceae (Miller, 1982: Fig. 3), and at the base of a subclade involving the Cephalotaxaceae and the Podocarpaceae. Thus the results are contradictory, and resolution will depend on additional work. Discovery of ovulate cones with internal structure preserved would certainly help.

2. Ullmanniaceae

The divergence of *Ullmannia* from a basal unresolved polytomy with other genera of the Majonicaceae in the analysis of basal conifers (Fig. 7D) rather than any of the genera of the Utrechtiaceae clearly places it on the Majonicaceae clade. Its relationships within the Majonicaceae, however, are not clear, because *Ullmannia* also branches from unresolved basal polytomies with the genera of the Majonicaceae when analyzed with group 1 and group 2 conifers. The latter analysis also includes the outgroup *Ernestiodendron*. Thus the Ullmanniaceae probably shares an ancestor with some member of the Majonicaceae that is as yet undiscovered and is more basal than any of the three known genera. The Late Permian age of *Ullmannia* is the same as that of the three genera of the Majonicaceae, which also supports the divergence of this lineage from basal Majonicaceae.

Ullmannia is unusual in having a single recurved ovule that is apparently free of an orbicular ovuliferous scale. The five vascular strands in the scale suggest that it was derived from the fusion of five sterile elements of an ancestral strobiloid dwarf shoot. The uniqueness of this construction supports treating *Ullmannia* in a distinct family (Clement-Westerhof, 1988; Mapes & Rothwell, 1991). The distinctiveness of this genus is also reflected by its lack of clear relationships with other genera in my earlier numerical and phylogenetic studies (Miller, 1982, 1988).

3. Voltziaceae

As used here, this family is an artificial grouping of genera not allied with other families. *Voltziopsis* and *Cycadocarpidium* are often included in this family as well, which further underscores the artificiality of the group, because the present work indicates that the affinities of these two taxa are different from those of the remaining genera. Although certain genera of the Voltziaceae appear in one analysis to be related to the Taxodiaceae (Miller, 1982: Fig. 4), other treatments (Miller, 1982: Fig. 3; 1988) do not support such a relationship.

Voltzia, the generitype of the Voltziaceae, typifies in its construction the remainder of the group. It has a bract with an acute apex that essentially free of an ovuliferous scale. The latter has five lobes that are partially fused with one another and in which the apical one-half of each is free (Schweitzer, 1963), although different authors interpret the amount of fusion from mostly fused to mostly free (Delevoryas & Hope, 1987). Three recurved ovules are associated with the middle and two lateral sterile lobes. The stalks of the ovules are fused to the associated sterile lobe, with only the tip free.

The analyses with basal conifers and with group 1 conifers show *Voltzia* diverging some-
what basal to the *Pseudovoltzia-Dolmitia* subclade (Fig. 6B). It occurs immediately basal to
this pair in the analysis of basal conifers and in two of the six equally parsimonious trees in the
analysis with group 1 conifers. Other positions have *Voltzia* as a sister taxon with *Majonica*
and in an unresolved basal polytomy with the Majonicaceae and the outgroup. Thus its rela-
tionships are clearly with the Majonicaceae, and there is no indication of involvement in the
evolution of the modern conifers.

Aethophyllum clearly diverges from within the Majonicaceae closer to *Dolmitia* and *Pseu-
dovoltzia* than to *Majonica*. It shares an unresolved trichotomy with these two genera when
analyzed with basal conifers (Fig. 7C). It occurs on a similar trichotomy in the strict consen-
sus with group 1 conifers and in two of the three equally parsimonious trees with group 2 coni-
fers. Thus the genus probably shares an ancestor with some member of the *Dolmitia-
Pseudovoltzia* subclade that is basal to either of these genera. Such a relationship was also ap-
parent in my earlier cladistic study (1988).

The construction of the bract-scale complex in *Aethophyllum* also reflects this divergence.
It is made up of five sterile elements that are only partially fused to one another and five re-
curved ovules. Thus there is greater fusion and reduction in numbers of parts in *Pseudovoltzia*
than in *Aethophyllum*. The Triassic age of the latter genus is also consistent with divergence
from Permian ancestors.

