Early Seed Plants

Recent fossil discoveries shed light on the evolution of the seed and on seed-plant progenitors.

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Within the last few years highly significant discoveries have been made that have brought us much closer to an understanding of the origin of seed plants. The gaps in our knowledge are still great, but it is clear that they are being narrowed. Here I summarize certain paleobotanical evidence that bears on the origin of gymnospermous plants, particularly of the group known as the pteridosperms or seed ferns, and consider briefly some older fossils that may be the progenitors of the early pteridosperms.

It is difficult to discuss plant evolution on the basis of paleobotanical evidence without being called on to deal with the problem of the origin of the angiosperms (flowering plants). The latter problem is touched on here only briefly; it should be recognized that a better understanding of angiosperm interrelationships and origins must be based on (or at least will be greatly aided by) an understanding of the earlier gymnosperms.

Extant Groups of Gymnosperms

The gymnosperms are represented today by several distinct groups, and some of these are known to everyone. I review them briefly for the benefit of the nonbotanist, pointing out relevant problems of evolution. The fundamental character that separates them from the angiosperms is the manner in which the seeds are borne. In the angiosperms, such as, for example, the pea or bean, seeds are enclosed within the pod or carpel wall. The seed in the gymnosperms is not enclosed; an example is the cone of the pine, where seeds are borne in pairs on the upper surface of each woody scale.

The Coniferales is the largest group of living gymnosperms and includes such familiar plants as the pine, spruce, redwood, and juniper. The "conifers" probably originated from the Carboniferous cordaites, and a good deal is known about the evolution of their seed-bearing cones. This sequence was worked out largely through the researches of the Swedish botanist Rudolf Florin and constitutes one of the really monumental contributions to our knowledge of plant evolution. I might add that some specialists now segregate the familiar evergreen yew (*Taxus*) as a separate order, the Taxales, in view of the fleshy seed organ, which is quite unlike the woody seed cone of most other members of the Coniferales.

The Ginkgoales includes one living species, *Ginkgo biloba*, that has several unique characters: the leaves are fan-shaped, having two veins in the petiole that dichotomize freely in the blade, and the leaves as well as the seeds and microsporangiate catkins are borne on distinctive short shoots. The group was much larger and quite diverse during the Mesozoic; 16 or more genera are recognized for that era.

The Cycadales are also plants of ancient lineage. The nine living genera are not abundant but are widely distributed through the tropics and subtropics. In a good many of them the trunk is columnar; it is covered with a heavy armor consisting of the persistent basal part of the leaf stalk and it is rarely branched. In gross form the leaves are much like those of the palms. The seed cones may be huge structures with numerous appendages each of which, in most species, bears a pair of seeds. Each of the appendages of the pollen cones has several dozen spherical sporangia on the under side. These appendages are quite unlike those of the Coniferales and Ginkgoales. *Ginkgo* and the cycads have a primitive character in common—male gametes which are free-swimming within the seed.

There are several other living gymnosperms about whose origins and relationships there has long been uncertainty. *Gnetum* is a genus predominantly composed of great scrambling vines that somewhat resemble the dicotyledonous angiosperms in leaf form and wood anatomy. The staminate organs are unique, and the seeds, with their three integuments (seed coats), are particularly striking. *Ephedra* is a profusely branched shrub of our Southwest, and the wholly fantastic *Welwitschia*, found only in southwest Africa, is a low-growing desert plant with a stem like a turnip and two large strap-shaped leaves which lie on the ground and split lengthwise into numerous segments as the plant grows older.

Extinct Groups of Gymnosperms

The gymnosperms first appear in early Lower Carboniferous horizons, some 250 million years ago, but it will not be surprising if they eventually are traced back to the underlying Devonian period. I might add that the first generally accepted flowering plants have been found in the mid-Lower Cretaceous, but fossils that have been attributed to this group come from the Jurassic and Triassic, and a few botanists have expressed the opinion that they originated as far back as the Permian.

The best known of the major groups of extinct gymnosperms are the Pteridospermae (seed ferns), the Cordaitales (cordaites), and the Bennettitales (bennettites). I discuss the seed ferns in some detail later on; the cordaites were abundant in the Carboniferous and are important as a group that was ancestral to the conifers; the bennettites bear a close resemblance to some of the Cycadales in their general habit but differ profoundly in the organization of their reproductive organs and in certain aspects of leaf anatomy. T. M. Harris, a leading authority on the group, has expressed the view (*1*) that the Cycadales and the Bennettitales are not closely related and should be regarded as independent gymnospermous orders equal in rank to the Coniferales.

