RECONSTRUCTIONS OF ARCHAEOPTERIS, AND FURTHER CONSIDERATION OF ITS PHYLOGENETIC POSITION[1]

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ABSTRACT

BECK, C. B. (U. Michigan, Ann Arbor.) Reconstructions of Archaeopteris, and further consideration of its phylogenetic position. Amer. Jour. Bot. 49(4): 373–382. Illus. 1962.—Two reconstructions, one of a branch bearing the basal part of 3 leaves and the other of the habit, are presented with the evidence upon which they are based. An analysis is made of some features which characterize the ferns. These, and characters of *Archaeopteris*, are considered in the light of present knowledge of evolutionary trends, and the conclusion is reached that *Archaeopteris* was neither a primitive fern nor a fern ancestor. Additional evidence is discussed which supports the view that the plant was a progymnosperm.

THE CORRELATION of *Archaeopteris* and *Callixylon* (Beck, 1960a,b) makes possible the preparation of relatively accurate reconstructions of the Upper Devonian and Lower Mississippian plant represented by these organ genera. Two reconstructions and presentation of the evidence on which they are based form the first objective of this paper. The second is to discuss further the phylogenetic position of this plant, including additional evidence which supports the view that *Archaeopteris* is a progymnosperm (Beck, 1960b).

RECONSTRUCTIONS—No single species of *Archaeopteris* is known in sufficient detail to provide an accurate picture of a large part of the plant, but such a picture can be obtained by pooling information from several species. Figure 1 shows a branch segment bearing the basal parts of 3 leaves, one of which is fertile. This reconstruction, including the size and spatial relationships of various structures portrayed, is based largely on the illustrations of *Archaeopteris fimbriata* in Nathorst (1902) and on the specimen which I have recently described and identified as *Archaeopteris* cf. *macilenta* (Beck, 1960b). *Archaeopteris fimbriata* Nathorst (1902) is considered a synonym of *A. macilenta* Lesquereux (1884) by Kräusel and Weyland (1941).

The spiral arrangement of the leaves was determined by Arnold (1930) on the basis of the sequence of leaf-trace departure in *Callixylon zalesskyi*. This is confirmed by the specimen of *A.* cf. *macilenta* in which several leaf fragments are borne spirally on a branch identified as *C. zalesskyi*. Arnold reported the origin of 4 leaf traces within a distance of 1.5 cm in his specimen which suggests that the leaves were closer together than those illustrated in Fig. 1. This apparent discrepancy may be explained by assuming that the leaf traces diverged in their passage from the stele to the leaf bases. Or, I may have incorrectly identified the wood of *A.* cf. *macilenta* as *Callixylon zalesskyi*, since the identification was based on only a few slides of pyritized wood. The distance between leaves may be related to leaf size; the larger the leaves, the more widely spaced. And considerable variation in leaf size among the several species of *Archaeopteris* is to be expected.

In this regard, a rather intriguing suggestion has been made by W. S. Lacey (personal communication, 1961) who wonders if *Archaeopteris* might not have borne both simple and compound leaves. There is no evidence of simple leaves on the specimen of *A.* cf. *macilenta*, unless the stipules fall into this category. The stipules do appear to be attached to the stem, immediately subtending the leaves, rather than to the petiole (Beck, 1960b, pl. 25, Fig. 2, 3). Lacey's suggestion is especially interesting in view of the proposal of the occurrence of both microphylls and megaphylls in some members of the Zygopteridaceae by Eggert (1961).

The presence of a stipule at the base of the *Archaeopteris* leaf has been illustrated by Nathorst (1902) in both *A. fimbriata* and *A. roemeriana* (*halliana*), Johnson (1911) in *A. hibernica*, Beck (1960b) in *A.* cf. *macilenta*, and possibly others. The forked nature of this structure is well illustrated by Nathorst.

The basal enlargement of the rachis (petiole) is illustrated in Nathorst (1902) and Johnson (1911). The adaxial concavity near the base and the convex abaxial surface of the rachis are entirely hypothetical, since only compressions have been uncovered in the fossil record. The rachial pinnules near the base of the leaves have been often observed and may be documented by reference to Lesquereux (1884), Nathorst (1902) and Johnson (1911). Opposite to sub-opposite, rachial pinnules between both fertile and vegetative pinnae are illustrated in the 2 latter papers and by Arnold (1939) in a vegetative specimen. I have recently

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2 cm

collected beautifully preserved specimens which also show this feature.

Although, rarely, the pinnae may be alternate (Arnold, 1939), the most common arrangement in the genus is opposite to sub-opposite. Occasionally, the basal pinna may occur opposite a rachial pinnule instead of opposite a pinna (Lesquereux, 1884; Arnold, 1939).

