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Hizemodendron, gen. nov., a Pseudoherbaceous Segregate of *Lepidodendron* (Pennsylvanian): Phylogenetic Context for Evolutionary Changes in Lycopsid Growth Architecture

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ABSTRACT. The classic coal-swamp lycopsid genus *Lepidodendron* (Lepidodendrales) is transformed from apparent paraphyly to monophyly by segregating '*L.*' *serratum* as a new genus, *Hizemodendron*, currently containing only *H. serratum*. All potential organs of *H. serratum* have been correlated, with varying degrees of confidence, to yield a conceptual whole-plant. Secondary tissues were probably confined to the rhizomorph and putatively short stem, which generated a repeatedly branched leaf- and cone-bearing crown. This pseudoherbaceous habit resulted in a scrambling, recumbent growth form that allowed the development of dense ground-cover in some Carboniferous coal-swamp forests of Euramerica. Truly prostrate growth (and accompanying bilateral symmetry of axes) was precluded by ontogenetic constraints, notably determinate growth and the centralized rhizomorphic rootstock. *Hizemodendron* and *Lepidodendron* are very similar in reproductive characters but differ in several vegetative characters. *Hizemodendron serratum* is the only recorded non-tree in the apomorphic (monosporangiate-coned) portion of the lepidodendralean clade, implying that it originated from an arboreous, *Lepidodendron*-like ancestor. If so, *Hizemodendron* retained the ancestral reproductive organs and bauplan, but decreased in body size and acquired a new, pseudoherbaceous growth habit that prompted other vegetative modifications. The pseudoherbaceous habit is iterative within the arboreous lycopsids, also occurring in *Oxroadia* and *Paurodendron*; it probably reflects precocious apical dichotomy. This in turn may be caused by mutation of genes regulating early development, which offers a range of heterochronic mechanisms for repeated saltational macroevolution within the lycopsids.

The lepidodendralean lycopsids epitomize the vegetation of the Carboniferous lowland tropics. Their distinctive morphologies in general, and bizarre architectures in particular, demonstrate that most extant plants are remarkably unrepresentative of the distant past. Together with the zosterophylloids, the lycopsids represent the sister-group for the remainder of the tracheophyte clade (cf. fig. 31 of Taylor 1988). The lepidodendraleans, a strongly derived group within the lycopsids, can be regarded as an exceptional "experiment" in parallel evolution, acquiring many key traits (e.g., secondary growth, tree habits, seed-like structures, bipolar root-shoot systems) independently of similar structures in other vascular plant lineages.

The rise to dominance of tree-sized (arboreous) lepidodendraleans in coal-swamps was accompanied by considerable morphological diversification and ecological specialization (e.g., Chaloner 1967; DiMichele and Phillips 1985; Phillips 1979; Stewart 1983). Although the extent of this diversity has become increasingly clear as arboreous lycopsids have been recon-

structed from their constituent organs, only recently has this diversity been recognized at an appropriate taxonomic rank. The consequent proliferation of genera (fig. 1), several resulting from the disaggregation of the genus *Lepidodendron* (e.g., DiMichele 1979, 1980, 1981, 1983, 1985), partitioned this variation into ostensibly monophyletic groups.

Recently, we tested the monophyly of the genera, and investigated their phylogenetic relationships, by means of an experimental cladistic analysis (Bateman et al., in press). The results strongly support monophyly of the genera with a single exception; the two species of *Lepidodendron*, *L. hickii* Watson [the anatomically-preserved equivalent of the addressed type, *L. aculeatum* Sternberg (DiMichele 1983, 1985)] and '*L.*' *serratum* Felix emend Leisman & Rivers, were similarly strongly supported as a paraphyletic sister-group to the most apomorphic lepidodendralean genus, *Lepidophloios* (fig. 1A). '*Lepidodendron*' *serratum* is perceived as plesiomorphic relative to *L. hickii* primarily because of character states that relate directly or indirectly to its bauplan and its habit, which is pseu-

doherbaceous (Bateman 1988, 1989; DiMichele and Bateman 1989) rather than arboreous (see below). On this evidence, we have chosen to further restrict the generic delimitation of *Lepidodendron* by segregating 'L.' *serratum* as a new genus, *Hizemodendron* Bateman & DiMichele. Slight emendments to the diagnosis accommodate our observations on the morphology of *H. serratum*.

TAXONOMY

Hizemodendron Bateman & DiMichele, gen. nov.—TYPE: *Hizemodendron serratum* (Felix emend Leisman & Rivers) Bateman & DiMichele. BASIONYM: *Lepidodendron serratum* Felix, Ann. Missouri Bot. Gard. 39: 276. 1952. Emended diagnosis: Leisman and Rivers, C. R. 7me. Cong. Int. Strat. Géol. Carb. 3:355. 1974. Lectotype: Designated herein, WCB 707. Paratypes: Part of original hypodigm, WCB 798 and WCB 815. Lectotype and paratypes housed in the paleobotanical collections, University of Connecticut.

