

EVOLUTIONARY-DEVELOPMENTAL CHANGE IN THE GROWTH ARCHITECTURE OF FOSSIL RHIZOMORPHIC LYCOPSIDS: SCENARIOS CONSTRUCTED ON CLADISTIC FOUNDATIONS

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I. INTRODUCTION

This wide-ranging paper uses a botanical cladistic case-study to explore four basic premises:

(1) A numerical, character-based phylogenetic context is essential for meaningful discussion of organismal architecture. Although current concerns regarding the relative merits and applications of various cladistic methods and interpretations may in part be justified, these reservations do not impinge on the fundamental truth of cladistic principles. No other approach rivals cladistics in generating explicit hypotheses of both evolutionary relationships and patterns of character change.

(2) Some radical macroevolutionary changes in organismal architecture can yield erroneous phylogenetic histories (topologies). This paper focuses on some of the more problematic architectural transitions, including those reflecting a suite of developmental changes that are collectively termed paedomorphosis.

(3) The preferred most-parsimonious cladogram (or the consensus tree summarizing all the most-parsimonious cladograms) is often regarded as an incontrovertible truth and treated as the end-point of a phylogenetic analysis. However, phenomena such as paedomorphosis are better addressed by reciprocal illumination – the initial cladistic analysis prompts increasingly interpretative (and thus subjective) cycles of scenario building and testing.

(4) The distribution of character-state transitions across the cladogram can in theory be used to reconstruct hypothetical ancestors on internal nodes (Hennig, 1966), and to test competing hypotheses purporting to explain the underlying evolutionary mechanism(s). In other words, a cladogram must be viewed as an evolutionary tree if it is to be fully exploited. This assertion is unashamedly pragmatic; I concede that the pattern cladistic view of a cladogram as merely a nested set of shared derived characters is more philosophically defensible (cf. Hull, 1988; *Auct. Mult.*, 1993).

The scenarios discussed below focus on the evolutionary origins of contrasting growth architectures in plants. The range of inferred morphological transitions is greater than can be readily accommodated in strict definitions of heterochrony (e.g. Alberch *et al.*, 1979) and heterotopy (e.g. Sattler, 1988). For this reason, I herein define a broader term, *evolutionary-developmental change*: any phenotypically expressed genetic change in a lineage that profoundly alters the shape and/or size of any developmental stage (semaphoront) in the putative descendant relative to the putative ancestor. Table 1 presents definitions of several related terms.

The example used to illustrate these premises is in some ways unusually challenging – a bizarre group of dominantly fossil plants known as the rhizomorphic clubmosses (Class Lycopsidea, Order Rhizomorphales *sensu* DiMichele & Bateman, 1994 = Lepidodendrales plus Isoetales of traditional classifications). Now generally recognized as the most derived portion of the lycopsid clade, the rhizomorphales are delimited by determinate centralized growth with secondary thickening. They were important components of many land-plant communities in the Late Palaeozoic, attaining considerable taxonomic and ecological diversity (e.g. DiMichele & Phillips, 1985; Bateman, 1991 *a*, 1992 *a*; Bateman, DiMichele & Willard, 1992; DiMichele *et al.*, 1992; Phillips & DiMichele, 1992). Together with the unrelated progymnospermopsids, they were one of the first clades to attain tree-sized dimensions in the Mid–Late Devonian (e.g. Scheckler, 1986; Mosbrugger, 1990; DiMichele *et al.*, 1992; Niklas, 1993 *a*, *b*).

Table 1. *Definitions of selected evolutionary-developmental terms*

[Note that several of these terms have been awarded widely divergent definitions by different workers (sources consulted include Gould, 1977; Riedl, 1979; Levinton, 1988; McKinney & McNamara, 1991; Bateman & DiMichele, 1994). Asterisked terms were coined specifically for this paper.]

*Evolutionary-developmental change**

Any phenotypically expressed genetic change in a lineage that profoundly alters the shape and/or size of any developmental stage (semaphoront) in the putative descendant relative to the putative ancestor.

Heterochrony

A temporal change in the expression of a trait between putative ancestor and putative descendant.

Heterotopy

A spatial (positional) change in the expression of a trait between putative ancestor and putative descendant.

Pleiotropy

A single genetic modification that is expressed in widely disparate elements of the organismal phenotype ('genetic pleiotropy' *sensu* Levinton, 1988).

Polygeny

Control of a single phenotypic feature by more than one gene.

Burden

The functional responsibility of a trait, as measured by the number and magnitude of dependent traits.

Canalization

Buffering of development, and thereby conservation of phenotype, against the effects of genotypic change.

Developmental cascade

A temporal sequence of developmentally related phenotypic changes occurring within the ontogeny of an organism.

*Domino effect**

Indirect but immediate and inevitable modifications to phenotypic traits that are expressed later in an ontogenetic cascade than a trait directly modified by an evolutionary-developmental change.

*Selective cropping**

Selectively-mediated, population-level phenotypic modifications to features whose function has been lost or transferred as a result of an evolutionary-developmental change.

*Evolutionary parsimony**

Evolutionary modification of pre-existing phenotypic features.

Epigeny

Modification of gene expression by the internal microenvironments encountered by cells during development.

Ecophenotypy

Phenotypic variation within a single genotype that is ascribable to variation in the external environment.

Mosaic evolution

At least partially independent evolution of different organs within an organism.

Saltation

A genetic modification that is expressed as a profound phenotypic change across a single generation and results in a potentially independent evolutionary lineage.

Despite their Palaeozoic successes, today the rhizomorphaleans are represented by only a highly derived and specialized clade that is most commonly divided into two closely related genera, *Isoetes* (ca. 60 spp.) and *Stylites* (2 spp.), though current evidence suggests that *Stylites* is nested within, and hence should be synonymized with, *Isoetes* (cf. Rauh & Falk, 1959; Kubitzski & Borchert, 1964; Bierhorst, 1971; Hickey, 1986; Gifford & Foster, 1989). Species range from small to diminutive in stature. Thus, it is obvious that any study of the evolutionary pattern within the rhizomorphic

lycopsids must focus on the extinct species. It might seem equally obvious that study of their growth architecture, ontogeny and life history should begin with the extant species, wherein these phenomena can be observed directly. However, it is impossible to determine how far process-related observations on the very limited range of extant species can be generalized to the remainder of the rhizomorphic lycopsid clade without an explicit hypothesis of their phylogenetic relationships. If *Isoetes* is highly derived (a strong *a priori* hypothesis), many of its biological properties could have been acquired long after the initial, Palaeozoic radiation of the rhizomorphic lycopsids. Hence, for process as well as pattern, the extinct species offer at least as much information as their extant descendants (albeit inferential).

Several topics warrant review prior to interpreting the evolution of architecture in the rhizomorphic lycopsids. Section II below outlines relevant aspects of phylogenetic analysis, and Section III summarizes the architecture and physiology of the rhizomorphic lycopsids; details of individual taxa are not presented (see Bateman *et al.*, 1992; Phillips & DiMichele, 1992). Determinate modular growth is considered in Section IV, and the formalization of comparative developmental patterns in Section V(1). The second half of the paper then attempts to weave these different conceptual threads into a broad-based evolutionary synthesis.

II. CLADISTIC ANALYSIS

Thorough accounts of cladistic methodology were presented by Wiley *et al.* (1991) and Forey *et al.* (1992), and of its underlying principles and applications by Wiley (1981) and Funk & Brooks (1990). The following brief (and of necessity oversimplified) overview of morphological cladistics focuses on issues that are underdeveloped in the literature or particularly relevant to the chosen case-study – a detailed experimental cladistic analysis of the rhizomorphic lycopsids that was originally performed in 1989 (Bateman *et al.*, 1992). This paper reviews relevant aspects of that analysis in the light of four years additional consideration, using substantially updated versions of the preferred analytical software: PAUP 3.1.1 (Swofford, 1993) and MacClade 3.0 (Maddison & Maddison, 1992). The original character coding has been retained, though both the coding and the topologies are reinterpreted in the light of evolutionary-developmental theory. Many of the issues raised are contentious, and it should be emphasized that some of the opinions expressed below are shared by few other practising cladists.

(1) *Selection of operational taxonomic units*

The basic analytical units of a cladistic analysis are most appropriately termed 'operational taxonomic units' (OTUs) rather than the more commonly used 'terminal taxa': each OTU is coded as a single row of data, with each datum being a specific state for a particular character (a column in the asymmetric primary 'nexus' matrix). Although a few cladistic analyses have coded ostensibly infraspecific OTUs (given diagnosability and non-reticulation: cf. Davis & Manos, 1991; Davis & Nixon, 1992; Hillis *et al.*, 1992; *Auct. Mult.*, 1993) and many have coded supraspecific OTUs (e.g. Doyle & Donoghue, 1986; Gauthier, Kluge & Rowe, 1988; Loconte & Stevenson, 1990; Kenrick & Crane, 1991), putative species are by far the most appropriate analytical units. When viewed over substantial periods of time, relationships among

infraspecific taxa are almost inevitably reticulate and therefore incompatible with the repeatedly dichotomous structure inherent in cladograms. Also, to avoid troublesome ambiguities, a character should be discarded from a cladistic analysis unless every OTU is characterized by a fixed (ubiquitous) state for that character. Thus, attempting to code a *supraspecific* taxon as a single row of data (i.e. summarizing several species in a single OTU) generates extensive polymorphism, and hence requires the exclusion of undesirably large numbers of characters.

In any cladistic study the range of potential OTUs is delimited *a priori* using morphological criteria. In practice, one or more higher taxa are chosen that are assumed to constitute a clade (a monophyletic group consisting of a single ancestor and all of its descendants; in this case, the Rhizomorphales). As computational capacity limits most cladistic analyses to a maximum of 20–30 OTUs, some further selectivity is often required within this *a priori* taxonomic spectrum. Sadly, the importance of such sampling procedures has escaped serious discussion in the literature. The OTUs included in this study were self-selecting, as only 17 fossil species met the minimum criteria imposed by preservational constraints: that all component organs (nine obligatory – rootlet, rhizomorph, stem, microphyll leaf, cone, megasporophyll, megaspore, microsporophyll, microspore – and two optional – isotomous crown branches, lateral branches) are known in cellular-anatomical detail and have been reconstructed from disarticulated assemblages into a conceptual whole-plant (Bateman & Rothwell, 1990; Bateman, 1991*c*). As the two *Oxroadia* species recognized by Bateman (1992*a*) yielded identical cladistic scores, one was discarded. The remaining 16 OTUs all occupied the Euramerican palaeocontinent during the Carboniferous period (*ca.* 360–300 Ma: Bateman *et al.*, 1992). The putative isoetalean clade, delimited by the possession of bilaterally symmetrical rhizomorphs, was under-represented (by *Chaloneria cormosa*: Pigg & Rothwell, 1983; Pigg, 1992). A future analysis will feature selected species of the extant genus *Isoetes* (including those generally assigned to *Stylites*), as well as the recently reconstructed fossil *Sporangiostrobus puertollanensis* (Wagner, 1989; Wagner, Coquel & Brousmitche, 1992).

(2) Selection of characters and partitioning into character states

Cladistic coding decisions are always a trade-off between several perceived advantages and disadvantages. A basically phenetic approach was taken to initial coding of characters for the present study; any recognizable and putatively homologous feature was described in detail, as objectively as possible (e.g. Sneath & Sokal, 1973). At this stage, no effort was made to eliminate covariance of characters that was suspected of being due to scalar hierarchies or to developmental correlation. These phenomena, and their relationship with homology (arguably the most fundamental and problematic of all cladistic concepts: e.g. Riedl, 1979; Patterson, 1982; Bryant, 1989; Roth, 1991), are discussed at greater length in later sections. Although methods have been developed to transform continuous (metric) and quasi-continuous (meristic) characters for cladistic coding (e.g. Archie, 1985; Chappill, 1989), such ‘soft’ characters are of questionable value in a cladistic context and were minimized in this study. Also excluded were all characters recognized as polymorphic (i.e. more than one state occurs within a species).

The uniformly binary coding simplified algorithmic analysis and the subsequent representation of character-state changes on cladograms. Each potentially multistate

character was split into two or more characters by additive binary coding (Brooks, 1984), thereby avoiding (1) the *de facto* down-weighting relative to binary characters that is inherent in unordered multistate characters, and (2) the *de facto* up-weighting that is inherent in fully ordered multistate characters. For some character suites, X-coding (Doyle & Donoghue, 1986) was used to weight against statistically feasible but biologically nonsensical changes of state, albeit at the expense of introducing additional missing values (and thereby analytical ambiguities) into the primary matrix. Future reanalysis will allow multistate coding and replace X-coding with character-state trees (e.g. Maddison & Maddison, 1992; Swofford, 1993).

(3) *Polarization of characters*

Polarization imposes a preferred direction of change among two or more states of a character. When two states are compared, the more primitive is said to be plesiomorphic and the more derived apomorphic. Of the three basic methods of polarization currently available, relative timing of appearance in the fossil record (Fisher, 1992) is here regarded as insufficiently reliable; the plant fossil record is too fragmented and knowledge of the species too restricted in time (cf. Fortey & Jefferies, 1982). This criterion does, however, provide a useful independent test when selecting among competing most-parsimonious topologies (e.g. Bateman *et al.*, 1992). Satisfactory application of the second method, the ontogenetic criterion (cf. Nelson & Platnick, 1981; Patterson, 1982; de Queiroz, 1985; Weston, 1988; Mabee, 1989; Williams, Scotland & Blackmore, 1990), requires direct observation of the ontogeny of individuals, and thus cannot in practice be applied to fossil plants (though in the following sections I strive to demonstrate that ontogeny can be inferred from fossils). There remains only the most popular method of character-state polarization and tree rooting, namely outgroup comparison (e.g. Maddison, Donoghue & Maddison, 1984). If expressed at its simplest and shorn of its philosophical trappings, this approach involves selecting one OTU as being the most primitive among the species coded, and assuming that all its character states are plesiomorphic (the logic is more complex and the results more ambiguous if more than one outgroup is chosen; Maddison *et al.*, 1984; Wiley *et al.*, 1991). The remaining OTUs are described as the ingroup.

Outgroup comparison is weakened by large morphological differences between the outgroup and ingroup (and among multiple outgroups), giving cause for concern as the procedure profoundly affects the resulting cladograms. Bateman *et al.* (1992) regarded the gap separating the rhizomorphic clade from the other lycopsid groups as too wide to confidently identify its sister-group. Within the coded rhizomorphic lycopsids, all four reproductively unsophisticated, bisporangiate-coned OTUs (the small-bodied genera *Oxroadia*, *Paurodendron* and *Chaloneria*, and the ulodendroid tree *Paralycopodites*) were screened as potential outgroups. However, they differed considerably in vegetative morphology and anatomy, and each possessed character states that were regarded as clearly apomorphic and thus inappropriate for an ideal outgroup. *Oxroadia gracilis*, by far the oldest OTU and (together with *Paurodendron fraipontii*) possessing the least complex vegetative anatomy, was eventually chosen as the basic model for constructing a *hypothetical* outgroup, which differed from *Oxroadia* in lacking both spore ornamentation and a ligule pit. Subsequent process-based interpretation of the cladograms suggests that *Paralycopodites* would have been a better model of vegetative plesiomorphy (see *Broader Implications*).

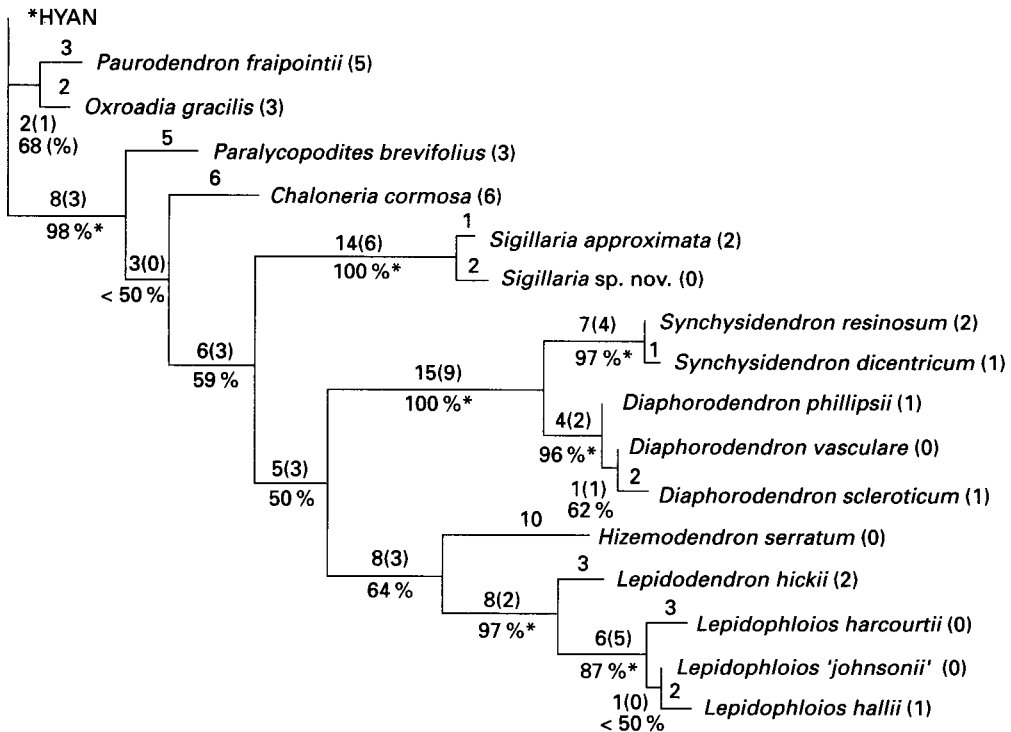


Fig. 1. Preferred most-parsimonious cladogram for 16 whole-plant species of fossil rhizomorphic lycopsid. Based on a data-matrix of 115 additive binary characters (80 phylogenetically informative) that contains 5% missing values. The fully resolved tree was rooted using a hypothetical ancestor (HYAN) based largely on *Oxroadia gracilis*, detected by branch-and-bound search, and optimized using the MinF algorithm of PAUP 3.1.1 (Swofford, 1993). 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 recovery of the node under 500 bootstrap replications (e.g. Felsenstein, 1985) is given below the line; figures are asterisked for the stronger nodes (> 80%). The number of species-level autapomorphic character states is given in parentheses following each binomial. (cf. Bateman *et al.*, 1992, fig. 6.)

(4) *The data matrix*

The 16 OTUs were coded for 115 binary characters (described in detail by Bateman *et al.*, 1992). Of these, eight proved to be coded uniformly among all ingroup OTUs ('holapomorphies') and 27 were apomorphic in only one ingroup OTU (autapomorphies). This left 80 truly synapomorphic characters to determine the phylogenetic relationships of the 16 OTUs analyzed. The resulting ratio of synapomorphic states over ingroup OTUs (5.0) greatly exceeds the minimum necessary to yield fully resolved topologies (*ca.* 2: Bateman, 1992*a, b*). Moreover, despite the user-imposed X-coding, the proportion of missing values in the matrix is low (5%), thereby minimizing serious ambiguities in tree-length calculations and in the positions of character-state transitions across specific topologies (Nixon & Davis, 1991; Platnick, Griswold & Coddington, 1991; Bateman *et al.*, 1992; Maddison, 1993).

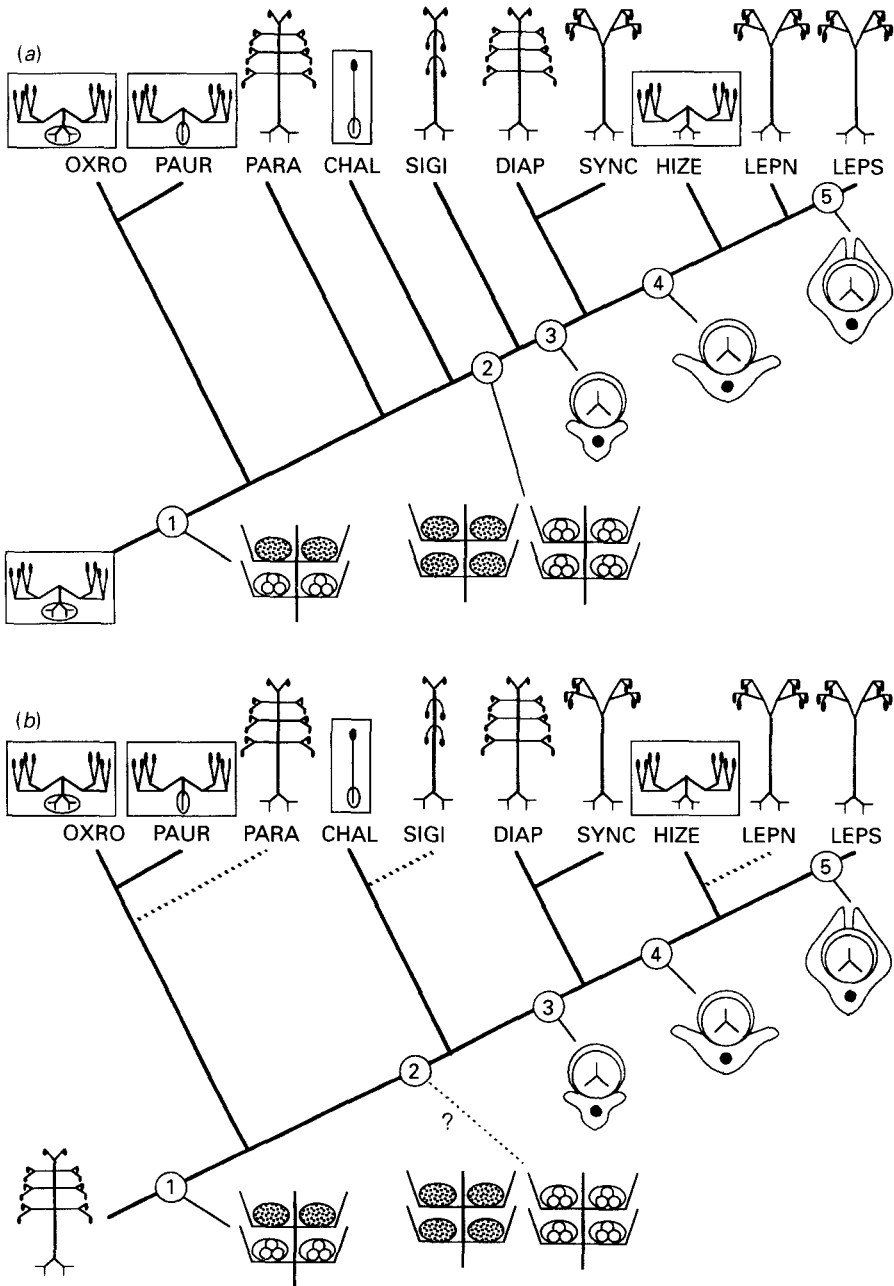


Fig. 2. (a) Preferred most-parsimonious cladogram depicted in Fig. 1, collapsed from 16 species to 10 monophyletic genera for ease of interpretation. (b) An alternative, user-imposed topology that was rooted using a *Paralycopodites*-like rather than *Oxroadia*-like hypothetical ancestor; differences from topology (a) are dashed. The growth architectures depicted in both topologies are the main focus of this paper. Unlike trees, small-bodied genera are boxed; within these boxes, ellipses denote compact, 'cormose' rhizomorphs. Also, key reproductive innovations particularly important in determining generic relationships are shown on the major axis: (1) plesiomorphic cone – ligulate and bisexual, resembling that of *Selaginella*, (2) segregation of megasporophylls and microsporophylls into separate unisexual cones, (3) reduction to a single functional megaspore, dispersal unit switched from megaspore only to megaspore plus megasporangium plus megasporophyll, (4) lateral expansion of sterile megasporophyll alations, (5)

(5) Parsimony analysis and optimization

Cladograms were generated by the now standard Wagner parsimony method, and definitive sets of most-parsimonious trees were identified using the branch-and-bound algorithm (Hendy & Penny, 1982). Species-level autapomorphies were excluded from tree-length calculations (Brooks, O'Grady & Wiley, 1986). The position of a specific character-state transition on a specific topology is fixed if the character is coded for all OTUs and changes only once across the tree. However, if the character changes more than once, due to parallel acquisition or loss (together termed homoplasy), more than one position is often possible for each change within the constraints of parsimony. Missing and polymorphic values cause similar positional ambiguities, which are practically (if not conceptually) resolved *a posteriori* using one of several optimization algorithms. Bateman *et al.* (1992) selected only one optimization algorithm, to help focus discussion. The chosen algorithm, MinF, concentrated character changes in the basal and terminal branches of the tree (Swofford, 1993). However, most of the architectural characters that are the focus of this study are highly homoplastic, so that optimization has a crucial effect on interpretations of their evolutionary pattern. Consequently, in the most recent analyses presented below (*Hypothesis Testing*), two algorithms have been used to determine and contrast the logical extremes of optimization: Acctran favours reversals over parallelisms, whereas Deltran favours parallelisms over reversals.

