Origin and evolution of lycopods

C. G. K. Ramanujam

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The lycopods are known from as early as Sieginean Stage of the Lower Devonian. Lower and Middle Devonian lycopods were all herbaceous. Arborescent taxa appeared by Upper Devonian (e.g., *Cyclostigma* and *Lepidosigillaria*). The microphyllous foliage of lycopods seem to have originated from enations as well as telomic trusses. The lycopods attained peak of their evolution during the Upper Carboniferous. Towards the close of the Carboniferous and dawn of the Permian, with gradual dwindling and disappearance of swamps, the lepidodendrids suffered drastic decline numerically and phytogeographically. General aridity of the Triassic resulted in acute dwarfing as evidenced by *Pleuromeia*. This trend continued further resulting in the highly telescoped *Nathorstiana* during the Cretaceous. The earlier lycopods were homosporous; heterospory appeared by Upper Devonian. Heterospory ran rampant in the Lepidodendrales. The ultimate in heterospory and the approach to seed habit could be witnessed in *Lepidocarpon*. Four discrete types of strobilus organization could be recognized by the Lower Carboniferous, viz., 1. *Lepidostrobus* type, 2. *Mazocarpon* type, 3. *Achlamydocarpon* type, and 4. *Lepidocarpon* type. Recent studies point towards the origin of lycopods along two different pathways, with both Zosterophyllopsida and Rhyniopsida representing the progenitors. All available evidence show that Lycopsida constitutes a "*Blind Alley*" in the evolution of vascular plants.

Key-words—Lycopsida, Origin, Geological history, Evolution.

C. G. K. Ramanujam, Department of Botany, P. G. College of Science, Osmania University, Saifabad, Hyderabad 500 004, India.

सारांश

लाइकोपोडी पौधों की उत्पत्ति एवं विकास

सी० जी० के० रामानुजम

लाइकोपोडी पौधों के अवशेष अधरि डिवोनी कल्प के सिजीनियन चरण से भी पहले से मिलते हैं। अधरि एवं मध्य डिवोनी से प्राप्त सभी लाइकोपोडी पौधे शाकीय थे। वृक्षवत् वर्गक (**साइक्लोस्टिग्मा** एवं **लेपिडोसिजिलेरिया**) उपरि डिवोनी कल्प में विकसित हुए। उपरि कार्बनीफ़री कल्प में इन पौधों का सर्वाधिक विकास हुआ। परन्तु कार्बनीफ़री कल्प की समाप्ति तथा परमी कल्प के प्रारम्भ में दलदली परिस्थितियों की शनैः शनैः समाप्ति के फलस्वरूप संख्या एवं भौगोलिक दोनों ही दृष्टि से इनका अत्याधिक ह्रास हुआ। त्रिसंधी कल्प में शुष्क परिस्थितियों के कारण इनका काफी छोटा आकार हो गया जैसा कि **प्लूरोमिआ** से प्रमाणित है और यही प्रवृत्ति इसके पश्चात् क्रीटेशी कल्प में भी चलती रही जिसके फलस्वरूप इनका आकार सूक्ष्म हो गया।

लाइकोपोडी पौधे पहले समबीजाणविक थे परन्तु उपरि डिवोनी कल्प में इनमें विषमबीजाणविक प्रवृत्ति विकसित हो गई। विषमबीजाणविक प्रवृत्ति तथा बीज का विकास **लेपिडोडेन्ड्रॉन** से जाना जा सकता है। अधरि कार्बनीफ़री कल्प तक चार विशेष प्रकार के शंकु अभिनिर्धारित किये जा सकते हैं—1. **लेपिडोस्ट्रोबस** प्ररूप, 2. **मेज़ोकार्पन** प्ररूप, 3. **एक्लेमाइडोकार्पन** प्ररूप, तथा 4. **लेपिडोकार्पन** प्ररूप। सभी उपलब्ध प्रमाणों से यह व्यक्त होता है कि वाहीनिकीय पौधों के विकास हेतु लाइकोपोडी पौधे एक "अन्धी गली" के समान हैं।

