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The Rhizomorphic Lycopsids: A Case-study in Paleobotanical Classification

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ABSTRACT. The rhizomorphic lycopsids are a putatively monophyletic group delimited by the rhizomorphic syndrome: centralized determinate growth and secondary thickening in their rooting systems. A cladistic analysis of the most completely understood species provides the basis for two alternative, new classifications of the group, one following strict phylogenetic classification criteria, the other more traditionally Linnean. Both are based on the same preferred most-parsimonious cladogram and place the rhizomorphic lycopsids in one order, the Isoëtales. Also, both classifications delimit the same suprageneric groups: *Hizemodendron* + *Lepidodendron* + *Lepidophloios*, *Diaphorodendron* + *Synchysidendron*, *Sigillaria*, and *Chaloneria* + *Isoetes* are well supported as monophyletic clades, but the basal plexus of bisporangiate-coned ulodendrids (*Paralycopodites* + *Oxroadia* + *Pauroidendron*) is paraphyletic. Both classifications differ from all previous studies in 1) assigning all rhizomorphic lycopsids to a single order, and 2) recognizing the trees *Diaphorodendron* plus *Synchysidendron* as a distinct family, the Diaphorodendraceae. A generally applicable paleobotanical taxonomic philosophy is outlined that broadly reflects a phylogenetic framework based on living species (if available) and reconstructed whole-plant fossil species. These core species provide a framework into which are interpolated satellite taxa: fossil isolated organs and partial plants.

Much has been written regarding the relationship between classification and phylogeny. Most authors supported an explicit role for evolution, arguing that "taxonomy follows phylogeny". This debate has gained momentum from the insistence by most cladists that taxonomic ranks should reflect only strictly monophyletic relationships, thereby permitting full recovery of cladistic pattern from the resulting classification (e.g., Wiley 1979; Wiley et al. 1991; Forey 1992b). While philosophical debates took place among systematists at large, most paleobotanists continued traditional taxonomic practice, apparently constrained by the supposedly unique problems presented by fossil plants. Problems such as disarticulation and variation in form with preservational state have been used to justify, for example, placing reproductive organs and vegetative organs of the same whole-plant species in different families, as part of a larger debate about "form" species and "organ" species (cf. Faegri 1963; Krassilov 1969; Meyen 1973, 1975, 1978a, b, 1987; Jansonius 1974; Schopf 1978; Harris 1979; Meyen and Traverse 1979; Chaloner 1986; Cleal 1986; Bateman et al. 1992a).

For paleobotanical data to be most effective in

addressing larger questions of evolution and systematic philosophy, studies of fossil plant phylogeny should take the same approaches as systematics of modern organisms. Although consideration should be given to the special problems posed by fossils (notably disarticulation and preservational vagaries), paleobotanists should aim for a fundamentally biological approach to the study of evolutionary relationships and classification. In this paper we attempt to meld a philosophy of classification with a phylogenetic study of the Carboniferous rhizomorphic lycopsids (Bateman et al. 1992), and demonstrate a practical yet biological approach to classification.

MATERIALS AND METHODS

The Rhizomorphic Concept. Rhizomorphic lycopsids produce woody tissue (secondary xylem) somewhere in their shoot and root systems and thus are arborescent. The defining characteristic of the group is bipolar growth from a centralized, shoot-like rootstock, the 'rhizomorph'. We use the term 'rhizomorph' for the rooting structures of this monophyletic group for several reasons. First, root

systems among the major lineages of lycopsids differ greatly in architectural and developmental patterns, and homologies appear to be few. Second, the term 'rhizophore' has been suggested by some authors; however, rhizophore commonly has been used to describe the non-homologous root-like structure that originates within stem bifurcations of bilaterally symmetrical species of *Selaginella* P. Beauv. Note that the selaginelloids are the likely sister clade of the rhizomorphic lycopsids. Although the term 'rhizomorph' is used to describe certain fungal structures, this is far less likely to confound interpretation than use of the same term (rhizophore) for non-homologous structures in sister-groups within the Lycopsidea. Third, the term rhizomorph is already available in the literature as a descriptor of the rooting structure of stigmarian lycopsids (Bierhorst, 1971; Rothwell and Erwin 1985; Pigg 1992). Use of this established, accurate descriptor seems preferable to coining yet another term.

Current Knowledge of the Rhizomorphic Lycopsids. The zenith of rhizomorphic lycopsid diversity, both taxonomic and structural, was reached during the Carboniferous, particularly in wetland habitats (DiMichele et al. 1992). The only extant genus attributable to this clade, *Isoetes* L. (including *Stylites* Amstutz), is a pale shadow of ancestors that ranged in habit from pseudoherbaceous ground cover to towering trees. The arboreous lycopsids (those with tree habit: Bateman et al. 1992) are a non-monophyletic group within the more generalized monophyletic arborescent clade, which is the most derived portion of the Lycopsidea (Bateman 1990, 1992a).

The fossil record of the arborescent lycopsids begins in the Late Devonian. By the Early Carboniferous several widely recognized genera existed, including most of those that would become common in Late Carboniferous coal swamps (Bateman et al. 1992: Fig. 3). These plants are preserved most commonly as adpressions (compressions and impressions: Shute and Cleal 1987; Bateman 1991), which reveal features of external axial ornamentation, branching patterns, and, in exceptional cases, body size. Petrifications also occur, beginning in the Lower Carboniferous, when they generally are associated with fluvial and volcanogenic landscapes (Scott et al. 1984; Scott and Rex 1987; Bateman and Scott 1990). The most detailed anatomical information comes from petrified peats within Upper Carboniferous coals (coal balls: see Phillips et al. 1976; Scott and Rex 1985),

which preserve a remarkable spectrum of details on anatomy, reproduction and growth form. Thus, most of the described Late Carboniferous genera are now known in great anatomical detail. Correlations between vegetative and reproductive organs, and between petrified and adpressed remains, have allowed reconstruction of numerous rhizomorphic lycopsids as whole plants, providing the basis to infer life history, ontogeny, physiology, and palaeoecology of each (for review see Bateman et al. 1992).

Phylogenetic Analysis: Background. We undertook a phylogenetic analysis of the most completely known species of arborescent lycopsids—those for which the anatomy, growth habit, and reproductive biology had been characterized. Species known only from adpressed preservation, or only from isolated petrified vegetative or reproductive organs, were excluded for two reasons. From a strictly methodological perspective, large tracts of missing data dramatically reduce the effectiveness of a cladistic analysis. Also, we wished to reconstruct relationships as accurately as possible, and our studies showed that stable phylogenies cannot be recovered when only vegetative or only reproductive organs are used (Bateman and DiMichele 1991; Bateman et al. 1992; R. M. Bateman, unpublished data).

The present analysis used without modification the data-matrix of Bateman et al. (1992). This was based on 16 reconstructed whole-plant species of ten genera: the large-bodied trees *Paralycopodites* E. D. Morey and P. R. Morey, *Sigillaria* Brongniart, *Diaphorodendron* DiMichele, *Synchysidendron* DiMichele and R. M. Bateman, *Lepidodendron* Sternberg, and *Lepidophloios* Sternberg, and the smaller-bodied pseudoherbs/shrubs *Oxroadia* Alvin, *Paurodendron* Fry, *Hizemodendron* R. M. Bateman and DiMichele, and *Chaloneria* Pigg and Rothwell.

Our preferred most-parsimonious cladogram is presented in Fig. 1a (details of supporting characters, alternate topologies, and experimental manipulation of data are presented in Bateman et al. 1992). The cladogram summarizes the morphological variation among these plants and suggests several distinct clades.