(6) Experimentation and the preferred most-parsimonious tree

The data-matrix compiled by Bateman *et al.* (1992) generated nine equally most-parsimonious topologies, of average overall homoplasy for a matrix of this size (cf. Archie, 1989*a, b*; Sanderson & Donoghue, 1989). Six of these reflected trivially ambiguous relationships of the three species of *Lepidophloios*, leaving three competing topologies that differ in the relative placements of *Paralycopodites* and *Chaloneria*. One of these was preferred as (1) it indicated homoplasy in a range of characters considered most vulnerable to parallel evolution or secondary loss, and (2) it proved more robust during subsequent experimental analyses of various sub-matrices.

That original topology is redrafted in Fig. 1 to show each branch length as proportional to the number of character-state changes occurring on that branch. Longer branches tend to be more robust, surviving modifications of the primary data-matrix, a property tested by the bootstrap figures that are also given in Fig. 1 (e.g. Felsenstein, 1985). The longest and most robust branches subtend genera; branches closer to the root of the tree that link genera or groups of genera are shorter. This pattern of large morphological discontinuities separating genera (all but *Oxroadia* are represented by species of Westphalian – that is mid-Late Carboniferous – age) is open to two contrasting interpretations. A gradualist model would require divergence of the genera far earlier than the Westphalian (Bateman *et al.*, 1992), whereas a saltational model, involving simultaneous, developmentally mediated changes in many characters, would allow later and more rapid diversification (Bateman & DiMichele, 1994).

enclosure of megasporangium by alations. Genera as follows: OXRO, *Oxroadia*; PAUR, *Paurodendron*; PARA, *Paralycopodites*; CHAL, *Chaloneria*; SIGI, *Sigillaria*; SYNC, *Synchysidendron*; DIAP, *Diaphorodendron*; HIZE, *Hizemodendron*; LEPN, *Lepidodendron*; LEPS, *Lepidophloios*. (Adapted from Bateman, 1992*a*, fig. 12; DiMichele & Bateman, 1992, fig. 15; Bateman & DiMichele, 1994, fig. 5.)

Where more than one species of a genus has been included in the analysis, the differences among those species are trivial and the genus is depicted as unquestionably monophyletic (indeed, two of the congeneric 'species' of *Lepidophloios*, *L. johnsonii* and *L. harcourtii*, have since been recognized as conspecific: W. A. DiMichele, oral comm., 1993). Moreover, with one minor exception within *Diaphorodendron*, all congeneric species share a single growth architecture. The robust taxonomy of the genera is no coincidence; although taxonomic revision was initiated prior to this analysis (e.g. DiMichele, 1979, 1981, 1983, 1985), it was completed *a posteriori*, using perceived monophyly and shared growth architecture as fundamental criteria for delimiting genera (Bateman & DiMichele, 1991; Bateman, 1992*a*; DiMichele & Bateman, 1992, 1994). Thus, rhizomorphic lycopsid growth architecture can be discussed at the less complex generic level without significant loss of information; this taxonomic reduction has been performed in generating Fig. 2*a*.

This procedure simplifies but does not alter the preferred topology. The resulting 'analytically correct' tree faithfully reproduces the most parsimonious relationships among the genera and the character-state changes resulting from rooting via an *Oxroadia*-like outgroup. However, a series of evolutionary interpretations based on the phylogeny (Bateman, 1991*b*; Bateman & DiMichele, 1991, 1994; Bateman, 1992*a, c*; Bateman *et al.*, 1992; DiMichele & Bateman, 1992, 1994) inexorably led to the conclusion that all four small-bodied genera (*Oxroadia*, *Paurodendron*, *Hizemodendron*, *Chaloneria*) had evolved from large-bodied arboreous ancestors by profound paedomorphosis. In this scenario, the decreases in body size and growth architecture had a domino effect (Table 1) on many other smaller scale features, causing the paedomorphic genera to be placed misleadingly close to the root of the 'analytically correct' cladogram and thereby depicting some potentially monophyletic groups as paraphyletic.

Given this interpretation, a more fundamental and controversial transformation of the phylogeny has also been performed in this paper. Fig. 2*b* presents an alternative, slightly less parsimonious, 'user-imposed' topology that was generated by artificially attaching each small-bodied genus to the reproductively most similar large-bodied genus. In each case, this involved the tree genus attached to the major axis of the cladogram immediately above its small-bodied putative descendant. It should be emphasized that the *ad hoc* simplification and restructuring of the topology mean that the alternative, user-imposed phylogeny of Fig. 2*b* is no longer a cladogram – rather, it is a tree that is broadly based on a cladogram but modified to incorporate process-based hypotheses. It is further modified by being rooted using a tree-sized, *Paralycopodites*-like outgroup.

Both topologies are discussed at much greater length below. However, neither can be satisfactorily interpreted without first considering the cast of characters – it is necessary to outline the reconstructed architecture, ontogeny and physiology of the rhizomorphic lycopsids.

III. GROWTH ARCHITECTURE AND ONTOGENY: GENERAL

(1) *Phylogenetic context of the rhizomorphic lycopsids*

The gradual elucidation of the palaeobiology of the rhizomorphic lycopsids, with many researchers each adding successive pieces to the puzzle, is one of the greatest

successes of twentieth century palaeobotany (e.g. Stewart & Rothwell, 1993). The most synthetic account to date (Phillips & DiMichele, 1992, *q.v.* for earlier references) focused on the best-known taxa – tree-sized (arboreous) fossil genera of Carboniferous age that are subtended by large, radially symmetrical stigmarian rhizomorphs. Although these remarkable trees have long been recognized as *bona fide* lycopsids (e.g. Grand'Eury, 1877; Williamson, 1893), comparisons have generally been made primarily with extant trees of the Coniferales and Angiospermales, using terminology developed specifically for these seed-bearing 'spermatophytes'. However, the arboreous lycopsids and spermatophytes share little more than a large body size and erect stem, which in turn necessitate bipolar growth, a robust centralized rootstock subtending the stem, and extensive production of structural support tissues. Each recent study has added to the lengthening list of fundamental differences in growth architecture, anatomy, ontogeny and physiology that separate lycopsid from spermatophyte trees (e.g. Phillips, 1979; Rothwell, 1984; DiMichele & Phillips, 1985; Rothwell & Erwin, 1985; Rothwell & Pryor, 1991; Phillips & DiMichele, 1992).

Far from being surprising, the number and magnitude of these differences is predictable when the rhizomorphic lycopsids and spermatophytes are placed in their phylogenetic context (Fig. 3), as they are separated by the maximum phylogenetic distance possible within the true vascular plants ('eutracheophytes'). Indeed, the 'lycophytes' (Lycopsida plus its extinct Devonian sister-group, the Zosterophylloids) are now most commonly identified as the earliest major lineage to diverge from the remainder of the eutracheophytes (Crane, 1990; Kenrick & Crane, 1991; Bateman, 1992*a*; Gensel, 1992; Hueber, 1992; Raubeson & Jansen, 1992), though attempts at molecular phylogenetic resolution of this question have thus far proved unsatisfactory (e.g. Manhart, 1993). The plesiomorphic growth form for the eutracheophytes, which characterizes most major groups that originated in the Late Silurian and Devonian (*ca.* 425–360 Ma), is undoubtedly unipolar. The most common unipolar architecture is a horizontal, indeterminate rhizome that periodically emits determinate modules: negatively geotropic aerial axial systems and positively geotropic adventitious roots (e.g. Callaghan *et al.*, 1986).

Eventually, a few 'pre-ferns' such as the Devonian-Carboniferous cladoxylaleans and, later, *bona fide* ferns such as the Marattiales, Cyatheaceae and Dicksoniaceae experimented with increased body size and upright growth, supported by limited and poorly differentiated secondary tissues and/or basally concentrated adventitious roots. However, a *centralized bipolar* upright growth form became dominant only in the most derived portion of the non-lycophyte clade, namely the progymnospermopsid-spermatophyte clade ('lignophytes': Fig. 3). Bipolar growth is programmed into the earliest stages of lignophyte ontogeny (the familiar shoot and root apices of spermatophyte embryogeny), leading to a specialized, repeatedly branched, subterranean rootstock with peripheral axes that produce abundant root-hairs to increase absorbance. In the aerial parts of the plant, wood and bark are generated by an indeterminate bifacial cambium, and photosynthetic activity is concentrated in large, many-veined leaves. Meristems are more numerous and more diverse, including axillary buds capable of long-term dormancy (e.g. Rothwell, 1994; Trivett, 1993). Although the rhizomorphic lycopsids originated at about the same time as the lignophytes (Mid- to Late Devonian), they acquired the tree habit by a radically

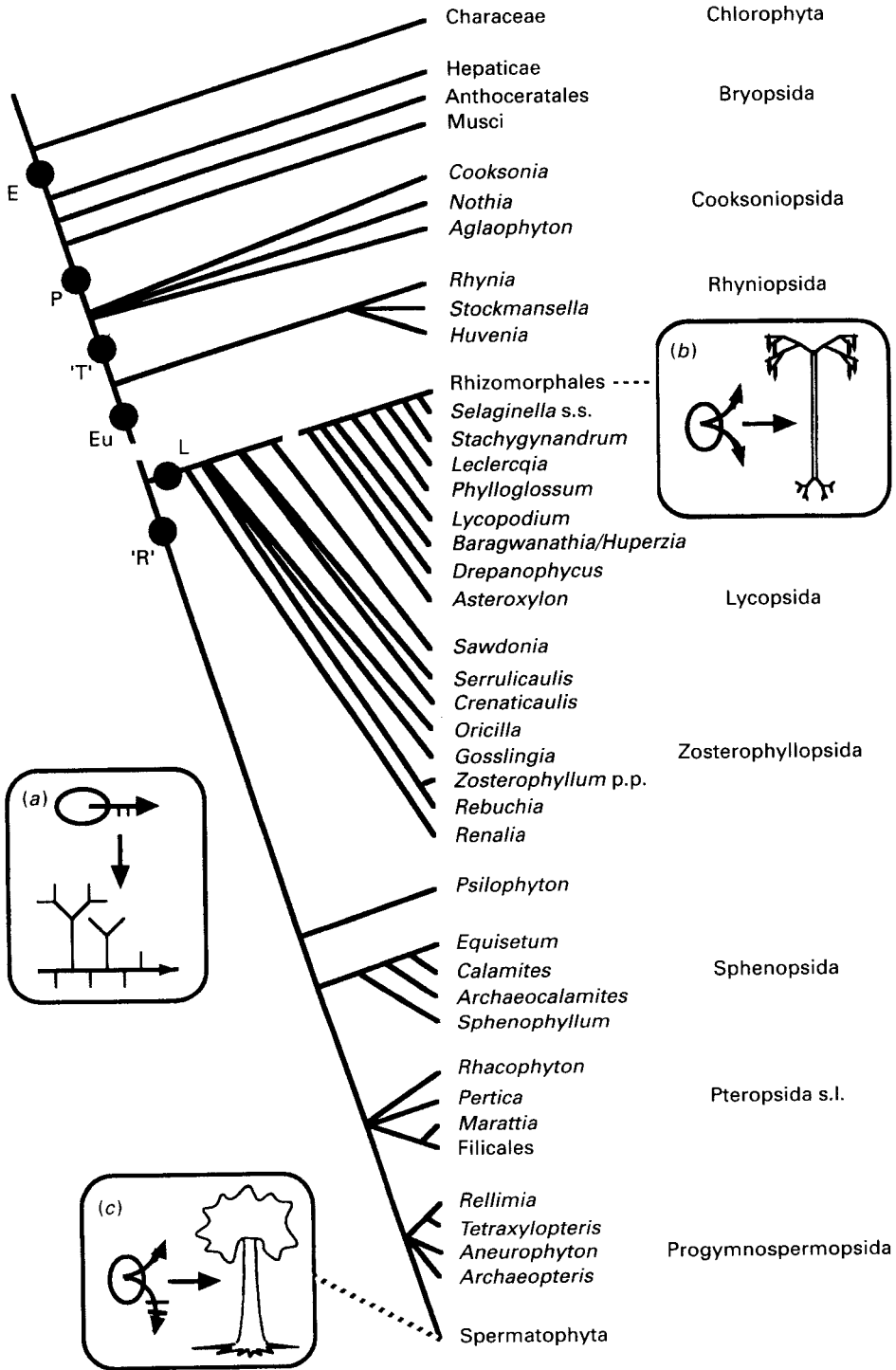


Fig. 3. Composite phylogeny of supraspecific taxa representing many major groups of bryophytic and pteridophytic land-plants. This illustrates the independent evolution of distinct modes of bipolar growth in the progymnospermopsid-seed-plant (c) and lycopsid (b) clades, in both cases from the plesiomorphic

different evolutionary route (cf. Corner, 1949, 1954; Carlquist, 1962; McMahon, 1973; Mabblerley, 1974; Borchert, 1976; Bostrack, 1993; Niklas, 1993*a, b*).

(2) *Architecture, ontogeny and physiology inferred from anatomy*

Predictably, all zosterophylloids and most lycopsids share the plesiomorphic unipolar mode of growth. The bipolar 'rhizomorphic syndrome' first appeared in Late Devonian lycopsids, apparently altering so many characters simultaneously (i.e. without intermediate forms) that the unipolar sister-group of the bipolar rhizomorphic clade has yet to be satisfactorily identified (cf. Crane, 1990; Bateman, 1992*a*; Gensel, 1992; Hueber, 1992). Bipolar growth typically involved an initial dichotomy of the embryonic vasculature, analogous to that in spermatophytes but essentially by shoot–shoot rather than shoot–root dichotomy (Phillips, 1979; Stubblefield & Rothwell, 1981; Rothwell & Erwin, 1985; Rothwell & Pryor, 1991; Phillips & DiMichele, 1992). Thus, the aerial axial system was, to a large extent, replicated in the subterranean system.

Determining the precise degree of developmental parallelism between the two poles – the aerial and subterranean systems – is hampered by our inability to observe directly the ontogeny of fossils and by the apparent non-preservation of demonstrably intermediate (post-embryonic but pre-reproductive) growth stages of the larger-bodied rhizomorphic lycopsids. Nonetheless, positional homologies of shoot and root modules strongly suggest similar genetic and epigenetic controls.

These issues highlight a further phylogenetic conundrum – one that exists within the rhizomorphic lycopsids, and concerns the relationship between genera with radially symmetrical, often branched rhizomorphs ('lepidodendraleans' *sensu lato*) and genera with bilaterally symmetrical, unbranched rhizomorphs ('isoetaleans' *sensu lato*). A broad cladistic analysis of the lycopsids suggested that they are discrete sister-groups (Bateman, 1992*a*, fig. 16*a*), whereas a more detailed analysis confined to the rhizomorphic clade suggested that the 'isoetaleans' are nested well within (and thus evolved from) the lepidodendraleans (Bateman *et al.*, 1992, fig. 6; the isoetaleans are represented by *Chaloneria* in Figs 1 and 2 of this study). This contradiction can be explored using extrinsic evidence, specifically the relative timing of appearance of clades in the fossil record, and embryogenic comparison. Putatively bilaterally symmetrical rhizomorphs occur in the Famennian *Lepidosigillaria* (e.g. Grierson & Banks, 1963) and an unnamed isoetalean (Chitaley, 1982), and the Strunian *Cyclostigma* (Chaloner, 1984); they have also been well described for the Tournaisian *Protostigmaria-Lepidodendropsis* (Jennings, Karrfalt & Rothwell, 1983). The earliest well described radially symmetrical rhizomorph – that of *Oxroadia* (Long, 1986; Bateman, 1992*a*) – is also Tournaisian. Thus, the fossil record tentatively suggests that bilateral

unipolar condition (*a*). Near-basal clades labelled include the embryophytes (E), polysporangiophytes (P), 'tracheophytes' ('T'), eutracheophytes (Eu), lycophytes (L) and the remaining eutracheophytes ('R'). Note that the bipolar clades are the two most derived groups within the two major clades of eutracheophytes. Note also that this phylogeny already requires revision; for example, the illustrated position of *Cooksonia* is challenged by the recent discovery that it possessed vascular tissue. (Sources of partial cladograms – bryophytes and rhyniophytes: Kenrick & Crane, 1991, fig. 26; non-rhizomorphic lycopsids: Bateman, 1992*a*, fig. 16; other groups: Crane, 1990, fig. 2. Bateman's (1992*a*, fig. 16*a*) treatment of the lycopsids is consistent with Gensel (1992, fig. 13) but not Crane (1990, fig. 1). Crane's (1990, fig. 2) treatment of the zosterophylloids is not consistent with Gensel (1992, fig. 13), but his treatment of the sphenopsids is consistent with Bateman (1991*c*, fig. 14*a*).

rhizomorphs antedate radial rhizomorphs (Rothwell & Erwin, 1985; Scheckler, 1986; Bateman *et al.*, 1992).

However, this interpretation is contradicted by developmental evidence. Firstly, the radially symmetrical branched rhizomorph most closely resembles the putatively homologous shoot system (Rothwell & Erwin, 1985). Also, the Lower Cretaceous isoetalean *Nathorstiana* undergoes a transition from radial to bilateral rhizomorph symmetry during ontogeny (Karrfalt, 1984*a*); in von Baerian terms this observation implies that the bilateral condition is derived relative to the radial condition. Rothwell & Erwin (1985, fig. 18) attempted to correlate rhizomorph symmetry with embryogenic patterns. They noted that the embryo of the radially symmetrical tree *Lepidophloios-Lepidocarpon* underwent an acutely angled primary vascular dichotomy within the megaspore wall, yielding sparsely vascularized stem and rhizomorph initials (e.g. Phillips, 1979) (Fig. 4*a*). They contrasted this pattern with axial bipolarity in the embryo of the bilaterally symmetrical pseudoherb *Isoetes*, which is preceded by the development, and obtusely angled vascularization, of the first root and first leaf (Stubblefield & Rothwell, 1981; Karrfalt, 1984*b*). However, this formerly reliable positive correlation between embryogeny and symmetry is contravened by *Oxroadia*, which has a radially symmetrical rhizomorph but an embryological vasculature resembling that of the bilaterally symmetrical *Isoetes* (Bateman, 1992*a*). Rather than the profound phylogenetic dichotomy envisaged by Rothwell and co-workers (Stubblefield & Rothwell, 1981; Rothwell & Erwin, 1985; Stewart & Rothwell, 1993), the earlier emphasis of the first-formed appendages in *Isoetes* and *Oxroadia* may simply reflect the small size of the megaspores relative to the larger *Lepidophloios*, which is better provisioned for immediate axial expansion.

Overall, it seems better to weight the combined phylogenetic and developmental evidence over the sparse fossil record (Bateman *et al.*, 1992, fig. 3). This would imply that the bilateral rhizomorph, and probably also early embryological rootlet-leaf vascularization, are derived characteristics.

In *Lepidophloios-Lepidocarpon*, rapid radial expansion of the stem and rhizomorph apical meristems followed the primary embryonic dichotomy as resources were shared between the first-formed leaves and rootlets, creating the 'transition zone' that links the two axial systems. Two closely spaced, isotomous apical divisions then produced the radially symmetrical stigmarian rhizomorph (thereby severely disrupting the pith). Both the stigmarian branches and stem possessed large, domed, determinate apical meristems that emitted in tight helices more-or-less terete, hispid, monarch appendages (undivided microphylls and often once-divided rootlets respectively; Fig. 4*b*). Exarch centripetal maturation of the primary xylem was followed by rapid development of secondary xylem immediately behind the apical dome. Secondary tracheids were fairly narrow (*ca.* 100 μm), and in *Paralycopodites* offered a modified specific conductance equivalent to that of a typical modern woody angiosperm (estimated at $117 \pm 20 \text{ m}^4 \text{ MPa}^{-1} \text{ S}^{-1} \times 10^{-7} \text{ cm}^{-2}$ by Cichan, 1986). However, the wood cylinder was proportionately narrow, thus offering efficient water conduction but little structural support. The support role was largely fulfilled by the external cylinder of secondary cortex, which formed a relatively rigid, decay- and desiccation-resistant periderm (DiMichele & Phillips, 1985; Speck, 1991; Speck & Vogellehner, 1992). Continuity of the narrow leaf traces through the wood and periderm suggest that the periderm also

formed rapidly and largely centripetally. Evidence for a peridermal bifacial cambium varies among families, being strongest for the Diaphorodendraceae (DiMichele, 1979, 1981, 1985; DiMichele & Bateman, 1992; Phillips & DiMichele, 1992), but the wood cambium appears uniformly unifacial (Eggert & Kanemoto, 1977; Cichan, 1985). Xylem maturation differed between the stem plus aerial branches (exarch, medullated protostele or siphonostele) and the rhizomorph (arguably the product of a primary thickening meristem, with wide rays dissecting the wood into wedges to give the false impression of a dictyostele). Nonetheless, as growth proceeded in the branches of both the stem and the rhizomorph, the apical dome gradually increased in diameter (reflected in increasing medullation), whereas the amounts of wood and periderm decreased (Figs 4c, 5 left: Walton, 1935; Eggert, 1961; Frankenberg & Eggert, 1969). Rothwell & Pryor (1991) plausibly suggested that these observations imply a significant modification in the behaviour of the apical meristems during ontogeny. Beyond the transition zone, the first-formed unifacial vascular cambium behaved as a primary thickening meristem, analogous to those of monocotyledonous angiosperms such as palms (DeMason, 1983; Tomlinson, 1990).

Indeed, other aspects of rhizomorphic lycopsid ontogeny parallel those of palms (Figs 4a-c vs. d-f). Common sense suggests that stem elongation was preceded by extensive development of the rhizomorph, to provide firm anchorage and a reliable nutrient supply. Subsequent stem growth was rapid and confined to a narrow zone immediately below the huge apical meristem. Only limited radial expansion could be accommodated by the rhombohedral leaf-bases cladding the stem, either by passive inter-cushion fissuring or by active inter- or sub-cushion cortical expansion (DiMichele & Phillips, 1985). Similarly, neither leaf bases nor leaves were capable of substantial post-meristematic enlargement. All reconstructed Carboniferous lycopsid trees underwent some aerial branching, either lateral and highly anisotomous (Fig. 4i) or terminal and near-isotomous (Fig. 4g). This isotomous terminal crown also generally contained anisotomous branches (W. A. DiMichele, lit. comm., 1993). Branching inevitably yielded daughter meristems of lesser diameter than the parent meristem (Andrews & Murdy, 1958; Eggert, 1961), eventually exhausting the determinate apical meristem. Bateman (1992a) argued that exhaustion occurred upon attaining a predetermined minimum size, though DiMichele (1981) noted that putative ultimate branches of *Diaphorodendron* and *Lepidophloios* diminished to very few rows of tracheids. Leaf and leaf-base size diminished in tandem with axial diameter (Chaloner & Meyer-Berthaud, 1983). In contrast, meristematic diminution in the rhizomorph was less rapid (i.e. occurred along a shallower developmental gradient: Rothwell & Pryor, 1991).

The least intuitive feature of the rhizomorphic lycopsids is their lack of secondary phloem, a severe physiological constraint. The apparent paucity and radial distortion of primary phloem in the transition zone imply that the rhizomorph and aerial axes endured near-independence in terms of photosynthate transport potential, prompting suggestions that the rootlets may have been photosynthetic (Phillips & DiMichele, 1992; Stewart & Rothwell, 1993). Admittedly, such photosynthetic activity would have been inefficient, given the small proportion of rootlets emergent from the substrate and the need to rely on CO₂ in the rhizosphere. Certainly, many morphological features indicate that photosynthetic activity was dispersed throughout the aerial parts of the plant. Although the leaves were long (both leaves and rootlets could exceed 50 cm: e.g.