Generic Stratigraphic Range. Union Seam, Britain (Westphalian A) to Springfield Coal, Illinois Basin, U.S.A. (Desmoinean, Westphalian D equivalent); Early and Middle Pennsylvanian.

Generic Description. Vegetative axes medullated, all but the smallest axes protostelic. Central parenchymatous area sharply delimited from tracheids, composed of elongate cells. Xylem maturation exarch. Protoxylem continuously distributed. Cortex three-zoned; inner cortex thin in radial dimension, of compact, near-isodiametric parenchyma; middle cortex of larger, irregular, thin-walled cells; outer cortex broad in radial dimension, homogenous and composed of vertically-elongate, thick-walled parenchyma cells. Secondary xylem and periderm absent from aerial axes. Branching frequent, strongly anisotomous. Leaves persistent. Leaf bases strongly elongate on small-diameter axes, less so (but still longer than wide) on larger diameter axes. Leaf cushions (particularly those on smaller diameter axes) characterized by deep folds (plications) on the lower field, below the point of leaf attachment. Parichnos small, confined to the leaf lamina and leaf base (i.e., without infrafoliar expression). Distinct

keel present on lower leaf-base field. Ligule present in pit on leaf base immediately above leaf attachment. Megasporangiate cone assignable to *Achlamydocarpon*, borne on unmodified axis with identical morphology to the smaller vegetative axes. Pedicel with prominent abaxial keel and laterally expanded alations; alations short, less than one third the length of the sporangium and acutely angled relative to the pedicel. Sporangium dorsiventrally elongate, containing a single gulate functional megaspore assignable to *Cystosporites*.

Species Description. As in Leisman and Rivers (1974, p. 355).

Etymology. *Hizemodendron* is derived from the Greek "hizemos" (to settle down or sink) and "dendron" (tree), referring to the hypothesized origin of the genus by heterochronically-induced reduction of the stem of an arboreous ancestor. The name is neuter. *Serratum* refers to the often deeply plicated lower field of the leaf cushion (Felix 1952).

PHYLOGENETIC POSITION OF HIZEMODENDRON WITHIN THE LEPIDODENDRALES

Bateman et al. (in press) resolved much of the variation among lepidodendralean genera into a vegetative trend, reflecting the morphological and anatomical expression of different growth habits, and a reproductive trend, reflecting increasingly sophisticated reproductive strategies that eventually approached the seed habit in *Lepidophloios* (e.g., DiMichele and Phillips 1985; Phillips 1979). However, the vegetative and reproductive trends are phylogenetically contradictory; cladograms based on vegetative characters only (fig. 1B) and reproductive characters only (fig. 1C) have substantially different topologies. In the vegetative cladogram, five apomorphic trees are distinguished from four plesiomorphic pseudoherbs and shrubs. In the reproductive cladogram, the five most apomorphic genera possess a suite of characters that reflects partitioning of mega- and microsporangia into monosporangiate cones (these are absent from the four bisporangiate plesiomorphs). The genera with the greatest positional differences between the two cladograms are the bisporangiate tree *Anabathra* (Pearson 1986; Witham 1833, =*Paralycopodites* of DiMichele 1980 and Morey and Morey 1977; see appendix 1B of Bate-