Most species included in the phylogenetic analysis were trees (arboreous habit): *Paralycopodites brevifolius* (Morey and Morey) DiMichele (Morey and Morey, 1977; DiMichele 1980), *Sigillaria* sp. nov. from the Westphalian A (see Bateman et al. 1992), *Sigillaria approximata* Delevoryas (Delevoryas 1957),

Diaphorodendron vasculare (Binney) DiMichele, *D. scleroticum* (Pannell) DiMichele, *D. phillipsii* DiMichele (DiMichele 1981, 1985; Wnuk 1985; DiMichele and Bateman 1992, 1993), *Synchysidendron dicentricum* (Felix) DiMichele and R. M. Bateman, *S. resinosum* DiMichele and R. M. Bateman (DiMichele 1979b, 1985; Wnuk 1985; DiMichele and Bateman 1992), *Lepidodendron hickii* Watson (Watson 1907; DiMichele 1983), *Lepidophloios hallii* (Evers) DiMichele (DiMichele 1979a), *L. harcourtii* (Witham) Seward and Hill (Bertrand, 1891; Calder 1934), and its probable conspecific *L. "johnsonii"* (Arnold) DiMichele (DiMichele 1979a; Winston 1988). Of the non-trees, *Hizemodendron serratum* (Felix) R. M. Bateman and DiMichele (Baxter 1965) was a sprawling pseudoherb, but clearly is closely related to *Lepidodendron* and appears to have evolved by changes in developmental timing (Bateman and DiMichele 1991). *Paurodendron fraipontii* Fry (Phillips and Leisman 1966; Schlanker and Leisman 1969; Rothwell and Erwin 1985) was a sprawling, centrally rooted pseudoherb, smaller than but similar in vegetative growth habit to the only Lower Carboniferous species in the analysis, *Oxroadia gracilis* Alvin (Alvin 1965; Long 1986). *Chaloneria cormosa* Pigg and Rothwell (Pigg and Rothwell 1983a, b) was columnar and unbranched, with an estimated height of 1-2 m.

The species were coded for 115 bistate characters (80 phylogenetically informative), giving a primary matrix that contained only 5 % missing values. The matrix was subjected to two separate analyses for the present paper. Both studies analyzed ordered characters using the branch-and-bound search algorithm and MNF optimization algorithm of PAUP 3.1.1 (Swofford 1993) and excluded autapomorphies from tree-length calculations.

RESULTS

The first analysis mirrored the core analysis of Bateman et al. (1992). The cladograms included all 16 species and were rooted and polarized using a hypothetical ancestor that closely resembled *Oxroadia gracilis*. Figure 1a shows the preferred most-parsimonious topology, which intermingles trees and non-trees (pseudoherbs). Among the trees, *Lepidodendron* plus *Lepidophloios* and *Diaphorodendron* plus *Synchysidendron* are depicted as both highly derived and closely related. *Sigillaria* lies outside these genera, and most primitive of all the trees is *Paralycopodites*. If trivially different permutations of the three *Lepidophloios* species are ignored,

the analysis yielded only two other most-parsimonious topologies. They differ from Fig. 1a in the relative positions of *Paralycopodites* and *Chaloneria*, which can either be unresolved or transposed; neither rearrangement alters the perceived relationships of the tree-sized genera.

In the present analysis, the strength of empirical support for nodes was assessed using three criteria: 1) the number of character-state transitions (either all transitions, or non-homoplastic transitions only); 2) bootstrap analysis based on an overnight run of 500 replications (e.g., Felsenstein 1985), and 3) decay index values based on progressively less parsimonious strict consensus trees (e.g., Bremer 1988). The positive correlation observed between the two measures is poor, though replication values greater than 95% and decay indices of at least three can be expected for nodes supported by more than five non-homoplastic transitions or more than eight transitions of any kind. Together, these measures show that the preferred most-parsimonious cladogram offers strong support for monophyly of most of the revised genera but for few relationships among species or, more importantly, among genera. The notable exceptions are the generic pairings of *Diaphorodendron* plus *Synchysidendron*, and *Lepidodendron* plus *Lepidophloios*. This relative weakness of the tree at higher taxonomic levels was attributed primarily to topological instability caused by putative broadly paedomorphic, independent origins of all the small-bodied genera from tree-sized ancestors (Bateman and DiMichele 1991; Bateman 1992a, 1994; Bateman et al. 1992).

In the light of this paedomorphic hypothesis, we reanalyzed the matrix after omitting the small-bodied taxa. If relationships among the *Lepidophloios* species are again ignored, the reanalysis results in a single most-parsimonious tree (Fig. 1b). The topology and branch lengths closely resemble those of Fig. 1a, though there is one significant difference: *Sigillaria* is depicted as sister-group to *Diaphorodendron* plus *Synchysidendron* alone rather than *Diaphorodendron* plus *Synchysidendron* and *Lepidodendron* plus *Lepidophloios*. However, obtaining the latter topology for the trees-only analysis requires only one extra step, and the crucial node linking *Sigillaria* with the diaphorodendroids in Fig. 1b has low values for bootstrap (67%) and decay index (2). Moreover, three of the four character-state transitions supporting the node reflect reversals of polarity, which resulted from the omission of the non-trees and the use of *Paralycopodites* as an

arboreous outgroup. In fact, only one synapomorphy (microspores bear a distinctive equatorial thickening termed a crassitude) genuinely unites the putative clade. Thus, of the two hypotheses of relationship among the tree-sized genera, we tentatively prefer Fig. 1a to Fig. 1b.

TAXONOMIC TREATMENT

General Problems. There are numerous challenges in the classification of fossil plants that are rarely encountered when dealing with extant forms. These include fragmentary preservation, missing data (systematic studies of extant plants, particularly tropical woody species analogous to the coal-swamp lycopsids, reveals similar difficulties), and preservational factors. In particular, different modes of preservation can reveal suites of characters so different that few direct comparisons of homologous characters are possible (e.g., Galtier 1986). Poorly known taxa, or those preserved in a manner different from the best known taxa, should be omitted a priori from phylogenetic analysis, though they can be inserted into topologies a posteriori.

Many of the aforementioned difficulties affect poorly known lycopsids but do not apply to the classification of the best known Carboniferous species. The most significant problem in the phylogenetic study of the rhizomorphic lycopsids is the paucity of whole-plant reconstructions of Upper Devonian and Lower Carboniferous species. The phylogenetic position of plants such as *Lepidodendropsis* J. Lutz, *Cyclostigma* Haughton, and *Valmeyerodendron* J.R. Jennings relative to bona fide "stigmarian" taxa and *Chaloneria* will strongly influence suprafamilial taxonomy. Consequently,

the present taxonomy of the group should reflect primarily what is known with confidence, generally a system that will inevitably change as important new data accrue.

Criteria for Paleobotanical Classification. We suggest the following criteria as a basis for classifying fossil plants, and have applied them in the classification of the rhizomorphic lycopsids.

(1) Taxonomy should broadly reflect inferred phylogenetic relationships. Phylogenetic rationale and pattern should be presented clearly, an objective that is most readily achieved by cladistic methods. Explicit phylogenies need not be cladistic, however, and not all cladistically constructed phylogenies are presented in a sufficiently explicit manner (for example, many cladograms are published without supporting data matrices).

(2) In attempting to aggregate species into higher taxa we have emphasized both the circumscription of monophyletic groups and the large morphological discontinuities separating some of the sister groups. In other words, we desire a classification that contains information on morphological distinctiveness as well as the primary pattern of evolutionary relationships inferred from nested sets of synapomorphies. Monophyletic taxa are preferred, but paraphyletic taxa are considered acceptable if they can be readily delimited using explicit criteria (e.g., Stein and Beck 1987).