The vegetative pinnules are sub-opposite to alternate, sessile to short-stalked, and obovate, spatulate, or rarely cuneiform, with the margin varying from nearly entire in *A. obtusa* and *A. halliana* (see Arnold, 1939) to deeply and finely dissected in *A. macilenta* (*fimbriata*) (Nathorst, 1902; Arnold, 1936; Beck, 1960b) and *A. fissilis* (Schmalhausen, 1894). Venation is dichotomous. The vegetative pinnules in Fig. 1 are based on those of the specimen of *A. macilenta* illustrated by Arnold (1936, Fig. 1). Within the genus, the pinnules vary greatly in size—from 1 cm or less to 2 cm or more—and may overlap or be spaced, as in *A. macilenta.* Figures in numerous papers show that pinnules of both fertile and vegetative pinnae gradually decrease in size distally.

The fertile pinnae, which occur basally on some fronds, bear proximally several alternate vegetative pinnules which are followed by a series of fertile pinnules bearing 1 or 2 rows of sporangia. Several vegetative pinnules terminate the pinna. Agreement has not been reached on whether there is only 1 or whether there are 2 rows of sporangia on the fertile pinnules. Johnson (1911) thought there was a single row, whereas Kräusel and Weyland (1941) suggested that there were 2 rows. Arnold's illustrations of fertile pinnules of *A. latifolia* (1939, pl. 9, Fig. 3, 4) suggest only 1 row, but he does not give an opinion on this question. The occurrence of proximal vegetative pinnules on the fertile pinnae has been observed frequently (Lesquereux, 1879, pl. 50, Fig. 3; Schimper, 1869, Atlas pl. 36; Nathorst, 1902; Johnson, 1911, and others). The existence of terminal vegetative pinnules has been less frequently reported due, undoubtedly in some specimens, to poor preservation of the tips of the pinnae. Good illustrations appear in Schimper (1869), Nathorst (1902) and Johnson (1911). It is, of course, quite possible that in some specimens, or in some species, the pinnae were terminated by fertile pinnules, or that the pinnae were wholly fertile, lacking vegetative pinnules entirely. The homology between the fertile and vegetative pinnules is shown in those cases where a pinnule is partly fertile and partly vegetative (see Schmalhausen, 1894, pl. II, Fig. 19–21; Johnson, 1911). The fertile pinnules often extend out into a sterile tip, sometimes forked (Nathorst, 1902; Johnson, 1911; Arnold, 1939, pl. 9, Fig. 3, 4; Kräusel and Weyland, 1941).

The reconstruction in Fig. 1 represents, specifically, *Archaeopteris macilenta* Lesquereux. In general features, it and the following habit reconstruction portray the genus *Archaeopteris.* The reconstruction (Fig. 2) is based in large part on the discussion of the habit of *Callixylon* by Arnold (1931) and the specimen of *Archaeopteris* cf. *macilenta* which consists of *Archaeopteris* leaf fragments attached to a branch of *Callixylon* (Beck, 1960b). Figure 2 depicts a tree 60 or more ft tall, the trunk tapering from a base of about 5 ft in diameter. Perhaps the largest known specimen of *Callixylon* is a stump about 5 ft in diameter from the Woodford chert of Oklahoma, now reconstructed on the campus of East Central State College in Ada, Oklahoma (Wilson, 1958). Logs 2–3 ft in diameter are common in the New Albany shale in Indiana and Kentucky, and a 28-ft segment of a log has been discovered in the Caballos chert of Southwest Texas (Bennett, 1959). On the basis of the taper of specimens in the Museum of Paleontology of the University of Michigan and the U. S. National Museum, Arnold estimated the tree represented by the Oklahoma stump to have had "a minimum height of sixty feet." The absence of exposed lateral branches on *Callixylon* logs has suggested to Arnold (1931) that the branches did not attain a great diameter, probably indicating their caducous character. This indicates a tree of excurrent habit with an apical crown of branches much as in the living pines. The main lateral branches would probably be nearly horizontal or inclined upward only slightly as illustrated in Fig. 2, and the more distal parts might have been bent downward by the weight of the large, compound leaves which varied in length from 2 ft or less to as much as 5 ft (see Johnson, 1911). Smaller branches diverged from the main laterals at angles as great as 45° (Arnold, 1931).

The form of the crown of leafy branches is, of course, primarily speculative, based on that of living conifers which branch in a manner similar to that proposed for *Archaeopteris.* A somewhat similar branching pattern is illustrated in the reconstruction of *Callixylon* in Life Magazine, September 7, 1953, page 63, which was prepared in consultation with Professor C. A. Arnold.