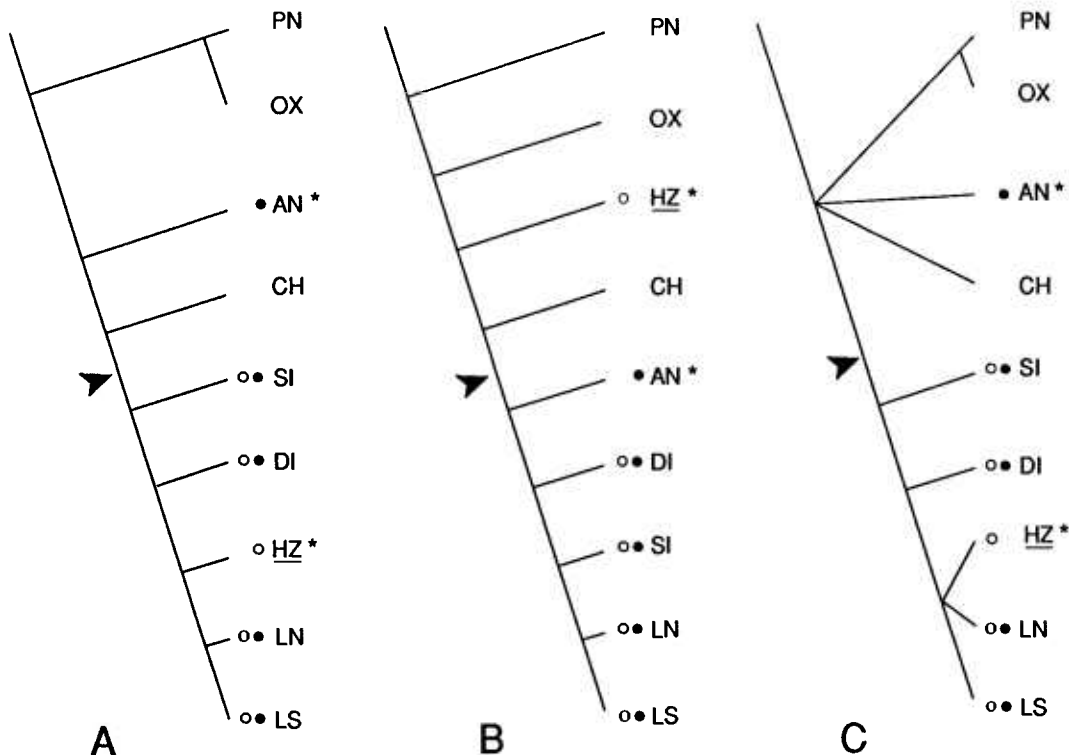


FIG. 1. Preferred most parsimonious cladograms of anatomically-preserved arboreous lycopsid genera, based on 69 vegetative and 46 reproductive characters (A), the vegetative characters only (B), and the reproductive characters only (C). *Hizemodendron* (formerly *Lepidodendron serratum*) is underlined. The boundary separating the four most plesiomorphic genera and five most apomorphic genera in each cladogram is arrowed, and the two genera (*Hizemodendron* and *Anabathra*) that transgress this boundary among the three cladograms are asterisked. Solid circles indicate trees, open circles indicate monosporangiate cones. Genera: *Paurodendron* (PN), *Oxroadia* (OX), *Anabathra* (AN), *Chaloneria* (CH), *Sigillaria* (SI), *Diaphorodendron* s.l. (DI), *Hizemodendron* (HZ), *Lepidodendron* (LN), *Lepidophloios* (LS). Modified after Bateman et al. (in press).

man et al., in press), which is reproductively plesiomorphic and vegetatively apomorphic, and the monosporangiate pseudoherb *Hizemodendron* (Baxter 1965; DiMichele 1981; Felix 1952; Leisman and Rivers 1974), which is reproductively apomorphic and vegetatively plesiomorphic. On the cladogram using both vegetative and reproductive characters (fig. 1A), the reproductively-defined monosporangiate-coned clade (open circles) is retained at the expense of the tree habit (closed circles), which is consequently depicted as homoplastic.

Hizemodendron is the only non-tree in the apomorphic (monosporangiate) portion of the lepidodendralean clade (fig. 1A), implying that it underwent reversal from tree to non-tree and is secondarily pseudoherbaceous (Bateman et

al., in press). To assess this phylogenetic hypothesis, we will review evidence for the pseudoherbaceous habit of *Hizemodendron* and for the similarity of *Hizemodendron* to *Lepidodendron*. First, we will briefly define key terms that describe the gross morphology of plants in general and lycopsids in particular.

BAUPLANS, HABITS, AND GROWTH FORMS

Studies of growth architectures in fossil plants are rare (e.g., Trivett and Rothwell 1988). Comparison with architectures of extant species suggests that determinate growth distinguishes lepidodendraleans from most other tracheophyte lineages, allowing closer analogy with the ontogeny of vertebrates. Thus, it is reason-

