CURRENT STATUS OF THE PROGYMNOSPERMOPSIDA

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ABSTRACT

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The three progymnosperm orders, Aneurophytales, Protopityales, and Archaeopteri-
dales, are characterized and analyzed. The possibility that some of the apparent taxonomic
diversity of the Aneurophytales and Archaeopteridales might reflect developmental
variation is considered as well as the probability that much of it reflects evolutionary
change. A detailed discussion of the phylogenetic position of the Progymnospermopsida
concludes the paper.

INTRODUCTION

Establishment of the Progymnospermopsida followed the discovery of
Archaeopteris lateral branch systems attached to stems of *Callixylon*
structure (Beck, 1960a, b).

The group is comprised of plants of gymnospermous anatomy and free-
sporing, homosporous or heterosporous reproduction. Plants of some genera
attained the stature of large trees (Beck, 1962a, 1964), and produced
secondary vascular tissues and periderm. Branching in lateral branch systems
is three-dimensional in many forms, but occurs in one plane in some Upper
Devonian and Lower Mississippian genera (e.g., *Archaeopteris, Siderella*).
Ultimate appendages (leaves) may be laminate or finely divided, and when
of the latter type may be either three-dimensional or flattened (see
Scheckler and Banks, 1971b).

Three orders have been recognized: Aneurophytales (Kräusel and
Weyland, 1941), Protopityales (Walton, 1957), and Archaeopteridales
(Arnold, 1930).

ANEUROPHYTALES

The order is characterized predominantly by three-dimensional branching.
Branching patterns of vegetative branch systems are either helical (*Rellimia*
[formerly *Protopteridium*], *Aneurophyton, Triloboxylon, Cairoa*) or

decussate (*Tetraxylopteris*) or in one plane (*Triloboxylon, Proteokalon*). The ultimate appendages are arranged helically in *Rellimia, Aneurophyton*, and *Triloboxylon*, and decussately in *Tetraxylopteris*. In *Proteokalon* an adaxial pair alternates with a single abaxial ultimate appendage (Scheckler and Banks, 1971b). The arrangement of ultimate appendages in *Cairoa* is unclear.

Sporangia are borne terminally, and in several genera (*Tetraxylopteris* [Bonamo and Banks, 1967], *Rellimia* [Leclercq and Bonamo, 1971, 1973], and *Triloboxylon* [Scheckler and Banks, 1972], on two-ranked (planated) lateral branch systems. Second order branching in the fertile systems of *Rellimia* and *Tetraxylopteris* is dichotomous, but sporangia are borne on terminal axes arranged in an irregularly pinnate manner (Bonamo and Banks, 1967; Leclercq and Bonamo, 1971).

Primary xylem forms a ribbed protostele except in ultimate appendages where it is a terete strand (Beck, 1957; Scheckler and Banks, 1971a). The secondary wood is pycnoxylic with generally tall, narrow rays that in some genera (*Triloboxylon, Tetraxylopteris*) contain some ray tracheids (Scheckler and Banks, 1971a). One species, *Triloboxylon hallii*, possesses secondary wood with tracheary pits arranged in radially banded groups like that of *Callixylon* (*Archaeopteris*) of the Archaeopteridales. Secondary xylem is unknown in *Cairoa* (Matten, 1973).

The secondary phloem, where known (*Tetraxylopteris* [Beck, 1957], *Triloboxylon* [Scheckler and Banks, 1971a], *Proteokalon* [Scheckler and Banks, 1971b]), is characterized by abundant thick-walled fibers. Phloem rays vary in width from one to several rows of cells, and are usually dilated in comparison with their counterparts in the secondary xylem.

The outer cortex of all members of the Aneurophytales (with the possible exception of *Aneurophyton* in which it is unknown) is characterized by thick-walled sclerenchyma cells, often forming a network of longitudinally oriented, interconnected strands, the so-called dictyoxylon cortex of earlier authors (Beck, 1957; Matten and Banks, 1966; Leclercq and Bonamo, 1971; Scheckler and Banks, 1971a, b; Matten, 1973).

The Aneurophytales extend through the geologic column from lowermost Middle Devonian (early Eifelian) to middle Upper Devonian (late Frasnian). Ranges of individual genera are given in Fig.1.

Six genera are currently assigned to the order. These are: (1) *Aneurophyton* Kräusel et Weyland, 1923; see also Leclercq (1940); (2) *Cairoa* Matten, 1973; (3) *Proteokalon* Scheckler et Banks, 1971b; (4) *Rellimia* Leclercq et Bonamo, 1973; see also Leclercq and Bonamo (1971); (5) *Tetraxylopteris* Beck, 1957; see also Matten and Banks (1967); Bonamo and Banks (1967); Scheckler and Banks (1971a); (6) *Triloboxylon* Matten et Banks, 1966; see also Scheckler and Banks (1971a, 1972).

Another genus, *Sphenoxylon*, has been shown to represent poorly preserved, petrified stem axes of *Tetraxylopteris* (Matten and Banks, 1967; Scheckler and Banks, 1971a).