If classification is to encapsulate both phylogenetic history and the magnitude of morphological difference between species or groups of species, higher taxa may be circumscribed best by excluding one or more highly derived monophyletic ingroups to leave a paraphyletic residuum. Internodes supported by unusually large numbers of character-state transitions, or by character-state

FIG. 1. Preferred most-parsimonious cladograms based on 115 bistate characters coded for (a) 16 whole-plant species of rhizomorphic lycopsids (cf. Bateman et al. 1992, fig. 6), rooted and polarized using a hypothetical ancestor based largely on *Oxroadia*, and (b) a reanalysis based on the same data-matrix but including only the 12 arboreous (tree-sized) species, rooted and polarized using *Paralycopodites*. The length of each internode is proportional to the number of supporting character-state transitions; this figure is given above the horizontal line, followed in parentheses by the number of those character-state transitions that are non-homoplastic. The percentage bootstrap replicability and decay index respectively of the node are given below the line; wide branches are the strongest nodes (bootstrap > 80%; decay index ≥ 3). The number of species-level autapomorphic character states follows in parentheses following each binomial. Vital statistics as follows: analysis (a), length 128 steps, consistency index 0.625, retention index 0.813, rescaled consistency index 0.508; analysis (b), length 82 steps, consistency index 0.744, retention index 0.869, rescaled consistency index 0.646. Species as follows: HYAN, hypothetical ancestor; OXGR, *Oxroadia gracilis*; PNFR, *Paurodendron fraipontii*; PSBR, *Paralycopodites brevifolius*; CHCO, *Chaloneria cormosa*; SIAP, *Sigillaria approximata*; SINS, *S. sp. nov.*; SYRE, *Synchysidendron resinosum*; SYDL, *S. dicentricum*; DIPH, *Diaphorodendron phillipsii*; DIVA, *D. vasculare*; DISC, *D. scleroticum*; HZSE, *Hizemodendron serratum*; LNHI, *Lepidodendron hickii*; LSHC, *Lepidophloios harcourtii*; LSJO, *L. 'johnsonii'* (see Winston 1988); LSHL, *L. hallii*.

transitions given heavy a posteriori weighting, could be severed by the analyst when constructing a classification from a phylogeny (long-branch partitioning sensu Bateman 1992b, 1995). Such a classification remains fundamentally phylogenetic while retaining the flexibility necessary to incorporate information on the distinctiveness of taxa (particularly at higher levels).

(3) The phylogeny should be based on whole-plant *species*. Because species (paleontological or neontological) are biological hypotheses, many lines of evidence can be brought to bear on their reconstruction (the precise definition of a whole-plant species, its nature, and the taxonomic treatment of its component parts, are all highly controversial). Frequent assertions that organic connection is the only satisfactory evidence for reconstructing fossil plants fail to recognize this hypothetical (and fundamentally probabilistic) nature of whole-plant species constructs (Bateman and Rothwell 1990).

(4) Supraspecific taxa should be based on reconstructed whole-plant species. Taxa at all ranks should possess character states that permit them to be recognized unambiguously, and that specify particular levels of universality. Species may have particular combinations of character states that permit them to be recognized, even if none of the states are uniquely derived (they may in theory be the direct ancestors of relatively derived forms). For example, *Diaphorodendron vasculare* lacks bistate autapomorphies (DiMichele and Bateman 1992) and hence is a "metaspecies" (sensu Donoghue 1985; Donoghue and Cantino 1988; de Queiroz and Donoghue 1988). Nevertheless, it is morphologically distinct from all other species of the genus, and thus can be circumscribed unequivocally.

Our emphasis on species in classification, most notably as the core units of higher taxa, reflects two underlying concepts. First, whole-plant species represent the smallest hypothetical units we can hope to specify using morphology (only in rare instances is it possible to describe a complete, fully articulated individual). Although their perceived relationships to each other may change, the fundamental circumscription of whole-plant species tends to remain reasonably stable following addition of new information. Second, studies of the rhizomorphic lycopsids (and of many other groups of fossil plants) have entailed excessive lumping at the generic level. For example, the traditional concept of *Lepidodendron* is based solely on the possession of higher-than-wide leaf cushions; this

defining character is a plesiomorphy and encompasses so much variation that in practice it is of little phylogenetic value (DiMichele 1983, 1985; Bateman et al. 1992; see also Thomas and Meyen 1984). In addition, uncritical use of form-genera has resulted in the agglomeration of organs from distinct whole-plant species into polyphyletic organ-genera, and has led to classifications where different organs from the same whole-plant species are placed in different families. Such nightmarish entanglements can be minimized by basing generic concepts primarily on whole-plant species rather than isolated organs.

(5) Satellite designation (sensu Thomas and Brack-Hanes 1984) should be employed for the classification of organ-based form-genera that cannot be placed into acceptable whole-plant constructs. Nonetheless, satellite taxa represent species-level hypotheses, and as such can be assigned to higher taxa based on the presence of diagnostic characters. Any polyphyletic satellite taxon (one that appears in two or more higher taxa that are not sister groups) should be dismantled if possible.

This protocol generates paleontologically-based, natural higher taxa of whole plants, biological entities comparable to those of neobotany (where in practice the morphospecies remains pre-eminent, despite occasional homage to biological and other species concepts). It also allows the inclusion of form-taxa (for those who wish to use them) as satellite taxa.

The system that we have constructed for the rhizomorphic lycopsids is both explicitly biological and based on cladistic phylogenies. We have focused on conceptual whole-plant species, circumscribed using available data on organ connection, association/dissociation, and anatomical similarity.

Suprageneric Classification of the Rhizomorphic Lycopsids. Here we restrict discussion to those Carboniferous whole-plant species that were included in the phylogenetic analysis shown in Fig. 1a. Omitted from the analysis were additional species of *Oxroadia* and *Chaloneria* that differed from the included species only in continuous characters such as size, and several named entities best classified as satellite taxa. Incompletely known Late Carboniferous taxa include *Sublepidophloios* Sterzel (Hopping 1956), *Asolanus* Wood (Wood 1860; Daber and Kahlert 1970), *Bothrodendron* Lindley ex Hutton (Wruck 1989), *Sporangiostrobus* Bode (Wagner 1989) and *Miadesmia* C. E. Bertrand (Benson 1908). From the Early Carboniferous the adpressions *Lepidodendropsis* (Turina and Lemoigne

1975; Jennings et al. 1983) and *Valmeyerodendron* (Jennings 1972), and the petrifications *Levicaulis* C. B. Beck (Beck 1958), *Landeyrodendron* Meyer-Berthaud, and *Trabicaulis* Meyer-Berthaud (Meyer-Berthaud 1981, 1984), and the problematic species "*Lepidodendron*" *calamopsoides* A. G. Long (Long 1971) and "*Lepidodendron*" *brownii* Chodat (Meyer-Berthaud 1981), are at present too incompletely known for inclusion in the cladistic analysis, as are enigmatic species from near the Devonian-Carboniferous boundary (Matten 1989; Roy and Matten 1989). The inability to include these taxa leaves in doubt many suprafamilial relationships.

CLASS. Within the Linnean hierarchy, we classify the lycopsids as a Class, Lycopsidea (the name Lycopodiopsida, rooted in the extant genus *Lycopodium* L., is preferred by some authors), within the Phylum Tracheophyta (e.g., Stewart and Rothwell 1993), rather than as the Subphylum Lycophytina (e.g., Banks 1975; Niklas and Banks 1990) or the Phylum Lycophyta (e.g., Bold 1967; Taylor and Taylor 1992; see Bateman 1990). In the strict cladistic classification, however, we use the grade Lycophytina. The inflationary practice, in which the rank of this group is raised, is part of a larger system in which all traditional orders of non-angiospermous seed plants (Cycadales, Coniferales, Ginkgoales, Gnetales, and numerous extinct seed-plant orders) are elevated to Phylum rank, with each Phylum encompassing only one Class and each Class encompassing only one Order (e.g., Bold 1967); Coniferales is subdivided into more than one order in some classifications but the inflationary problem remains. Also elevated to Phylum in such inflated systems are the Classes Sphenopsida and Pteropsida (= Polypodiopsida of some authors), as well as the angiosperms, which are traditionally treated as one or two classes (e.g., Cronquist 1988). The lack of phylogenetic structure in the inflated classification is apparent. Unless evolutionary relationship is to be denied, it is clear that the eutracheophytes (sensu Kenrick and Crane 1991) are monophyletic and divided basally into two major clades: 1) the zosterophylls—lycopsids ("lycophytes" of Kenrick and Crane 1991; see also Gensel 1992), and 2) the 'trimerophytes' and their descendents: sphenopsids, pteropsids, progymnospermopsids, and seed plants.