Finally, there are several fossil assemblages, such as the Jurassic Pentoxyleae from the Rajmahal Hills of

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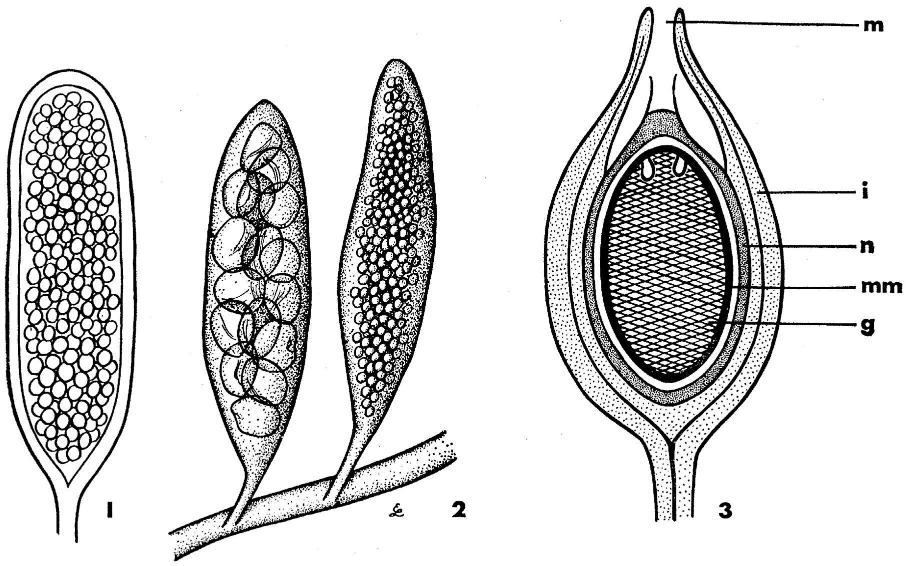
India (*2*) and the Vojnovskyales, described by the late Maria F. Neuburg (*3*), from the Permian of Russia. These do not compare at all closely with the plants in the recognized major groups that I have cited.

Thus, the great diversity of form in the living and the extinct groups strongly suggests that the "gymnosperms" constitute, not a natural group of plants, but an assemblage of several different lines in which seeds probably have evolved independently. This point is subject to argument, but the fact that the two early fossil groups that we know best, the seed ferns and the cordaites, have few features in common may be of particular importance.

Unless it is otherwise noted, the fossils that I describe here are pteridosperms. Members of the group first appear in the Lower Carboniferous; they became numerous and diverse in the succeeding Upper Carboniferous and Permian. They are characterized by fernlike foliage that bore seeds. The stems, in different species, are from a few centimeters to half a meter in diameter; some were vines and others grew upright. The stems possessed a cambium that produced secondary wood and strongly developed fiber strands in the bark. The pollen-bearing organs are quite massive in some species, being cup-shaped or bell-shaped, with numerous elongate pollen sacs. The group was a dominant one in the later Paleozoic forests and of great botanical interest as a possible source of the flowering plants. Recent discoveries that bear on pteridosperm evolution concern developments as follows: (i) the evolution of the seed and particularly of its coat or integument; (ii) some special modifications of early pteridosperm seeds; (iii) the evolution of a structure, the cupule, which enclosed a seed or seeds and which may be homologous with the angiosperm seedpod; and (iv) some possible progenitors of the pteridosperms.

Evolution of the Seed

A seed may be described as an integumented megasporangium. The most primitive "spore state" in vascular (woody) plants seems to have been one in which all the spores produced by a plant were of the same size (see Fig. 1)—that is, the plant was homosporous. In some lines of vascular plants there is abundant evidence that heterospory (see Fig. 2) evolved independently. That is, certain sporangia on a plant produced microspores which, in turn, developed into the male gametophytes, while others produced megaspores that formed the female gametophytes. When the number of megaspores is reduced to one and the sporangium is enclosed, the organ is an "integumented megasporangium"—in other words, a seed.



Figs. 1–3. Probable basic stages in the evolution of the seed. Fig. 1. The earliest vascular plants were homosporous, all of the spores being of approximately the same size. Fig. 2. Heterospory characterizes more advanced plants; some sporangia (see right-hand member of the pair) include numerous small microspores from which male gametophytes develop, while others (see left-hand member of the pair) contain a smaller number of relatively large megaspores which produce the female gametophytes. Fig. 3. A generalized drawing of a pteridosperm seed in median longitudinal section. The nucellus (megasporangium) includes and retains only one megaspore, within which the female gametophyte develops. The nucellus is enclosed by the integument, and the two are shown here as partially united. (*i*) Integument (light stipple) with a conspicuous vascular strand; (*n*) nucellus (dark stipple); (*mm*) megaspore membrane (the thickness is somewhat exaggerated); (*g*) female gametophyte (cross-hatching), with two archegonia at the distal end; (*m*) micropyle.

Figure 3 is a generalized drawing of a pteridosperm seed. The nucellus is regarded as a megasporangium that has been surrounded by a coat or integument with a small opening (micropyle) at the distal end. The nucellus produces a single functional megaspore (in Fig. 3 the thickness of its wall is somewhat exaggerated); the female gametophyte develops within the wall. At a later developmental stage the egg contained in one of the archegonia (the female organs; two are shown in Fig. 3) may be fertilized and an embryo develops within the gametophyte.

The transition from megasporangium (Fig. 2) to seed (Fig. 3) involves, particularly, the enclosing of the nucellus by the integument and certain modifications of the distal end of the nucellus. Let us consider these two points.

In the past, several botanists have suggested that the integument consisted of a ring of fused filaments or branches of one sort or another. For example, T. G. Halle wrote (*4*), "In the light of the Psilophytales, both cupule and integument are easily accounted for as syntelomes." ("Syntelomes" means fused terminal branchlets.)

