ARCHAEOSPERMA ARNOLDII—A CUPULATE SEED FROM THE UPPER DEVONIAN OF NORTH AMERICA

BY

JOHN M. PETTITT and CHARLES B. BECK
Department of Botany, The University of Michigan

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JOHN M. PETTITT[1] and CHARLES B. BECK[2]

Department of Botany, The University of Michigan

ABSTRACT—A new seed, *Archaeosperma arnoldii,* n. gen. and n. sp., from the Upper Devonian of North America, provides evidence for the existence of gymnospermous plants in pre-Mississippian times. This discovery is significant in relation to the origin and evolution of the seed habit.

INTRODUCTION

IN AN EARLIER PUBLICATION (Pettitt & Beck, 1967) we briefly reported the occurrence of fossils which demonstrate the existence of seed plants in the Upper Devonian. The purpose of the present paper is to present a formal description of the fossils and a more detailed discussion of their possible significance and bearing on the origin and evolution of gymnospermous seeds.

Arnold (1935) reported cupule-like structures from the Upper Devonian (Oswayo Formation, Famennian Series) of Northern Pennsylvania. The fossils, which he likened to small detached seed cupules, were associated with vegetative and fertile *Archaeopteris.*

Arnold described the cupule-like structures as borne in pairs on forked pedicels, each cupule being about 10 mm long measured from the point of bifurcation of the pedicel, and composed of 4 or 5 long, tapering prongs (Arnold, 1935). The close association of the cupules with *Archaeopteris* led him to speculate that they might belong to that plant. In 1939 Arnold showed unquestionably that the *Archaeopteris latifolia* specimens from Port Allegany were free-sporing and heterosporous and the discovery led him to change his view with regard to the possible connection of the cupules with *Archaeopteris* (Arnold, 1948).

The discovery of these fossils that resembled the cupules of some Mississippian and Pennsylvanian pteridosperm seeds raised the probability of the presence of pre-Mississippian

seeds, but structures identifiable as seeds were not found associated with the cupules (Arnold, 1948, p. 451).

TECHNIQUE AND PROCEDURE

From two slabs of fossiliferous shale from Arnold's original collection, four cupulate pairs were transferred to glass slides following the standard balsam transfer procedure (see Lacey, 1963). The only modification of the method was the substitution of the thermoplastic cement "Lakeside 70" for Canada balsam as the transferring medium. After the completion of acid treatment the transfers were washed in water and any adherent particles of mineral were cleaned away with fine tungsten needles.

One of the seed cupules (similar in appearance to that in plate 2) was removed from a transfer and treated with Schulze's solution (nitric acid and potassium chlorate). The oxidation process was closely observed with a binocular dissecting microscope. Immersion in the oxidizing solution caused the cupule to disintegrate and as this occurred a single megaspore tetrad was released (plate 5, figs. 1, 2). The megaspore tetrad remained in the Schulze's solution for several hours, was then washed in water, extracted in dilute ammonium hydroxide, washed again and mounted in glycerine jelly.

The tetrad comprises a large, axially elongated, presumably functional megaspore some 4.5 mm long and 2 mm in greatest width and two or possibly three very much smaller, pre-

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sumably abortive spores situated at one end (the apical end) of the large spore.

The exine of the functional spore is thinner at the apical end than in the middle and thickens noticeably towards the basal end. Covering the entire tetrad and closely associated with the spore exines is a thin tapetal membrane in places bearing the outlines of a cellular reticulum. The cells of the reticulum are polygonal in outline and their pattern is most distinct in the middle region of the functional spore and rather less distinct at the extreme apical end. At the basal end of the large spore the tapetal membrane is extended and forms a short stalk-like projection. The megaspore is not involved in the formation of this projection.

Additional megaspore tetrads similar to that released from the seed cupule were obtained from hydrofluoric acid digestions of the seed-bearing sediment. The tetrads so obtained were cleared and mounted as described above.

Because of the complete disruption of the fossil during the maceration procedure the location of the megaspore tetrad within the seed-cupule complex could not be ascertained. We suspected, however, that the cupule appendages completely enveloped and obscured from view a seed positioned as those in text-figure 1. As the correct interpretation of the fossil as a seed-bearing cupule rested on the recognition of a megaspore tetrad within the structures now identified as seeds, the spiny integumentary covering of one of the specimens was removed with fine needles (plate 4, figs. 1, 2). This procedure revealed the outline of a structure situated towards the base of the seed which from its shape, relative size and position we identify as the large spore of a megaspore tetrad. Text-figure 3 is a diagrammatic representation drawn from the dissected seed, and in the drawing the unshaded oval body occupying the basal two-thirds of the seed is the functional megaspore. The large number of free integumentary lobes shown at the apex of the seed in the drawing results from two seeds overlying one another in this position. The integumentary lobes of both specimens have been splayed out by compression.