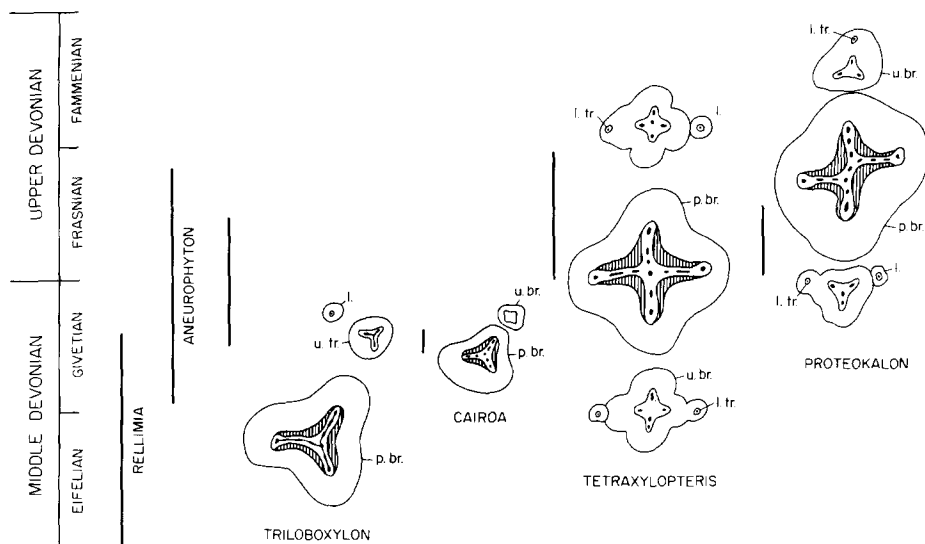*Stauroxylon* Galtier, 1970 from the Lower Carboniferous of France is

Fig.1. Geologic ranges (heavy lines to left of names and diagrams) and morphologic features of some members of the Aneurophytales. Some aspects of the primary and secondary xylem, branching patterns, and phyllotaxy are shown. Lined secondary xylem encloses unshaded metaxylem that contains black protoxylem strands. The smallest appendages containing traces, terete in sectional view, are considered to be the basal parts of leaves. Genera are arranged from left to right in order of increasing levels of morphologic specialization. *l* = leaf; *l. tr.* = leaf trace; *p. br.* = penultimate branch; *u. br.* = ultimate branch.

remarkably similar to *Tetraxylopteris*. It is characterized by decussate branching and a four-ribbed protostele. Parenchymatous protoxylem occurs in mesarch strands. Opposite to subopposite pairs of traces (terete in section), apparently the vascular supply to ultimate appendages, diverged from the irregularly shaped vascular column of the second-order branches. It is not clear whether ultimate appendages were two-ranked or decussately arranged. The vascular column of the second order branches (as seen in transverse view) elongated in the plane of trace divergence. Following the production of the first pair of traces, this column, at a higher level, became elongate at right angles to the region from which the first pair had diverged. Although a second pair of traces is not preserved in Galtier's specimen, this evidence supports the possibility of a decussate arrangement of ultimate appendages.

Although Galtier believes that *Stauroxylon* is probably an aneurophytalean progymnosperm, he hesitates to assign it definitely to this group because of several divergent characters, and because its fructifications are unknown. Primary among the differences he cites is the presence of scalariform pits in the secondary xylem. Because of poor preservation, however, the details of tracheary pitting are not clear. The pits may have been similar to the elliptical bordered pits of the inner secondary wood of *Protopitys scotica*. As Smith (1962) has shown, tracheids in later-formed secondary wood of

this genus were circular-bordered. Whether or not this was true also of *Stauroxylon* must await the discovery of specimens with larger amounts of secondary xylem.

I agree with Galtier that *Stauroxylon* is almost certainly a member of the Aneurophytales. If subsequent study corroborates this view, this genus will become the first record of a Lower Carboniferous aneurophyte.

Childanophyton, from the Lower Mississippian of southwestern Virginia, recently established by Gensel (1973), and the Upper Devonian genus *Rhacophyton*, have been suggested as possible aneurophytes (for discussion of the taxonomic affinities of the latter genus, see Andrews and Phillips, 1968). *Childanophyton* is very similar in some features to *Rhacophyton*, and also to *Protocephalopteris* (see Schweitzer, 1968). *Rhacophyton*, is considered to be a coenopterid fern by Leclercq and Bonamo (1971) who base their conclusion on the presence of clepsydroid primary xylem strands with peripheral loops. The genus is also characterized by scalariform tracheids in the secondary xylem. *Rhacophyton*, *Protocephalopteris*, and *Childanophyton* may well be primitive members of the *Zygopteridaceae* (Coenopteridales).

Andrews et al. (1974) have described probable Middle Devonian specimens from Chaleur Bay, New Brunswick with aneurophytalean features. They assign a new name, *Chaleuria*, to this material. Whereas only two orders of branches are illustrated in their restoration (the second order bearing dichotomous sterile or fertile ultimate appendages), Andrews et al. (1974) describe some specimens as having three orders of branches. *Chaleuria* produced spores of variable size that fall into two intergrading size classes, considered by Andrews et al. (1974) to represent "incipient heterospory". Although I have not seen the specimens, the published descriptions and photographs seem to present many of the important characteristics of *Aneurophyton* as described by Kräusel and Weyland (1923, 1926, 1929), and as amplified and modified by Leclercq (1940), Streel (1964) and Potonié (1967). Andrews et al. (1974) compare *Chaleuria* with *Arctophyton*, a poorly understood plant from the early Middle Devonian of Spitsbergen which Schweitzer (1972) suggests might have been related to Aneurophyton. Both *Chaleuria* and *Arctophyton* are considered to be possible members of the Progymnospermopsida.

Further study of *Chaleuria*, *Arctophyton*, and *Aneurophyton* is required to clarify the status and relationships of these genera.

Two form genera, *Eospermatopteris* and *Callixylon*, include fossils that represent parts of several of the genera listed above. *Eospermatopteris* is the name for sandstone stump casts commonly thought to belong to *Aneurophyton* (Kräusel and Weyland, 1941). They might also belong to some other aneurophytes. *Callixylon*, the type of secondary wood with groups of circular bordered pits arranged in radial bands, is a feature of at least one aneurophyte, *Triloboxylon hallii* (Scheckler and Banks, 1971a), as well as of *Archaeopteris* and *Eddya* of the Archaeopteridales (Beck, 1960b, 1967).