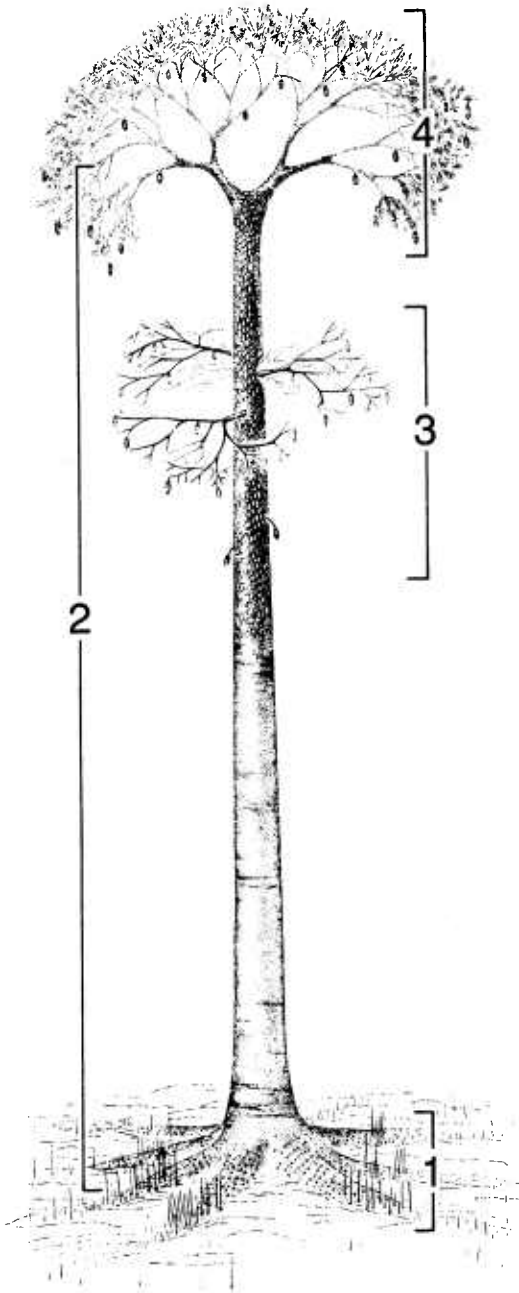


FIG. 2. Diagrammatic representation of a hypothetical arboreal lycopsid that possesses well-developed examples of all four major structural units. 1 = rhizomorph, 2 = stem, 3 = lateral branches/cauline peduncles, 4 = crown branches.

able to compare the "body sizes" of mature lepidodendrales, and to speak of a developmentally highly constrained, genetically-imposed body plan ("bauplan" of Meeuse 1986, "architectural model" of Hallé et al. 1978). This is further constrained by the limited number of major structural units available to the lepidodendrales. We recognize four (fig. 2; Bateman et al., in press; DiMichele and Bateman 1989): rhizomorph, stem (defined as the length of the axis from the point of root-shoot divergence to the first isotomy of the apical meristem), crown branches (resulting from isotomy of the apical meristem), and lateral branches/cauline peduncles (resulting from strong anisotomy of the apical meristem). All units are modules (shoot units of determinate growth; Hallé et al. 1978; Tomlinson 1982).

Rhizomorph and stem are ubiquitous modules within the Lepidodendrales, but lateral branches/peduncles and crown branches are each absent from (or, in the case of crown branches, rare in) some species, thus defining three bauplans (lateral branches only, crown branches only, neither type of branch). The four modules vary greatly in size, frequency of branching (except stems and peduncles, which are unbranched by definition), and secondary tissue content within each bauplan, thus generating a range of growth habits. Growth habit is defined as the ultimate form of a plant as expressed in its physiognomy (Hallé et al. 1978, p. 388), thereby encompassing ecophenotypic modification of the genetically-programmed bauplan. In this case, we suspect that growth was largely deterministic (genetically-induced), with relatively little potential for opportunistic modification of growth architecture by environmental influences or chance factors (cf. Tomlinson 1982). Thus, for lepidodendrales, the conceptual architectural model will be unusually faithfully reproduced in the actual habit.

Body size and body shape in the vertical plane together allow the aggregation of habits into three commonly-used (but rarely defined) growth forms: trees, shrubs, and herbs. To these, we add a fourth, the pseudoherb (Bateman 1988, 1989).

In summary, we recognize three concepts of body size and shape, listed in order of increasing breadth: genetically determined bauplan (architecture), ecophenotypically modified

habit, and the more nebulous classification of form.

GROSS MORPHOLOGY OF *HIZEMODENDRON*

In his original description of '*Lepidodendron serratum*', Felix (1952) noted the consistent absence of secondary xylem and periderm from many specimens of aerial axes spanning a wide range of diameters, and concluded that it was probably "a lax, flexuose plant which branched frequently, and . . . [was] afforded . . . very little support" (Felix 1952, p. 279). While explaining his determinate growth paradigm, Eggert (1961) suggested that Felix may have described small non-woody distal axes from the crown of an arboreous lycopsid that bore wood in larger, more proximal axes (see also Chaloner 1967, p. 568). After examining over 200 axes of *H. serratum*, Baxter (1965) refuted Eggert's arguments by citing the following evidence: 1) none of the axes exhibited secondary tissues; 2) of the many axes measured, the few largest all approximated the same size (ca. 100 mm in overall diameter and 15 mm in xylem bundle diameter), suggesting that this was indeed the maximum axial diameter of the species; 3) branching is profuse and sufficiently anisotomous to appear monopodial; 4) one axis, 14 mm in overall diameter, was strongly bilaterally symmetrical in transverse section; the eccentric stele occurred diametrically opposite a longitudinal zone of excessive outer cortical development. Baxter (1965, p. 3) argued that the least developed portion of the cortex was in contact with the ground surface, and concluded that *H. serratum* was a "semi-prostrate, . . . semi-herbaceous, . . . scrambling, semi-bushy plant."

Observations (1) to (3) were endorsed by the subsequent large-scale empirical studies of Leisman and Rivers (1974) and DiMichele (1981), but the axis described in (4) remains a unique anomaly. It is surprising that all larger (i.e., 15-100 mm diameter) axes remained radially symmetrical, as they would have been even less capable of independent support and, therefore, even more likely to adopt a prostrate posture. Frequency of branching (3) is a poor criterion for distinguishing upright/pendent from recumbent axes. Angle of branching, a character ignored by all previous contributors to this debate, is more informative (e.g., Honda 1971). Wider angles, such as those observed in *H. ser-*

ratum, generally incur greater physical stresses and are more likely to occur in recumbent plants (Bateman 1988).

