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EXPERIMENTAL CLADISTIC ANALYSIS OF ANATOMICALLY PRESERVED ARBORESCENT LYCOPSIDS FROM THE CARBONIFEROUS OF EURAMERICA: AN ESSAY ON PALEOBOTANICAL PHYLOGENETICS[1]

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ABSTRACT

This evolutionary cladistic analysis of the arborescent (wood-producing) lycopsids, an exclusively fossil group of vascular plants, is confined to the strongest available data: anatomically preserved fossils that have been painstakingly reconstructed into conceptual whole plants. Ten Carboniferous genera are represented by 16 species: four pseudoherbs/"shrubs" and 12 of the arboreous (tree-sized) species that epitomize the Pennsylvanian coal swamps of Euramerica. The 69 vegetative and 46 reproductive characters are described in detail; several key terms are redefined and homologies reassessed. Binary coding was imposed throughout the data matrix, which contained only 5% missing values despite limited X-coding. Lack of an acceptable outgroup necessitated construction of a hypothetical ancestor for character polarization and tree rooting.

Our experimental approach analyzed the full data matrix plus four submatrices (growth habit characters excluded, *Chaloneria* excluded, vegetative characters only, reproductive characters only) and screened topologies of subminimal as well as minimal length. Interpretation focuses on the ten monophyletic genera and marginally favors the topology ((*Paurodendron, Oxroadia*) (*Anabathra* (*Chaloneria* (*Sigillaria* ((*Diaphorodendron, Synchysidendron*) (*Hizemodendron* (*Lepidodendron, Lepidophloios*)))))). Other parsimonious topologies allow dissociation of the *Paurodendron–Oxroadia* clade (probably justified), transposition or unification of *Anabathra* and *Chaloneria*, and addition of *Sigillaria* to the *Diaphorodendron–Synchysidendron* clade. The analysis confined to vegetative characters translocates *Hizemodendron* close to the base of the clade, thus uniting the non-trees as an ostensibly paraphyletic basal group. The analysis confined to reproductive characters more closely resembles the analysis of all characters, but fails to resolve relationships among the four basal, bisporangiate-coned genera, and between *Hizemodendron* and *Lepidodendron.* These observations cast doubt on the value of partial-plant and isolated-organ phylogenies.

Parsimonious use of the increasingly sophisticated and *K*-selected reproductive strategies as the basis of the overall phylogeny inevitably renders homoplastic the partly discordant vegetative architectures (including the tree habit). Consequently, a poorly resolved paraphyletic plexus of four primitive, bisporangiate-coned genera (*Paurodendron, Oxroadia, Anabathra, Chaloneria*) subtends a monophyletic monosporangiate-coned clade of three well-supported, monophyletic families: the Sigillariaceae (*Sigillaria*) are primitive relative to the Diaphorodendraceae (*Diaphorodendron* sens. str., *Synchysidendron*) and the Lepidodendraceae (*Hizemodendron, Lepidodendron* sens. str., *Lepidophloios*), which together are characterized by a single functional megaspore per megasporangium. This apparently progressive evolutionary trend toward seedlike reproduction increased ecological specialization and is consistent with adaptive scenarios.

In contrast with reproductive features, vegetative features such as the determinate growth, centralized rhizomorphic rootstock, and small number of module types that constitute the bauplan (rhizomorph and stem essential, lateral and crown branches optional) apparently predisposed the arborescent lycopsids to nonadaptive saltational evolution. Mutation of genes controlling early development allowed radical changes in growth architecture, and consequent

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epigenetic readjustment and adaptive honing affected many other vegetative characters. The progenetic (heterochronic) origin postulated for the pseudoherb *Hizemodendron* may also apply to *Chaloneria* and the other pseudoherbs (*Paurodendron*, *Oxroadia*), arguably comprising their value in scoring habit characters for the hypothetical ancestor.

Other limitations of the present data matrix are the large number of genus-level autapomorphies (at least partly reflecting the absence of pre-Pennsylvanian arboreous species), the inclusion of only one bisporangiate-coned tree (*Anabathra*) and of only one putative isoetalean (*Chaloneria*). More primitive OTUs are needed to investigate the origins of profound character states shared by all OTUs in the present study (e.g., secondary thickening, determinate growth, centralized rhizomorph, heterospory), and to confirm the crucial hypotheses of monophyly for the monosporangiate cone and the single functional megaspore. Repeated simplification of growth architecture by progenesis and of megaspore ornamentation by functional redundancy show that evolution did not consistently increase morphological complexity among the arborescent lycopsids. Synapomorphies of highest burden (and therefore lowest homoplasy) tend to represent features of intermediate scale.

We have not identified any significant drawbacks of cladistically analyzing an exclusively extinct set of OTUs. Rather, we recommend further study of some under-researched aspects of phylogeny reconstruction in general: (1) the effect of missing values on tree length calculations and on character state optimization; (2) the minimum acceptable level of empirical support (apomorphic states per OTU); (3) means of recognizing heterochrony in cladograms; and (4) less methodologically constrained phenetic adjuncts to strict cladistic analyses.

Coal-swamp floras from the Pennsylvanian of Euramerica have remained the most intensively investigated and best known of all Paleozoic plant communities throughout the last two centuries of detailed scientific study. Their popularity largely reflects the unusual abundance of spores, adpressed megafossils, and anatomically preserved megafossils in these depositional environments and the economic importance of coal (e.g., Scott, 1987). Studies of permineralized coal-ball floras (e.g., Scott & Rex, 1985) have been especially important in providing detailed information on the morphology and anatomy of the plants that comprised the coal-swamp communities (e.g., Taylor, 1981; Stewart, 1983; Bateman, 1991b; DiMichele et al., 1992). Early workers (e.g., Grand'Eury, 1877; Williamson, 1893; Scott, 1908; Seward, 1910) soon recognized that the majority of the coal-ball floras were of low diversity and dominated (both in terms of body size and biomass) by trees that exhibited clear morphological (and, by inference, phylogenetic) similarities to an extant group of ecologically insignificant, exclusively herbaceous, free-sporing plants, the lycopsids or "clubmosses" (see Appendix 1A for discussion of the nomenclature and systematics of higher taxa).

The fossil tree-lycopsids occur in a severely disarticulated condition, and must be painstakingly reconstructed if they are to be understood as biological entities. Some early speculative *restorations* of these plants were remarkably accurate (e.g., Grand'Eury, 1877). Recently, more rigorous *reconstructions* (DiMichele, 1979a, b, 1980, 1981, 1983, 1985; DiMichele & Phillips, 1985) have been achieved using evidence of organic connection supported by quantified association/dissociation values (e.g., Bateman & Rothwell, 1990) and paralleled by increased knowledge of ontogeny (Walton, 1935; Eggert, 1961; Chaloner & Meyer-Berthaud, 1983; Phillips & DiMichele, 1992) and reproductive biology (e.g., Thomas, 1978, 1981; Phillips, 1979).

Earlier higher classifications of the arborescent lycopsids focused on ostensibly well-known genera such as *Sigillaria*, *Bothrodendron*, *Lepidophloios*, and '*Lepidodendron*' sens. lat. and remained fairly stable throughout much of this century (see Chaloner, 1967, for the most detailed account). More recently, these conventional supraspecific classifications have been challenged. Thomas & Brack-Hanes (1984) devised a controversial system of satellite taxa that more accurately reflects the variable and fragmentary nature of the paleobotanical data, albeit at the expense of emphasizing reproductive structures rather than whole plants. Using a contrasting philosophy (but generating an equally controversial result), DiMichele (1979a, b, 1980, 1981, 1983, 1985) revised several arborescent lycopsid genera as part of a program of whole-plant reconstruction, implicitly intended to delimit potentially monophyletic taxa within *Lepidodendron* sens. lat. This revision has been extended by Bateman & DiMichele (1991) and DiMichele & Bateman (1992).

We believe that sufficient credible whole-plant reconstructions of arborescent lycopsids are now available (Figs. 1, 2) to allow explicit phylogenetic analysis, using cladistic methods. To date, cladistic analysis has been applied sparingly to long-extinct (i.e., paleobotanical) species, which have invariably been admixed with their extant putative descendants. Most of these studies focused on seed plants (Hill & Crane, 1982; Crane, 1985a, b; Doyle & Donoghue, 1986a, b, 1987a, b; Donoghue & Doyle,

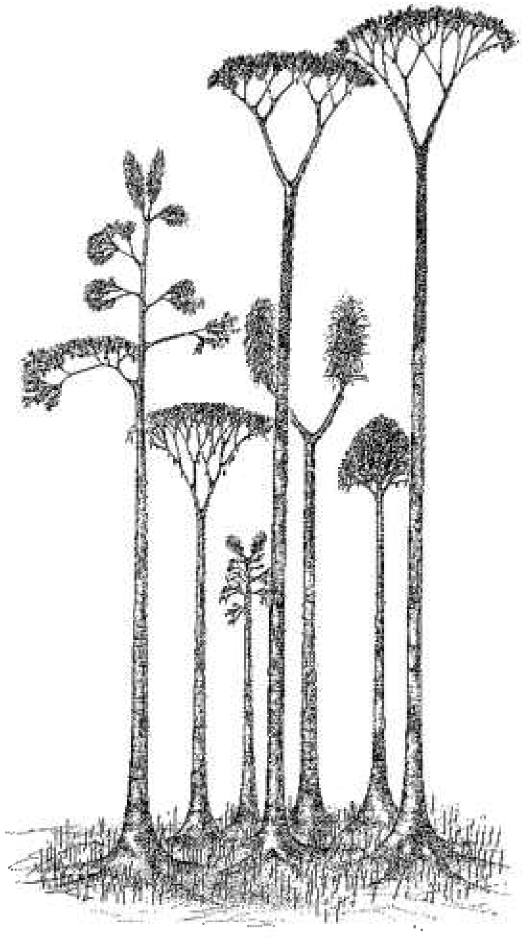

FIGURE 1. Reconstructions of tree lycopsids, listed from left to right: *Diaphorodendron scleroticum* (modified after Wnuk, 1985, fig. 19), *Lepidophloios hallii* (modified after DiMichele & Phillips, 1985, fig. 2), *Anabathra pulcherrima* (redrawn from DiMichele & Phillips, 1985, fig. 2), *Synchysidendron dicentricum* (modified after Wnuk, 1985, fig. 19), *Sigillaria approximata* (modified after Hirmer, 1927, fig. 284, and Stewart, 1983, fig. 11.19). *Diaphorodendron phillipsii*, *Lepidodendron hickii* (after Wnuk, 1985, fig. 12, and Thomas & Watson, 1976, textual description). All ×0.003.

1989a, b; Donoghue, 1989; see also Hill & Camus, 1986, on marattialean "ferns"). Conceptually, our study owes much to Doyle & Donoghue (1986b) in particular, but differs from all the above studies in focusing on relationships of taxa within a widely accepted order (Class Lycopsida, Order Lepidodendrales) that may lack extant descendants; certainly, all of the genera analyzed are extinct. The lycopsids are of particular phylogenetic interest as a potential sister group of the remainder of the tracheophyte clade (Doyle & Donoghue, 1986b, fig. 1; DiMichele & Skog, 1992).

Our purpose was not merely to unravel the historical relationships of various arborescent lycopsids. We chose to analyze our data within the now well-established framework of evolutionary cladistics (e.g., Wiley, 1981; Farris, 1983; Funk & Brooks, 1990; Wiley et al., 1991) in order to test scenarios concerning patterns and underlying mechanisms of evolution within the group. In particular, we wished to assess preconceived hypotheses concerning the phylogenetic distributions, functional roles, and ecological significance of aspects of growth architecture and reproductive biology.

The structure and content of this paper reflect the philosophical framework outlined by Neff (1986) and elaborated by Bryant (1989). Bryant (1989, fig. 1b) emphasized the creative, deductive nature of a priori character analysis and a posteriori phylogenetic interpretation relative to the purely synthetic, empirical, inductive procedure of tree construction. Our phylogenetic analysis investigates all three of these phases in detail, attempting to exploit the main benefit of cladistics: conceptual and methodological explicitness.

SELECTION AND PARTITIONING OF WHOLE-PLANT SPECIES

In order to qualify for inclusion in this study, plants had to be (1) either members or potential outgroups of the Order Lepidodendrales (lycopsids possessing rhizomorphs, secondary thickening, periderm, ligules, and heterospory: Stewart, 1983), (2) anatomically preserved, and (3) known in sufficient detail that all disarticulated component organs could be reconstructed to form a conceptual whole plant (Chaloner, 1986; Bateman & Rothwell, 1990; Bateman, 1991a); only whole-plant species can be thoroughly characterized. In practice, these three prerequisites confined our study to the Carboniferous of Euramerica (Fig. 3), specifically to two species of *Oxroadia* from Mississippian volcanigenic terrains (Bateman, 1988, 1992) and 15 species of nine genera (Appendix 1C) from Pennsylvanian coal swamps (e.g., Hirmer, 1927; Phillips, 1979; DiMichele & Phillips, 1985). (We have deliberately avoided formal reclassification in this paper, though several recommendations for taxonomic revision are outlined in Appendix 1C. Papers derived from this study segregated *Hizemodendron* from *Lepidodendron* sens. str. (Bateman & DiMichele, 1991) and *Synchysidendron* from *Diaphorodendron*, as well as erecting the new family Diaphorodendraceae (DiMichele & Bateman, 1992). Our use of the generic name *Anabathra* rather than *Paralycopodites* follows Pearson (1986) and is justified in Appendix 1B).

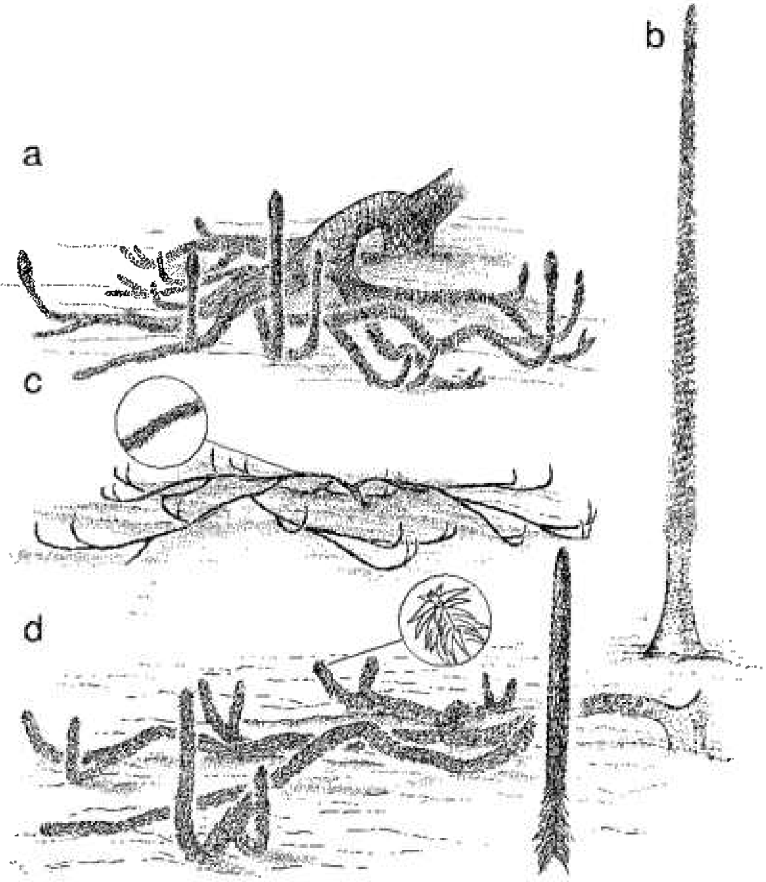

FIGURE 2. Reconstructions of small-bodied lycopsids.—a. *Hizemodendron serratum*.—b. *Chaloneria cormosa* (redrawn from Pigg & Rothwell, 1983a, fig. 1).—c. *Paurodendron fraipontii* (redrawn from Schlanker & Leisman, 1969, fig. 13).—d. *Oxroadia gracilis* (modified after Bateman, 1988, fig. 7.11). Aspects of the *Hizemodendron* reconstruction in particular are speculative, and it is more appropriately described as a restoration (Bateman & DiMichele, 1991). a, b = ×0.03, c, d = ×0.12.

These conceptual whole-plant species of arborescent lycopsid are listed in Table 1, together with the bibliographic sources of much of our data. Each conceptual whole plant encompasses at least nine readily distinguished organs (rootlet, rhizomorph, stem, branch, leaf, megasporophyll, megaspore, microsporophyll, microspore) that are formally named, either individually or in aggregates, as organ-species. Table 2 correlates the more important of the organ-species that have been awarded Linnean binomials. Some organ-species binomials encompass more than one organ; most of the larger-bodied whole-plant species encompass five named organ-species (rootlet/rhizomorph, stem/branch/leaf, strobilus/megasporophyll/microsporophyll, megaspore, microspore) and the smaller-bodied four (rootlet/rhizomorph is not nomenclaturally distinguished from stem/branch/leaf). Other binomials are applied to homologous organs of more than one whole-plant species (i.e., form-species sensu Bateman & Rothwell, 1990: an organ whose morphological expression is indistinguishable in two or more whole-plant species). Confining our study to anatomically preserved material avoided the further complication of correlating the same organs of the same whole-plant species in different preservation states (e.g., Galtier, 1986; Bateman, 1991a).

Evidence for the reconstruction of these organ-species into whole-plant species can be ascribed to three main categories (in order of increasing probability of correct correlation): association/dissociation (co-occurrence in space and time), anatomical similarity, and organic connection (this has traditionally been regarded as proof of successful reconstruction, though Bateman & Rothwell (1990) argued that at best it constitutes only a strong hypothesis). In practice, anatomical similarity is

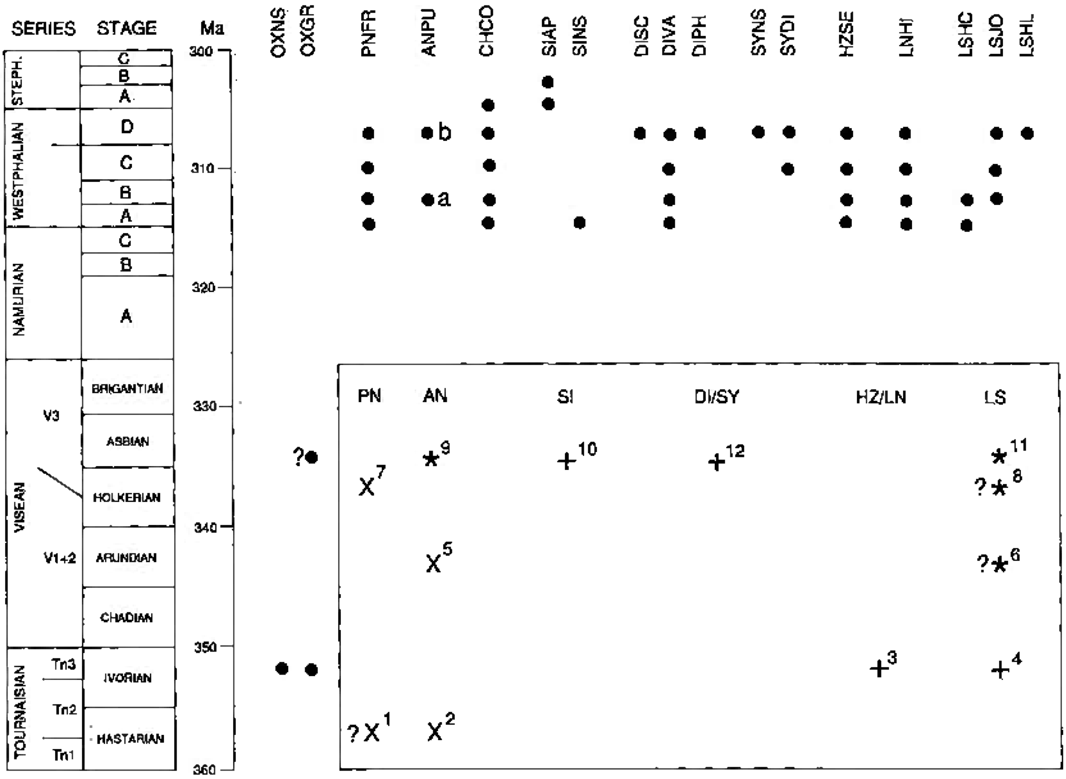

FIGURE 3. Reported time ranges of OTUs (see caption to Table 3 for key to abbreviations). In general, last appearances are more reliable than first appearances. Inset shows first recorded occurrences of the genera (× = vegetative remains only, + = reproductive remains only, * = vegetative and reproductive remains). Superscripts denote bibliographic sources; Montagne Noire, south-central France: Rowe & Galtier, 1989, Bateman, 1992 (1), Meyer-Berthaud, 1984 (2); Burnmouth, northeastern England: Long, 1964 (3), Long, 1968 (4); Glenarbuck, southwestern Scotland: Smith, 1962 (5), Smith, 1962, 1964 (6); Laggan, Arran, southwestern Scotland: Fry, 1954 (7), Walton, 1935, Scott, 1990 (8); Pettycur, southeastern Scotland: Williamson, 1872, 1893, Scott, 1900, 1920, Gordon, 1910, Jongmans, 1930, DiMichele, 1980, Pearson, 1986 (9), Benson, 1908 (10), Scott, 1901, Gordon, 1908 (11); Kingswood, southeastern Scotland: Scott et al., 1986 (12) (see also Scott et al., 1984). Time scale follows Leeder (1988). ᵃ *Flemingites schopfii* cone. ᵇ *F. diversus* cone.

usually employed in conjunction with association/dissociation, and both are used as an adjunct to organic connection, especially when attempts to reconstruct whole plants by organic connection are only partially successful. In the case of our tree-lycopsids, organic connection is particularly difficult to demonstrate between reproductive organs and vegetative axes. It is easier to achieve correlations between different organs within these two main categories; for example, by extracting in situ megaspores and microspores from cones (e.g., Thomas, 1987; Willard, 1989a, b). Additional information acquired since our analyses were performed suggests a closer relationship between *Lepidophloios johnsonii* and *L. hallii*. Otherwise, the least conclusive reconstructions in our analysis are *Hizemodendron serratum*, where doubts surround its habit and tentatively correlated microsporangiate cone (cf. Baxter, 1965; Leisman & Rivers, 1974; Bateman & DiMichele, 1991), and *Sigillaria* "sp. nov.," which is strictly a Westphalian A composite from more than one locality.

It should be emphasized that the inevitable disarticulation of their constituent individual organisms into organ-aggregates or single organs renders the reconstructed whole-plant species both conceptual and typological. Each species is conceptual in the sense that it is a summation of several probabilities of correlation of pairs of organs rather than an integral, demonstrable fact. It is typological in the sense that intraspecific variation can only be documented among different specimens of the same organ; complete data sets cannot be compiled for specific individuals, in contrast with morphometric studies of extant plants (e.g., Bateman & Denholm, 1989a, b). This prevents objective de-

TABLE 1. List of OTUs (1–16) with selected synonyms and bibliographic sources. *Oxroadia* sp. nov. (2a) was not used as an OTU as it did not differ from *O. gracilis* (2) in the qualitative characters scored.

Number	Taxon
1	*Paurodendron fraipontii* (Leclercq) Fry (syn. *Botryopteris fraipontii, Selaginella fraipontii*) Fry (1954); Phillips & Leisman (1966); Schlanker & Leisman (1969); Rothwell & Erwin (1985)
2	*Oxroadia gracilis* Alvin Alvin (1965, 1966); Long (1964, 1971, 1986); Bateman (1988, 1992)
2a	*Oxroadia* sp. nov. Bateman (1988, 1992)
3	*Anabathra pulcherrima* Witham (syn. *Paralycopodites brevifolius, Lepidodendron brevifolium* pro parte) Felix (1954); Brack (1970); Morey & Morey (1977); DiMichele (1980)
4	*Chaloneria cormosa* (Newberry) Pigg & Rothwell (syn. *Polysporia mirabilis*) DiMichele et al. (1979); Pigg & Rothwell (1979, 1983a, b, 1985)
5	*Sigillaria approximata* Fontaine & White Schopf (1941); Delevoryas (1957); Eggert (1972)
6	*Sigillaria* sp. nov. Brongniart (1836); Benson (1918); Lemoigne (1961)
7	*Synchysidendron* sp. nov. DiMichele (1979b, 1981); DiMichele & Bateman (1992)
8	*Synchysidendron dicentricum* (Felix) DiMichele & Bateman (syn. *Lepidodendron dicentricum, Diaphorodendron dicentricum*) Arnold (1960); DiMichele (1979b, 1981, 1985); DiMichele & Bateman (1992)
9	*Diaphorodendron phillipsii* DiMichele (syn. *Lepidodendron phillipsii*) DiMichele (1981, 1985)
10	*Diaphorodendron vasculare* (Binney) DiMichele (syn. *Lepidodendron vasculare*) Carruthers (1869); Hovelacque (1892); Seward (1910); DiMichele (1981, 1985)
11	*Diaphorodendron scleroticum* (Pannell) DiMichele (syn. *Lepidodendron scleroticum*) Pannell (1942); DiMichele (1981, 1985)
12	*Hizemodendron serratum* (Felix) Bateman & DiMichele (syn. *Lepidodendron serratum*) Felix (1952); Baxter (1965); Leisman & Rivers (1974); DiMichele (1981, 1983); Bateman & DiMichele (1991)
13	*Lepidodendron hickii* Watson (syn. *L. aculeatum* pro parte, *L. obovatum* pro parte) Scott (1906); Seward (1906); Watson (1907); DiMichele (1983); Willard (1989a)
14	*Lepidophloios harcourtii* (Witham) DiMichele (syn. *Lepidodendron harcourtii*) Bertrand (1891); Seward (1899); Zalessky (1912); Koopmans (1928); Calder (1934)
15	*Lepidophloios johnsonii* (Arnold) DiMichele Arnold (1940); DiMichele (1979a); Winston (1988)
16	*Lepidophloios hallii* (Evers) DiMichele Evers (1951); Felix (1952); Andrews & Murdy (1958); Brotzman & Schabiliov (1972); DiMichele (1979a)

limitation of individual organisms into species using morphological discontinuities and hinders attempts to distinguish genetic (and thereby taxonomically and phylogenetically useful) contributions to phenotype from those caused by ontogeny and ecophenotypy (e.g., Bateman & Denholm, 1989c). Ironically, this inability to resolve variation at the whole-organism level can be considered advantageous in a cladistic analysis. In most cases, less information is discarded when a paleobotanical spe-

TABLE 2. Correlations of organ-species that constitute the whole-plant OTUs listed in Table 1. Asterisked whole-plant species lack recognized autapomorphies (see caption to Table 3 for explanation of abbreviations).

OTU	Rhizomorph	Vegetative axes	Cones
PNFR	←	*Paurodendron fraipontii*	→ *Selaginellites crassicinctus* (⚥)
OXGR*	←	*Oxroadia gracilis*	→
OXNS*	←	*Oxroadia* sp. nov.	→
ANPU	*Stigmaria ficoides*	*Anabathra pulcherrima*	*Flemingites diversus/schopfii* (⚥)
CHCO	←	*Chaloneria cormosa*	→
SIAP	*Stigmaria* sp. nov.	*Sigillaria approximata*	*Mazocarpon oedipternum* (♀+♂)
SINS*	*Stigmaria* sp. nov.	*Sigillaria* sp. nov.	*Mazocarpon schorense/cashii* (♀+♂)
SYNS	*Stigmaria ficoides*	*Synchysidendron* sp. nov.	*Achlamydocarpon varius* (♀+♂)
SYDI	*Stigmaria ficoides*	*Synchysidendron dicentricum*	*Achlamydocarpon varius* (♀+♂)
DIPH	*Stigmaria ficoides*	*Diaphorodendron phillipsii*	*Achlamydocarpon varius* (♀+♂)
DIVA*	*Stigmaria ficoides*	*Diaphorodendron vasculare*	*Achlamydocarpon varius* (♀+♂)
DISC	*Stigmaria ficoides*	*Diaphorodendron scleroticum*	*Achlamydocarpon varius* (♀+♂)
HZSE*	←	*Hizemodendron serratum*	*Achlamydocarpon* sp. nov. (♀) *Lepidostrobus minor* (♂)
LNHI	*Stigmaria ficoides*	*Lepidodendron hickii*	*Achlamydocarpon takhtajanii* (♀) *Lepidostrobus* cf. *oldhamius* (♂)
LSHC*	*Stigmaria ficoides*	*Lepidophloios harcourtii*	*Lepidocarpon lomaxi* (♀) *Lepidostrobus oldhamius* (♂)
LSJO*	*Stigmaria ficoides*	*Lepidophloios johnsonii*	*Lepidocarpon lomaxi* (♀) *Lepidostrobus oldhamius* (♂)
LSHL	*Stigmaria ficoides*	*Lepidophloios hallii*	*Lepidocarpon lomaxi* (♀) *Lepidostrobus oldhamius* (♂)

cies is reduced to a single unvarying (and thus, by definition, typological) data set (the normal procedure prior to cladistic analysis) than in comparable studies of extant species. Also, the paleobotanist is effectively constrained to conceptual morphospecies and is therefore spared the trauma experienced by neobotanists when selecting an appropriate species concept (cf. de Queiroz & Donoghue, 1988, 1990; Nelson, 1989; Wheeler & Nixon, 1990; Nixon & Wheeler, 1990). Although we wished primarily to investigate generic relationships, our use of species (of whatever kind) as basic operational taxonomic units (OTUs) created fewer difficulties when typologically eliminating intra-OTU variation than the more common approach of selecting sets of OTUs from higher (and often variable) levels in the taxonomic hierarchy (cf. Doyle & Donoghue, 1986b).