The reconstructions shown as text-figures 1 and 2 are based on these interpretations and on our understanding of the structure of the cupule and seed.

SYSTEMATIC DESCRIPTION
Class GYMNOSPERMAE

ARCHAEOSPERMA Pettitt & Beck n. gen.

Type species.—Archaeosperma arnoldii Pettitt & Beck n. sp.

ARCHAEOSPERMA ARNOLDII Pettitt & Beck n. sp.
Pls. 1–5; text-figs. 1–3

Combined diagnosis.—Two-seeded cupules borne in pairs. Common axis branched dichotomously into two cupule axes, cupule axes branched in plane at right angles to first dichotomy and at different levels distally, each producing two inner, short, seed-bearing axes or pedicels and two outer axes bearing a series of free cupular segments. Free cupule segments dorsiventral, bifurcated, extended distally into two long, tapering tips. Seed integument spiny, especially at basal end, lobed at micropylar end, containing single tetrad of megaspores, one spore of tetrad axially elongated, the other three small, abortive, arranged at apex of large spore.

Types.—Holotype, UMMP 16069. Paratypes, UMMP 57289.

Type locality.—Roadside exposure on Pennsylvania route 59, six miles west of Port Allegany, McKean County, Pennsylvania. Oswayo Formation (Famennian Series), Upper Devonian.

Cupule.—All four specimens of *Archaeosperma* disclosed by transfer show the morphology of the cupule. The most complete cupular specimen of the four, however, is that shown on plate 1. The specimen is 15 mm in total length and shows that the dichotomy of the common axis gives rise to two second order branches or cupule axes of equal width. At a

EXPLANATION OF PLATE 1

Archaeosperma arnoldii. This is the most complete cupular specimen. Dichotomy of the common axis gives rise to two cupule axes. Dichotomy of each cupule axes is at right angles to that of the common axis and produces the seed stalks or pedicels (P) to the inside, and outer branches bearing dorsiventral, bifurcate appendages with attenuate tips. Scale line corresponds to 5 mm. Paratype, UMMP 57289.

PLATE 1

PLATE 2

position about 1.5 mm above the dichotomy, the cupule axis on the right dichotomizes in a plane at right angles to that of the first division to produce two short inner branches or pedicels, and two somewhat stouter outer branches. Immediately distal to this dichotomy, each outer branch shows evidence of division into a number of (probably four) separate, dorsiventrally flattened appendages. That these appendages are individual and separate elements becomes more apparent farther from their origin. Some distance above the origin, each appendage bifurcates and extends distally as two long, tapering projections. The appendages are 1.0–1.3 mm wide immediately below the point of bifurcation and narrower at their origin.

The left cupule axis produced by the dichotomy of the common axis divides in the same manner as the right, but the division occurs at a slightly higher level. Consequently, the pedicels on the left cupule are somewhat above the level of the corresponding pedicels on the right and the tips of the terminal appendages on the left extend beyond those on the right (plate 1; text-figure 1).

In our interpretation of the fossils, the axes produced by the dichotomy of the common stalk together with the terminal aggregations of flattened appendages represent two seed cupules and the pedicels or seed axes arise by division of the cupule axes.

Although the seeds are missing from the specimen in plate 1, their position of attachment can be clearly seen (P) and would correspond to the same position in the cupule (described below) in which the seeds are retained.

A second specimen, comprising part of a detached cupule, is illustrated on plate 2. Although incomplete, the specimen shows the form of the free cupule appendages and the position of the seed stalks (P) in relation to them. The specimen corresponds to the left terminal part of the cupule on plate 1, and the crushed remains of the right cupule of the pair can be seen to the right of the figure. The seed stalk (P) of the right cupule is also evident.

Seeds.—The relationship of the seeds to the cupules is shown in the transfer illustrated on plate 3, The specimen has been compressed

in a way such as to separate the cupule elements and reveal the position of the enclosed seeds. The separated cupule elements are seen to the right and left of the figure and we interpret these as belonging to a pair of cupules produced by the dichotomy of a common axis in exactly the same way as those described above.

The four seeds are more or less flask-shaped structures and lie to the inside of the cupule appendages. The position of attachment of the seeds to the four pedicels and the origin of the pedicels inside and near the base of the elements of the cupules is clearly seen at the bottom of the picture (P). The pedicels in this specimen are in precisely the same position and have the same relationship to the cupular elements as the pedicels in the less compressed and more complete cupular specimens first described.

The seeds are about 4.2 mm in length and 1.4–1.7 mm wide at their widest point about mid-way along their length. On the outer surface of the integument is a covering of small spines. These are more densely crowded at the basal ends of the seeds than at the micropylar ends (plate 3; plate 4, figures 1, 2).