The inflation of taxonomy appears to have resulted from the restrictions placed on angiosperm classification by the limited number of traditional Linnean ranks. In a temporally top-down approach (i.e., beginning with extant plants and only later

considering their evolutionary history), the angiosperms naturally occupy center stage, and taxonomy is distorted to accommodate their much greater (if taxonomically superficial) diversity. In an explicitly historical, bottom-up approach (one focusing mainly on the larger pattern of descent with modification), the angiosperms are perceived more clearly within the context of the Mesozoic seed-plant radiation; structural differences between the angiosperms and the other seed-plant orders are no greater than those among the non-angiospermous orders. We would classify angiosperms as an order and emphasize their exceptional present-day species diversity only at infra-ordinal levels. Conferral of informal names for higher-order plant groups of the Silurian and Devonian (Crane 1990; Kenrick and Crane 1991) offers an alternative nomenclatural approach.

ORDERS. It is almost universally accepted that there are three extant orders of lycopsids: Lycopodiales, Selaginellales, and Isoëtales. The Isoëtales possess rhizomorphs and are related closely (if somewhat ambiguously) to the Carboniferous rhizomorphic forms (Bateman et al. 1992; Bateman 1992a; Pigg 1992).

In principle, we believe a strong argument can be made for including *all* rhizomorphic lycopsids, including *Isoëtes*, in one order, following the suggestion of Meyen (1987). Key synapomorphies for this group together constitute the rhizomorphic syndrome: rootstock with centralized determinate growth and secondary thickening, wood produced from a unifacial cambium; lateral appendages (rootlets) leaf-like, unbranched or with single isotomous branch, borne plesiomorphically in helical rhizotaxy (as opposed to phyllotaxy, which describes the pattern of leaf display). Other characters diagnostic of the clade that reflect shoot organization and vegetative anatomy and are not enumerated here (see Bateman et al. 1992). The phylogenetic and ontogenetic significance of this suite of characters has been widely discussed elsewhere (Eggert 1961, 1972; Paolillo 1963; Karrfalt 1984; Rothwell and Erwin 1985; Rothwell and Pryor 1991; Bateman et al. 1992; Bateman 1994).

Naming this order is problematic. Either the traditional Isoëtales or the Lepidodendrales could be expanded to include the several currently recognized orders that include rhizomorphic lycopsids, but the circumscription of both names is deeply entrenched. Because ordinal names are free of the laws of priority, we prefer a new ordinal name, *Rhizomorphales*; however, we are prevented

from formalizing this name here due to nomenclatural convention. Thus, we here follow the usage of Meyen (1987) and use the name Isoëtales.

FAMILIES. The traditional, Carboniferous-age 'stigmarian' lycopsids, comprise four groups in our cladistic analyses (Figs. 1a, b). Three of these are both unambiguously monophyletic and supported by several synapomorphies, and hence can be classified as bona fide families: the Sigillariaceae (*Sigillaria*), Diaphorodendraceae (*Diaphorodendron*—*Synchysidendron*), and Lepidodendraceae (*Hizemodendron*—*Lepidodendron*—*Lepidophloios*). *Paralycopodites* can be included in the family Ulodendraceae, although this family will be a relatively poorly delimited parataxon when compared with the other families. Part of the difficulty in classifying *Paralycopodites* and its bisporangiate-coned relatives reflects the paucity of Early Carboniferous tree forms in the analysis, and the effect of this absence on the perceived positions of the pseudoherbs *Oxroadia* and *Paurodendron*. Sprawling pseudoherbs, such as *Oxroadia* and *Paurodendron*, probably evolved by profound paedomorphic reduction from Early Carboniferous arboreous ancestors. This obscured their true relationships within the bisporangiate-coned parataxon that is basal to the rhizomorphic lycopsids (Bateman 1994, 1996). We now present two classifications of the rhizomorphic lycopsids that focus on the ranks that separate genus and order. Together they illustrate how the phylogenetic relationships shown in Fig. 1a and the supporting character-state changes can be translated into significantly different classifications, even when broadly similar philosophies are applied to the same basic data. First we present a 'relaxed' phylogenetic classification, which was constructed largely by the senior author.

Relaxed Phylogenetic Classification. All taxa are encompassed by the Phylum Tracheophyta, the Class Lycopsida and the order Isoëtales.

LEPIDODENDRACEAE. DEFINING CHARACTERS. Synapomorphies—Megasporangium bilaterally flattened; megasporangium dehiscence distal (within the context of the megasporangium-sporophyll complex). Parallelisms—Complex microspore cingulum (shared with *Paralycopodites*); densely granulate microspores (shared with *Paralycopodites*).

The evolutionary simplification of *Hizemodendron* (Bateman and DiMichele 1991) caused the apparent loss of many characters or their reversion to less complex, more primitive states. If the anomalous *Hizemodendron* is removed from consideration, the arboreous members of the Lepidodendraceae share

the following additional characters: Synapomorphies—Infrafoliar parichnos present below leaf scar; periderm massive, with two to three histologically distinct zones. Parallelisms—Periderm "resinous" (shared with Sigillariaceae); leaf cushion height : width ratio 1 : 1 or less on terminal branches (shared with Sigillariaceae); leaf vascular strand dorsiventrally flattened (shared with *Diaphorodendron scleroticum*); paired abaxial grooves on leaf (shared with Sigillariaceae and *Diaphorodendron scleroticum*).

The Lepidodendraceae is universally recognized (in some instances under the name Lepidocarpaceae: e.g., Chaloner 1967; Thomas and Brack-Hanes 1984) as encompassing the most highly derived species of arboreous lycopsids, consisting of five or more species distributed among at least three genera: *Hizemodendron*, *Lepidodendron*, and *Lepidophloios*. Recent discovery of anatomically preserved specimens shows that *Sublepidophloios* (Hopping 1956) is also a member of the family (W. A. DiMichele, unpubl. data).

Lepidodendron has been at the root of extensive confusion and overlumping in the taxonomy of arboreous lycopsids for more than 150 years (see discussion in DiMichele 1983, 1985; Bateman and DiMichele 1991; Bateman et al. 1992). This resulted from unwarranted reliance on a narrow set of plesiomorphic leaf-cushion characteristics to circumscribe the genus (higher-than-wide tangential dimensions; foliar parichnos; small leaf scar; ligule pit above leaf scar), thereby including a broad spectrum of taxa that prove to be vegetatively and reproductively distinct when a wider range of characters is considered. Additional confounding factors also have contributed to this taxonomic morass. For example, the bisporangiate cones of *Paralycopodites* (*Flemingites* Carruthers pro parte: Brack-Hanes and Thomas 1983) have been mistakenly correlated with *Lepidodendron* s.l., resulting in placement of all or part of the genus in a family of more primitive pleisomorphic forms (*Flemingitaceae* of Thomas and Brack-Hanes 1984). As an experiment, Bateman et al. (1992) reconstructed the rhizomorphic lycopsid phylogeny with the traditional *Lepidodendron* s.l. constrained as monophyletic; this proved an untenable hypothesis. The phylogeny was far less parsimonious, and the resulting taxon lacked synapomorphies. It is largely through disassembly of the paraphyletic *Lepidodendron* into highly distinctive monophyletic genera that we have been able to delimit more clearly the other families of arboreous lycopsids.