SELECTION, PARTITIONING, AND POLARIZATION OF CHARACTERS

The provisional selection of whole-plant species preceded the partitioning of the conceptual organisms into characters and, subsequently, of the characters into putatively homologous character states. Our chosen characters are listed below; they are identified by numbers prefixed by the letter C.

Partitioning a representative, conceptual organism of a species into morphological characters is based on the assumption that each character represents a discrete, recognizable, and homologous feature. This is the most subjective and ultimately most influential phase of any cladistic analysis; it is especially unfortunate that the only sources of evidence to support assertions of homology are circumstantial; consequently, such assertions cannot be conclusively verified (e.g., De Beer, 1971; Riedl, 1979; Patterson, 1982; Kaplan, 1984; Roth, 1984, 1988, 1991; Tomlinson et al., 1984; Neff, 1986; Ridley, 1986; Bryant, 1989; G. P. Wagner, 1989). Features that do not vary among the chosen OTUs provide no information on their phylogenetic relationships, though such characters are valuable in characterizing the entire ingroup (they may, of course, have a greater level of universality than the ingroup alone). Continuously variable characters can be artificially partitioned into binary or multiple character states (e.g., by gap coding (Archie, 1985) or segment coding (Chappill, 1989)), but we believe that such "soft" characters are more appropriately analyzed by phenetic methods (cf. Bateman, 1990a; Farris, 1990). We therefore excluded continuous (metric) and quasicontinuous (meristic) characters from our data matrix, even though they were the only potential source of unique

TABLE 2. Continued.

Megaspore	Microspore
Triangulatisporites triangulatus	*Cirritriradiates annulatus*
Setispora subpalaeocristata	*Auroraspora* cf. *asperella* 'A'
Setispora pannosa	*Auroraspora* cf. *asperella* 'B'
Lagenicula rugosa	*Lycospora orbicula*
Valvisisporites auritus	*Endosporites ornatus*
Tuberculatisporites reinschii	*Crassispora kosankei*
Tuberculatisporites mamillarius	*Crassispora* sp. nov.
Cystosporites varius	*Granasporites medius*
Cystosporites varius	*Granasporites medius*
Cystosporites varius	*Granasporites medius*
Cystosporites varius	*Granasporites medius*
Cystosporites varius	*Granasporites medius*
Cystosporites giganteus	*Lycospora* cf. *pusilla*
Cystosporites giganteus	*Lycospora pusilla*
Cystosporites giganteus	*Lycospora pellucida*
Cystosporites giganteus	*Lycospora* sp. nov.
Cystosporites giganteus	*Lycospora granulata*

(and thereby distinguishing) characters for eight of the 17 species initially selected for study (Table 2).

We opted for a uniformly bistate data matrix, on the grounds that bistate characters are more readily analyzed algorithmically and the distributions of character states on the resulting trees are more easily interpreted. This decision had three potentially deleterious consequences:

First, the hierarchy of organs that constitute the plants introduced a degree of character duplication; we often found it necessary to include a character scoring an organ present or absent (e.g., the rhizomorph: C8) before partitioning additional characters (C9–C13) to describe its detailed morphology in those OTUs that possess that structure. This is to be expected, given the strongly hierarchical nature of morphological and anatomical homologies (Riedl, 1979; Fortey & Jefferies, 1982; Wimsatt & Schank, 1988; Roth, 1991). We adopted a similarly relaxed attitude to the inclusion of potentially coupled characters "correlated for developmental-genetic reasons" (Doyle & Donoghue, 1986b: 338); indeed, we hoped that our analysis would reveal such character correlations, which are by no means intuitively obvious a priori.

Second, even more complicated hierarchies of related characters, such as stelar (C14–C19) and periderm (C39–C43) anatomy, occur in complexes. In such cases, a broad concept of character can be selected, allowing coding in multistate rather than bistate format. Such multistate characters tend to be especially difficult to polarize satisfactorily and may have to be input unordered. If they are to be ordered, several methods are available for coding and polarizing such characters (e.g., O'Grady & Deets, 1987). The preferred options are additive binary coding (Brooks, 1984) or nonredundant linear coding (O'Grady & Deets, 1987; O'Grady et al., 1989). Both operate via a hypothetical tree representing transitions between the polarized multiple states of the character in question. By reducing the character states to a set of bistate subsets, additive binary coding labels every node of the character tree and thus generates a large number of narrowly defined operational characters. Nonredundant linear coding avoids this proliferation of characters, but at the expense of retaining characters in a multistate format and arbitrarily designating within the tree a major axis that forms the basis for coding the remaining branches (minor axes). Once mixed with other (typically mostly bistate) characters, multistate characters complicate the generation and subsequent interpretation of cladograms (e.g., Gensel, 1992). We therefore preferred the more primitive but also more intuitive additive binary system, despite the risk of eliminating a priori some ambiguities in the data.

Third, polarization of spore ornamentation characters was rendered especially problematic. They tend to be evolutionarily displacive rather than additive; there appears to be a developmental constraint on the range of features exhibited by the exine of any one species, so that a new type of ornamentation supplants rather than supplements the previous type. We spurned the option of scoring these characters as unordered multistate in order to maintain a uniformly polarized binary matrix. Thus, we treated each type of spore ornamentation as a separate character and assumed a hypothetical plesiomorphic spore lacking all features.

Polarization also presented a more general problem. All three OTUs (*Oxroadia gracilis–Oxroadia* sp. nov., *Paurodendron fraipontii*, *Chaloneria cormosa*) originally screened as potential outgroups (Maddison et al., 1984) exhibited some character states that we were reluctant to regard as plesiomorphic. In *Oxroadia* and *Paurodendron*, we initially believed that such characters were few and almost confined to spore ornamentation. However, *Chaloneria* proved too derived to root the tree successfully. Consequently, we constructed a hypothetical ancestor possessing putatively plesiomorphic states for all characters; it largely reflected character states shared by *Oxroadia* and *Paurodendron*, though for a few problematic characters we elected to screen more distantly related lycopsids for presumed plesiomorphic states.

As in all cladistic analyses, our recognition of alternative character states as *plesiomorphic* and *apomorphic* preceded tree-building. We restrict these terms to character states and use *primitive* and *derived* to describe the relative positions of OTUs on the resulting trees.

Many of the characters considered for inclusion were rejected on the grounds that they were known for less than two-thirds of the OTUs. The most important examples are the detailed histology of the rhizomorph and rootlets (which are well known for the form-species *Stigmaria ficoides* but not for the different types of this rhizomorph correlated with specific whole-plant species), of the leaves (well-documented only for *Oxroadia*: Bateman, 1988), and of the gametophyte (described for few cone-species; e.g., Galtier, 1964, 1970; Brack, 1970; Phillips, 1979; Stubblefield & Rothwell, 1981; Pigg & Rothwell, 1983b), and ultrastructure of spore walls (e.g., T. Taylor, 1973; W. Taylor, 1990).

One hundred fifteen bistate characters were eventually accepted: 69 are vegetative (C1–C4, C8–C72) and 46 are reproductive (C5–C7, C73–C115). The large number of characters reflects the stringent selection criterion of detailed knowledge that was applied to potential OTUs; inclusion of poorly known OTUs would have increased the proportion of missing values in some characters sufficiently to warrant exclusion of those characters from the data matrix.

THE CHARACTERS

Characters are apportioned into 11 categories: the overall habit of the organism (A) and ten constituent organs (B–K). For each category, lists of characters and character states are preceded by discussions of relevant homologies and descriptive terms.

A. Habit (7 characters)

We perceived habit as an overall property of an organism, expressed as a specific bauplan. We describe the group of habits colloquially known as trees (C1) as "arboreous," and use "arborescent" strictly to describe the ability to generate secondary tissues (C29). Thus, all 16 OTUs are considered arborescent, but only 12 are truly arboreous. We reject the frequently used term "secondary wood," because wood is by definition secondary. Only mature woody plants greater than 2 m in overall height are termed trees; *Chaloneria* does not qualify as a tree on this criterion, despite possessing wood (albeit poorly developed) and an elongate, unbranched, upright stem (Pigg & Rothwell, 1983a, b). Recumbent OTUs generating limited amounts of wood are termed pseudoherbs (Bateman, 1988, 1992; DiMichele & Bateman, 1989; Bateman & DiMichele, 1991).

In lepidodendraleans, the main aspects of habit are stem length (C2), frequency of lateral and terminal branching (C3–C4, C6), and the position on the bauplan of reproductive structures (C5–C7). Various combinations of these character states generate several distinct architectures (Figs. 1, 2). Four of these characters (C3–C4, C6–C7) reflect the mode and timing of branching during ontogeny. Lepidodendralean stems branched isotomously (or near-isotomously) only during the final stages of growth (Walton, 1935; Andrews & Murdy, 1958; Eggert, 1961; Wnuk, 1985); terminal branching is profuse in most OTUs, but infrequent in *Anabathra*, *Sigillaria*, and *Diaphorodendron*, and absent in *Chaloneria* (C3). Strongly anisotomous apical divisions during stem growth result in lateral branches that were deciduous (C4) in all OTUs except *Diaphorodendron scleroticum*, where thick bark and wood suggest retention (DiMichele, 1981). The anisotomies terminate in cones (C6), either individually on short peduncles (*Sigillaria*) or collectively on large, repeatedly dichotomous peduncle systems (C7; *Anabathra* and *Diaphorodendron*). In all other OTUs, anisotomous cone-bearing branches were borne only on the terminal, isotomously branched, determinate crown. We regard cauline peduncles and cone-bearing lateral branches as homologous (DiMichele & Bateman, 1989). *Chaloneria* lacked cones (C5), instead bearing sporophylls directly on fertile zones of the unbranched stem (Pigg & Rothwell, 1983a, b). Consequently, it is scored as missing for C6 and C7.

Polarity decisions for several of the habit characters were taken with considerable reservations (especially C1, C2 and C7). Also, in retrospect, the addition of a character representing equality of "crown" branching among the pseudoherbs would have distinguished *Oxroadia* (dominantly isotomous) from *Paurodendron* and *Hizemodendron* (both dominantly anisotomous).

1. Nonarboreous (0); arboreous (1).
2. Stem short (relative to any branches), plant recumbent (0); stem tall, plant upright (1).
3. Dichotomy of trunk apex frequent (0); infrequent or absent (1).
4. Persistent lateral branches absent (0); present (1).
5. Cone present (0); cone absent (1).
6. Lateral branches and/or cone peduncles borne on dichotomous crown (0); excurrent trunk (1).
7. Number of cones on lateral branches one (0); more than one (1).

B. Rootstock (6 characters)

Until recently, the stigmarian rhizomorph (C8) was regarded as arguably the most reliable ubiquitous character state defining the Lepidodendrales (e.g., Phillips & DiMichele, 1992). Rothwell (1984) and Rothwell & Erwin (1985) suggested that the stigmarian rhizomorph is a shoot system modified for rooting; we recognize that it is a shootlike developmental system, but prefer to regard it as a unique organ reflecting limited developmental options within the arborescent lycopsid bauplan. The rhizomorph is radially symmetrical (C9), undergoes repeated isotomous apical dichotomy (C10), is woody (C11), and emits in helical rhizotaxy rigid absorbent rootlets (C12), each containing a single monarch vascular strand. Rothwell & Pryor (1990, 1991) concluded that the tracheary elements of such rhizomorphs are derived largely from the equivalent of a primary thickening meristem. Such branched rhizomorphs were considered radically different from other unbranched rootstocks, whether radial, as in *Paurodendron* (Rothwell & Erwin, 1985), or bilateral, as in *Protostigmaria-Lepidodendropsis* (Jennings, 1975; Jennings et al., 1983), *Chaloneria* (Pigg & Rothwell, 1983a; Pigg & Taylor, 1985), and *Isoetes* (Karrfalt & Eggert, 1977 et seq.; Karrfalt, 1984). However, other studies of rhizomorphs have rendered less profound the distinctions between radial and bilateral symmetry (Karrfalt, 1981, 1984; G. W. Rothwell, pers. comm. 1989) and branched and unbranched vasculature (Bateman, 1988). In our analysis, bilateral symmetry (C9) is retained as a character state; it is scored as an autapomorphy of *Chaloneria* and thus does not affect tree topologies. Scoring the rhizomorph of *Oxroadia* as branched is an oversimplification; it is extremely compact, so that the cortex branches shallowly and less frequently than the vascular system (Long, 1986; Bateman, 1988).

Stigmarian axes exhibit a suite of anatomical character states that, with sufficient study, can be shown to parallel those of correlated stem genera. Given the current paucity of such studies, we used only one such character: the ovoid rootlet gaps (C13) found in *Chaloneria* (Pigg & Rothwell, 1983a) and *Sigillaria approximata* (Eggert, 1972).

8. Rhizomorph absent (0); present (1).
9. Rhizomorph symmetry radial (0); bilateral (1).
10. Rhizomorph branched (0); unbranched (1).
11. Secondary xylem in rhizomorph absent (0); present (1).
12. Rootlets absent (0); present (1).
13. Rootlet gap in wood fusiform (0); ovoid (1).

C. Stele (18 characters)

The morphology and histology of lepidodendralean vascular systems, described in detail by previous authors, are valuable for distinguishing both genera and species (Fig. 4a). Unfortunately, much less attention has been paid to determining homologies and polarizing these complex characters. We recognize six distinct forms of stelar medullation (C14–C19). All genera but *Diaphorodendron* and *Synchysidendron* are regarded as primitively protostelic (C14). The protosteles of *Anabathra*, *Chaloneria*, *Sigillaria*, *Hizemodendron*, *Lepidodendron*, and *Lepidophloios* are medullated (C15). The core of the stele consists of unlignified cells whose dimensions are typical of tracheids, suggesting that they are procambial de-

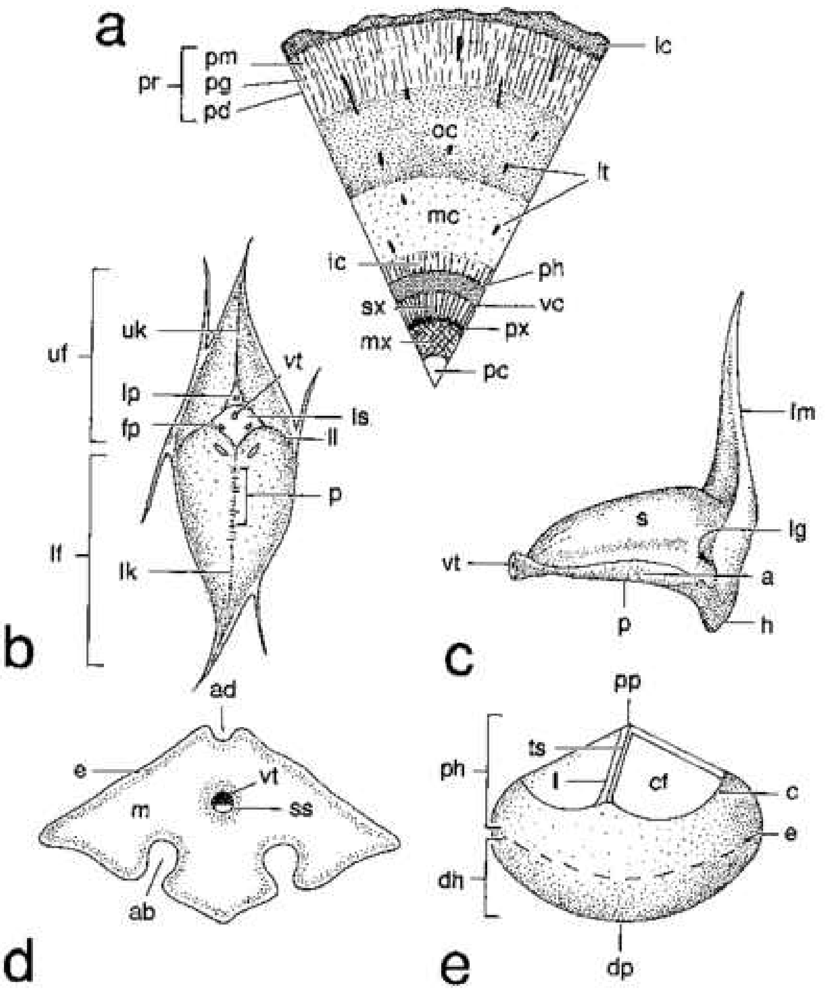

FIGURE 4. Morphological and anatomical terminology for arborescent lycopsids.—a. Axial anatomy (redrawn from fig. 9.44 of Gifford & Foster, 1989: pc = parenchymatous core, px = protoxylem, mx = metaxylem, sx = secondary xylem, vc = vascular cambium, ph = phloem (primary), ic = inner cortex, mc = middle cortex, oc = outer cortex, pr = periderm, pd = phelloderm, pg = phellogen, pm = phellem, lt = leaf traces, lc = leaf cushions).—b. External morphology of leaf base following leaf loss (modified after fig. 11.3B of Stewart, 1983: ls = leaf scar, vt = vascular trace, fp = foliar parichnos, lp = ligule pit, uf = upper field, uk = upper keel, lf = lower field, lk = lower keel, p = plications).—c. External morphology of sporophyll (modified after fig. 11.16C of Stewart, 1983, and fig. 2A of Phillips, 1979: p = pedicel, a = alations, h = heel, lm = lamina, lg = ligule, s = sporangium, vt = vascular trace).—d. Leaf anatomy in proximal transverse section (modified after fig. 11.9E of Stewart, 1983, and fig. 1A of Reed, 1941: vt = vascular trace, ss = sclerenchymatous sheath, m = mesophyll, e = epidermis, ab = lateral abaxial grooves, ad = median adaxial groove).—e. External morphology of spore (pp = proximal pole, dp = distal pole, ph = proximal hemisphere, dh = distal hemisphere, e = equator, ts = triradiate (trilete) suture, l = laesura, c = curvatura, cf = contact face).

rivatives that remained parenchymatous (Walton, 1935; DiMichele, 1979a, b). In *Lepidodendron* and two of the three *Lepidophloios* species, randomly oriented filamentous cells apparently infilled a central cavity (C16; DiMichele, 1979a). In *Diaphorodendron* and *Synchysidendron*, central parenchyma cells are distinctly smaller than those of associated tracheids, suggesting that these genera had a true pith sensu Beck et al. (1982). The two *Synchysidendron* species share the synapomorphy of a solidly parenchymatous pith (C17), and each possesses a histological autapomorphy: secretory cells in *Synchysidendron* sp. nov., and secondarily thickened cells in *S. dicentricum*.

Deep parenchymatous invaginations in *S. dicentricum* and *Synchysidendron* sp. nov. (C20) are not considered homologous with the shallower invaginations of *Chaloneria* (C21); in the *Synchysidendron* species, the parenchymatous wedges are raylike, many cells wide and high, and are often confluent with the pith parenchyma (DiMichele, 1980, 1981). In contrast, the invaginations of *Chaloneria* are smaller and do not reach the central parenchymatous area of the stele (DiMichele et al., 1979; Pigg & Rothwell, 1983a).

Protoxylem configuration and leaf trace emission comprise an integrally linked complex of characters (C22–C28; Fig. 4). Protoxylem is exarch in all OTUs and, with the exception of *Oxroadia* and *Paurodendron*, forms a continuous sheath enclosing the metaxylem (C22). Concentrations of protoxylem observed in transverse sections of axes of many genera are often described individually as "poles" or "points" and collectively as a "corona." This two-dimensional terminology is misleading; protoxylem actually occurs as more-or-less longitudinal strands that are raised to form ridges in "coronate" genera (Bateman, 1988). These protoxylem strands are longitudinal and linear in *Oxroadia*, *Paurodendron*, and *Lepidodendron*, but reputedly anastomose in *Lepidophloios* (C28; Bertrand, 1891).

We have coined new terms for four distinct modes of leaf trace emission (C23–C25; Fig. 5). Leaf traces departing from a longitudinal protoxylem ridge are termed *evaginate*. Those of *Oxroadia* and *Paurodendron* are emitted from a single uninterrupted ridge and are termed *evaginate-direct* (Fig. 5a). Those of *Lepidophloios* originate within a protoxylem ridge at the point where it bifurcates and are termed *evaginate-internal* (C25; Fig. 5d). Most of the genera lack discernable protoxylem ridges and are said to emit *superficial* leaf traces (C23; Fig. 5b). In *Chaloneria*, the trace originates from a submarginal position in the stele and is associated with shallow parenchymatous invaginations (C24, Fig. 5c; DiMichele et al., 1979; Pigg & Rothwell, 1983a). We used X-coding (Doyle & Donoghue, 1986b) to permit evolution of evaginate-internal and invaginate states directly from

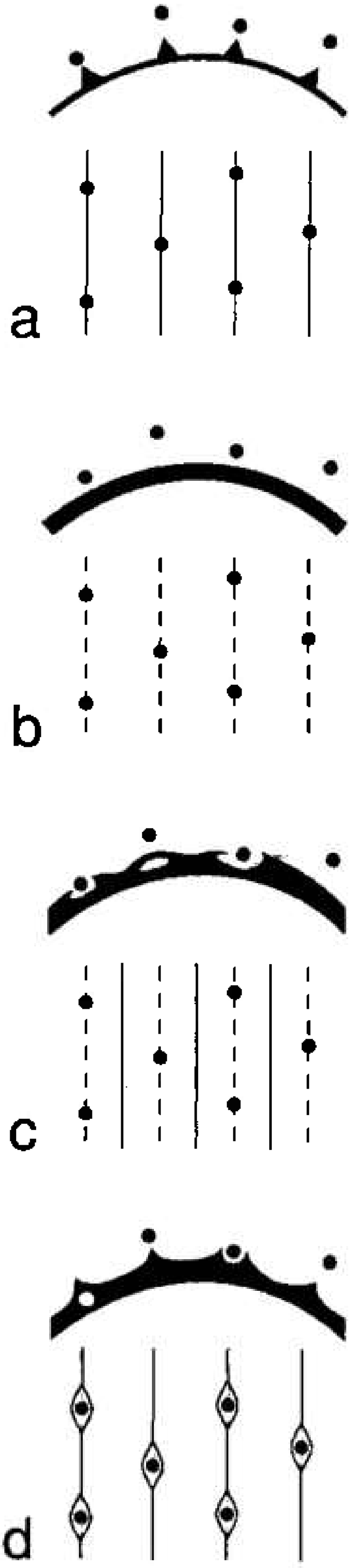

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FIGURE 5. Protoxylem morphology and modes of leaf trace emission. Transverse section above, longitudinal projection of surface of xylem bundle below. Protoxylem in black, spots = leaf traces, solid lines = ridges, dashed lines = leaf trace orthostiches where these do not coincide with ridges.—a. Evaginate direct: *Paurodendron* and *Oxroadia*.—b. Superficial: *Anabathra*, *Hizemodendron*, and *Lepidodendron*.—c. Invaginate: *Chaloneria*.—d. Evaginate internal: *Lepidophloios*.

the plesiomorphic evaginate-direct state (thus bypassing the superficial state), but to inhibit improbable evolutionary routes that treat the evaginate-internal and invaginate states as intermediate.

The stele morphology and leaf trace emission of *Sigillaria* are especially difficult to interpret. The undulatory outer margin of the continuous primary xylem sheath represents tangential variation in the amount of primary xylem produced; protoxylem thickness is greatest on the flanks of the undulations. In contrast with other genera possessing discernable protoxylem ridges, sigillarian leaf traces appear to originate from the intervening troughs, leading to suggestions that each trace may be derived from both of the adjacent protoxylem ridges (e.g., Lemoigne, 1961). However, we were unable to confirm their putative bipolar origin and therefore scored *Sigillaria* leaf traces as superficial. The alternative option of recognizing *Sigillaria* traces as bipolar would generate an additional genus-level autapomorphy.

Secondary xylem occurs in the stem and at least the more proximal crown branches (if present) of all OTUs (C29), but extends into the lateral branches (C30) only in *Diaphorodendron vasculare* and *D. scleroticum*. Most OTUs possess homogeneous rays composed of small-diameter cells, though heterocellular rays characterize *Synchysidendron*. Consistent nonpreservation prevented characterization of the phloem.

14–19. Solid protostele (000000); medullated protostele (010000); medullated protostele with filamentous core (011000); siphonostele with mixed pith (100000); siphonostele with solidly parenchymous pith including secretory cells (100110); siphonostele with solidly parenchymous pith including cells with secondary wall thickenings (100101).
20. Deep parenchymatous invaginations or radial partings absent (0); present (1).
21. Shallow parenchymatous invaginations absent (0); present (1).
22. Exarch protoxylem sheath discontinuous (0); continuous (1).
23–25. Leaf trace origin evaginate, direct (000); superficial (100); invaginate (X10); evaginate, internal (X01).
26. Longitudinal ridges of protoxylem strands discernable (0); indiscernable (1).
27. Leaf trace originates from one protoxylem strand (0); two protoxylem strands (1).
28. Anastomoses of protoxylem strands absent (0); present (1).
29. Secondary xylem in trunk absent (0); present (1).
30. Secondary xylem in lateral branches and/or peduncles absent (0); present (1).
31. Rays homogeneous (0); heterogeneous (1).

D. Cortex (5 characters)

All OTUs possess a three-zoned cortex (C32; Fig. 4a). It consists of a narrow inner cylinder of compact, barrel-shaped parenchyma cells, a thick middle cylinder of even thinner-walled, more-or-less isodiametric parenchyma cells that often decay to leave a cavity, and a broader outer zone of thicker walled cells that are longitudinally elongate (especially in the central portion of the cylinder of tissue) and often grade into sclerenchyma (particularly in the smallest diameter cells, close to the epidermis). This peripheral sclerenchyma is especially well developed in *Diaphorodendron scleroticum*. Leaf traces passing through the middle cortex are ensheathed with cells characteristic of, and in continuity with, the inner cortex; they are secretory in several OTUs (C33) and adaxially concentrated in *Synchysidendron* sp. nov. (C34). In *Sigillaria* sp. nov., *Synchysidendron*, and *Diaphorodendron*, each leaf trace is surrounded by a broad cylinder of thinner-walled cells when passing through the outer cortex (C35), increasing apparent cellular heterogeneity. No attempt was made to divide variations in the angle of passage of the leaf traces through the cortex into discrete character states. Vertically elongate cavities at the cortex-periderm transition (C36) characterize *D. phillipsii*.

32. Outer cortex two-zoned (0); three-zoned (1).
33. Intracortical leaf-trace sheaths not secretory (0); secretory (1).
34. Intracortical leaf-trace sheaths circumferential (0); adaxial (1).
35. Thin-walled parenchyma surrounding leaf trace in thick-walled outer cortex absent (0); present (1).
36. Cavities at outer cortex-periderm transition absent (0); present (1).

E. Periderm (14 characters)

Periderm occurs in all of the OTUs (C37), though its distribution (and thereby its protective and supportive function) is extremely restricted in the bauplans of *Oxroadia* and *Paurodendron*. Common references to periderm as "secondary cortex" are an anatomical non sequitur; cortex is a region of an axis (between the stele and the epidermis) rather than a specific tissue type. The periderm of most genera cannot be differentiated histologically into phellem and phelloderm. The exceptions are *Diaphorodendron* and *Synchysidendron*, where clear bizonation is strong evidence for a bifacial cambial layer that produced much greater quantities of centripetal phelloderm than centrifugal phellem (C38; DiMichele, 1981). Additional, indirect evidence indicates bifaciality in *Anabathra* (DiMichele, 1980) and *Lepidophloios* (DiMichele, 1979a). Given the determinate growth and early onset of peridermal cambial function that are evident in lepidodendraleans, the cambial layer may have fully differentiated or been active only near the apices of stems and rhizomorph axes. Either phenomenon would inhibit preservation of the cambial layer per se. It is also possible that the centripetal and centrifugal products of cell division are sufficiently similar to prevent recognition of a potentially fully differentiated cambium.