Pararaucaria was first thought to exhibit features of the Araucariaceae (Calder, 1953) and
later believed to show a combination of features of the Pinaceae and the Taxodiaceae (Stockey,
1977). It branches from the base of a subclade consisting of the Araucariaceae and Pinaceae in
my 1988 study. However, affinities with none of these modern families are supported by the
present analyses. Although the genus is clearly aligned with the Majonicaceae, its position
within the clade is not well resolved. When analyzed with other Voltziaceae, *Pararaucaria*
branches from an unresolved basal polytomy. Thus there is no evidence of affinities with other
members of this family. With group 2 conifers it diverges basal to the *Dolmitia-Pseudovoltzia*
subclade but distal to *Majonica*. With group 1 conifers it exhibits this same position in about
one-third of the equally parsimonious trees, occurs as a sister genus with *Majonica* in another
one-third, and diverges from an unresolved polytomy in the final one-third.

Although the analyses indicate the divergence of *Schizolepis* from the Majonicaceae, its
position within this clade is not well resolved. Harris (1979) speculated that this genus was re-
lated to the *Pinus*, because it has two ovules per ovuliferous scale, and in the modern family.
However, there is no indication of such a relationship. Indeed, in the analysis of this genus
with group 2 conifers, it branches from an unresolved trichotomy distal to the *Pinus*. Thus the
putative relationship is unsubstantiated.

The various trees indicate the divergence of *Swedenborgia* from within the Majonicaceae
distal to *Majonica* and basal to the *Dolmitia-Pseudovoltzia* subclade (Fig. 7C). With group 2
conifers *Swedenborgia* is linked with the latter pair and *Araucaria* in an unresolved trichot-
omy. With group 1 conifers the genus shares an unresolved trichotomy with *Cunninghamia*
and *Cryptomeria*, and in two of the four equally parsimonious trees *Swedenborgia* and *Cryp-
tomeria* are sister taxa. The association of *Swedenborgia* and *Araucaria* with group 2 conifers
supports its relationship with *Cryptomeria* and *Cunninghamia* in group 1 conifers because
Araucaria is part of the latter clade was well. When analyzed with other Voltziaceae, *Sweden-
borgia* and *Aethophyllum* are sister genera, but there is no indication of the latter genus assort-
ing with any of the modern genera that *Swedenborgia* does.

In the analysis with basal conifers (Fig. 7C) *Tricranolepis* diverges basal to *Dolmitia* and
Pseudovoltzia and distal to *Majonica*, whereas it is linked in an unresolved trichotomy with

these two genera in the analysis with group 2 conifers. Twelve of the 20 equally parsimonious trees in the analysis with group 1 conifers shows a similar lack of resolution, but there is a pairing with *Majonica* in two trees and a linkage with *Cryptomeria* and *Cunninghamia* in 6 of the 16 trees.

In four of the five equally parsimonious trees *Voltziopsis* occurs as a sister taxon with *Walchiostrobus meyenii* (Fig. 5). In the fifth tree *Voltziopsis* shares a node with the Majonicaceae clade, and this overall group shares a node with *Walchiostrobus meyenii*. Thus the latter tree is the only one in which a relationship between *Voltziopsis* and the Majonicaceae can be inferred, and the other four trees indicate that *Voltziopsis* probably branched from within the Utrechtiaceae. This relationship was also apparent in my earlier cladistic work (Miller, 1988: Fig. 10.1), in which the genus branched in the cladogram basal to modern groups and Voltziaceae but distal to a composite OTU that included taxa now in the Emporiaceae, Utrechtiaceae, and Majonicaceae.

Voltziopsis has been regarded as relatively primitive because it retains the bifurcate bract apex that is more typical of *Emporia* and certain, but by no means all, genera of the Utrechtiaceae (Table II). Other features, such as the relative lack of fusion between segments of the fertile dwarf shoot, also contribute to this aspect (Townrow, 1967b). Yet there appears to be more reduction in number of parts of the fertile dwarf shoot than is typical of the Utrechtiaceae, and this argues against including *Voltziopsis* in that family.

Townrow (1967b) compared the genus with *Swedenborgia* while acknowledging the greater fusion of parts in the latter genus. He concluded that it was premature to classify the genus in any family other than the Voltziaceae. Townrow (1967b) also commented that he could not see an obvious connection with *Emporia* (*Lebachia*) and that both genera probably evolved from an early complex of conifers. The cladogram (Fig. 5) in the present report supports that idea and points more specifically to an ancestral source within the Utrechtiaceae. The Early Triassic occurrence of *Voltziopsis* is consistent with this derivation.