Hizemodendron, a pseudoherb, evidently represents a reduction from arboreal ancestors, probably within *Lepidodendron* (Bateman and DiMichele 1991). This simplifies and thus potentially broadens delimitation of the Lepidodendraceae. We believe that it would be appropriate to treat *Hizemodendron* as sister group to *Lepidodendron* alone, not to *Lepidodendron*—*Lepidophloios*. Rather than never having possessed the synapomorphies that unite *Lepidodendron* and *Lepidophloios*, *Hizemodendron* apparently lost these characters by reversal to earlier plesiomorphic states, thereby placing *Hizemodendron* lower in the tree.

DIAPHORODENDRACEAE. DEFINING CHARACTERS.

Synapomorphies—Protostele with parenchymatous core; parenchyma cells formed independently of protracheids, thus forming a true pith; phellem and phelloderm histologically distinct; phelloderm composed of alternating bands of thick- and thin-walled cells; sporangium wall heterocellular; megasporangium dorsiventrally flattened; megasporangium dehiscence proximal (within context of megasporangium—sporophyll unit); megaspore bears massa; microspore contact face granulofoveolate; microspore distal ornamentation papillate. Parallelisms—Thin-walled parenchyma surrounding leaf trace (shared with *Sigillaria* sp. nov.); leaf-cushion upper field plicate (shared with *Hizemodendron*); leaf-cushion upper and lower fields separated by lateral line (shared with *Lepidodendron*); megasporophyll alations short, horizontal (shared with Sigillariaceae); equatorial crassitude on microspore (shared with Sigillariaceae).

The Diaphorodendraceae encompasses a well studied, distinctive group of lycopsids segregated from *Lepidodendron* (DiMichele 1985; DiMichele and Bateman 1992). The family consists of at least five anatomically preserved species in two genera, *Diaphorodendron* and *Synchysidendron*. Many of the common Late Carboniferous species of compressions described as *Lepidodendron* are in fact assignable to these genera. For example, '*Lepidodendron*' *brettonense* Bell and '*L.*' *rimosum* Sternberg as described by Wnuk (1985) appear to be species of *Diaphorodendron* and *Synchysidendron* respectively.

SIGILLARIACEAE. DEFINING CHARACTERS. Synapomorphies—Leaf trace originates from two protoxylem strands; periderm includes bands of "resinous" cell clusters; massive parichnos strands present in periderm; leaf vascularized by two xylem strands (paired leaf central vascular bundle); medial adaxial groove on leaf; echino-conate distal ornamentation on microspore. Parallelisms—Cone pe-

duncles or cone-bearing lateral branches borne on main trunk (shared with *Paralycopodites* and *Diaphorodendron*); tangential interarea expansion between leaf cushions (shared with *Synchysidendron*); periderm "resinous" (shared with Lepidodendraceae); leaf-cushion height : width ratio 1 : 1 or less on terminal branches (shared with Lepidodendraceae); 'V'-shaped vascular strand (shared with *Chaloneria*); paired abaxial grooves on leaf (shared with Lepidodendraceae and *Diaphorodendron sclerotium*); short, horizontal megasporophyll alations (shared with Diaphorodendraceae); equatorial crassitude on microspore (shared with Diaphorodendraceae).

The family Sigillariaceae (Sigillariostrobaceae of Thomas and Brack-Hanes 1984) is probably the most universally recognized and accepted family of rhizomorphic lycopsids (e.g., Chaloner 1967). Numerous species of *Sigillaria* have been described from both petrified and adpressed preservation states. Detailed analysis of this genus probably will result in segregation of several genera (e.g., Lemoigne 1961). However, *Sigillaria* is less commonly preserved as petrifications than genera of the Diaphorodendraceae and Lepidodendraceae, so its breadth and variation in anatomical characters are less well understood. We tentatively included *Asolanus* in the Sigillariaceae; indeed it may be congeneric with *Sigillaria* (Daber and Kahlert 1970).

ULODENDRACEAE. DEFINING CHARACTERS. Synapomorphies—Prominent leaf traces in periderm; rugose ornamentation of megaspore contact faces; microspores with distally ornamented cingulum complex. Parallelisms—cone peduncles or cone-bearing lateral branches borne on main trunk (shared with Sigillariaceae and Diaphorodendraceae); more than one cone per lateral branch (shared with *Diaphorodendron*); angle between mature leaf and subtending axis acute (shared with *Pauroidendron*, *Chaloneria*, and *Hizemodendron*); microspore with equatorial cingulum complex (shared with Lepidodendraceae); microspore distal ornamentation densely granulate (shared with Lepidodendraceae).

A natural group cannot be circumscribed by a suite of characters that is, in the present analysis, entirely plesiomorphic. However, relative to the rest of the arboreal lycopsids, the Ulodendraceae has a unique combination of primitive and derived traits (Bateman et al. 1992).

The Ulodendraceae includes the anatomically preserved genus *Paralycopodites* (DiMichele 1980), which ranges through the c. 45 myr of the Viséan,

Namurian, and Westphalian stages of the Carboniferous. Minor quantitative differences among associated cones suggest that this genus includes at least three species (Brack-Hanes and Thomas 1983). We expect that the family eventually will include several additional genera, particularly from the Early Carboniferous. It presently includes the most primitive of the six arboreal "stigmairian" genera analyzed by us. Pearson (1986) suggested that the predominantly Late Carboniferous *Paralycopodites* as emended by DiMichele (1980) is synonymous with the Early Carboniferous *Anabathra* Witham. Initially we accepted this synonymy (Bateman et al. 1992: appendix 1e), but we have since examined the type of *Anabathra* in the Natural History Museum (London) and find that it is too incomplete to synonymize confidently with *Paralycopodites*. As described by Pearson (1986), *Anabathra* is a composite based on several specimens that range in age from Tournaisian to Westphalian (Appendix 1).

The Ulodendraceae as we envision it is both paraphyletic and basal to the rhizomorphic clade. There is less taxonomic precedent for the Ulodendraceae than for the more derived families. The closest approximation is the Flemingitaceae of Thomas and Brack-Hanes (1984), which in their system is based on reproductive morphology. The Flemingitaceae, as seen in the light of more recent whole-plant reconstructions, is polyphyletic (due to the inclusion of "*Lepidodendron*" s.l.), but being based on bisporangiate cones it contains a central character of the Ulodendraceae. The cone genus *Flemingites*, and hence the family Flemingitaceae, is united only by the shared primitive feature of bisporangiate morphology. If broadly construed (for the time being) the Ulodendraceae could include as satellite taxa problematic forms such as the large bisporangiate cone *Flemingites brownii* (Unger) Brack-Hanes and Thomas, which clearly is related only distantly to smaller forms such as *F. diversus* (Felix) Brack-Hanes and Thomas.

The Ulodendraceae of Chaloner (1967) is based on the adpression genus *Ulodendron* Lindley & Hutton. As recircumscribed by Thomas (1967), *Ulodendron* appears to be congeneric with *Paralycopodites* (DiMichele 1980), although this may be confirmed ultimately only by finding an exceptional specimen that combines diagnostic anatomical features of both anatomy and external morphology. We have chosen the name Ulodendraceae for this family because: 1) current evidence supports the correlation between petrifications and adpressions, albeit equivocally; 2) Ulodendraceae has

priority over any new name that may be created; 3) the name is already in current use, and 4) it is more pronounceable than its possible alternative, "Paralycopoditaceae."