Although we now have a fairly good knowledge of *Archaeopteris* as an entire plant, there is much yet to learn. Was the genus heterosporous or were some species homosporous? Arnold (1939) has presented evidence for heterospory in *A. latifolia,* and Kräusel and Weyland (1941) suggest the possibility of heterospory in *A. halliana* and *A. hibernica,* based on variation in sporangium size. Spores of only one size, however, were found in *A.* cf. *macilenta* (Beck, 1960b). Concerning this problem, Professor T. M. Harris (personal communication, 1961) writes: "May I suggest the

Fig. 1. *Archaeopteris.* Reconstruction of a branch bearing the basal parts of 3 leaves. Based largely on *A. macilenta.* About natural size.

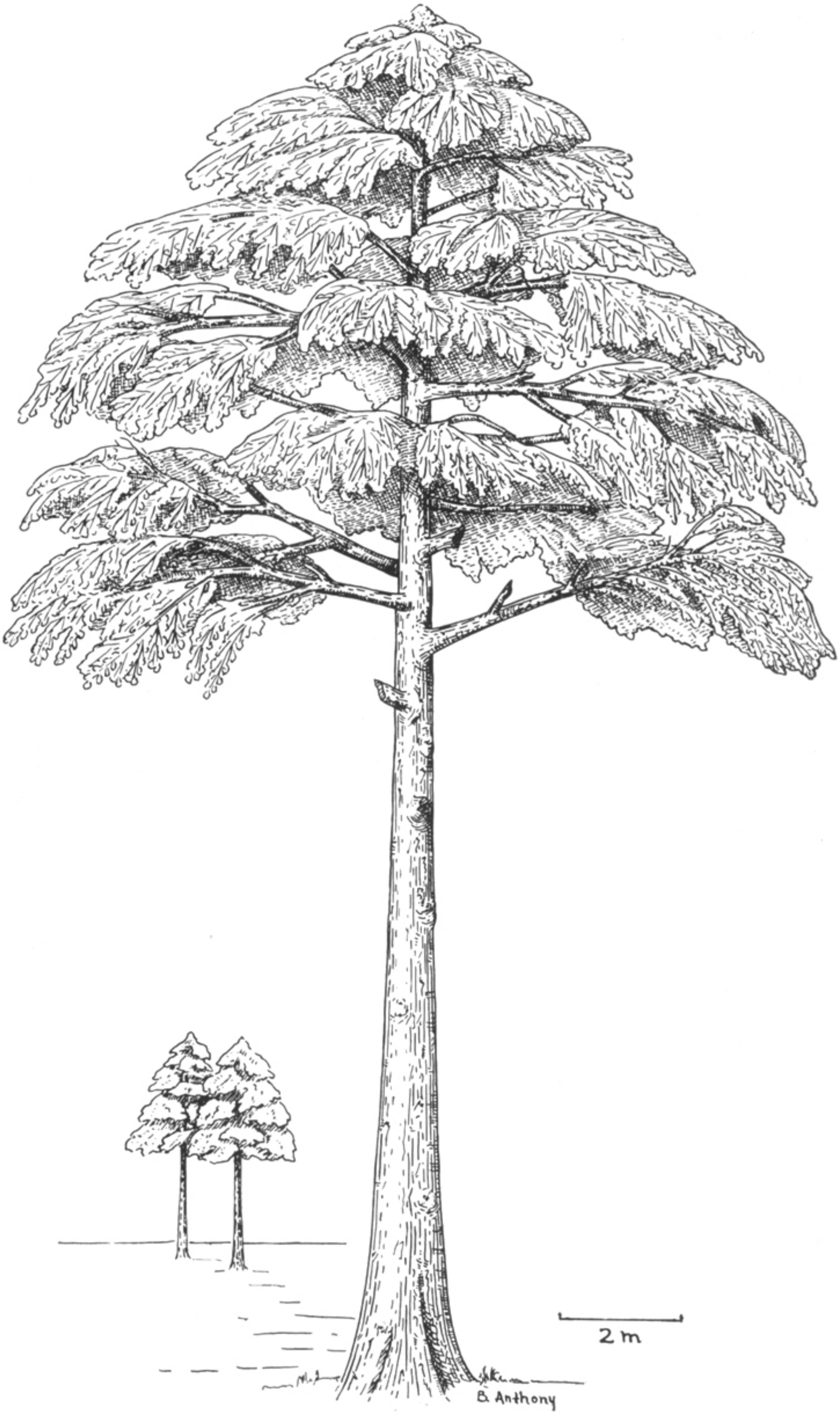

Fig. 2. *Archaeopteris*. Habit reconstruction.

likelihood that some [species] are monoecious and others dioecious, or at least tend to have mega- and microsporangia on different leaves or branches." Such a condition could account for the isolation of spores of but one size from *A.* cf. *macilenta.*

Did any species produce seeds? Arnold (1935) discovered seed-like compressions in association with *Archaeopteris* foliage, but none has ever been found attached.