Absence of secondary tissues from large axes (observations 1 and 2) is equivocal evidence of herbaceousness unless at least one such axis can be shown to be a mature stem; this is most readily achieved by demonstrating organic connection between a large axis and a rootstock. This correlation is especially crucial because recent reconstructions of pseudoherbaceous (and shrubby) lycopsids have demonstrated that secondary tissues can be very restricted: to the rhizomorph, short stem and longer, recumbent primary branches of *Oxroadia* (Bateman 1988, 1989; Long 1986), to the rhizomorph and base of the unbranched, upright stem in *Chaloneria* (Pigg and Rothwell 1983), and to the rhizomorph and extreme stem base only in the very short-stemmed, recumbent *Paurodendron* (Phillips and Leisman 1966; Rothwell and Erwin 1985; Schlanker and Leisman 1969). Such restriction of wood and periderm, combined with a very short stem incapable of raising branches clear of the ground, defines the pseudoherbaceous habit sensu Bateman (1988, 1989).

Current evidence (including unpubl. data) suggests a growth architecture for *Hizemodendron* similar to that of *Oxroadia* (Bateman 1988); a very short (possibly woody) stem subtended by a repeatedly branched, woody, stigmatic rhizomorph, and undergoing frequent, wide-angle dichotomies to cover much of the ground surface with non-woody, microphyll-bearing axes. Admittedly, the analogy is incomplete. Firstly, *Hizemodendron* is a much larger plant than *Oxroadia* when mature. Secondly, aerial branching is dominantly isotomous in *Oxroadia* but dominantly strongly anisotomous in *Hizemodendron*, which more closely resembles *Paurodendron* in this character (cf. Fry 1954; Schlanker and Leisman 1969).

The vine-like habit attributed to *Hizemodendron* by Baxter (1965) and DiMichele (1983) is highly improbable, given its 10 cm maximum axial diameter, lack of specialized structures for gaining purchase on other plants, and its frequent high-angle branching. Rather, we postulate a scrambling, recumbent but not truly prostrate habit. Non-terminal axes were vertically sinuous, touching the ground only infrequently and thereby permitting leaves on the lower surface of the axis to photosynthesize.

TABLE 1. Binary characters discordant between *Hizemodendron serratum* and *Lepidodendron hickii*, numbered following Bateman et al. (in press). For each character, the putative apomorphic state is listed after the plesiomorphic state and occurs in *L. hickii* unless marked "HZ." Autapomorphies (derived states currently perceived as unshared) are asterisked.

Habit

1. Non-arboreous : arboreous
2. Stem short, recumbent : stem tall, plant upright

Stele

16. Protostele core non-filamentous : filamentous
26. Longitudinal ridges of protoxylem discernible : indiscernible (HZ)

Periderm

46. Cushion retention mechanism absent : sub-cushion cellular expansion (*)
47. Non-glandular : glandular
48. Non-resinous : resinous

Leaf bases

53. Length/width ratio of cushions on small branches/twigs $>1 : <1$
54. Upper keel absent : present
56. Upper field non-plicate : plicate (HZ)
58. Lateral line separating upper and lower fields absent : present
62. Intrafoliar parichnos absent : present
63. Consistent basal limit to leaf atrophy absent : present

Leaves

66. Angle of leaf attachment \pm horizontal : acute (HZ)
68. TS vascular strand terete : dorsiventrally flattened
70. Lateral abaxial grooves absent : present
72. Sheath of sclerenchyma surrounding leaf trace absent : present

Cones

73. Stellar vascular gap subtending peduncle absent : present
74. Pith in peduncle absent : present

Sporangia

78. Sporangium wall uniseriate : multiseriate (*)
-

bodied *Oxroadia* (Bateman 1988, 1989) and much smaller-bodied *Paurodendron* (Schlanker and Leisman 1969). All three genera appear to have shared the determinate growth pattern that characterizes their arboreous relatives (e.g., Andrews and Murdy 1958; Delevoryas 1964; Eggert 1961; Walton 1935), though it is unclear whether they were strictly monocarpic.

These reconstructions suggest that all three genera possess the same basic bauplan. This consists of a woody, radially symmetrical rhizomorph and a very short arborescent stem, which branches to form an extensive leaf- and cone-bearing crown. These pseudoherbs share Schoute's architectural model (sensu Hallé et al. 1978, p. 128) with better-known arboreous genera such as *Lepidodendron* (DiMichele 1981, 1983, 1985) and *Lepidophloios* (DiMichele 1979; DiMichele and Phillips 1985), but their smaller body-sizes and much shorter stems relative to the proximal branches result in a pseudoherbaceous rather than arboreous habit.