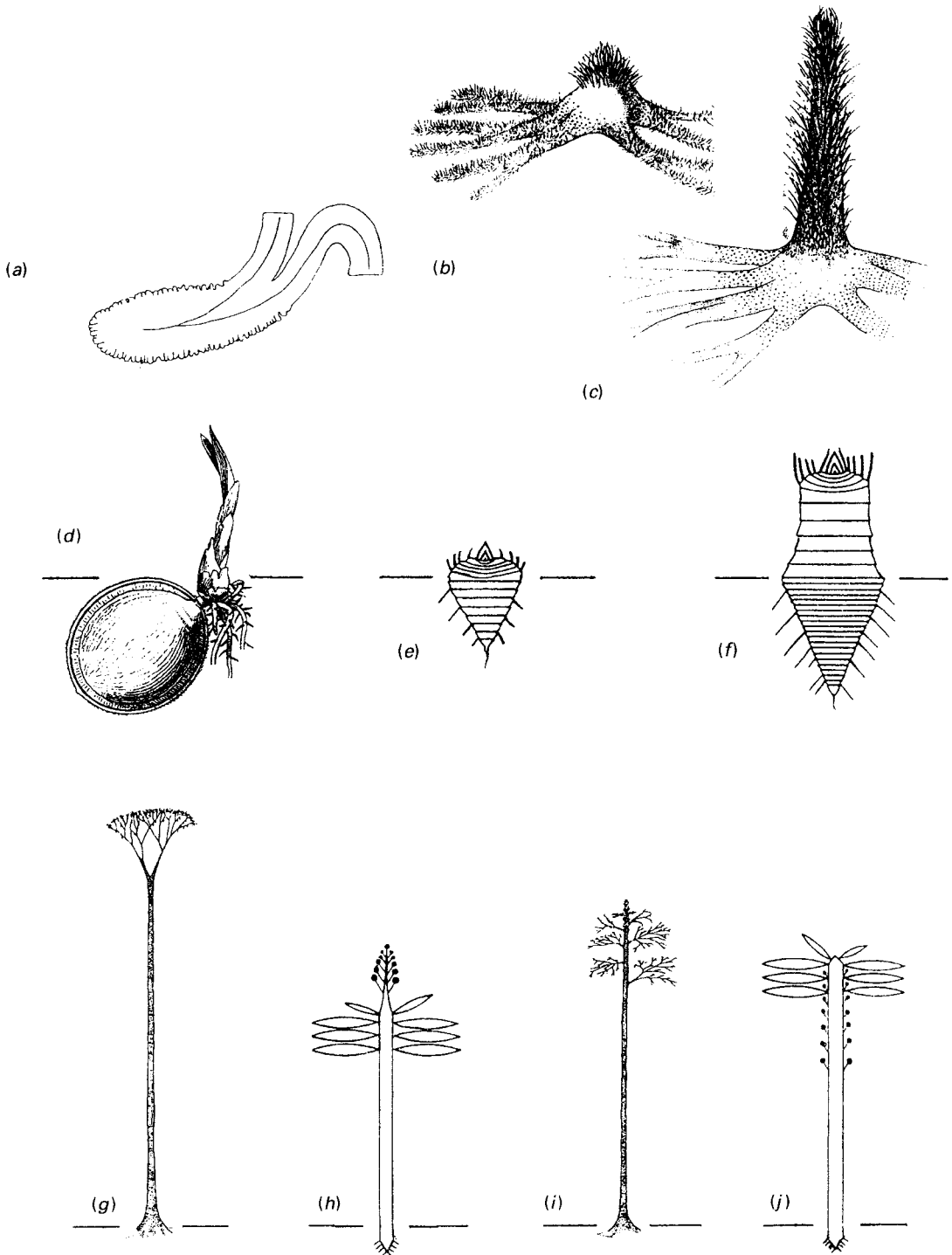


Fig. 4. Comparison of ontogenies and life histories of typical rhizomorphic lycopsid and palm trees. (a-c) Megaspore germination, rhizomorph establishment and early stem elongation respectively of typical lycopsid tree. (d-f) Seed germination, rootstock establishment and early stem elongation respectively of

Kosanke, 1979), their acicular, near-terete morphology greatly limited their light-trapping potential. Moreover, leaves were shed during ontogeny, leaving distinct 'abscission scars' in the more derived tree genera. The presence of stomata on the more persistent leaf cushions suggests that they were capable of continued photosynthesis following leaf loss (e.g. Thomas, 1977). Branches resulting from anisotomies also tended to be shed as units (Jonker, 1976), reflecting their primary function of rapid cone production and propagule dispersal rather than photosynthesis *per se* (DiMichele & Phillips, 1985; Phillips & DiMichele, 1992). The highest photosynthetic activity probably occurred where it was most needed – around the apical meristem, aided by the unusually high leaf densities, and in the cones, aided by the unusually broad distal laminae of the sporophylls (Phillips, 1979; Phillips & DiMichele, 1992).

The aerenchymous nature of the stigmarian rootlets and radial air channels (lacunae and parichnos) in the leaves and/or cortex indicate a need for local aeration, perhaps to maintain an optimal $O_2:CO_2$ balance. The xylary system may also have facilitated transfer of an inferred CO_2 surplus from the rhizomorph to the stem, though this process would have been inefficient and the amount of carbon fixed would have been low (J. A. Raven, lit. comm., 1993). Phillips & DiMichele (1992) argued that CAM-type photosynthesis is probably characteristic of the rhizomorphic lycopsids, given that they possess several characters usually associated with CO_2 conservation. CAM plants have temporal separation of nocturnal 4-carbon and diurnal 5- to 3-carbon pathways, with stomata closed during the day to increase CO_2 concentration. CAM characterises many groups that prefer high-stress (often xeric) habitats (Spicer, 1989), and has been demonstrated in several extant isoetales (e.g. Raven *et al.*, 1988). Moreover, the areally restricted, often sunken stomata, near-terete undivided leaves, and armoured, fibrous periderm together appear xeromorphic, implying a need to limit evapotranspiration despite the typically wetland habitats of the plants. However, preliminary studies of tree lycopsid carbon isotopes indicate the more common, mesic, C_3 metabolism (Raven & Spicer, 1993). Irrespective of metabolic details, the plants give an overall impression of considerable physiological conservatism.

Recently, it has become fashionable to describe the arboreal lycopsids as 'giant herbs' (Rothwell & Pryor, 1991; Phillips & DiMichele, 1992). The trunks could exceed 1 m in basal diameter and 35 m in height, with dichotomous crowns and rhizomorphs both reaching 12 m in diameter. The weight:volume ratio was well below that of any similarly-sized extant spermatophyte – the main benefit of using circumferential periderm for support, restricting wood to a transport role, and packing the rest of the axial interior with unligified tissues composed largely of thin-walled parenchyma (Bierhorst, 1971; Mosbrugger, 1990; Speck & Vogellehner, 1992). DiMichele & Phillips (1985) argued that such 'cheap construction' probably allowed rapid maturation, with a life cycle measured in years rather than decades (contrary views, measured in centuries, have also been expressed: e.g. J. M. Robinson, lit. comm., 1989). However, there were adaptive prices to be paid for cutting these structural corners. Firstly, the high degree of physiological independence inferred for the

typical palm tree. (g-h) Comparison of mature monocarpic lycopsid and palm respectively. (i-j) Comparison of mature polycarpic lycopsid and palm respectively. (Sources – a: Rothwell & Stubblefield, 1981; b, c, g, i: Phillips & DiMichele, 1992; d: Gifford & Foster, 1989; e, f, h, j: Tomlinson, 1990.)

individual growth modules borders on the symbiotic-colonial. Secondly, the rhizomorphic axes penetrated the substrate only shallowly, dichotomized infrequently, and produced rootlets that branched at most only once and lacked *bona fide* root hairs and caps (but for a root-cap analogue see Rothwell & Erwin, 1985). Not surprisingly, the efficiency of these organs for penetrating well consolidated substrates, anchoring the plant in poorly consolidated substrates, and obtaining some key nutrients from water-unsaturated substrates, have all been questioned (DiMichele & Phillips, 1985; Thomas, 1985; Phillips & DiMichele, 1992). Significant pre-reproductive mortality is suspected, though this inference is inconsistent with the rarity of preservation of intermediate growth stages (cf. Kosanke, 1979). In this context, quantitative estimates of anchorage potential are desirable. The trees in particular seem to be prime candidates for mycorrhizal associations (Raven *et al.*, 1988), but mutualistic fungi have not been detected in any of the abundant *in situ* stigmarian rootlets that penetrate Westphalian petrified peats.

To summarize, many morphological and ontogenetic similarities are evident between the two main developmental poles (rhizomorph and aerial) of the rhizomorphic lycopsids. Homologies are relatively easily identified among organs, both between and within poles, because they have been modified from the presumed plesiomorphic condition only sufficiently to adequately fulfil their respective tasks: examples include stigmarian versus crown branches, rootlets versus microphyllous leaves, microphyllous leaves versus sporophyll distal laminae, leaf bases versus sporophyll pedicels, and cone axes versus ultimate vegetative axes. The frequent use of similar growth modules for different functional roles (Bateman & DiMichele, 1991; Bateman, 1992*a*; Bateman *et al.*, 1992), lack of major phase changes (Poethig, 1990), and somewhat idiosyncratic physiology, together imply an unusually high degree of what is here termed *architectural parsimony*: the plants made the most of the developmental units that they already possessed. This Heath Robinson approach to architectural change also implies that the rhizomorphic lycopsids were not adept at evolving genuinely novel module types. If this relative simplicity extended to developmental control, ontogenetic trajectories (and thereby growth architectures) could be unusually easily modified by mutation. Only the initial embryonic vascular dichotomy (including the modified embryogeny of small-bodied genera) appears to have been an unbreakable evolutionary constraint. The crux of the rhizomorphic syndrome, its suppression would have generated economically inviable progeny that lacked either root or shoot systems.

The remainder of this paper develops evolutionary hypotheses based on the above assumptions.

IV. GROWTH ARCHITECTURE AND ONTOGENY: SPECIFIC CASES

(1) *Growth modules and architectures*

Determinate, modular growth distinguishes the rhizomorphic lycopsids from most other tracheophyte lineages; indeed, vertebrate ontogeny provides a more apt comparison (e.g. Harper, Rosen & White, 1986), even though vertebrates are more holistically integrated (Bateman & DiMichele, 1994). This high degree of developmental programming suggests that both body size and body plan ('bauplan' of Meeuse, 1986; 'architectural model' of Hallé, Oldemann & Tomlinson, 1978; see also McMahan, 1975; Tomlinson, 1982; Tomlinson, Sattler & Stevens, 1984; Hallé, 1986;

Mosbrugger, 1990; Mattheck, 1991) were largely genetically imposed. This assumes a broad definition of genetic control, encompassing both pleiotropic responses (one gene directly effects several distinct developmental events: Table 1) and epigenetic interactions (gene expression is modified by the internal environment of the developing organism). There was relatively little potential for opportunistic modification of growth architecture by ecophenotypic effects (gene expression is modified by the external environment of the developing organism) or chance factors. In other words, the conceptual architectural model was unusually faithfully reproduced in the actual growth habit (Bateman & DiMichele, 1991).

After surveying rhizomorphic lycopsid growth architectures, DiMichele & Bateman (1989) and Bateman & DiMichele (1991) recognized four fundamental, large-scale growth modules (axial units of determinate growth: Fig. 5). Here, the four units are recircumscribed and formally defined:

(A) rhizomorph: the entire axial system generated by the positively geotropic product of the initial embryonic vascular dichotomy.

(B) stem: that part of the negatively geotropic product of the initial embryonic vascular dichotomy that precedes the first isotomous division of the stem apical meristem.

(C) terminal crown: non-repetitive, isotomous aerial axial branch system terminating the stem and initiated by the first isotomous division of the stem apical meristem.

(D) lateral branches: repetitive aerial axial systems, each initiated by a strongly anisotomous division of the stem apical meristem (cauline lateral branches: D₁) or of the apical meristems of its isotomous products in the crown (crown lateral branches: D₂).

Lateral branches, the most problematic modules, require further discussion (W. A. DiMichele, lit. comm., 1993). Unlike other module types they are positionally flexible; they can be expressed either before or after the first isotomy of the stem apical meristem. Those situated in the crown (D₂) tend to be smaller than those attached directly to the stem (D₁); they are distinguished in this paper as two submodules that are structurally but not positionally homologous. Both submodules invariably bear reproductive cones; indeed, in *Sigillaria* the lateral branch unit consists only of a cone plus a peduncle (DiMichele & Bateman, 1989; Bateman *et al.*, 1992). The homology of unbranched peduncles with extensively dichotomous lateral branches is supported by the strong (if circumstantial) evidence that no known rhizomorphic lycopsid produces both extensive lateral branches and peduncles directly on the stem (W. A. DiMichele, lit. comm., 1993).

Of the four modules, rhizomorph and stem (i.e. the first-formed axial organs of root and shoot respectively) are essential components of rhizomorphic growth and thus are ubiquitous among the genera. In contrast, both types of branch are optional, though most genera possess at least one branch type. All modules vary greatly among genera in relative and absolute size, frequency of branching (except stems, which by definition exclude any lateral branches and ontogenetically precede any terminal branches), and development of secondary tissues. Thus, several different morphs are recognized within each of the four basic categories of module (Fig. 5).

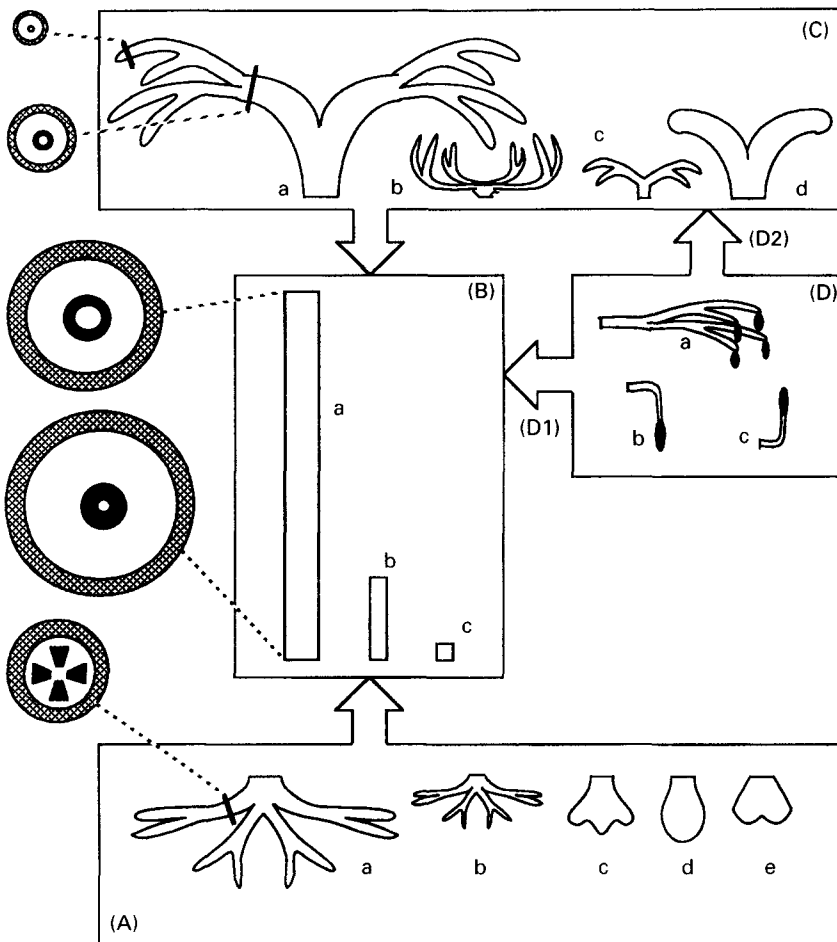


Fig. 5. 'Identikit' scheme for rhizomorphic lycopsid architecture, illustrating variation among the ten study genera in the morphology of the four main growth modules: (A) rhizomorph; (B) stem; (C) isotomous crown branches; (D) lateral branches (D₁ = cauline lateral branches, D₂ = crown lateral branches). Organs are not shown to scale. The modular composition of each genus is listed in the order (A)-(B)-(C)-(D₁)-(D₂): *Oxroadia*, ccb-c; *Paurodendron*, dcba; *Paralycopodites* and *Diaphorodendron*, aacaa; *Chaloneria*, eb---; *Sigillaria*, aadbb; *Synchysidendron*, *Lepidodendron* and *Lepidophloios*, aaa-a; *Hizemodendron*, bcb-a. Also shown on the left are transverse sections of axes of the dominantly crown-branched tree *Lepidophloios* (modified after Walton, 1935), illustrating ontogenetic variations in tissue composition; periderm is cross-hatched and wood is solid black.

(2) Architectures and specific ontogenetic trajectories

The ten analysed genera of rhizomorphic lycopsids can be regarded as 'identikit' composites, each possessing specific morphs of two or more of the four basic modules (Fig. 5). However, this perspective is too static and atemporal; by considering only mature individuals, valuable ontogenetic information is ignored. It is preferable to depict the ontogenetic trajectories of individual modules on bivariate plots of time versus size (note that both axes of Figs 6 and 7 are of necessity crude estimates of relative values, scaled arithmetically). Each modular trajectory is bounded by the times

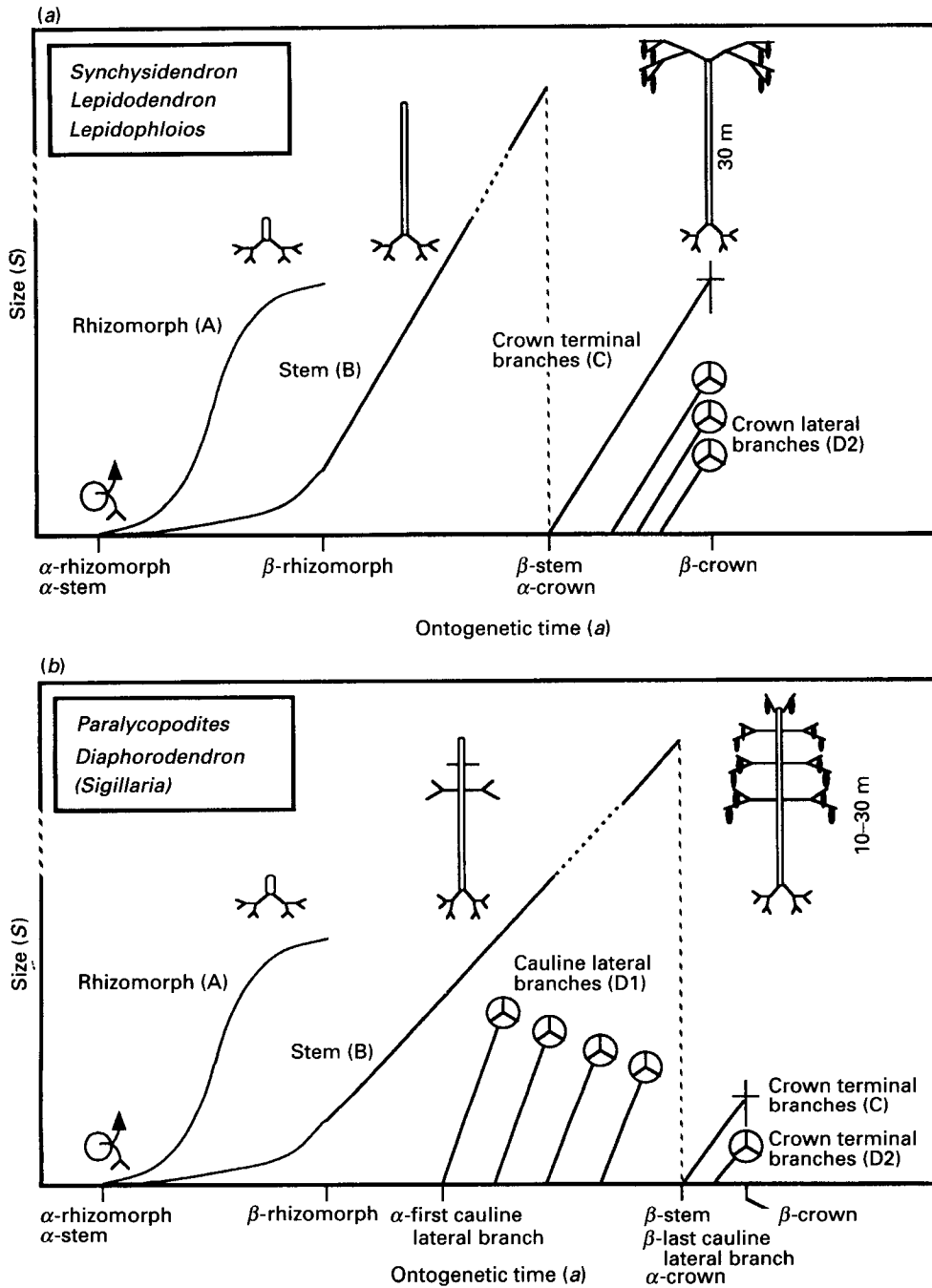


Fig. 6. Inferred allometric trajectories of ontogenetic time versus size for growth modules of (a) the dominantly crown-branched trees *Synchysidendron*, *Lepidodendron* and *Lepidophloios*, and (b) the dominantly laterally-branched trees *Paralycopodites*, *Diaphorodendron*, and (with undivided cauline lateral branches) *Sigillaria*. α , onset of module growth; β , offset of module growth; bipolar megaspore indicates germination; triradiate spore indicates sporogenesis; cross indicates death of the sporophyte.

of onset and offset of growth. Also indicated are key points in the life history of the entire sporophytic individual: germination, sporulation, and death.

All four plots in Figs 6 and 7 begin with the simultaneous onset of growth in the rhizomorph and stem that immediately followed megaspore germination. Early resource allocation was concentrated in the rhizomorph, which is interpreted as accomplishing most of its growth prior to appreciable upward growth of the stem. Although their early trajectories are similar, the four main architectures then diverge ontogenetically:

(A) As described by DiMichele & Phillips (1985) and Phillips & DiMichele (1992), the dominantly crown-branched trees *Synchysidendron*, *Lepidodendron* and *Lepidophloios* (Fig. 6a) produced large, repeatedly and isotomously branched 'stigmarian' rhizomorphs. The stem then grew rapidly (in effect it 'bolted') to produce a 'telegraph pole', which greatly exceeded the rhizomorph in size and lacked cauline lateral branches. At an approximately predetermined height the domed apical meristem divided isotomously, terminating stem growth and initiating extensive crown development. Repeated lower-order isotomous branching in the crown was followed by anisotomous divisions to produce crown lateral branches. Together these axial systems generated an extensive physical framework, transient and with poorly developed secondary tissues, to display the abundant reproductive cones. Because crown production exhausted the products of the stem apical meristem, reproduction was rapid and immediately preceded the death of the individual (monocarpism). Analogous life histories occur in some palms (cf. Figs 4g, h).

Architectural variation within this group was limited to the degree of anisotomy in the lower-order branches of the crown, though all three genera produced linear arrays of cones by repeated, strongly anisotomous branching. Note, however, that lateral branches were invariably restricted to the crown; they were not expressed directly on the stem.

(B) The smaller-bodied genera *Hizemodendron*, *Oxroadia* and *Paurodendron* were composed of the same four growth modules: rhizomorph, stem, terminal branches and crown lateral branches (Fig. 7a). Cauline lateral branches were absent, as in architecture (A). However, the overall body size was much smaller and the rhizomorph-stem assembly was more compact, reflecting the more closely-spaced isotomous divisions of the apical meristems. The precocious division of the stem meristem caused the crown to develop close to the soil surface and altered the relative sizes of the modules; the stem more-or-less equalled the rhizomorph, and both were greatly exceeded by the crown. Although smaller and recumbent, the branching pattern and function of the crown paralleled those of architecture (A): cheap construction, rapid growth, reproduction, and death. Such unintuitive growth forms, which combine small body size with secondary thickening, have been termed pseudoherbaceous (Bateman & DiMichele, 1991; Bateman, 1992a).