UNEQUIVOCAL members of Lycopsida could be recognized from as early as Sieginean Stage of the Lower Devonian coexisting with the zosterophyllopsids and rhyniopsids. They soon underwent rapid multiplication and radiation qualitatively and quantitatively all through the Devonian, and by Carboniferous Period attained developmental climax, both vegetatively and reproductively, as exemplified by numerous herbaceous and arborescent taxa that dominated the swampy environment. The Permian Period, which witnessed rapid dwindling and disappearance of swamps, heralded their decline. The overall arid Triassic Period triggered drastic physical, numerical and phytogeographic diminution of the lycopods. The geological history of the Lycopsida closely parallels that of the Sphenopsida which, however, suffered

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much more drastic decline. Thomas (1978), Phillips (1979) and DiMichele and Phillips (1985) have provided superb overviews of the morphology, reproductive biology and ecological adaptation of the Palaeozoic arborescent lycopods.

The extant Lycopsida comprises five genera, viz., *Phylloglossum, Lycopodium* (Lycopodiaceae), *Selaginella* (Selaginellaceae) and *Isoetes* and *Stylites* (Isoetaceae). If *Stylites* is considered as a subgenus of *Isoetes* (see Kramer & Green, 1991), only four genera constitute the extant lycopods. In the geological past, however, the lycopods enjoyed better representation at the genus, family and order levels.

GENERAL CHARACTERS AND CLASSIFICATION

The lycopods are a well-knit, homogeneous group of lower vascular plants. The essential features of lycopods are: plants usually herbaceous but occasionally arborescent with dichotomous or a combination of dichotomous and monopodial branching; leaves helically disposed microphylls with a prominent unbranched midvein that does not leave any leaf gap in the stele of stem; vasculature of stems protostelic or siphonostelic with protoxylem in exarch position; arborescent taxa with limited secondary xylem; a single sporangium borne in the axil or on adaxial surface of sporophyll; sporophylls generally aggregated to form discrete strobili; plants homosporous or heterosporous.

Drepanophycales, Protolepidodendrales, Lycopodiales, Selaginellales, Lepidodendrales, Pleuromeiales and Isoetales are usually recognized in various systems of classification proposed since 1960 (Delevoryas, 1962; Sporne, 1966; Bierhorst, 1971; Stewart, 1983; Taylor, 1983; Meyen, 1987). Bierhorst (1971) included Asteroxylales also under lycopods, and Meyen's (1987) Isoetales encompasses the Lepidodendrales and Pleuromeiales of others. The author, however, agrees with Stewart (1983) that *Asteroxylon* notwithstanding its similarities with lycopods, deserves inclusion only under Zosterophyllopsida. Further, the traditional treatment of Isoetales is followed in this contribution. Lycopodiales, Selaginellales and Isoetales consist of both extinct and extant members; the remaining taxa are represented by only extinct members. The following are the geological ranges of the various lycopod orders:

Drepanophycales	— Devonian
Protolepidodendrales	— Devonian to Lower Carboniferous
Lepidodendrales	— Upper Devonian to Permian
Pleuromeiales	— Triassic to Cretaceous
Lycopodiales	— Upper Carboniferous to Recent
Selaginellales	— Upper Carboniferous to Recent
Isoetales	— Triassic to Recent