Periderm is the most abundant tissue type produced by arboreous lycopsids and often occurs as abundant disarticulated fragments in coal-ball assemblages (Phillips & DiMichele, 1981; DiMichele et al., 1986). Fortunately, the detailed anatomy and histology of the periderm (C39–C43) allow identification of five groups of OTUs. Primitive genera (*Oxroadia*, *Paurodendron*, *Anabathra*, *Chaloneria*) have a uniform periderm, which is modified to include bands of resinous cells in *Sigillaria* (C40). *Diaphorodendron* and *Synchysidendron* possess bifacial periderm (C41); *Synchysidendron* is distinguished from *Diaphorodendron* by its uniform (C43) rather than banded (C42) phelloderm. *Lepidodendron* and *Lepidophloios* have two- or three-zoned periderm (C39) and are X-coded for resinous cell clusters to suppress improbable evolutionary routes that attain histological modifications via the acquisition of zonation.

Glandular periderm histology (C47) is shared by *Lepidodendron* and two of the three *Lepidophloios* species, and resinous sacs (C48) occur in *Sigillaria*, *Lepidodendron*, and *Lepidophloios*. The passage of leaf traces and infrafoliar parichnos strands through the periderm also distinguish OTUs. Prominent leaf traces, more-or-less perpendicular to the length of the axis and surrounded by thin-walled parenchyma (C49), are an autapomorphy of *Anabathra*. Similarly, well-developed infrafoliar parichnos strands (C50) characterize *Sigillaria* periderm.

Many lepidodendraleans retained leaf cushions on the stem surface as periderm production expanded axial girth. We recognize three retention mechanisms (C44–C46). The first two are, by definition, mutually exclusive; interareas exhibit either a plastic response and expand (C44; *Sigillaria* and *Synchysidendron*) or a brittle response and fissure (C45; *Diaphorodendron*) (DiMichele, 1981). In contrast, *Lepidodendron hickii* accommodates growth by expansion of cells beneath the cushion (C46; DiMichele, 1983). This character state could have replaced interarea expansions or fissuring, or it could have arisen directly from the plesiomorphic state; it is X-coded to allow any of these options. Evidence for the interarea expansion of *Lepidodendron* is confined to compression fossils (Thomas, 1966).

37. Periderm in stems absent (0); present (1).
38. Phellem and phelloderm not histologically differentiable (0); histologically differentiable (1).
39–43. Cellular composition of periderm uniform (00000); cells form two or three distinct zones (1X000); bands of resinous cell clusters (01000); periderm bifacial, alternating bands of thick- and thin-walled cells in phelloderm (00110); periderm bifacial, phelloderm ± uniform (00101).
44–46. Leaf cushion retention mechanism absent (000); tangential interarea expansion (100); interarea fissuring (010); subcushion cellular expansion (XX1).
47. Periderm nonglandular (0); glandular (1).
48. Periderm nonresinous (0); at least partially resinous (1).
49. Leaf traces in periderm obscure (0); prominent (1).
50. Infrafoliar parichnos strands in periderm absent (0); present (1).

F. *Leaf bases* (15 characters)

Lepidodendralean leaf base characters are well reviewed by DiMichele (1979a, b, 1981, 1983) for anatomically preserved species and by Thomas (1970b, 1977, 1978) and Thomas & Meyen (1984) for adpressed species.

Lycopsid leaves attenuate bilaterally close to the stem, where they are consequently most readily detached. The area proximal to the constriction persists as a symmetrical structure raised above the surface of the axis and is termed a leaf base; aggregates of leaf bases preserve the phyllotaxy of the axis after leaf loss. In our more primitive OTUs (*Oxroadia*, *Paurodendron*, *Anabathra*, *Chaloneria*), leaf bases are small, ellipsoid in transverse section, widely spaced on the axial surface, and are fully transitional into the leaf lamina (C51). In the more derived OTUs, the leaf base is more elaborate and only a portion emits the leaf; it is then termed a leaf cushion (Fig. 4b). Such cushions typically exhibit a simple angular outline in tangential section: hexagonal in *Sigillaria*, and diamond-shaped in *Diaphorodendron*, *Synchysidendron*, *Hizemodendron*, *Lepidodendron*, and *Lepidophloios* (this character was not coded). Cushions are further elaborated by the development of raised upper (C54) and lower (C55) keels, and by division into upper and lower fields that are usually separated by a lateral line (C58) and are independently plicate (C56–C57). *Sigillaria* is plesiomorphic for all five characters, while *Diaphorodendron* and *Synchysidendron* are apomorphic for all five. *Lepidophloios* only possesses keels. *Hizemodendron* possesses plications but lacks an upper keel, while *Lepidodendron* lacks upper field plications but possesses a lateral line.

The leaf cushion can be regarded as an elaborated leaf base and thus as fundamentally foliar and appendicular in nature. This interpretation is supported by the leaflike structural and positional attributes of leaf cushions; rejection of the foliar nature of leaf cushions would require their recognition as developmentally distinct organs of a kind unknown in other plants. Even the relatively simple cushions of *Sigillaria* are helically arranged, closely packed but discrete, well-defined features. Leaf bases of all the arborescent lycopsids analyzed bear ligules, which are ancestrally foliar in the class (Bonamo et al., 1988). All of these characters are features of appendicular organs produced laterally to the apical meristem through the formation of primordia. In order to be axial rather than foliar, leaf cushions would have to be epidermal/subepidermal elaborations that enlarged below, and concurrently with, leaf primordia as the leaves expanded. There is no evidence in any arborescent lycopsid (with or without cushions) for such an unintuitive developmental mechanism wherein the leaf determines differentiation of the axis. Moreover, stomata occur on leaves and leaf bases, but are absent from axes; they are exclusively foliar.

Together, the above qualitative characters separate all of the cushion-bearing genera studied here, though morphometric quantification is necessary to separate species within each genus (Thomas, 1970b; DiMichele, 1983; Chaloner & Meyer-Berthaud, 1983; DiMichele et al., 1984; Wnuk, 1985). Although we have deliberately excluded metric characters from our analysis, to avoid arbitrary division of such characters into states, we made an exception for the length : width ratio of the leaf cushions (C52–C53). Since the early nineteenth century, the plesiomorphic condition of greater leaf cushion length than width has been crucial for delimiting *Lepidodendron* sens. lat. (DiMichele, 1983). Despite early knowledge that awarding primacy to this character resulted in the lumping of morphologically and anatomically dissimilar species (e.g., Scott, 1908; Seward, 1910), only recently has *Lepidodendron* sens. lat. been disaggregated into the morphologically distinct segregates *Anabathra* (DiMichele, 1980), *Diaphorodendron* sens. str. (DiMichele, 1983), *Synchysidendron* (DiMichele & Bateman, 1992), *Hizemodendron* (Bateman & DiMichele, 1991), *Lepidodendron* sens. str., and *Lepidophloios* (DiMichele, 1979a, 1983). Horizontally (i.e., tangentially) elongate leaf cushions are, however, a valid generic autapomorphy of *Lepidophloios*, together with radial elongation (C64–C65). Obscure evolutionary relationships of the arched and the perpendicular states of radial elongation among different *Lepidophloios* species necessitated X-coding.

All OTUs possess ligules (C59), and most recess the ligule in the cavity that communicates with the adaxial surface of the leaf base via a deep pit (C60). The plesiomorphic exceptions are *Paurodendron*, where the ligule is fully exposed (Phillips & Leisman, 1966), and *Anabathra*, where it is afforded some protection by the leaf cushions (DiMichele, 1980). Foliar parichnos (C61) occur in all OTUs but *Oxroadia* and *Paurodendron* (Bateman (1988) was unable to substantiate Long's (1986) tentative identification of parichnos in *Oxroadia*). In contrast, infrafoliar parichnos (C62) are confined to *Lepidodendron* (Weiss, 1907; DiMichele, 1983) and *Lepidophloios* (W. A. DiMichele, pers. obs.).

The presence of a leaf cushion (C51) is positively correlated with deciduousness (C63) in all OTUs but *Hizemodendron*, where retention is probably secondary (Bateman & DiMichele, 1991). We deliberately avoid describing leaf loss in lepidodendraleans as abscission (cf. Chaloner & Meyer-Berthaud, 1983). Despite the consistent absence of leaf laminae from axes (including almost all twigs), an abscission layer has not been detected in any OTU at any stage of development. We suggest that lycopsid leaves atrophy and are mechanically removed. This occurred more readily in trees such as *Sigillaria* than in smaller erect plants such as *Chaloneria* and recumbent pseudoherbs such as *Oxroadia*, due to the higher basal stresses imposed by the long microphylls of the arboreous species. Fracture occurs where the lamina constricts to form the leaf base; its position relative to the axis and lamina is more consistent in OTUs possessing leaf cushions, where a sharp structural (and, presumably, physiological) boundary is represented as a leaf scar. The scar is situated within the leaf rather than at the leaf-axis junction. Deciduous lateral branches may also have been shed by this mechanism; according to Jonker (1976), triangular marks below ulodendroid scars indicate that the branches were torn away at their junctions with the stem. However, R. A. Gastaldo (pers. comm. 1990) argued that most specimens lack these features, which may be taphonomic overprints.

51. Leaf is outgrowth of entire leaf base (0); portion of leaf base (1).
52. Length : width ratio of cushions on stems and large branches >1 : 1 (0); <1 : 1 (1).
53. Length : width ratio of cushions on small branches and twigs >1 : 1 (0); <1 : 1 (1).
54. Upper keel absent (0); present (1).
55. Lower keel absent (0); present (1).
56. Upper field nonplicate (0); plicate (1).
57. Lower field nonplicate (0); plicate (1).
58. Lateral line separating upper and lower fields absent (0); present (1).
59–60. Ligule absent (00); superficial or in shallow depression (10); in deep cavity with narrow neck (11).
61. Foliar parichnos absent (0); present (1).
62. Infrafoliar parichnos absent (0); present (1).
63. Consistent basal limit to leaf atrophy absent (0); present (1).
64–65. Leaf cushion not radially elongate (00); elongate, strongly arched (1X); elongate, ± perpendicular to axis (X1).

G. Leaves (7 characters)

Leaves are the organs most frequently neglected when attempts are made to reconstruct lepidodendraleans. Admittedly, their deciduousness and consequent absence from the upper axes hinders organ correlation by organic connection, but even more consistent disarticulation has not prevented indirect correlation of cone species with the vegetative axes that bore them. Failure to correlate leaves with their parent plants is unfortunate, as Graham (1935) and Reed (1941) demonstrated the wide range of potentially phylogenetically valuable characters present in isolated lepidodendralean leaves, and Bateman (1988) recorded many characters (including details of the cuticle, epidermis, and stomata) of leaves attached to *Oxroadia* axes. We discarded most of these characters for this analysis, because they would have contained unacceptably large proportions of missing values.

The presence of two vascular strands (C67) is autapomorphic for *Sigillaria*, which also shares V-shaped strands (C68) with *Chaloneria*. Dorsiventrally flattened strands (C69) occur in *Lepidodendron*, *Lepidophloios*, and *Diaphorodendron scleroticum*; ambiguous evolutionary pathways from plesiomorphic terete strands necessitated X-coding. All OTUs whose leaves possess nonterete strands also possess pronounced lateral abaxial grooves (furrows) containing stomata (C70; Fig. 4d); these are supplemented with a median adaxial groove in *Sigillaria* (C71). The vascular strands of most of the more apomorphic OTUs are surrounded by a sclerenchymatous sheath (C72), though this is absent from *Hizemodendron*.

Angle of leaf attachment (C66) refers only to the angle subtended by the basal portion of the mature lamina relative to the distal portion of the axis, thus avoiding the effect of recurvation in OTUs such as *Oxroadia*. This character distinguishes genera with hispid, generally short leaves (*Paurodendron*, *Anabathra*, *Chaloneria*, *Lepidodendron*), but can result from one of several developmental mechanisms and is therefore prone to homoplasy.

66. Angle of leaf attachment relative to axial apex ± horizontal (0); acute (1).
67. Number of vascular strands per leaf one (0); two (1).
68–69. Transverse section of vascular strand terete (00); dorsiventrally flattened (1X); V-shaped (X1).
70. Lateral abaxial grooves absent (0); present at least near base (1).
71. Median adaxial groove absent (0); present at least near base (1).
72. Sheath of sclerenchyma around trace absent (0); present (1).

H. Cones (4 characters)

Intensive study of lepidodendralean reproductive structures has generated thorough reviews of both anatomically preserved (Arber, 1914; Balbach, 1967; Brack, 1970; Hanes, 1975; Phillips, 1979; Brack-Hanes & Thomas, 1983; Willard, 1989a) and adpressed (Lesquereux, 1880; Kidston, 1923–1925; Willard, 1989b) organ-species. Reproductive characters played important roles in the delimitation of the genera; not surprisingly, many are genus-level autapomorphies. Moreover, many of the traits are functionally linked and can be used to define reproductive strategies in the same manner that vegetative morphology defines growth habits.

All of the lycopsids included in this analysis are heterosporous (C75). *Oxroadia*, *Paurodendron*, and *Anabathra* have primitively bisporangiate strobili (C76), with microsporangia concentrated toward the cone apex. The fertile zones of *Chaloneria* (arguably a derived condition) are similarly bisporangiate; all other OTUs bore monosporangiate cones.

Characters 73 and 74 describe the relationships to the parent stem of the lateral cone-bearing axes, whether peduncles or branches (*Chaloneria* is unbranched and was scored as missing for C73). Lateral branches are subtended by stelar gaps (C73) in *Diaphorodendron*, *Synchysidendron*, *Lepidodendron*, and *Lepidophloios*, and are medullated (C74) in *Sigillaria*, *Diaphorodendron*, *Lepidodendron*, and *Lepidophloios*.

73. Stelar vascular gap associated with departure of peduncle or lateral branch absent (0); present (1).
74. Pith in trace of peduncle or lateral branch absent (0); present (1).
75. Plants homosporous (0); heterosporous (1).
76. Cones/fertile zones bisporangiate (0); monosporangiate (1).

I. Sporophylls and sporangia (15 characters)

Literature review suggests that the terms describing most components of the sporangium-sporophyll complex have become standardized (Fig. 4c). The sporophyll is divided into a proximal portion ("pedicel"), perpendicular to the cone axis, and a distal portion ("distal lamina"), parallel to the cone axis and oriented toward the cone apex. The adaxial surface of the pedicel bears the sporangium and (immediately distal to the sporangium) the ligule. The pedicel is triangular in median transverse section and attenuates abaxially, to a structure that has been termed a keel if sufficiently prominent (Phillips, 1979), and laterally, to structures that have received various names. "Lateral laminae" is used most commonly; alternatives are "lateral extensions" (e.g., Meyen, 1987), "wings" (e.g., Arber, 1914), "flanges" (e.g., Sporne, 1975), and "alations" (e.g., Phillips, 1979). Some authors (e.g., Phillips, 1979) have distinguished the most developed state of this character (long and enrolled) as "integuments," by analogy with the true seeds of "spermatophytes." The apically directed distal lamina is much less three-dimensional and usually appears as a shallow "V" in transverse section. An antapically directed extension from the right-angled junction of the pedicel and distal lamina is termed the heel.

Comparing sporophylls with sterile microphylls, we believe that the pedicel is homologous with the leaf base (including the leaf cushion), and the sporophyll distal lamina is homologous with the leaf lamina. We suggest that the qualifier "distal" should be abandoned for the sporophyll lamina (there is no *proximal* lamina), and that the lateral extensions of the pedicel should be termed alations, irrespective of size and orientations (use of the term "integuments" for extensive enrolled alations misleadingly implies homology with the integuments of true seeds).

Little attention is paid in the literature to angle of pedicel attachment relative to the cone axis (C77), which may be prone to ontogenetic change as an aid to passive spore dispersal (Bateman, 1988). Thus, our identification of *Oxroadia* as autapomorphic for obtuse sporangia is tentative. With this exception, all sporophyll and sporangium characters (C78–C91) are scored as plesiomorphic for the four most primitive OTUs possessing bisporangiate cones (*Oxroadia*, *Paurodendron*, *Anabathra*, *Chaloneria*), which differ quantitatively rather than qualitatively. A good example is the number of megaspores per megasporangium, which also separates species of the same genus (e.g., *Anabathra*: Felix, 1954; Brack, 1970; see also Appendix 1B). It is tempting to distinguish qualitatively between megasporangia containing four spores, derived from one spore mother cell, and those containing more than four spores, derived from more than one spore mother cell. However, each condition characterizes one of the two species of *Oxroadia* (Bateman, 1988), and spore counts are complicated by frequent and apparently random abortions.

Differences among the remaining (monosporangiate) genera focus on megasporangiate cones and reflect their shared transition in the nature of the dispersal unit from isolated megaspores to a megasporangium-sporophyll complex (C81). The apomorphic state of this character encapsulates a broad spectrum of morphologies (elaborated in C80 and C82–C90) that may reflect parallel (i.e., homoplastic) responses to similar selective regimes. In all monosporangiate genera but *Sigillaria*, this evolutionary trend results in reduction to a single functional megaspore (C90) that germinates within the sporangium (C80; Phillips, 1979). Probably as an aid to dispersal and/or protection, these changes are accompanied by lateral expansion of the pedicel to form alations (C82–C84). These are coded as short and horizontal in *Sigillaria*, *Diaphorodendron*, and *Synchysidendron*, short and erect in *Hizemodendron* and *Lepidodendron*, and long and erect (typically enrolled) in *Lepidophloios*. These characterizations require further revision; the lateral margins of the pedicel can be proportionately longer in *Anabathra* (e.g., fig. 9 of Brack, 1970) and more erect in *Diaphorodendron* and *Synchysidendron* (e.g., pl. 8.4 of Phillips, 1979) than those of *Lepidodendron* (e.g., pl. 5.4 of Phillips, 1979). Moreover, shortness may not be homologous between vertical and horizontal alations; hence, X-coding was used to allow evolution of short, erect alations from either absence of alations or short, horizontal alations, and to suppress evolution of short, horizontal alations from short, vertical alations.

Megasporangia of *Diaphorodendron* and *Synchysidendron* are strongly dorsiventrally flattened (C85–C86) and dehisce proximally (C87–C89), while those of *Hizemodendron*, *Lepidodendron*, and *Lepidophloios* are strongly bilaterally flattened and dehisce distally. *Sigillaria approximata* undergoes indehiscent fragmentation (C89), presumably an apomorphic character state. We have used X-coding to allow its evolution by one step from any of the three dehiscence mechanisms. *Sigillaria approximata* possesses another autapomorphy, the enclosure of megaspores with parenchyma (C91).

Heterocellular sporangium walls (C79) characterize *Diaphorodendron* and *Synchysidendron*. Only *Lepidodendron* possesses a multiseriate sporangium wall; together with greater sporangium size (a quantitative character and therefore not coded), this distinguishes *Lepidodendron* sporangium-sporophyll complexes from the otherwise identical equivalents of *Hizemodendron*.

77. Angle of sporophyll attachment relative to cone apex ± horizontal (0); obtuse (1).
78. Sporangium wall uniseriate (0); multiseriate (1).
79. Sporangium wall homocellular (0); heterocellular (1).
80. Megaspores shed from sporangium prior to germination (0); megaspores germinate within sporangium (1).
81. Dispersal unit megaspore (0); megasporangium-sporophyll complex (1).

82–84. Alations of megasporophyll pedicel absent (000); short, horizontal (100); short, suberect (X10); long, erect (011).

85–86. Transverse section of megasporangium ± circular (00); strongly bilaterally flattened (10); strongly dorsiventrally flattened (01).

87–89. Megasporangium dehisces longitudinally (000); distally (100); proximally (010); indehiscent fragmentation (XX1).

90. Functional megaspores per megasporangium more than one (0); one (1).
91. Parenchyma enclosing megaspores absent (0); present (1).

J. Megaspores (10 characters)

Figure 4e summarizes terms describing the "geography" of the exteriors of lycopsid spores.

Morphological and ultrastructural studies of lycopsid megaspores preserved in situ in cones have been undertaken since the earliest applications of palynology to biostratigraphic and paleoecological problems (Schopf, 1938; Bocheński, 1939; Brack, 1970; Taylor, 1990; see also Bartram, 1987).

Polarity decisions for laesural (C94–C96) and equatorial (C92–C93) characters were problematic; they are generally poorly developed in distantly related lycopsids, but better developed and more complex in putatively more closely related outgroups (e.g., *Selaginella*: Stanier, 1965; Tryon & Lugardon, 1978; Minaki, 1984) and in the more primitive ingroup members (*Oxroadia*, *Paurodendron*, *Chaloneria*) than in the more derived OTUs. Prominent laesural expansions characterize *Oxroadia*, where they are fimbriate and do not extend beyond the curvaturae (C95: Alvin, 1965, 1966; Bateman, 1988), and *Paurodendron*, where they are plicate and extend to the equatorial flange (C96: Guennel, 1952). The laesurae of *Diaphorodendron* and *Synchysidendron* megaspores are gulate (C94); the spongy, trilobate proximal massa is a key taxonomic character. Equatorial expansions provide autapomorphies for *Paurodendron*, in the form of a perisporial plicate flange (C93: Guennel, 1952), and *Chaloneria*, in the form of auriculae (ear-shaped expansions of the exine) opposite laesural rays (C92: Pigg & Rothwell, 1983b).

Most OTUs lack dispersed proximal and distal ornamentation. Contact-face ornamentation is confined to *Oxroadia* (sparse, robust, buttressed spines: C97), *Paurodendron* (reticulate: C98), and *Chaloneria* (rugose: C99). The megaspore of *Sigillaria* sp. nov. could not be scored for this character, but its distal surface clearly bears short spines (C100: Benson, 1918; Pigg, 1983). Large and more complex buttressed spines typify *Oxroadia* megaspores. *Paurodendron* megaspores bear a striking distal reticulum (C101).

92–93. Equatorial ornamentation absent (00); auriculate (10); flanged (01).

94–96. Laesural ornamentation absent (000);

gulate (100); fimbriate (01X); plicate (0X1).

97–99. Contact-face ornamentation absent (000); echinate (100); reticulate (010); rugose (001).

100–101. Distal ornamentation absent (00); echinate (10); reticulate (01).

K. Microspores (14 characters)

Several lycopsid microspores commonly encountered in dispersed miospore assemblages (sensu Chaloner, 1970) have been correlated with source cones, both anatomically preserved (Brack, 1970; Courvoisier & Phillips, 1975; Willard, 1989a) and compressed (Thomas, 1970a, 1987; Willard, 1989b). Classification of lycopsid microspores has focused on equatorial elaboration and general surface ornamentation. The only exception in our list of characters, strongly raised laesurae (C105), occurs in *Chaloneria* and *Lepidophloios harcourtii*.

In *Chaloneria*, separation of the sexine and nexine layers distal to the contact faces has generated a pseudosaccus (C102: Brack & Taylor, 1972). All of the monosporangiate-coned genera exhibit some form of equatorial elaboration (C106–C108). *Anabathra*, *Hizemodendron*, *Lepidodendron*, and *Lepidophloios* microspores possess a thickened equatorial band (cingulum: C106); in *Hizemodendron*, *Lepidodendron*, and some *Lepidophloios* species, this is supplemented with an external membranous flange (zona: C108). *Sigillaria*, *Diaphorodendron*, and *Synchysidendron* microspores bear a crassitude equatorial thickening (C107) that appears structurally distinct from a cingulum. Cingula of some OTUs are further elaborated; those of *Hizemodendron*, *Lepidodendron*, and *Lepidophloios harcourtii* are bizonate (C103) and those of *Anabathra* are distally ornamented (C104).

Characterization of microspore general surface morphology is increasingly dependent on the greater resolution of scanning electron microscope (SEM) studies relative to light microscopy (LM). As in the megaspores, ornamentation is described separately for contact faces (C109–C111) and the distal hemisphere (C112–C115), though *Lepidophloios johnsonii* is insufficiently known to be scored. Contact faces of *Hizemodendron*, *Lepidodendron*, and *Lepidophloios* microspores are granulate (C109; Leisman & Rivers, 1974; Willard, 1989a), those of *Diaphorodendron* and *Synchysidendron* grade into a more foveolate texture (C110; Courvoisier & Phillips, 1975), and those of *Oxroadia* and *Paurodendron* are echinate (C111; Schlanker & Leisman, 1969; Bateman, 1988). Several OTUs lack contact-face ornamentation, but only *Chaloneria* and *Lepidophloios harcourtii* lack distal ornamentation. In *Oxroadia* and *Paurodendron*, the echinate contact faces are paralleled by the distal ornamentation (C115). *Diaphorodendron* and *Synchysidendron* microspores are papillate (C114), those of *Sigillaria* are characterized by a mixture of spines and cones (C113), and those of *Hizemodendron*, *Lepidodendron*, and *Lepidophloios hallii* bear dense grana (C112).

102. Pseudosaccus absent (0); present (1).

103–104. Equatorial expansion absent (00); unornamented bizonate cingulum complex (10); distally ornamented cingulum complex (01).

105. Laesurae subdued (0); strongly raised (1).

106–108. Equatorial ornamentation absent (000); cingulum complex (100); crassitude (010); zona (001).

109–111. Contact-face ornamentation absent (000); granulate (100); granulo-foveolate (010); echinate (001).

112–115. Distal ornamentation absent (0000); densely granulate (1000); echino-conate (0100); papillate (0010); echinate (0001).

THE DATA MATRIX

After all 115 characters had been scored, two whole-plant species (*Oxroadia gracilis* and *Oxroadia* sp. nov.) possessed identical data sets, demonstrating that they differ in quantitative but not qualitative characters. The duplicate data set provided no useful information and was therefore omitted, reducing the original 17 whole-plant species to 16 OTUs that, in our opinion, represent 10 genera. This gave a ratio of characters : OTUs of 115 : 16 (7.2 : 1).

The resulting 1,840-byte data matrix (Table 3, excluding HYAN) contained 94 missing values that each reflected one of four factors. Two of these factors result from ignorance of whether the OTU possesses the feature or what state the feature exhibits, one from unwillingness to specify the precursor state of the character (the X-coding procedure discussed in detail by Doyle & Donoghue, 1986b: 344–350; see also Appendix 2), and one from absence of the relevant feature, which therefore cannot be scored. The first three categories indicate varying degrees of ignorance concerning the nature of the character and can be replaced by a posteriori optimization, substituting values most parsimonious with the cladogram in question. The fourth type of missing value (coded # in Table 3) is also replaced during optimization, but here the result is merely an operational necessity. It does not generate a potentially biologically meaningful hypothesis; there is no obvious meaning in scoring a character state as present for an OTU that completely lacks the feature in question (for example, in Fig. 6 *Chaloneria* is optimized as possessing peduncle/branch gaps (C73) but actually lacks both types of organ). This situation is more frequent in data matrices that include OTUs of highly divergent morphology, where the probability of obtaining fully compatible sets of homologous features is less. The most gap-ridden (12% missing values) of our data sets is *Chaloneria cormosa*, where 11 of the 14 missing values reflect lack of the coded feature (i.e., absence rather than ignorance). Compared with OTU selection, we were less rigorous when excluding gap-ridden characters from the matrix; the worst examples (C34, C40, C69) possess 31% missing values, most of these X-coded to represent ambiguity of precursor states. Nevertheless, the overall proportion of missing values in our data matrix (5%) compares favorably with those of other studies (e.g., 24% in Table 2 of Doyle & Donoghue, 1986b).

We believe that every cladistic data matrix should routinely carry character:OTU ratios to indicate the average strength of empirical support for nodes and percentage missing values to indicate the completeness of the data matrix, just as the resulting trees now routinely carry consistency indices to summarize levels of homoplasy (Kluge & Farris, 1969; Brooks et al., 1986).

OPTIMIZATION, CHARACTER STATES, AND MISSING VALUES

The distribution of an apomorphic character state among all the OTUs can be assigned to one of three categories:

1. The apomorphic state is confined to a single OTU and is thus an autapomorphy at the least inclusive (species) level in the taxonomic hierarchy. It is important to note that the autapomorphic condition is a relative concept; a synapomorphy (shared derived character) at the species level in our analysis can be an autapomorphy (unshared derived character) at the more inclusive level of genus. Autapomorphies at the least inclusive level analyzed distinguish OTUs, but are phylogenetically uninformative. Consequently, they are omitted from algorithmic analysis to avoid artificially increasing length and decreasing perceived levels of homoplasy by including characters that are, by definition, nonhomoplastic (e.g., Brooks et al., 1986; Kluge, 1989; Sanderson & Donoghue, 1989).