We suspect that the pseudoherbaceous condition, at least in *Hizemodendron*, arose by reduction from an arboreous ancestor (fig. 1A). Precocious division of the primary apical meristem minimized the length of the stem, and prompted many subsequent character changes to accommodate the new growth habit (see Heterochrony, below). In particular, relieved of the necessity for a self-supporting crown, epigenetic stress-strain induction of secondary tissue would progressively diminish (there is ample evidence that plants produce support tissues in response to physical stimuli).

Nevertheless, many characters of the arboreous ancestor of *Hizemodendron* persisted. Most notably, axial symmetry remained radial, and roots remained confined to the highly differentiated basal rhizomorph. These characters suggest an insurmountable developmental commitment to determinate growth and a centralized rootstock, and contrast with the bilateral axial symmetry and adventitious roots of lycopsids adapted to a truly prostrate growth habit, such as many species of heterophyllous *Selaginella* and *Lycopodium* s. str. (e.g., Bierhorst 1971; Bold et al. 1980).

Oxroadia and *Paurodendron* may also have originated from arboreous ancestors, albeit much less apomorphic than the ancestor of *Hizemodendron* (Bateman et al., in press).

Terminal axes, both vegetative and cone-bearing, were probably more-or-less erect. The resulting dense ground-cover of *Hizemodendron* would have resembled a briar patch.

A similar growth habit occurs in the smaller-

COMPARISON OF *HIZEMODENDRON* WITH
LEPIDODENDRON S. STR.

Lepidodendron is the arboreal lycopsid most closely related to *Hizemodendron* (fig. 1A). For the purposes of argument, we will ignore the evidence of paraphyly, and compare the two genera to consider whether *Hizemodendron* could have been derived from a *Lepidodendron*-like ancestor by reduction.

Bateman et al. (in press, table 3) noted differences between *H. serratum* and *L. hickii* in 20 of 107 non-holapomorphic (i.e., non-ubiquitous) characters scored. The discordant characters are summarized in table 1; two (arborescence and relative length of stem) directly describe the habit differences already discussed, most of the others represent more detailed aspects of the vegetative anatomy.

The acute (rather than perpendicular) leaf insertion of *Hizemodendron* may be an adaptation to contact with the ground surface. Both *Hizemodendron* and *Lepidodendron* possess leaf bases that are differentiated into distinct cushions, but these are more complex in *Lepidodendron*; the upper field is separated from the lower field by a lateral line and possesses a keel. At least some of the distinct morphological attributes of *Hizemodendron* may reflect the greater persistence of its leaves; examples are the absence of a consistent basal limit to leaf atrophy, the strongly plicate upper and lower leaf-cushion fields, the absence of infrafoliar parichnos, and the poor development of foliar parichnos. Many of the character states found in *Lepidodendron* but not *Hizemodendron* may simply reflect the greater body size of the former; examples include the filamentous core to the protosteles that accommodates axial elongation, the subcushion cellular expansion that accommodates axial radial expansion, the histological elaborations of the periderm, the dorsiventrally-flattened traces and lateral abaxial grooves of the leaves, the stelar vascular gap associated with the departure of a peduncle, and the medullated stele of the peduncle itself (peduncles of arboreal lycopsids inevitably resemble ultimate vegetative axes in anatomy).

In contrast with the numerous vegetative differences, we are able to list in table 1 only one qualitative difference between the reproductive organs of *H. serratum* and *L. hickii*: sporangium

walls are uniseriate in the former and autapomorphically multiseriate in the latter. Otherwise, only more subtle, quantitative differences distinguish the megasporangiate cone of *H. serratum* (an unnamed species of *Achlamydocarpon*, found in organic connection with a vegetative axis by Leisman and Rivers 1974) from that of *L. hickii* (*Achlamydocarpon takhtajanii*; DiMichele 1983). Evidence for attributing the microsporangiate cone-species *Lepidostrobus minor* to *H. serratum* is associational (Leisman and Rivers 1974) and, therefore, more equivocal. If correctly correlated, it differs only quantitatively from the microsporangiate cone of *L. hickii* (*Lepidostrobus* cf. *oldhamius*; DiMichele 1983; Willard 1989). Similarly, megaspores and microspores of *H. serratum* and *L. hickii* possess identical qualitative character states. Thus, any hypothesis of relationship between *Hizemodendron* and *Lepidodendron* s. str. need only explain the numerous vegetative differences.

HETEROCHRONY

In attempting to explain the postulated reductive evolution of *Hizemodendron*, *Oxroadia*, and *Paurodendron*, it is tempting to invoke a class of developmentally-mediated evolutionary mechanisms termed heterochrony: a change in the timing of appearance of a trait between ancestor and descendant (Alberch et al. 1979; Gould 1977; Levinton 1988; McNamara 1982; Raff and Kaufman 1983; Rothwell 1987).