VEGETATIVE CHARACTERS

The Lower and Middle Devonian lycopods were all herbaceous (e.g.) *Baragwanathia, Drepanophycus, Protolepidodendron, Colpodexylon*, etc.). Shrubby or moderately arborescent habit appeared by the Upper Devonian as evidenced by *Lepidosigillaria* and *Cyclostigma* which often attained a height of 8 m and a girth of 30 cm. During the Carboniferous the arborescent lycopods had their best expression in forest giants such as *Lepidodendron, Lepidophloios, Sigillaria* and *Bothrodendron*. It is generally suggested that the Upper Devonian taxa, such as, *Lepidosigillaria* and *Cyclostigma* constitute the transitional forms and the possible precursors of the Carboniferous arborescent lycopods. Banks (1960) opined that there was a group of diverse herbaceous Devonian lycopods with eligulate foliage, lack of leaf cushions and homospory which subsequently gave rise to arborescent forms along one line and newer herbaceous forms along the other. Andrews (1961) visualized a common stock from which all the arborescent taxa developed. The lycopods of the Carboniferous and Permian furnished greatest diversity of form incorporating small, insignificant herbaceous taxa referable to Lycopodiaceae and Selaginellaceae (e.g., *Lycopodites, Selaginellites, Paurodendron*, etc.), moderately arborescent (some species of *Lepidodendron, Paralycopodites*), and huge, majestic arborescent Lepidodendrales often attaining a height of 50 m and occupying extensive tracts of swamps (*Lepidodendron, Lepidophloios, Sigillaria*, etc.) in the Euramerica.

The branching of the axes was almost exclusively dichotomous in the earliest forms and a combination of dichotomous and monopodial nature in the later forms. The foliage of lycopods should be technically designated as microphylls irrespective of their size as they possess a single unbranched midvein not associated with any leaf gap in the central vascular cylinder of the stem. The leaves disposed in a lax or close-knit helix or pseudowhorls may be scale-like, linear, deltoid and more or less laminar (Fairon-Demaret & Banks, 1978). They may be entire or as in some Devonian

taxa forked (*Protolepidodendron*), trifurcate (*Colpodexylon*) or split up into five lobes (*Leclereqia*). Further, the leaves may be perennial or show abscission leaving prominent leaf cushions of varied shapes (e.g., Lepidodendrales).

The stelar anatomy of the lycopod stems shows well-defined trends of evolution from various types of protostele to mixed protostele and ultimately the siphonostele. The protosteles of the Devonian lycopods may be lobed, as in, *Drepanophycus, Colpodexylon* and *Archaeosigillaria*, or with numerous small marginal, teeth-like ridges, as in, *Protolepidodendron* and *Leclereqia*. The lobed protostele resembles the steles in some of the modern species of *Lycopodium*; the ridged type is comparable with the primary xylem of some of the arborescent lepidodendrids (e.g., *Lepidophloios*). The lepidodendrids show solid protosteles (*Lepidodendron scleroticum*), mixed protosteles (*Lepidodendron vasculare*) and siphonosteles (*Lepidodendron hickii, Sigillaria approximata*). The arborescent forms possess cambial activity resulting in secondary tissues. The vascular cambium is, however, unifacial forming only secondary xylem and no secondary phloem (Eggert & Kanemoto, 1977).

The microphylls of lycopods are generally considered to have been evolved from enations (Bower, 1935; Banks, 1968; Gensel, 1975). According to this concept, the microphylls originated from non-vascularized spine-like enations seen in some zosterophyllopsid taxa, viz., *Sawdonia, Kaulangiophyton*, etc. The enations of *Asteroxylon*, where in a vascular trace emanating from the axial protostele stops short abruptly at the base of the enation rather than entering it, represent obviously the intermediate step in the evolution of microphylls. The extension of the vascular trace into the enation results in a microphyll with a single midvein as exemplified by *Drepanophycus* and *Baragwanathia*, two of the earliest lycopods. A continued elaboration of the simple microphyll could result in the variously lobed microphylls of the protolepidodendralean taxa.