2. The apomorphic state is ubiquitous among the OTUs (including the outgroups if used), thereby justifying their status as a potential clade. Although such character states are conventionally described as "basal synapomorphies" or "invariant characters" (e.g., Sanderson & Donoghue, 1989), we prefer to coin the more parsimonious term "holapomorphy." It could be argued that such character states are merely plesiomorphies, but they cannot be defined as such in the absence of an equivalent apomorphic state. Our definition of the term synapomorphy is also unconventional in implicitly excluding holapomorphic character states. Holapomorphy, like autapomorphy, is a relative concept; addition to the suite of taxa analyzed of an OTU lacking the apomorphic character state transforms a formerly ubiquitous holapomorphy into a nonubiquitous synapomorphy. Holapomorphies also resemble autapomorphies in being phylogenetically uninformative within the confines of a particular data matrix. Hence, like autapomorphies, holapomorphies should be (and in this study were) omitted from tree length calculations.

3. When the apomorphic state occurs in more than one but less than all of the OTUs, it is deemed phylogenetically informative and included in the algorithmic computation of tree length. Most such character states are synapomorphic, although category (3) also encompasses homoplasies (these are generally regarded as refuting the initial hypothesis of homology between the plesiomorphic and apomorphic states: e.g., Wiley, 1981; Funk & Brooks, 1990). The perception of synapomorphies as homoplastic (i.e., as parallelisms and/or reversals) or nonhomoplastic (evolving only once and persisting throughout the derived portion of the clade) is the least stable aspect of cladistic analysis, since these conditions are a property only of the interaction of a specific tree topology with a specific optimization algorithm (see below). Also, character states can be both homoplastic and partially synapomorphic; for example, a particular state may be a meaningful synapomorphy of the OTUs forming clade A+B but be represented as a parallelism in their non-sister OTU D (J. I. Davis, pers. comm.' 1990). Surprisingly, the terminologically rich discipline of cladistics does not appear to have generated unique terms to describe the important (albeit ad hoc) distinction between synapomorphies sens. str. (i.e., holapomorphies excluded) that are homoplastic and those that are not; only the latter

TABLE 3. Cladistic data matrix. Operational taxonomic units: Hypothetical ancestor (HYAN), *Paurodendron fraipontii* (PNFR), *Oxroadia gracilis* sp. nov. (OXGR), *Anabathra* (*Paralycopodites*) *pulcherrima* (ANPU), *Chaloneria cormosa* (CHCO), *Sigillaria approximata* (SIAP), *Sigillaria* sp. nov. (SINS), *Synchysidendron* (*Diaphorodendron*) sp. nov. (SYNS), *Synchysidendron dicentricum* (SYDI), *Diaphorodendron phillipsii* (DIPH), *Diaphorodendron vasculare* (DIVA), *Diaphorodendron scleroticum* (DISC), *Hizemodendron* (*Lepidodendron*) *serratum* (HZSE), *Lepidodendron hickii* (LNHI), *Lepidophloios harcourtii* (LSHC), *Lepidophloios johnsonii* (LSJO), *Lepidophloios hallii* (LSHL). Known values: primitive (0), derived (1); missing values (coded 9 in PAUP; functional states in preferred most parsimonious tree are indicated by subscripts): not known whether OTU possesses relevant feature

	Habit (1–7)							Rootstock (8–13)					
OTU					5					10			
				+	+			@	+		@	@	
HYAN	0	0	0	0	0	0	0	0	0	0	0	0	0
PNFR	0	0	0	0	0	0	0	1	0	1	1	1	$?_0$
OXGR	0	0	0	0	0	0	0	1	0	0	1	1	$?_0$
ANPU	1	1	1	0	0	1	1	1	0	0	1	1	0
CHCO	0	1	1	0	1	$\#_0$	$\#_0$	1	1	1	1	1	1
SIAP	1	1	1	0	0	1	0	1	0	0	1	1	1
SINS	1	1	1	0	0	1	0	1	0	0	1	1	$?_0$
SYNS	1	1	0	0	0	0	0	1	0	0	1	1	0
SYDI	1	1	0	0	0	0	0	1	0	0	1	1	0
DIPH	1	1	1	0	0	1	1	1	0	0	1	1	0
DIVA	1	1	1	0	0	1	1	1	0	0	1	1	0
DISC	1	1	1	1	0	1	1	1	0	0	1	1	0
HZSE	0	0	0	0	0	0	0	1	0	0	1	1	0
LNHI	1	1	0	0	0	0	0	1	0	0	1	1	0
LSHC	1	1	0	0	0	0	0	1	0	0	1	1	0
LSJO	1	1	0	0	0	0	0	1	0	0	1	1	0
LSHL	1	1	0	0	0	0	0	1	0	0	1	1	0

	Cortex (32–36)					Periderm (37–50)						
OTU				35					40			
	@		+		+	@	*		*	*	*	*
HYAN	0	0	0	0	0	0	0	0	0	0	0	0
PNFR	1	0	$?_0$	0	0	1	0	0	0	0	0	0
OXGR	1	0	0	0	0	1	0	0	0	0	0	0
ANPU	1	0	0	0	0	1	0	0	0	0	0	0
CHCO	1	$?_1$	0	0	0	1	0	0	0	0	0	0
SIAP	1	1	0	0	0	1	0	0	1	0	0	0
SINS	1	$?_1$	$?_0$	1	0	1	0	0	1	0	0	0
SYNS	1	1	1	1	0	1	1	0	0	1	0	1
SYDI	1	0	0	1	0	1	1	0	0	1	0	1
DIPH	1	1	$?_0$	1	1	1	1	0	0	1	1	0
DIVA	1	1	0	1	0	1	1	0	0	1	1	0
DISC	1	1	0	1	0	1	1	0	0	1	1	0
HZSE	1	0	0	0	0	$-_1$	$-_0$	$-_0$	$-_0$	$-_0$	$-_0$	0
LNHI	1	0	0	0	0	1	0	1	X_0	0	0	0
LSHC	1	$?_1$	$?_0$	0	0	1	0	1	X_0	0	0	0
LSJO	1	1	$?_0$	0	0	1	0	1	X_0	0	0	0
LSHL	1	1	0	0	0	1	0	1	X_0	0	0	0

reliably characterize an entire monophyletic portion of a clade.

We are also surprised at the paucity of literature concerning optimization, as it proved to be a crucial aspect of our analysis. Optimization is an a posteriori procedure performed using one of a range of algorithms that are designed to apply specific logical precepts to specifying the nature (e.g., reversal vs. parallelism) and location of each character transition on a tree whose topology and length

TABLE 3. Continued.
(–), OTU possesses relevant feature but character state unknown (?), OTU lacks relevant feature (#), precursor state ambiguous (X; X-coded sensu Doyle & Donoghue, 1986b). Functional level of generality of derived character state in preferred most parsimonious tree: + = species level autapomorphy (character state restricted to a single OTU; these provide no information on historical relationships of species or genera), * = genus level autapomorphy (character state restricted to a single genus but occurring in more than one species; these provide no information on historical relationships of genera), @ = holapomorphy (= basal synapomorphy; these provide no information on historical relationships of species or genera).

Stele (14–31)																	
	15					20					25					30	
*			*	+	+	*	+			+	*		*	*	@	*	*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0
0	1	0	0	0	0	0	1	1	X_1	1	0	1	0	0	1	$\#_0$	0
0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0
0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0
1	0	0	1	1	0	1	0	1	1	0	0	1	0	0	1	0	1
1	0	0	1	0	1	1	0	1	1	0	0	1	0	0	1	0	1
1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0
1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0
1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0
0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	$?_1$	0	0
0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
0	1	0	0	0	0	0	0	1	X_1	0	1	0	0	1	1	0	0
0	1	1	0	0	0	0	0	1	X_1	0	1	0	0	1	1	0	0
0	1	1	0	0	0	0	0	1	X_1	0	1	0	0	1	1	0	0

Periderm (cont'd.)							Leaf bases (51–65)									
	45					50					55					60
	*	+			+	*		*							@	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	1	0
0	0	0	0	0	0	0	0	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	1	1
0	0	0	0	0	1	0	0	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	1	0
0	0	0	0	0	0	0	0	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	1	1
1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	1	1
1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	1	1
1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1
1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1
0	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1
0	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1
0	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1
0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1
X_0	X_0	1	1	1	0	0	1	0	1	1	1	0	1	1	1	1
0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	1	1
0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	1	1
0	0	0	0	1	0	0	1	1	1	1	1	0	0	0	1	1

have already been fixed. In theory, optimization cannot alter the length of a tree (though see below for a critical reappraisal of this conventional wisdom).

Rooting the tree using the hypothetical ancestor had the advantage of maximizing the number of optimization algorithms that could legitimately be applied (Swofford, 1985: 3.10). We tested all five optimization algorithms available in PAUP 2.4: ACCTRAN maximizes reversals, as in practice does

TABLE 3. Continued.

	Leaf bases (cont'd.)					Leaves (66–72)						
OTU					65					70		
				*	+		*				*	
HYAN	0	0	0	0	0	0	0	0	0	0	0	0
PNFR	0	0	0	0	0	1	0	0	0	0	0	0
OXGR	0	0	0	0	0	0	0	0	0	0	0	0
ANPU	1	0	0	0	0	1	0	0	0	0	0	0
CHCO	1	0	0	0	0	1	0	X_0	1	1	0	0
SIAP	1	0	1	0	0	0	1	X_0	1	1	1	1
SINS	1	0	1	0	0	0	1	X_0	1	1	1	1
SYNS	1	0	1	0	0	0	0	0	0	0	0	1
SYDI	1	0	1	0	0	0	0	0	0	0	0	1
DIPH	1	0	1	0	0	0	0	0	0	0	0	$?_1$
DIVA	1	0	1	0	0	0	0	0	0	0	0	1
DISC	1	0	1	0	0	0	0	1	X_0	1	0	1
HZSE	1	0	0	0	0	1	0	0	0	0	0	0
LNHI	1	1	1	0	0	0	0	1	X_0	1	0	1
LSHC	1	$?_1$	1	1	X_0	0	0	1	X_0	1	0	$?_1$
LSJO	1	$?_1$	1	1	X_0	0	0	1	X_0	1	0	1
LSHL	1	1	1	X_1	1	0	0	1	X_0	1	0	1

	Megaspores (92–101)									
OTU				95					100	
	+	+	*	+	+	+	+	+		+
HYAN	0	0	0	0	0	0	0	0	0	0
PNFR	0	1	0	X_0	1	0	1	0	0	1
OXGR	0	0	0	1	X_0	1	0	0	1	0
ANPU	0	0	0	0	0	0	0	1	0	0
CHCO	1	0	0	0	0	0	0	0	0	0
SIAP	0	0	0	0	0	0	0	0	0	0
SINS	0	0	0	0	0	$?_0$	$?_0$	$?_0$	1	0
SYNS	0	0	1	0	0	0	0	0	0	0
SYDI	0	0	1	0	0	0	0	0	0	0
DIPH	0	0	1	0	0	0	0	0	0	0
DIVA	0	0	1	0	0	0	0	0	0	0
DISC	0	0	1	0	0	0	0	0	0	0
HZSE	0	0	0	0	0	0	0	0	0	0
LNHI	0	0	0	0	0	0	0	0	0	0
LSHC	0	0	0	0	0	0	0	0	0	0
LSJO	0	0	0	0	0	0	0	0	0	0
LSHL	0	0	0	0	0	0	0	0	0	0

FARRIS; in contrast, DELTRAN maximizes parallelisms. MINF concentrates character state transitions toward the terminal branches, MINRES concentrates all possible transitions toward the root, then concentrates the remainder toward the terminal branches. For our preferred most parsimonious tree (PMPT), FARRIS yielded similar (though not identical) results to ACCTRAN, and MINRES yielded similar results to DELTRAN and, to a lesser degree, MINF. We preferred MINRES and MINF, as they minimized perceived homoplasy in the lower (genus-level and above) branches that were of greatest interest to us; they also tended to yield the greatest number of intuitively satisfactory selections when (1) choosing between reversals and parallelisms, and (2) substituting 0 or 1 for missing values of specific characters (see below). Reservations expressed by Swofford (1985: 3.9–3.10)

TABLE 3. Continued.

Cones (73–76)				Sporophylls & Sporangia (77–91)														
		75					80					85					90	
		@		+	+	*					*		*		*	+		+
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
$\#_1$	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
$?_1$	1	1	1	0	0	0	0	1	1	0	0	0	0	X_0	X_0	1	0	1
$?_1$	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
1	0	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0
1	0	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0
1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0
1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0
1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0
0	0	1	1	0	0	0	1	1	X_0	1	0	1	0	1	0	0	1	0
1	1	1	1	0	1	0	1	1	X_0	1	0	1	0	1	0	0	1	0
1	1	1	1	0	0	0	1	1	0	1	1	1	0	1	0	0	1	0
1	1	1	1	0	0	0	1	1	0	1	1	1	0	1	0	0	1	0
1	1	1	1	0	0	0	1	1	0	1	1	1	0	1	0	0	1	0

Microspores (102–115)													
			105					110					115
+		+				+		*			*	*	
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	1	0	0	1	0	0	1	0	0	0	1
0	0	0	0	0	0	0	0	0	1	0	0	0	1
0	0	1	0	1	0	0	0	0	0	1	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	1	0	0
0	0	0	0	0	1	0	0	0	0	0	1	0	0
0	0	0	0	0	1	0	0	1	0	0	0	1	0
0	0	0	0	0	1	0	0	1	0	0	0	1	0
0	0	0	0	0	1	0	0	1	0	0	0	1	0
0	0	0	0	0	1	0	0	1	0	0	0	1	0
0	0	0	0	0	1	0	0	1	0	0	0	1	0
0	1	0	0	1	0	0	1	0	0	1	0	0	0
0	1	0	0	1	0	0	1	0	0	1	0	0	0
0	1	0	1	1	0	0	0	0	0	0	0	0	0
0	$?_1$	0	0	1	0	0	$?_1$	$?_0$	$?_0$	$?_1$	$?_0$	$?_0$	$?_0$
0	0	0	0	1	0	0	1	0	0	1	0	0	0

concerning MINRES encouraged our consistent use of MINF.

During optimization, each missing value (coded 9 in the PAUP data matrix) is replaced with 0 or 1 in accordance with (1) the topology of the tree and (2) the intended effect on patterns of character state transformation of the chosen optimization algorithm (this is an a priori opportunity to modify evolutionary interpretations). The substitutions that result are different for every tree of every analysis; for example, those presented as subscripts to missing values in our data matrix (Table 3) refer only to the preferred MPT of analysis A following application of the MINF optimization algorithm. Replacement of missing values is achieved parsimoniously in accordance with the topology of the tree, so that further homoplasy will not be introduced. Hence, we presume that this procedure artificially reduces levels of homoplasy relative to those that would have been determined from the same matrix if complete (i.e., gap-free).

Doyle & Donoghue (1986b: 352) imposed dual origin (parallelism) where a structure was simplified, and an origin and a loss (reversal) where a structure became more complex, on the assumption that "it is easier to reduce or lose a complex structure than to elaborate one from a simple structure." We did not consider this generalization sufficiently reliable to warrant a posteriori modification of our algorithmically optimized character state distributions, though we did emphasize complex, apparently conservative characters in subsequent evolutionary interpretations.

According to Bateman (in prep.), when all OTUs are scored as possessing either the plesiomorphic or apomorphic state for a character, the assignment of that character to one of these three ostensibly exclusively categories (autapomorphy, holapomorphy, synapomorphy sens. str.) is *definitive*; its condition is fixed for that data matrix. However, this principle does not apply if the character column contains at least one missing value (9), when the results of optimization determine the status of the character as informative or uninformative. For example, in our data matrix, a character scored as fifteen 1s and one 9 (e.g., C29) will be holapomorphic if the 9 is replaced a posteriori with a 1, but synapomorphic if the 9 is replaced with a 0 (in practice, this will occur only if the OTU scored 9 is placed at the base of the cladogram). Similarly, a character scored as fourteen 0s, one 1, and one 9 (e.g., C94, C98) will be autapomorphic if the 9 is replaced with a 0 but nonautapomorphic if the 9 is replaced with a 1. Hence, there is a need for the concepts of *transient* autapomorphy, *transient* holapomorphy, and *transient* synapomorphy, to accommodate characters that contain missing values. These concepts are relative, even within a single data matrix; they characterize only a single combination of a specific topology and a specific optimization algorithm. In our novel terminology, definitive and transient autapomorphies together constitute *operational* autapomorphies (likewise for holapomorphies and synapomorphies).

In contrast with definitive autapomorphies and holapomorphies, transient autapomorphies and holapomorphies cannot be screened out of an analysis a priori. Consequently, they contribute to tree length as calculated during cladistic analysis; they introduce spurious extra steps in an unpredictable manner, often generating alternative trees that are incorrectly considered of equal length by the parsimony algorithm. For example, a data matrix generates two topologies, A and B, both X steps in length. A posteriori screening for transient autapomorphies/holapomorphies reveals four in topology A and two in topology B. A is then preferred over B as its true length is X − 4, relative to X − 2 in topology B. Unfortunately, topology C, perceived by the algorithm as X + 1 steps long but containing six transient autapomorphies/holapomorphies, has a true length of X − 5 steps and is actually the most parsimonious tree. Thus, the true lengths of trees generated from a data matrix containing missing values can only be calculated a posteriori. Algorithmically determined tree lengths are unreliable, and trees other than those that are ostensibly the most parsimonious must also be screened individually via apomorphy lists for spurious additional steps. The alternative option of omitting all *potential* transient autapomorphies and holapomorphies a priori (appendix 1 of Sanderson & Donoghue, 1989) deleteriously discards potential synapomorphies merely because their frequencies among the OTUs approach zero or unity.

PARSIMONY ANALYSIS

Cladograms were generated from the data matrix using Version 2.4 of PAUP (Swofford, 1985), which employs unrestricted parsimony via the Wagner method (Kluge & Farris, 1969; Farris, 1970; Felsenstein, 1982; Swofford & Maddison, 1987; Wiley et al., 1991). Some of the computational difficulties encountered by us and discussed below have been at least partially surmounted by more recent software (see Appendix 2). Despite the long run-times incurred on our IBM-PS2/#80, the branch-and-bound option (a modification of the algorithm devised by Hendy & Penny, 1982) was used routinely to obtain the definitive shortest trees.

Once character scoring had been finalized, five different configurations of the data matrix were analyzed:

A. All 16 OTUs and all 115 characters included. This basic analysis provided a yardstick by which to measure the remaining analyses.

B. All OTUs included, "habit" characters (C1–C7) excluded. We wished to reassess the phylogeny without these characters for two reasons. First, they describe the most generalized aspects of plant morphology and are thus most prone to epigenesis. Second, we wished to map the distribution of lycopsid bauplans onto a phylogeny constructed independently of such characters (see also Bateman & DiMichele, 1991; Phillips & DiMichele, 1992).

C. All characters included, but *Chaloneria cormosa* excluded. Survey of tree topologies from analyses A and B demonstrated that *Chaloneria* is the most unstable OTU; it is supported by the least robust node, characterized only by homoplastic and autapomorphic characters, and possesses more autapomorphies (six) than any other OTU (Fig. 6). This most awkward OTU was omitted in order to determine how the topologies of the more parsimonious trees would be altered and whether homoplasy would decrease significantly.

D. All OTUs included, analysis restricted to vegetative characters (C1–C4, C8–C72).

E. All OTUs included, analysis restricted to reproductive characters (C5–C7, C73–C115). Analyses D and E were performed to determine the relative contributions of vegetative and reproductive characters to the whole-plant phylogeny (cf. Bateman & DiMichele, 1991), and to assess the likely accuracy of phylogenies based on the partial plants that constitute most paleobotanical "species." Data matrices for organ-species phylogenies are much easier to construct than those for whole-plant phylogenies, given the difficulty of correlating vegetative and reproductive organs.

After some experimentation, we developed an analytical routine that was applied to each of our main groups of analyses (A–D above; analysis E generated more equally most parsimonious trees than PAUP 2.4 can store). In each case, an initial run used the BANDB command to find all equally most parsimonious topologies by branch-and-bound, and the combination of the OPT=MINF optimization algorithm and APOLIST print command to identify the putative location and direction of each character state transition. Having thus determined the length of the shortest tree(s) (L_{min}), we then reanalyzed the data matrix by replacing the BANDB command with BB = 'X', where 'X' was one step longer than the shortest tree (i.e., L_{min+1}). This second run found and saved trees of lengths L_{min} and L_{min+1}; in order to determine the number of topologies of length L_{min+1}, the total number of topologies found at BB = L_{min} was subtracted from the total number of topologies found at BB = L_{min+1}. This procedure was repeated up to lengths of about L_{min+4} (depending on the particular submatrix under scrutiny). Tree number increases more-or-less exponentially with increase in length; the maximum capacity of PAUP 2.4 to store trees (N = 100) is soon exceeded, so that it becomes untenable to routinely scrutinize topologies much longer than L_{min}.

We found such scrutiny desirable for two reasons. First, we wished to know how many genus-level topologies occurred at each length, as opposed to species-(OTU-)level topologies routinely detected by the tree-building algorithm. Second, we wished to use lists of apomorphies following optimization to assess each tree for transient holapomorphies and autapomorphies, so that they could be subtracted to obtain its true length (determined entirely by synapomorphies sens. str.). In practice, this time-consuming screening procedure was not applied to trees longer than L_{min+1} (a new algorithm is required for this purpose), rendering optimization and the retention of apomorphy lists redundant from L_{min+2} onward (analyses A, B, D) or L_{min+3} onward (analysis C).

Having surveyed all optimally (L_{min}) and suboptimally ($L_{min+\leq 3}$) parsimonious trees, we focused on particular trees of interest, including all most parsimonious trees (MPT, i.e., tree of length L_{min}). These were reprinted with APOLIST (a list of node by node character state transitions) and CHGLIST (a list of character by character state transitions) for full interpretation (e.g., Figs. 6, 7). Topologies of potential interest longer than those routinely surveyed (i.e., longer than ca. L_{min+4}; Fig. 7) were specified using the TOPOLOGY command in "user tree" mode (Swofford, 1985: 2.20–2.22).

In summary, our cladistic analyses were experimental sensu Doyle & Donoghue (1986b). The basic philosophy of this approach was well summarized by Johnson (1982) and Bryant (1989: 218): "Parsimony determines the *order* by which viable hypotheses should be tested; one *starts* with the simplest" (our italics). Alternative hypotheses are then considered in order of increasing complexity until a self-imposed threshold is reached. In contrast, nonexperimental cladistic studies both start *and finish* with the simplest.

SPECIES-LEVEL RELATIONSHIPS

Although this experimental cladistic study was aimed primarily at elucidating genus-level relationships, we chose to perform our analyses at the species level. This decision partly reflected a subsidiary interest in species-level relationships, but was taken primarily because species-level OTUs provide a test of the presumed monophyly of genera. Genera can then be re-delimited if necessary. The following discussion is based primarily on analysis A, but also applies to analyses B–D (analysis E produced an untenably large number of equally most parsimonious trees).

Only four of the ten genera in the data matrix are represented by more than one OTU (Table 1): *Sigillaria* (two species), *Diaphorodendron* (three species), *Synchysidendron* (two species), and *Lepidophloios* (three species, but see Appendix 1D).

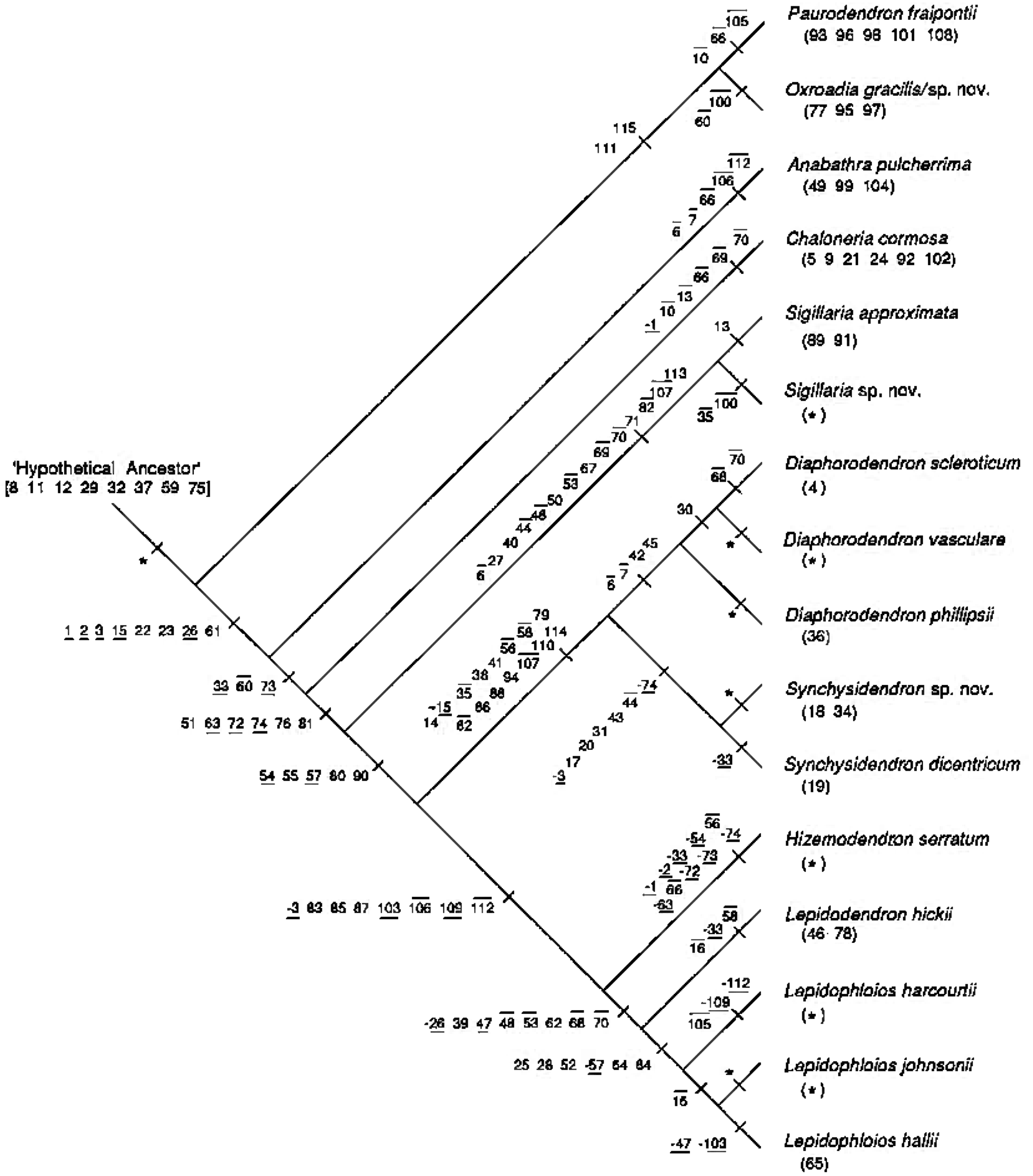


FIGURE 6. Preferred most parsimonious cladogram for analysis A (all OTUs and all characters). Holapomorphies are placed in square brackets below the hypothetical ancestor, and autapomorphies are placed in parentheses below OTUs; all character state transitions on terminal branches are therefore homoplastic. Characters that experience reversal are underlined (with a minus sign where a reversal occurs), parallelisms are overlined. Asterisks indicate absence of character state transitions at specific nodes.

Each of these four genera proved very robust (i.e., dismantling each genus in any way resulted in much longer trees), but relationships of the species within at least two of the genera are less clear (the two species of *Sigillaria* and *Synchysidendron* respectively do not allow multiple topologies).