At the micropylar end the integument is divided into a number of separate lobes which come together at the seed apex to form a definite micropyle. The exact number of lobes involved is unclear, but there seem to be at least four. A series of low ridges separated by shallow furrows is discernible on the main body of the seed which match the micropylar lobes in position and number. The ridges are more apparent at the chalazal end of the seed, diminishing in amplitude toward the micropyle (text-fig. 1).

A shallow but distinct notch at the chalazal end of the seed marks the area of attachment of the seed to the pedicel and probably represents the point of abscision of the mature seed from the pedicel.

Isolated megaspore tetrads.—Some twenty-five megaspore tetrads similar in form to that released from the seed were obtained by bulk hydrofluoric acid digestion of the seed-bearing sediment (plate 6, figures 1–5).

There is some variation in the size of the tetrads, the smallest being 1.0 mm long and 0.5 mm wide and the largest is more than 3.8
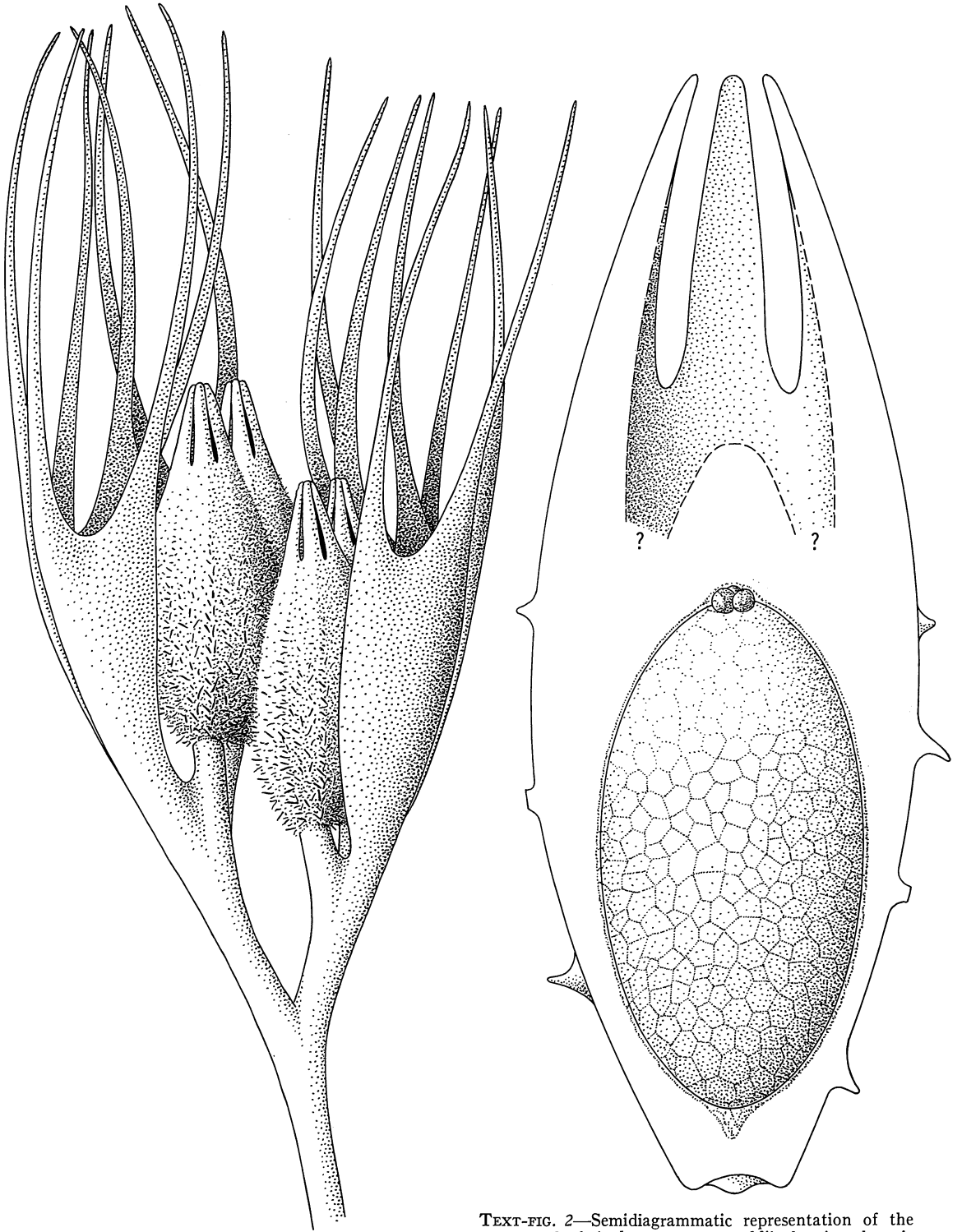
TEXT-FIG. *1*—Reconstruction of cupule complex of *Archiaeosperma arnoldii*. The cupules are arranged in pairs, and each cupule contains two seeds. Based on holotype and paratypes.