The telomic origin of microphylls originally proposed by Zimmermann (1952) did not receive much support for a long time. The recent studies of Schweitzer (1980) and Bonamo and Grierson (1981) which highlight the 3-dimensional nature of the fertile and sterile microphylls of *Protolepidodendron* and *Leclereqia* have provided fairly convincing evidence for the origin of some microphylls by overtopping and reduction of telomic trusses (see also Stewart, 1983). In accordance with this concept, the variously lobed microphylls would represent primeval condition in some lycopods. It now appears probable that the microphylls of lycopods could have evolved along two divergent pathways, one involving enations and the other, telomic trusses. Concomitantly, the microphylls of all the lycopods need not necessarily be considered as homologous structures.

With the dwindling and large scale disappearance of swampy habitats by the end of the Upper Carboniferous and the dawn of the Permian, many of the arborescent lycopods such as *Lepidodendron* and *Lepidophloios* suffered drastic decline but *Sigillaria*, and smaller lepidodendrids such as *Paralycopodites* survived along with a number of herbaceous forms. The Triassic witnessed acute diminution in the arborescent habit resulting in much smaller forms like *Pleuromeia* which attained a maximum height of 2 m. Both the aerial and subterranean systems of the lepidodendrids such as *Sigillaria* underwent extreme reduction as exemplified by *Pleuromeia*. Further reduction in the aerial system could have led to *Nathorstiana* (10-15 cm) of the Cretaceous. Earlier it was felt that *Isoetes* probably represents the end product of this continued trend of reduction starting from *Sigillaria* (Magdefrau, 1956). Based on his study of *Protostigmaria*, Jennings (1975) argued that the lobed rhizophore of *Isoetes* might not have evolved from the dichotomous stigmarian root system of arborescent lycopods. Pigg and Rothwell (1979) recently suggested that *Isoetes* and *Stylites* may have had their origin in *Lepidodendron* plants of smaller stature possessing basal cormose rhizophore, instead of a regular stigmarian type of branched rooting system. The bisporangiate strobili, and the similarity between the megagametophytic structures of *Isoetes* and Lepidodendraceae furnish additional support to this line of thinking (Brack-Hanes, 1978). The Upper Devonian moderately arborescent lycopods like *Lepidosigillaria* and *Cyclostigma* with basal once- or twice-lobed corm-like rhizophores could be the progenitors of the line that resulted in Isoetes-like plants. The recent discovery of *Isoetites* from the Triassic (Brown, 1958; Bock, 1962) lends support to this view. *Pleuromeia* and *Nathorstiana* thus appear to have evolved (or devolved!) along a different pathway than that of *Isoetes* and *Stylites*.

REPRODUCTIVE CHARACTERS

One of the diagnostic features of Lycopsida is the presence of a single, globose, reniform or elongated sporangium either in the axil or on the adaxial facet of the sporophyll. Many of the Lower and Middle Devonian lycopods, viz.,

Baragwanathia, Drepanophycus, Protolepidodendron, Cyclodendron, Leclereqia, etc. do not show any perceptible difference between the sporophylls and vegetative leaves. The sporophylls in these taxa may be seen interspersed among the leaves or loosely grouped into discrete fertile zones alternating with the leaves, simulating the situation seen in the modern *Lycopodium selago*. In other words, no organized strobili were known in the Lower and Middle Devonian lycopods. Well-organized strobili were encountered only from the Upper Devonian onwards. The absence of organized strobili may then be considered as a primeval condition in lycopods.

The Lower and Middle Devonian lycopods were all homosporous. By the Upper Devonian time heterospory appeared as evidenced by the bisporangiate strobili of *Cyclostigma* (Chaloner, 1968). Phillips (1979) has provided a masterly analysis of the strobilus organization and reproductive biology of the arborescent lycopods.