The three-taxon problem presented by *Diaphorodendron phillipsii*, *D. vasculare*, and *D. scleroticum* is very poorly resolved (Fig. 6), resting entirely on the nonhomoplastic synapomorphy of secondary xylem in lateral branches (C30) that unites *D. scleroticum* and *D. vasculare* (Fig. 8d). Treating C30 as a synapomorphy of the clade and as a secondary loss in *D. phillipsii* (a tenable hypothesis more consistent with stratigraphic evidence; Fig. 3) costs only one extra step and col-

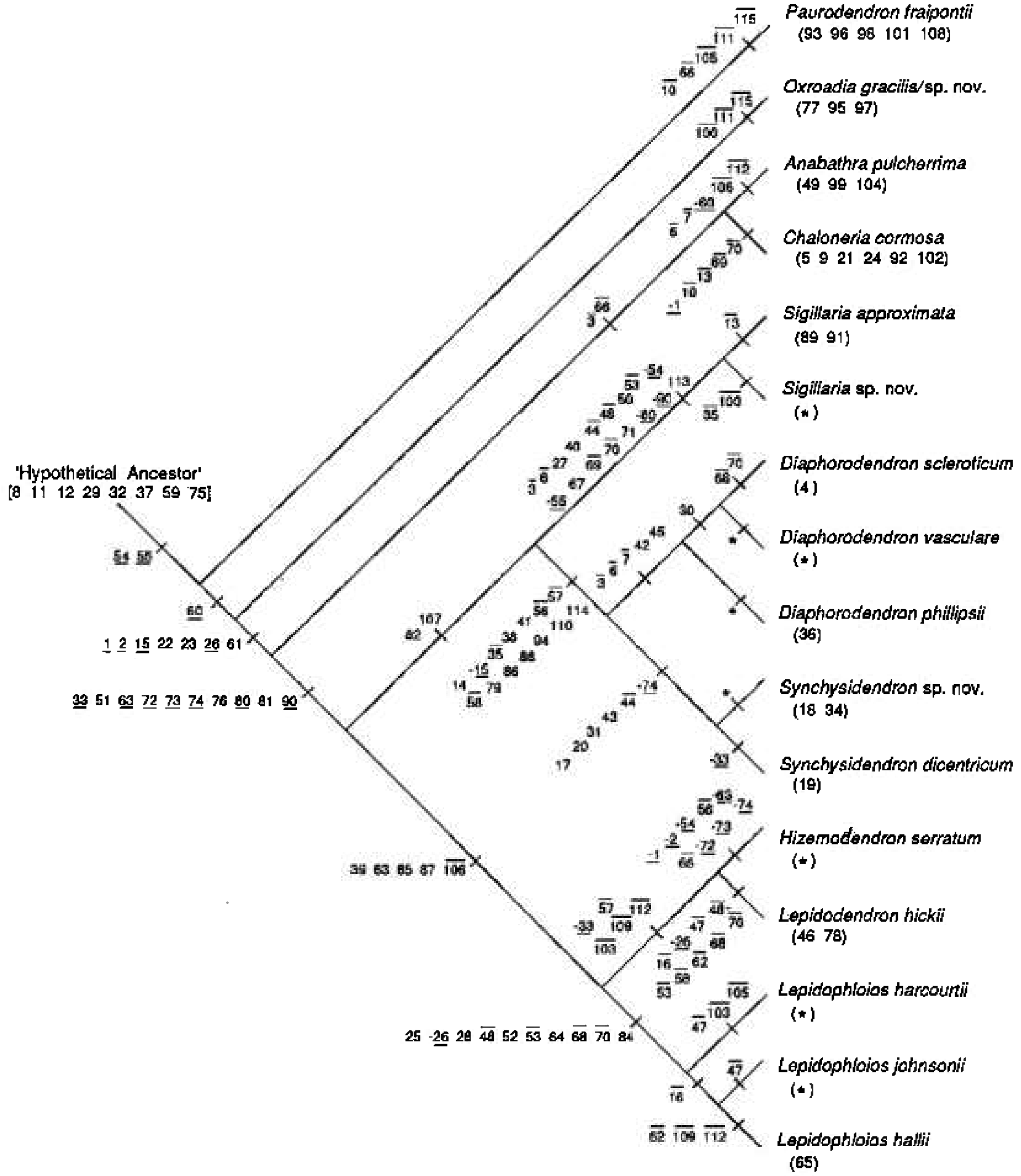
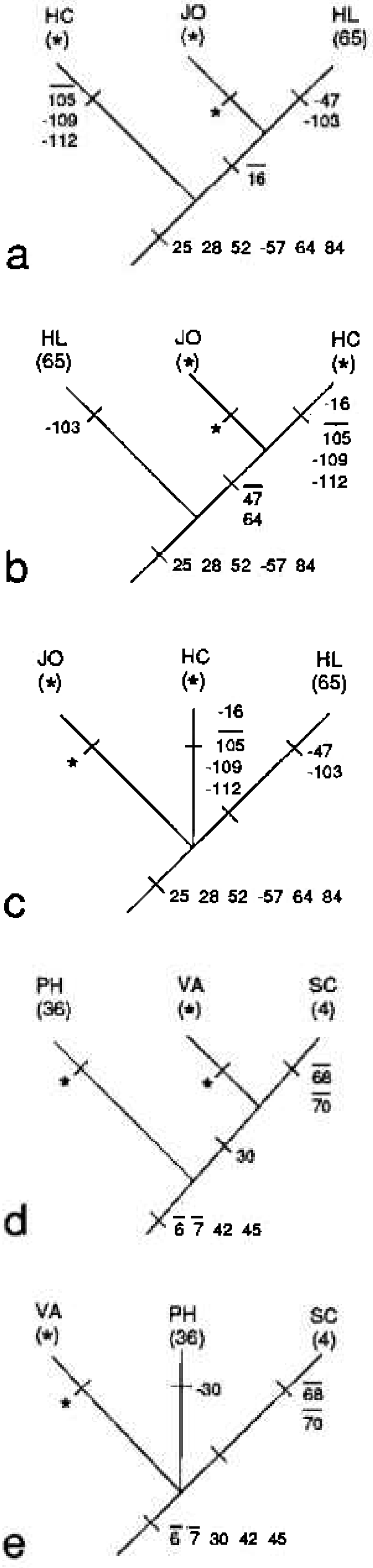


FIGURE 7. Fully annotated cladogram for analysis A showing alternative generic topologies of potential interest. It differs from Figure 6 in that (1) *Paurodendron* is a sister group of *Oxroadia* (cost = two steps), (2) *Anabathra* and *Chaloneria* form a clade (cost = nil). (3) *Sigillaria* and *Diaphorodendron* form a clade (cost = one step), and (4) *Hizemodendron* and *Lepidodendron* sens. str. form a clade (cost = five steps). Character notation follows Figure 6.

lapses the relationship into an uninformative trichotomy (Fig. 8e). This polychotomy was a persistent cause of trivially multiple topologies in our analyses (see Appendix 2).

The phylogenetic relationship of the three putative *Lepidophloios* species is obscured by extensive homoplasy that is compounded by ambiguities caused by missing values for some characters. *Lepidophloios hallii* and *L. harcourtii* are subtended only by homoplasies, while *L. johnsonii* is not subtended by any characters (it even lacks qualitative autapomorphies; Fig. 6). We obtained three equally most parsimonious solutions to this three-taxon problem (Fig. 8a–c). The first (Fig. 8a) links *L. johnsonii* and *L. hallii* by the homoplastic synapomorphy of a filamentous core to the protostele



(C16). The second (Fig. 8b) links *L. johnsonii* and *L. harcourtii* by the homoplastic synapomorphy of a glandular periderm (C47) and by the ostensibly nonhomoplastic synapomorphy of arched leaf cushions (C64). Unfortunately, this character is scored as missing for *L. hallii* as a result of X-coding (Table 3) and can therefore be treated as either apomorphic or plesiomorphic during optimization. As a result of inconsistent replacement during optimization, the apomorphic state is depicted as characterizing all three *Lepidophloios* species in Figure 8a but only two species in Figure 8b. The third topology (Fig. 8c) treats C16 as a loss in *L. harcourtii* and C64 as present in all three species, which consequently collapse to a trichotomy.

Given that all three solutions are equally most parsimonious, every topology that differed in the positions of OTUs other than *Lepidophloios* species was repeated three times by the tree-building algorithm to accommodate the multiple solutions to the *Lepidophloios* problem (hence our division by three of the algorithmically determined numbers of species-level topologies to yield the smaller, more meaningful values listed in Table 4). The arrangement of *Lepidophloios* species shown in Figure 8a best fits their reported sequence of relative appearance in the fossil record (Fig. 3); on the basis of this weak evidence, it was preferred when selecting the trees shown in Figures 6 and 7.

EXPERIMENTAL CLADISTICS: A SURVEY OF GENUS-LEVEL TOPOLOGIES

In all analyses, *Synchysidendron* and *Diaphorodendron* sens. str. consistently remained united as a monophyletic group and are not distinguished in Figures 9 and 10. Also, the following discussion occasionally refers to *Synchysidendron* as derived relative to *Diaphorodendron* and *Lepidophloios* as derived relative to *Lepidodendron*. As these pairs of genera are sister groups (Fig. 6), these assertions of derivation are subjectively imposed by us, based on comparison of the number and inferred evolutionary significance of the character state transitions supporting each genus.

←

FIGURE 8. Poorly resolved relationships between species of the same genus (see caption to Table 3 for key to abbreviations). a–c show three equally parsimonious (12-step) solutions to the three taxon problem presented by the *Lepidophloios* species. d and e show two solutions to the three taxon problem presented by the *Diaphorodendron* species (d = 7 steps, e = 8 steps). Notation largely follows Figure 6, though lines below character numbers emphasizing reversals are omitted.

TABLE 4. Comparison of cladistic parameters for five permutations (A–E) of the data matrix in Table 3. A = all taxa and all characters included; B = all taxa included, habit characters (C1–C7) omitted; C = *Chaloneria cormosa* omitted, all characters included (the total number of characters declines from 115 to 109 due to the elimination of *Chaloneria*'s six autapomorphies; also one former synapomorphy becomes an autapomorphy of *Paurodendron*); D = vegetative characters (C1–C4, C8–C72) only; E = reproductive characters (C5–C7, C73–C115) only. For numbers of trees, the initial figure is the number of species-level topologies of that length, the figure in parentheses is the number of genus-level topologies of that length, and the figure in square brackets is the cumulative total of genus-level tree topologies (ND = not determined). Figures for topologies longer than L_{min+1} may be inaccurate, as it was not feasible to screen by eye large numbers of trees for transient holapomorphies and transient autapomorphies (see "Optimization, character states, and missing values"). Strictly, each species-level value should be multiplied by three to reflect three equally parsimonious solutions to the relationships of the three species of *Lepidophloios* (this triangular relationship became unreliable in all analyses at L_{min+4}). The figure for analysis E remains greatly inflated by repeated dichotomies. Note that *Hizemodendron serratum* was treated as a new genus distinct from *Lepidodendron* sens. str. when calculating the genus-level values. Segregating *Synchysidendron* from *Diaphorodendron* sens. str. did not affect calculation of tree numbers, as the two genera consistently behaved as a monophyletic group.

Parameter		Analysis				
		A	B	C	D	E
Number of OTUs (excluding HYAN)		16	16	15	16	16
Total number of characters		115	108	109	69	46
Number of operational holapomorphies		8	8	8	7	1
Number of operational species-level autapomorphies		27	25	22	11	16
Number of informative characters remaining (synapomorphies sens. str.)		80	75	79	51	29
Minimum length (L_{min}; steps)		128	115	121	77	43
Consistency index at L_{min}		0.625	0.652	0.653	0.662	0.674
Number of trees of minimum and near-minimum length	L_{min}	3 (3) [3]	2 (2) [2]	1 (1) [1]	2 (2) [2]	270 (ND) [ND]
	L_{min+1}	14 (11) [11]	9 (7) [7]	3 (2) [2]	13 (11) [11]	—
	L_{min+2}	31 (19) [22]	28 (18) [18]	5 (4) [5]	44 (ND) [ND]	—
	L_{min+3}	62 (ND) [ND]	70 (ND) [ND]	14 (10) [11]	129 (ND) [ND]	—
	L_{min+4}	134 (ND) [ND]	133 (ND) [ND]	32 (ND) [ND]	—	—
	L_{min+5}	—	—	51 (ND) [ND]	—	—

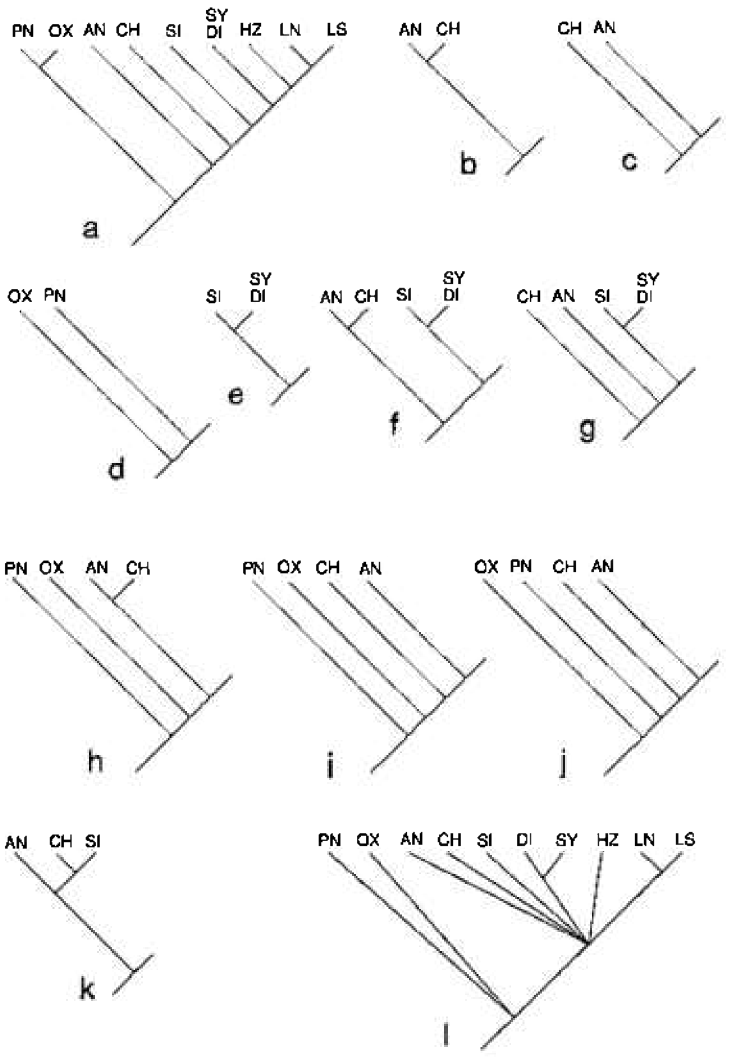


FIGURE 9. Generic topologies of analysis A at L_{min} (a–c) and L_{min+1} (d–k) (see caption to Table 3 for key to abbreviations). For analysis B (habit characters omitted), a and b occur at L_{min} and c–f, h at L_{min+1} (the relationship between *Chaloneria* and *Anabathra* became unresolved in c). For analysis C (*Chaloneria* omitted), only single generic topologies occur at L_{min} (that seen in a–c less *Chaloneria*) and at L_{min+1} (that seen in e–g). l is a strict consensus tree for analysis A at L_{min+2}, analysis B at L_{min+2}, and analysis C at L_{min+3} (less *Chaloneria*). *Synchysidendron* and *Diaphorodendron* are not distinguished in Figures a–g as they consistently behave as sister groups. All character information is omitted.

Analysis A (all OTUs and all characters included). Analysis A yielded three equally most parsimonious trees (MPTs; Fig. 9a–c) that unite *Oxroadia* and *Paurodendron* as a basal clade. The preferred most parsimonious tree (PMPT) depicts the remaining genera as a perfectly nested sequence of increasingly apomorphic OTUs (Figs. 6, 9a). The three MPTs differ in the position of *Chaloneria*, which occurs immediately above *Anabathra* in the preferred MPT (Fig. 9a), immediately below *Anabathra* in the second MPT (Fig. 9c), and is united with *Anabathra* to form a monophyletic clade in the third MPT (Fig. 9b).

Decreasing the level of parsimony by adding one step (L_{min+1}) yields another eight generic topologies (Fig. 9d–k). Three of these unite *Sigillaria* with *Diaphorodendron–Synchysidendron* (Fig. 9e–g), otherwise repeating the three possible relationships between *Chaloneria* and *Anabathra* seen in Figure 9a–c. Four others dissociate the *Oxroadia–Paurodendron* clade, so that each arises directly from the major axis (Fig. 9d, h–j); three of these (Fig.

9h–j) also involve changes in the relative positions of *Anabathra* and *Chaloneria*. It is then equally parsimonious to have *Oxroadia* (Fig. 9d, j) or *Paurodendron* (Fig. 9h, i) as the basal OTU of the tree. The eighth topology unites *Sigillaria* and *Chaloneria*, linking both to *Anabathra* to form a substantially different topology (Fig. 9k).

At $L_{\mathrm{min}+2}$, some topologies unite *Chaloneria* and *Sigillaria*, others allow the exchange of *Hizemodendron* and *Sigillaria* across *Diaphorodendron–Synchysidendron* (cf. Fig. 9a). The putative *Sigillaria–Diaphorodendron–Synchysidendron* clade can be placed above *Hizemodendron*. Alternatively, placing *Chaloneria* immediately below *Anabathra* allows the *Sigillaria–Diaphorodendron–Synchysidendron* clade to be situated between or immediately below these genera. Together, the five genera can form a sister clade to *Hizemodendron–Lepidodendron–Lepidophloios*, either with *Chaloneria–Anabathra* and *Sigillaria–Diaphorodendron–Synchysidendron* as sister groups or as a nested clade ((((*Diaphorodendron–Synchysidendron*) *Sigillaria*) *Anabathra*) *Chaloneria*).

Analysis B (all OTUs, "habit" characters C1–C7 omitted). The two MPTs of analysis B are identical to two of the three MPTs of analysis A (Fig. 9a, b). Five additional topologies occur at $L_{\mathrm{min}+1}$; one fails to resolve the relationship between *Chaloneria* and *Anabathra* (dashed line on Fig. 9c), two unite *Sigillaria* and *Diaphorodendron–Synchysidendron* (Fig. 9e, f), and two allow dissociation of the *Oxroadia–Paurodendron* clade (Fig. 9d, h). At $L_{\mathrm{min}+2}$, *Chaloneria* can be united with *Sigillaria*, *Hizemodendron* and *Sigillaria* can be transposed across *Diaphorodendron–Synchysidendron*, and the putative *Diaphorodendron–Synchysidendron–Sigillaria* clade shown in Figure 9e can be placed above *Hizemodendron* or below *Anabathra* and *Chaloneria*. All topologies found in analysis B at $L_{\mathrm{min}+2}$ were also found in analysis A at $L_{\mathrm{min}+2}$.

Analysis C (Chaloneria omitted, all characters included). The only MPT from analysis C merely deletes *Chaloneria* from the preferred MPT of analysis A (Fig. 9a). Increasing the number of steps allow a *Sigillaria–Diaphorodendron–Synchysidendron* clade, either below ($L_{\mathrm{min}+1}$) or above ($L_{\mathrm{min}+2}$) *Hizemodendron*, and disaggregation of the *Oxroadia–Paurodendron* clade ($L_{\mathrm{min}+2}$). The range of topologies substantially increases at $L_{\mathrm{min}+3}$. Once again, *Sigillaria* and *Hizemodendron* can be exchanged across *Diaphorodendron–Synchysidendron*. A putative *Sigillaria–Diaphorodendron–Synchysidendron* clade can be placed low in the tree, between *Oxroadia–Paurodendron* and *Anabathra*, or it can be appended to *Anabathra* to yield a more innovative topology.

A strict consensus tree (Nelson, 1979, 1983) at $L_{\mathrm{min}+2}$ (analyses A, B) or $L_{\mathrm{min}+3}$ (analysis C), has only four nodes (Fig. 9l); only *Oxroadia* and *Paurodendron* (at the base of the tree), *Diaphorodendron* and *Synchysidendron*, and *Lepidodendron* and *Lepidophloios* (at the apex) are consistently conjoined and/or juxtaposed.

Analysis D (all OTUs, vegetative characters only). The preferred MPT for analysis D (Figs. 10a, 11) is pectinate (each genus is connected directly to the major axis) and differs substantially from the preferred MPT of analyses A–C (see also Bateman & DiMichele, 1991). *Lepidodendron* and *Lepidophloios* remain linked at the top of the tree, but two pairs of adjacent branches are transposed (*Sigillaria* and *Diaphorodendron–Synchysidendron*, *Anabathra* and *Chaloneria*). The *Oxroadia–Paurodendron* clade is split into its constituent genera, each of which forms an equally parsimonious sister group to the rest of the ingroup (Fig. 10a, b). *Hizemodendron* is sister group to the most derived genera *Lepidodendron* and *Lepidophloios* in the preferred MPT of analysis A (Fig. 9a), but is derived relative only to *Oxroadia* and *Paurodendron* in the preferred MPT of analysis D.

All of the variation among the eight additional generic topologies at $L_{\mathrm{min}+1}$ occurs below *Diaphorodendron–Synchysidendron* in the tree, indicating that the more apomorphic portion of the tree is the most robust. An unresolved trichotomy replaces the *Oxroadia–Paurodendron* clade (Fig. 10c). The remaining topologies place *Anabathra* below *Chaloneria* (Fig. 10d–f) or unite *Anabathra* and *Chaloneria* as a separate clade (Fig. 10g–j). *Hizemodendron* is the least stable genus; it can occur below (Fig. 10a–e, g, i) or above (Fig. 10f, h, j) *Anabathra* and *Chaloneria*. In the most radical topology, *Hizemodendron* is the sister group of *Anabathra* and *Chaloneria*, together forming a separate clade (Fig. 10k).

Analysis E (all OTUs, reproductive characters only). In contrast with the other analyses, it was not possible using PAUP 2.4 to store and thereby screen all 810 MPTs for analysis E (270 trees, if the equally most parsimonious solutions to the *Lepidophloios* species relationships are ignored). Available evidence suggests that the number of MPTs was grossly exaggerated by repeated polychotomies and conceals a much smaller number of substantially different topologies. A representative and fully annotated MPT is shown in Figure 12a.

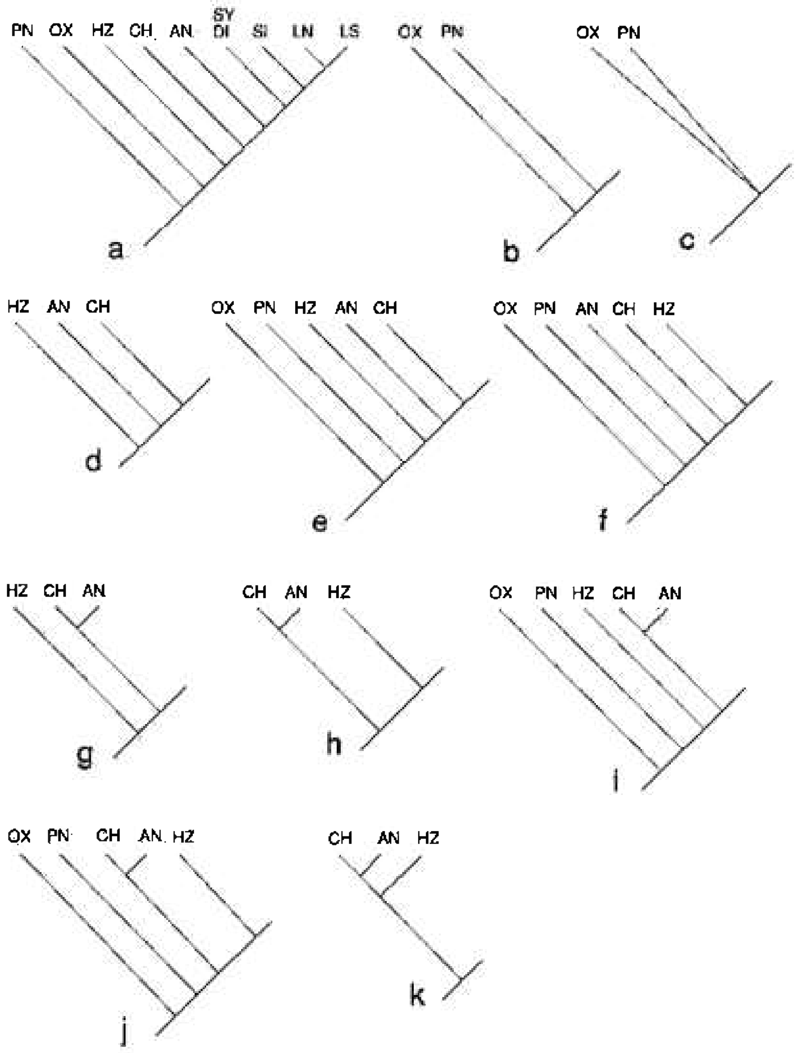


FIGURE 10. Generic topologies of analysis D (vegetative characters only) at L_{min} (a, b) and L_{min+1} (c–k). (See caption to Table 3 for key to abbreviations.) Only those portions of trees that differ from the preferred most parsimonious tree (a) are shown, and all character information is omitted.

Unlike analyses A–D, the relationship between the four most primitive OTUs is unresolved, as are the relationships between (1) the three species of *Diaphorodendron* sens. str., and (2) *Hizemodendron* and *Lepidodendron*. The most radical innovation is the depiction of *Lepidophloios* as polyphyletic; the relatively primitive *L. harcourtii* is separated from *L. johnsonii* and *L. hallii* by *Lepidodendron* and *Hizemodendron*. Restoring *Lepidophloios* to monophyly costs one additional step (Fig. 12b).

Methodological conclusions. For any cladistic matrix, progressive one-step increases in length relative to the MPT result in a rapid increase in the number of topologies obtained (Table 4). The gradient of this increase provides an estimate (albeit crude and dependent on matrix size) of the relative resolution of different data matrices; more confidence can be placed on a most parsimonious tree from a matrix that yields few alternative trees of optimal or near-optimal length (more rigorous, statistical methods are now available for determining confidence limits of specific topologies; e.g., Felsenstein, 1985; Archie, 1989b; Sanderson, 1989).

For our data, the complete data matrix (analysis A) provides a yardstick by which to measure the relative resolution of analyses based on selectively reduced permutations of the matrix presented in Table 3 (i.e., analyses B–E). Omitting the five synapomorphic habit characters (analysis B) yield-

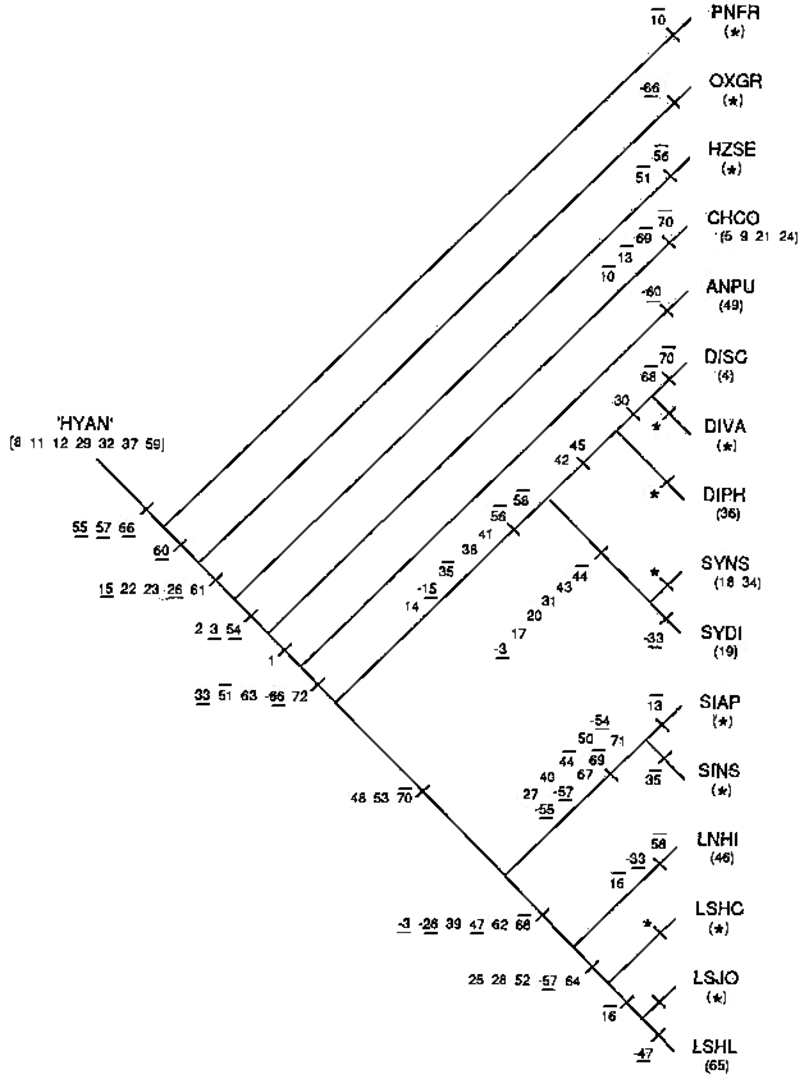


FIGURE 11. Preferred most parsimonious cladogram for analysis D (vegetative characters only). Character notation follows Figure 6, OTU notation follows Table 3.

ed fewer topologies of length L_{min}–L_{min+1} and slightly increased the consistency index (Table 4). Omitting *Chaloneria*, the least stable OTU (analysis C), increased the consistency index by a similar amount to that of analysis B and generated an even more highly resolved set of trees that included only one most parsimonious topology (Fig. 9a).