PROTOPITYALES

This order is represented by a single genus, *Protopitys* Göppert, of Lower Carboniferous age, recently studied by Walton (1957, 1969) and Smith (1962). The plant was probably pteridophytic in reproduction, and bore dichotomous fertile organs within which sporangia were produced terminally on pinnately arranged ultimate branches (Walton, 1957; Smith, 1962).

The sporangia, approximately 3 mm long, dehisced by a longitudinal slit. Spherical, trilete spores are of variable size (80—360 μm in diameter) and are characterized by an enclosing, cutinized membrane. According to Smith (1962) "it is possible that . . . the membrane is homologous with the air sac or saccus of some monosaccate spores and pollen . . . " Because the spores fall into two distinct size classes, Smith endorses Walton's view that *P. scotica* represents an early stage in the evolution of heterospory. He believes that the intact spore (with saccus or "perine" present) can reasonably be "compared to a monosaccate type such as . . . *Remysporites* B. and W., a genus whose only known species, *R. magnificus* (Horst) B. and W., is the pollen of a pteridosperm, *Paracalathiops stachei* Remy . . . "

This arborescent plant whose stems are known to have exceeded 45 cm in diameter, produced massive, dense secondary wood of gymnospermous aspect. Pitting on the radial walls of tracheids is uniseriate to multiseriate circular-bordered, the tracheids adjacent to the metaxylem often uniseriate with elliptical, bordered pits (Smith, 1962); vascular rays are uniseriate and small (2—3 cells high) in *P. scotica*, but sometimes biseriate and up to 15 cells high in *P. buchiana*.

Metaxylem encloses the pith, elliptical in transverse view. Protoxylem developed in the inward regions of two adjacent "strands" along opposite, narrow sides of the pith. These pairs of strands divided in succession to form leaf traces, each consisting of two vascular bundles. Consequently, leaves were borne alternately and distichously. Unfortunately, nothing is known of the anatomy and morphology of vegetative leaves of lateral branch systems of *Protopitys*.

ARCHAEOPTERIDALES

This group is composed of genera with three-dimensional or bilaterally symmetrical (planated) lateral branch systems. The main axis of *Svalbardia* is often considered to bear lateral branches in a helical pattern (Carluccio et al., 1966; Andrews, 1970; Chaloner, 1972), but Høeg's (1942) descriptions do not provide a clear picture of the branching pattern of this genus (Beck, 1971). Branching is helical in *Actinoxylon* (Matten, 1968) and bilateral opposite to alternate in *Archaeopteris* and *Siderella*. *Actinopodium* (Høeg, 1942) is characterized by a transverse stelar configuration apparently identical with that of *Archaeopteris*, and its branching was probably also bilateral.

Ultimate appendages (simple leaves) are dichotomously branched and finely divided in *Svalbardia, Actinoxylon* and some species of *Archaeopteris.* In other species of *Archaeopteris* and in *Eddya* they are broadly laminate. Leaves are arranged helically on the penultimate branches of *Svalbardia, Actinoxylon, Archeopteris,* and *Siderella,* and in the two latter genera, at least, they are decurrent on the axes that bear them. On the ultimate branches leaves are arranged helically in *Svalbardia* (Høeg, 1942), decussately in *Actinoxylon,* decussately and/or helically in *Archaeopteris,* and, apparently, bilaterally in *Siderella.*

Fertile structures are known only in *Svalbardia* and *Archaeopteris.* Høeg (1942) noted that the fertile foliage of *Svalbardia* is apparently identical with that of *Archaeopteris.* No subsequent study has provided data which alter this evaluation. Fertile ultimate appendages of *Archaeopteris,* considered to be homologous with vegetative leaves, were borne typically in the basal parts of lateral branch systems that otherwise are vegetative. (Phillips et al. (1972) suggest that some lateral branch systems may be entirely fertile.) The branching pattern in fertile and vegetative regions is identical (Beck, 1971). Fertile ultimate appendages are apparently laminate structures, often dichotomously branched, distally. The linear components of which these appendages are comprised vary from narrowly (Andrews et al., 1965; Carluccio et al., 1966) to rather broadly laminate (Phillips et al., 1972).The more broadly laminate ones occur in regions of transition between fertile and vegetative parts of lateral branch systems, and do not, as far as we know, reflect the general condition in any species. Fertile appendages of *A. fissilis* bear small epidermal emergencies (Andrews et al.,1965).

Sporangia, which stand erect in one or more rows on adaxial surfaces of fertile ultimate appendages, vary in length from about 1.5—4.0 mm. Dehiscence was by a longitudinal slit.

Heterospory has been demonstrated in *Archaeopteris latifolia* (Arnold, 1939), *A.* cf. *jacksoni* (Pettitt, 1965), *A. halliana* and *A. macilenta* (Phillips et al., 1972). The spores, apparently identical in these species, have finely ornamented exines (megaspores "rugulate to incompletely reticulate" [Phillips et al., 1972]) and trilete tetrad scars. Microspores range in diameter from 35—75 μm, and megaspores from 110—370 μm (Pettitt, 1970). Spore measurements of Phillips et al. (1972) are similar, but they observed megaspores, within sporangia, no smaller than 210 μm, and some dispersed megaspores as large as 460 μm in diameter. Megaspores of *Archaeopteris* resemble the dispersed spore genus, *Biharisporites* Potonié.