Theories come and go. I suppose very few of them mature into established fact, but in the case of the integument, the brilliant discoveries of A. G. Long of Duns, Berwickshire, Scotland, seem to fit the theory very well. In a series of recent reports (*5, 6*) he has described several seeds from the Lower Carboniferous of Scotland that fill a significant part of the gap in our knowledge. A few of these, as well as two seeds described by previous workers, are shown in Figs. 4–9 as representative of some probable stages in the evolution of the integument.

The most primitive fossil that may be called a seed is *Genomosperma kidstoni* (see Fig. 4). The integument, which in most gymnosperms is an essentially uniform cylindrical envelope enclosing the nucellus, consists of eight filaments that are separate down to the base. There is no micropyle as the filaments (integument) flare outward. The micropyle in modern seed plants is a minute apical opening in the integument at the distal end of the seed, and it is through this that pollen grains pass to reach the inner part of the seed.

In another Lower Carboniferous species, *Genomosperma latens* (see Fig. 5), the integumentary lobes are fused from the base for about a third of their length and are closely appressed at the distal end, forming at least a rudimentary micropyle.

I have selected an Upper Carboniferous seed, *Physostoma elegans* (see Fig. 7), to show a somewhat more advanced degree of fusion of the integument lobes. Finally, in the integument of two more of Long's seeds, *Eurystoma angulare* (Fig. 8) and *Stamnostoma huttonense* (Fig. 9), fusion is almost or wholly complete. In *E. angulare* the inetgument is only slightly lobed; in *S. huttonense* fusion is complete.

Some of the Lower Carboniferous seeds developed a considerable degree of specialization; an example is the unique *Salpingostoma dasu* (*7*) (Fig. 6). It is elongate and spindle-shaped and has an overall length of 50 millimeters and a maximum diameter of 6 millimeters. The integument, above the level of the distal part of the nucellus, is divided into five or six slender tentacle-like lobes whose basal portions enclose the elongate, tubular, and slightly flaring salpinx (described in the next section). The basal outer part of the seed is covered with stiff, unicellular hairs which become confined to six grooves above the base. These hairs disappear at the level of the distal end of the nucellus; more delicate hairs occur on the inner surface of the integument lobes.