The putative evolutionary transition from a *Lepidodendron*-like ancestor to *Hizemodendron* cannot be simply attributed to proportioned dwarfism (sensu Alberch et al. 1979; Gould 1977), as it involves non-allometric change of shape as well as decrease in size. In theory, these two criteria define the progenetic mode of heterochrony (fig. 3A), provided that growth rate (k) and age of onset of growth (α ; in this case, of a module) are unchanged between ancestor and descendant (these assertions are difficult to test in lepidodendraleans, where lack of suitable modern analogues has rendered both parameters highly contentious). Progenesis is expressed as paedomorphosis (retention of ancestral juvenile characters in the descendant adult).

The presumed precocious dichotomy of the stem would both reduce its size and change its shape, supporting the progenetic hypothesis for

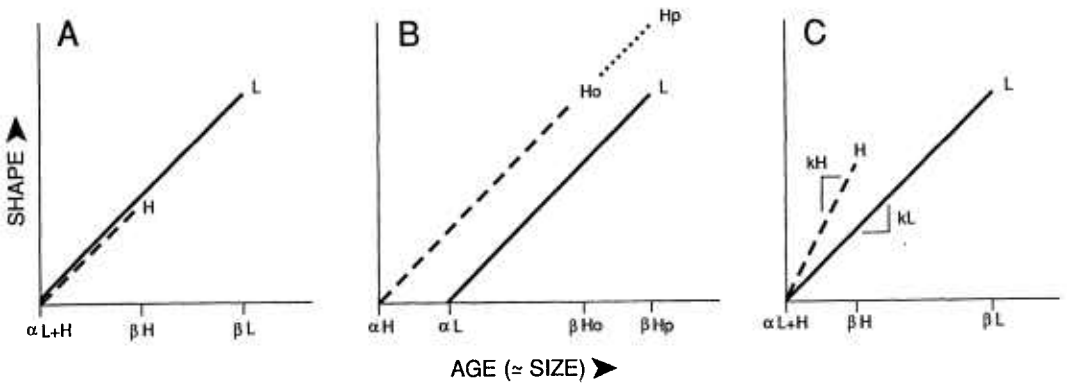


FIG. 3. Shape- and age-determined ontogenetic trajectories inferred for the stems (A), crowns (B), and overall bodies (C) of *Hizemodendron* (H: dashed line) and its putative *Lepidodendron*-like ancestor (L: solid line). A) A typical progenetic (paedomorphic) relationship. B) Two alternative forms of pre-displacement; the dashed line depicts correspondingly early offset of growth (β_{Ho}), which prevents peramorphosis, whereas the dotted extension reaches the ancestral age of offset of growth (β_{Hp}) and thus allows peramorphosis. C) A phenomenon not readily classified within the currently accepted heterochronic framework. α = age of onset (initiation) of growth, β = age of offset (cessation) of growth, k = rate of growth. See text and Alberch et al. (1979) for further explanation.

that organ. However, this simple interpretation is complicated by the sequential modular growth of lepidodendraleans. By severely restricting growth of the stem, precocious initial apical dichotomy would also have caused earlier onset of crown production. This heterochronic phenomenon, termed pre-displacement (fig. 3B), usually results in peramorphosis (the morphology of the ancestral adult is matched by the descendant juvenile and further elaborated by the descendant adult, i.e., the converse of the paedomorphosis attributed to the stem). However, repeated branching diminishes the primary body, providing prima facie evidence of limited development (Eggert 1961). Determinate growth in *Oxroadia* (and, presumably, *Hizemodendron*) ceases when the number of protoxylem strands marginal to the stele reaches a predetermined minimum (Bateman 1988). Thus, the period of crown growth ($\beta - \alpha$) is unlikely to have been altered, so that offset (cessation; β) of crown growth was probably similarly precocious. This form of pre-displacement does not cause peramorphosis; the crown of *Hizemodendron* decreased in size but probably remained similar in shape to that of its ancestor (fig. 3B).

As a result of the sequential growth of stem followed by crown, a mature *Hizemodendron* did not wholly resemble a juvenile *Lepidodendron*-like tree lycopsid as it should if progenesis af-

fected the whole organism. A juvenile *Lepidodendron* has a stem but no crown (e.g., fig. 2 of DiMichele and Phillips 1985), whereas a mature *Hizemodendron* has a crown but little stem. The net ontogenetic result resembles progenesis s. str. in that it involves change in shape and decrease in size (fig. 3A), but differs in that the ontogenetic trajectory of the descendant is distinct from that of the ancestor (we suspect that growth rate is increased). The resulting overall size: shape relationship (fig. 3C) is not readily accommodated in any category of heterochrony s. str. (cf. figs. 15-17 of Alberch et al. 1979), suggesting that zoocentric ontogenetic terms and concepts may require modification when applied to vascular plants. Nevertheless, heterochrony s.l. remains a compelling explanation for the origins of *Hizemodendron* and several other lycopsid genera (Bateman et al., in press; DiMichele and Bateman 1989).