Primarily on the basis of rootstock morphology, Karrfalt (1981) suggested that *Oxroadia* represents a distinct group of rhizomorphic lycopsids. This argument was further developed in a whole-plant context by Bateman (1989) and Stewart and Rothwell (1993), who inferred a close relationship between *Oxroadia* and *Paurodendron*. Indeed, in Fig. 1a the two genera are depicted as a clade within the primitive bisporangiate-coned basal group, though in fact their monophyly is supported only by the echinate ornamentation of their microspores (Bateman et al. 1992). Bateman (1992a, 1994) subsequently argued that the two genera are equally likely to have evolved independently, by broadly paedomorphic reduction from different tree-sized, ulodendrid ancestors. Given present knowledge of the basal rhizomorphic plexus, it would certainly be premature to recognize formally the 'Paurodendraceae' of Bierhorst (1971) as a separate family.

ISOËTACEAE. DEFINING CHARACTERS. Synapomorphies—Bilaterally symmetrical rhizomorph. Sporophylls grouped into fertile areas on aerial stems.

The taxonomically diverse isoetean lineage was represented in this analysis by only one species (*Chaloneria cormosa*). Consequently, the presumed monophyly of the family could not be tested. Moreover, the topological position of *Chaloneria* in the cladogram is especially equivocal (Fig. 1a). Despite the lack of an analytical context, there is strong circumstantial evidence that several lycopsid genera with bilaterally symmetrical rhizomorphs form a distinct clade, which diverged from (or alternatively was ancestral to) the radially symmetrical lineage during the Devonian (e.g., Jennings et al. 1983; Rothwell and Erwin 1985; Pigg 1992). The isoetean clade is well represented throughout the fossil record by genera that on average became smaller-bodied and less branched with time, though probably not gradually nor in the unidirectional, linear reduction series envisaged by Mägdefrau (1956). They include *Protostigmaria* Jennings, *Sporangioostrobus*, *Chaloneria*, *Pleuromeia* Giebel, *Nathorstiana* P. R. Richt., *Takhtajanodoxa* Snigirevskaya, and *Isoëtes* (including *Isoëtites* Münster and the extant *Stylites*) (summarized by Pigg 1992). These genera differ greatly in body plan, varying from highly branched arboreal forms, such as *Lepidodendropsis* (the "parent plant" of *Protostigmaria*, Jennings et al. 1983) to pseudoherba-

ceous forms such as the extant *Isoëtes*. As a result, many authors have apportioned the genera among different families (e.g., Chaloner 1967; Pigg and Rothwell 1983b; Thomas and Brack-Hanes 1984; Meyen 1987; Stewart and Rothwell 1993), and some authors have even segregated certain genera as the basis of separate orders (e.g., Taylor and Taylor 1992). Multiple orders are difficult to justify, and assignment to several families must be regarded as provisional at best in the absence of well supported phylogenies.

A more narrowly circumscribed and morphologically uniform family Isoëtaceae can be delimited by exclusion of the few large, arboreous forms, such as *Lepidodendropsis/Protostigmaria* and possible relatives *Eospermatopteris* Goldring and *Lepidosigillaria* Kräusel and Weyland (Pigg 1992). This exclusion leaves a group of genera that possess unbranched or sparsely branched stems with sporangia aggregated in terminal cones or more commonly non-terminal fertile zones on the aerial shoot, characters that are potential synapomorphies of the more narrowly circumscribed family. In this more restricted sense the Isoëtaceae would share bilaterally symmetrical rhizomorphs with another, less well understood group of Late Devonian and Lower Carboniferous isoëtoids characterized by arboreous habit and frequent branching. The evolutionary reductions that gave rise to the smaller-bodied, unbranched forms appear to have begun early in the evolution of the clade and became increasingly extreme during the Mesozoic and Cenozoic.

Strict Phylogenetic Classification. The following alternative outline classification of the rhizomorphic lycopsids is favored by the junior author and accepted (although not preferred) by the senior author. It is based on the preferred most-parsimonious cladograms of Kenrick and Crane (1991: Fig. 26) and Bateman (1992a: text-fig. 16a; Fig. 1a of this paper) for ordinal and supraordinal taxa, and that of Bateman et al. (1992: Fig. 6) for infraordinal taxa. With the exception of the ulodendrid basal plexus, all taxa (including the listed whole-plant genera) are hypothesized to be monophyletic. Listing of genera is highly conservative, and is confined to ten fossil genera that include at least one fully reconstructed whole-plant species, plus the one extant genus of rhizomorphic lycopsids (*Isoëtes*, including *Stylites*).

Choice of supporting character states was also highly conservative. All are non-homoplastic synapomorphies supporting the relevant nodes of the cladograms; even of those some (for example, the

relatively poorly conserved spore characters) were discarded in order to maximize the robustness of the classification. Single key character states (italicized) also have been selected to delimit each monophyletic taxon. This unashamedly typological approach deliberately renders the classification highly robust; the addition of further whole-plant species to the analysis can break up suites of character states treated here as diagnostic, but the taxon per se will only be fragmented if the italicized key character state is rendered homoplastic as a result of reanalyzing the expanded cladistic matrix. Thus, the following classification is reduced not only to the best known core genera but also to the best known core characters. No attempt has been made to include satellite taxa; this would have required a far more detailed discussion and classification.

Phylum Tracheophyta

Helical/annular water-conducting cells in axes.

Subphylum Lycophytina

Sporangia reniform; borne laterally.

Class Lycopsidea

Metaxylem tracheid perforations contain Williamson striations (fimbrials). Sporangia borne helically or pseudohelically.

Order Isoëtales (Rhizomorpha sensu Bateman 1992a)

True bipolar rhizomorph emitting monarch rootlets, conferring centralized determinate growth and secondary thickening; the latter reflected in the presence of wood, periderm and a three-zoned cortex.

Parataxon 'Ulodendrineae'

Rhizomorphic lycopsids lacking both bilaterally symmetrical rhizomorphs and monosporangiate cones.

Core genera: *Paratycopodites*, *Oxroadia*, *Paurodendron*.

Suborder Isoëtineae

Rhizomorph bilaterally symmetrical.

Core genera: *Chaloneria* (also extant *Isoëtes*, including *Stylites*).

Suborder Dichostrobiles

Leaf is an outgrowth of only a portion of the leaf base ('cushion'). *Cones monosporangiate;*

dispersal unit sporangium-sporophyll complex.

Superfamily Sigillarianae

Leaf contains two vascular traces arising from adjacent protoxylem strands in axis. Intrafoliar parichnos penetrate periderm.

Core genus: *Sigillaria*.

Superfamily Monomegasporae

Single functional megaspore per megasporangium; germinates within sporangium.

Family Diaphorodendraceae

Stem with true pith (medullated). Periderm clearly bifacial with distinct phellem and phelloderm. Megasporangium dorsiventrally flattened with proximal dehiscence and heterocellular wall. Megaspore bears massa.

Core genera: *Diaphorodendron*, *Synchysidendron*.

Family Lepidodendraceae

Megasporangium bilaterally flattened with distal dehiscence. Megasporophyll alations suberect or erect.

Core genera: *Hizemodendron*, *Lepidodendron*, *Lepidophloios*

Three of these nested higher taxa have been given new names that reflect their key diagnostic characters. The rhizomorph-bearing Order Isoëtales comprises the Orders Lepidodendrales and Isoëtales of most authors; here, the traditional Isoëtales, including the extant genera, is downgraded to the Suborder Isoëtinae. The Suborder Dichostrobiles (Greek: *dicha*, in two, *strobilos*, cone—referring to the separation of megasporangia and microsporangia in discrete cones) corresponds to the traditional Lepidodendrales less the arboreous members of the bisporangiate-coned ulodendroids. The Monomegasporae, characterized by seed-like megasporophyll complexes, corresponds to the traditional Lepidodendraceae less the arboreous members of the bisporangiate-coned ulodendroids, prior to the revision of DiMichele (1983, 1985).