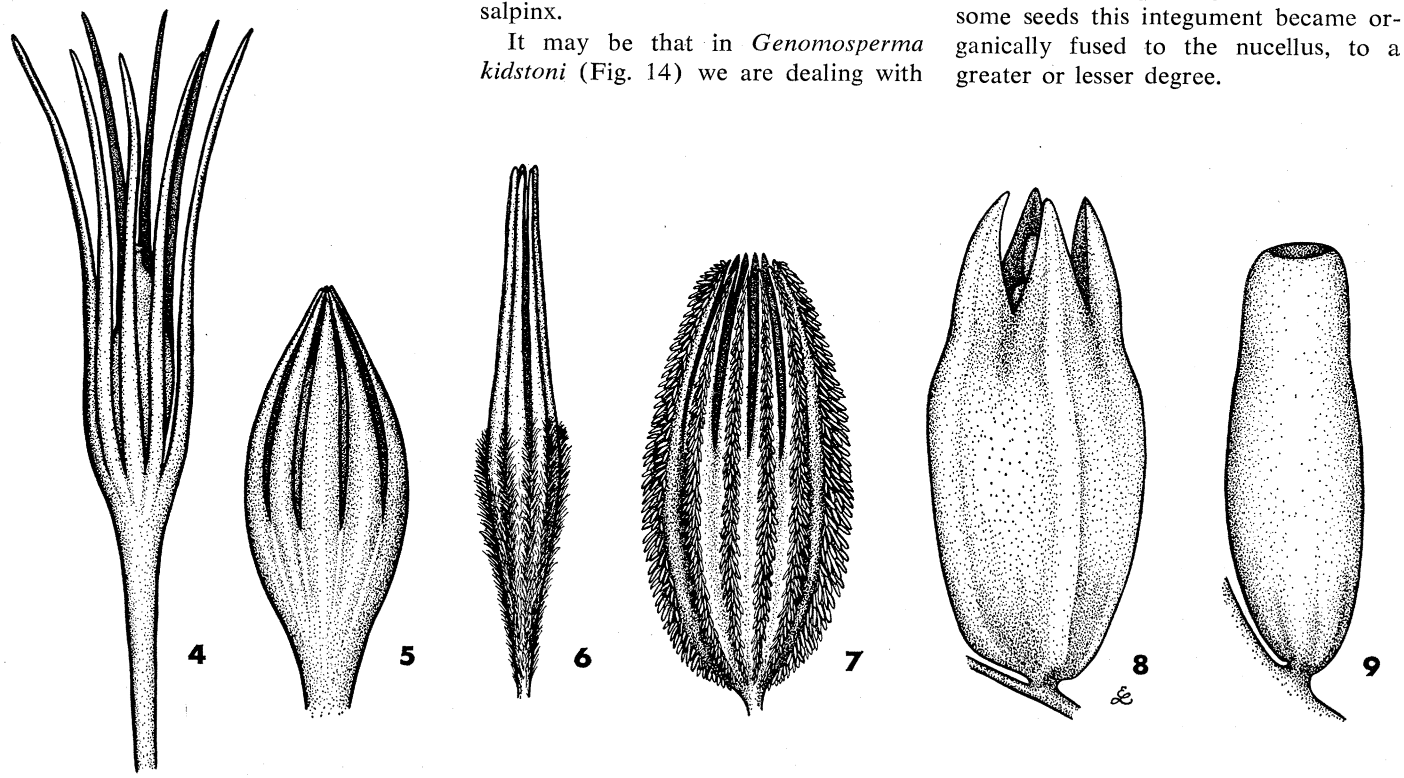
Modifications for Pollen Reception

A significant sidelight on the early evolution of the pteridosperm seed lies in the development of the salpinx, the specialized distal portion of the nucellus (see Figs. 10–14). In seeds such as *Stamnostoma huttonense* and *Eurystoma angulare* (Fig. 12), where a micropyle is lacking, it seems likely that the strongly developed salpinx would have been of significant aid in directing the pollen into the pollen chamber. The case is less clear in *Salpingostoma dasu* (Fig. 13), where the greatly elongated distal extremities of the integument serve no obvious purpose, but in which the pollen, once it was within the long micropylar tube, would have been directed into the pollen chamber by the lining of hairs and the trumpet-shaped salpinx.

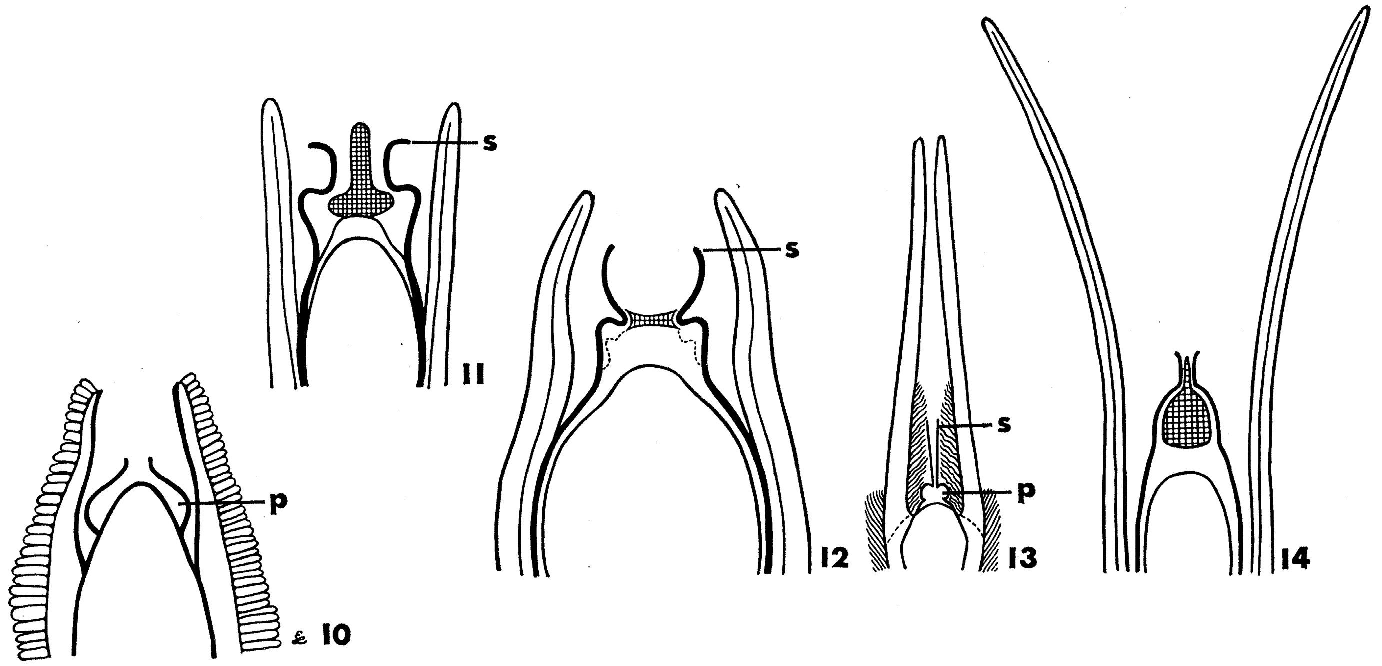
It may be that in *Genomosperma kidstoni* (Fig. 14) we are dealing with a seed that is so primitive that the bizarre development of the salpinx had not yet evolved, and in Upper Carboniferous seeds such as *Physostoma elegans* (Fig. 10), perhaps the pollen-drop mechanism had evolved, reducing the necessity for the salpinx. (In modern gymnosperms, such as the cycads and ginkgo, a portion of the apical part of the nucellus produces a droplet of fluid which partially oozes out of the micropyle; pollen grains are caught in this, and, as the droplet dries, the grains are drawn into the apical part of the seed.)

With reference to the unique salpinx, Long notes (*6*), "the evolution of a well developed salpinx may have been one of the earliest structural refinements of the megasporangial apex or 'nucellar beak' following the establishment of heterospory." He also says (*6*), "the development of a salpinx and its variation in size and form was an evolutionary phase preceding the establishment of the integumental micropyle."

It must be emphasized that the seeds illustrated in Figs. 4 through 9 do not represent a straight-line evolutionary series. They represent significant stages in the envelopment of the nucellus by a ring of vegetative lobes which later fused together to form a nearly completely enclosing integument, and in some seeds this integument became organically fused to the nucellus, to a greater or lesser degree.