We cannot yet answer these questions with any certainty. We know nothing about the leaf trace immediately prior to its entry into the leaf base, or about the internal structure of the rachis, and there is still much to learn about variation within species, valid criteria for distinguishing species, etc. Nevertheless, *Archaeopteris* is more completely known than any other Upper Devonian plant—better, possibly, than any other Paleozoic plant. Consequently, one can determine its general phylogenetic position with a good deal of certainty, although its precise position in relation to its immediate ancestors and descendants presents a more difficult problem.

THE PHYLOGENETIC POSITION OF ARCHAEOPTERIS—Of several suggestions regarding the phylogenetic position of this plant, 2 have seemed to merit the most serious consideration. These are that it is: (1) a primitive fern, representing a major group from which Coenopteridales, Ophioglossales, Marattiales and Filicales, or some of these, evolved; and, (2) a progymnosperm, representing a major group of pteridophytes from which one or more groups of gymnosperms has evolved. I have elsewhere expressed the view that the second of these alternatives is the correct one. Because, however, some other morphologists support the former, I feel that it is important to present, in much greater detail than previously (Beck, 1960b), my reasons for rejecting it.

To consider *Archaeopteris* a fern, or a member of a group of fern ancestors, one must be able to show that its characteristics are those generally recognized as attributable to ferns, or are of a type from which those of ferns could logically have been derived; or there must be evidence of the existence of forms of character intermediate between this group and plants generally accepted as ferns. It is generally accepted that ferns are megaphyllous pteridophytes bearing foliar sporangia, and that most of them possess mesarch primary xylem. These characters, also features of *Archaeopteris,* do not, however, adequately define a fern. There are other important and distinctive features which must be considered. It is recognized, of course, that within the Filicineae the several orders, Coenopteridales, Ophioglossales, Marattiales and Filicales, each has its own distinctive characters. Eames (1936) suggests that the "...'ferns'... are,... if considered a unit group, polyphyletic." That they are at the same time a group of genetically related members sharing many common characters has been supported recently by the recognition of a fern division, called Pterophyta by Bold (1956) and Filicophyta by Cronquist (1960), which includes the orders listed above.

I should like to note and discuss some important common characters in addition to those listed above which seem to me to characterize generally the groups comprising the Filicineae, and then to consider their applicability to *Archaeopteris.*

(1) *Primary growth only and the consequent lack of cambial activity are characteristic of the Filicineae*—This feature is not only restricted to the low, "shrubby," forms, but also characterizes the large, arborescent genera of the Dicksoniaceae, and the Marattiales, the latter considered to be among the most primitive groups of ferns, including the widespread Carboniferous and Permian genus, *Psaronius.*

Opinion of the number of extant genera in the Filicineae varies from about 145 (Bower, 1926, 1928) to 308 (Copeland, 1947); and Holttum (1949) recognizes approximately 180 genera. Including the structurally preserved fossil genera, it seems conservative to conclude that there are at least 225 widely recognized genera of ferns. Of these, only 4 or 5 seem to be characterized by the production of secondary tissues. Although Sahni (1932) and others have referred to secondary wood in *Zygopteris,* Baxter (1952) presents an argument for the primary nature of this tissue. Kräusel and Weyland (1941) describe and illustrate secondary xylem in the stem of *Rhacophyton incertum,* and Leclercq (1951) refers to a similar, though less extensive tissue in *R. zygopteroides.* Among the living genera, aside from *Botrychium,* only *Angiopteris* has been reported to produce secondary xylem (Farmer and Hill, 1902), and this locally, in very small amounts. This report needs further substantiation before it can be accepted without reservation. Scott (1920) reports secondary xylem in *Ankyropteris corrugata* and *Metaclepsydropsis duplex,* but recent studies of American species of *Ankyropteris* (Baxter, 1951; Eggert, 1959b) include no mention of secondary xylem, and it is probable that this tissue was not a constant feature in these genera. The Cladoxylales, sometimes grouped with the ferns (Arnold, 1947), sometimes with the pteridosperms (Scott, 1923), and admittedly of uncertain systematic position, produced secondary xylem. This group is of interest because of its polystelic vascular system. Leclercq and Banks (1959) have shown that *Pseudosporochnus,* previously called a psilophyte, had cladoxylalean anatomy. The report of secondary xylem in *Osmundites kidstoni* by Stopes (1921) was shown by Posthumus (1924) to be in error.