Substantially reducing the size of the data matrix analyzed by including only vegetative characters (analysis D) or only reproductive characters (analysis E) also increased consistency index values relative to those of analysis A. However, in contrast with analyses B and C, analyses D and E yielded less resolved sets of topologies (Table 4). Analysis D provided acceptable results (Fig. 10), but analysis E yielded 270 equally most parsimonious trees, all containing at least one polychotomy. Thus, it is tempting to argue that vegetative characters are more phylogenetically informative (i.e., less homoplastic) than reproductive characters, but levels of homoplasy are very similar in the MPTs of the vegetative and the reproductive submatrices (consistency index values = 0.66 and 0.67 respectively; Table 4). Rather, the crucial difference apparently lies in the different sizes of the submatrices, which are reflected in different values for the average number of synapomorphic character states per OTU: 3.2 in analysis D and 1.8 in analysis E. For the preferred MPT of our complete matrix, the number of steps per synapomorphy (1.6) and

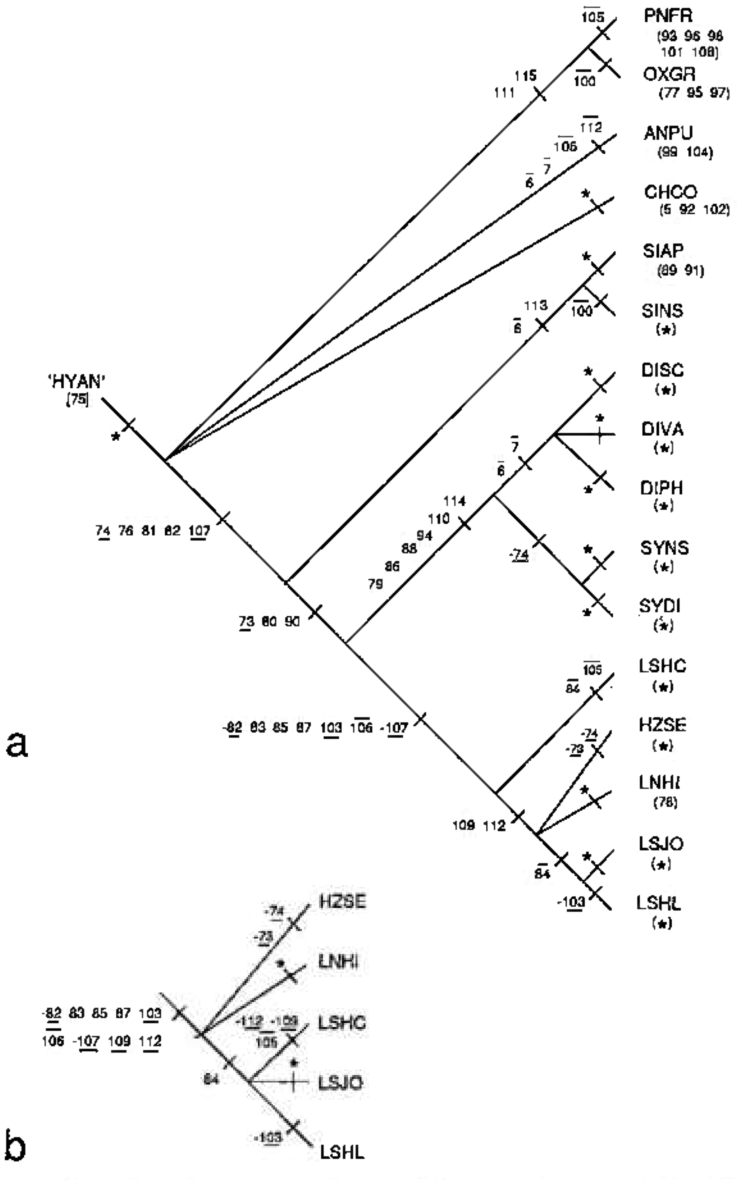


FIGURE 12. a. Preferred most parsimonious cladogram for analysis E (reproductive characters only). Character notation follows Figure 6, OTU notation follows Table 3.—b. Terminal portion of an alternative topology at L_{min+1}.

the resulting consistency index (0.63) are average relative to those of other cladistic data matrices containing similar numbers of OTUs (the main variable influencing consistency index values: cf. figs. 2a and 3 of Archie, 1989a; fig. 1b of Sanderson & Donoghue, 1989). Thus, we suggest that for a data matrix of average homoplasy (as here), there is a threshold of minimum empirical support (2–3 synapomorphies per OTU) below which well-resolved sets of fully dichotomous trees cannot be expected (see also Felsenstein, 1985; Guyer & Slowinski, 1991).

EMPIRICAL SUPPORT FOR ALTERNATIVE HYPOTHESES OF GENERIC RELATIONSHIPS

The relative merits of the topologies described above are best assessed by examining the optimized distributions of character state transitions across the trees and subjectively estimating the probabilities of alternative evolutionary scenarios for particular suites of characters. To this end, many of the near-optimally parsimonious pairings of genera obtained during the topological survey of analysis A are summarized in a single fully annotated tree

(Fig. 7), to enable comparison with the preferred most parsimonious tree (Fig. 6).

Oxroadia and Paurodendron. Oxroadia and *Paurodendron* share only two synapomorphies (Fig. 6). Both are nonhomoplastic and describe echinate distal and proximal surfaces of microspore exines (C111, C115). Disaggregating this clade induces parallelism in these characters, at the cost of one step (Fig. 7). Given that echinate microspore exines could be regarded as a single character, the status of these two genera as a monophyletic group may be even less well supported than parsimony suggests. A phylogenetic study focusing specifically on these and other similarly primitive genera is required to resolve this ambiguity.

Anabathra and Chaloneria. Topologies treating this group as paraphyletic (Fig. 6) or as a monophyletic clade (Fig. 7) are equally parsimonious, differing only in the distributions of a few homoplasies. When united, the genera possess only two synapomorphies: weakly branched or unbranched trunk apex (C3) and acutely angled leaf attachment (C66). Both characters are parallelisms: trunks with little or no branching are depicted as homoplastic, also occurring in *Sigillaria* and *Diaphorodendron*. Angle of leaf attachment, a character prone to ontogenetically related variation and ecophenotypic modification, is represented as a parallel trait in *Paurodendron* and *Hizemodendron*. Thus, evidence for an *Anabathra–Chaloneria* clade is weak.

Uniting *Anabathra* and *Chaloneria* affects optimized character state transitions elsewhere in the tree. In Figure 6, unbranched trunk apex (C3) is perceived as reversed in *Synchysidendron* and in the *Hizemodendron–Lepidodendron–Lepidophloios* clade, but in Figure 7 this character state is depicted as a parallel acquisition in *Anabathra–Chaloneria*, *Diaphorodendron*, and *Sigillaria*. The absence of a ligule cavity (C60) in *Anabathra* is a plesiomorphy in Figure 6 but a reversal in Figure 7. Missing values for C33 (secretory intracortical leaf sheaths) and C73 (branch gap associated with peduncle) in *Chaloneria* allow these characters to be optimized as apomorphic in Figure 6 (despite the absence of a cone in *Chaloneria*) but plesiomorphic in Figure 7.

Anabathra, Chaloneria, and Sigillaria. In analysis A, these genera formed a clade at $L_{\min+1}$ (Fig. 9k). *Chaloneria* and *Sigillaria* are united by two nonhomoplastic character states, fusiform rootlet gaps (C13) and V-shaped leaf traces (C69), and by the homoplasy of abaxial grooves in the leaf (C70). The apparent synapomorphy for C69 may be false if the V-shaped leaf trace of *Sigillaria* reflects origination from two protoxylem strands, and the abaxial grooves may be developmentally related to leaf trace morphology. *Anabathra* is united with *Chaloneria* and *Sigillaria* on the basis of two homoplasies reflecting habit: the trunk possesses an apex that shows little if any branching (C3) and bears lateral branches and/or cones (C6; a character that could not be coded for the branchless and coneless *Chaloneria*). Both states also characterize *Diaphorodendron* (Fig. 6).

Diaphorodendron and Synchysidendron. The distinction between the segregate *Synchysidendron* (*S. dicentricum* and *Synchysidendron* sp. nov.) and the three species of *Diaphorodendron* sens. str. is well supported (Fig. 6), the former by seven synapomorphies (four nonhomoplastic) and the latter by four synapomorphies (two nonhomoplastic). These characters, which represent habit sens. lat. (C3, C6–C7, C74), leaf base retention (C44–C45), stele histology (C17, C20, C31), and periderm histology (C42–C43), reflect two substantially different growth habits (see Evolutionary Patterns). Nesting *Synchysidendron* within *Diaphorodendron* requires a minimum of four extra steps in analyses A, C, and D, and three extra steps when habit characters C1–C7 are omitted (analysis B). Placing the genera on separate terminal branches is even less parsimonious. Although there is little doubt that *Diaphorodendron* sens. lat. (i.e., sensu DiMichele, 1985) is monophyletic, we believe that the differences between the two monophyletic groups of species that it contains are sufficiently profound to warrant segregation of the new genus, *Synchysidendron* (Appendix 1C).

Sigillaria and Diaphorodendron–Synchysidendron. Sigillaria and *Diaphorodendron–Synchysidendron* are empirically the best supported of all the clades under scrutiny; *Sigillaria* is supported by 14 characters (six nonhomoplastic), and *Diaphorodendron–Synchysidendron* by 15 characters (nine nonhomoplastic). Uniting *Sigillaria* with *Diaphorodendron–Synchysidendron* adds only one step and transforms two reproductive character states from parallelisms into nonhomoplastic synapomorphies: short, horizontal alations on the megasporophyll pedicel (C82), and crassitude microspore laesurae (C107). Balancing these gains, homoplasy is induced by losses in three character states: the presence of a lower keel on the leaf cushion (C55), germination of megaspores within the sporangium (C80), and reduction of viable megaspores to one per sporangium (C90, a logical functional correlate of C80). Although Figure 7 portrays these character state transitions as reversals in *Sigillaria*, they are more likely to represent parallel acquisitions in *Diaphorodendron–Synchysidendron* and in the more derived *Hizemodendron–Lepidodendron–Lepidophloios* clade (loss of these traits in *Sigillaria* would probably confer a severe competitive disadvantage). As all five of the above characters are considered potentially homoplastic, the possible monophyly of *Sigillaria–Diaphorodendron–Synchysidendron* remains equivocal.

Differential optimization alters perceptions of evolutionary patterns of three other characters in Figure 7. The first is stem apical branching (C3, already discussed under *Chaloneria–Anabathra*), and the remaining two describe leaf cushion morphology. In Figure 6, the plicate lower field (C57) evolves below *Diaphorodendron–Synchysidendron* and is subsequently lost in *Lepidophloios*, whereas in Figure 7 it is represented as a parallel acquisition in *Diaphorodendron–Synchysidendron*, *Hizemodendron*, and *Lepidodendron*. Similarly, in Figure 6, the upper keel evolves below *Diaphorodendron–Synchysidendron* and is lost in *Hizemodendron*, whereas in Figure 7 it evolves below the *Oxroadia–Paurodendron* clade (despite the absence of leaf cushions in these highly plesiomorphic genera) and is independently lost in *Sigillaria* and *Hizemodendron*. For both characters, the optimizations in Figure 6 are more intuitive.

Hizemodendron and Lepidodendron. As depicted in Figure 6, the branches immediately subtending *Hizemodendron* and *Lepidodendron* share only one character state transition: the loss of secretory intracortical leaf-trace sheaths (C33). The other four characters that support the *Hizemodendron–Lepidodendron* clade in Figure 7 are all parallelisms. Three describe microspore equatorial (C103) and contact face (C109, C112) ornamentation and are homoplastic among *Lepidophloios* species. Their frequencies and distributions differ between topologies, due to inconsistent optimization of missing values. These characters are more appropriately treated as reversals within *Lepidophloios* (Fig. 6) than as parallelisms in *Lepidophloios* and *Hizemodendron–Lepidodendron* (Fig. 7). In Figure 6, the fourth character state, plication of the lower field of the leaf cushion (C57), originates below *Diaphorodendron–Synchysidendron* and is reversed in *Lepidophloios*. In Figure 7, this character state originates twice, in *Diaphorodendron–Synchysidendron* and in *Hizemodendron* (a less probable scenario). Missing values allow demotion of infrafoliar parichnos from a nonhomoplastic synapomorphy of *Lepidodendron* and all *Lepidophloios* species (Fig. 6) to a parallelism of *Lepidodendron* and *Lepidophloios hallii* only (Fig. 7). Similarly, a missing value in *Hizemodendron* for multizoned periderm (C39) allows the genus to be plesiomorphic for this character in Figure 6 but apomorphic in Figure 7.

However, the most deleterious consequence of uniting *Hizemodendron* and *Lepidodendron* is the generation between *Lepidodendron* and *Lepidophloios* of five vegetative parallelisms: discernable protoxylem ridges on the stele (C26), resinous periderm (C48), tangentially elongate leaf cushions on twigs (C53), and a leaf with a dorsiventrally flattened vascular strand (C68) and lateral abaxial grooves (C70). The overall cost to parsimony (five steps) appears sufficient to reject the hypothesis of monophyly. Nevertheless, treating these hypothesized character state transitions as reversals in *Hizemodendron* suggests a heterochronic evolutionary mechanism that could allow monophyly (see Evolutionary Patterns).

Lepidodendron sens. lat. Prior to the studies of DiMichele (1985), Bateman & DiMichele (1991), and DiMichele & Bateman (1992), '*Lepidodendron*' sens. lat. encompassed four of the anatomically preserved genera analyzed by us: *Lepidodendron* sens. str., *Hizemodendron*, *Diaphorodendron*, and *Synchysidendron*. Forcing these four genera into a single clade representing the traditional concept of *Lepidodendron* (not illustrated) cost nine additional steps and revealed only one synapomorphy uniting the clade: a plicate lower field to the leaf cushion, which is reversed in *Lepidophloios* in the preferred MPT (Fig. 6). In contrast, five nonhomoplastic synapomorphies in Figure 6 are rendered homoplastic: short, erect megasporophyll alations (C83) and bilaterally flattened (C85), distally dehiscent (C87) megasporangia are lost in *Diaphorodendron–Synchysidendron*, and zoned periderm (C39) and infrafoliar parichnos (C62) become parallelisms in *Lepidodendron* and some *Lepidophloios* species as a result of ambiguous missing values in the latter. Moreover, homoplasy is increased in other characters already depicted as homoplastic in Figure 6. We conclude that '*Lepidodendron*' sens. lat. is clearly a paraphyletic group.

MULTIVARIATE ANALYSIS

In order to examine patterns of morphological variation free from the rigid constraints imposed by cladistic nested hierarchies, we subjected the cladistic data matrix (Table 3) to multivariate analysis. A value of zero or unity was substituted a priori for each missing value according to optimized distributions of character state transitions in the preferred most parsimonious cladogram (Table 3 subscripts, Fig. 6). The resulting uniformly binary matrix allowed generation of a symmetrical matrix comparing OTUs without a priori standardization, simply using the number of character state conflicts (i.e., 0 vs. 1) as a direct measure of dissimilarity between pairs of OTUs. The dissimilarity values were used to construct an unrooted minimum spanning tree (Gower & Ross, 1969); links in the tree represent specific sets of character state transitions, thus contradicting frequent assertions that phenetic trees inevitably lack such information. Also, principal coordinates (Gower, 1966) were calculated from the data matrix via Manhattan distances, using unpublished software written by J. Alroy. Holapomorphies (which are invariant) were excluded (as in cladistic analysis), but autapomorphies contributed to both the unrooted tree and the ordination.

Links between genera on the minimum spanning tree (Fig. 13a) represent at least 10 character conflicts, those within genera represent no more than five. The 21 conflicts between *Hizemodendron* and *Lepidodendron*, and 14 conflicts between *Synchysidendron* and *Diaphorodendron*, emphasize the need to segregate these new genera (Appendix 1C).

The minimum spanning tree resembles the preferred most parsimonious cladogram (Fig. 6) in depicting a progression from *Paurodendron* and *Oxroadia* through *Anabathra*, *Hizemodendron*, and *Lepidodendron* to *Lepidophloios* (though *L. johnsonii* is shown as ancestral to the two remaining species). However, *Anabathra* is also depicted as the ancestor of a second lineage, consisting of *Chaloneria*, *Sigillaria*, *Diaphorodendron*, and *Synchysidendron*, that is not represented among the range of cladograms shown in Figure 9. This second lineage is held together by the weakest links in the tree (*Chaloneria–Sigillaria* = 29 conflicts, *Sigillaria–Diaphorodendron* = 33 conflicts) and consequently can be dissociated at the cost of very few additional steps (Fig. 13b), demonstrating that these genera are the most problematic in both the cladistically and phenetically generated phylogenies. Attaching *Sigillaria* directly to *Anabathra*, rather than via *Chaloneria*, creates an intuitively more credible evolutionary hypothesis at the expense of two steps. *Diaphorodendron* and *Synchysidendron* can be attached to *Hizemodendron* at the cost of only one step, but this results in the putatively more derived *Synchysidendron* giving rise to the more primitive *Diaphorodendron*. *Paurodendron* can replace *Oxroadia* as the closer relative of *Anabathra* at the cost of one step.

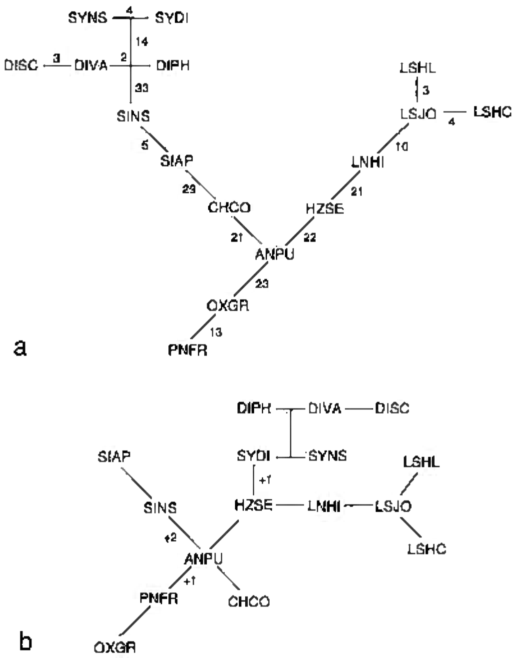


FIGURE 13. a. Minimum spanning tree (unrooted phenetic tree) as based on cladistic data matrix (Table 3, q.v. for key to OTUs). Links represent numbers of character state conflicts.—b. Alternative links that are almost maximally parsimonious; additional steps relative to a are marked.

In summary, the phenetic trees serve primarily to emphasize the potentially pivotal role of *Anabathra* as the most primitive arboreous lycopsid analyzed.

The first three principal coordinates (Fig. 14) account for an unusually large proportion (91%) of the total variance. The first coordinate separates *Diaphorodendron–Synchysidendron* from the other genera, the second coordinate separates *Lepidodendron–Lepidophloios* from the bisporangiate-coned group of *Paurodendron–Oxroadia–Anabathra–Chaloneria* (with *Hizemodendron* intermediate), and the appreciably weaker third coordinate separates *Sigillaria* (and, to a lesser extent, *Chaloneria*) from the remainder. The resulting tetrahedral arrangement of four clusters (excluding *Hizemodendron*), separated by broad morphological discontinuities, underlines the distinctiveness of the three groups of monosporangiate-coned trees (*Sigillaria*, *Diaphorodendron–Synchysidendron*, *Lepidodendron–Lepidophloios*) and the consequent difficulties of resolving their phyloge-

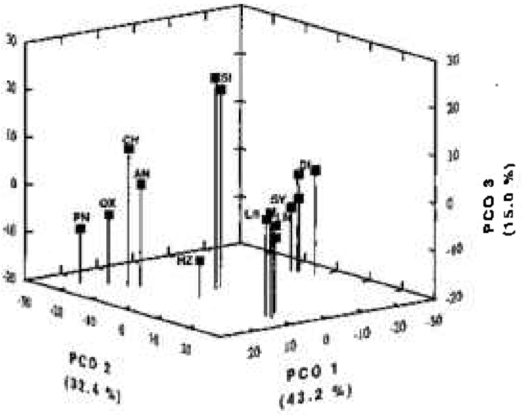


FIGURE 14. Principal coordinates ordination of the OTUs, based on Table 3 (q.v. for OTUs). Only genera are labeled. Two *Diaphorodendron* species are indistinguishable on the first three coordinates.

netic relationships relative to each other and to *Anabathra*, their most likely sister group.

EVOLUTIONARY PATTERNS AND PROCESSES

Overall trends. Much of the variation among arborescent lycopsids can be resolved into a vegetative trend, reflecting in particular morphological and anatomical expression of different growth architectures, and a reproductive trend, representing increasingly sophisticated reproductive strategies. The phylogenetic analyses show that the two trends are not entirely concordant; the preferred MPTs using vegetative characters only (analysis D; Fig. 11) and reproductive characters only (analysis E; Fig. 12) have substantially different topologies. The following discussion of these trends emphasizes characters for which we developed strong (often a priori) hypotheses of high burden and pays particular attention to the relative temporal order of appearance of apomorphic states of different characters (e.g., Donoghue, 1989).

Many (possibly all) of the MPTs of analysis E (reproductive characters only) distinguish the four bisporangiate-coned genera (*Paurodendron*, *Oxroadia*, *Anabathra*, *Chaloneria*) from the five relatively derived genera that possess a suite of characters reflecting the developmental partitioning of mega- and microsporangia into monosporangiate cones (Fig. 12). In contrast, the preferred MPT of analysis D (vegetative characters only) distinguishes four primitive pseudoherbs/shrubs (*Paurodendron*, *Oxroadia*, *Hizemodendron*, *Chaloneria*) from five derived arboreous genera (the derived clade is supported by the tree habit *only*; Fig. 11) and depicts *Sigillaria* as derived relative to *Diaphorodendron–Synchysidendron*. The genera whose positions differ most between the reproductive and vegetative cladograms are the bisporangiate-coned tree *Anabathra*, which is reproductively plesiomorphic and vegetatively apomorphic, and the monosporangiate-coned pseudoherb *Hizemodendron*, which is reproductively apomorphic and vegetatively plesiomorphic (see also Bateman & DiMichele, 1991).

Thus, monosporangiate cones (Fig. 12) and the tree habit (Fig. 11) cannot both be nonhomoplastic, though a full analysis using vegetative and reproductive characters together could have yielded a compromise solution involving homoplasy in both suites of characters. In fact, although its topology differs in detail from those of analyses D and E, the preferred MPT for analysis A (all characters and OTUs; Fig. 6) more closely resembles the exclusively reproductive cladogram (Fig. 12) than the exclusively vegetative cladogram (Fig. 11); in particular, the monosporangiate-coned clade is retained at the expense of depicting the tree habit as homoplastic.

The two subsections that follow discuss in greater detail the reproductive and vegetative trends, focusing on the functional morphology and adaptive (or nonadaptive) significance of specific character states, before returning to the evolutionary implications (and limitations) of the preferred whole-organism cladogram.

Reproductive morphology. Reproductive characters proved to be of little value in elucidating phylogenetic relationships within the plesiomorphic group of bisporangiate-coned OTUs, which differ primarily in autapomorphic spore character states (Fig. 12). Careful revision of bisporangiate cones is desirable, to search for potential synapomorphies less inclusive than the entire group. It is particularly important to understand the ontogeny and reproductive biology of the bisporangiate cones in order to determine how they could have given rise to monosporangiate-coned descendants. All bisporangiate cones have apically concentrated microsporangia and basally concentrated megasporangia irrespective of presumed geotropic orientation, suggesting a shared developmental control of sporogenesis.

In contrast, the functional morphology of reproductive characters within the monosporangiate-coned portion of the lepidodendralean clade has prompted much discussion (e.g., Thomas, 1978; Phillips, 1979; DiMichele & Phillips, 1985; Phillips & DiMichele, 1992; see Appendix 1D for the taxonomic implications). In Figures 6 and 12, the appearance of monosporangiate cones (immediately below *Sigillaria*) is accompanied by lateral expansion of the sporophyll pedicel to form alations and by the functionally important transition in basic dispersal unit from isolated megaspores to the megasporophyll-megasporangium complex. All three character states persist without reversal throughout the derived clade, indicating strong functional linkage that may be evolutionarily tied to elaboration of the leaf bases.

Current evidence suggests that the leaf lamina and leaf base are derived from the same primordium; the leaf cushion, an elaborated leaf base, is also fundamentally foliar. Furthermore, we believe that the sporophyll lamina is homologous with the leaf lamina, and that the sporangium-bearing pedicel is homologous with the leaf base, including an elaborated cushion if present. The strongest evidence supporting these homologies is provided by the ligule (e.g., Phillips, 1979; Bateman, 1988), which occurs adaxially on (*Paurodendron*) or within (all other OTUs) the bases of leaves (Fig. 4b) but on sporophylls occurs close to the distal end of the pedicel, between the sporangium and the more-or-less perpendicular junction of the pedicel and lamina (Fig. 4d). Regarding the attachment of the ligule as a homologous point implies that the pedicel is indeed homologous with the leaf base. Both the leaf base (and thereby cushion) and lamina originate from the same primordium, as do the sporophyll pedicel and lamina. Leaf and sporophyll both bear a ligule and both are fundamentally appendicular in origin. Moreover, there is a strong positive correlation between the complexity of the pedicel-sporangium unit and that of the leaf base; definable leaf cushions appear at the same node of the cladogram as monosporangiate cones, and both structures progressively increase in complexity through the remainder of the clade, culminating in the large, elaborate leaf cushions and equally large, seedlike megasporophyll of *Lepidophloios* (e.g., Reed, 1941; Phillips, 1979). Thus, the evolution of the leaf cushion may have been developmentally linked to that of the sporophyll (T. L. Phillips, pers. comm. 1989). It is not clear whether elaboration of the leaf prompted modification of the sporophyll, or whether increase in size of the appendicular primordial meristems allowed simultaneous expansion and elaboration of both leaf bases and sporophyll pedicels.

Whatever its driving mechanism, the transition from bisporangiate to monosporangiate cones (immediately below *Sigillaria* on Figs. 6 and 12) represents a crucial release from developmental constraints (cf. Endress, 1987, on angiosperms). In particular, it allowed spatially independent development of the mega- and microsporophylls, thereby permitting modifications of the megasporophyll-megasporangium units that could have impaired the function of microsporophyll units if similarly modified (a likely consequence in bisporangiate cones, where mega- and microsporophylls form a developmental continuum). Thus, free megaspores were superseded as the basic dispersal unit by the megasporophyll-megasporangium complex.

The remaining reproductive modifications that delimit increasingly exclusive portions of the monosporangiate-coned clade can be envisioned as a progressive evolutionary trend toward *K*-selection (sensu Pianka, 1970). Megaspores decrease in number and increase in size, and the pedicellate tissues surrounding the megasporangium become adapted for increasingly specialized modes of microspore/microgametophyte capture and diaspore dispersal (e.g., Phillips, 1979). However, arguments that the most derived product of this evolutionary trend, *Lepidophloios–Lepidocarpon*, possesses true seeds (Zhang et al., 1986) are phylogenetically unhelpful; the megasporophylls are clearly analogs rather than homologs of gymnosperm ovules.

Reduction in megaspore number to one per sporangium, and concomitant germination of megaspores within the sporangium, distinguish the remainder of the monosporangiate-coned clade from *Sigillaria* (Figs. 6, 12). The dichotomy immediately above *Sigillaria* results in two clades well supported by reproductive characters: *Diaphorodendron–Synchysidendron* (proximally dehiscent, dorsiventrally flattened, heterocellular megasporangium containing gulate megaspores; granulate-foveolate *Granasporites* microspores), and *Hizemodendron–Lepidodendron–Lepidophloios* (distally dehiscent, cylindrical sporangium subtended by suberect alations; cingulate *Lycospora* microspores). Enveloping, integumentlike alations delimit *Lepidophloios* (Fig. 6; in the analysis of reproductive characters only (Fig. 12a), this single character is insufficient to override differences in microspore ornamentation between *Lepidophloios* species, resulting in depiction of the genus as polyphyletic; inducing monophyly in *Lepidophloios* costs one extra step (Fig. 12b)). Interestingly, the vegetatively well-differentiated species of *Diaphorodendron* and *Synchysidendron* (Fig. 11) are effectively uniform in reproductive characters (the medullated stele attributed to *Diaphorodendron* (C74) strictly applies to the cone-bearing lateral branches rather than the cones per se; Appendix 1D).

Distinguishing between monoecious and dioecious strategies is especially valuable in interpreting the phylogeny and the functional morphology of extant plants (e.g., Bawa, 1980; Givnish, 1980, 1982; Donoghue, 1989). Unfortunately, the almost inevitable disarticulation of cones from vegetative axes undermines attempts to identify the reproductive strategies adopted by members of the monosporangiate-coned lycopsid clade. Were individual plants monoecious or dioecious? If monoecious (as seems more likely), did megasporangiate and microsporangiate cones mature synchronously or sequentially? Or were arborescent lycopsids capable of even more complex strategies, such as gynodioecy?