With the exception of *Callixylon* and *Eddya,* the primary xylem of the "main" axis of all genera forms a multi-ribbed stele. The stele of *Actinoxylon* may be a protostele (Matten, 1968), but a pith characterizes *Archaeopteris, Actinopodium* and *Siderella.*

Callixylon, the large axes on which *Archaeopteris macilenta* (Beck, 1960a, b) and presumably other species were borne, is characterized by a large number of vascular bundles, apparently forming a eustele similar to that of the calamopityeans, lyginopterids and conifers (Beck, 1970, 1971). The

details of morphology and the three-dimensional architecture of the *Calli-xylon* stele, now being studied in this laboratory, are not yet fully understood.

Axes with ribbed steles in archaeopteridalean genera are probably main axes of lateral branch systems. It is possible that like *Archaeopteris*, all genera characterized by such axes represent lateral branch systems, or the more distal regions, of large plants whose main axes had an anatomy similar or identical to that of *Callixylon*. We already know that secondary wood of the *Callixylon*-type occurs in both some species of *Archaeopteris* and in *Triloboxylon hallii* (Scheckler and Banks, 1971a) as well as in *Eddya*. *Callixylon*, therefore, is a form genus (Beck, 1967).

Protoxylem is mesarch in the order. Leaf and branch traces of the main axes of lateral branch systems diverge radially from continuing strands or ribs, differing in detail from trace divergence in *Callixylon* in which, apparently, traces initially diverge from axial bundles along tangential planes as in the eusteles of seed plants.

There is evidence of secondary growth in *Actinoxylon*, *Actinopodium*, and *Archaeopteris* as well, of course, as in *Callixylon* and *Eddya*. In all of these genera tracheids of the compact secondary xylem bear multiseriate, circular-bordered pits (with the exception of *Callixylon arnoldii* [Beck, 1962b] in which pitting is predominantly uniseriate). The pits of *Archaeopteris macilenta* (Beck, 1960a, b), *Eddya sullivanesis* (Beck, 1967), and *Callixylon* occur in groups that are radially banded. Radial banding of grouped pits has not been observed in *Actinoxylon* and *Actinopodium*, but available data are so meagre that this possibility cannot be ruled out. My observations indicate that even in *Callixylon*, banding of pits is not characteristic of apparent secondary wood just outside the primary xylem. No specimens of *Actinoxylon* and *Actinopodium* described thus far have possessed more than a few layers of presumed secondary xylem tracheids. Secondary xylem is unknown in *Siderella*. The secondary wood of *Calli-xylon* has been studied in great detail; readers wishing more information should refer to Beck (1970).

Archaeopteridales appear first in the late Middle Devonian (early Givetian), and extend into the Lower Mississippian (Tournaisian). The known ranges of individual genera are shown in Fig.2.

The following genera have been assigned to the order:
(1) *Actinopodium* Høeg, 1942; (2) *Actinoxylon* Matten, 1968;
(3) *Archaeopitys* Scott et Jeffrey, 1914, (4) *Archaeopteris* Dawson, 1871 (see also Arnold, 1939; Kräusel and Weyland, 1941; Beck, 1960a, b, 1962, 1971; Andrews et al., 1965; Carluccio et al., 1966; (5) *Eddya* Beck, 1967; (6) *Siderella* Read, 1936 (see also Beck, 1971, pp.778—779); (7) *Svalbardia* Høeg, 1942 (see also Andrews, 1970; Chaloner, 1972).

The form genus *Callixylon* (Zalessky, 1911; Arnold, 1930a, 1970, Beck, 1967, 1970; Scheckler and Banks, 1971a) includes fossils that represent the stem of *Archaeopteris macilenta* (Beck, 1960a, b) and *Eddya sullivanensis* (Beck, 1967).
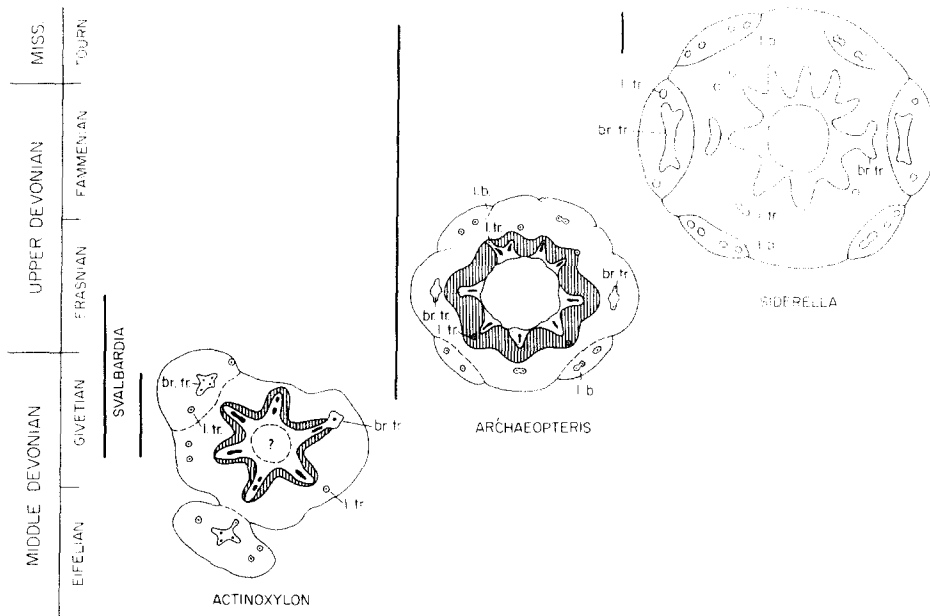
Fig. 2. Geologic ranges (heavy lines to left of names and diagrams) and morphologic features of some members of the Archaeopteridales. Some aspects of the primary and secondary xylem, branching patterns, and phyllotaxy are shown. Lined secondary xylem encloses unshaded metaxylem that contains black protoxylem strands. The smallest appendages containing one or more traces, terete in sectional view, are the basal parts of simple leaves. Note that the leaf bases of *Archaeopteris* and *Siderella* are decurrent on the axes that bore them. Genera are arranged from left to right in order of increasing levels of morphologic specialization. *br. tr.* = branch trace; *l. b.* = leaf base; *l. tr.* = leaf trace.