There was considerable variation in architectural detail, both among and within the three pseudoherbaceous genera. In general, *Hizemodendron* had the largest body size and *Paurodendron* the smallest. Lower-order branching in the crown was dominantly isotomous only in *Oxroadia*, where cauline lateral branching was probably restricted to the cone peduncles (cf. Bateman, 1992a). In contrast, cauline lateral branches, each probably bearing several cones, dominated the crowns of *Paurodendron* and *Hize-*

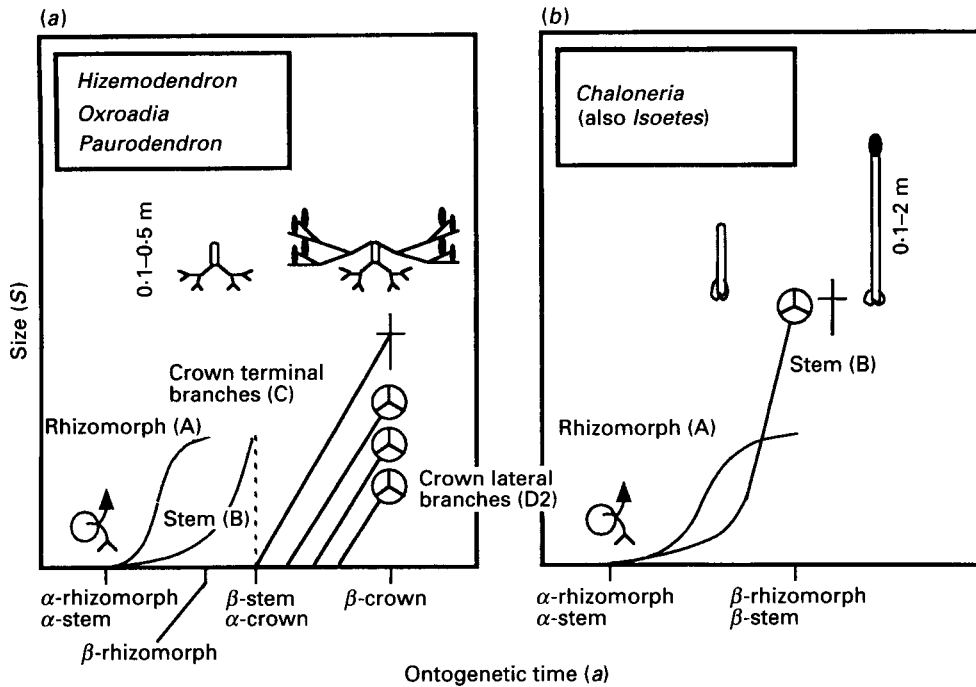


Fig. 7. Inferred allometric trajectories of ontogenetic time versus size for growth modules of (a) the small-bodied pseudoherbs *Hizemodendron*, *Oxroadia*, and (with unbranched rhizomorph) *Paurodendron* and (b) small-bodied unbranched shrubs such as the isoetalean *Chaloneria*.

modendron. More important differences concern rhizomorph architecture. That attributed to *Hizemodendron* resembled a small stigmarian rootstock, having repeatedly branched vasculature surrounded by deeply lobed cortex (Bateman & DiMichele, 1991). *Oxroadia* maintained a similar pattern of vascular division to stigmaria but its cortex was only shallowly lobed (Long, 1986; Bateman, 1992a). In contrast, neither vasculature nor cortex branched in the rhizomorph of *Paurodendron*, though the corm-like product retained the radial symmetry of the other genera (Phillips & Leisman, 1966; Rothwell & Erwin, 1985).

(C) Like architecture (A), the relatively complex architecture (C) is restricted to tree-sized genera possessing stigmarian rhizomorphs (*Paralycopodites*, *Diaphorodendron*, *Sigillaria*; Fig. 6b). Early growth stages resembled those of the dominantly crown-branched genera, though their stems contained more secondary tissue, sequestering photosynthate and therefore indicating less rapid development (Phillips & DiMichele, 1992). However, once stem growth was well underway the apical meristem progressively 'pinched off' cauline lateral branches by strongly anisotomous divisions. Except for *Sigillaria*, the lateral branches underwent repeated dichotomies of similar degrees of inequality, thereby forming sufficient 'daughter' meristems for extensive cone production. As each cauline lateral branch was an integral determinate axial system, they are plotted individually in Fig. 6b. In most of the species that possessed them, cauline lateral branches were ephemeral, containing little secondary tissue and being shed as cohesive units following cone maturation. The branches developed

progressively up the stem, together allowing a prolonged (polycarpic) reproductive phase. Cauline lateral branch production is assumed to have gradually diminished the stem apical meristem, so that the terminal phase of dominantly isotomous crown-branching was small-scale and heralded death. Thus, with the possible exception of *Sigillaria*, cauline lateral branching was achieved at the expense of both isotomous crown branching and crown lateral branching. Again, analogous polycarpic life histories occur among the palms (cf. Figs 4*i, j*).

This basic architecture of cauline lateral branch dominance encompasses considerable variation. Reconstructed species of *Paralycopodites* were relatively small-bodied, and *Sigillaria* had a small, compact rhizomorph relative to its robust stem. Cauline lateral branches of *Diaphorodendron scleroticum* contained considerably greater quantities of wood and periderm than those of *D. vasculare* or *D. phillipsii*, suggesting that they were more persistent (DiMichele, 1981, 1985). More significantly, *Sigillaria* lacks obvious (i.e. dichotomous) cauline lateral branches. However, its cone peduncles, which emerged directly from the stem, are probably homologous with the more extensive dichotomous lateral branches of the other genera (DiMichele & Phillips, 1985; DiMichele & Bateman, 1989; W. A. DiMichele, lit. comm., 1993). Isotomous terminal branching was comparatively rare in *Sigillaria* but generated unusually large daughter axes. The resulting open crowns continued to produce numerous unbranched cone peduncles identical to those borne on the stems. The great similarity of cauline lateral branches to crown lateral branches in *Sigillaria* suggests that producing cauline peduncles exhausted the apical meristem less severely than producing dichotomous cauline lateral branches in *Paralycopodites* and *Diaphorodendron*. The relative positions of cauline lateral branches also differed among the genera. Two vertical orthostiches are often discernible in *Paralycopodites* (e.g. Taylor & Taylor, 1992, fig. 9.45) and its putative close relative *Bothrodendron* (Wnuk, 1989), whereas peduncles of *Sigillaria* often occur in zones that approximate whorls.

(D) The least complex architecture characterises the isoetalean clade, which here is represented only by *Chaloneria* but also contains several other fossil genera (Pigg, 1992) and the only extant rhizomorphic lycopsid genus, *Isoetes* (including 'Stylites'). In most species neither of the two first-formed meristems undergoes further division, thereby restricting the architecture to an unbranched stem and rhizomorph (Fig. 7*b*). Some cortical lobing is evident in the rhizomorph; both the cortex and vasculature show a distinctive bilateral symmetry, in contrast with the radial symmetry that characterizes architectures (A)–(C) (e.g. Rothwell & Erwin, 1985). Temporally prolonged growth of the rhizomorph is evident in the living genus and suspected in at least some of its fossil progenitors.

In the absence of branching only one cone can be produced. In this extreme monocarpic strategy the cone is terminal in both senses of the word, marking a change in the behaviour of the apical meristem and heralding the death of the plant. Most isoetaleans avoided this potentially serious constraint by substituting sporophylls for similar (both morphologically and developmentally) microphyllous leaves on the stem, either entirely or in zones that alternate with microphylls. This classic example of heterotopy (see below) allows a more leisurely, polycarpic life history in the extant *Isoetes* (e.g. Pfeiffer, 1922; Bierhorst, 1971). At least one isotomy of the stem apex, analogous to that of the tree *Sigillaria*, occurs frequently in the two species of 'Stylites'

(e.g. Rauh & Falk, 1959) and occasionally in some other species of *Isoetes* (Karrfalt & Eggert, 1977; Hickey, 1986). Although *Isoetes* and *Chaloneria* were small-bodied and produced little secondary tissue, other fossil putative isoetaleans such as *Lepidosigillaria* and *Sporangiostrobus* grew several metres tall (e.g. Wagner, 1989; Pigg, 1992; DiMichele & Bateman, 1994).

In summary, the rhizomorphic lycopsids exhibit a wide range of architectures when fully mature. Note that the interaction of these growth architectures with the equally great diversity of reproductive biologies (Thomas, 1978, 1981; Phillips, 1979) largely determines the life history and ecological role of each species of rhizomorphic lycopsid. These interesting topics have been discussed in detail elsewhere (DiMichele & Phillips, 1985; DiMichele *et al.*, 1987; Bateman, 1991a; Phillips & DiMichele, 1992). Circumstantial evidence suggests that all rhizomorphic lycopsids were monoecious, thereby ruling out the potential for architectural dimorphy evident in some dioecious plants (e.g. *Cycas circinalis*: Hallé, 1978). The vegetative architectures can be classified *atemporally*, in terms of the static plant bauplans recognized by Hallé *et al.* (1978); architectures (A) and (B) correspond with Schoute's model, architecture (C) with Stone's model, and architecture (D) with Corner's model (Bateman *et al.*, 1992). Interestingly, Schoute's and Stone's models together encompass most palm species (Figs 4g–l), further extending the developmental analogy with rhizomorphic lycopsids. More importantly, the architectures can be interpreted *temporally*, in terms of different ontogenetic trajectories. This knowledge allows us to return to comparative morphology at a higher interpretational level (Harvey & Pagel, 1991), in order to address key macroevolutionary questions. How many times did each basic architecture evolve? What was the architecture of the first recognizable rhizomorphic lycopsid? Which of the many potential evolutionary transitions between architectures actually occurred? Were some transitions precluded by developmental constraints? How typical are the few extant representatives of this once dominant clade? And, even more speculatively, did the postulated architectural transitions occur gradually or saltationally, and by what mechanism(s)?

V. EVOLUTIONARY-DEVELOPMENTAL CHANGE: PATTERN

(1) *Terms and concepts*

Gould's (1977) influential treatise *Ontogeny and Phylogeny* prompted a renaissance in the study of development in an evolutionary context. Building on the foundations of von Baer (1828), Haeckel (1868, 1905) and de Beer (1940, 1971), both the treatise and the renaissance were dominated by neontological and palaeontological zoologists (e.g. Alberch *et al.*, 1979; Cheverud, 1982; Fink, 1982; Raff & Kaufman, 1983; Arthur, 1984; Kluge & Strauss, 1985; Kluge, 1988; McKinney, 1988a; Raff & Wray, 1989; McKinney & McNamara, 1991; Kauffman, 1993). Neobotanical applications have been few (e.g. Takhtajan, 1972; Guerrant, 1982, 1988; Iltis, 1983; Lord & Hill, 1987; Tomlinson, 1987; Gottlieb & Jain, 1988; Sattler, 1988, 1993; Weston, 1988; Lord, 1991; Pryer, 1993) and palaeobotanical applications even fewer (Doyle, 1978; Stidd, 1980; Rothwell, 1987; Meyen, 1988; DiMichele, Davis & Olmstead, 1989; Bateman & DiMichele, 1991; Bateman *et al.*, 1992). Most such studies have focused on a suite of evolutionary-ontogenetic transitions collectively termed *heterochrony*: a *temporal* change in the expression of a trait between ancestor and descendant. A companion

concept also relevant to this discussion is *heterotopy*: a *spatial* (positional) change in the expression of a trait between ancestor and descendant (note that both of the above definitions are unusually broad: cf. Sattler, 1988). Key variables that affect both concepts and are relevant to the current discussion include:

(1) Is the pairwise comparison genealogically constrained – that is, must it involve a putative ancestor and its putative descendant? [No, though this is the simplest approach. In contrast, cladistic comparison requires a monophyletic group of at least three OTUs (see *Cladistic Analysis* above).]

(2) Is the comparison inter- or intraspecific? [Either option is analytically feasible, though all of the examples presented in this paper are interspecific.]

(3) Must comparison involve the ontogenies of whole organisms, or can it focus on putatively homologous parts of organisms? [Part-organisms are acceptable; indeed, this study suggests that they are preferable, provided that they can be readily delimited. This dilemma prompted McKinney & McNamara (1991) to label whole-organism changes as global heterochrony and more structurally restricted phenomena as dissociated heterochrony.]

(4) Is it more appropriate to perceive a temporal sequence of ontogenetic events as a mutually dependent ‘cascade’ or as a suite of potentially independent occurrences? [It is interpretationally helpful to view a particular problem from both perspectives. In practice, whole-organism ontogenies lie between these two extremes.]

(5) Does a change in the number of definable ontogenetic stages fall within the remit of either heterochrony or heterotopy? [For authors such as Fink (1982) the answer is ‘yes’. However, in my opinion, only changes involving repetitions of a particular pre-existing event, such as adding extra sets of lateral branches to *Diaphorodendron*, are acceptable. Excluding the addition or subtraction of events from the concepts of heterochrony and heterotopy prompted introduction of the more inclusive term ‘evolutionary-developmental change’ (Bateman, 1992c).]

(6) Is the number of possible ontogenetic events essentially infinite (von Baer, 1828) or constrained by a temporal limit to ontogeny, necessitating condensation of the previous developmental chronology when events are added during evolution (Haeckel, 1905)? [In the case of the rhizomorphic lycopsids, a severe limit to ontogenetic complexity is suspected, though it may be intrinsic to developmental potential – that is, it may reflect the limited genetic armoury of the clade – rather than reflecting strictly temporal limits.]

Other important points relate more specifically to heterochrony. In order to categorize several contrasting modes of heterochrony, Gould (1977) developed a clock model that allowed both size and shape to track relative time. Alberch *et al.* (1979) translated these parameters into more formalized ontogenetic trajectories that have strongly influenced most subsequent studies of ontogeny. However, several flaws in Alberch *et al.*’s paper have been largely overlooked by many subsequent authors, while other concepts discussed by Alberch *et al.* have been subjected to unwarranted modification in later texts (cf. Alberch, 1985; Kluge, 1988; McKinney, 1988b).

Most importantly, the pivotal hypothetical ‘ontogenetic trajectory’ of Alberch *et al.* (1979, fig. 9) occupied three-dimensional ‘age–size–shape’ space, whereas subsequent trajectories figured by them were two dimensional; all employed shape (σ) as the vertical axis but, for the horizontal axis, size (S) and age (a); perhaps better described

		Phenomenon		
Parameter(s) altered		Less morphological change in descendant (paedomorphosis)	Greater morphological change in descendant (peramorphosis)	
<i>Heterochronic</i>				
Onset of growth (α)		Delayed (post-displacement)		Precocious (pre-displacement)
Offset of growth (β)		Precocious (progenesis)		Delayed (hypermorphosis)
Rate of morphological development ($k = \sigma/t$)		Decreased (neoteny)		Increased (acceleration)
<i>Non-heterochronic</i>	$S (\cong t)$	Decreased (dwarfism)	$S (\cong t)$	Increased (giantism)
Rate of growth ($g = S/t$)				

Fig. 8. Definitions of 'pure', end-member modes of the two heterochronic spectra of paedomorphosis and peramorphosis, together with non-heterochronic allometric size changes. a = putative ancestor, d = putative descendant; σ = shape, S = size, t = time. (Modified after Alberch *et al.*, 1979; see also O'Grady, 1985; Funk & Brooks, 1990; McKinney & McNamara, 1991.)

as time, t) were treated as interchangeable (and unqualified) parameters. Obviously, they are not; size and age vary greatly among species, together determining the allometric growth rate ($g, = S/t$). All three basic parameters (shape, size, time/age) can be measured for a living organism by directly observing its ontogeny, but for most fossils (including extinct rhizomorphic lycopside) it is necessary to use measurable size as a crude proxy for unmeasurable time. The more phylogenetically disparate the taxa under consideration, the less justifiable is this assumption.

In either case, trajectories are bounded by the onset time/size (α) and offset time/size (β) of growth. Hypothetical examples used to define classes of evolutionary-developmental change are linear, thereby defining a constant rate of morphological development ($k, = \sigma/t$; k is not, as is frequently mis-stated, the growth rate). Onset time, offset time and development rate can each be shifted positively or negatively in the descendant relative to the ancestor while keeping the two remaining parameters fixed, thereby defining a total of six 'pure' (i.e. end-member) modes of heterochrony (Fig. 8). For each of the three parameters, a shift in one direction leads to relatively less morphological change in the descendant relative to the hypothetical ancestor (paedomorphosis), whereas a shift in the opposite direction gives greater morphological change in the descendant (peramorphosis). In addition, simple decreases and increases in growth rate between ancestor and descendant that leave shape unaltered are termed dwarfism and giantism respectively; these allometric properties lie outside the boundaries of heterochrony *sensu stricto* (Gould, 1977). Obviously, many ontogenetic

	Terminal	Non-terminal
Addition	$\frac{A-B-C}{A-B-C-D^*}$	$\frac{A-B-C}{A-B-D^*-C}$
Deletion	$\frac{A-B-C}{A-B-*}$	$\frac{A-B-C}{A-* -C}$
Substitution	$\frac{A-B-C}{A-B-D^*}$	$\frac{A-B-C}{A-D^*-C}$

Fig. 9. Classification of changes in the number of developmental events between putative ancestral and descendant ontogenies (above and below the horizontal line respectively). In each example only the asterisked event is altered. (Modified from a classification of developmental stages (semaphoronts) by O'Grady, 1985; see also Kluge, 1988.)

trajectories combine different modes of heterochrony and/or growth rate changes, presenting severe challenges to interpretational precision.

Other more specific difficulties are evident. Although Alberch *et al.* (1979) recognized the considerable scope for intraspecific variation in trajectories, most subsequent studies have been wholly typological. Moreover, the entities compared by Alberch *et al.* varied greatly in 'demographic' level, from individual organs to entire species, but the significance of these hierarchical differences was not discussed. Also, many studies have defined modes of heterochrony by substituting onset of sexual maturity for offset of growth. Unlike cessation of growth, sexual maturity is exclusively a property of the whole organism and hence reflects the interaction of many developmental factors. This key event in life histories would be better described by a set of terms independent of those given for heterochrony *per se* in Fig. 8. Finally, criteria for recognition of changes in timing, and for standardizing onset and offset times, have received insufficient attention. Recognition of heterochrony is easiest when two distinct ontogenetic events are transposed rather than merely shifted through time, though such changes are uncommon.

This last point emphasizes the relevance of O'Grady's (1985) classification of the number and/or nature of definable events in an ontogenetic sequence (Fig. 9). Events can be added (thereby increasing overall number), deleted (thereby decreasing overall number), or substituted (thereby maintaining overall number). Each such modification involves either the last event in an ontogenetic sequence (terminal) or an intermediate event (non-terminal). This distinction is especially relevant to a cascade model of ontogeny, wherein non-terminal modifications affect the course of subsequent ontogenetic events, unlike terminal modifications (Alberch, 1985; Wake, 1989). Beyond the six-fold classification of Fig. 9 lies the possibility of re-ordering pre-existing events (transposition).

Armed with these two contrasting perspectives on comparative ontogeny, we can now return to the case-study of the rhizomorphic lycopsids. The remarkable frequency and diversity of architectural transitions evident in Fig. 2 encompasses many of the phenomena defined in Figs 8 and 9. The transitions can be viewed either as ancestor-descendant pairs or cladistic triplets.

(2) *Selected comparisons : ancestor-descendant pairs*

I have selected three examples to illustrate the principles of pairwise comparison of putative ancestral and descendant ontogenetic trajectories. It should be emphasized that the rhizomorphic lycopsid phylogeny (Fig. 2) influenced only indirectly the choice of generic pairings. First, cladistic principles explicitly reject the concept of ancestor-descendant relationships, referring instead only to closeness of relationships among three or more OTUs in a monophyletic group (one such comparison is presented in the following subsection). Secondly, if an attempt is made to transform a cladogram into ancestor-descendant mode, in theory this is most appropriately done within the constraints of a monophyletic group (an ancestor plus all of its descendants). Here, the first two pairs of genera compared are depicted as paraphyletic (an ancestor plus only some of its descendants) in the analytically correct topology (Fig. 2*a*). They are perceived as monophyletic only in the user-imposed topology (Fig. 2*b*), which attempts to correct for inferred local perturbations in topology caused by profoundly pedomorphic evolutionary changes.

In each example, the bodies of the two genera have been disaggregated into the component modules recognized by Bateman & DiMichele (1991) (Fig. 5). Trajectories of relative shape versus relative time are plotted for all four modules, including both positional modes – D1 and D2 – of the lateral branch module. (The depiction of trajectories as linear – now traditional in such studies – is an over-simplification; Figs 6 and 7 indicate that at least some are non-linear.) The five trajectories can only be arranged in approximate temporal sequence, as the developmental periods of most modules overlapped to some degree. Moreover, the lateral branch module was iterative and thus described multiple trajectories, irrespective of whether it was expressed on the stem or in the crown. Thus, reliable onset–offset datum points are difficult to identify. The stem and rhizomorph undoubtedly shared the same onset time, though the rhizomorph tended to have a more rapid initial rate of development and an earlier offset time. Also, the onset of growth of isotomous crown branches by definition followed the offset of growth of the stem. The first-formed cauline lateral branches did not commence growth until stem elongation was well advanced (Figs 6, 7), and the last-formed cauline lateral branches must have been initiated prior to crown formation. Also, within the crown the onset of isotomous branching must have preceded the onset of anisotomous lateral branching. Overall, onset times are easier to infer than offset times.

The first example of a postulated speciation event describes the evolution of the crown-branched pseudoherb *Hizemodendron* from an ancestor resembling the crown-branched tree *Lepidodendron* (Fig. 10). The two genera share many synapomorphies; most notably, they are identical in almost all reproductive characters, possessing relatively apomorphic monosporangiate cones (Fig. 2). The obvious differences in vegetative architecture are supported by differences in many smaller-scale characters that reflect the anatomical simplicity of *Hizemodendron*; this genus therefore appears reproductively apomorphic but vegetatively plesiomorphic (Bateman & DiMichele, 1991; Bateman *et al.*, 1992). The postulated evolutionary transition involved parallel developmental changes in the stem and rhizomorph. Radical decreases in size and simplification of shape indicate precocious offset of growth in both modules, a mode of

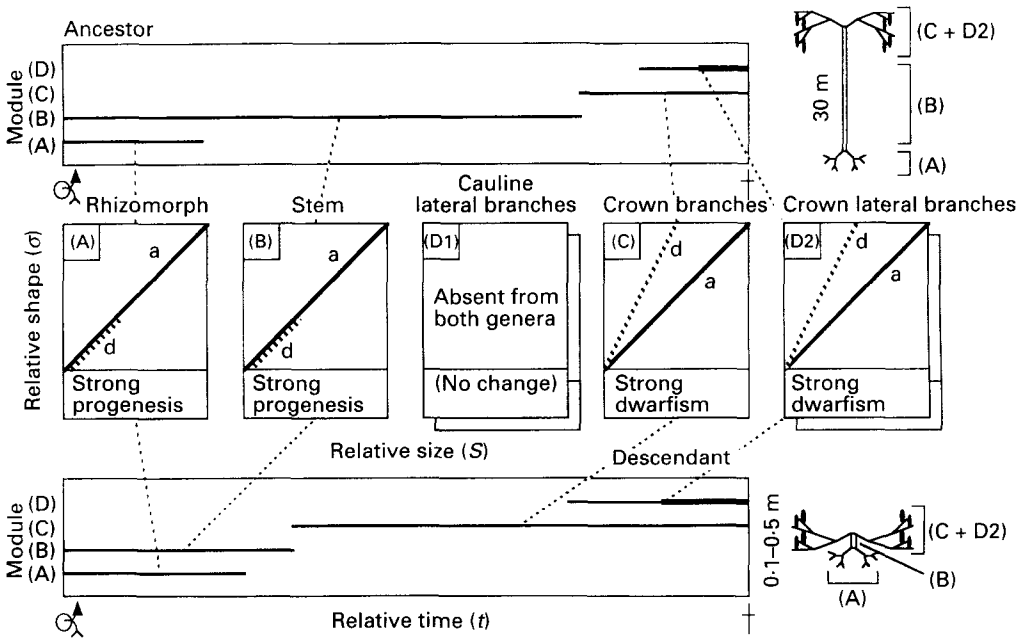


Fig. 10. Comparison of life histories of *Lepidodendron* and its putative descendant *Hizemodendron*, indicating inferred modes of evolutionary-developmental change for each growth module and the two submodules of lateral branches. Lines in the two horizontally elongate boxes indicate the estimated relative periods of growth of modules; thick lines denote inferred reproductive phases. The square boxes plot ontogenetic trajectories of relative size (S) against relative complexity of shape (σ) for each module in the ancestor (a , solid line) and descendant (d , dashed line). Architectures and average height at maturity of both genera are shown to the right. (Broadly based on formulations devised by Alberch *et al.* (1979) and O'Grady (1985); see also Figs 8 and 9.)

paedomorphic heterochrony that is termed progenesis. The precocious division of the stem apical meristem yielded an isotomous crown, and within that crown well developed lateral crown branches, that were both far smaller than those of the ancestor but similar architecturally. Thus, both modules changed in size but not shape (Bateman & DiMichele, 1991, fig. 3*b*); this is an example not of heterochrony *sensu stricto* but of dwarfism. Together, these developmental changes generated a far smaller-bodied plant and probably accelerated its overall life history. In terms of absolute time, *Hizemodendron* attained reproductive maturity far earlier than *Lepidodendron*. However, in terms of relative time, reproduction occurred synchronously in the two genera; in each case, cones were confined to the crown, and thus were produced monocarpically as the final event in the life history of each individual.