TEXT-FIG. *2*—Semidiagrammatic representation of the seed of *Archaeosperma arnoldii*, showing the micropylar lobes of the integument and the position of the megaspore tetrad within the seed. The elevation (dashed line) above the megaspore tetrad represents the supposed position of the nucellar apex.

mm long and 1.7 mm wide. The size of the majority of tetrads, however, is between these two extremes and they are, therefore, somewhat smaller than that macerated from the seed.

A complete tetrad consists of one large functional megaspore with three smaller abortive spores arranged at the apical end (plate 6, figures 1, 2). The tetrads are covered by a thin tapetal membrane bearing a clear cellular pattern (plate 6, figure 4), and the membrane in some specimens is extended basally into the short stalk-like projection previously mentioned (plate 6, figure 1).

A few specimens clearly show a triradiate mark at the apical end of the large functional spore when the abortive spores are missing (plate 6, figure 3). Occasionally, the laesurae of the triradiate mark can be detected between adjacent abortive spores of the tetrad (plate 6, figure 2).

Some of the tetrads have badly corroded triradiate miospores that are different from the aborted spores adhering to the exine of the large spore. The miospores are most frequently, although not invariably, attached to the apical region of the megaspore.

A thin and rather incomplete cuticle bearing a pattern of cells more or less longitudinally aligned with respect to the tetrad can be detected external to the tapetal membrane and investing the large spore in some specimens (plate 6, figure 5). If these tetrads were originally contained within seeds, as seems probable, this cuticle could be the cuticle of a nucellus, and its presence would indicate the absence of fusion between the nucellar and integumentary tissues in the region of the megaspore.

Discussion.—Stockmans (1948) described some fossils from the Upper Devonian of Belgium as *Moresnetia zalesskyi* and *Xenotheca bertrandi* which show some resemblance to *Archaeosperma*. Professor Stockmans kindly loaned us a number of his specimens for examination and balsam transfer. Two specimens from the Stockmans' collection (plate 5, figures 3, 4) were photographed before transferring.

There is obvious similarity between some features of *Moresnetia zalesskyi* and *Archaeosperma*. In the former, as Stockmans (1948) describes it, a dichotomously branched axis gives rise in the terminal region to a number of free, more or less flattened segments. Each segment is deeply divided into two "lobes" which extend distally as long narrow projections. In these respects they are exactly like the cupule segments in *Archaeosperma*. But whereas in *Archaeosperma* the free elements of the cupule terminate the outer axis produced by the dichotomy of the cupule axis they are not invari-

ably in only this position in *Moresnetia*. In some specimens of *M. zalesskyi* the common axis divides to give rise to two branches of unequal length, the shorter of which is directly terminated by the appendages. The longer branch, however, itself divides into two short but more or less equal axes, and it is each of these that is terminated by the free segments.

Notwithstanding the difference in some specimens, the evident structural resemblance between *Moresnetia* and the cupule of *Archaeosperma* cannot be lightly dismissed. Although the transfers of *Moresnetia* did not reveal structures which can be securely identified as seeds we do not feel that this necessarily precludes their presence. Our failure to detect seeds might well be a circumstance of the light metamorphic
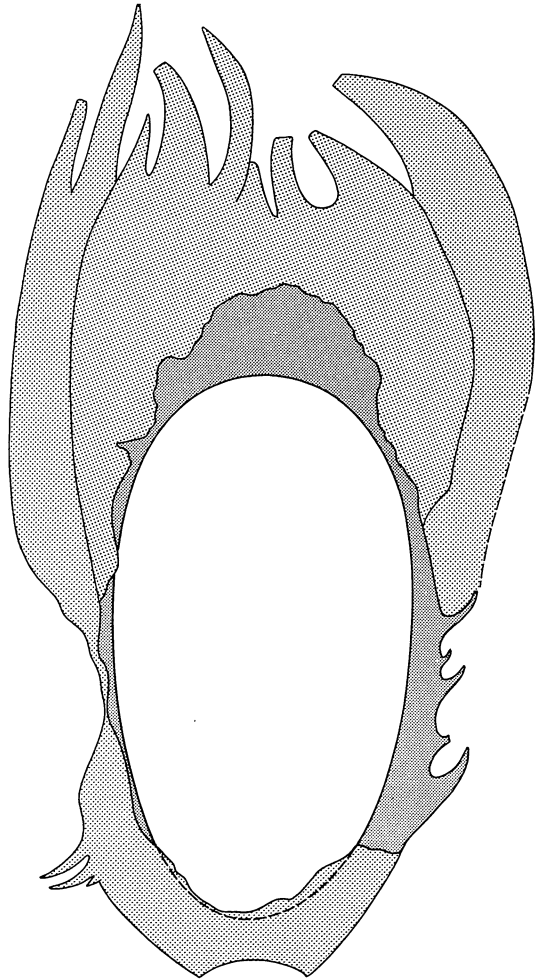
TEXT-FIG. *3*—Diagram of the dissected seed of *Archaeosperma arnoldii*. The unshaded body in the center is the large spore of the megaspore tetrad. Compare with plate 4, figures 1, 2. For full explanation see text.

alteration of the sediment in which the fossils occur and of the fossils themselves. It is our opinion that more satisfactorily preserved specimens might well show *Moresnetia* to be seed-bearing.