CONCLUSIONS

***Hizemodendron* as a Monotypic Genus.** The classic arboreous lepidodendralean genera that characterize coal-swamp communities (*Anabathra*, *Sigillaria*, *Diaphorodendron* s.l., *Lepidodendron*, *Lepidophloios*) have long stratigraphic ranges, but those of their constituent species are usually considerably shorter; often,

one species of a genus replaced another in the same ecological niche. With the exception of *Diaphorodendron*, species within these genera differ primarily in details of the reproductive organs.

For example, the only recognized vegetative organ-species of *Anabathra* (*A. pulcherrima* of Pearson 1986 and Witham 1833 = *Paralycopodites brevifolius* of DiMichele 1980 and Morey and Morey 1977) has a long temporal range from the Late Visean (Middle Mississippian) to the Westphalian D (Middle Pennsylvanian). However, this single vegetative organ-species is correlated with three species of the bisporangiate cone-genus *Flemingites* (sensu Brack-Hanes and Thomas 1983), which differ in quantitative characters not amenable to cladistic analysis (Bateman et al., in press) and have much shorter stratigraphic ranges than their shared vegetative correlate (DiMichele 1980).

We suspect that a similar situation exists in *Hizemodendron serratum*. The long stratigraphic range of *H. serratum* (almost the entire Early and Middle Pennsylvanian; DiMichele 1981) may indicate that it is an aggregate species. If so, it will be dissociated into more meaningful whole-plant species as knowledge of variation in its reproductive morphology through time increases from the present inadequate level.

Hizemodendron and Lepidodendron as a Monophyletic Group. Confident resolution to the question of whether these genera constitute a monophyletic or paraphyletic group requires greater knowledge of the rhizomorph, stem, and reproductive organs of *Hizemodendron*. Parsimony based on vegetative and reproductive organs strongly suggests that *Hizemodendron* and *Lepidodendron* comprise a paraphyletic sister-group to *Lepidophloios* (fig. 1A), but reproductive characters alone allow monophyly (fig. 1C).

We hypothesize that *Hizemodendron* was derived from a *Lepidodendron*-like arboreal ancestor by precocious apical branching and decrease in body size, and that these gross modifications are reflected in a large proportion of the vegetative character-state transitions that distinguish the two genera. These inferred character correlations render monophyly a more tenable hypothesis than raw parsimony would suggest.

Even if further data support monophyly for the *Hizemodendron-Lepidodendron* group, their

gross morphological differences alone merit generic separation. However, the precedent of delimiting genera within a monophyletic group using growth habits would then require the generic separation of two groups of species within the monophyletic genus *Diaphorodendron*, which are distinguished not only by different growth habits but also by different bauplans (Bateman et al., in press; DiMichele 1981, 1985).

Saltational Changes in Growth Habit as a Macroevolutionary Process in Lycopside. DiMichele and Bateman (1989) and Bateman et al. (in press) documented a wide range of body sizes and body plans among the rhizomorphic lycopsids. Rhizomorphs and stems are ubiquitous components, but lateral branches/peduncles and crown branches are more restricted in occurrence. These four components differ greatly between species in relative size and secondary tissue content. We believe that different combinations and morphological expressions of these components result from mutation of D-genes (regulatory and structural genes controlling early development; Arthur 1984, 1988), allowing geologically-instantaneous saltational macroevolution in lepidodendraleans that is expressed as heterochrony s.l. (e.g., Alberch et al. 1979; Gould 1977; DiMichele and Bateman 1989; Rothwell 1987). Many other correlated morphological and anatomical changes occurred immediately, as a result of epigenetic changes within the new bauplan or habit, or subsequently, as a result of adaptive honing by natural selection (e.g., Arthur 1984).

Phylogeny reconstruction indicates that many lycopsid growth architectures and habits are iterative, including the pseudoherbaceous habit that characterizes *Hizemodendron*, *Oxroadia*, and *Paurodendron*. This iteration implies that habit changes were a major macroevolutionary mechanism in the lycopsid clade. Heterochronic anomalies must have occurred frequently, as the chances of perpetuating such macromutants are very small, requiring a competition-free niche to allow establishment of the new population prior to adaptive honing (Arthur 1984, 1988; DiMichele et al. 1987). The high-stress ground layer of a coal-swamp may have provided just such an opportunity for *Hizemodendron*, which can be the dominant non-arboreal component in those tree-lycopsid forests where it occurs. Current evidence suggests that *Hize-*

modendron succumbed, along with most of its arboreous lycopsid cohabitants, to the climatically-driven Westphalian-Stephanian extinction (Phillips and Peppers 1984; Phillips et al. 1985), indicating a similar degree of ecological specialization and thereby vulnerability to long-term environmental change.

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