VI. Conclusions

The view of conifer evolution that prevailed during the past forty years held that modern families originated from Late Paleozoic ancestors of the Lebachiaceae via Early Mesozoic "transition conifers" of the Voltziaceae (Arnold, 1947; Miller, 1977; Stewart & Rothwell, 1993). In the last decade our knowledge of Late Paleozoic conifers has expanded significantly. The present cladistic work suggests that there is a phylogenetic basis for the Late Paleozoic conifer families Emporiaceae, Utrechtiaceae, and Majonicaceae and that most modern families diverged from different ancestors in the latter two families (Fig. 21). Early Mesozoic conifers of the Voltziaceae and Cheirolepidiaceae also diverged from these two Paleozoic families and, except for *Cycadocarpidium*, played no evident role in the evolution of living conifers.

The Majonicaceae branches from the Utrechtiaceae in cladograms and probably evolved from an ancestor in this family with an ovuliferous dwarf shoot and subtending bract resembling those of *Walchiostrobus meyenii*. Two other taxa included in the analyses branch from the Utrechtiaceae. *Voltziopsis* shares an ancestor with *Walchiostrobus meyenii*, and *Taxus* shares one with *Walchiostrobus florinii*.

The Taxaceae thus appears to have branched from ancestors within the Utrechtiaceae and is the only modern family to have done so. All others have their origins within the Majonicaceae. *Podocarpus* branches from basal Majonicaceae and may share an ancestor with *Majonica*. The Cupressaceae, Sciadopityaceae, and certain Taxodiaceae share an ancestor with
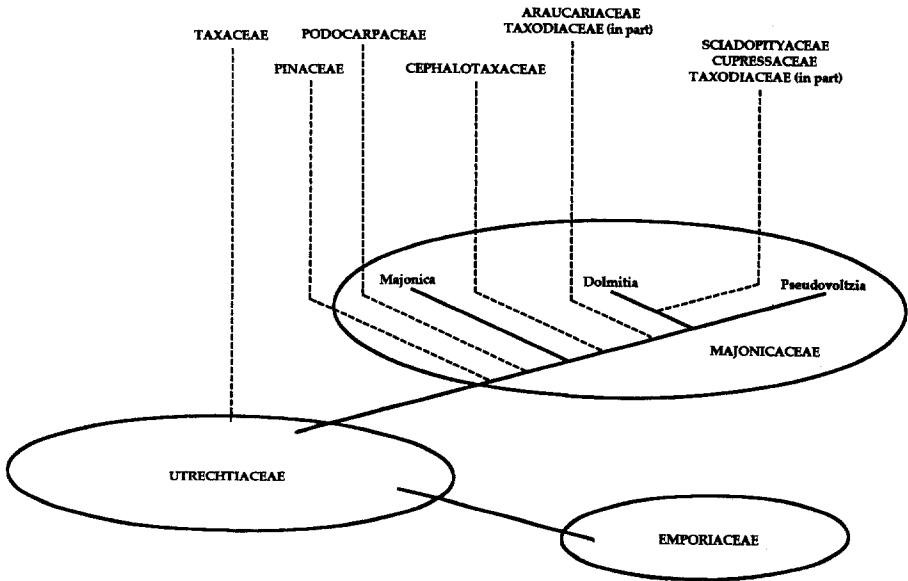
Fig. 21. Interpretive diagram showing the phylogenetic relationships of the modern families Majoni-caceae and Utrechtiaceae, inferred from the cladograms.

Dolmitia, whereas other Taxodiaceae, Araucariaceae, and *Cycadocarpidium* diverge from the *Dolmitia-Pseudovoltzia* subclade basal to *Dolmitia*. Thus the Taxodiaceae appears to have had a biphyletic origin. The Cephalotaxaceae occurs distal to the Pinaceae and Podocarpaceae and basal to other modern families. The Pinaceae is associated with the Majonicaceae clade and diverges from it basal to any of the known extinct or extant genera.

The above relationships in many cases are consistent with the results of others working on living conifers.

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