Xenotheca bertrandi is a cupule-like organ composed of a number of tapering segments some 8–10 mm long (Stockmans, 1948). Stockmans describes the cupule appendages as fused at the basal end, but this is a feature that is not altogether certain in our transferred specimens. The cupules are borne at the ends of long narrow axes and seemingly lack contents. Their true nature remains undetermined.

The structural organization of the cupule of *Archaeosperma* is superficially similar to the cupules of some Lower Carboniferous (Mississippian) ovules, those, for example, of *Eurystoma angulare* and *Stamnostoma huttonense* (Long, 1960a, b).

The seeds of *E. angulare* are borne on a reduced pedicel which possibly represents one of four main branches produced by repeated dichotomy. The branched structure was apparently curved round a single seed, the whole forming a rudimentary type of cupulate organ (Long, 1960a).

In *S. huttonense* the nature of the investing structure is much more cupule-like in the generally accepted sense and here, again, it is derived from a system of relatively simple cylindrical axes by repeated dichotomy. The seeds, of which there were four in each cupule, are borne near the dichotomies of the four principal lobes (Long, 1960b).

The free cupule elements in the Devonian seed cupule cannot satisfactorily be explained on the basis of derivatives directly from dichotomous divisions of the cupule axis in the manner of *S. huttonense*. Rather, the available evidence would suggest that they are probably foliar in nature, that is, that each cupule is formed from an aggregation of up to four leaf-like organs which surrounded the seeds. If this is the case, it calls into question the supposition that the cupules of cupulate ovules have evolved directly from a system of dichotomously branched axes.

The structure of the seed of *Archaeosperma* is also similar to that of some Lower Carboniferous genera although one feature of the Devonian seed, the covering of spines on the integument, is not known in seeds of Mississippian age.

Although a nucellus has not been proven its presence in *Archaeosperma* is suggested in the reconstruction (text-figure 2). In this, the position of the supposed nucellar apex is shown by a broken line below the level at which the integument lobes are connate, and it is represented as simply a centrally-placed elevation that is not in any way modified into salpinx or lagenostome. The question mark between the nucellar apex and the integument in the drawing indicates our uncertainty of the structural relationship between the nucellus and integument. It would be of greatest interest to know if and how the nucellar apex was modified for pollen reception in these seeds and at exactly what level the tissues of the nucellus and integument were adnate.

The occurrence of a complete tetrad of spores in a tatrahedral arrangement in *Archaeosperma* is a feature which is shared by several seeds of Lower Carboniferous age (Pettitt, 1966b). In both the Devonian and Lower Carboniferous seeds the tetrad is composed of a single, large, presumably functional spore and three smaller, presumably abortive ones. In all cases the tetrads are entirely surrounded by a thin membrane of tapetal origin which bears the outlines of a cellular reticulum, and in some specimens the tapetal membrane forms a short stalk-like projection at the distal end of the functional spore.