Similar, albeit more complex, transitions from tree to pseudoherb are envisaged from *Paralycopodites*-like (ulodendroid) ancestors to *Oxroadia* and to *Paurodendron* (Bateman, 1992*a*). As in the *Lepidodendron*-*Hizemodendron* pairing, these genera are united by similar reproductive characters (though cones of all these genera are, in contrast, primitively bisporangiate: Fig. 2), and the evolution of the pseudoherbs involved the loss of so many small-scale vegetative features that parsimony confidently dictates placement of the paedomorphic descendants immediately below the more probable (but less parsimonious) position on the cladogram (cf. Figs 2*a, b*). Their evolution also

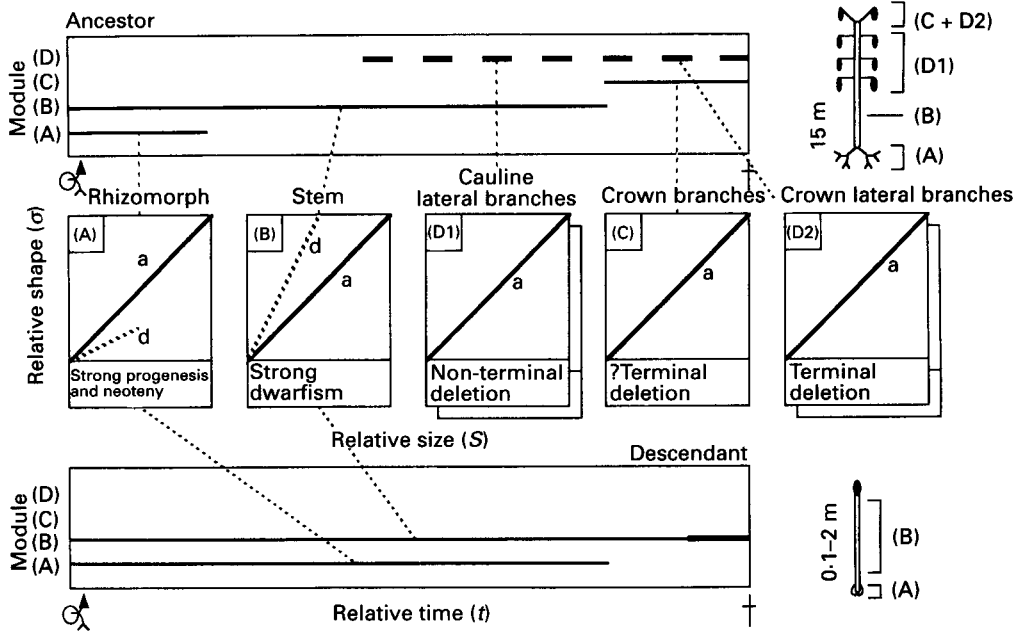


Fig. 11. Comparison of life histories of *Sigillaria* and its putative descendant *Chaloneria*, indicating inferred modes of evolutionary-developmental change for each growth module. For further details see Figures 8–10.

involved more radical architecture modifications. Assuming that a species of *Paralycopodites sensu stricto* was the ancestor of the pseudoherbs, a change from dominantly cauline lateral to dominantly isotomous crown branching would be required, though other ulodendroid trees with putatively extensive crown branching and better claims for direct ancestry are currently being reconstructed (cf. Bateman *et al.*, 1992, table 5). Rhizomorphs experienced size reduction and architectural compaction: suppression of cortical but not vascular branching in *Oxroadia*, and of cortical and vascular branching in *Paurodendron*. On current evidence, it is equally parsimonious to derive *Paurodendron* from *Oxroadia* or independently from a *Paralycopodites*-like ancestor.

The second example similarly involved a transition from tree to small-bodied shrub that is considered to be placed erroneously in the cladogram, one node below the ancestral tree (cf. Figs 2a, b). In this case, the ancestral tree is the *bona fide* 'lepidodendralean' *Sigillaria* and the descendant is one of the earliest *bona fide* 'isoetaleans', *Chaloneria* (Fig. 11: for discussion of this pre-cladistic ordinal classification see DiMichele & Bateman, 1994). Unlike the previous example, developmental changes in the stem do not precisely parallel those in the rhizomorph. The stem merely shows dwarfism; a reduced growth rate and consequent decrease in size within the original allometric ratio of cylinder length to cylinder diameter. The changes in the rhizomorph are broadly pedomorphic but cannot be attributed to a single end-member mode of heterochrony. A combination of decreased development rate (neoteny) and precocious offset of growth (progenesis) is suspected, reducing both size and shape. Profound changes also occur later in ontogeny, notably the suppression

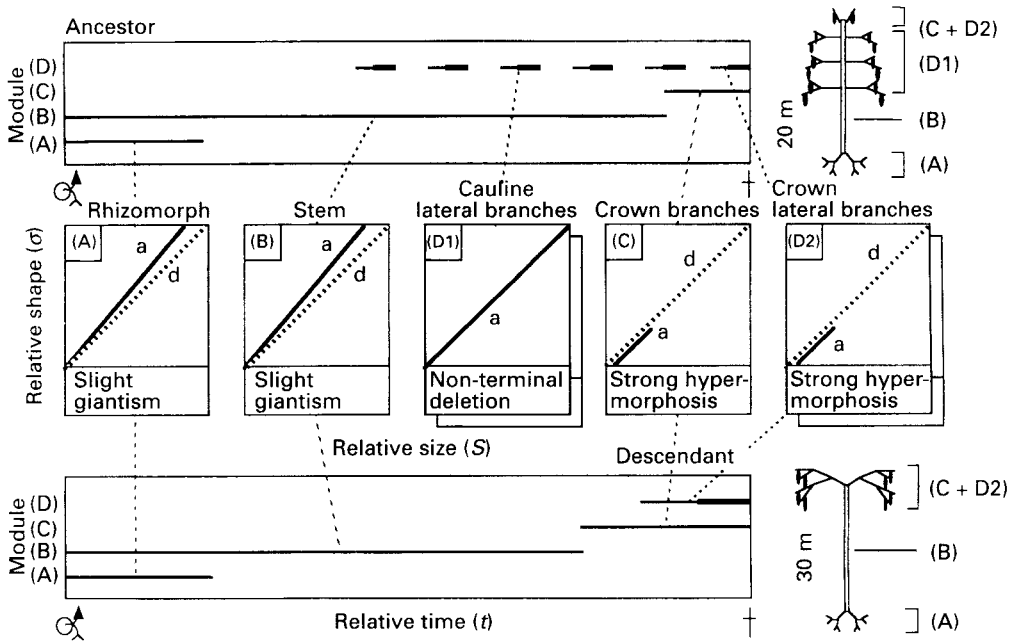


Fig. 12. Comparison of life histories of *Diaphorodendron* and its putative descendant *Synchysidendron*, indicating inferred modes of evolutionary-developmental change for each growth module. For further details see Figures 8–10.

of all axial branching. Taken at face value, the consequent losses of the cauline lateral branches and terminal branches are a non-terminal and a terminal deletion respectively, though it could be argued that loss of lateral branches within the crown is a terminal deletion and loss of earlier-formed isotomous crown branching is a non-terminal deletion. In either case, the total number of growth modules comprising the plant was reduced from four to two. Suppression of branching transferred to the stem reproductive responsibilities formerly held by the cauline lateral branches (in the case of *Sigillaria* these are unbranched peduncles); this, together with body size reduction, accelerated overall life history. This in turn caused precocious reproduction, especially in those isoetalean species where the sporophylls occurred in periodic zones (polycarpic) rather than single terminal clusters (monocarpic).

The third postulated evolutionary-developmental transition contrasts the architectures of *Diaphorodendron* and *Synchysidendron* (Fig. 12). As both genera are trees, thus precluding hypotheses of severe architectural pedomorphosis, they are correctly depicted as sister-groups in both topologies summarized in Fig. 2. Even so, cladistic techniques cannot legitimately attribute polarity to a pair of OTUs; at least three must be involved in any comparison. Hence, the evidence for *Diaphorodendron* as the predecessor (rather than merely the sister-group) of *Synchysidendron* is extrinsic, based primarily on its earlier occurrence in the unusually good lycopsid fossil record of the Westphalian of Euramerica (DiMichele & Bateman, 1992, fig. 3). The two genera share identical reproductive organs, together with a wide range of vegetative synapomorphies that reflect their siphonostelic vasculature and relatively complex peridermal-cortical anatomy. Indeed, the main generic distinction is architectural; *Diaphorodendron* is

dominated by cauline lateral branching, whereas *Synchysidendron* is strongly crown-branched and lacks cauline branches (Fig. 12). This implies evolutionary suppression of cauline lateral branching, ostensibly by a non-terminal deletion. However, the overall number of growth modules present in the descendant relative to the ancestor is not reduced, as expression of lateral branching and associated cones persists in the crown. Indeed, released from the need to generate cauline lateral branches, the stem apical meristem was free to produce a much more extensive and complex crown. The delayed offset of growth of both the isotomous and anisotomous branches of the crown defines hypermorphosis, a mode of peramorphosis (Fig. 8). Loss of cauline lateral branches caused the transfer of cone production to lateral branches in the crown, thus delaying reproduction and effecting a transition from polycarpism to ontogenetically terminal monocarpism. Modifications of earlier ontogenetic stages were confined to slight giantism in both the stem and the rhizomorph.

(3) Selected comparisons : cladistic triplets

Fink (1982, figs 3, 5) reformulated Alberch *et al.*'s (1979) heterochronic modes in order to allow cladistic testing. He retained the original definitions and parameters but extended the comparison to three OTUs (effectively a functional outgroup and two ingroup members), in order to distinguish heterochronic change from the null hypothesis of plesiomorphy (Fink, 1982, 1988; Kluge & Strauss, 1985). Such comparisons focus on the morphology inferred for the hypothetical common ancestor of the ingroup members (*hyan* on Fig. 13a). However, such comparison becomes unmanageably complex for highly homoplastic characters among several OTUs (as in Fig. 2). Hence, the method is here illustrated by extending the last of the pairwise comparisons described above (*Diaphorodendron* and *Synchysidendron*) to include, for the sake of argument, *Sigillaria* as an outgroup. This relationship among the three genera occurred in a near-optimal topology illustrated by Bateman *et al.* (1992, fig. 9e), and is in fact the most parsimonious topology if non-trees are excluded *a priori* from the analysis (DiMichele & Bateman, 1994, fig. 1b).

Although all three genera were trees, they exhibited contrasting architectures (Fig. 13a). They possessed stems and rhizomorphs of similar shape but somewhat different sizes. The most parsimonious explanation of this observation is progressive giantism, from the relative small sigillarian outgroup through the medium-sized *Diaphorodendron* and hypothetical ancestor *hyan* to the somewhat larger *Synchysidendron* (Fig. 13b). Three-way comparison cannot be made for trajectories representing the cauline lateral branches, as these are absent from *Synchysidendron*. The figure implies deletion in *Synchysidendron* and peramorphic hypermorphosis in *Diaphorodendron*. Isotomous and anisotomous crown branching offer the most interesting examples of three-way comparison, taking as a model *Sigillaria* with limited crown branching (admittedly, some *Sigillaria* may have lacked crown branching). Evolutionary transitions in crown branching are most parsimoniously explained by an increase in growth rate (k) from *Sigillaria* to *Diaphorodendron* and its common ancestor with *Synchysidendron* – that is, by acceleration (Fig. 13b). This increased growth rate was retained in *Synchysidendron*, but the evolution of *Synchysidendron* from hypothetical ancestor *hyan* involved delayed offset of growth (β) – that is, hypermorphosis. Inferred changes in the crown lateral branches are even more complex. Both increased growth rate (acceleration) and delayed offset of growth (hypermorphosis) are required to generate *Diaphorodendron* from

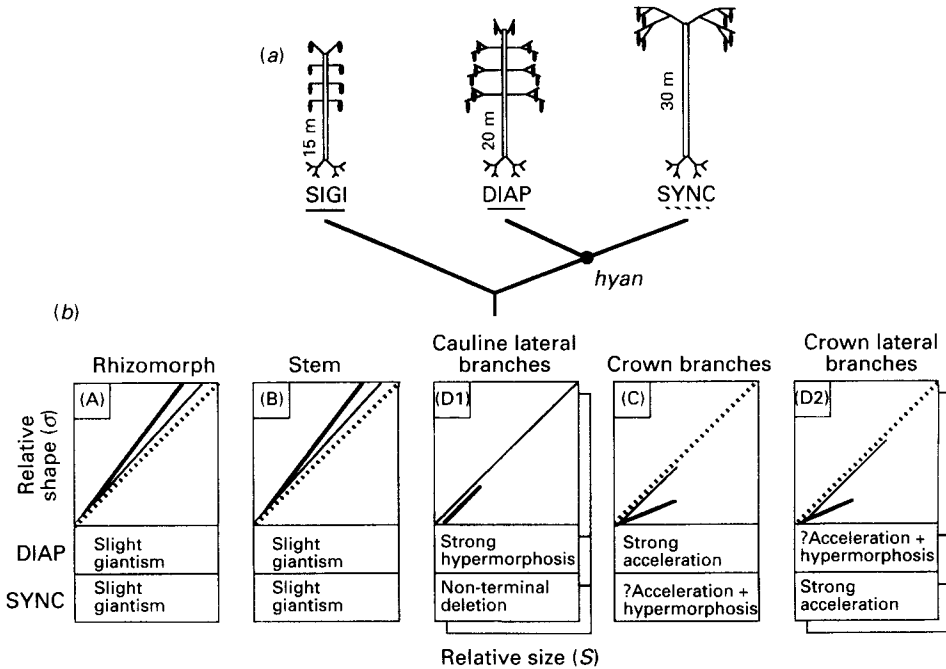


Fig. 13. Three-way comparison of life histories consistent with cladistic principles. For the sake of argument, *Sigillaria* (thick line) is used as an outgroup to re-examine without assumptions of ancestor-descendant relationships the pairwise comparison of *Diaphorodendron* (thin line) and *Synchysidendron* (dashed line) previously attempted in Figure 12. This is achieved via a hypothetical ancestor (*hyan*). Method devised by Fink (1982).

Sigillaria, with further acceleration required to yield the more elaborate *Synchysidendron*. For these crown modules at least, three-way comparison offers a useful insight into potential evolutionary mechanisms.

(4) Overview

The above examples illustrate several important general principles:

(1) Individual ontogenetic trajectories can be drawn more successfully for specific growth modules than for an entire, composite modular organism (cf. Cheverud, 1982; Guerrant, 1982, 1988; Lord & Hill, 1987; McNamara, 1988; Raff & Wray, 1989; Kampny, Dickinson & Dengler, 1993). An evolutionary-developmental change may affect the overall life history of the descendant organism, but this is usually the net effect of several contrasting (sometimes contradictory) changes occurring at smaller spatial and temporal scales – a manifestation of the domino effect. For example, many studies of heterochrony focus on the onset of reproductive maturity. Cases outlined above, notably the transitions between mono- and polycarpism, are determined by the cumulative ontogenetic changes in a range of growth modules (but see point (4) below).

(2) When comparing modular trajectories of different genera, it is difficult to decide whether to treat the timing of the onset and offset of growth as relative or absolute. For example, in absolute terms, crown production undoubtedly both began and ceased

much earlier in *Hizemodendron* than in *Lepidodendron* (Fig. 10); should the clock therefore be reset for each growth stage, so that the onset of growth of each module is treated as simultaneous in the two genera?

(3) Although logical, the modification of Alberch *et al.*'s (1979) pairwise comparison of ancestor-descendant by Fink (1982) and others to accommodate cladistic three-taxon statements is of limited value if (a) pedomorphosis has already undermined the cladogram itself (a form of 'Catch 22') and (b) the architectural changes are both diverse and highly homoplastic, spanning several OTUs rather than just three; the logical problem then becomes unmanageably complex and the cladistic inferences correspondingly ambiguous. Consequently, the scenarios discussed here were prompted by the cladistic analysis but are not wholly constrained by the preferred most-parsimonious topology. They are presented to facilitate discussion rather than as incontrovertible truths inherent in the phylogeny.

(4) Many important evolutionary-developmental changes are not strictly heterochronic. Some relate to changes in module size without accompanying changes in shape, such as the small crowns of the pseudoherbs. Others are caused by changes in the number of types of growth module present, notably the ontogenetic deletions of all aerial branch modules during the evolution of the shrub *Chaloneria* and of cauline lateral branches to generate the tree *Synchysidendron*. Yet others reflect a positional change in the expression of a module (heterotopy *sensu stricto*). Even when a particular evolutionary-developmental change can be attributed to one of the major groups of phenomena (heterochrony, heterotropy, allometric change, stage addition/deletion), it can often be difficult to classify within that group. For example, intermediate, 'impure' forms of heterochrony, such as that observed in the rhizomorph of *Chaloneria*, are frequent (though it is tempting to shoe-horn such observations into pure modes). Even changes in the number of modules present in an organism can be difficult to identify. The non-terminal deletion of cauline lateral branching inherent in the evolution of *Synchysidendron* (Fig. 12) would have been mis-labelled as a substitution (crown branching replacing cauline lateral branching) had the very poorly developed crown of most *Diaphorodendron* species escaped recognition. Indeed, this particular transition presents the greatest challenge to accurate classification of evolutionary-developmental changes. Lateral branches are unique among the axial modules of rhizomorphic lycopsids in being iterative, which allows them to be structurally homologous but positionally non-homologous on the stem (D1) and in the crown (D2). Suppression of this module in the cauline position allows greater expression of the same module in the newly-expanded crown. Hence, only one positional manifestation of the module is deleted, rather than the module *per se*. Moreover, heterotopy cannot strictly be invoked either, as the expression of the lateral branch module in the crown is not newly acquired – it is merely enhanced (cf. Tucker, 1988).

(5) Both heterochronic changes and modular deletions tend to have a domino effect. For example, many authors automatically attribute precocious reproduction to pedomorphic heterochrony, yet the rapid onset of reproduction in those species of *Chaloneria* that possess fertile zones rather than terminal cones reflects a late-stage deletion of the cone more than an early-stage pedomorphosis affecting the sporophylls. Also, the extensive crown branching in *Synchysidendron*, strictly defined as late-stage

peramorphosis, is merely an inevitable consequence of the deletion of the previous developmental stage, namely cauline lateral branch production. Note that the lateral branch module is not wholly lost; rather, its positional expression becomes confined to the crown.

(6) When the trajectories of two modules first diverge within the ontogeny of a single organism, the probability of parallel evolutionary-developmental changes in the modules is highest. Current evidence (albeit weak in some cases) suggests that in all of the above examples but *Sigillaria-Chaloneria*, parallel developmental changes occurred in the rhizomorph and stem, reflecting their synchronous bipolar growth in opposite directions following germination. Also, deletion of either of these two first-formed modules is inevitably lethal to the organism. Later developmental stages, such as those generating aerial branches, are less likely to show parallel transitions and more likely to experience non-lethal deletions.

(7) Lastly and most importantly, perception of the nature of an evolutionary-developmental change depends upon the degree of interpretation imposed on the empirical observation. For example, the losses of both lateral cauline branches and crown branches during the postulated evolution of *Chaloneria* from *Sigillaria* are most obviously described as non-terminal and terminal deletions respectively of recognizable modules (Fig. 11). However, the loss of both module types could in theory be achieved by a single developmental command: suppress all divisions of the stem apical meristem. It would then be more parsimonious to perceive the loss of both types of branch as a single, terminal deletion.

VI. HYPOTHESIS TESTING: ASSESSING THE POTENTIAL RANGE OF ARCHITECTURAL TRANSITIONS

Cladistic analysis eschews ancestor-descendant relationships in favour of sister-group relationships, placing all OTUs on terminal branches of the cladogram (i.e. as terminal taxa). However, if a cladogram is perceived as a phylogenetic tree (e.g. Hennig, 1966; Swofford & Maddison, 1987) rather than merely as a nested set of synapomorphic character states (e.g. Nelson & Platnick, 1981; Patterson, 1982), each internal node can be regarded as a hypothetical ancestor of the two (or more) lineages that diverge from that node. Given a particular data-matrix, a particular topology, and a particular optimization algorithm, the characteristics of those hypothetical ancestors can be reconstructed. This can be done using characters in the primary matrix that contribute to the topology. Alternatively, additional characters can be scored for the same range of OTUs and analyzed within the pre-determined topology (a procedure that is termed mapping).

Here, an attempt is made to reconstruct the architectures of the hypothetical ancestors by mapping a matrix of relevant characters. It should be emphasized that Table 2 presents but one of many viable coding schemes for these architectures. Some characters have been re-coded from the architectural data originally input into the analysis, primarily to accommodate more effectively the *a posteriori* hypothesis that reduction and loss of architectural modules tends to be apomorphic rather than plesiomorphic among the rhizomorphic lycopsids. Another character (C7) is new. Of the nine binary characters, four are confined to single genera (i.e. autapomorphic at the generic level; three of these characterize *Chaloneria*). A fifth character (C6: lack of

Table 2. Architectural characters of rhizomorphic lycopsid genera, used to characterize hypothetical ancestors in Figs 14 and 15

[Coding largely follows Bateman *et al.* (1992, *q.v.*), though the *a priori* hypothesized polarity of some characters has been reversed to accommodate *Paralycopodites* as the most satisfactory outgroup. Three possible outgroups are italicized: *Oxroadia* (the first OTU to appear in the fossil record), *Paralycopodites* (arguably the first tree-sized OTU to appear in the fossil record), and *Synchysidendron* (the most reproductively primitive OTU to possess similar developmental patterns in both shoot and root systems). Genera with similarly coded architectures are equated. Generic autapomorphies, phylogenetically uninformative at this level of comparison, are asterisked. For key to genera see caption to Fig. 2.]

Genus	PS = DI	SI	SY = LN = LS	OX	HZ	PN	CH
Character and alternative states (0:1)							
1 Arboreous (stem > 2 m tall): non-arboreous	0	0	0	0	0	1	1
2 Stem longer than branches, plant upright: shorter than branches, plant recumbent	0	0	0	0	0	1	1
3 Aerial terminal branching extensive: vestigial or absent	0	0	0	1	1	1	1
4* Aerial lateral branches absent or extensive: present but undivided	0	0	1	0	0	0	0
5* Aerial branching present: absent	0	0	0	0	0	0	1
6* Cones present: absent	0	0	0	0	0	0	1
7 Rhizomorphic cortical division deep: shallow or absent	0	0	0	0	0	1	1
8 Rhizomorphic vascular division present: absent	0	0	0	0	0	0	1
9* Rhizomorph symmetry radial: bilateral	0	0	0	0	0	0	1

rhizomorph vascular dichotomy) is scored as apomorphic only for *Chaloneria* and *Paurodendron*. As they do not form a clade in either the analytically correct (Fig. 2a) or the user-imposed (Fig. 2b) topology, this character is strongly suspected of being a parallel acquisition in the two genera. Thus, in practice, only the four remaining characters (C1–C3, C7) are likely to vary (1) between the two topologies or (2) between different optimizations of the character-state transitions across the same topology. Nonetheless, these few informative characters offer some strikingly different hypotheses of architectural evolution.

Here, the characters in Table 2 are mapped across the two contrasting generic topologies shown in Figs 2a and 2b. In each case, characters have been mapped twice, following the contrasting optimization procedures Acctran (which favours reversals over parallelisms) and Deltran (which favours parallelisms over reversals). As these are the two most extreme approaches to optimization, together they encompass all possible hypotheses of character change based on a particular matrix and a particular topology. The following discussion focuses on (1) transitions between tree and non-tree and (2) transitions among the three basic body plans: rhizomorph + stem only (AB), rhizomorph + stem + well developed crown branches subtending crown lateral branches (ABCD₂), and rhizomorph + stem + poorly developed crown branches + cauline lateral branches (ABcD1d₂). (This abbreviated notation will be followed in the remainder of the discussion.)