One may conclude, therefore, that clear-cut examples of secondary growth among the ferns are rare and that primary growth only is generally characteristic of the Filicineae.

(2) *Scalariform pits characterize the xylem of ferns*—Not only the primary xylem of most genera, but also the secondary xylem of all but one (excluding the Cladoxylales) of those which produce this tissue contain tracheids with scalariform pits. Distinct circular bordered pits are a known constant feature of only 3 genera of Filicineae, *Ophioglossum*, *Botrychium*, and *Helminthostachys* of the Ophioglossales. Circular bordered pits occur in the late protoxylem and metaxylem of these genera (Bierhorst, 1960) and also in the secondary xylem of *Botrychium*. Localized occurrences of circular bordered pits have been reported in the metaxylem of several coenopterid ferns and are discussed below. Bierhorst (1960) reports the rare presence of circular bordered pits in some predominantly reticulate elements of *Marattia alata*.

(3) *The primary xylem and phloem of the leaf traces and stelar bundles is always concentrically arranged*—I know of no exception to this character among plants usually included within the Filicineae, and the phloem always surrounds the xylem. In contrast, the traces and vascular bundles in the gymnosperms are, most commonly, collateral, although in a few genera such as *Calamopitys*, *Lyginopteris* and *Callistophyton* (Delevoryas and Morgan, 1954b) the petiolar bundles may be concentric.

(4) *The Filicineae are characterized by adventitious roots which often arise at the base of leaves*—In respect to this character a quotation from Bower (1923, p. 337) is appropriate: "The shoot is fixed in the soil by numerous roots, of which all the later are clearly adventitious. The nature and origin of the first root may be open to question. That origin is not constant in time or place for all Ferns. The root may actually be absent in *Salvinia*. Its emergence where there is a suspensor present is lateral. These facts indicate that it is accessory to the shoot, as are all those which follow accessory to the shoots which bear them." Little is known about the root-stem relationship of some fossil ferns, but the occurrence of adventitious roots in the Coenopteridales has been often demonstrated (e.g., Scott, 1920; Delevoryas and Morgan, 1952, 1954a).

In the preceding paragraphs I have presented a group of characters that I believe typify and unify the group Filicineae. In a sense, I have presented my own "type concept" of a fern. The ferns have, of course, never been static. As a group (or as several groups) they have diverged from one or more evolutionary lines; the primitive ferns have given rise to the more advanced groups; and, possibly, other major groups of vascular plants have been derived from some group or groups of ferns. The pro-ferns undoubtedly were different in many ways from the primitive filicineans, but, in my opinion, they could not have possessed the combination of characters of *Archaeopteris*.

If the paleozoic ferns had been derived from *Archaeopteris*, there should be evidence in the fossil record of a trend of reduction from the woody to the herbaceous habit. Such evidence is unknown at present. The genera reported to produce secondary wood are members of the more primitive eusporangiate groups of ferns, Coenopteridales, Ophioglossales and Marattiales, but the secondary activity in these groups, scattered among a few genera, in no way suggests a major line of evolutionary specialization toward the acquisition of the woody habit, or toward a reduction from a woody habit. Eames (1936), in comparing the Ophioglossales, Marattiales and Filicales, noted that: "So distributed are the differences that it is apparent that the three groups are not closely related, and that no one of them represents an ancestral stock from which the others may have been derived." Although the Coenopteridales have long been considered the ancestral fern stock, the view that they may be, rather, an independent branch of the main line of fern evolution is gaining adherents. At present, the occurrence of secondary xylem in several diverse groups of ferns and fern-like plants seems, therefore, to be of importance only in indicating the potential within the Filicineae for secondary growth, a potential which was not as fully exploited by the ferns as by several other major groups.

To derive the ferns from *Archaeopteris* or its close relatives, one must assume the evolution of the scalariform bordered pit from the circular bordered pit, since the Paleozoic ferns, which produced secondary xylem, possessed scalariformly pitted secondary tracheids. Although the circular bordered pit may very well be an equally primitive type, there is little evidence that the scalariform pit has evolved from the circular pit in any group of vascular plants. Bailey (1925, 1953) and Frost (1931) present strong support for the view that the circular bordered pit has been derived from the scalariform pit in the gymnosperms and angiosperms. Their conclusions regarding pit evolution in angiosperms have been supported by the observations of many other workers during the last several decades. Bierhorst (1960) has suggested, however, that the circular bordered pits in the primary xylem of conifers and some related groups as well as in *Equisetum* and the Ophioglossales might not have evolved by a phylogenetic break up of scalariform bordered pits in the metaxylem, but probably evolved as circular bordered pits in the protoxylem. His view is based on the presence of circular bordered pits in the late protoxylem of these groups, and the absence of transitional types between scalariform and circular bordered pits in the metaxylem of the genera studied.