The isolated megaspore tetrads recovered from the sediment in which *Archaeosperma* was contained are essentially similar to those described from the Upper Devonian of Quebec as *Cystosporites devonicus* (Chaloner & Pettitt, 1964) and could appropriately be included in this species. We do not think it begs the question to suppose that the tetrads associated with *Archaeosperma* were at one time contained within seeds of that genus and that they were released from the enclosing tissues by damage to the seeds during either fossilization or chemical digestion of the sediment. The size variation within the isolated tetrads could be explained as differences of seed maturity or, more prob-
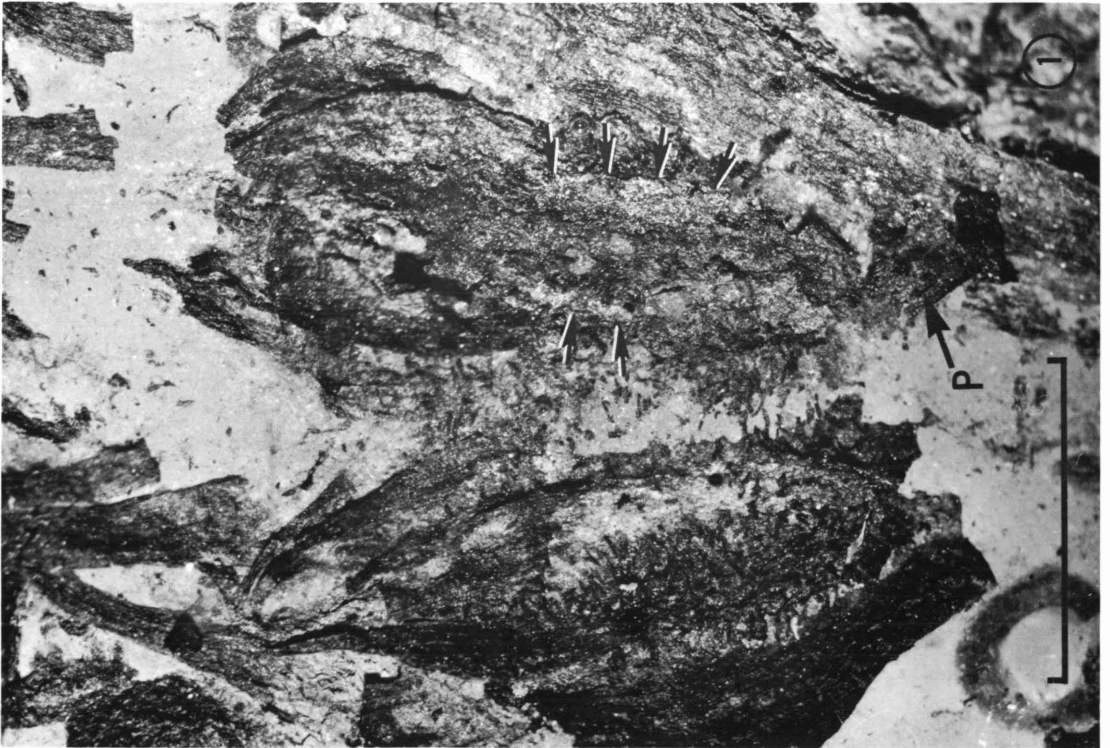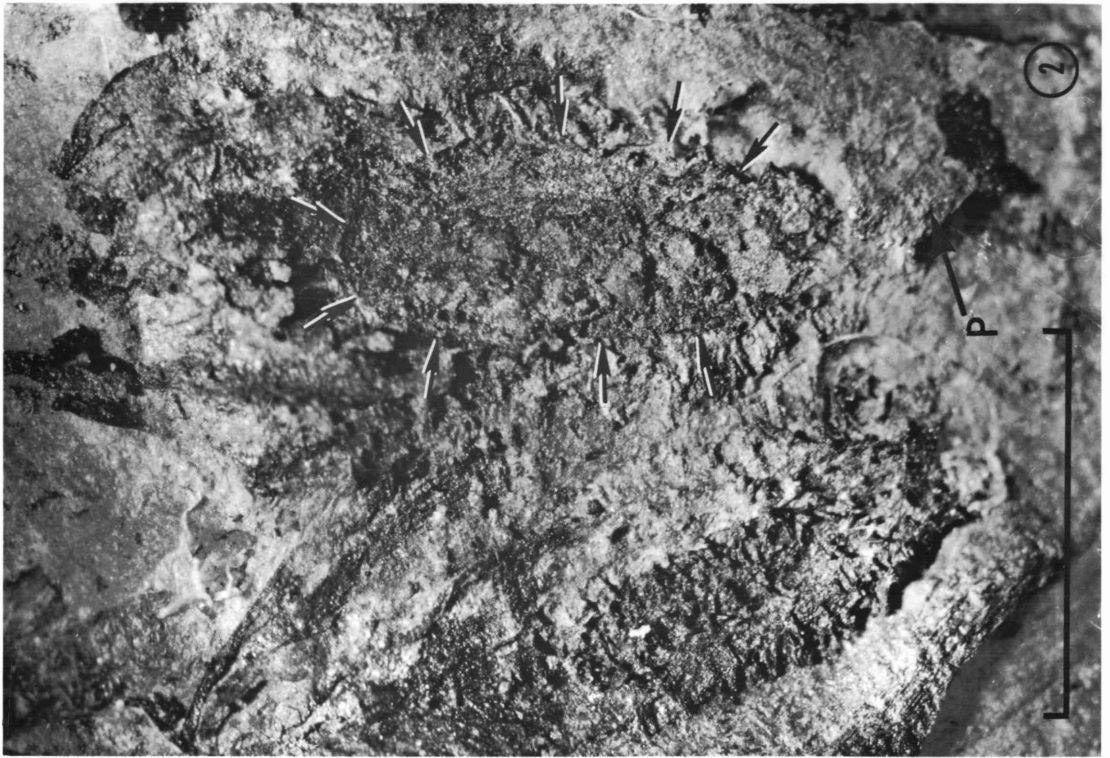

PLATE 3

PLATE 4

ably, as abortive development of the gametophyte or the entire ovule (Pettitt, 1966b). The presence of a cuticle, possibly representing a nucellus, associated with some of the tetrads adds to the interest of finding precisely how and in what they were originally enclosed.