Fig. 14 reproduces the analytically correct topology, rooted using a hypothetical outgroup that possesses the pseudoherbaceous growth architecture of *Oxroadia*. This has a strong influence on the hypothetical intermediates, which all resemble *Oxroadia*

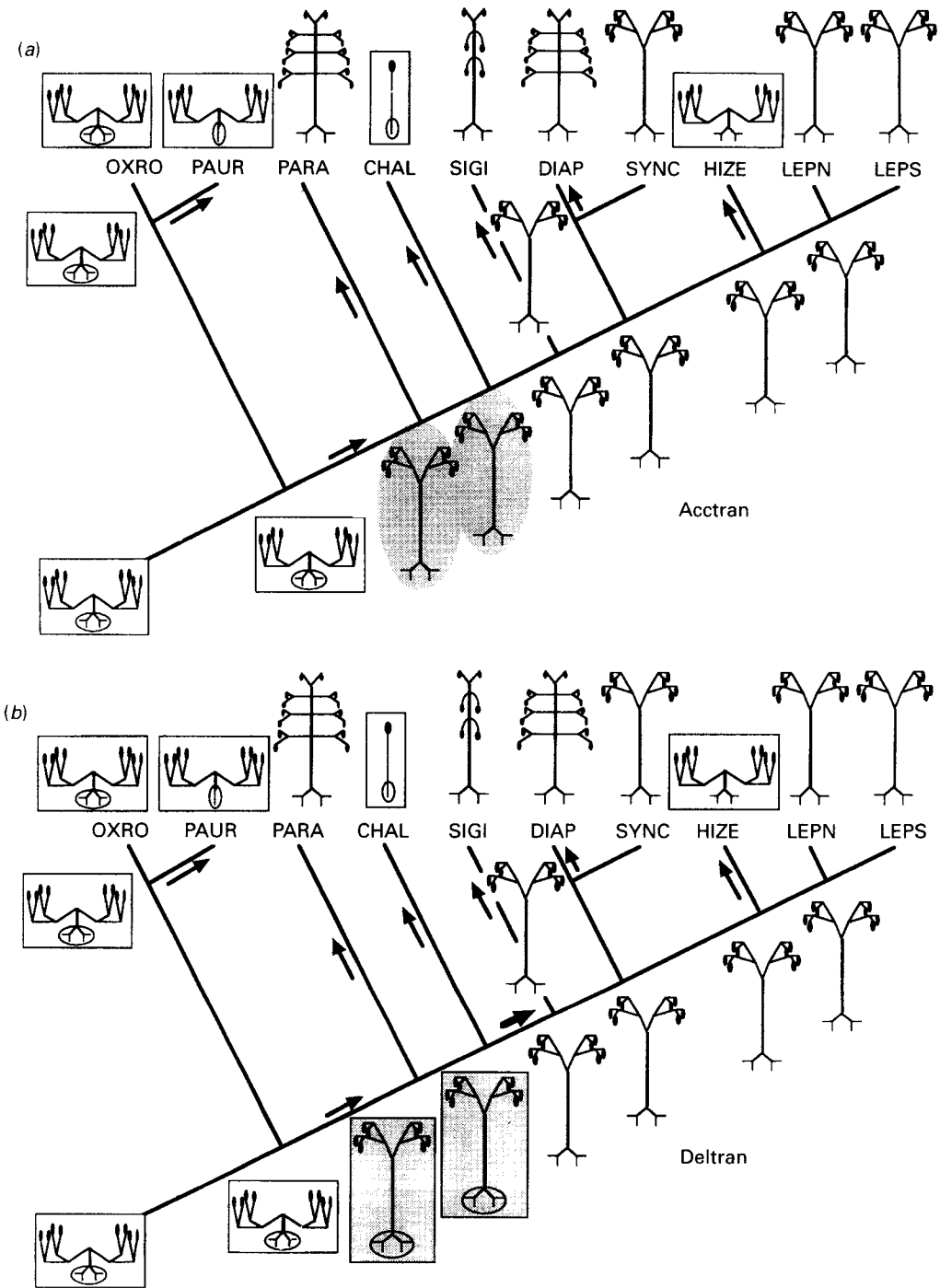


Fig. 14. Architectural characters presented in Table 2, mapped onto the analytically correct topology shown in Fig. 2a in order to reconstruct hypothetical ancestral architectures occupying internal nodes of the cladogram. Rooted using the architecture of *Oxroadia*. High levels of homoplasy in the characters

in lacking cauline lateral branches (D₁). Also, the transition from non-tree to tree occurs above the base of the cladogram. The two optimizations generate significantly different hypothetical ancestors at the two asterisked internal nodes in Fig. 14; Acctran (Fig. 14*a*) gives a standard ABCD₂ tree, but Deltran (Fig. 14*b*) creates an architecture that resembles *Oxroadia* in most characters (small-bodied, with an extensive crown rather than cauline lateral branches and a reduced rhizomorph lacking deep cortical lobing), but differs in possessing an extended stem (i.e. it is an erect shrub rather than a recumbent pseudoherb). Although clearly biologically sound, this architecture is not found in any of the ten genera under comparison – within the confines of this analysis it is hypothetical. Interestingly, however, it is thought to characterize some as yet incompletely reconstructed early rhizomorphic lycopsids, notably *Valmeyerodendron* (Jennings, 1972). Thus, cladistic character mapping has made a prediction of the existence of a novel architecture that is likely to be fulfilled by further empirical study.

The contrasting architectural transitions required by Acctran and Deltran are summarized in Figs 16*a* and 16*b* respectively. Both derive the simple AB architecture (one genus) and complex ABcD₁d₂ architecture (three genera) from intermediate ABCD₂ architectures, in four independent events. However, Deltran suggests only one tree-to-nontree transition, whereas Acctran suggests two such transitions. Both optimizations specify independent origins for the two genera of ABcD₁d₂ trees with cauline lateral branches that are dichotomous (i.e. excluding the unbranched lateral cauline peduncles of *Sigillaria*), but Acctran suggests that both genera evolved from tree ancestors whereas Deltran suggests that one of the ancestors was a shrub.

In Fig. 15, the same architectural characters are mapped across the author's preferred topology, rooted using a hypothetical ancestor possessing the architecture of *Paralycopodites*. This topology requires the same total number of state transitions among the four phylogenetically informative characters mapped, though the use of a ulodendroid outgroup reverses the *a posteriori* polarity of all four characters (Table 2). Consequently, most architectural transitions are pushed outward to ultimate or penultimate branches of the cladogram, and the hypothetical intermediates are very different in architecture from those predicted in Fig. 16. Laterally branched trees predominate, especially under Deltran optimization (Fig. 15*b*), which gives a later transition from dominantly lateral to dominantly crown branching among the derived genera than Acctran (Fig. 15*a*: compare the highlighted nodes).

Translation of these cladistic patterns into transition networks yields only one optimization ambiguity; Deltran (Fig. 17*b*) shows two parallel origins of ABCD₂ trees from ABcD₁d₂ trees, whereas Acctran (Fig. 17*a*) shows one such transition and one reverse transition (the only example in either topology of a hypothesis requiring the evolution of an ABcD₁d₂ tree from an ABCD₂ tree).

Overall, there are significant differences between the networks for the analytically correct topology (Fig. 16) and those for the author's preferred topology (Fig. 17). In the former, the focus is on dominantly crown-branched (ABCD₂) architectures, and there are reversible alternations between trees and non-trees. In the latter, the unbranched (AB) shrub and dominantly crown-branched (ABCD₂) trees and pseudoherbs all

result in significantly different architectures at the highlighted nodes, according to whether Acctran (*a*) or Deltran (*b*) optimization is used. Internodes involving state changes in at least one architectural character are arrowed; large arrows denote positional differences between the two optimizations.

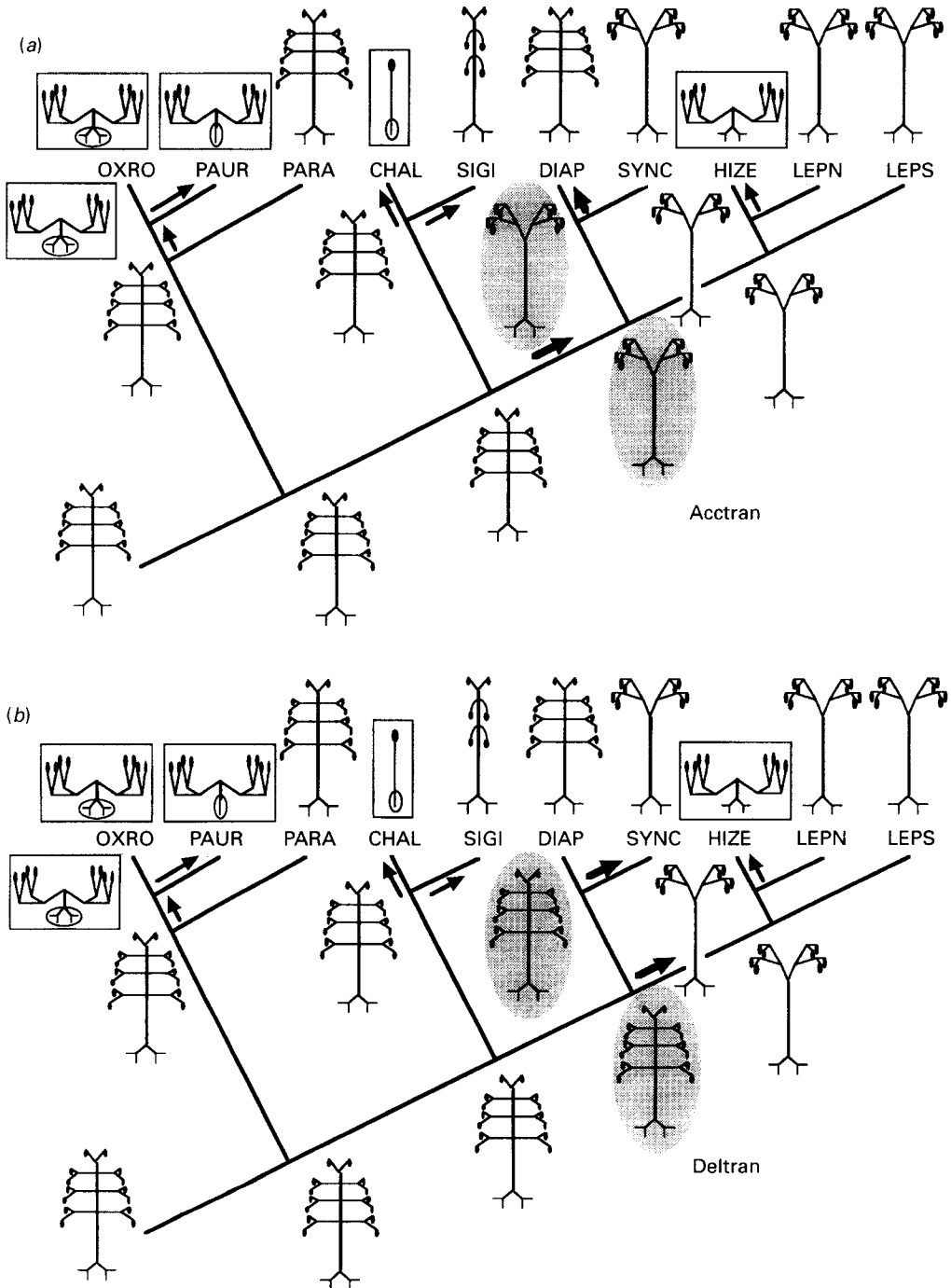


Fig. 15. Architectural characters presented in Table 2, mapped onto the author's preferred topology shown in Fig. 2b in order to reconstruct hypothetical ancestral architectures occupying internal nodes of the cladogram. Rooted using the architecture of *Paralycopodites*. High levels of homoplasy in the characters result in significantly different architectures at the highlighted nodes, according to whether Acctran (a) or Deltran (b) optimization is used. Internodes involving state changes in at least one architectural character are arrowed; large arrows denote positional differences between the two optimizations.

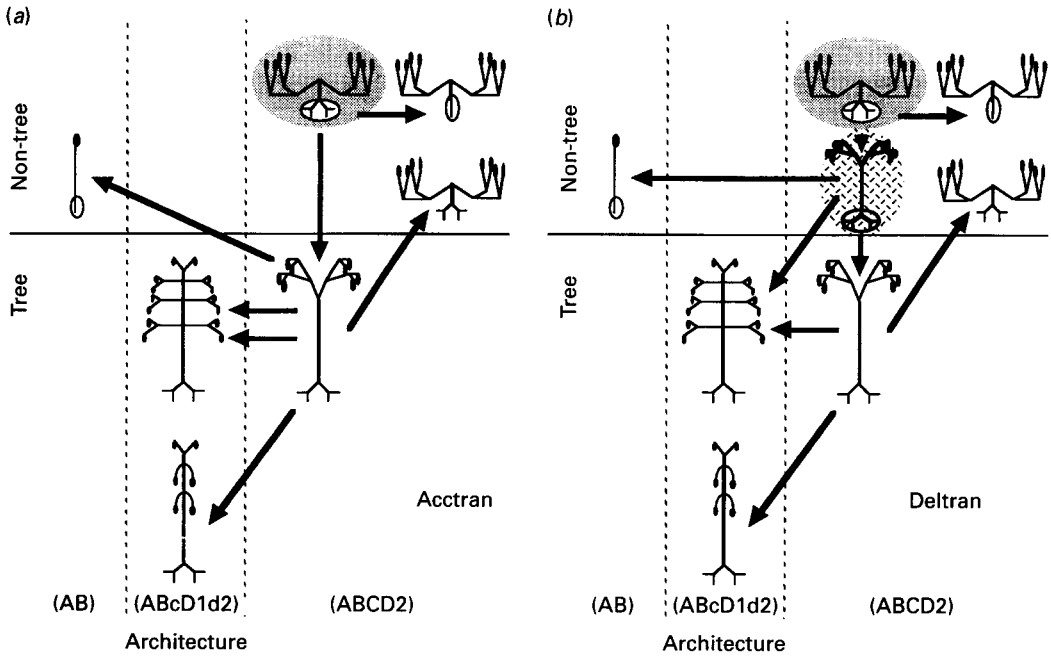


Fig. 16. Scheme of architectural transitions implied for the analytically correct topology by Fig. 14, focusing on changes in module composition and transitions between tree and non-tree. The designated plesiomorphic architecture is highlighted. (a) Acctran optimization; (b) Deltran optimization (note that the cross-hatched architecture has not yet been detected in nature).

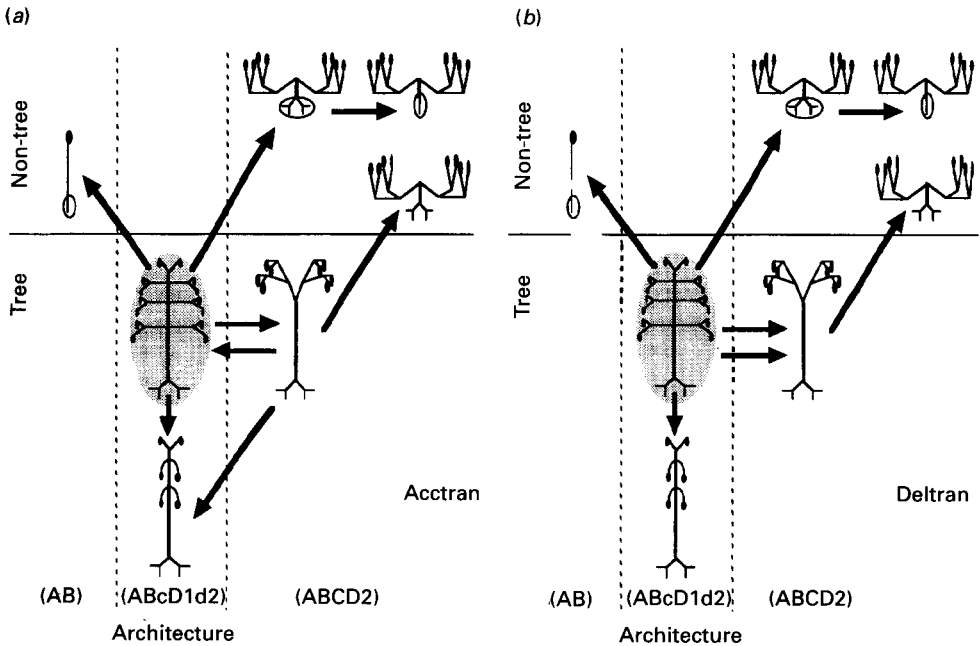


Fig. 17. Scheme of architectural transitions implied for the author's preferred topology by Fig. 15, focusing on changes in module composition and transitions between tree and non-tree. The designated plesiomorphic architecture is highlighted. (a) Acctran optimization; (b) Deltran optimization.

evolve from dominantly laterally branched (ABcD_{1d2}) trees (at least twice in the case of the ABCD₂ architectures). The primitive pseudoherbs evolve from an ABcD_{1d2} tree, and the derived pseudoherb evolves independently, from an ABCD₂ tree. There are no nontree-to-tree transitions.

In summary, each topology generates a range of hypotheses of architectural transitions that is bounded by contrasting optimization criteria. Substantial differences between the ranges of hypotheses for the two topologies are due more to the radically different choices of character-polarizing outgroup than to the topological differences *per se* or to optimization ambiguities within each topology. Nonetheless, some generalizations can be made. First, all the evolutionary hypotheses require three transitions between ABcD_{1d2} and ABCD₂ architectures; changes that were driven by the expression or suppression of the lateral branch module in its cauline position (D₁). Secondly, all hypotheses require three transitions between trees and non-trees, driven primarily by changes in the timing of the onset of developmental stages (heterochrony). Thirdly, any one of these schemes demonstrates that radical architectural change was rampant among the rhizomorphic lycopsids; of the 19 internodes in Figs 14 and 15, a minimum of 7–8 involved fundamental architectural transitions. Why were these transitions so common, and how did they occur?

VII. EVOLUTIONARY-DEVELOPMENTAL CHANGE: INFERRED PROCESSES

(1) *Developmental switches, cascades, and the domino effect*

The remarkable architectural variation among the rhizomorphic lycopsids can be explained largely in terms of modifications to the axial apical meristems – specifically, to their size and to the equality, spacing and ultimate number of divisions that they experienced under the influence of specific morphogens (cf. Wardlaw, 1965, 1968; Galston & Davies, 1969; Kaplan, 1971; Jong & Burt, 1975; White, 1979; Rosenblum & Basile, 1984; Gottlieb, 1986; Hardwick, 1986; Mishler, 1986; Watkinson & White, 1986; Poethig, 1988; Cheplick, 1989; Holmes, 1989; Goodwin & Saunders, 1992; Leyser & Furner, 1992; Mauseth, 1992; Bostrack, 1993). The vegetative transitions formed a developmental hierarchy; the earlier in ontogeny the meristematic modification was expressed, the more profound was its eventual phenotypic effect. If *Paralycopodites* is indeed the most appropriate outgroup among the rhizomorphic lycopsids, the most primitive architectures (and ontogenies) in the clade were the most complex. Subsequent evolution of the group entailed successively suppressing some developmental switches (thereby deleting specific modules) and altering the timing of expression of others (heterochrony *sensu stricto*).

This scenario is summarized in Table 3. *Paralycopodites* and *Diaphorodendron* possessed the maximum possible number of active hypothetical switches. In the only other ABcD_{1d2} tree, *Sigillaria*, all secondary divisions of the lateral branches were suppressed, leaving only primary lateral branches – cone peduncles attached directly to the stem. The transition from ABcD_{1d2} trees to ABCD₂ trees involved the suppression of a higher order switch that controls *primary* (anisotomous) lateral branching prior to the first isotomous division of the stem apical meristem. This yielded the relatively derived, expansively crown-branched trees *Synchysidendron*, *Lepidodendron* and *Lepidophloios* (Fig. 2).

Table 3. *Hypothetical hierarchy of meristematic controls determining the architecture of rhizomorphic lycopsid genera* ('+' = on, '-' = off)

[The type of meristematic division determines the number and type of developmental modules (A-D₂), whereas the timing of meristematic division determines body size and allows truly heterochronic transitions. For key to genera see caption to Fig. 2.]

Genus	PS = DI SI SY = LN = LS OX HZ PN CH									
	Tree					Non-tree				
	ABCD _{1d2}					ABCD ₂				
Tree: non-tree										
Basic architecture	ABCD _{1d2}					ABCD ₂				
TYPES OF MERISTEM DIVISION										
Embryonic bipolar division	+	+	+	+	+	+	+	+	+	+
Division of either bipole	+	+	+	+	+	+	+	+	+	-
Isotomous division of rhizomorph pole	+	+	+	+	+	+	+	+	+	-
Isotomous division of stem pole	+	+	+	+	+	+	+	+	+	-
Anisotomous division of stem pole	+	+	+	+	+	+	+	+	+	-
Anisotomous division of stem pole before first isotomy	+	+	+	-	-	-	-	-	-	-
Secondary division of anisotomous branch	+	+	-	-	-	-	-	-	-	-
TIMING OF MERISTEM DIVISION VERSUS AXIAL ELONGATION										
Early elongation of bipoles prior to extensive apical doming	-	-	-	-	-	-	+	+	+	+
Early isotomy prevents extensive elongation of stem	-	-	-	-	-	-	+	+	+	-
Early isotomy prevents extensive elongation of rhizomorph	-	-	-	-	-	-	+	-	-	-

The same switch was suppressed during the evolution of the ABCD₂ pseudoherbs, but here a series of heterochronic changes accelerated specific meristematic dichotomies. In the plesiomorphic trees, the primary meristems of the two germinal poles (rhizomorph and stem) expanded laterally into the huge apical domes necessary for subsequent extensive elongation (to 10–30 m in the case of the stem). In the non-trees, elongation of the two poles commenced before substantial lateral expansion had occurred, thereby increasing growth rate at the expense of ultimate body size. In the three pseudoherbaceous genera, stem elongation was rapidly followed by a precocious first isotomy of the stem apical meristem to generate a low-growing crown. The evolutionary response among their rhizomorphs was more varied. *Hizemodendron* apparently showed little change from the plesiomorphic tree morphology other than decreased size. In *Oxroadia*, vascular dichotomies were retained but became more closely spaced, allowing their enclosure by a compact, almost unlobed cortex. Rather than heterochronically condensed division, the rhizomorph of *Paurodendron* experienced a stage deletion; meristematic division of the rhizomorph pole was wholly suppressed, leaving an unlobed fusiform rootstock.

Lastly, the simple ontogeny of small-bodied isoetaleans such as *Chaloneria* could reflect inactivation of an even higher level switch; meristematic division was suppressed in both embryonic poles, as was lateral expansion and doming of the meristem.

As depicted in Table 3, only one meristematic switch remained active in all ten genera; that initiating the earliest axial vascular dichotomy, which typically occurred within the megaspore and generated the positively and negatively geotropic poles.

There can be little doubt that this earliest of switches was equally vulnerable to suppression by mutation, but in this case the phenotypic product would inevitably have been inviable. Loss of the stem would prevent photosynthesis and reproduction; alternatively, loss of the rhizomorph would prevent absorption of water and nutrients. In either case, the resulting plant would be deprived of the rhizomorphic syndrome and forced to undergo plesiomorphic unipolar growth without the other plesiomorphic necessities for such growth, notably a rhizome and adventitious roots. In short, the only inviolable developmental constraint on the rhizomorphic lycopsids was, appropriately, the presence of the rhizomorph. Within this constraint, the plants were free to experiment with various combinations and degrees of development of the four basic architectural modules; most possible architectural permutations appear to have been viable (note that their viability does not necessarily imply that such architectures conferred a high level of fitness).

This scenario requires a hierarchy of developmental switches; for example, relative to the most complex architecture (e.g. *Paralycopodites*), aerial branching can be suppressed (1) in the entire system (e.g. *Chaloneria*), (2) in primary cauline lateral branching (e.g. *Lepidodendron*), or (3) in secondary cauline lateral branching (e.g. *Sigillaria*). This particular example shows three parallel hierarchies; of time, the number of module types affected, and the relative size of the modules affected. The suppression of the switch operating earliest in ontogeny deleted both types of large-scale primary branching, whereas the late-stage suppression of secondary division in the cauline lateral branches deleted only small sub-modules. In this scenario, loss of secondary cauline lateral branching could occur by mutations affecting three different ontogenetic stages – in (3) the loss was a direct result of the mutation, but in (1) and (2) it was merely the inevitable consequence of changes occurring earlier in the various hierarchies. I refer to such changes occurring within a developmental cascade as the ontogenetic domino effect (Table 1).

Heterochronic changes affecting the timing of ontogenetic events can also have an indirect domino-type effect. For example, early elongation of the stem prevented lateral expansion of the meristem; under the constraint of determinate growth, this in turn prevented growth to tree-sized dimensions. Also, the highly precocious primary isotomy in the pseudoherbs would probably have prevented expression of lateral branching on the stem even if the developmental switch for such branching remained operative.