Pitys was considered earlier to be a member of this group of genera, many of which I assigned to the order Pityales (Beck, 1960b). Since Long's (1963) presentation of evidence suggesting that *Pitys* was a pteridosperm, the name, Archaeopteridales (Arnold, 1930a) has gained general acceptance as the preferred ordinal name for this group of progymnosperms. While Long's evidence is highly suggestive, it does not provide proof that *Pitys* was a lyginopterid. Organic connection between *Pitys* stems and *Lyginorachis papilio* has not been demonstrated.

Archaeopitys eastmanii, the most poorly known member of the Archaeopteridales, was considered by Scott and Jeffrey (1914) to be similar to *Pitys*. Considering the fact that no other specimens fitting the description of this fossil have been discovered, and considering its source (the New Albany Shale), I believe that it might be a specimen of *Callixylon*. The type specimen should be carefully re-examined.

DISCUSSION

In considering the Progymnospermopsida one is impressed both with the number of genera and their diversity of form and structure. It is equally apparent that the majority of genera fall into two major categories, the Aneurophytales and the Archaeopteridales.

As we consider each of these groups, several important questions arise: (1) Does the diversity reflect the evolution of many different genera, or merely developmental variation within a few genera? (2) Might not some of these genera represent the same group, but be maintained as separate taxa for lack of information?

The effect of incomplete information

Let us first consider that some genera are maintained apart for lack of proof of their common identities.

In the Aneurophytales, *Rellimia, Aneurophyton,* and *Triloboxylon* are remarkably similar, and their known vertical ranges are either overlapping or parallel. All are characterized by a basic helical branching pattern, and by dichotomous ultimate appendages. The primary vascular column of the main axis of each is a three-ribbed protostele. Secondary xylem is pycnoxylic, and characterized by multiseriate, circular-bordered pits (but additional evidence of such pits in *Rellimia* is needed). Rays are narrow and of variable height.

The fertile branch systems of *Rellimia* and *Triloboxylon* are planated and dichotomous with sporangia borne terminally on pinnately arranged (at least in *Rellimia*) ultimate appendages. Only a brief description of the fertile parts of *Triloboxylon* has been published (Scheckler and Banks, 1972) and reports on the morphology of *Aneurophyton* are conflicting (Leclercq and Bonamo, 1971). Such similarities suggest the possibility that *Rellimia, Aneurophyton* and *Triloboxylon* represent a single natural genus. *Triloboxylon* is maintained as a separate taxon, however, because relatively little information on the morphology of its vegetative and fertile branch systems has been published. Conversely, very little is known about the internal structure of *Rellimia*. Additional information about either might clarify the relationship of these taxa. *Aneurophyton* needs to be fully restudied before its status as a genus can be further clarified.

Similar problems characterize the Archaeopteridales. *Svalbardia* can hardly be distinguished from *Archaeopteris*, the only distinction being helical to irregular branching in *Svalbardia* and sub-opposite to alternate distichous branching in *Archaeopteris*. Vegetative morphology of *Actinoxylon* (in which fertile structures are unknown) is possibly indistinguishable from *Svalbardia* and differs from *Archaeopteris* only in branching pattern. Internal anatomy of *Actinoxylon* is similar to that of *Archaeopteris* and also to *Actinopodium*. Although poorly known, the structure of *Actinopodium* seems to be identical with that of main axes of lateral branch systems of

Archaeopteris. Carluccio, et al. (1966) have suggested that *Actinopodium* might represent the structure of *Svalbardia*, a viewpoint that I strongly support. *Actinopodium* and *Svalbardia polymorpha*, both established by Høeg (1942), were collected from the same locality at different times and from beds of probably the same age. The probability that *Actinopodium* represents the structure of *Svalbardia* supports the view that *Svalbardia* and *Archaeopteris* are congeneric (Beck, 1971). Additional information about *Svalbardia*, *Actinopodium* and *Actinoxylon* is needed in order to draw final conclusions about the relationship of these forms with each other and with *Archaeopteris.*

The possibility of ontogenetic variation

The question of variation during development is more interesting and more difficult to resolve because it is essentially impossible to study more than a very small part of a large, extinct plant. The very fact, however, that the primary vascular columns of *Cairoa* and *Proteokalon* vary from three to four-ribbed provides evidence of ontogenetic variation. Could, for example, *Triloboxylon* (stele three-ribbed) simply represent distal regions of *Tetraxylopteris* or *Proteokalon* (steles four-ribbed)? The rather unusual, semi-planated arrangement of vegetative ultimate appendages of *Proteokalon* perhaps makes this less likely in this genus; but, in fact, we know very little about either *Triloboxylon* or *Proteokalon* which, as is true of most fossil genera, are based on only a few specimens of variable size and preservation.

It is well known (see Beck, 1967, 1969; Eggert, 1961, Namboodiri and Beck, 1968a) that stelar anatomy and phyllotaxy may vary from more proximal to more distal regions of determinate branch systems, or between essentially indeterminate lead shoots and relatively more determinate lateral branch systems. We must, therefore, consider whether such ontogenetic variation might account for the differences in anatomy and branching patterns.

Rellimia and *Tetraxylopteris* are nearly identical in known details except that branching is helical in the former and decussate in the latter, their protosteles being three-ribbed and four-ribbed, respectively. An additional minor difference is the single bifurcation of the fertile branch system in *Rellimia* compared with the double bifurcation in *Tetraxylopteris.* It is, at least, possible that these differences reflect developmental (ontogenetic) variation relating to position in the plant and/or response to environment. (For more detailed discussions of developmental variation in morphology see Beck, 1967, 1969.) Bonamo and Banks (1967) and Leclercq and Bonamo (1971) emphasize the remarkable similarity between *Rellimia* and *Tetraxylopteris* and consider the possibility of their identity.