EVOLUTIONARY SIGNIFICANCE OF *ARCHAEOSPERMA*

The occurrence of *Archaeosperma* provides definite evidence for the presence of gymnosperms in the Upper Devonian and we are faced with several questions relating to the parent plant of the seed, the phylogenetic history of the reproductive structure and the phylogenetic significance of *A. arnoldii* in the evolution of the seed habit.

It is not impossible that *A. arnoldii* is the female reproductive structure of one of the plants now included in the progymnosperms. The progymnosperms comprise those plants of Upper Devonian and Lower Carboniferous age which possess typically pteridophytic reproductive structures and anatomical characters that are mainly gymnospermous (Beck, 1960). Among the Devonian genera included in the class at the present time are *Archaeopteris* Dawson, and *Tetraxylopteris* Beck. These plants are of especial interest because they are the only progymnosperms in which both the morphology of the fructification and the anatomy of vegetative axes are known with a great measure of certainty.

The association of *Archaeosperma* and isolated megaspore tetrads assignable to *Cystosporites devonicus* with heterosporous *Archaeopteris latofolia* at the Port Allegany locality should be noted. A species of *Barinophyton*—probably *B. citrulliforme*—also occurs at the locality, and this too has proven to be heterosporous as Arnold (1947) had suggested. *Cystosporites devonicus* tetrads also occur together with heterosporous *Archaeopteris* at Escauminac Bay, Quebec (Chaloner & Pettitt, 1964). These records raise the question of whether the association of *Archaeosperma* and *C. devonicus* with *Archaeopteris* may be more significant than is at the moment apparent.

Some species of *Archaeopteris* are known to be free-sporing and heterosporous (*A. latifolia,* Arnold 1939 & *A.* cf. *jacksoni,* Pettitt 1965). Krausel & Weyland (1941) have synonomyzed *A. jacksoni* with *A. halliana.* Others (*A. macilenta,* Beck 1960 & *A. fissilis,* Andrews, Phillips & Radforth 1965) are thought to be free-sporing and homosporous because only one size of spore (44–68 μ diameter in *A. macilenta,* 60 μ in *A. fissilis*) was found in macerations of the sporangia. However, Beck (1962) has suggested that the failure to demonstrate heterospory in his specimens of a *A. macilenta* could be due to the species being dioeceous or having microsporangia and megasporangia on different branches. The same interpretation could be advanced for the *A. fissilis* material investigated by Andrews *et al.* (1965).

Alternatively, it is equally possible that *A. macilenta* and *A. fissilis* were not free-sporing heterosporous plants, but gymnospermous seed plants. We see no *a priori* reason to preclude this suggestion. The explanation of dioecism advanced by Beck (1962) to explain the absence of megaspores in *A. macilenta* could also be used to explain the absence of attached seeds in the plant.