Figs. 4–9. Some seeds attributed to the pteridosperms that show variation in the degree of fusion of the integument lobes and in the presence or absence of a micropyle. Fig. 4. *Genomosperma kidstoni* (Calder) Long; seed length, approximately 15 mm. Fig. 5. *Genomosperma latens* Long; seed length, 8 mm. Fig. 6. *Salpingostoma dasu* Gordon; seed length, 50 mm. Fig. 7. *Physostoma elegans* Williamson; seed length, 6 mm. Fig. 8. *Eurystoma angulare* Long; seed length, 8 mm. Fig. 9. *Stamnostoma huttonense* Long; seed length, 3.7 mm.



Figs. 10–14. The distal end of several pteridosperm seeds, in median longitudinal section, showing modification of the tip of the nucellus to form pollen chamber (*p*) and salpinx (*s*). Fig. 10. *Physostoma elegans.* Fig. 11. *Hydrasperma tenuis* Long. Fig. 12. *Eurystoma angulare.* Fig. 13. *Salpingostoma dasu.* Fig. 14. *Genomosperma kidstoni.* [Figs. 11, 12, and 14, after Long; Fig. 13, after Gordon]

In some pteridosperm seeds the distal part of the nucellus (the salpinx) became elaborated as a pollen-collecting mechanism. With the development of a distinct, minute opening at the distal end of the integument (the micropyle) and the pollen-drop mechanism, the need for the salpinx disappeared.

Evolution of the Cupule

Several seeds attributed to the pteridosperms are known to have been enveloped, singly or in groups and to a greater or lesser degree, in a structure known as the cupule. Its importance lies in the strong suggestion that it may be homologous with the carpel (seed pod) of the flowering plants. The examples considered (see Figs. 15–19) illustrate certain phases in the evolution of the cupule, but in the case of several of the fossils little is known of the rest of the plant, and here again there is no implication of a direct evolutionary sequence.

Tyliosperma orbiculatum (Fig. 17) is known from small, nearly spherical seeds about 3.7 millimeters long (*8*). The integument and nucellus are united except at the apical end of the seed, where the integument is divided into seven free lobes. What the vascularization (conducting system) of the seed was is uncertain, but there were probably seven strands and they are thought to have been confined to the nucellus and not to have extended to the integument. The seed is, in turn, partially enclosed by seven or eight fleshy segments, free for the greater part of their length, which compose the cupule.

The seed by which others in the pteridosperm group have been judged is one described originally under the name *Lagenostoma lomaxi*, from the Upper Carboniferous of Britain; in 1904 it was demonstrated by Oliver and Scott (*9*) that this is the female organ of *Lyginopteris oldhamia*, a vine-like pteridosperm with rather primitive, fern-like foliage. The seed (Fig. 18) is barrel-shaped, about 5.5 millimeters long, and a little over 4 millimeters in diameter.

The integument and nucellus are united for about four-fifths the length of the seed, and the integument is slightly lobed in the distal free part; the extreme tip of the pollen chamber projects slightly through the micropyle. The cupule consists of about eight segments which are united for approximately half their length. The vascular strands at the base of the cupule branch several times. The exact number of these strands is not clear, but from Oliver and Scott's description it appears that each cupule lobe was supplied with more than one bundle, and this may mean that there were originally more than eight cupule segments. Rather abundant, large, and essentially spherical glands are a conspicuous feature of the fossil.

Several multiseeded cupules have been reported; the largest of them is the cupule of *Calathospermum* (*10, 11*), from the Lower Carboniferous of Scotland. The cupule of *C. scoticum* Walton (Fig. 19) is a tulip-shaped organ of six broad lobes; these are basally united, and there are five or six vascular strands in each. Several dozen seeds, each at the tip of a slender stalk, are borne within the cupule. Several cupules contain only stalks—a finding which indicates that the seeds were extruded and separated from the distal end of the stalk as they approached maturity. The seeds are similar if not identical to those described independently under the name *Salpingostoma dasu* (Fig. 6); some cupules give evidence of having contained as many as 70 seeds.

More recently Barnard (*11*) has described another species, *Calathospermum fimbriatum*, which has several features of special interest. The cupule is about 90 millimeters long, and it is thought that it was borne terminally on the primary rachis of a special fertile frond. It differs from *C. scoticum* Walton in the greater division of its cupule wall; each of the two primary halves of the wall divides into three segments near the base, and each segment, in turn, divides into five branches or pinnae, of which some were sterile and others were seed-bearing.

The most primitive cupulate organ found to date—and it is so rudimentary that there is some question as to whether it should be called a cupule—is that of *Eurystoma angulare* (see Fig. 15). The seed is roughly embraced by a system of dichotomizing terete branches, which may represent a slightly specialized portion of a primitive frond. The view that this branch system does represent an early stage in the development of a cupule is supported by Long's discovery of *Stamnostoma huttonense*, also from the Lower Carboniferous.