Similarly, *Actinoxylon* and *Archaeopteris* might represent ontogenetically variant parts of a plant. Certainly, the presence or absence of a distinct pith, one of the possible (but not certain) differences between these genera might be a variation of this kind, the smaller axes being protostelic, the larger

medullated. Even the difference in branching pattern might reflect ontogenetic variation. We do not know that the main axis of *Actinoxylon* (Fig.2) and the main axis of an *Archaeopteris* lateral branch system with which it is here compared are of equivalent order. The main axis of *Actinoxylon* might represent an axis that, in a young specimen or a distal region of *Archaeopteris*, bore lateral branch systems. At different times during the development of a plant equivalent axes might have had different internal anatomy. If the main axis of *Actinoxylon* were equivalent to such a stem, the helical pattern of branching would not be unexpected. Is it not possible that the helical/to irregular branching of *Svalbardia* might be accounted for in the same way?

When one considers this analysis and the strong probability that *Actinopodium* is identical with the structure of the main axis of *Archaeopteris* lateral branch systems, the conclusion that *Svalbardia*, *Actinopodium*, *Actinoxylon* and *Archaeopteris* might represent a single natural genus is inescapable, and parallels that regarding the possible identity of *Rellimia*, *Triloboxylon* and *Tetraxylopteris*.

I have previously provided a detailed rationale for the possibility that *Eddya* and *Archaeopteris* are different developmental stages of the same plant, *Eddya* being a young sporophyte of *Archaeopteris* (Beck, 1967).

These suggestions and the preceeding analyses are, of course, highly speculative, but they point to an important fact: We know relatively very little about the progymnosperms. This dilemma is common to paleobotany and related directly to the fact that plants are basically indeterminate in growth and that one is never able to study more than a small part of a single large plant.

Evolutionary change through time

I must emphasize again that these suggestions are highly speculative. Whereas it is clear that *some* of the diversity within Progymnospermopsida is probably the result of ontogenetic variation, a larger part of it is very likely the result of evolution through time. Indeed, one could argue that the major progymnosperm genera form a single continuum of evolutionary variation. The current state of our knowledge suggests, however, that some major taxonomic diversification had occurred within the group, and that at least two lines of evolution are represented.

In the Aneurophytales, *Rellimia* seems to have been a dominant group during mid-Devonian and *Tetraxylopteris* during late Devonian times. The remarkable morphological similarity between these genera suggests a very close genetic relationship. These homosporous genera even produced identical spores (*Rhabdosporites langii*, of the sporae dispersae) (Leclercq and Bonamo, 1971). Their differences may represent "straight line" evolutionary change through time, with the decussate branching pattern and four-ribbed stele of *Tetraxylopteris* representing an evolutionary advance over the helical branching and three-ribbed stele of *Rellimia*. Leclercq and Bonamo (1971) have suggested that the more complex fertile "organ" of

Tetraxylopteris is also an evolutionary specialization.

I believe that *Protopitys* which lived during early Mississippian times (although now assigned to a different order) may have been a still more highly specialized member of this same line of evolution. The alternate and distichous branching in this genus could have evolved from the decussate branching of *Tetraxylopteris*. It should be emphasized, furthermore, that entire *Protopitys* plants might not have been characterized by distichous branching. Unfortunately we know nothing of the leaves or vegetative branching systems of this plant. On the other hand, its secondary wood was similar to that of *Tetraxylopteris* and its fructifications and saccate spores remarkably similar, if not identical. As noted earlier, the presence of two fairly distinct size classes -- 75 to about 200 μm and about 200 to 355 μm — suggested to Smith (1962), as it had earlier to Walton (1957), the possibility that this variation in spore size reflects an intermediate stage in the evolution of heterospory. It is, indeed, interesting that the range of spore diameter in *Tetraxylopteris* (73– 176 μm) corresponds approximately to the smaller class of spores of *Protopitys*.

Information on the morphology and anatomy of lateral branch systems and leaves of *Protopitys* will clarify its phylogenetic position and might show it to be a Carboniferous member of the Aneurophytales. (It is intriguing, though entirely speculative, to suggest that *Stauroxylon* (Galtier, 1970) might represent a part of the lateral branch systems of *Protopitys*.) In the meantime *Protopitys* must remain in the Protopityales.

Very little is known about *Cairoa*, and its phylogenetic position is unclear. *Proteokalon* is also relatively poorly understood, but is characterized by two features of considerable interest. As in the case of *Cairoa*, it exhibits both four- and three-ribbed protosteles. In *Proteokalon*, the three-ribbed stele, T-shaped in transverse configuration, occurs in leaf-bearing axes. The most unusual feature of this plant is the arrangement of leaves along the axis in adaxial pairs that alternate with single abaxial leaves (Scheckler and Banks, 1971b), producing a sort of bilateral symmetry (Fig.1).

The helical branching and phyllotaxy of *Triloboxylon* (also of *Rellimia* and possibly *Aneurophyton*), the decussate branching and phyllotaxy of *Tetraxylopteris* and the decussate branching and semi-planated leaf arrangement of *Proteokalon* and the associated changes in stelar form provide another example of possible evolutionary specialization through time, and as Banks and Scheckler point out, may illustrate stages in the evolution of a planated compound leaf from a more primitive system of simple leaves exhibiting helical phylotaxy.