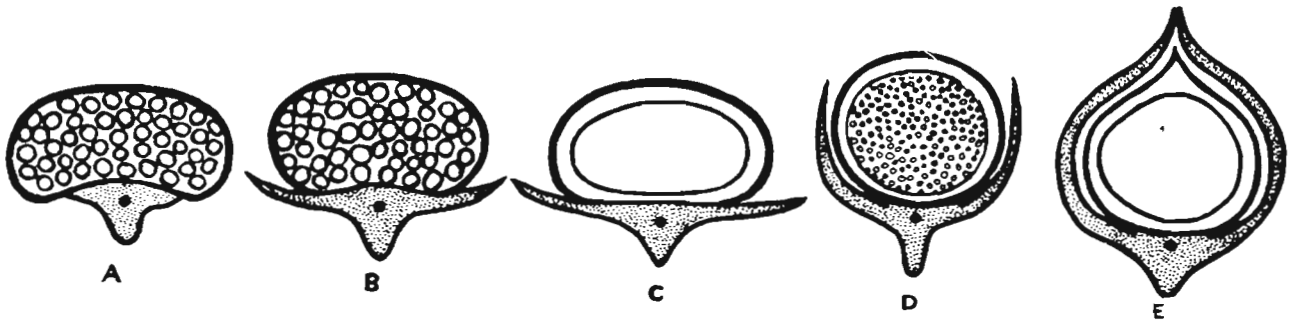
In addition to the Devonian herbaceous Drepanophycales and Protolepidodendrales, the modern Lycopodiales are homosporous. Lepidodendrales, Pleuromeiales, Selaginellales and Isoetales are, however, strictly heterosporous. The heterosporous taxa are invariably ligulate but the homosporous ones, are as a rule, eligulate notwithstanding the recent discovery of ligulate, homosporus *Leclereqia* (Banks, Bonamo & Grierson, 1972).

A gradual reduction in the number of megaspores per megasporangium and the concomitant increase in the size of the remaining megaspores seems to be most potent trend of evolution within the heterospory. The highly advanced heterospory is the one in which a large functional megaspore is retained within the megasporangium as exemplified by *Miadesmia, Achlamydocarpon, Lepidocarpon* and some species of *Selaginella (S. monospora, S. sulcata)*. The ultimate in the heterospory coupled with the approach to seed habit had its expression in *Lepidocarpon lomaxi* (strobilus referable to *Lepidophloios*) which for all intents and purposes functioned as a seed. The studies of Ramanujam and Stewart (1969) and Phillips (1979) have clearly shown that *Lepidocarpon* is an integumented dehiscent megasporangium with a single functional megaspore.

By the Early Carboniferous (Mississippian) four distinct types of strobilus architecture, primarily based upon megasporangium—megasporophyll units, could be recognized in the arborescent lycopods, viz. (i) free sporing bisporangiate Lepidostrobus-type exemplified by *Lepidostrobus (= Flemingites), Bothrodendrostrobus, Sporangiostrobus*, etc., and closely resembling the extant *Selaginella*, (ii) Mazocarpon-type showing intrasporangial modification in the form of a parenchymatous pad or cushion, (iii) Achlamydocarpon-type with megasporangial and sporophyll modification (the megasporangial wall being multilayered and sclerotic and the sporophyll pedicel prominently keeled), and (iv) lepidocarpon-type which is integumentary (Phillips, 1979). The latter three types are monosporangiate; of these *Achlamydocarpon* and *Lepidocarpon* are monosporic.

Unlike *Lepidostrobus*, in *Mazocarpon* the megasporangium-sporophyll complexes are shed from the cone and disseminated by wind and water. The megasporangium-sporophyll units of *Achlamydocarpon* and *Lepidocarpon* simulate boat-like structures and functioned as propagules (dissiminules) well adapted to dispersal by water. The fertilization and embryo development in these took place most probably after their separation from the parent plants and release into the swamp (Phillips, 1979; DiMichele & Phillips, 1985). The free sporing bisporangiate *Lepidostrobus* type with many small megaspores per sporangium, encountered more frequently than other types during the Lower Carboniferous, may be considered as least specialized structurally in its adaptation to swampy environment.