A common stalk bears a pair of cupules each of which was formed by two divisions (at right angles to each other) of the initial branch system; these four main branches (of each cupule) fork toward the distal extremity, with as many as 16 terminal divisions. Scars where other seeds may have been attached suggest that each cupule may have contained as many as four seeds. In *S. huttonense* the enclosing branchlets are organized into a more definite entity than in *Eurystoma*, and the fossil seems to represent an intermediate stage between the later and more highly evolved pteridosperms such as *Tyliosperma* and *Calathospermum.*

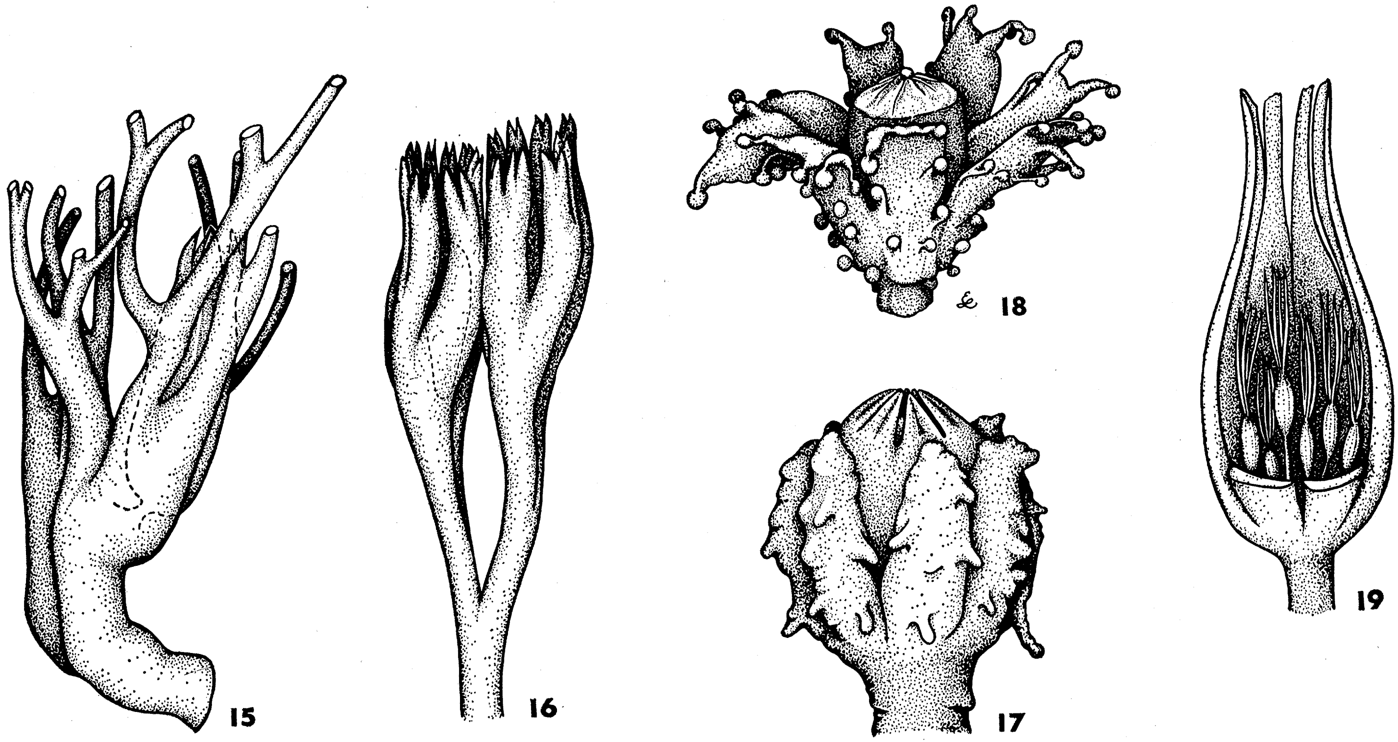
We have little information concerning the way in which the cupules were borne on the plants as a whole, but a few fossils have been found which reveal something of their group organization (see Figs. 20 and 21). Some years ago M. Benson (*12*) described *Calathiops bernhardti* (Fig. 21) as a simple pinnate branch system in which each primary division produced several branchlets that terminated in what seemed to be a multiseeded structure. At least *Calathiops* was so interpreted, and recent discoveries substantiate this opinion. Each cupule is a little over 3 centimeters long and contained perhaps a dozen seeds. There is a basic similarity to Walton's *Calathospermum,* but the cupule of *Calathiops* is smaller, with fewer seeds, and there are more divisions.

In the case of *Calathospermum fimbriatum* there appears to have been one large terminal cupule on a special(?) frond, and Barnard suggests that the two major divisions may be homologous with primary divisions of the main rachis (central axis) of the leaf or frond. This bifurcation of the main rachis of the frond is characteristic of several pteridosperms, and it seems probable that Barnard is correct.

Among his other contributions Long (*13*) has described some compression fossils (Fig. 20) which he identified with petrified cupules and seeds of *Stamnostoma huttonense* which he had described earlier. The compressions consist of bifurcating axes, with cupules usually borne in pairs at the distal extremities; some of them contained at least two seeds.