In the aneurophytes helical branching was probably primitive, decussate and distichous derived; the latter type had evolved in only fertile branch systems. If, as is quite possible, the presumed stems of *Protopitys* (as described by Walton, 1957, and Smith, 1962) are found to be axes of lateral branch systems and the presumed leaf traces, branch traces instead, we may extend this trend in vegetative branching patterns from helical through decussate to distichous (bilateral). Distichous (planated) branching in a

lateral branch system (as in *Archaeopteris*) is clearly adaptive; it would seem unlikely as the pattern of main axes of a large plant (as has been presumed to be the case in *Protopitys*).

A similar, clear-cut succession of changes in branching pattern, leaf arrangement, and anatomy can be described in the archaeopteridalean genera, *Actinoxylon, Archaeopteris* and *Siderella* (Fig.2). As in the aneurophytes these changes may be time-correlated, the known range of *Actinoxylon* being restricted to the late Middle Devonian (Givetian), *Archaeopteris* extending from late Middle Devonian into early Mississippian (Tournasian) and *Siderella* being known only from the early Mississippian. The presumed trend in branching patterns is from helical (*Actinoxylon* and possibly *Svalbardia*) to sub-opposite or alternate and distichous in *Archaeopteris* and *Siderella*. In phyllotaxy, the changes seem to have been from helical or decussate in *Actinoxylon* and *Archaeopteris* to alternate and bilateral (planated) in *Siderella*. These apparent trends, like those among aneurophytes, not only reflect different levels of evolutionary specialization of the several genera (Figs.1, 2), but also support the contention that compound leaves may have arisen through planation of three-dimensional lateral branching systems (Matten, 1968; Beck, 1970). It is important to understand, however, that *Archaeopteris* did not bear compound leaves. It bore planated lateral branch systems bearing helically arranged simple leaves (Carluccio et al., 1966; Beck, 1971) very similar to those of some modern conifers.

Unfortunately we do not know whether *Siderella* bore compound leaves or planated lateral branch systems bearing simple leaves. When we learn more about *Siderella* and other possible descendants of *Archaeopteris* such as *Rhacopteris, Palaeopteridium, Saaropteris, Noeggerathia*, etc., and *Protopitys* and other possible descendants of the aneurophytes, we may be able to determine positively whether the lateral branch systems of the progymnosperms do, in fact, represent intermediate stages in the evolution of compound leaves.

THE PHYLOGENETIC POSITION OF THE PROGYMNOSPERMS

The two major groups of progymnosperms, while apparently distinct, are tied together by some important common characteristics. There are, of course, the general characters of the class; but in addition, some or all members of both groups bore finely and dichotomously divided simple leaves, and produced ribbed steles. At least one member of each group produced secondary wood containing ray tracheids and axial tracheids bearing grouped and banded circular-bordered pits, characters that are known to occur elsewhere in the plant kingdom only in certain conifers.

When one considers all of the evidence, the Aneurophytales has clearly the more primitive aspect of the two orders. It extends farthest back in the geologic column. The Archaeopteridales might have diverged from a primitive member of this group (Beck, 1966); but it seems equally probable that

the two orders diverged from an unknown common ancestor.

In several other papers (Beck, 1960b, 1966, 1971) I have developed a rationale for the view that the gymnosperms evolved from the Progymnospermopsida. Since my original proposal in 1960, a large body of evidence has accumulated through the efforts of many workers. Studies in my laboratory (Beck, 1971) and by Harlan Banks and his students (Carluccio et al., 1966) of the anatomy and morphology of lateral branch systems have demonstrated beyond any doubt that they are planate, probably determinate, and bear helically arranged, simple leaves with decurrent, and adherent leaf bases. In other words, they have all of the characteristics of lateral branch systems of some members of the coniferales.

Analyses and reinterpretations of stelar morphology of primitive and extant gymnosperms by my students and me (Namboodiri and Beck, 1968a, b, c; Beck, 1970; Devadas and Beck, 1972; Blanc-Louvel, 1966; Galtier, 1970, 1973; and Slade, 1971) have clarified the three-dimensional morphology of the stele of seed plants and demonstrate its similarity to the stele of the progymnosperms. In both progymnosperms and gymnosperms, whether basically protostelic (including medullated protosteles) or eustelic, leaf traces diverge directly from longitudinal ribs or discrete vascular bundles. Namboodiri and Beck (1968c) and Beck (1970) have shown how the eustele may have been derived directly from the ribbed protostele. There is no morphologic discrepancy between the organization of progymnosperms, primitive gymnosperms and extant gymnosperms. This clarification of stelar morphology further strongly supports the contention that gymnosperms are descendants of progymnosperms.

Further support for this view comes from the many details of anatomy and morphology of aneurophytes, discerned largely through the studies of Harlan Banks and his students at Cornell, Patricia Bonamo of Binghamton, and Suzanne Leclercq of Liège. For example, the discovery of ray tracheids and grouped, radially banded, bordered pits in the secondary wood of *Triloboxylon hallii* by Scheckler and Banks (1971) not only supports the assumed close relationship of Aneurophytales and Archaeopteridales, but, importantly, also supports the proposed relationship of progymnosperms with gymnosperms, the only other major group in which these characters are known to occur.

The anastomosing strands of cortical sclerenchyma in aneurophytes strongly resemble similar structures in the calamopityeans and lyginopterid gymnosperms.

Secondary phloem characterizes all three orders of progymnosperms. In the opinion of Scheckler and Banks (1971a) this characteristic is "perhaps the strongest evidence for the gymnospermous affinity of the progymnosperms", because as they further point out, "cambial activity does not produce any secondary phloem in woody ferns, lycopods, and calamites . . . " The aneurophytes produced rather distinctive secondary phloem containing scattered strands or rows of thick-walled fibers (Beck, 1975, Scheckler and Banks, 1971a, b). The secondary phloem of *Callixylon*

(large axes of *Archaeopteris*) is parenchymatous, lacking fibers, and characterized by well-defined rays (Arnold, 1930b). The secondary phloem of *Protopitys* is poorly known, but a brief report by Walton (1969) suggests that it was more like that of *Callixylon* than that of the aneurophytes.