Overall, spore morphology proved less phylogenetically informative than cone morphology. Many of the spore character states are species-level autapomorphies, and the remainder exhibit significantly greater homoplasy than cone characters (in Fig. 6, the proportion of holapomorphies plus autapomorphies and consistency index for cone and sporophyll characters are 26% and 0.78 respectively, contrasting with values of 42% and 0.64 for mega- and microspore characters). In retrospect, some cases of mistaken homology are clearly evident among spore characters. For example, the distal spines (C100) of *Oxroadia* and *Sigillaria* sp. nov. megaspores differ in detail; those of the former are long and buttressed, those of the latter are short and almost papillate. Also, polarization of spore characters was especially problematic, as character states (especially those representing ornamentation) tend to replace each other in entirety rather than accumulating as sequential elaborations of form (i.e., they are displacive rather than additive). Consequently, patterns of increasing complexity cannot be expected. Indeed, many spore character states (including the more elaborate forms of ornamentation) are confined to the primitive, bisporangiate OTUs. Reduction to a single functional megaspore resulted in the loss of all types of dispersed ornamentation (Table 3), suggesting that they were redundant once megaspores had ceased to be the basic units of dispersal.

Relatively little attention has been paid to the functional morphology of lycopsid spores. Prominent equatorial (*Paurodendron*, *Chaloneria*) and laesural (*Paurodendron*, *Oxroadia*, *Diaphorodendron*, *Synchysidendron*) megaspore ornamentation has been invoked as an aid to flotation and thereby dispersal. Phillips (1979) argued that openings in the massa of *Diaphorodendron* and *Synchysidendron* megaspores trapped microspores to facilitate fertilization, and a similar function was attributed to the anastomosing fimbriate laesural ornamentation of *Oxroadia* megaspores by Bateman (1988). The pseudosaccus of *Chaloneria* microspores and cingulum of *Hizemodendron*, *Lepidodendron*, and *Lepidophloios* microspores probably acted as buoyancy aids.

Vegetative morphology. Vegetative characters uniting the arborescent lycopsids are those associated with the production of rhizomorphs and wood, together with ligules and exarch xylem maturation (inferred centrifugal maturation in stigmarian rhizomorphs (Frankenberg & Eggert, 1969) is suspect (Phillips & DiMichele, 1992)). Beginning at the root of the preferred MPT and passing along its major axis (Fig. 6), the node above *Paurodendron–Oxroadia* is characterized by the appearance of the tree habit (habit is discussed more fully in subsequent subsections) and by modifications to vascular tissue that probably reflect greatly increased body size: medullation of the stele, continuous protoxylem sheath, loss of protoxylem ridges (together causing superficial leaf trace emission: Fig. 5b), and the advent of foliar parichnos in the leaf bases, now much more distant from the axial vasculature following acquisition of the arboreous habit. Beyond *Anabathra*, the ligule pit is ubiquitous, though it also occurs in the ostensibly primitive genus *Oxroadia*.

Beyond *Chaloneria*, the evolution of discrete leaf cushions provided a consistent basal limit to leaf atrophy. Many of the characters that support nodes higher in the cladogram represent elaborations of leaf cushion morphology, notably in cushion complexity below *Diaphorodendron–Synchysidendron*, and in overall shape below *Lepidodendron–Lepidophloios*. In contrast, cushion and leaf-trace simplification is evident in *Hizemodendron*. The analysis of vegetative characters only (Fig. 11) places *Hizemodendron* much lower in the tree, eliminating the many character losses shown in Figure 6 but depicting the leaf cushion per se as iterative in (a) *Hizemodendron* and (b) all of the arboreous genera, shown clustered above *Chaloneria* in Figure 11 (also, arbitrary optimization of missing values representing the absence of coded structures led to the nonsensical apparent evolution of specific leaf cushion features below *Paurodendron*, prior to the evolution of the cushions themselves). Further modifications of cushion shape, together with the appearance of infrafoliar parichnos and a return to longitudinal protoxylem ridges, characterize the highly derived *Lepidodendron–Lepidophloios* clade (Fig. 6).

Stelar characters, together with peridermal features, play important roles in the more derived portion of the arborescent lycopsid clade, particularly in delimiting the three main cushion-bearing clades: *Sigillaria*, *Diaphorodendron–Synchysidendron*, and *Hizemodendron–Lepidodendron–Lepidophloios*. The solid protosteles of *Oxroadia* and *Paurodendron* give way to medullation by parenchymatous vitalization in the remaining genera. In most of these, the central portion of the stele consists of parenchyma cells that have lengths and diameters similar to those of the innermost metaxylem tracheids; these appear to be procambial cells that remained unlignified and thus metabolically active throughout the life of the plant. In the largest axes of *Lepidodendron* and *Lepidophloios* (less *L. harcourtii*), the stelar core consists of filamentous cells that probably proliferated into a central void. In contrast with the other lycopsid genera but in parallel with ferns, the *Diaphorodendron–Synchysidendron* clade evolved a true siphonostele. Pith parenchyma cells are much shorter and narrower than the adjacent metaxylem tracheids, suggesting different developmental origins for these tissues. *Diaphorodendron* has a mixed pith of parenchyma and tracheids, with parenchyma increasing in relative abundance toward the centers of larger axes. *Synchysidendron* has a pith region sharply delineated from the tracheary cells, and wood with heterogeneous rays and deep parenchymatous invaginations.

Most characters of the stelar margin constitute genus-level autapomorphies, notably the distinctly different modes of leaf trace emission observed in *Chaloneria*, *Sigillaria*, and *Lepidophloios* (Fig. 5). Of greater interest is the apparent switch from distinct longitudinal protoxylem ridges (yielding "coronate" cross sections) to no discernible ridges immediately above the primitive *Paurodendron–Oxroadia* clade, followed by a return to similar (but not identical) coronate morphology in the most derived *Lepidodendron–Lepidophloios* clade; the protoxylem ridges are further modified in *Lepidophloios*, where they anastomose (Fig. 6). Derivation of *Hizemodendron* from *Lepidodendron* (contra Fig. 12; see Heterochrony) would imply loss of protoxylem ridges. We suggest that the loss of ridges does not reflect complete absence of discrete protoxylem strands, even though the strands are no longer discernible.

Cortical characters of the arborescent lycopsids are surprisingly conservative compared with the other axial tissues. The persistent inner cortex may have provided a barrier of live cells along the outer margin of the phloem, protecting this delicate tissue from exposure to the central void created by the presumed in vivo disintegration of the thin-walled parenchyma of the middle cortex. The medullated steles of *Diaphorodendron* and *Synchysidendron* emit leaf traces that are sheathed by parenchyma when passing through the outer cortex, a character state also found in *Sigillaria* sp. nov. Leaf traces are secretory in most of the arboreous species analyzed.

Periderm is arguably the most unusual and developmentally intriguing vegetative tissue in arborescent lycopsids. As with stelar morphology, the *Diaphorodendron–Synchysidendron* clade is distinct from the other cushion-bearing arboreous genera. Bifaciality in the former group is evident in the clear histological distinction between the thin phellem and much thicker phelloderm. The relatively homogeneous periderm of the latter group may conceal cryptic cambial bifaciality (for example, this may be manifested in the peridermal trizonation of *Lepidodendron–Lepidophloios*), especially if the phellem is very weakly developed or the phellem and phelloderm are histologically identical. Details of periderm histology tend to be homoplastic or species-level autapomorphies, and therefore of limited phylogenetic value. In the analysis of vegetative characters only (Fig. 11), promotion of *Sigillaria* to sister group of the *Lepidodendron–Lepidophloios* clade united the three genera that possess resinous periderm. However, the other two characters supporting this node (cushions on twigs wider than long, leaves with lateral abaxial grooves) are almost certainly miscoded as homologs shared by *Sigillaria* and *Lepidodendron–Lepidophloios*.

Periderm, the main support tissue of the arboreous lycopsids, reached thicknesses of at least 20 cm in some species (DiMichele, 1979a, b, 1981; Phillips & DiMichele, 1981). This considerable increase in trunk girth over that of the primary tissues is difficult to reconcile with the persistence of primary leaf cushions, which probably remained photosynthetic after leaf loss; they are covered in stomata (Thomas, 1970b, 1977; DiMichele, 1979a, b), and both leaf traces and parichnos connections with leaf cushions were maintained through the periderm (Delevoryas, 1957; DiMichele, 1980). Several specialized mechanisms for accommodating girth increase evolved: tangential interarea expansion in *Sigillaria* and *Synchysidendron*, interarea fissuring in *Diaphorodendron*, and subcushion cellular expansion in *Lepidodendron* (DiMichele, 1981, 1983). In arboreous genera with well-developed crowns (*Synchysidendron*, *Lepidodendron*, *Lepidophloios*), periderm thickness diminished through the branching systems and the cortex was probably a major support tissue.

Given the determinate growth of arborescent lycopsids (Andrews & Murdy, 1958; Eggert, 1961), most of the periderm probably formed and differentiated near the stem apex, during (though probably continuing after) differentiation of the primary cortex, leaf cushions, and traces. This coordinated development is indicated by the persistence of the vascular linkages between the stele and leaf cushions through the periderm, and the occurrence of arboreous genera lacking specialized cushion-retention mechanisms (*Anabathra*, *Lepidophloios*). This mode of growth implies a stem apex analogous to the primary thickening meristem of some monocotyledonous angiosperms, an assertion previously made for stigmarian apices (Rothwell & Pryor, 1990, 1991). Unfortunately, there have been few discoveries of anatomically preserved stigmarian apices (Rothwell, 1984; Rothwell & Pryor, 1991) and none of stem apices, despite detailed and prolonged studies of coal balls. Their rarity may be at least partly explained by preferential decay of the apex, as observed in *Oxroadia* branches (Bateman, 1988). Rapid trunk elongation is suspected in the arboreous species (Phillips & DiMichele, 1992).

The most significant transitions in leaf base characters are the evolution of leaf cushions immediately below *Sigillaria* and their elaboration immediately above, involving the advent of upper and lower keels and lower field plications. The upper keel was subsequently lost in *Hizemodendron*, as were the lower field plications in *Lepidophloios*. Moreover, iteration is evident in several cushion characters: upper field plication in *Diaphorodendron–Synchysidendron* and *Hizemodendron*, the lateral line in *Diaphorodendron–Synchysidendron* and *Lepidodendron*, and the undoubtedly nonhomologous broader-than-long leaf cushions on the twigs of *Sigillaria* and *Lepidophloios*. Such convergences extend beyond the coded characters; for example, the similarity between *Synchysidendron* and *Lepidodendron* leaf cushions is reflected even in patterns of shape change from large to small branches. Also, cushions of both genera are protuberant and therefore have deep ligule pits. Only the infrafoliar parichnos of *Lepidodendron* allow distinction of its axial surface from that of *Synchysidendron*. Thus, many of the characters detailing leaf cushion morphology that have figured so prominently in previous classifications of Paleozoic lycopsids are shown to be homoplastic.

We regard the leaf cushions of derived genera as elaborated leaf bases of their more primitive antecedents such as *Anabathra*, which lacks a clear lamina-cushion distinction. Several features of the leaf base, notably the position of the ligule, suggest development from a leaf primordium. If so, the so-called "abscission" of leaves, which leaves a scar immediately external to the ligule pit aperture, occurred within the leaf rather than at the leaf-axis junction. Moreover, there is no evidence of a discrete abscission layer. Thus, we suspect that leaf laminae merely withered and sheared off at the physically weakest point, where the leaf constricts and is perforated by the ligule pit and, in the more derived genera, by the foliar parichnos.

Acute leaf posture is strongly homoplastic, characterizing unrelated genera with relatively short, broad laminae (*Paurodendron*, *Anabathra*, *Chaloneria*, *Hizemodendron*). The derived arboreous genera (above *Chaloneria*) all possess leaves with sclerenchymatous sheaths, which presumably supported the long, narrow laminae. Interestingly, the sheaths were lost in the short-leaved pseudoherb *Hizemodendron* (Fig. 6). Expansion and invagination of traces may also have aided structural support; dorsiventrally flattened traces characterize the *Lepidodendron–Lepidophloios* clade and *Diaphorodendron scleroticum*, V-shaped traces occur in *Chaloneria* and *Sigillaria*. Such vascular elaboration is invariably manifested externally as lateral abaxial grooves. The V-shaped trace of *Sigillaria* is an inevitable consequence of the vascularization of each leaf by two adjacent protoxylem strands of the parent axis and results in a median abaxial groove in addition to the lateral grooves. Postmortem accentuation of the grooves may have occurred (cf. Rex, 1986).

Arborescent lycopsids as integrated homeostatic organisms. Analogizing arborescent lycopsids with woody seed plants or tree ferns is unsatisfactory when considered in detail; in particular, periderm rather than wood constitutes the main physical support system, and the primary function of branches is reproduction rather than light capture (DiMichele & Phillips, 1985; Phillips & DiMichele, 1992). Perhaps the most profound character distinguishing the arborescent lycopsids is their determinate growth (Walton, 1935; Andrews & Murdy, 1958; Eggert, 1961), which allows analogy with the ontogeny of vertebrates and legitimate use of the terms body and bauplan (Bateman & DiMichele, 1991).

The body of each arborescent lycopsid is composed of at least two of four major determinate structural units (modules): rhizomorph, stem (defined as the length of the axis from the point of root-shoot divergence to the first isotomy of the apical meristem), crown branches (resulting from isotomy of the apical meristem), and lateral branches/cauline peduncles (resulting from strong anisotomy of the apical meristem) (DiMichele & Bateman, 1989; Bateman & DiMichele, 1991). Rhizomorph and stem are ubiquitous modules, though both occur in a severely reduced form in some OTUs. Lateral branches/cauline peduncles and crown branches are each rare or absent from some OTUs, thus defining three basic bauplans: (1) neither type of branch present, (2) crown branching frequent, lateral branching generates peduncles only, and (3) crown branching infrequent, lateral branching dominant. Variations in the sizes and secondary tissue contents of all four modules, and in the frequency of dichotomy of lateral and crown branches, generate a range of growth habits (e.g., Hallé & Oldeman, 1970; Hallé et al., 1978; White, 1979; Tomlinson, 1982, 1983). We suspect that growth of the arborescent lycopsids in general, and arboreous taxa in particular, was largely deterministic (genetically induced), offering much less potential than angiosperms for opportunistic modification of growth architecture by environmental influences or chance factors (e.g., Tomlinson, 1982). Consequently, the conceptual architectural model was unusually faithfully reproduced in the actual habit (Bateman & DiMichele, 1991).

The three basic bauplans outlined above broadly correspond to three of the growth models reviewed by Hallé et al. (1978); two can be subdivided using growth habit.

Bauplan (1) corresponds to Corner's architectural model. In our analysis, this exclusively monoaxial growth is confined to *Chaloneria*, though several penecontemporaneous lycopsids apparently possessed the same habit; these include *Spencerites* (Leisman & Stidd, 1967), *Sporangiostrobus* (Wagner & Spinner, 1976; R. H. Wagner, 1989), *Porostrobus* (Leary & Mickle, 1989), and the as yet unnamed, almost fully articulated compression from the Upper Devonian Cleveland Shale of Ohio (Chitaley, 1982, 1988; S. Chitaley & K. B. Pigg, in prep.). *Chaloneria* is the only OTU in our analysis that consists only of the two ubiquitous modules, a rhizomorph and an unbranched stem (Pigg & Rothwell, 1983a). We have classified its repeated zones of cauline sporophylls as lateral rather than terminal fructifications, as their production did not necessarily result in cessation of stem growth. The wood cylinder is narrow and the stem erect but much shorter than those of the truly arboreous OTUs (cf. Fig. 2b with Fig. 2a–g). The low wood content and lack of branches and cones in *Chaloneria* demonstrate highly economical construction, implying rapid growth. Distributional evidence suggests that *Chaloneria* was an ecological dominant in marshlike associations (DiMichele et al., 1979).

Bauplan (2), which corresponds to Schoute's architectural model, is the most widespread among the OTUs. Stems divide acrotonously (distally) by equal division of the apical meristem, yielding modular (determinate), orthotropic (three-dimensional) branches. The bauplan encompasses two distinct subgroups categorized by the arboreous and pseudoherbaceous habits respectively.

The first subgroup includes the classic arboreous genera *Lepidodendron* and *Lepidophloios*, together with *Synchysidendron* (Fig. 1). Throughout much of their life history, these trees consist of a rhizomorph and telegraph polelike stem capped by a massive primary body, undergoing frequent dichotomous branching to form a determinate crown only during the final phase of growth and subsequent monocarpic reproduction (DiMichele & Phillips, 1985). The cones were borne on stout peduncles that we regard as the homologs of more elaborate lateral branches found in bauplan (3); although evolutionarily significant, the peduncles do not *define* the architecture of bauplan (2) trees. These trees were cheaply constructed. Secondary thickening ceased well before termination of growth; the resulting poor development of wood in both the crowns and the trunks meant that they relied primarily on periderm for structural support (DiMichele, 1979a, b, 1983; Wnuk, 1985). This probably allowed channeling of more photosynthate into reproduction. Rapid generation times and an opportunistic life strategy were postulated for the subgroup by DiMichele & Phillips (1985).

The second subgroup, consisting of *Paurodendron*, *Oxroadia*, and *Hizemodendron*, is delimited by the pseudoherbaceous growth habit (Bateman, 1988, 1989, 1992; Bateman & DiMichele, 1991). These genera possess the same modules as *Lepidodendron* and *Lepidophloios*, but differ in the relative sizes and shapes of the modules (Fig. 2a, c, d). Also, overall body size of mature individuals is one to two orders of magnitude less than those of comparable arboreous species (cf. Fig. 1 with Fig. 2). In particular, the ubiquitous modules of rhizomorph and stem are greatly reduced (most drastically in *Paurodendron*) relative to the crown, which develops much earlier in the life histories of these genera. Their minimal stems result in a recumbent growth habit (Baxter, 1965; Schlanker & Leisman, 1969; Bateman, 1988), though developmental constraints preclude adaptations typical of truly prostrate growth (Bateman & DiMichele, 1991). Nonetheless, these plants superficially resemble the basally branched architectural model of Tomlinson (Hallé et al., 1978). Restriction of wood to the rhizomorph and highly reduced stem defines the pseudoherbaceous habit sensu Bateman (1988). Rapid determinate growth and a strongly *r*-selected life strategy are inferred for these species, though whether their reproduction was extended, or monocarpic upon cessation of growth, remains equivocal (Bateman, 1988; Bateman & DiMichele, 1991).

Bauplan (3) also encompasses two subgroups. It characterizes *Anabathra*, *Diaphorodendron* sens. str., and *Sigillaria*, as well as the reconstructed adpression *Bothrodendron punctatum* (Wnuk, 1989). All share Stone's architectural model and the arboreous growth habit. Stone's model resembles Schoute's model in many parameters but exhibits clear differentiation between stem and lateral branches, which were produced throughout much of the life of the individual. Although a degree of dorsiventral flattening has been inferred for the lateral branches (Wnuk, 1985), their stable morphology and spiral phyllotaxy suggest persistent orthotropy sens. lat. rather than a transition to plagiotropy (cf. Hallé et al., 1978, table 7). Deviation from Stone's model occurs during the final phase of determinate growth, occasional isotomous divisions (Hirmer, 1927; DiMichele & Phillips, 1985; Wnuk, 1985), presumably heralding exhaustion of the apical meristem. However, the effect of such divisions is much less profound in bauplan (3) than in bauplan (2). Our assignment of *Sigillaria* to Stone's model, which contradicts Hallé et al.'s (1978, fig. 71) assertion that the genus conforms to Schoute's model, reflects our view that the stout cauline peduncles of *Sigillaria* (and the bauplan (2) genera) are homologous with entire lateral cone-bearing branches of *Anabathra* and *Diaphorodendron*; thus, by definition, *Sigillaria* possesses lateral branches, though we distinguish it as a separate architectural subgroup.

This group of polycarpic plants possessed excurrent trunks and deciduous lateral branches. Wide cylinders of wood and periderm occur in the trunks of all the members of the group; they extend into the lateral branches of *D. scleroticum*, suggesting greater persistence (DiMichele, 1980, 1981, 1985). Growth and reproduction were both prolonged and sustained, conferring greater tolerance to extrinsic stress and allowing these species to occupy suitable habitats for considerable periods (DiMichele & Phillips, 1985; DiMichele et al., 1987). Relatively sporadic reproduction and apomixis (presumably facultative) have been reported in *Sigillaria approximata* (Schopf, 1941; Phillips, 1979; DiMichele & Phillips, 1985).

DiMichele & Phillips (1985) argued that growth architecture and mode of reproduction largely determine the ecological niches of specific arboreous lycopsids, a hypothesis that can be broadened to encompass nonarboreous arborescent species (Bateman, 1988; Bateman & DiMichele, 1991). Bateman & DiMichele (1991) further suggested that transitions in many of the characters describing more detailed aspects of vegetative morphology reflect evolutionary changes in growth architecture. If so, it is especially important to assess the frequency and polarity of architectural changes during the history of the arborescent lycopsids.

Our character analysis (Table 3) focused on specific homologous structures, whereas the five growth habits outlined above are polythetic summaries of several individual character states, some apomorphic and some plesiomorphic (C1–C7). For example, the arboreous habit corresponds with the apomorphic state of C1, the pseudoherbaceous habit with the plesiomorphic state of C2, and the pedunculate habit with the plesiomorphic state of C7; Schoute's model with the apomorphic state of C3, Stone's model with the apomorphic state of C6, and Corner's model with the apomorphic state of C5. Despite their heterogeneity and partial dependence on the cladistic characters, there is considerable interpretative value in mapping the distributions of the growth habits across the preferred MPTs. The procedure is not wholly tautologous, as the preferred MPT for analysis B (habit characters omitted) is identical to that for the complete analysis (A; Fig. 9a), suggesting that habit characters had little direct effect on the topology of the latter.

Two of the five growth habits (Corner's model in *Chaloneria*, pedunculate Stone's model in *Sigillaria*) are autapomorphic at the generic level, preventing assessment of their phylogenetic significance. The preferred MPT for analysis A (Fig. 6) requires homoplasy in at least two of the remaining three growth habits (pseudoherbaceous Schoute, arboreous Schoute, laterally branched Stone). It is equally parsimonious to assume a pseudoherbaceous or arboreous hypothetical ancestor. In the first case, pseudoherbaceousness is replaced by arboreousness immediately below *Anabathra*, with a reversal to pseudoherbaceousness in *Hizemodendron*. The transition to Stone's model also occurs immediately below *Anabathra*, with resumption of Schoute's model in *Diaphorodendron* and the *Hizemodendron–Lepidodendron–Lepidophloios* clade. The only sister groups that unequivocally possess the same habit are *Paurodendron* and *Oxroadia* at the base of the cladogram and *Lepidodendron* and *Lepidophloios* at the apex. Moreover, there is no clear evolutionary trend through the clade; Schoute's model characterizes both the most primitive and most derived genera.

We expected analysis D, based only on vegetative characters, to provide a less homoplastic distribution of the major vegetative architectures. The most profound difference is the unification of the pseudoherbs (all attributed to Schoute's model) as a basal paraphyletic group, thus depicting *Hizemodendron* as much more primitive than it appears in the full analysis (cf. Fig. 11 with Fig. 6). The topology for Figure 11, unlike that for Figure 6, requires recognition of the pseudoherbaceous habit as plesiomorphic. Although *Anabathra* is promoted to sister group of *Diaphorodendron–Synchysidendron*, a transition from Schoute's to Stone's model immediately above the pseudoherbs, followed by independent re-acquisition of Schoute's model in the derived *Synchysidendron* and *Lepidodendron–Lepidophloios* clades, remains the most parsimonious distribution of major architectures.

Heterochrony. The strongly iterative occurrence of the tree habit among the arborescent lycopsids is mirrored in extant tree ferns and seed plants (Hallé & Oldeman, 1970; Hallé et al., 1978; White, 1979; Funk, 1982; Tomlinson, 1983). We believe that radical changes in growth architecture are more readily achieved instantaneously, by mutation of genes involved in the production of the morphogens that control early development (D-genes of Arthur, 1984, 1988), than gradually, by selectively driven adaptation. The resulting morphological change would appear instantaneous on a geological time-scale. In this case, we believe that such saltational events were expressed as heterochrony sens. lat.: a change in the timing of the appearance of a trait between ancestor and descendant (e.g., Gould, 1977; Alberch et al., 1979; Fink, 1982; McNamara, 1982; Rothwell, 1987; DiMichele & Bateman, 1989; Bateman & DiMichele, 1991). Many other correlated morphological and anatomical changes probably occurred immediately, as a result of epigenetic changes within the new bauplan and habit, or subsequently, as a result of adaptive honing by natural selection (Arthur, 1984; Bateman & DiMichele, 1991). This scenario predicts that such macromutants very rarely generated evolutionary lineages, requiring a competition-free niche to allow establishment of the new population prior to adaptive honing (Valentine, 1980; Arthur, 1984, 1988; DiMichele et al., 1987). Hence, heterochronic anomalies must arise frequently to overcome their almost inevitable failure.

Bateman & DiMichele (1991) argued that *Hizemodendron* became pseudoherbaceous by heterochronic reduction from an arboreous ancestor. Precocious division of the primary apical meristem minimized the length of the stem and prompted many subsequent character changes to accommodate the new growth habit. Reduction in size and change in shape of the stem of *Hizemodendron* imply progenesis, a form of paedomorphosis (retention of ancestral characters in the descendant adult).

In this paper, we are concerned less with the details of the postulated mechanism of vegetative reduction than its potential consequences for phylogenetic reconstruction. The preferred MPT for all characters (Fig. 6) depicts *Hizemodendron serratum* as primitive relative to its former congener, *Lepidodendron hickii*; together, the two genera constitute a paraphyletic sister group of *Lepidophloios*. The preferred MPT for reproductive characters only (Fig. 12) shows an unresolved trichotomy, thus allowing monophyly of *Hizemodendron* and *Lepidodendron*. In contrast, the preferred MPT for vegetative characters only (Fig. 11) depicts a very distant relationship between these two genera.

Although the phylogeny based on the greatest number of characters (Fig. 6) has the highest overall probability of accuracy, it may be misleading in this case. If *H. serratum* evolved by progenesis directly from *L. hickii* (admittedly an improbable event, but a useful working hypothesis) and thereby lost all autapomorphies of *L. hickii* (*H. serratum* and *L. hickii* have no exclusive synapomorphies; Table 3), *H. serratum* would be depicted as primitive sister group of *L. hickii*. Losses of character states that the ancestor (*L. hickii*) shared with its former sister group (*Diaphorodendron–Synchysidendron*) are often depicted as reversals on the branch of the descendant (*H. serratum*) (this is only guaranteed if ACCTRAN optimization is used), whereas losses of character states not present in *Diaphorodendron–Synchysidendron* are not recognized as character transitions at all; it is more parsimonious to assume that the ancestor of *Hizemodendron* never possessed them. Thus, heterochrony in general and progenesis in particular can undermine phylogenetic reconstruction, and monophyly of *Hizemodendron* and *Lepidodendron* remains a viable hypothesis.

Bateman (1988, 1992) and Bateman & DiMichele (1991) postulated a similar progenetic origin for the other two pseudoherbs, *Oxroadia* and *Paurodendron*. They are shown as the most primitive OTUs in all analyses (cf. Figs. 6, 11, 12), though they form a polychotomy with the remaining bisporangiate-coned genera (*Chaloneria* and *Anabathra*) in Figure 12. As in the case of *Hizemodendron*, their primitiveness relative to OTUs with similar reproductive morphology is determined by vegetative characters. *Anabathra* is the only bisporangiate-coned tree included in our analysis and therefore provides the only potential arboreous ancestor for *Oxroadia* and *Paurodendron*. However, the three OTUs differ in many spore characters, and the unbranched rhizomorph and superficial ligules of *Paurodendron* label the genus as relatively primitive or relatively derived, depending upon near-arbitrary polarization decisions. Other bisporangiate-coned trees, once reconstructed, will provide more credible ancestors.

A heterochronic origin for *Oxroadia* and *Paurodendron* would weaken our analysis, as an a priori assumption of their primitiveness was used to polarize most of the characters (i.e., they were used as partial outgroups). Inclusion in the data matrix of even more primitive OTUs may support our original assumption that *Paurodendron* and *Oxroadia* are sister groups to the remainder of the arborescent lycopsid clade. Our concern is largely driven by our opinion that the first arborescent lycopsid would have generated secondary tissues throughout its bauplan (the most simple developmental transition from inability to generate secondary tissues), and that restriction of wood to certain modules reflects subsequent developmental modifications. Moreover, determinate growth and a centralized rhizomorphic rootstock are characters shared by all the OTUs, suggesting that they have exceptionally high burden (i.e., they play pivotal roles in the development and function of the organism and influence other dependent characters: Riedl, 1979; Fortey & Jefferies, 1982; Donoghue, 1989). These high-burden characters represent serious ontogenetic constraints to a truly prostrate growth habit (Bateman & DiMichele, 1991), and the bauplan appears much better adapted to upright growth. Increase in body size to arboreous proportions may have occurred subsequently rather than concomitantly with acquisition of wood.