The nature of sporangial protection in arborescent lycopods also furnishes distinct trends of evolution. The sporangium in *Lepidostrobus*, where the pedicel of sporophyll is simply T-shaped in cross section, is least protected and represents the primitive condition. The *Lepidocarpon* sporangium ensheathed by well-developed lateral lamina ("*integument*") is best protected and evolutionarily, more advanced. *Lepidostrobopsis* and *Lepidocarpopsis* of Abbott (1963) are intermediate between the above two extremes. In *Achlamydocarpon*, a multilayered sclerotic wall affords protection to the sporangium (Schumaker-Lambry, 1966). Balbach (1962) and Ramanujam and Stewart (1969) have provided detailed information on the developmental stages of the lateral lamina in *Lepidocarpon. Lepidostrobus, Lepidostrobopsis, Lepidocarpopsis* and *Lepidocarpon* show the following trends of evolution in the sporangial protection by its progressive ensheathment, viz. (i) lateral extension or alation of the pedicel on either side of its vein portion, (ii) gradual upturning of the alation to enfold the sides of the basal half of sporangium, and (iii) further elaboration and upward growth of the alation to form well-developed lateral lamina that



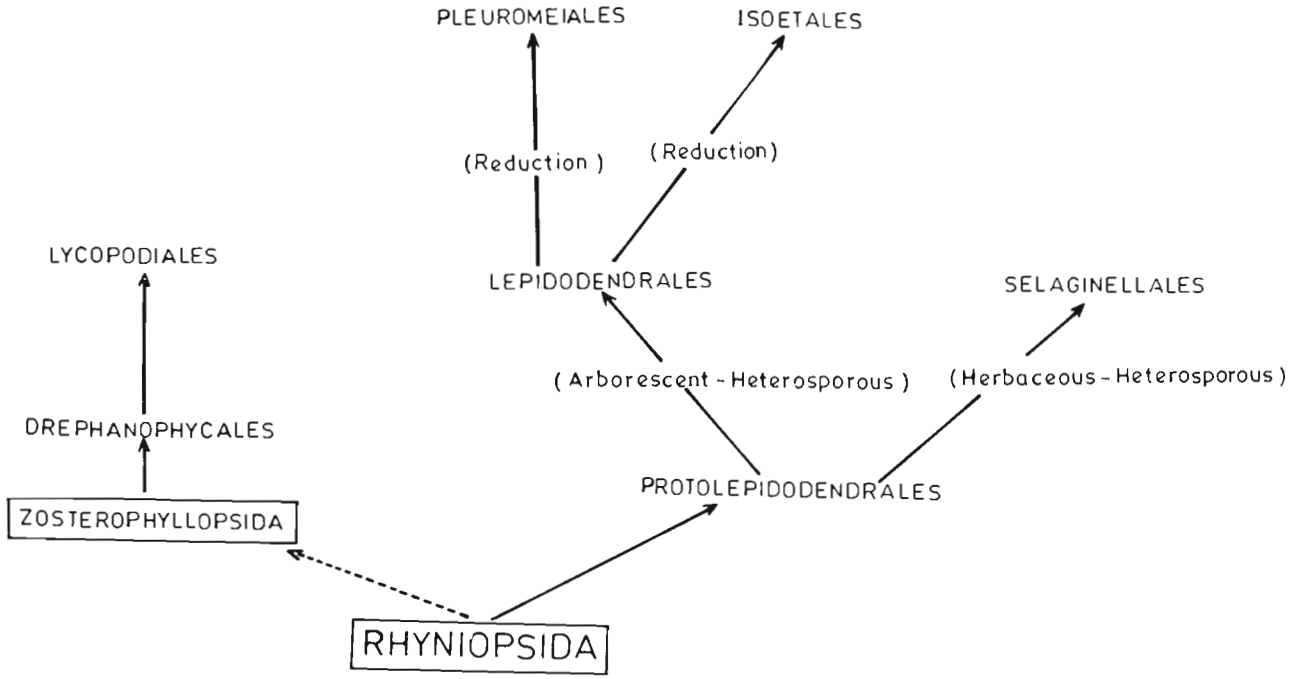
Text-figure 1—Diagrammatic cross sections of sporophylls of: **A.** *Lepidostrobus*, **B.** *Lepidostrobopsis*, **C.** *Lepidocarpopsis lanceolatus*, **D.** *L. semialata*, and **E.** *Lepidocarpon* showing progressive ensheathment of the sporangia (redrawn from Ramanujam & Stewart, 1969).