The generally gymnospermous features of the secondary xylem of progymnosperms, and, especially, the remarkably detailed similarity between the wood of *Callixylon* and members of the Coniferales has been recently documented (Beck, 1970) and will not be discussed again here.

The production of periderm in several progymnosperms is another feature believed to support their close relationship with gymnosperms (Scheckler and Banks, 1972b).

A recent, significant development that tends to relate the progymnosperms and gymnosperms is the discovery of 'pseudosaccate' spores (*Rhabdosporites* of the Sporae dispersae) in two aneurophytes, *Tetraxylopteris* (Bonamo and Banks, 1967) and *Rellimia* (Leclercq and Bonamo, 1971), and similar spores (compared with the monosaccate pteridosperm pollen grain, *Remysporites*) in *Protopitys* (Smith, 1962). The spores of both the aneurophyte genera and *Protopitys* are spherical and consist of a corpus enclosed by a thin, bladder-like membrane attached proximally in the region of the trilete mark. This type of spore may have been a precursor of monosaccate pteridosperm or cordaite pollen grains in which the saccus was attached at both proximal and distal ends and in which had evolved a clear proximo-distal differentiation. Millay and Taylor (1974) have described two new pollen genera, *Sullisaccites* and *Felixipollenites*, that they consider to be related taxonomically to the Cordaitales. Whereas *Felixipollenites* is believed to be the more primitive, they are, together, intermediate in morphology between a pseudo-saccate spore such as *Rhabdosporites* and a relatively highly specialized saccate pteridosperm pollen grain such as *Vesicaspora* (pollen of *Callistophyton*) or a cordaitean grain such as *Florinites* (pollen of Cordaites). Indeed, Millay and Taylor believe that "spores of *Tetraxylopteris* . . . possess most of the features that would be required of the ancestor of *Felixipollenites*".

Phillips et al. (1972) have contributed to a better understanding of the morphology of fertile ultimate appendages of *Archaeopteris*. They have shown that sporangia of *A. halliana* occur extensively over the adaxial surface of thrice-dichotomized appendages, extending to but not beyond the third dichotomy. They suggest that such appendages might have evolved ihto cupulate structures like those of the Upper Devonian fructification, *Archaeosperma* Pettitt et Beck, 1968, in which seeds were enclosed. Pettitt and Beck (1968) postulated that "evolutionary reduction of an *Archaeopteris* fertile ultimate branch and its appendages could result in several megasporangia, each surrounded by an integument derived either from sterile sporangia . . . or from the laminar fertile leaves, borne in cupules derived from the basal vegetative leaves."

There is no evidence that any species of *Archaeopteris* produced seeds or that those of any primitive gymnosperm were derived directly from

Archaeopteris fructifications. Morphological similarities of parts of these fructifications to primitive seed cupules and integuments are, however, consistent with the belief that some progymnosperms might have been precursors of some gymnosperms.

A gradually growing fund of data tends to support the hypothesis that gymnosperms evolved from the Progymnospermopsida. In 1966 I suggested that the lyginopterid Pteridosperms probably evolved from the aneurophytes. This view was based then, and supported with more detail later (Beck, 1970), on the similarity between stelar morphology of the aneurophytes and the calamopityeans and the apparently closely related lyginopterids (Galtier, 1974). The Archaeopteridales seem to be the most likely source of the coniferophytic gymnosperms, this view based largely on the remarkable resemblance between the secondary wood (*Callixylon*) and lateral branch systems of *Archaeopteris* and those of Coniferales (see Beck, 1970, 1971).

Although aneurophytes and archaeopterids at present seem to represent distinct, clearly defined lines of evolution, it is only prudent to recognize that the progymnosperms may comprise only one, branching line of evolution from which the two main lines of evolution among gymnosperms originated. If so, the gymnosperms could be considered to be of monophyletic origin as has been suggested by Scheckler and Banks (1971a).

Much has been written about the probable seed-plant descendants of the progymnosperms, but almost nothing about possible pteridophytic descendants. Is it not possible that some progymnosperms persisted well into and, perhaps, through the Carboniferous? *Archaeopteris* and *Siderella* occur in the early Mississippian, as does *Protopitys*. In strata of comparable and younger age, in both North America and Europe, there occur also a large number of vegetative foliage genera such as *Rhacopteris*, *Sphenopterididium*, *Triphyllopteris*, *Adiantites*, *Palaeopteridium*, and *Saaropteris*, of unknown taxonomic affinity. Some of these may represent ferns, others primitive gymnosperms (as has been shown recently to be true of *Rhodea* [Jennings, 1974]). Still others might be progymnosperms. *Palaeopteridium* and *Saaropteris* have been grouped with *Noeggerathia* on the basis of similarity of leaf (or leaflet) form (Hirmer, in Hirmer and Guthörl, 1940). The fructifications of *Noeggerathia* are similar to those of *Archaeopteris* as is, possibly, the arrangement of vegetative leaves. (The latter possibility is suggested by my recent unpublished re-interpretation based on published photographs.) This very preliminary evidence and analysis suggests at least the possibility that *Noeggerathia* is a Pennsylvanian progymnosperm. Further, intensive study of this genus is planned. This and studies of other possible Carboniferous progymnosperms and primitive gymnosperm descendants, with continuing investigations of Devonian progymnosperms, will further clarify the phylogenetic relationship between the progymnosperms and the gymnosperms.

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