Summary, and Some Unsolved Problems

Discoveries of Lower Carboniferous fossils in Scotland indicate that the integument and the cupule wall of the pteridosperms evolved from an enclosing ring of vegetative lobes that fused together. But there are still unsolved problems of interpretation. We know very little about the origin of the integumentary lobes of *Genomosperma.* In those species in which the integument is united for much of its length with the nucellus, it is not always possible to distinguish between the two. In some

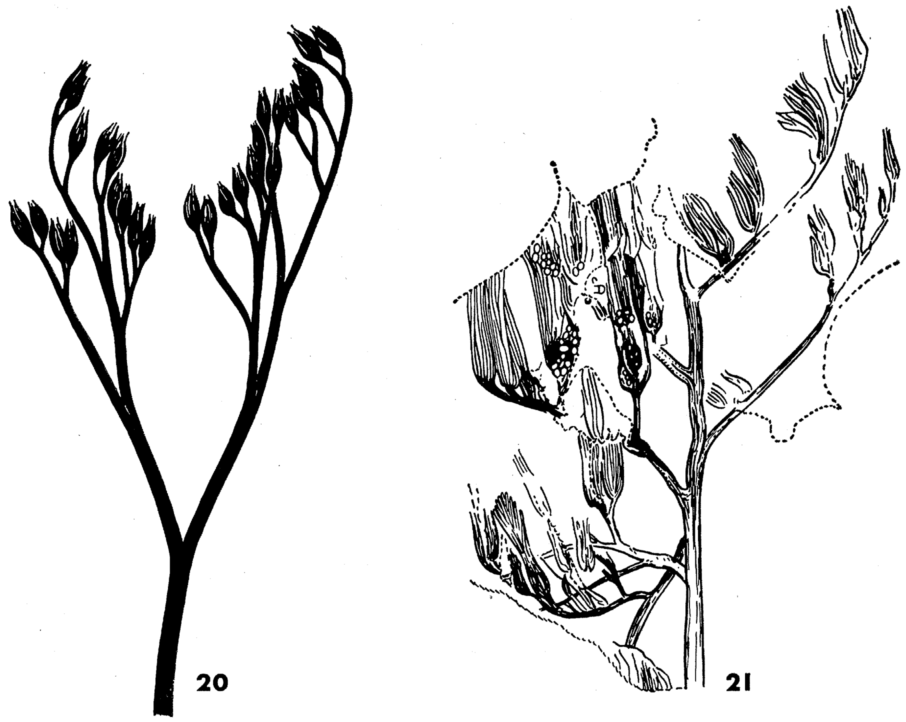


Figs. 15–19. Some seed-bearing organs attributed to the pteridosperms, showing variations in the degree of fusion of the cupule lobes. For explanation and dimensions, see text. Fig. 15. *Eurystoma angulare*; dotted line indicates position of one seed. Fig. 16. *Stamnostoma huttonense*; dotted line indicates position of one seed. Fig. 17. *Tyliosperma orbiculatum* Mamay. Fig. 18. *Lyginopteris oldhamia.* Fig. 19. *Calathospermum scoticum* Walton. [Figs. 15 and 16, after Long; Fig. 17, after Mamay; Fig. 18, after Oliver and Scott; Fig. 19, after Walton]

pteridosperm seeds, possibly those borne by the medullosan subgroup (relatively large plants with highly complex wood anatomy), the nucellus, or what is interpreted as being the nucellus, is heavily vascularized; in most pteridosperm seeds, and so far as I know in the seeds of all living gymnosperms, the nucellus is nonvascularized. It is thus uncertain in such cases whether we are dealing with a closely investing integument or whether the nucellus is actually vascularized.

Some botanists refer to the cupule as simply an outer integument. The evidence does suggest that it originated from an outer or secondary ring of branchlets, as in *Tyliosperma*; this is, however, an oversimplification in that the outer ring in some species enveloped several seeds, in fact a few dozens in the case of *Calathospermum*. Here the cupule is not just another integument but is, rather, a distinct morphological structure and quite possibly the progenitor of the seed pod in flowering plants. In *Calathospermum fimbriatum* the cupule wall may be the modified terminal bifurcation of the frond and its accompanying subdivisions (pinnae).

Clearly we need to know a great deal more about the plants that bore these seeds, and it is my impression that we are still viewing only fragments of what may be several distinct lines of development within the pteridosperms. The evidence at hand, however, is impressive, and Long's discoveries stand among the most significant in recent decades.



Figs. 20 and 21. Drawings of two pteridosperms, illustrating the manner in which the cupules were borne; the branch system may be a modified portion of a frond. Fig. 20. *Stamnostoma huttonense*. Fig. 21. *Calathiops bernhardti*. [Fig. 20, after Long; Fig. 21, after Benson]

Possible Precursors of Seed Plants

It is hardly possible to study the fossil remains of the early seed plants without wondering what they in turn evolved from. A very brief summary of some of the earlier (pre-seed) plant groups seems appropriate as a prelude to consideration of certain fossils that may be ancestral to the early seed plants.

Although fragmentary bits of evidence, including spores, suggest that vascular plants may have existed on the land in Cambrian times, the earliest generally acceptable evidence is an interesting assemblage of late Silurian plants from Australia, which may possibly be of Lower Devonian age. To be on the safe side we may say that vascular land plants appeared in some abundance in the lower Devonian, that by mid-Devonian times vegetation of considerable diversity clothed the land; and in the late Devonian not only was there considerable structural diversity but forest trees of respectable size had evolved. Some of these early and mid-Devonian fossils seem to represent ancestral members of the lycopod (club moss) and articulate (horse-tail rush) lines; others may be regarded with some confidence as early members of certain fern families, and not a few are referred to as "early fern-like plants" whose relationships are unknown. Some may be the beginnings of the pteridosperms and some may represent dead ends in the stream of evolution, but the diversity, which increased year by year, points clearly to the fact that there were many lines of evolution which we are just beginning to untangle.