Although *Chaloneria* is not a pseudoherb and is erect, the cladograms for all characters (Fig. 6) and vegetative characters only (Fig. 11) show that its unbranched, bilaterally symmetrical rhizome, unbranched stem, and cauline sporophylls (all autapomorphies in our analysis) are derived. This conclusion is tempered by the possibility that *Chaloneria* is not a genuine member of the ingroup, which would explain its numerous autapomorphies and its role as the greatest cause of topological instability in each analysis (Figs. 9, 10). The only well-supported conclusion from our study is that *Chaloneria* is more primitive than the most primitive member of the clade delimited by reduction to a single functional megaspore per megasporangium (i.e., than *Diaphorodendron–Synchysidendron*).

The phylogenetic position of *Chaloneria* is especially significant because it is the oldest reconstructed genus currently assigned to the Isoetales (Pigg & Rothwell, 1983a; Rothwell & Erwin, 1984). A sister-group relationship with a widely recognized lepidodendralean genus such as *Sigillaria* (e.g., Fig. 9k) would imply paraphyly of the Lepidodendrales and support Meyen's (1987: 70–81) decision to synonymize the Lepidodendrales into the Isoetales. Further resolution of these problems requires a broader cladistic analysis that includes other bona fide isoetaleans (including *Isoetes*), potential arboreous ancestors (e.g., *Lepidodendropsis–Protostigmaria*: Jennings, 1975; Jennings et al., 1983), and ostensibly more primitive OTUs (e.g., *Selaginella*) (see Bateman, 1992).

Outgroups and ancestors. Thus, we return to the fundamental questions that prompted this study. What character states delimit the Lepidodendrales? Is the group monophyletic? If so, what is the most appropriate outgroup? The chosen answer to this question leads to an even more loaded question: What is the most probable ancestor of the ingroup? It also largely determines perception of the phylogenetic relationships among the ingroup members.

We believe that the greatest weakness of our analysis is the narrow temporal and ecological range represented by our OTUs; most of the species are restricted to at most the ca. 10 Ma of the Westphalian (Fig. 3) and to the coal swamps of Euramerica. However, the main phylogenetic groups within the Lepidodendrales (or at least species possessing many of their diagnostic character states; whole-plant reconstructions have not yet been achieved for pre-Westphalian arboreous lycopsids) can be traced back at least another 20 Ma, to the Ashbian. Moreover, reproductive organs consistent with the most apomorphic genus, *Lepidophloios*, have been recovered from Ivorian strata, a further 15 Ma older (Fig. 3, inset; Long, 1968). This implies that all of the sister groups of this genus had diverged by the Ivorian; unfortunately, only one of our OTUs (*Oxroadia gracilis–Oxroadia* sp. nov.) was reconstructed from such early assemblages. As yet incompletely reconstructed arboreous lycopsids (not necessarily bona fide lepidodendraleans) were widespread and at least locally ecologically dominant by the latest Devonian (e.g., Scheckler, 1986a, b; DiMichele et al., 1992).

Thus, the combination of the stratigraphic record and our phylogeny suggests that the three main groups of monosporangiate-coned genera recognized in our cladistic analysis (*Sigillaria*, *Diaphorodendron–Synchysidendron*, *Hizemodendron–Lepidodendron–Lepidophloios*) diverged at least 35 Ma prior to the Westphalian coal-swamp lagerstätten that provided most of our OTUs. This would explain why these groups show similarly large degrees of divergence from their putative bisporangiate-coned ancestor(s) (Fig. 14) and are supported by many character-state transitions (Fig. 6). Alternatively, the saltational evolutionary scenario erected for major vegetative changes may be extended to encompass reproductive innovations, eliminating the need for intermediate taxa during the early radiation of the group.

Current evidence suggests that our morphologically divergent OTUs together exhibit most of the character states possessed by the arborescent lycopsids as a whole, including other Pennsylvanian species and their Mississippian and Devonian antecedents. However, the paucity of genera in our analysis, and the fact that most represent only the final period of the history of the group, implies that we have sampled only a restricted range of the *combinations* of character states that existed. This would explain the large number of character states that occur as genus-level autapomorphies in our cladogram (Fig. 6), leaving few character states to support the consequently weak links that constitute the main axis of the cladogram and determine perceived genus-level relationships. Inclusion of older OTUs, dating back to the main radiation of the group, would probably alleviate this problem by transforming genus-level autapomorphies into genus-level synapomorphies. In an alternative less gradualistic scenario, the large number of genus-level autapomorphies may reflect evolutionary dynamics, particularly the simultaneous origin of blocks of characters linked by pleiotropic or epigenetic factors (e.g., Levinton, 1988). This mode of evolution may be difficult to resolve cladistically for a variety of methodological reasons (these will be discussed in a future paper; see also Lemen & Freeman, 1989).

Older OTUs are also needed to determine convincingly whether the Lepidodendrales are monophyletic and in particular to provide more satisfactory outgroups. However, before these questions can be addressed, the character states that supposedly delimit the Lepidodendrales should be reviewed. Four are most commonly cited: the possession of rootlet-bearing rhizomorphs, secondary tissues (wood and periderm), ligules, and heterospory (Chaloner, 1967; Stewart, 1983). These structures provided the holapomorphies that unite all the OTUs included in our analysis (Fig. 6), but most (possibly all) have a greater level of universality. For example, a wide range of enigmatic latest Devonian and earliest Mississippian lycopsids possessed wood (Meyer-Berthaud, 1981, 1984; Scheckler, 1986a, b; Matten, 1989; Roy & Matten, 1989). Rhizomorph-like, rootstocks, ligules, and heterospory all characterize homophyllous *Selaginella*, the type genus of the Selaginellales (e.g., Bierhorst, 1971; Bold et al., 1980). Moreover, *Paurodendron* (and therefore, by implication, its sister genus *Oxroadia*) was assigned by Schlanker & Leisman (1969) to *Selaginella*, and it is widely accepted as a member of the Selaginellales (e.g., Taylor, 1981; Stewart, 1983; Meyen, 1987). On these criteria, the Lepidodendrales could be circumscribed to include both *Paurodendron* and homophyllous *Selaginella*.

Moving progressively up the clade, the next OTU encountered is the most primitive tree, *Anabathra*. Regarding this OTU as the most primitive lepidodendralean would allow delimitation of the order using the arboreous habit and associated modifications of stelar anatomy, together with foliar parichnos. Unfortunately, many of these character states are homoplastic as a result of loss during the hypothesized progenetic evolution of pseudoherbs from trees: *Hizemodendron* from a *Lepidodendron*-like ancestor, and possibly *Oxroadia* and/or *Paurodendron* from *Anabathra*-like ancestor(s). Although phylogenetically valuable, these character states are not ubiquitous within the clade. Many workers would argue that the clade is delimited primarily by possession of a stigmarian rhizomorph. However, we were unable to identify any profound characters that distinguish the stigmarian rhizomorph of *Anabathra* from the supposedly nonstigmarian rhizomorph of *Oxroadia*, which is much smaller and more compact but otherwise very similar. Also, this clade contains *Chaloneria*, another nonarboreous OTU. *Chaloneria* possesses several autapomorphies, notably an unbranched stem lacking cones and a bilaterally symmetrical rhizomorph, that suggest affinities with the extant genus *Isoetes*. If Pigg & Rothwell (1983a) correctly ascribed *Chaloneria* to the Isoetales, and if the genus is correctly positioned in our phylogeny (which is by no means certain; Fig. 9), inclusion of *Anabathra* in the Lepidodendrales and continued recognition of the Isoetales would render the former order paraphyletic (Appendix 1A).

Perhaps the most cohesive clade includes *Sigillaria* as its most primitive genus. It is delimited by the nonhomoplastic synapomorphies of leaf cushions and monosporangiate cones that generate megasporangium-megasporophyll disseminules. We are confident of the monophyly of the three main groups of OTUs that constitute the clade (*Sigillaria*, *Diaphorodendron–Synchysidendron*, *Hizemodendron–Lepidodendron–Lepidophloios*), and our parsimony analysis strongly supports monophyly of the clade as a whole (nevertheless, we note that such an adaptively valuable suite of character states could reflect parallel responses in two or more lineages to similar selective regimes, thus confounding parsimony: cf. Coddington, 1988). Given that our assumption of homology among the three lineages in monosporangiate cones and the megasporangium-megasporophyll complex as disseminule is the crux of the preferred MPT (Fig. 6), these characters merit even more careful scrutiny. For now, we refer to this clade, more narrowly defined than most perceptions of the Lepidodendrales, as the "Segregationists" (referring to the segregation of megasporangia and microsporangia in different cones). Members of the less inclusive clade that excludes *Sigillaria* and is delimited primarily by reduction to a single functional megaspore that germinates within the sporangium are the "Isolationists."

CONCLUSIONS

Empirical observations. We are confident that each of the 10 genera analyzed by us is monophyletic. This conclusion is not especially profound, as six of the genera are here represented by only one species and thus not cladistically testable (Fig. 8). The analysis prompted segregation of two new genera: *Hizemodendron* from *Lepidodendron* (Bateman & DiMichele, 1991), and *Synchysidendron* from *Diaphorodendron* (DiMichele & Bateman, 1992). However, these decisions were taken primarily on the grounds of differences in several characters (many directly or indirectly reflecting different growth architectures) rather than as attempts to disaggregate para- or polyphyletic groups. *Diaphorodendron–Synchysidendron* is undoubtedly monophyletic; *Hizemodendron–Lepidodendron* is depicted in Figure 6 as paraphyletic but, as we have argued, may nonetheless be monophyletic. Derived (monosporangiate-coned) genera constitute three distinct monophyletic clades that are most appropriately regarded as families: Sigillariaceae (*Sigillaria*), Diaphorodendraceae (*Diaphorodendron–Synchysidendron*), and Lepidodendraceae (*Lepidophloios–Lepidodendron–Hizemodendron*). Each family is supported by several character state transitions (Fig. 6).

Evidence for the postulated monophyly of the monosporangiate-coned clade, and for the primitiveness of the Sigillariaceae relative to the Diaphorodendraceae and Lepidodendraceae, is more equivocal. This largely reflects our inability to make confident statements concerning phylogenetic relationships among the four primitive, bisporangiate-coned genera. They form a highly heterogeneous, paraphyletic (or possibly polyphyletic) plexus of disparate morphologies that share a free-sporing mode of reproduction. *Oxroadia* and *Paurodendron* differ in many characters and are united in Figure 6 by arguably only one synapomorphy; we doubt their apparent monophyletic status. Only *Anabathra* is a tree; the pseudoherbs *Oxroadia* and *Paurodendron* and possibly even the shrub-sized phallos *Chaloneria* are potential progenetic descendants of trees broadly similar to, but probably distinct from, *Anabathra*.

Determining the origin(s) of the monosporangiate-coned clade will require inclusion of pre-Pennsylvanian monosporangiate-coned species and a broader selection of bisporangiate-coned trees; several potential candidates, all requiring further reconstruction before they can be used with confidence in cladistic analyses, are listed in Table 5. Determining the origin(s) of the arboreous lycopsids, and of putatively progenetic bisporangiate-coned genera such as *Oxroadia* and *Paurodendron*, also necessitates inclusion of more distantly related nonarborescent lycopsids (e.g., *Selaginella* sens. lat., *Leclercqia*) to reassess character state polarities. Given these observations, we envisage eventual redelimitation, or possibly amalgamation, of three widely recognized lycopsid orders (Appendix 1A; see also Bateman, 1992).

Absence from the present analysis of nonarborescent species and of any credible ancestor of the most primitive arboreous genus (*Anabathra*) together prevent determination of whether arborescence (secondary thickening) and arboreousness (large body and upright growth) evolved simultaneously or sequentially. Other especially important and potentially linked innovations that possess a higher level of universality than our ingroup are determinate growth and the centralized rhizomorphic rootstock. In general, the most significant evolutionary advances within the bisporangiate-coned plexus appear to have involved vegetative rather than reproductive organs, indicating that

TABLE 5. Selected genera that are potentially phylogenetically informative but are currently insufficiently known to provide satisfactory cladistic data sets (listed in order of appearance in the stratigraphic record). We note that '*Lepidodendron*' *calamopsoides* is not closely related to *Lepidodendron* sens. str. (R. M. Bateman, unpublished obs.) and that *Bothrodendron* sens. lat. is probably a polyphyletic aggregate of several disparate species (Scott, 1920; Thomas & Meyen, 1984). See also reviews by Chaloner (1967), Meyer-Berthaud (1981, 1984), and Matten (1989).

Lepidosigillaria whitei Kräusel & Weyland
White (1907); Arnold (1947); Grierson & Banks (1963)
[Late Givetian-Early Famennian: New York State]
Protolepidodendropsis spp. Gothan & Zimmermann
Høeg (1942); Schweitzer (1965)
[Famennian: Euramerica]
Trabicaulis spp. Meyer-Berthaud
Meyer-Berthaud (1981, 1984); Roy & Matten (1989)
[Famennian-Early Tournaisian: south-central France; New York State]
Cyclostigma kiltorkense Haughton
Johnson (1913); Chaloner (1967, 1968, 1984); Chaloner & Meyer-Berthaud (1983)
[Strunian: southwestern Ireland]
Landeyrodendron spp. Meyer-Berthaud
Meyer-Berthaud (1981, 1984)
[Early Tournaisian: south-central France]
Lepidodendropsis spp. Lutz–*Protostigmaria eggertiana* Jennings
Lutz (1933); Iurina & Lemoigne (1975); Jennings (1975); Jennings et al. (1983)
[Tournaisian: Euramerica]
Valmeyerodendron triangularifolium Jennings
Jennings (1972)
[?Tournaisian: Illinois]
Bothrodendron spp. Lindley & Hutton
Scott (1908); Weiss (1908); Calder (1933b); Stubblefield & Rothwell (1981); Wnuk (1989)
[Tournaisian-Westphalian: Euramerica]
'*Lepidodendron*' (?*Anabathra*) *calamopsoides* Long
Long (1964, 1971, 1986); Scott & Galtier (1988)
[Late Tournaisian: northern Britain]
Levicaulis arranensis Beck
Beck (1958); Pant & Walton (1961)
[Mid-Visean: southwestern Scotland]
'*Lepidodendron*' (?*Phytokneme*) *brownii* Unger
Chodat (1911); Calder (1933a); Meyer-Berthaud (1981)
[Visean: southern Scotland]

they are economic adaptations (sensu Eldredge, 1989) employed continuously in competition for resources. The cladograms imply that the well-documented sequence of reproductive innovations in the monosporangiate-coned clade, which ultimately led to seed analogs in *Lepidophloios* (e.g., Phillips, 1979), occurred later, though they may have been developmentally linked to additional vegetative modifications (this hypothesis requires further study). Interestingly, the equally well-documented, climatically driven end-Westphalian extinctions of specific elements of the coal-swamp floras (Phillips et al., 1977, 1985; Phillips & Peppers, 1984) most seriously affected the most derived portion of the arborescent lycopsid clade, eliminating the "Isolationist" families Diaphorodendraceae and Lepidodendraceae (Fig. 3). Such extinctions of major monophyletic groups are uncommon (Smith & Patterson, 1988) and require a causal rather than a purely stochastic explanation.

These analyses provide useful (if circumstantial) evidence for the relative burden of particular types of character, in the guise of amounts of homoplasy. Interestingly, this partly reflects the physical scale (dimensions) of the feature represented by the character relative to that of the plant body. Characters of largest scale (notably overall growth habit) and smallest scale (e.g., various details of cellular histology and spore ornamentation) are generally more homoplastic than those of intermediate scale, such as stelar and associated trace morphology, the basic structure of leaf bases and sporophylls, and the nature of the dispersal unit. As a broad generalization, large- and small-scale features delimit species and genera, intermediate scale features delimit families or still higher taxa.

The results of our study will not encourage proponents of organ phylogenies. Merely bisecting our data matrix into submatrices representing vegetative (Fig. 11) and reproductive (Fig. 12) organs generated substantially different preferred MPTs that were clearly inferior to the preferred MPT of the full matrix (Fig. 6). The analysis of reproductive organs could not satisfactorily resolve the relationships among the four most primitive and three most derived genera. The analysis of vegetative organs misplaced *Hizemodendron* as unduly primitive and *Sigillaria* as unduly derived and could only distinguish *Synchysidendron* from *Diaphorodendron* using cone axis characters that mirror those of ultimate vegetative axes. Nonetheless, the arboreous members of the three most derived families (Sigillariaceae, Diaphorodendraceae, Lepidodendraceae) persist as clades in the analyses of both submatrices. This shows that the families as currently known can be approximately delimited using either vegetative or reproductive characters alone, even if their relationships cannot be determined accurately.

Our results are even less encouraging for classifications based on even more reduced suites of characters. We have identified homoplasy in many supposedly diagnostic character states, including some of the leaf-base details that are traditionally used to classify adpressed lycopsid axes. On the basis of these observations, we support in principle the hierarchical system of well-known core taxa and less well-known satellite taxa proposed for the Lycopsida by Thomas & Brack-Hanes (1984), but are convinced that reconstructed, anatomically preserved whole plants provide better core taxa than the reproductive organs favored by Thomas & Brack-Hanes. Certainly, whole-plant reconstructions are essential prerequisites for convincing phylogenetic and ecomorphic interpretations.

Methodological observations. We do not regard phylogenetic reconstruction as an isolated, objective procedure divorced from hypotheses of evolutionary mechanisms; rather, it is positive feedback between the two sets of paradigms that leads to greater understanding. The evolutionary history of the arborescent lycopsids is not a simple story of progressively increasing complexity expressed throughout the bauplan. In particular, high-burden characters such as determinate growth and a centralized rhizomorphic rootstock, together with the small number of module types that constitute the bauplan, predisposed the plants to profound heterochronic changes in body size and body plan; we believe that these were manifested as geologically instantaneous events resulting from changes in developmental regulation. This saltational evolutionary scenario has considerable predictive value, particularly if considered in tandem with advances in understanding of the ontogeny, functional morphology and physiology of these remarkable organisms (e.g., Phillips & DiMichele, 1992). Moreover, saltational scenarios can be falsified (or at least highly modified) by cladograms, if the predicted positively correlated suite of character state transitions is dissociated (e.g., by the interpolation of additional OTUs onto the internode in question: R. M. Bateman, in prep.).

We have been unable to discern any substantive differences between reconstructing the morphological phylogenies of extinct and extant species (cf. Stein, 1987; Gauthier et al., 1988; Donoghue et al., 1989; Boy, 1990). The inevitable typological nature of conceptual whole-plant fossils is not detrimental in the essentially typological realm of cladistics. Our 16 OTUs undoubtedly represent a highly rarified sample of all the arboreous lycopsid species that ever existed. This contributed to several problems, notably the broad morphological discontinuities separating some clades (Fig. 14) and the absence of satisfactory outgroups. However, cladistic analyses based exclusively on extant species are even more selective; unique character combinations found only in the fossil record, especially during the initial radiation of a major clade, are deliberately excluded. Similarly, opportunities to use stratigraphic-temporal evidence to assist polarization and characters, and (more importantly) to select among alternative topologies generated from the same data matrix, are squandered. The question of excluding fossils does not arise in the case of the monosporangiate-coned lycopsid clade, which apparently lacks extant descendants. Despite the serious problems posed by incomplete preservation in the fossil record, we were able to score a large number of characters representing all organs of our OTUs and generated a large data matrix containing only a small proportion of missing values. Although technically feasible, inclusion of less well-known, partially reconstructed OTUs should be postponed pending further investigation of the effects of missing values on tree-length calculation and character state optimization.

This study indicates that well-understood fossils are as valuable for phylogenetic studies as any extant organisms and do not require any special methodological concessions. We note that profound gaps in the fossil record caused by nonpreservation are matched by equally profound gaps in extant floras, namely those resulting from extinction of their precursors. Access to the time dimension, and thereby to character states (and combinations of character states) no longer in existence, justifies a pivotal role for paleontological data in phylogenetic reconstruction.

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APPENDIX 1. NOMENCLATURAL AND TAXONOMIC NOTES

A. Higher taxa. Bateman (1990b) recommended the supra-ordinal classification of Knoll & Rothwell (1981) and ordinal classification of Stewart (1983); together, these classifications imply monophyly of the Division Tracheophyta and Class Lycopsida, but present a provisional, egalitarian (grade) arrangement of six orders within the Lycopsida (Drepanophycales, Protolepidodendrales, Lycopodiales, Selaginellales, Lepidodendrales, Isoetales). Acquisition of further phylogenetic information will require re-delimitation of these orders and their rearrangement into a more hierarchical classification (Bateman, 1990b, 1992; Hueber, 1992). Colloquial (informal) names are consistently rooted in their formal counterparts; thus, "lycopsid" is used for the Class Lycopsida and "lepidodendralean" for the Order Lepidodendrales (Bateman, 1990b).

At present, the Lycopsida are perceived as being delimited by exarch protostele, scalariform metaxylem with Williamson fimbrils, vascularized "microphylls," and foliar/axillary eusporangia (e.g., Stewart, 1983). With the possible exception of stigmarian rhizomorphs, none of the characters traditionally used to delimit the Lepidodendrales (secondary thickening, periderm, ligules, heterospory) is confined to the order. The present analysis shows that the Lepidodendrales as currently delimited may not be monophyletic, and even if monophyletic may not be the most meaningful clade to use as the basis of an ordinal level classification (see also Matten, 1989). Together with the Isoetales and Selaginellales, the Lepidodendrales require redelimitation or amalgamation.

B. Anabathra versus Paralycopodites. We accept Pearson's (1986) arguments that *Paralycopodites brevifolius* (Williamson) DiMichele (formerly '*Lepidodendron*' *brevifolium* Williamson) is identical to, and a junior synonym of, *Anabathra pulcherrima* Witham (cf. Witham, 1833; Williamson, 1872). We also recognize that the adpression genus *Ulodendron* Lindley & Hutton (1831) both resembles and nomenclaturally pre-dates *Anabathra*, but suspect that *Ulodendron* is considerably more inclusive (i.e., more broadly delimited) than *Anabathra*.

Unfortunately, *A. pulcherrima* is a form-species (sensu Bateman & Rothwell, 1990), having been correlated with several cone-species of the plesiomorphic bisporangiate genus *Flemingites* (DiMichele, 1980; Pearson, 1986). The type material of *A. pulcherrima*, from the Late Tournaisian of Allanbank, southeastern Scotland, co-occurred with *Lagenicula horrida* megaspores (these were incorrectly referred to *L. subpilosa* by Pearson, 1986: K. M. Bartram, pers. comm. 1987; H. L. Pearson, pers. comm. 1987), which have been found in *Flemingites gracilis* cones (Chaloner, 1953; Brack-Hanes & Thomas, 1983). Elsewhere, *A. pulcherrima* co-occurs with *F. scottii* at the Late Visean locality of Pettycur, southeastern Scotland (e.g., Williamson, 1872; Jongmans, 1930; DiMichele, 1980; Scott et al., 1984; Pearson, 1986), and with either *F. diversus* or *F. schopfii* at many Westphalian coal-ball localities in Euramerica (DiMichele, 1980). The differences between these cone-species are subtle and not readily resolved cladistically. In particular, our scoring of *A. pulcherrima* focused on Pennsylvanian rather than Mississippian assemblages; *F. diversus* (Westphalian D: Felix, 1954) and *F. schöpfii* (Westphalian B: Brack, 1970) differ primarily in the mean number of megaspores per megasporangium and thus were not differentiated in our data matrix (Table 3, Fig. 3).

We anticipate taxonomic revision of vegetative and reproductive organs of *Anabathra* as increased knowledge (particularly of Mississippian forms) allows further whole-plant reconstructions; for example, '*Lepidodendron*' *calamopsoides* Long (1964), which co-occurs with stigmarian rootstocks, *Flemingites*-like strobili and *Lagenicula crassiaculeata* megaspores (Scott & Meyer-Berthaud, 1985; Scott & Galtier, 1988; Scott, 1990), may be a species of *Anabathra* (cf. Table 2). Such plants will form the basis of a new arborescent lycopsid family, the Anabathraceae.

C. Erection of new genera and species. We have deliberately avoided formal reclassification of the 17 whole-plant species included in our study. Thus, the three new species (one each of *Oxroadia*, *Sigillaria*, and *Synchysidendron*) remain unnamed (but see Bateman, 1992; DiMichele & Bateman, 1992).

However, the results of this study encouraged us to restrict further the range of variation encompassed by *Lepidodendron* sens. str., a process that was begun by DiMichele (1981, 1983, 1985) when clarifying the delimiting parameters of *Lepidodendron*, *Lepidophloios*, and *Diaphorodendron* sens. lat. In order to transform

Lepidodendron from an apparently paraphyletic (Fig. 6) to a monophyletic entity, we retained only the anatomically preserved equivalent (*L. hickii*) of the type species (*L. aculeatum*) and erected '*Lepidodendron*' *serratum* as the type species of a new genus, *Hizemodendron* (Bateman & DiMichele, 1991). The two genera share similar reproductive organs, but differ in many vegetative characters; at least most of these differences may reflect the imposition of radically different growth habits on a shared bauplan.

Although our study strongly supports monophyly for *Diaphorodendron* sens. lat. (i.e., sensu DiMichele, 1985; see Fig. 6), the precedent of generic distinction of species sharing similar reproductive organs but exhibiting major differences in growth habit and ontogeny requires the recognition of the two most apomorphic species, '*D.*' *dicentricum* and '*Diaphorodendron*' sp. nov., as a new genus of arboreous lycopsid, *Synchysidendron*. In contrast with the more plesiomorphic *Diaphorodendron* (epitomized by the type species, *D. vasculare*), *S. dicentricum* and *Synchysidendron* sp. nov. lack lateral branches and were probably monocarpic (DiMichele, 1981, 1985; Bateman & DiMichele, 1991; DiMichele & Bateman, 1992), thus possessing the same bauplan, growth habit, and reproductive strategy as *Lepidodendron* sens. str. (Fig. 1).

D. Revision of the cone-genera. As currently delimited, cone form-genera serve as shorthand for co-occurring complexes of character states. A few cone-genera are assignable to single stem-genera (Table 2), notably *Mazocarpon* to *Sigillaria* (e.g., Schopf, 1941; Feng & Rothwell, 1989) and *Lepidocarpon* to *Lepidophloios* (DiMichele, 1983). The microsporangiate genus *Lepidostrobus* characterizes *Hizemodendron*, *Lepidodendron*, and *Lepidophloios*; cone-species of each of these stem-genera can only be distinguished by continuous quantitative characters and microspore morphology (e.g., Willard, 1989a). In contrast, *Achlamydocarpon* is a greatly inflated form-genus (e.g., Leisman & Phillips, 1979) encompassing three main morphological groups: (1) megasporangiate *A. takhtajanii*-type, (2) megasporangiate *A. varius*-type, and (3) microsporangiate *A. varius*-type (Table 2). Groups (2) and (3) are restricted to *Diaphorodendron–Synchysidendron*; cones of all three *Diaphorodendron* species and both *Synchysidendron* species can only be distinguished by the medullated steles of the latter, despite major differences in growth architecture and vegetative anatomy between the two genera (DiMichele, 1981). Group (1) cones characterize *Hizemodendron* and *Lepidodendron* (DiMichele, 1983; Bateman & DiMichele, 1991). We believe that megasporangiate *A. takhtajanii* and *A. varius* are sufficiently distinct to merit generic distinction (the latter would require a new organ-genus). Assignment of megasporangiate and microsporangiate *A. varius* to different cone-genera would be more consistent with the systematic treatment of *Hizemodendron*, *Lepidodendron*, and *Lepidophloios* cones in Table 2, though Phillips (1979: 256, 259) presented several arguments against this option.

APPENDIX 2. ANALYTICAL ADVANCES

Given the appropriate microcomputers and software, more elegant solutions are now available to some of the difficulties that we encountered when performing these analyses in 1989. For example, the problem of storage of only superficially different topologies, resulting from polychotomies, has been solved in Version 3.0 of PAUP (Swofford, 1991). There is much to commend an analytical approach that entails initial parsimony analysis in PAUP 3.0, subsequent comparison of MPTs with those generated by using Hennig86 Version 1.6 (Farris, 1989), and printing of interesting topologies and character state distributions using MacClade Version 3.0 (Maddison & Maddison, 1991). Estimation of degrees of support for particular nodes using bootstrapping (Efron, 1982; Felsenstein, 1985; Sanderson, 1989) is gaining in popularity, though there is no statistical substitute for detailed examination of suboptimal-length topologies.