Working on this hypothesis, the "microspores" of the presumed dioecious species of *Archaeopteris* would be botanically, pollen grains, and the megaspores would be seed megaspores enclosed within an integument, similar perhaps to *Archaeosperma.* It is known that the pollen grains (so-called prepollen) of some early Carboniferous gymnospermous seed plants are morphologically and structurally indistinguishable from triradiate miospores (Halle, 1933; Pettitt, 1966a, b). A number in fact had, and presumably germinated by means of, a proximal triradiate suture, just as in the spores of many modern pteridophytes. Such pollen is only known to be pollen because the corresponding megaspores were contained within seeds as seed megaspores. The spores of *A. macilenta* cannot be separated from the triradiate prepollen of some Carboniferous pteridosperms on purely morphological criteria alone. The resemblance extends even to similarity of exine ornamentation of some forms
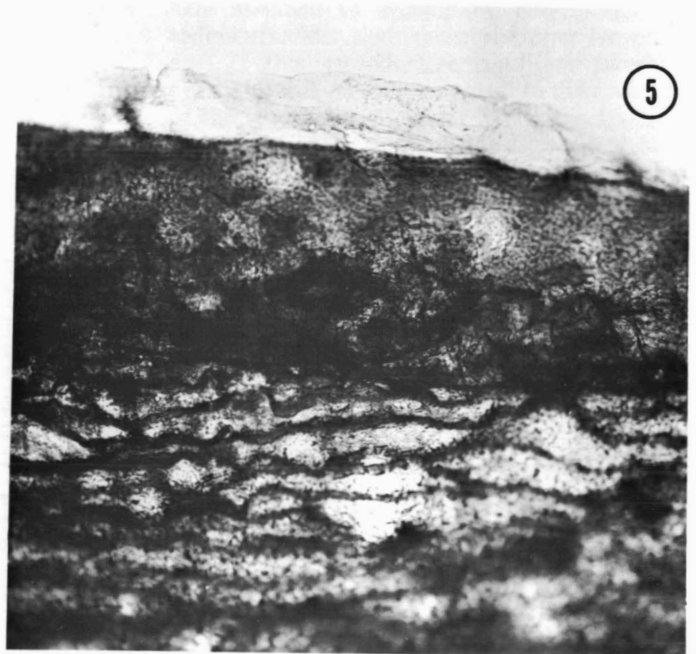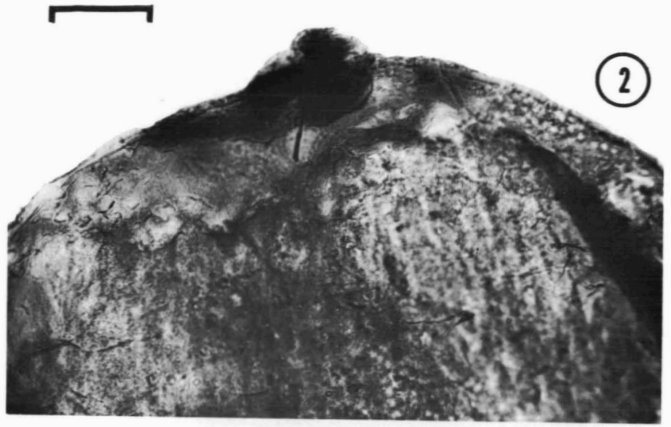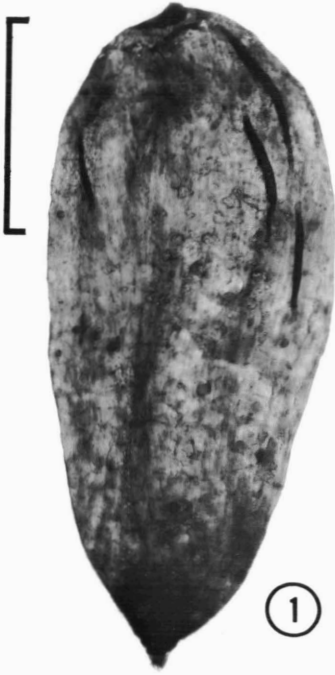

PLATE 6

morphological heterospory. As Thomson (1927) has suggested, such a reproductive condition could be directly ancestral to free-sporing heterospory on the one hand and to the seed habit on the other.

Finally, it should be noted that Read (1955) has synonymized *Archaeopteris latifolia* with *Rhacopteris latifolia* on the basis of some specimens he found in the lower part of the Pocono near Altoona, Pennsylvania. Characteristic Mississippian genera *Adiantites, Rhodea Alcicornopteris* and *Lepidodendropsis* were associated with the *Rhacopteris*. Read believes that the fossils included in *A. latifolia* by Arnold (1939) are more correctly assigned to *Rhacopteris* because of the close agreement of the pinnule form with certain species of that genus, and his transference of *A. latifolia* to *Rhacopteris* extends the known age of *Rhacopteris* from the Mississippian into the Upper Devonian.

The recognition of *Rhacopteris* in the Upper Devonian would effectively bring together the Devonian genus *Archaeopteris* and the morphologically very similar plants of the Lower Carboniferous.

We know from Arnold's (1939) investigations that the Upper Devonian plants Read assigns to *Rhacopteris latifolia* are free-sporing and heterosporous. To judge from Read's illustrations, the fructification he considers as possibly that of *R. latifolia* from the Pocono (Read, 1955, plate 18, figure 2) appears to be exactly similar to those described by Arnold. We do not, however, know the contents of the sporangia of Read's specimen.

The fructifications of the other Mississippian species of *Rhacopteris* are unknown. Numerous seeds have been discovered in association with genera of similar vegetative morphology in the Lower Carboniferous of Great Britain. It is at least possible, therefore, that some species of *Rhacopteris* were seed-bearing plants and that the line to which *Archaeosperma* belongs represents an intermediate linking plants such as *Archaeopteris* and *Rhacopteris* of the Devonian with gymnosperms of the Mississippian.

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EXPLANATION OF PLATE 6

FIGS. *1–5—Cystosporites devonicus.* Specimens released by bulk digestion of seed-bearing sediment. *1,* an entire tetrad. *2,* apex of the same specimen, showing the three abortive spores, their relationship to the large functional spore, and a commissure of the triradiate mark. *3,* apex of one specimen from which the abortive spores are missing, showing the triradiate mark. *4,* details of the tapetal membrane which surrounds the tetrad. *5,* part of the surface of the functional megaspore of one tetrad, showing the thin cuticle bearing a pattern of longitudinally-aligned cells (center of the picture) which overlies the tapetal membrane. Scale line in figure 1 corresponds to 1 mm; that in figure 2 to 100 μ.

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