One of the more interesting assemblages of fossils from the Devonian and Carboniferous—one that may have some bearing on the evolution of early fern and pteridosperm groups—is the assemblage of the Coenopterid ferns. These are characterized by the simple stelar (woody) structure of their stems, a rudimentary distinction between stems and leaves, and a tendency (at least in some of them) to produce the sporangia in rather massive aggregates. Botanists, for good reasons, attribute a good deal of importance to reproductive organs in establishing systems of classification, and the coenopterids display a considerable degree of diversity in the structure of their spore-producing organs.

According to the standards that we use in classifying modern plants, several extinct families are represented in these fernlike assemblages of the Devonian and the Carboniferous. The significance of this diversity is that there is an abundant "ancestor potential" for the seed plants. A few of these fossils combine characters that are more advanced than anything associated with true ferns, yet they fall short of the seed-plant level. Charles B. Beck, a leader in the discovery and interpretation of these plants, has proposed (*14*, *15*) the group name Progymnospermopsida—a name which implies that the plants immediately preceded the early seed plants.

I consider one member of this group in some detail instead of attempting a cursory survey of the half dozen or more genera that are included, particularly since their relationships are not entirely clear.

For more than a century, fernlike leaves assigned to the genus *Archaeopteris* have been known from Upper Devonian horizons in the northeastern

United States, from the Gaspé region of Canada, from Ireland, and from such Arctic sites as Ellesmere and Bear Islands. The leaves attain a length of about 1 meter and consist of a central rachis (midrib) with primary branches departing in two rows. These, in turn, bear leaflets that in some species are nearly entire, wedge-shaped, and about an inch long and in other species are quite strongly divided into slender lobes. On some of the primary branches these leaflets or pinnules are replaced by rather dense rows of elongate spore sacs. Very few of the 25 or 30 recorded species of *Archaeopteris* have afforded critical information on the spore contents, but in 1939 C. A. Arnold (*16*) made the important discovery that a species from Pennsylvania (*A. latifolia*) was heterosporous—that is, the plant bore two kinds of sporangia. The sporangia are all about 2 millimeters long, but some are 0.5 millimeter in diameter while others are more slender, about 0.3 millimeter in diameter. The slender ones contain about 100 spores, each approximately 35 microns in diameter, while the larger ones contain 8 to 16 spores, each some 300 microns in diameter. The most exciting development in our accumulating knowledge of this plant came in 1960 when Beck announced (*14*) that he had found a partially petrified stem 3 centimeters wide bearing several *Archaeopteris* fronds. The anatomy is that of *Callixylon*, a widely distributed Upper Devonian genus known to us from petrified stems some of which are reported to be as much as 1½ meters in diameter. The wood structure of *Callixylon* is quite like that of some of the coniferales, and it had been generally regarded as a seed plant, but no fossil seeds of *Callixylon* had been found.

It is thus evident that we have in the "new *Archaeopteris*" a plant that is neither fern nor seed plant. It is probably incorrect, as Beck emphasizes, to associate the plant in any way with the ferns. He considers that the Progymnospermopsida represent "a major group of pteridophytes from which one or more groups of gymnosperms has evolved" (*15*). And he adds, "I believe that *Archaeopteris* was not derived from any group which could reasonably be called a fern. . . ."

The *Archaeopteris*-*Callixylon* complex, like the other plants included in the Progymnospermopsida, presents both problems and answers. For example, were all the *Archaeopteris*-type leaves borne on stems with *Callixylon* anatomy? How many species of *Archaeopteris* were heterosporous? Did any of them come closer to the seed-plant level than *A. latifolia*?

A notable feature in the several other generic entities that are included in the group is the presence of a cambium, the tissue that is responsible for the more or less continuous production of secondary wood. A cambium is characteristically found in the seed plants but not in the ferns. A good deal remains to be learned of the reproductive structures of these fossils, and there is at present no positive evidence that they are directly ancestral to the plants from the Lower Carboniferous of Scotland that are known from their very primitive seeds. In a general way, however, great strides have been made in understanding the nature of early seed plants and their origins; there is reason to hope that our knowledge of this critical phase of plant evolution will expand in the near future (*17*).

General Summary

Recent discoveries of fossils from the Lower Carboniferous and the Upper Devonian reveal primitive seed plants and advanced pteridophytic ones, respectively, that bring us much closer to understanding the origins of the former. The Lower Carboniferous plants are represented by a series of primitive seeds in which the integument originated as an enclosing ring of filaments; in some of these seeds the distal end of the nucellus is modified to aid in gathering pollen, a modification that was apparently lost when a more efficient integument, and the pollen-drop mechanism, evolved. A secondary enclosing ring of branchlets has been demonstrated in some species; this formed the cupule, which may be the progenitor of the angiosperm seedpod. In late Devonian horizons pteridophytic plants have been found with pronounced cambial activity and other advanced features, and these may be ancestral to the earliest seed plants.

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17. Many investigators in addition to those whose work is cited have contributed directly and indirectly in bringing paleobotanical knowledge to its present level. I especially thank Ellen K. Lissant for preparing the drawings. Her careful attention to dimensions and proportions has produced what I believe are drawings that accurately depict the plants' organs, so far as one can judge from the fossil remains.