In the coenopterid ferns, *Anachoropteris clavata* (Delevoryas and Morgan, 1954a), *Apotropteris minuta* (Morgan and Delevoryas, 1954), *Tubi-*

caulis stewartii, and *T. scandens* (Eggert, 1959a), pitting of the protoxylem is uniseriate-scalariform, whereas the metaxylem is typically multiseriate-scalariform in the first 3 and multiseriate-reticulate in the last species, and in *T. sutcliffii*, the larger metaxylem elements are characterized by bordered pits (Delevoryas and Morgan, 1952). Such developmental sequences suggest a possible derivation of the circular bordered pit from the scalariform in these groups. In *Anachoropteris clavata* and *Tubicaulis stewartii*, transitional and circular bordered pits characterize the petiolar xylem, whereas tracheids of the stem possess the typical scalariform pits. It should also be noted that pits approaching a circular bordered type occur in the Osmundaceae and in some other extant leptosporangiate ferns. Some of the last-formed metaxylem elements of *Osmunda cinnamomea* stem bear some very short, opposite scalariform pits, pairs of which approximate the relative position of single, vertically adjacent, scalariform pits (Bierhorst 1960, Fig. 137). Earlier differentiated metaxylem elements of this species are characterized by uniseriate scalariform bordered pits. Bierhorst (Fig. 155) also illustrates oval or lens-shaped pits from the rachis of *Onoclea sensibilis*. Similar pits have also been observed in several other higher Filicales by Richard A. White (unpublished). It may also be significant that in the Paleozoic ferns such as *Zygopteris* and *Rhacophyton*, which produced secondary xylem, the pits were scalariform, and that the single genus within the Filicineae that typically produces secondary tracheids bearing bordered pits, *Botrychium*, is a living group with no fossil record.

This evidence suggests that in the ferns (with the possible exception of the Ophioglossales), as in the angiosperms, the circular bordered pit has been derived from the scalariform.

If *Archaeopteris* represents an ancestral fern group, the typical concentric arrangement of primary xylem and phloem in the leaf traces and stelar bundles of the typical fern must have been derived from the collateral arrangement. The collateral arrangement is characteristic of the gymnosperms and angiosperms and is generally considered the advanced condition. Certain paleozoic genera, primitive gymnosperms or progymnosperms such as *Calamopitys*, *Lyginopteris* and *Callistophyton*, are intermediate in character, possessing collateral stelar bundles and concentric leaf traces, and suggest a derivation of the collateral condition in the gymnosperms from the concentric condition. Although we do not know in detail the appearance of the stem of *Archaeopteris* in the solely primary condition, the vascular bundles of the stele were probably collateral, judging from the absence of internal phloem. This seems to eliminate *Archaeopteris* as an ancestral form from which the typical concentric arrangement of the ferns might have evolved.

Archaeopteris roots have not been discovered in attachment to stems (*Callixylon*), but because of the nearly identical anatomy of the secondary wood of root and stem there is no question as to the identity of the roots of this plant (Beck, 1953). This similarity in structure, the production of secondary tissues, and the habit of the plant make it most unlikely that the roots were adventitious, rather, they were probably an important part of the axial system. I am not aware of any evidence to suggest that *Archaeopteris*, through reduction, has become modified into an herbaceous plant with adventitious roots.

Because *Archaeopteris* does not possess some of the important distinguishing characters of the ferns, because there are no recognizable intermediates, and because, considering our knowledge of evolutionary trends of cell types and tissues, it does not possess characters of the type from which ferns probably evolved, I must conclude that *Archaeopteris* is not a primitive, woody, arborescent fern.

I believe that *Archaeopteris* was not derived from any group which could reasonably be called a fern, although I realize the probability of the common ancestry of these groups, and the possibility that *Archaeopteris* might be of fern origin. Even if the group of which *Archaeopteris* was a member had been derived from a group of primitive ferns, the evidence suggests that its evolution was not in the direction of any other group of ferns, but rather, in the direction of the gymnosperms, and that it had evolved beyond the level at which it could reasonably be called a fern. The fern-like characters of this plant such as megaphyllous leaves, pteridophytic reproduction, foliar sporangia, and mesarch order of maturation of primary xylem do not conflict with this view. Megaphylly is common not only to ferns and progymnosperms, but also to pteridosperms and angiosperms. Pteridophytic reproduction characterizes all vascular plant groups except the gymnosperms and angiosperms, and the seed habit in these groups probably evolved from the pteridophytic condition by way of heterospory. Foliar sporangia occur in the lycopsids, the cycadophytes, the angiosperms, and, in the opinion of many, the coniferophytes, in addition to the ferns. Mesarch primary xylem is characteristic of, but not unique to, ferns, occurring also in primitive gymnosperms.