completely ensheaths the sporangium leaving a narrow slit (Text-figure 1). *Lepidocarpon* may then be considered as a highly advanced reproductive organization of arborescent lycopods that closely mimicked the seed habit, which incidentally was also evolving during the Carboniferous. In *Lepidocarpon*, however, the integument-like lateral laminae were outgrowths of the sporophyll pedicel, while the integuments of seed plants had their origin from the reduction and concrescence of a branching system.

ORIGIN OF LYCOPODS

Recent thought provoking studies on the antiquity, origin and evolution of early vascular plants (Banks, 1967, 1968; Banks & Davis, 1969) have brought to light convincing evidence for treating Zosterophyllopsida as the progenitors of lycopods. Banks (1968) proposed that lycopods are monophyletic and had their origin from zosterophylls, with *Asteroxylon*, or taxa of similar nature, as transitional forms. In the possession of massive elliptic or terete protosteles with exarch protoxylem and globose to reniform stalked lateral sporangia with distal dehiscence in addition to dichotomous or pseudomonopodial branching with spirally disposed spine-like enations, the zosterophylls are, no doubt, genetically related to lycopods.

Stewart (1983), who included Asteroxylales under Zosterophyllopsida, has argued that lycopods



Text-figure 2—Phylogenetic concepts of Lycopsida based upon recent studies.

had two different sources of origin, viz., Zosterophyllopsida and Rhyniopsida. He considers Zosterophyllopsida as ancestral to Drepanophycales which subsequently gave rise to the eligulate, homosporous Lycopodiales. The second source in this concept involves the Rhyniopsida as the progenitors of Protolepidodendrales which later on evolved into Lepidodendrales and from thence to Pleuromeiales and Isoetales, on one hand, and Selaginellales on the other (Text-figure 2). Recent interpretation of the variously lobed fertile and sterile microphylls in diverse Protolepidodendrales as 3-dimensional telome trusses (Schweitzer, 1980; Bonamo & Grierson, 1981) lends credence to the concept of rhyniopsid ancestry of protolepidoden drids. Further, the possibility that Zosterophyllopsida itself could have probably originated from Rhyniopsida merits serious consideration, as indicated by the discovery of *Renalia hueberi* (Gensel, 1976) in the Lower Devonian, furnishing tantalizing evidence for the pathway leading to stalked lateral sporangia with distal dehiscence.

In conclusion, it appears that Drepanophycales and Protolepidodendrales constitute a constellation of Devonian lycopods from which the remaining lycopods evolved along two different lines, viz., Lycopodiales from Drepanophycales, and Lepidodendrales, Pleuromeiales, Isoetales and Selaginellales from protolepidodendralean stock. Triassic *Pleuromeia*, and Cretaceous *Nathorstiana* could represent the products of extreme reduction from Sigillaria-like Upper Carboniferous-Permian arborescent lycopods. As regards Isoetales, however, it now appears fairly convincing that this group originated from small Lepidodendron-like plants with basal cormose rhizophore by further diminution.

All available data indicate in no uncertain manner that the lycopods which appeared in the Lower Devonian, radiated and multiplied through the Upper Devonian reaching their peak of evolution during the Upper Carboniferous-Permian, but declined drastically since then, have not given rise to any other group of Tracheophyta and hence constitute a "Blind Alley".

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