All of the above phenotypic changes, both direct and indirect, are manifested in the original mutant individual(s). However, other results of evolutionary-developmental change are expressed in subsequent generations, as a result of selectively-mediated phenotypic modifications that reflect loss or transference of function following the mutation; this phenomenon is here termed 'selective cropping' (Table 1). Evolutionary-developmental change, the domino effect, and selective cropping can all influence 'burden': the functional responsibility of a trait, as measured by the number and magnitude of dependent traits (cf. Riedl, 1979; Fortey & Jefferies, 1982; Donoghue, 1989). This concept ties the connectivity of traits to their temporal sequence, spatial relationships, scale of phenotypic expression, and adaptive value.

Whatever the underlying cause, it is clear that different types of evolutionary-developmental change can cause morphological convergence. For example, three of the

ten genera studied possessed small, compact, 'cormose' rhizomorphs with little or no cortical lobing. However, careful examination of the evidence suggests that this reflects high-level suppression of all polar vascular division in *Chaloneria*, a lower level suppression of vascular division in the rhizomorph pole only in *Paurodendron*, and merely precocious (and thus closely-spaced) secondary dichotomies of the rhizomorph vasculature in *Oxroadia*.

The putative early-stage suppression of meristematic division in both poles of isoetaleans such as *Chaloneria* explains, either directly or indirectly, their entire architecture. Deprived of the ability to branch in either stem or rhizomorph, the plants were obliged to improvise. Cones could be produced only as a single terminal structure, thereby constraining the plant to relatively low reproductive output and monocarpy. However, this constraint was relatively easily overridden. Several lineages (including that leading to *Isoetes*) abandoned the aggregation of sporophylls into cones and reverted to a deeply plesiomorphic condition; microphyll leaves attached to the stem were replaced with sporophylls in a clear-cut example of heterotopy (e.g. Meyen, 1988; Sattler, 1988). The resulting 'fertile zones' allowed increased reproductive output and polycarpy. Meanwhile, in the unbranched rhizomorph, the lack of meristematic branching (and the lack of doming in smaller-bodied genera) greatly restricted rootlet production. One way to increase rootlet number was to evolve the characteristically elongated (and thus bilaterally symmetrical) apical meristem and/or exaggerated lobing.

The overall impression gained is that plants experienced 'unwanted', non-adaptive changes in growth architecture and then, having survived these indignities, attempted adaptive adjustments to generate a fitter morphology within the new architectural constraints. Is this a viable evolutionary scenario?

(2) *Relative roles of adaptive selection and non-adaptive saltation*

Most evolutionary scenarios are now couched in strictly neoDarwinian terms, relying primarily on small-scale, non-lethal mutations as the source of genetic novelty and on natural selection to drive evolution by gradual, population-level changes in gene frequencies (e.g. Dawkins, 1986). A rare dissenting voice, Goldschmidt (1940) argued that major taxonomic groups of animals evolved by 'systemic mutations'; large-scale chromosomal rearrangements that altered early developmental trajectories to create 'hopeful monsters' – teratological lineages of radically different body-plans that by chance possessed high levels of fitness. Such monsters effectively represented speciation events across a single generation (here termed *saltational* evolution; see Bateman & DiMichele, 1994). Goldschmidt's scenario was overwhelmed by the collective might of contemporary geneticists such as Fisher (1930), Haldane (1932), Dobzhansky (1951) and Mayr (1963), who wielded the then recently forged *New Synthesis* like a sword to cut heretics such as Goldschmidt down to size. Thus, history labelled 'hopeful monsters' as 'hopeless' and Goldschmidt's opinionated Germanic pronouncements as 'politically incorrect'.

Writing with the benefit of hindsight (and of the molecular revelations of Watson & Crick, 1953*a, b*), Gould (1982) was able to identify two cardinal errors made by Goldschmidt (1940): appealing to large-scale genetic modifications to explain large-

scale phenotypic changes, and requiring competitively high levels of fitness in those few monsters whose hopefulness was rewarded by successful establishment – that is, who passed the acid test of historical continuity. Goldschmidt's hypothesis was most effectively resurrected and reformulated in a broadly neoDarwinian context by Arthur (1984, 1988), who recognized that the key causal factor in teratology is not the number of base-pairs affected by a mutation but the position of the modified genes in the hierarchies of phenotypic expression. Specifically, Arthur envisaged a molecular universe of enzyme-producing structural genes that are in turn controlled by regulatory genes. If the enzyme in question is concerned only with biochemical maintenance functions, the structural genes are termed S-genes and the regulatory genes R-genes. However, if the enzyme is a morphogen affecting early ontogeny, both the structural and regulatory genes are termed D-genes. These were subdivided by McKinney & McNamara (1991) into type I D-genes, which control intercellular development (i.e. rearrange cells), and type II D-genes, which control intracellular development (i.e. determine cell type). In plants, modifications to type II D-genes are most likely to generate evolutionary novelties (Bateman & DiMichele, 1994).

Within a specific ontogeny, the relative time of activation of a particular D-gene is crucial. On average, mutations of early acting D-genes have more profound phenotypic effects than those operating later in ontogeny. Also, the model suggests that later developmental stages will be controlled by a greater number of D-genes of lesser effect, often acting in concert to generate continuous variation (polygenic) or with complex expression heavily modified by the internal environment of the organism (epigenetic: e.g. Goodwin & Saunders, 1992). In contrast, early-acting D-genes are more likely to be expressed in a wide range of characters distributed widely across the bauplan (pleiotropic). Any mutation suppressing a strategic D-gene can cause a complex series of biochemical interactions to collapse like a house of cards, particularly if the developmental system affected is relatively simple and devoid of viable alternative pathways.

Back-mutation is also conceivable, restoring a temporarily suppressed developmental switch. During its period of non-expression, the system controlled by the switch will have been released from selection but will remain subject to random genetic drift (e.g. Kimura, 1983). Thus, restoration of the switch can result in the expression of a phenotype significantly different from the plesiomorphic homologue. For example, a cladistic analysis by Mooi (1990) demonstrated the suppression, and subsequent reinstatement in a different form, of the feeding apparatus of clypeasteroid echinoderms during their evolution.

For the remainder of this discussion I will assume that the deliberately enigmatic 'developmental switches' of Table 3 are, in fact, high-ranking type II D-genes. The architectural changes documented in the rhizomorphic lycopsids are consistent with probable point mutations of key D-genes controlling early development (dichotomous saltations *sensu* Bateman & DiMichele, 1994). Their presumably simple developmental controls and consequent lack of alternative developmental pathways probably rendered the rhizomorphic lycopsids particularly prone to such modification.

Turning to the second major question – that of fitness – all of the main protagonists in the original hopeful monster controversy were zoologists (cf. Gould, 1982; Dawkins, 1986). They were intimidated by the awesome difficulties faced by any hopeful

monster, both in terms of initial economic existence (ecological establishment) and eventual reproductive potential (lineage establishment). Although the *ad hoc* nature of saltation undoubtedly results in organisms possessing a wide range of fitnesses, the high degree of fitness attributed by Goldschmidt to the most fortunate of the hopeful monsters has justifiably been challenged; it seems certain that even the fittest hopeful monsters were competitively weak relative to well established pre-existing species that had been honed to near-optimal fitness in their chosen habitats by natural selection; indeed, the monsters would have been competitively inferior to their own genealogical parents. The best solution to this conundrum is to temporarily release the monsters from competition and thus from selection (Waddington, 1957; Valentine, 1980; Arthur, 1984, 1988; DiMichele *et al.*, 1987; Levinton, 1988; Bateman & DiMichele, 1994, fig. 6). This is most readily achieved by establishing the monster(s) in a vacant niche or, better still, the somewhat abstract ensemble of vacant niches that comprise a vacant habitat. Under these circumstances, the monster need only be sufficiently efficient to allow day-to-day economic survival (*sensu* Eldredge, 1989) and eventual reproduction. This economic threshold would be surpassed by any rhizomorphic lycopsid still capable of producing aerial and subterranean axes, rootlets, and sporangia containing viable spores (even leaves were probably superfluous; much of the overall photosynthetic activity must have occurred in the axes).

Today, well adapted plant species (dominantly angiosperms in most habitats) occupy all but the most stringent habitats of the globe. They form complex, speciose, integrated communities held together by extensive biotic interactions (Clementsian). However, during the main radiation of the rhizomorphic lycopsids in the Late Devonian and Carboniferous, communities occupying comparable habitats were less complex, less speciose (DiMichele *et al.*, 1987, 1992), and arguably less well integrated (more Gleasonian: Bateman, 1991 *a*). Occupied niches were broader and unoccupied niches more numerous; at least some arid environments were ecological vacuums devoid of vascular plants. This non-uniformitarian view of communities prescribes an increasing probability of release from selection backward through time, and thus an increasing hope of survival for monsters (e.g. Valentine, 1980; DiMichele & Aronson, 1992; Bateman & DiMichele, 1994).

Even in the relatively rich communities of the Late Carboniferous coal-swamps, which yielded most of the species used as OTUs in this analysis, many habitats offered a surfeit of free water and/or deficits in many nutrients, thereby generating the high levels of intrinsic stress that discourage intense biotic competition (DiMichele *et al.*, 1987). Thus, albeit rarely, adaptively inferior architectural mutants occupied by chance niches or habitats offering minimal competition, where they were able to reproduce to form the first population of a new, radically different and geologically instantaneous species. Early selection pressures would be generated by intraspecific competition within the new population, but as the population expanded to occupy greater geographical (and thus ecological) ranges, it would experience increasing interspecific competition. Such gradual re-introduction to selection allows a slim chance of honing to greater fitness the new lineage within the constraints of the new architecture while avoiding selection pressures sufficiently intense to drive the population to extinction. Many ancestral characters are lost instantaneously as a direct result of the saltational architectural transition, but many more lose their adaptive function and are eliminated

subsequently and gradually by *bona fide* neoDarwinian selection. The small initial size of such populations renders them especially prone to unusually rapid, non-Mendelian changes in gene frequencies (parasaltation *sensu* Bateman & DiMichele, 1994).

Only this saltational hypothesis can explain the unintuitive morphology of, for example, the pseudoherbaceous lycopsid lineages (Bateman & DiMichele, 1991; Bateman, 1992*a*; Bateman *et al.*, 1992). The rhizomorphic syndrome has all the hallmarks of an adaptive breakthrough that facilitated the tree habit – that is, a large body size and upright, genuinely bipolar growth. However, in the context of the pseudoherbs, this inescapable developmental constraint more closely resembles a serious handicap; the pseudoherbs evolved as best they could within their newly-acquired developmental shackles. The repeated evolution of pseudoherbs from trees is most consistent with non-adaptive saltational origin of the new architecture. Subsequent adaptive restructuring of the smaller-scale anatomy of the plant to accommodate its new overall growth form (Bateman & DiMichele, 1994, fig. 7) improved its fitness in its new interstitial understorey niche within the open forests of the coal-swamps. Nevertheless, among the lycopsids, the rhizomorphic (bipolar) pseudoherbs appear less well adapted to such niches than their distant ancestors among the rhizomatous (unipolar) herbs. The secondary thickening of the pseudoherbs is energetically wasteful to little structural advantage, given their recumbent growth habit. Moreover, their retention of centralized, determinate growth denied them the ancestral benefits of truly prostrate growth and vegetative reproduction that characterize non-rhizomorphic lycopsids. In this context, their ontogeny is a strong phylogenetic constraint (cf. McKittrick, 1993).

Discussion of the relationship between evolutionary-developmental change and ecology can be further extended to take account of the ‘maturity’ of the clade. A major climatic warming and drying phase began in the Euramerican tropics at the Westphalian–Stephanian boundary and spread diachronously across the globe during the Stephanian and Early Permian (e.g. Phillips & Peppers, 1984; Phillips, Peppers & DiMichele, 1985; DiMichele *et al.*, 1987; DiMichele & Aronson, 1992). The most persistent of the tree-sized rhizomorphic lycopsids was *Sigillaria*, which was less tied to peaty substrates and may have been liberated from dependence on free water for reproduction by apomixis (DiMichele & Phillips, 1985; Phillips & DiMichele, 1992). Nonetheless, global drying eventually eliminated all but the developmentally simplest, isoetalean lineage of rhizomorphic lycopsids. These remained relatively diverse and locally ecologically dominant in some habitats during the Mesozoic, but by the Cenozoic were represented only by small-bodied, *Isoetes*-like plants (e.g. Pigg, 1992). Most were (and are) confined to habitats that are of high intrinsic stress and thus of low biotic competition, typically occurring as specialized riparians with large polyploid chromosome complements and unwieldy genomes (e.g. W. Taylor & Hickey, 1992). These last relicts of a once globally co-dominant clade wholly fulfil Hyatt’s (1889) predictions that such ‘living fossils’ are likely to be developmentally simple, genetically ‘saturated’, and confined to ecological refugia (Gould, 1977).

They also raise the intriguing possibility of ploidy changes among Palaeozoic lycopsids (Bateman, 1992*a*; see also Soltis & Soltis, 1988); allopolyploidy also generates new species in a single generation, and hence was termed reticulate saltation by Bateman & DiMichele (1994). Interestingly, Brack-Hanes & Vaughn (1978) inferred

a low haploid karyotype of $n = 8$ or 9 for exceptionally preserved microspores that were probably produced by the relatively primitive rhizomorphic lycopsid *Paralycopodites*, suggesting that any ploidy increases occurred later in the evolutionary history of the group.

To summarize, the new formulation of neoGoldschmidtian saltation outlined above does not require 'systemic mutations' to generate the hopeful monsters or high degrees of fitness to perpetuate them. It merely requires non-uniformitarianism in community structure and establishment (however rare) of lineages of radical developmental mutants in the temporary absence of competitively-mediated selection. Saltation is not, as is commonly misconceived, anti-Darwinian – rather, it is supra-Darwinian (cf. Gould & Lewontin, 1979; Bateman & DiMichele, 1994).

VIII. BROADER IMPLICATIONS

(1) *Fossil rhizomorphic lycopsids as a test case of evolutionary-developmental change*

The rhizomorphic lycopsids were chosen by Bateman *et al.* (1992) as the clade offering the best available data for applying cladistic principles to a group of fossil plants; the resulting implications for study of evolutionary-developmental change were an unexpected by-product of that study. Their remarkable determinate, modular growth and presumed simple genetic control of development appear to have rendered them unusually prone to saltational architectural changes; these in turn were unusually clearly expressed and thus easily detected. The Palaeozoic age of the species analyzed (OTUs), and consequent differences in community composition and interactions, allowed far more frequent establishment of architecturally divergent mutant lineages.

More generally, a wide range of opinions have been expressed regarding the use of fossils in phylogeny reconstruction: optimists argue that fossils should be given the same treatment as living OTUs (Gauthier *et al.*, 1988; Donoghue *et al.*, 1989; Bateman, 1992*b*; Bateman *et al.*, 1992; Doyle & Donoghue, 1992), pragmatists that certain extrinsic factors such as completeness of the fossil record and primitiveness of the fossils should be considered (Fortey & Jefferies, 1982; Huelsenbeck, 1991; Fisher, 1992), and pessimists that fossils are inexcusably troublesome and should be inserted into phylogenies *a posteriori* (Patterson, 1981; Loconte & Stevenson, 1990; Forey, 1992).

Here, the fact that the clade is almost extinct (it is represented in the modern flora only by the highly derived, ecologically specialized, paedomorphic isoetalean lineage) has not deleteriously affected the range of morphological–anatomical data that could be acquired, nor has it weakened the data-matrix with large tracts of missing values. Rather, the main problem posed by fossils is the inability to observe directly (or experiment on) the ontogeny of individuals through time, their morphology and those of other co-occurring (and potentially completing) species, and their preferred habitats. Fortunately, all these criteria can be inferred with some confidence for the best-known fossil species.

(2) *Architectural versus smaller-scale characters in lycopsid phylogeny*

Table 4 presents a breakdown of the relative levels of phylogenetically useful information obtained from different organs of the rhizomorphic lycopsids. The total

Table 4. Comparison of the number and phylogenetic information content of bistate characters from different organs (and, in the case of vegetative axes, different tissues) of 16 species of rhizomorphic lycopsid

Organ/ tissue	Total no. of characters scored	No. (and percentage) of			Mean value per informative character (and sample standard deviation) of		
		Informative characters ⁵	Non-homoplastic synapomorphies	No. of changes	Retention index	Rescaled consistency index	
Cones <i>sensu lato</i> ¹	19	14 (74)	11 (79)	1.29 (0.61)	0.95 (0.10)	0.86 (0.28)	
*Stele	18	13 (72)	10 (77)	1.23 (0.44)	0.94 (0.14)	0.85 (0.28)	
*Periderm	14	11 (79)	8 (73)	1.27 (0.47)	0.91 (0.17)	0.82 (0.32)	
Vegetative axes*	52	39 (75)	24 (62)	1.44 (0.64)	0.89 (0.17)	0.75 (0.33)	
*Leaf bases	15	13 (87)	6 (46)	1.54 (0.52)	0.86 (0.16)	0.66 (0.33)	
Microspores ²	14	11 (79)	5 (45)	1.64 (0.67)	0.72 (0.34)	0.58 (0.41)	
Megaspores ²	10	2 ⁶ (20)	1 (50)	1.50 —	0.50 —	0.50 —	
Leaves ³	7	7 (100)	2 (29)	2.29 (1.25)	0.66 (0.35)	0.45 (0.40)	
*Cortex	5	2 ⁶ (40)	0 (0)	3.00 —	0.65 —	0.26 —	
Architecture ⁴	10	6 (60)	0 (0)	2.50 (0.55)	0.52 (0.26)	0.21 (0.12)	
Rhizomorph ³	3	1 ⁶ (33)	0 (0)	2.00 —	0 —	0 —	
All Organs	115	80 (70)	43 (54)	1.60 (0.77) ⁷	0.81 (0.28) ⁷	0.66 (0.38) ⁷	

¹ Cone axis, sporophyll and sporangium.

² Organ under-described, due to lack of wall ultrastructural characters.

³ Organ under-described, due to insufficient study of some OTUs.

⁴ Includes three characters (C8-C10), one phylogenetically informative, that were listed under 'Rhizomorph' by Bateman *et al.* (1992).

⁵ To be deemed informative, characters must be scored as apomorphic for more than one OTU but not for all OTUs.

⁶ Sample statistically too small for meaningful discussion, due largely to high proportions of autapomorphic states.

⁷ Mean rather than ensemble values (cf. Farris, 1989; Wiley *et al.*, 1991).

number of bistate characters scored and, more importantly, the number of phylogenetically informative characters scored, varies greatly among organs. Admittedly, these figures are somewhat distorted by insufficiently careful study of rhizomorphs and leaves in some OTUs and of spore ultrastructure in all OTUs. Nonetheless, they largely reflect the contrasting levels of complexity in different organs, which is highest in cones and, especially, vegetative axes (the rhizomorphic lycopsids are best viewed as large-scale axial frameworks bearing cones: DiMichele & Phillips, 1985). In the case of the character-rich vegetative axes, the comparison in Table 4 is extended to contrast their four component tissues (listed centrifugally: stele, cortex, periderm, leaf bases). Four measures of information content per character are presented: the proportion of non-homoplastic synapomorphies (i.e. apomorphic states confined to, and ubiquitous among, the members of a single clade), the mean number of changes depicted for a character (the reciprocal of this value is the widely used consistency index), the mean retention index (a better measure of information than the consistency index, as it is adjusted to give a potential minimum value of zero), and the mean rescaled consistency index (the arithmetic product of the consistency index and the retention index: for further discussion see Farris, 1989; Swofford & Olsen, 1990; Wiley *et al.*, 1991). These four measures of homoplasy are all inter-related and therefore as expected show strong positive correlation. Here, the rescaled consistency index is considered to have the strongest logical support and the organs are listed accordingly in Table 4, from the most to least reliable. Contradictions to this ordering of organs among other listed parameters are largely confined to the mean number of state changes, in organs represented by few informative characters. (Alternative approaches to sub-matrix comparison, based on contrasting topologies rather than characters, are currently being developed; e.g. Page, 1993.)

Table 4 confirms the opinion expressed by Bateman *et al.* (1992) that organs which are intermediate in both size and timing of ontogenetic expression (vegetative axes, cones) show less homoplasy, and thus play a greater role in determining cladogram topologies, than small-scale organs (leaves, spores). These in turn show less homoplasy than the largest-scale, architectural characters. Leaves and spores occur at the termini of ontogenetic trajectories, and thus are of low burden; they can be modified without causing generally deleterious changes later in their respective developmental cascades. The small and developmentally simple microphyllous leaves of the rhizomorphic lycopsids were probably pre-programmed, rather than interacting with the apical meristem via the physiological feedback loops favoured by the megaphyllous lignophytes (Steeves, 1993). In addition, spores are single cells, and thus in aggregate are capable of expressing an unusually limited range of morphological variation (admittedly, rhizomorphic lycopsid spores indulge in a wide variety of surficial ornamentation). This constraint makes convergence far more likely to occur and far less likely to be detected *a priori*. Thus, the focus of most current plant developmental studies – on transient organs such as leaves (e.g. Allsop, 1967; Jones, 1993; McLellan, 1993; Steeves, 1993) and flowers (e.g. Lord, 1981; Tucker, 1988; Guerrant, 1989; Coen & Meyerowitz, 1991; Coen & Carpenter, 1992; Green, 1992; Kampny *et al.*, 1993; Gustafson-Brown, Savidge & Yanofsky, 1994) – tells us little about larger-scale architectural evolution.

In contrast to determinate appendages, axial architecture is determined early in

ontogeny by primary meristem behaviour. Although of high burden and influencing many smaller-scale features, architectural changes could clearly be accommodated without rendering the resulting lineage inviable due to severely impaired physiology or reproductive capacity. Indeed, it was the features of vegetative anatomy and cone morphology, most intimately connected with physiology and reproduction respectively, that were most highly conserved and least prone to reversal (a conclusion that would undoubtedly have pleased Linnaeus).

(3) *Architectural studies of extant clades*

Hallé (1978) documented major architectural mutants within several species of dominantly tropical angiosperm trees. These included the loss of branching and consequent cauline expression of reproductive organs in *Manihot esculenta*, *Hevea brasiliensis* (both Euphorbiaceae), *Corchorus capsularis* (Tiliaceae), *Gossypium hirsutum* (Malvaceae) and the gymnosperm *Pinus caribaea* (Pinaceae); architectural changes analogous to the inferred origin of the isoetalean lycopsids. In contrast, a switch from unbranched stem and lateral reproduction to rhizomatous growth and terminal reproduction has been observed in *Ravenula madagascariensis* (Strelitziaceae). Rapid suppression of the stem terminal meristem in angiosperms such as *Gossypium hirsutum* and *Abroma augusta* (Sterculiaceae) yields smaller-bodied architectures similar to those of pseudoherbaceous rhizomorphic lycopsids such as *Oxroadia* and *Hizemodendron* (Hallé & Oldeman, 1975). Not all of these modern architectural transitions reflect mutations in the nuclear genome (Hallé, 1978), but those that are heritable offer obvious opportunities for saltational evolution of architecture.

Most of the few comparative studies of extant tracheophyte clades that have given serious consideration to overall architecture also indicate high frequencies of evolutionary iteration in large-scale features of plant form. These suggest that previous use of architecture to arrange related species in linear evolutionary sequences of vectorial (unidirectional and progressive) stepwise size/shape changes, such as the often reproduced 'paedomorphoclines' inferred for living and fossil isoetalean lycopsids by Mägdefrau (1956) and for extant species of the bromeliad genus *Tillandsia* by Tomlinson (1970), are probably gross over-simplifications that would be contradicted by rigorous cladistic analyses.

To date, most phylogenetic studies of architectural radiations have focused on relatively recent morphological radiations among dicotyledonous angiosperms on physical or ecological islands. Funk's (1982) morphological cladistic analysis of the tropical American asteracean genus *Montanoa* suggested repeated evolution of polyploid tree-sized species that specialized in upland cloud-forest habitats from diploid shrubs and lianas of the lowlands (Funk & Brooks, 1990; Bateman & DiMichele, 1994). This scenario may now require modification, as a recent cpDNA phylogeny contradicts the preferred morphological topology (Panero & Jansen, 1993). Nonetheless, similar radiations have been documented in the asteracean *Stenopadus* among the tepuis of South America (Funk & Brooks, 1990). East African *Senecio* and *Lobelia* also show repeated origins of unusually large and woody, tetraploid and hexaploid upland specialists from diploid, herbaceous ancestors (Knox & Kowal, 1993; Knox, Downie & Palmer, 1993), as do island endemic species of *Echium*. Studies of the

recent radiations in the Hawaiian islands of two other asteracean clades, *Tetramolopium* (Lowrey & Crawford, 1985; Lowrey, 1993) and the silverswords (Baldwin *et al.*, 1990, 1991; Baldwin, 1992), graphically illustrate that major morphological radiations can occur very rapidly and with minor genetic changes; the degree of phenotypic change does not reflect the number of genes that are modified but rather the magnitude of their effect.