Evidence previously presented (Beck, 1960b) supports the second alternative listed above, that *Archaeopteris* was one of a large group of progymnosperms. Its arborescent, probably excurrent habit, megaphyllous leaves, secondary growth, circular bordered pits, ray tracheids, collateral vascular bundles, and probable heterosporous reproduction suggest that it was a type intermediate between the psilophyte and the seed plant: one advanced considerably beyond the primitive Lower and Middle Devonian psilophytic level and approaching that of the primitive Carboniferous gymnosperms.

ADDITIONAL SUPPORT FOR THE VIEW THAT

ARCHAEOPTERIS IS A PROGYMNOSPERM—The view that *Archaeopteris* is a progymnosperm is further supported by the nature of its fertile foliage, since the morphology of its leaves suggests a type from which some pteridosperm fructifications might have evolved. In fact, Walton (1949a), in discussing *Alcicornopteris hallei,* a microsporangiate pteridosperm fructification, noted that "the structure of the branching axes indicated that they were parts of a frond and not stems"; and further, that "... [this fructification] seems relatively simple and may possibly be regarded as occupying an intermediate position between the type of organization found in the Upper Devonian *Archaeopteris* and the Upper Carboniferous synangial types."

Walton (1953a) proposed that the cupule of the Lagenostomales might have evolved by the fusion of sterile foliar segments around a cluster of ovules, a view supported by the morphology of the *Calathospermum* cupule, composed of 6 basally fused leaf-like segments, which surrounded a cluster of stalked seeds. Walton (1949b) writes: "The presence of a crescentric strand in the stalk of the cupule clearly suggests that the whole structure is morphologically equivalent to a frond or part of a frond." And further: "It is evident that in the evolution of the *Calathospermum* cupule, the telome system from which it was derived must have acquired the status of a dorsiventral lateral foliar organ not only in external features but in the structure of its vascular system before modification into an almost radially symmetrical cupule."

Support for Walton's view is presented in several recent papers. *Eurystoma* (Long, 1960) and *Geminitheca* (Smith, 1959), primitive lagenostomalean seeds from the Lower Carboniferous of Scotland, were borne on cupules considered to be derived from bilateral, dorsiventral leaves or branch systems. The "cupule" of *Eurystoma* was, in fact, little more than a somewhat curved, dorsiventral branch system.

Barnard (1960) has described a new species of *Calathospermum, C. fimbriatum,* and, on excellent evidence, like Walton, interprets the *Calathospermum* cupule as the equivalent of a large part of a dorsiventral frond. The main axis of the fructification described by Barnard has the morphology of a rachis. The basal part is slightly concave adaxially and contains vascular strands which form a shallow U with the open end facing the adaxial surface. Proximal to the cupular segments, there are 2 opposite pairs of lateral pinnae in 1 plane. The main axis (rachis) is interpreted as branching, in the manner of many pteridosperm leaves. Primary pinnae, alternately arranged, arise from the branches of the main axis. The 2 proximal pinnae are fertile and bear seeds on branched secondary pinnae (pinnules), whereas the 3 distal are vegetative. The basic segments of the cupule are composed of the primary pinnae.

There are some close similarities between the fertile frond of *Archaeopteris* and the *Calathospermum* fructification. In *Archaeopteris,* as in *C. fimbriatum,* the most basal lateral appendages are frequently vegetative, most often taking the form of pinnules, but sometimes of pinnae (Johnson, 1911, pl. IV). These are followed by a series of fertile pinnae bearing predominantly fertile pinnules, but with the most proximal and distal pinnules often being vegetative. The fertile pinnae are succeeded by a series of solely vegetative pinnae. In these features the *Archaeopteris* fertile leaf and *Calathospermum* are remarkably alike. If Barnard's interpretation is correct, and I see no reason for scepticism, the fertile leaf of *Archaeopteris* differs from *Calathospermum* in basic architecture only in its unbranched main rachis. It is not difficult to conceive of a fructification of the *Calathospermum-Salpingostoma* type having evolved through several intermediates from a fertile frond of a type similar to that of *Archaeopteris.* The strong evidence that some of the primitive pteridosperm seed-bearing fructifications were morphologically bilateral and dorsiventral foliar organs supports the view that *Archaeopteris* and similar gymnospermous pteridophytes might have been ancestral to some of the pteridosperms.