Two parataxa are relevant to this classification. Our Subphylum Lycophytina should not be confused with the Division "Lycophyta" of Thomas and Brack-Hanes (1984), which is synonymous with our Class Lycopsidea. Within the Subphylum Lycophytina, the putatively monophyletic Class Lycopsidea is nested within the Parataxon 'Zostero-

phyllopsida' (cf. the cladograms of Crane 1990; Gensel 1992). The second parataxon, the 'Ulodendrineae', is explicitly included in the present classification. It is used as a temporary repository for primitive rhizomorphic lycopsids whose precise phylogenetic relationships remain ambiguous. Although the group is partly delimited using plesiomorphies (or more accurately the absence of apomorphies), it nonetheless can be diagnosed readily.

DISCUSSION

Comparison of the Relaxed and Strict Classifications. The aforementioned relaxed and strict classifications are based on the same cladogram (Fig. 1a) and hence are similar in most characteristics. Both assign all of the rhizomorphic lycopsids to one order, the Isoëtales. Within this order, genera are apportioned to the same higher taxa, which, except for the basal ulodendrid plexus, are all putatively monophyletic. Although some of the names given to the suprageneric taxa are novel, they differ between the classifications only in the suffix that denotes taxonomic rank.

There are, however, two important differences between the two classifications. First, the preference for uniformly familial assignments in the relaxed classification contrasts with the use in the strict classification of superfamilial and subordinal ranks to encompass more of the phylogenetic structure of the cladogram (though note that the provisional recognition of the paraphyletic ulodendrids means that even the strict classification includes some ambiguity; it does not allow complete reconstruction of the cladogram). Second, the relaxed classification employs a much larger number of characters that include homoplasies, though these are distinguished from the more diagnostic non-homoplastic characters. The more heavily culled strict classification uses a far smaller number of exclusively non-homoplastic characters.

Comparison of Present with Previous Classifications. Table 1 compares both of the present classifications with five previous classifications of the rhizomorphic lycopsids. Note that the table focuses on family and order levels, and its compilation required some reinterpretations of aspects of the earlier studies.

Only the present study assigns all of the rhizomorphic lycopsids to a single order. Rather than recognizing the Isoëtales as a coherent group, most previous studies, elected to distinguish the

TABLE 1. Strict and relaxed classifications of the rhizomorphic lycopsids analyzed in this study, compared with five contrasting schemes. Generic names follow Bateman et al. (1992), as modified by Bateman and DiMichele (1991) and DiMichele and Bateman (1992). Note that the present classification employs suborders and superfamilies, whereas the remaining classifications are confined to orders and families (NF = no family affinity suggested). Names shown in single quotation marks are paraphyletic. Classifications broadly similar to, but less detailed than, that of Stewart and Rothwell (1993) were presented by Sporne (1975) and Taylor and Taylor (1992). The relationship of *Paralycopodites* to *Anabathra* sensu Pearson (1986) is ambiguous; see Appendix 1. Symbols have the following meanings: (*) small-bodied shrubs and pseudoherb regarded as strongly simplified (Bateman 1992, 1994; Bateman et al. 1992); (!) listed as *Selaginellites* in Thomas and Brack-Hanes (1984); (!!) taxonomic assignment did not note evidence of heterospory in Alvin's (1965) original description of the genus; (!!!) assignment of whole-plant inferred by us through assignment of a diagnostic organ-species or organ-genus; (+) genus not yet segregated from *Lepidodendron* and thus not recognized at the time of publication; *Paralycopodites* by Morey and Morey (1977), *Diaphorodendron* by DiMichele (1985), *Synchysidendron* by DiMichele and Bateman (1992), and *Hizemodendron* by Bateman and DiMichele (1991); (++) there is little doubt that Bierhorst (1971) would have assigned *Chaloneria* to the Isoetales, given his assignment of *Synchysidendron* not distinguished from *Diaphorodendron*; (#) there is little doubt that Bierhorst (1971) would have assigned *Chaloneria* to the Isoetales, given his assignment of other closely related genera; (##) listed as *Polysporia*; the name *Chaloneria* had not yet been applied to petrified specimens by Pigg and Rothwell (1983a).

Whole-plant genus	Present study (strict)	Present study (relaxed)	Thomas & Brack-Hanes (1984)	Meyen (1987)	Stewart & Rothwell (1993)	Bierhorst (1971)	Chaloner (1967)
<i>Paurodendron*</i>	Isoetales 'Ulodendrineae' Isoetales	Isoetales 'Ulodendraceae' Isoetales	Selaginellales Selaginellaceae! Protolepidodendrales!!	Selaginellales NF Lycopodiales!!	Isoetales NF Isoetales	Selaginellales Paurodendraceae —	'Incertae sedis' NF Protolepidodendrales!!
<i>Paralycopodites</i>	'Ulodendrineae' Isoetales	'Ulodendraceae' Isoetales	Elutherophyllaceae Lepidocarpaceae!!!	NF Isoetales	NF Lepidodendrales	— Lepidodendrales	Elutherophyllaceae Lepidodendrales
<i>Chaloneria*</i> (also <i>Isoetes</i>)	'Ulodendrineae' Isoetales	'Ulodendraceae' Isoetales	Flemingitaceae Isoetales	Lepidocarpaceae Isoetales	Lepidodendraceae Isoetales	Lepidodendraceae —#	Ulodendraceae Isoetales##
<i>Sigillaria</i>	Isoetinae Isoetales Sigillariaceae	Isoetaceae Isoetales Sigillariaceae	Chaloneriaceae Lepidocarpaceae	Chaloneriaceae Isoetales	NF Lepidodendrales	— Lepidodendrales	'Incertae sedis' Lepidodendrales
<i>Diaphorodendron</i>	Isoetales Diaphorodendraceae	Isoetales Diaphorodendraceae	Sigillariostrobaseae Lepidocarpaceae Lepidocarpaceae!!; +	Sigillariaceae Isoetales Lepidocarpaceae++	Sigillariaceae Lepidodendrales Lepidodendraceae	Sigillariaceae Lepidodendrales Lepidodendraceae+	Sigillariaceae Lepidodendrales Lepidodendraceae+
<i>Synchysidendron</i>	Isoetales Diaphorodendraceae	Isoetales Diaphorodendraceae	Lepidocarpaceae Lepidocarpaceae!!; +	Isoetales Lepidocarpaceae+	Lepidodendrales Lepidodendraceae!!; +	Lepidodendrales Lepidodendraceae!!; +	Lepidodendrales Lepidodendraceae+
<i>Hizemodendron*</i>	Isoetales Lepidodendraceae	Isoetales Lepidodendraceae	Lepidocarpaceae Lepidocarpaceae!!; +	Isoetales Lepidocarpaceae!!!; +	Lepidodendrales Lepidodendraceae!!!; +	Lepidodendrales Lepidodendraceae!!!; +	Lepidodendrales Lepidodendraceae+
<i>Lepidodendron</i>	Isoetales Lepidodendraceae	Isoetales Lepidodendraceae	Lepidocarpaceae Lepidocarpaceae!!; +	Isoetales Lepidocarpaceae!!!; +	Lepidodendrales Lepidodendraceae!!!; +	Lepidodendrales Lepidodendraceae!!!; +	Lepidodendrales Lepidodendraceae+
<i>Lepidophloios</i>	Isoetales Lepidodendraceae	Isoetales Lepidodendraceae	Lepidocarpaceae Lepidocarpaceae	Isoetales Lepidocarpaceae	Lepidodendraceae Lepidodendraceae	Lepidodendraceae Lepidodendraceae	Lepidodendraceae Lepidodendraceae

Lepidodendrales (Lepidocarpaceae of Thomas and Brack-Hanes 1984) and Isoëtiales s. str. at ordinal level. However, in this configuration the Lepidodendrales is paraphyletic relative to the Isoëtiales. Only Meyen (1987) subsumed the Lepidodendrales into the Isoëtiales, an action that we support. However, he did not include all the rhizomorphic forms in the order, following earlier authors who assigned *Paurodendron* and *Oxroadia* to other orders.