In summary, all of these angiosperm radiations are consistent with saltational scenarios. However, they differ from the rhizomorphic lycopsid case-study in one important characteristic. The dominant evolutionary pattern in the lycopsids is pedomorphosis and the generation of non-trees from trees, but with one exception (the Hawaiian lobelioids studied by Lammers, 1990) the dominant pattern among the island angiosperms is the generation of trees from non-trees (see also D. Taylor & Hickey, 1993). This discrepancy could indicate different developmental controls of the independently evolved secondary thickening of the rhizomorphic lycopsids and the seed-plants, but it is more likely to be caused by contrasting ecological filters that reflect differences in niche partitioning and occupancy.

(4) *Outgroups, rooting, long branches, and character polarization : a role for developmental parsimony*

The most serious phylogenetic problem presented by the rhizomorphic lycopsids is unrelated to their status as fossils; indeed, it plagues cladistic studies of extant plant groups. It is the search for the most appropriate method and/or taxon to root the cladograms. The use of developmental criteria to polarize characters in fossils is precluded by the inability to directly observe ontogeny. Moreover, I regard the plant fossil record as clearly inadequate to allow the use of earliest occurrences of OTUs for polarization (though many palaeontologists would disagree with this assertion). Rejecting these options leaves only outgroup comparison (e.g. Maddison *et al.*, 1984), using either one or more real species or a hypothetical construct (for example, the slight modification of *Oxroadia gracilis* used to root Figs. 1 and 2*a*). Choosing such a species is both critical and problematic.

Most higher taxa are separated by long branches from their closest sister group – that is, in any objective analysis, the taxon would be separated from its sister group by many character-state changes, reflecting a large phenetic (and, usually, patristic) distance. Both recognition of homologous features and scoring of homologous states are especially difficult to achieve across such discontinuities. Moreover, selecting two or more disparate, distant taxa as multiple outgroups rather than using a single outgroup merely adds to the ambiguities of character change between outgroup(s) and ingroup. For example, the most probable known sister group of the rhizomorphic lycopsids is the homophyllous selaginellas (Bateman, 1992*a*). However, an immense morphological discontinuity separates the two groups, delimited in part by the many characters that define the rhizomorphic syndrome and hence are absent from the selaginellaleans. Long outgroup–ingroup branches can be avoided by selecting an outgroup from within the higher taxon under scrutiny as being its most primitive member. Possible criteria for recognizing primitiveness in a phenetic outgroup may sound familiar to the reader. They include the criteria offered as alternatives to outgroup comparison: morphological

and/or developmental simplicity, earliest occurrence in the fossil record, and generality (frequency) of character states among the OTUs.

Bateman *et al.* (1992) chose *Oxroadia* as a model for constructing their outgroup primarily because it was much the earliest of their OTUs to have been satisfactorily reconstructed; it also appeared to be morphologically simpler than all other OTUs but *Paurodendron fraipontii* and *Chaloneria cormosa*. This paper has gradually developed a different criterion for recognizing primitiveness, based on the inferred functional morphology of species. I have argued above that the morphologies of the small-bodied isoetalean shrubs such as *Chaloneria* and pseudoherbs such as *Oxroadia* only make biological sense if they are the developmentally constrained descendants of tree-sized ancestors; much of their morphological simplicity is misleading, reflecting not primitiveness but paedomorphosis *sensu stricto* and/or ontogenetic stage deletion (an error that has probably been made in the choice of outgroups for many other cladistic studies). Irrespective of first observed occurrences (see Section III(2)), the first *bona fide* rhizomorphic lycopsid must have been a tree. This conclusion transferred the focus of the search for the best outgroup from the small-bodied genera back to the earliest known fully reconstructed tree, the relatively modestly-sized *Paralycopodites brevifolius* (DiMichele & Bateman, 1989). This species has the added advantage of possessing relatively simple anatomy and being the only reconstructed tree to produce bisporangiate cones, a key primitive state that characterizes all of the potential sister-groups of the rhizomorphic lycopsids (e.g. Bateman, 1992 *a*). Moreover, *Paralycopodites* proved to be the focus of an unrooted phenetic tree generated from the cladistic matrix (Bateman *et al.*, 1992, fig. 13). However, it shares with *Diaphorodendron* the cauline laterally branched architecture (ABcD1d2); can this most complex of lycopsid body-plans really be plesiomorphic?

An alternative approach to inferring architectural primitiveness is to apply *developmental parsimony* – specifically, to assess the smallest number of modifications necessary to generate a bipolar arborescent lycopsid tree from a putatively ancestral unipolar, non-arborescent herb. First, it seems likely that the earliest rhizomorphic lycopsid would express its newly acquired secondary thickening throughout its axial systems; more localized expression (such as that generating the almost wood-free, disposable lateral branches of *Paralycopodites*) would require the subsequent evolution of more sophisticated developmental controls. The only OTU that expressed extensive secondary thickening throughout its body – the monosporangiate coned tree *Diaphorodendron scleroticum* (DiMichele, 1985) – is unquestionably relatively derived (Fig. 1). Secondly, the same principle can be applied to the homologies inferred between the two main axial systems, root and shoot, which reflect the architectural innovation of bipolarity that first allowed the evolution of the rhizomorph. Strong developmental parallels have been demonstrated between the two systems, not only in terms of homologies (e.g. of microphyll leaves with rootlets) but also in terms of the similar evolutionary-developmental changes shown by the concurrently growing rhizomorph and stem (e.g. Figs 10, 12). The earliest rhizomorphic lycopsid is thus likely to have possessed whichever architecture incorporated a shoot system most closely resembling the corresponding root system. Using the large, frequently and isotomously branched stigmarian system as a model of primitiveness in rhizomorphs would place the emphasis for primitive aerial axes not on trees with well developed cauline lateral branching such

as *Paralycopodites*, *Sigillaria* and *Diaphorodendron* but on extensively crown-branched (and, unfortunately, reproductively derived) trees such as *Synchysidendron*, *Lepidodendron* and *Lepidophloios* – trees with architectures of intermediate (ABCD₂) complexity.

Two main conclusions can be drawn regarding perceived primitiveness and phylogenetic rooting. First, if the earliest rhizomorphic lycopsid is ever reconstructed (of course, we will never be sure), it is most likely to fulfil the prediction obtained by Deltran optimization of architectural characters in Fig. 14*b* – that is, it will have a novel architecture not yet documented in the clade. Secondly, our understanding of the phylogeny of the group will be advanced most rapidly by the reconstruction of species that bridge the wide gap between the most primitive known rhizomorphic lycopsid (whether modelled on *Oxroadia* or *Paralycopodites*) and the most derived known non-rhizomorphic lycopsid (probably a selaginellalean).

Bateman (1992*b*) noted that such newly described, morphologically intermediate species would break up the large suite of characters separating the rhizomorphic lycopsids from their closest relatives, thereby testing the saltational hypothesis of their origin and offering much greater insights into the sequence of character state changes that eventually resulted in the evolution of the rhizomorphic syndrome (for a detailed account see Bateman & DiMichele, 1994). As well as improving the effectiveness of outgroup polarization, breaking up a set of characters that change together across a single internode provides tests of competing evolutionary mechanisms. Determining the relative positions on a cladogram of transitions in form and function allows falsification of hypotheses of adaptation and exaptation (Coddington, 1988; Lauder, 1990). Also, failure to disaggregate a resilient set of character-state changes following the addition of OTUs to a cladistic matrix supports the *a priori* hypothesis that those characters originated together as a saltational event (Bateman, 1992*b*; Bateman & DiMichele, 1994).

(5) *Cladistics, scenario building, and reciprocal illumination*

As described in *Cladistic Analysis*, this study is based on morphological and anatomical characters that were first scored in 1989. Organisms were progressively partitioned into organs, tissues and smaller-scale features, to describe all parts of the organism. This was achieved as thoroughly and objectively as possible within the *a priori* constraint of requiring characters that show qualitative rather than mere quantitative differences among species. The extensive experimentation that followed (Bateman & DiMichele, 1991; Bateman *et al.*, 1992; DiMichele & Bateman, 1994) was based on this original matrix. However, it is now tempting to re-examine the species and then recode the characters to better accommodate those interpretations, perhaps replacing the homogeneous additive binary coding with a more heterogeneous matrix that incorporates multistate characters: unordered or ordered, linear or bifurcating (e.g. Mickevich & Weller, 1990; Maddison & Maddison, 1992; Swofford, 1993). The problems of implicit weighting, polarity determination, and contributions of autapomorphic states to tree-length calculations should also be considered carefully. Certainly, the incorporation of process-based interpretations into the recoded matrix will render the resulting cladograms appreciably more subjective than their predecessors.

Beyond these issues lies the question of whether (and how) interpretations of the original descriptive characters should influence recoding. Arguments developed in this paper suggest that character-based morphological analyses are performed within the sphere of at least four overlapping and inter-related hierarchies:

(1) *Spatial*: the physical scale of a particular developmental unit (= stage; in this case, ranging from the architecture of the entire lycopsid plant to the morphology of the dust-like unicellular microspores).

(2) *Temporal*: the commencement and cessation of a particular developmental stage relative to other stages during ontogeny.

(3) *Burden*: in this context, the profundity of effect of an evolutionary–developmental change in a particular developmental stage relative to the ontogeny of the entire organism. Note that the effect can be direct and immediate (mutation), indirect and immediate (domino effect), or indirect and expressed in subsequent generations (selective cropping) (Table 1).

(4) *Phylogenetic*: the historical inclusiveness (relative commonality) of the comparable homologous developmental stage as coded for, and tested by, cladistic analysis – in other words, viewing the developmental stages as nested sets of synapomorphies constituting a cladogram.

Note that (1)–(3) are intrinsic to any one species, whereas (4) can be determined only by interspecific comparison. In practice, (1)–(3) show strong positive correlation; indeed, (1) tends to be used as a surrogate for (2) and (3). All three parameters result in a hierarchy of characters. In contrast, (4) results in a hierarchy of taxa. Ever since von Baer (1828), many authors have argued for strong correlation among all four hierarchies: early ontogenetic events are of larger scale, have a higher burden, and characterize a greater number of species within a clade than later events. It is perturbations of the parallels among these hierarchies that both complicate character coding and potentially undermine cladistic analyses. For example, extensive crown branching (six genera) is more common than cauline lateral branching (three genera) among the rhizomorphic lycopsids, yet cauline lateral branching occurred earlier in ontogeny and determined both the physical scale and the biological significance of subsequent crown branching. Such inconsistencies among hierarchies are especially problematic if a specific perturbation is repeated during the evolution of the clade, such as the repeated transitions among different modes of aerial branching and the iterative evolution of small-bodied pseudoherbs from tree lycopsids. Such paedomorphic events offend another (perhaps unreasonable) expectation of evolution – that it should lead to increasing complexity. Complexity should not be confused with sophistication and, like fitness, is impossible to measure objectively (cf. Wimsatt, 1986; Wimsatt & Schank, 1988; Atchley & Hall, 1991; McShea, 1991; Lewin, 1993).

These difficulties are epitomized by the hypothetical hierarchy of developmental controls summarized in Table 3. These could in theory be translated directly into cladistic characters, but the same problems would be encountered – representing in the coding (1) hierarchies of ontogenetic timing of activity and (2) morphological scale of effect, and (3) imposing on those hierarchies both order and polarity when the true pattern – both multidirectional and locally reversible – is far more complex. For example, the preferred scenario of architectural evolution (Figs 15, 17) requires that complexity in terms of the number of ontogenetic stages should generally be regarded

as plesiomorphic (i.e. ‘+’ = 0, ‘-’ = 1), but that complexity of the control of the timing of developmental stages (heterochrony *sensu stricto*) should generally be regarded as apomorphic (‘-’ = 0, ‘+’ = 1). Although phylogeneticists will continue to seek better solutions to these problems, I have little doubt that repeated paedomorphosis and/or ontogenetic stage deletion within a clade will always pose serious problems. Rather than attempting to force cladograms to accommodate paedomorphosis, it may be better to focus on improving our ability to recognize such phenomena and to predict their effects on cladogram topologies.

Such problems in no way detract from the power of cladistics. This lies less in the much-debated use of parsimony (better regarded as a necessary evil) than in inherent explicitness – of the conceptual underpinnings, numerical character coding, analytical algorithms, and specific statements of character evolution inherent in the positions of state changes across the resulting topology. Phenetic methods abandon the last feature in exchange for greater flexibility of character coding and greater robustness, notably the guarantee of obtaining only one topology. Non-numerical or non-algorithmic approaches (e.g. Sporne, 1974; Dahlgren, 1975; Takhtajan, 1980; Cronquist, 1987; Hay & Mabberley, 1991) can in theory offer specific statements of relationship and character change, but in practice rarely succeed. In any case, such statements lack both empirical and conceptual support – they are authoritarian rather than authoritative (admittedly, this accusation can also be levelled at cladistic studies published without the support of the primary data-matrix).

For example, Hay & Mabberley (1991) and Mabberley & Hay (1994) rejected the concept of a character in favour of a non-explicit ‘holistic’ approach to comparative morphology. In this paper I have focused on the most holistic aspect of the morphology of any plant – its overall growth architecture, as determined by the behaviour of apical meristems. In one sense, Hay & Mabberley provided a valuable reminder that plants are holistic organisms subject to phenotypic interaction. Even so, architecture, perhaps more than any other suite of characters, is the sum of its parts. In most scientific endeavours, a researcher analyzes an entity by dividing it into comparable components in a recognizable hierarchy (usually one of physical scale). For example, we understand molecules by studying atoms and atoms by studying subatomic particles; subsequent interpretations benefit from reciprocal illumination between these different levels of scrutiny. I doubt whether anyone will be able to develop a viable approach to comparative biology that is independent of hierarchy theory and reciprocal illumination – that is, of characters and character states. If we are to gain further insights into the evolution of plant form, we will be obliged to continue addressing the remaining problems of phylogenetic reconstruction rather than evading them.

(6) *Future trends*

In the case of extinct species such as the tree-lycopsids, biological hypotheses cannot be tested directly. In contrast, molecular phylogenies can now be constructed for living (or recently extinct) species as OTUs. However, nucleic acid sequence data are biochemical signals rather than truly interactive elements (cf. Albert, Backlund & Bremer, 1994); few base-pairs are actually expressed in the phenotype. Thus, genotype *per se* is less useful for biological interpretations than is phenotype (cf. O’Brien & Clegg,

1993). Of greater significance is the possibility of comparing morphological and molecular data (notably base-pair sequences) for the same range of OTUs (e.g. Lowrey & Crawford, 1985; Baldwin *et al.*, 1990, 1991; Meyer *et al.*, 1990; Baldwin, 1992; Conti, Fischbach & Sytsma, 1993; Cantino, Wagstaff & Olmstead, 1993; Doyle, 1993; Hoot, Culham & Crane, 1993; Patterson, Williams & Humphries, 1993; Smith, Kress & Zimmer, 1993). As phylogenetic indicators, nucleic acid sequences offer the opportunity of testing hypotheses based on phenotypic data; they would, for example, be particularly valuable to test the hypothesis of reduced complexity (paedomorphosis *sensu lato*) advanced to explain the independent origins of multiple lineages of small-bodied rhizomorphic lycopsids (Bateman & DiMichele, 1991, 1994; Bateman, 1992a; Bateman *et al.*, 1992) – events capable of undermining phenotypically-based phylogenetic reconstructions (cf. Figs 2a, b).

Hypotheses of paedomorphosis in some angiosperm clades have already been tested by molecular cladistics. For example, a morphological phylogeny suggested that the highly structurally reduced but ecologically specialized aquatics of the Lemnaceae are nested well within, and evolved from, the Araceae (Mayo, 1993); this hypothesis of paedomorphosis was supported by a cpDNA phylogeny (French, Hur & Chung, 1993). Similarly, cpDNA sequences suggest that the morphologically reduced aquatic *Callitriche* is nested within the more generalized Scrophulariaceae (Reeves & Olmstead, 1993), and the riparian annual *Navarretia* within the Polemoniaceae (Spencer, 1993). In contrast, both morphological (Les, 1988; Crepet *et al.*, 1993) and molecular (Chase *et al.*, 1993) phylogenies suggest that the reproductively unsophisticated aquatic angiosperm *Ceratophyllum* is sister-group to all other extant angiosperms; it is thus plesiomorphic rather than paedomorphic.

I believe that the greatest advances in evolutionary biology will be made by studying yet another hierarchical relationship – the interface between genotype and phenotype. Current work relating phenotypic features to the activities of specific D-genes, a fundamental form of reciprocal illumination, will eventually generate sufficient data for cladistic coding of gene expression, akin to that in Table 3 but based on direct observation rather than indirect speculation (cf. Gottlieb, 1984, 1986; Sattler, 1993).

To date, the most valuable information on gene expression has described the floral morphogenesis of dicotyledonous angiosperm herbs such as *Arabidopsis thaliana* (e.g. Bowman, Smyth & Meyerowitz, 1991; Coen & Meyerowitz, 1991; Meyerowitz *et al.*, 1991; Mandel *et al.*, 1992; Crone & Lord, 1993; Weigel & Meyerowitz, 1993; Gustafson-Brown *et al.*, 1994), *Antirrhinum majus* (Schwartz-Sommer *et al.*, 1990; Coen & Meyerowitz, 1991; Endress, 1992), *Primula vulgaris* (Webster & Grant, 1990), *Clarkia concinna* (Ford & Gottlieb, 1992), *Petunia inflata* (Angenent *et al.*, 1994; Lee, Huang & Kao, 1994), *Solanum lycopersicum* (Szymkowiak & Sussex, 1992; Rasmussen & Green, 1993), and *Glycine max* (Crozier & Thomas, 1993). A few examples of radical changes in floral (and vegetative) architecture have proved to be caused by environmental perturbations (Hallé, 1978; Crozier & Thomas, 1993), epigenesis (Green, 1992; Stebbins, 1992; Gallie, 1993), or cytoplasmic inheritance (Demarly, 1974), but most studies have identified control of expression of each floral part and pigment by only one or two nuclear D-genes. Recent work on *Arabidopsis* (Leyser & Furner, 1992) and the monocot *Zea mays* (Poethig, 1988, 1990; Smith *et al.*, 1992; Kellogg & Birchler, 1993; Jackson, Veit & Hake, 1994) suggests that there is no reason

to assume that vegetative morphogenesis is any more complex than floral morphogenesis. Moreover, thus far, the evolutionary implications of these exciting discoveries (Chasan, 1993) have consistently been under-explored.

When they are reappraised (e.g. Bateman & DiMichele, 1994), these observations on D-genes offer particular encouragement to neoGoldschmidtian proponents of hopeful monsters, and imply that the continuity of plant form reported by Sattler & Jeune (1992) need not reflect continuous, gradual evolution (e.g. Croizat, 1962; Lewis, 1962; van Steenis, 1969, 1976; Hallé, 1978; Fournier, 1979; Sattler, 1986; Levinton, 1988; Levin, 1993; Bateman & DiMichele, 1994). Developmental canalization may indeed improve species survival (Kerszberg, 1989), but it also prevents radical evolutionary innovation. In contrast, non-adaptive saltation releases a lineage from the constraints of canalization (albeit usually at the cost of immediate extinction) – the developmental ratchet (Vermeij, 1987; Levinton, 1988) and the evolutionary clock (Gould, 1989) are effectively reset. Several other modes of unusually rapid evolution in small populations (e.g. Gould, 1982; Arthur, 1984; Levin, 1993), collectively termed parasaltation by Bateman & DiMichele (1994), also merit reconsideration in the light of recent developments in development.

Saltation is more credible for higher plants than for higher animals (e.g. van Steenis, 1976; Bateman & DiMichele, 1994). Their sedentary life-style renders competition for resources indirect and active mate recognition inviable; it also places less selection pressure on overall architecture. Consequently, plants are better able to accommodate saltational changes than animals, just as they are better able to accommodate ploidy changes (cf. Thompson & Lumaret, 1992; Stace, 1993) – plants suffer far less profound decreases in relative fitness (e.g. van Steenis, 1976; Bateman & DiMichele, 1994). Also, the open, meristem-based growth of higher plants offers many more targets for mutations that can subsequently pass into germ cell lineages once the plant enters a reproductive phase. Moreover, one teratological organism is sufficient to establish a plant lineage unless it is dioecious or self-incompatible (cf. Goldschmidt, 1940; Arthur, 1984). Hence, saltation is especially readily accommodated in the lower vascular plants, which increase in importance relative to seed-plants backward through geological time. Simpler development in such plants would also enhance expression of D-gene mutations, and simpler ecosystems would increase the probability of establishing new lineages.

Unlike holistic higher animals, higher plants are differentiated into permanent core organs and transient appendicular organs, which generally terminate ontogenetic cascades and thus are immune to the domino effect. Such organs have high degrees of developmental independence and hence can become individually canalized. This in turn allows a high degree of evolutionary independence and results in mosaic evolution (Stebbins, 1983; Meyen, 1987).

Thus, saltation via single-gene mutations is more likely to lead to successful lineage establishment in higher plants than in higher animals, and in fossil rather than living species (Bateman & DiMichele, 1994). Plant architecture is especially prone to saltational evolutionary–developmental change. Other, smaller-scale features are altered in turn, either as a direct ontogenetic consequence of the architectural change or subsequently, as a result of functional redundancy eventually leading to adaptive elimination. Given these conclusions, the best opportunity for significantly improving

our understanding of the evolution of plant form lies in positive feedback between such hypotheses and empirical observations of gene expression analyzed in a cladistic context.

IX. SUMMARY

The Rhizomorphales, the most derived portion of the lycopsid (clubmoss) clade, is now represented only by the diminutive genus *Isoetes*. However, during their Late Palaeozoic acme the rhizomorphic lycopsids exhibited a wide range of architectures and body sizes, from recumbent pseudoherbs to trees 40 m high. All possessed the rhizomorphic syndrome: a centralized rootstock and secondary thickening, reflecting an inescapable developmental constraint of bipolar determinate growth. These features in turn allowed acquisition of the tree habit by the lycopsids, independently of the physiologically and ontogenetically distinct lignophyte clade that includes the seed-plants. Differences among lycopsid genera in the number and size of four major growth modules – rhizomorph, stem, lateral branches (two positionally distinct submodules), and isotomous crown branches – resulted from differences in the relative size, number and equality of dichotomies of the apical meristems.

A detailed experimental cladistic analysis of the best known fossil rhizomorphic lycopsids demonstrates extensive iteration among several distinct growth architectures characterizing ten genera. Scenarios can be constructed for the type of morphogenetic transitions necessary to (1) derive one genus from a putative ancestor or (2) explain the relationship of two genera relative to a putative outgroup. The scenarios are best formulated within a synthesis of terminology devised primarily by zoologists to describe via size–shape trajectories various modes of evolutionary–developmental change: heterotopy, heterochrony *sensu lato*, and allometric modifications. Many examples of these phenomena are evident among the rhizomorphic lycopsids, and can be explored by reconstructing hypothetical ancestors occupying interior nodes of the cladogram. Iterative origination of the small-bodied genera from tree-sized ancestors is inferred, by various forms of paedomorphosis and decreases in the number of developmental stages that are sufficiently profound to locally perturb perceived phylogenetic relationships. This study highlights several problems of cladistic analysis in general and of fossils in particular, especially the significance for character polarization of both perceived primitiveness and large phenetic gaps. Many phylogenetic studies of several extant angiosperm clades also imply frequent architectural transitions, but few suggest repeated origins of non-trees from trees.

A simple model for control of development focuses on D-genes: switches that control morphogen production. This perspective emphasizes the importance of a series of inter-related hierarchies reflecting ontogenetic time, size, burden and complexity within species, and phylogeny among species. The increasingly evident simplicity and common origin of D-gene control in all living organisms is used to formulate a neoGoldschmidtian paradigm of instantaneous, non-adaptive, saltational speciation via teratological ‘hopeful monsters’ that escape the constraints of developmental canalization. The scenario does not require large-scale mutations or high levels of fitness in the mutants – merely temporary release from competitive selection by establishing the new lineage in a vacant niche. The model is more appropriate to higher plants than to the more developmentally complex and constrained higher animals, and

more appropriate to fossil plants than to their more ecologically complex and developmentally constrained living descendants. Future progress in understanding transitions in plant form requires reciprocal illumination between such scenarios and empirical observations of gene expression analyzed in a cladistic context.

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