I have previously suggested that the cordaites as well as the pteridosperms might have evolved from the Progymnospermopsida. There is a conspicuous similarity in internal structure of both root and stem. In view of the foregoing discussion and of the clearly leaf-borne sporangia of *Archaeopteris,* however, those who adhere to the view that the cordaites are stachyosporous (i.e., with seeds borne terminally on axillary shoots or branches) will, no doubt, disagree. The concept of stachyospory as applied to the coniferophytes by Sahni (1920), and upheld by Lam and others, has never been acceptable to Florin, the foremost authority on the morphology and evolution of cordaite and primitive conifer fructifications. Schoute (1925), Florin (1939) and Eames (1952) agree that ovules as well as microsporangia of the cordaites are (in the words of Eames), "... borne terminally on an appendage, not terminally on an axillary shoot." One who studies Florin's massive and scholarly work on the evolution of the female coniferophyte cone, or who carefully reads his summary of this work (1951), can hardly fail to concur in this conclusion. The cordaitean fructification is, of course, very different from that of *Archaeopteris.* A single sporophyll of the axillary fertile shoot (strobilus) of *Cordaites* is, apparently, homologous with the entire fertile leaf of *Archaeopteris.* This difference, however, is not as basic as that between phyllospory and stachyospory, and the evolution of the primitive coniferophyte fructification from some progymnosperm remains a distinct possibility.

The evolution of the cordaite leaf from the pinnately compound type of the progymnosperm does, of course, present an organographic problem. But Delevoryas and Morgan (1954b), in discussing the possible relationship between *Callistophyton* and *Poroxylon*, have hypothesized that a simple cordaite-like leaf could be derived from a pinnate type by a suppression of the lateral leaf segments and a concurrent flattening and lateral expansion of the rachis.

Archaeopteris was, predominantly, an Upper Devonian genus, with several species extending into the Lower Mississippian whereas *Cordaites* seems to have existed primarily in the Pennsylvanian and later periods, possibly occurring earliest in the Upper Mississippian (see Walton, 1953b). The identification of a Lower Mississippian specimen as *Cordaites*, solely on the basis of secondary wood, by Cribbs (1935) is probably in error. These genera are, therefore, separated temporally by about 30 million years (see Kulp, 1961, for a new geologic time scale), during which time major evolutionary changes could have occurred. There is a large group of cordaite-like petrifaction genera including *Endoxylon*, *Eristophyton*, *Bilignea*, the "*Cordaites*" of Cribbs, *Pycnoxylon*, and others, all of Lower Mississippian age. Lacey (1953) has suggested that the first 3, often included with the Calamopityeae, should be grouped with the Cordaitales. Is it not possible that some of these genera represent intermediates between the progymnosperms of the Upper Devonian and the later Paleozoic cordaites and/or conifers?

There is an obvious similarity in leaf morphology between *Archaeopteris* and Lower Mississippian foliage genera such as *Sphenopteridium*, *Adiantites*, *Rhodea*, *Rhacopteris*, and *Triphyllopteris* (see Walton, 1931; Read, 1955). Some of these genera occur with fructifications, previously discussed, which are believed to belong to primitive pteridosperms, and with petrifaction genera such as *Stenomyelon*, *Eristophyton*, *Protopitys*, *Bilignea* and *Calamopitys*. *Callixylon* (the stem of *Archaeopteris*) occurs in great abundance in association with several of these same petrifaction genera in the New Albany shale, and shares many structural characteristics.

Archaeopteris is closely similar in foliage and fructifications to the pteridosperms. It is similar in the anatomy of its primary body to both pteridosperms and some coniferophytes. In its secondary wood structure there is a remarkable resemblance to the coniferophytes.

Just where *Archaeopteris* fits in the scheme of progymnosperm and primitive gymnosperm evolution is impossible at present to conclude. That it is, indeed, a progymnosperm, not a fern precursor, is supported by much evidence. It seems to have been one of the more advanced genera among the progymnosperms and, as suggested by Arnold (1930) and Leclercq (personal communication, 1960), might have evolved concurrently with, and in some ways parallel to, both the primitive pteridosperms and coniferophytes. To determine finally whether this is a sound conclusion, as seems probable, or whether the genus was directly ancestral to some pteridosperms or coniferophytes, or some members of both groups, must await a more comprehensive knowledge of the plants represented by the numerous foliage and petrifaction genera of the Devonian and Mississippian.

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