Among the non-trees, all studies recognized the close affinity of *Hizemodendron* to *Lepidodendron*, albeit implicitly as organ-species rather than explicitly as whole-plant species. All also recognized the close affinity of *Chaloneria* to *Isoëtes*, the archetypal isoëtalean. However, no consensus was reached regarding the other pseudoherbs. Only Stewart and Rothwell (1993) acknowledged *Paurodendron* as a rhizomorphic lycopsid; most authors assigned the genus to the Selaginellales and some treated it as synonymous with *Selaginella* or *Selaginellites* Zeiller (e.g., Thomas and Brack-Hanes 1984). Even more bizarre is the repeated misassignment of the woody, ligulate, heterosporous *Oxroadia* to non-woody, eligulate, homosporous orders: to the Protolepidodendrales by Chaloner (1967) and Thomas and Brack-Hanes (1984), and to the Lycopodiales by Meyen (1987) and Taylor and Taylor (1992). Stewart and Rothwell (1993) chose to assign both *Oxroadia* and *Paurodendron* to the Isoëtiales, despite their fundamentally radially symmetrical rhizomorphs (cf. Rothwell and Erwin 1985; Long 1986; Bateman 1992a).

There is more agreement regarding the taxonomy of the tree-sized genera. All of the tabulated studies awarded *Sigillaria* its own family, the Sigillariaceae (Sigillariostrobaceae of Thomas and Brack-Hanes 1984), and assigned most of the remaining tree genera to the Lepidodendraceae (Lepidocarpaceae of Thomas and Brack-Hanes 1984; Meyen 1987). Only we have separated *Diaphorodendron* and *Synchysidendron* from the true lepidodendrids (*Hizemodendron*, *Lepidodendron*, and *Lepidophloios*) as the new and highly distinct family Diaphorodendraceae (Figs. 1a, b). The main taxonomic variable is *Paralycopodites*, which was lumped with the lepidodendrids sensu lato by Bierhorst (1971), Meyen (1987), and Rothwell and Stewart (1993), but given its own family of bisporangiate-coned trees by Chaloner (1967) as the Ulodendraceae and by Thomas and Brack-Hanes (1984) as the Flemingitaceae. We have no hesitation in supporting the segregation of *Paralycopodites* from the other reproductively more sophisticated trees, but have chosen

to recognize taxonomically its many similarities (body size notwithstanding) and close phylogenetic relationship with smaller bodied bisporangiate-cone rhizomorphic lycopsids such as *Oxroadia* and *Paurodendron* (Fig. 1a).

Thus, earlier classifications of the rhizomorphic lycopsids less accurately reflected evolutionary relationships. This is not surprising, as systems that arrange organs into phenetic groups, often delimited by shared primitive characters, reflect phylogeny only partially and ambiguously.

Many authors have advocated a hierarchy among organ-taxa, giving primacy not to whole plants but to reproductive organs (e.g., Meyen 1978a, 1987; Thomas and Brack-Hanes 1984). Although reproductive organs are on average the most reliable taxonomic indicators, they are, for example, insufficient to determine relationships among the genera of the Ulodendraceae and Diaphorodendraceae. We obtained credible, fully resolved cladograms for the rhizomorphic lycopsids only by including a full range of reproductive and vegetative characters (Bateman and DiMichele 1991; Bateman et al. 1992). Admittedly, the 'correct' topology can be fairly well approximated using only stem anatomy and cone morphology, but this conclusion could only be reached *after* having determined the best topology using all the available characters (Bateman 1994). Thus, it is isolated organs and partial plants rather than all fossils that should be fitted a posteriori into phylogenies and thus into classifications (Donoghue et al. 1989; Bateman 1992b; but see Patterson 1981; Forey 1992a).

Moreover, emphasis on particular organ types is both artificial and unnecessarily restrictive. Given that different organ systems evolve at different rates (mosaicism sensu Knoll et al. 1984), no one system should be granted taxonomic precedence a priori. We have therefore adapted the core taxa plus satellite taxa system of Meyen and Thomas and Brack-Hanes, using whole-plants rather than reproductive organs as our core taxa. Satellite designation is useful for tentative placement of organs that so far lack a whole-plant context yet exhibit characters that allow their assignment to a supraspecific taxon. It also allows permanent supraspecific classification of organ-species that have been placed in a whole-plant context but are known to lack any of the defining autapomorphies of that particular whole-plant (for example, we are not sanguine that species-level autapomorphies will ever be found in *Stigmara* Brongniart).

The approaches advocated here incorporate a

degree of flexibility into fundamentally Linnean classifications and contravene strict cladistic principles (e.g., Wiley et al. 1991; Forey 1992b). Nonetheless, we have ensured that the classifications are *consistent* with the preferred cladogram even though they do not reflect its entire structure. Future empirical research will lead to more confident phylogenetic hypotheses and thus to further taxonomic revisions.

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APPENDIX 1.

In an earlier paper (Bateman et al. 1992, Appendix 1c) we presented a brief discussion of the nomenclatural conundrum surrounding the relationships of three fossil genera that were all based on vegetative axes: the adpression genus *Ulodendron* Lindley and Hutton and the petrification genera *Anabathra* Witham emend. Pearson (1986) and *Paralycopodites* Morey and Morey (1977). We accepted that *Ulodendron* had nomenclatural priority but argued the genus was too broadly defined (i.e., its supposedly delimiting characters were too generalized) to regard it as synonymous with the petrification genera. However, we accepted Pearson's (1986) arguments that *Anabathra* is synonymous with, and pre-dates, *Paralycopodites*; we therefore used the former rather than the latter in a series of recent papers on the rhizomorphic lycopsids (Bateman 1991, 1992a; Bateman and DiMichele 1991; DiMichele et al. 1992; Bateman et al. 1992; DiMichele and Bateman 1992). However, in September 1992 we re-examined the type and other materials studied by Pearson (1986) at the British Museum (Natural History). Following this study, we are obliged to reject *Anabathra* for the same reason that we originally rejected *Ulodendron*, and have chosen to resurrect the far more narrowly delimited *Paralycopodites sensu* DiMichele (1980).

Anabathra is based on a nodule containing a single axis that includes only a stele, secondary xylem, and a small lateral branch trace, embedded in a matrix of clastics and detrital plant material. We believe that sediment filled the rotting cortical region of the stem; the periderm was removed later by decay or abrasion. The stele appears to be non-coronate with a large pith; an associated 4 mm-diameter lateral branch trace is associated with a *bona fide* stelar gap. These features are consistent with *Paralycopodites* but they are plesiomorphic and thus not diagnostic of the genus.

Pearson (1986: 278–9) noted that leafy twigs and reproductive remains associated with the holotype of *Anabathra* are also broadly consistent with *Paralycopodites*. However, many of these characters, such as leaf retention, are similarly plesiomorphic. Pearson (1986, figs. 18–20) also illustrated an Early Westphalian nodule from Yorkshire that consists of an anatomically preserved but somewhat vertically compressed stem bearing two opposite rows of small (c. 10 cm diameter) ulodendrid branch scars. Short leaves remain attached to the approximately equidimensional leaf bases. The small (c. 1 cm diameter) stele has a relatively large pith and shows evidence of lateral branch traces, but lacks wood. Overall, this specimen is more like *Paralycopodites* than is the type of *Anabathra*.

In summary, the holotype of *Anabathra* cannot be confidently united with either the associated plant material or with the holotypes of *Paralycopodites* or *Ulodendron*, though all three genera share several characters and are probably all attributable to the basal group of the rhizomorphic lycopsid clade (Fig. 1a). Although *Paralycopodites* is the most recent of the three generic names, it is also by far the most precisely delimited and is the only one of the three genera that has yielded a fully reconstructed species.