A NEW SPECIES OF *AULACOTHECA* (PTERIDOSPERMALES) FROM THE MIDDLE PENNSYLVANIAN OF IOWA

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ABSTRACT. *Aulacotheca iowensis* sp. nov. is described from the Middle Pennsylvanian of Iowa; it is distinct from previously described forms in synangial dimensions, number of sporangia per synangium, and size range of pollen grains. The Iowa material demonstrates that pollen organs of the *Aulacotheca* type were borne in large numbers on ultimate axes of either an entirely fertile frond or portion of frond lacking planated foliar structures. Orientation of the synangia suggests that the fertile regions were three-dimensional and bushy prior to fossilization.

THE genus *Aulacotheca* was instituted by Halle (1933) for certain synangiate pollen organs believed to have been produced by medullosan pteridosperms. The exact nature of remains assigned to this genus was entirely problematical until the work of Halle, and included leaves (see, for example, White 1900) and seeds (Kidston 1890–8, Crookall 1929). Older generic designations of remains now assigned to *Aulacotheca* include *Whittleseya*, *Rhabdocarpus*, and *Holcospermum*. Four of the six previously described species (*A. elongata* (Kidston) Halle 1933, *A. hemingwayi* Halle 1933, *A. campbelli* (White) Halle 1933, *A. idelbergeri* Halle 1933, *A. dixiana* Hemingway 1941, and *A. hallei* Hemingway 1941) occur in the Upper Carboniferous of Great Britain. *Aulacotheca idelbergeri* occurs in continental Europe in strata designated as Westphalian A. In North America, *Aulacotheca* has been reported from the Pottsville Series of the Appalachian region (White 1900), the Pocahontas and New River Beds of West Virginia (Jongmans 1937), and the Michigan coal basin (Arnold 1949). Arnold (1949) has discussed the occurrence of the genus in North America and has compared this material, which is referred for the most part to the species *A. campbelli*, with that from Europe.

Methods of study. Elucidation of the various features of the specimen was carried out by excavation of the individual synangia to insure completeness. Isolated synangia were treated with either Schulze solution or dilute sodium hypochlorite (Clorox) to remove dark occluding materials. Subsequent to these treatments the synangia were carried through a standard dehydration series and mounted between coverslips so that both sides of the synangium could be examined and photographed at relatively high magnifications. Attempts to separate the individual pollen grains in the adherent masses were unsuccessful so that individual pollen grains were observed and measured within the

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Figs. 1–5. *Aulacotheca iowensis* sp. nov. 1, Over-all view of one-half of specimen (part) showing general organization; 1324a, ×1. 2, Over-all view of counterpart of specimen after additional excavation had been carried out; 1324b, ×2. 3, Two synangia apparently borne as a pair; 1324b, ×5·5. 4, Single synangium showing the narrow stalk; 1324b, ×8. 5, Isolated synangium after treatment with Schulze solution; Slide 2934, ×22.

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pollen masses. Measurements parallel and perpendicular to the long axis were carried out on a sample of 250 grains to determine the dimensional range, percentage distribution, and average dimensions of the pollen.

SYSTEMATIC SECTION

Order PTERIDOSPERMALES
?Family MEDULLOSACEAE
Genus AULACOTHECA Halle 1933

Aulacotheca iowensis sp. nov.

Diagnosis. Fertile frond material lacking planated foliar structures, primary laterals apparently borne alternately and having numerous groups of stalked synangia along their entire lengths. Individual synangia about 5 mm. in length, 1·5 mm. in maximum width, and having either 3 or 4 pollen sacs. Pollen sacs with elongate pollen masses of adherent bilaterally symmetrical *Monoletes*-type pollen grains 88 (135) 165μ long by 44 (81) 121 μ broad.

Holotype. Specimen 1324a and b (part and counterpart), and slide preparations 2926 through 2980, Paleobotanical Collections, Department of Biological Sciences, University of Illinois at Chicago Circle.

Stratigraphic position. Clay pit approximately $\frac{1}{2}$ mile south-west of Redfield, Iowa (Sec. 5T 78N, R29W, Adel Quadrangle), Cherokee Group (Des Moines Division).

Age. Middle Pennsylvanian (Des Moines Series).

Description. Initial cleavage of the matrix combined with subsequent excavation for more complete exposure yielded an extensive mass of synangia approximately 8 cm. in length (Pl. 76, figs. 1, 2). The arrangement of the synangia suggests that the specimen consisted of a major axis bearing approximately 6 primary laterals. These laterals, apparently borne alternately along the major axis, bear the individual synangia. Little in the way of clearly definable remains of the major axis are preserved, but the presence of such a structure may be inferred from the orientation of the synangium-bearing laterals. Each bears a large number of synangia which are radially disposed in the matrix surrounding the position of the lateral axis. This apparent 3-dimensional disposition was presumably a feature of the plant in life and suggests that this portion of the frond was non-planated and probably had a rather bushy appearance. Synangia are stalked (Pl. 76, fig. 4) and in some instances borne in pairs (Pl. 76, fig. 3). Individual synangia are spatulate in outline, broadest just back of the tip, and gradually tapered toward the base into a delicate stalk. Average dimensions of the synangia are 5 mm. long and 1·5 mm. in maximum width. Relatively few, somewhat distantly spaced dark lines run longitudinally along the synangia (Pl. 76 fig. 3) and apparently represent intervening walls between individual sporangia. As is seen in Pl. 76, fig. 3 and 4, these dark lines designate furrows that separate somewhat curved ridges. A number of representative synangia are shown in place in the matrix in Pl. 77, fig. 1.

Entire synangia consist of either 3 or 4 elongate masses of pollen (Pl. 76, fig. 5, Pl. 77, fig. 5). Each mass apparently represents the contents of a single sporangium, little else remains. In some instances, a thin layer of dark material is present covering

portions of the synangium (Pl. 76, fig. 5), which when cleared in Clorox consists of a single layer of extremely thin-walled cells that are axially elongate and have horizontally orientated end walls. Whether this tissue represents all or part of the sporangial walls, or is some sort of tapetal structure, is not known. Individual pollen masses illustrate that the sporangial cavities were relatively narrow in comparison to their lengths and reflected the exterior shape of the synangium in being broader near the tip (Pl. 77, fig.3) and gently tapering toward the base of the synangium. Disposition of the pollen within the masses (Pl. 77, figs. 3, 4) further illustrates that the sporangial cavities were probably circular in cross section rather than radially elongate. Material embedded in paraffin and sectioned did not provide any pertinent information concerning the central portion of the synangium.

Pollen grains of *A. iowensis* are similar to those found in a large number of pollen organs thought to have affinities with the Medullosaceae. Grains are bilaterally symmetrical, have a prominent suture on the proximal face (Pl. 77 fig. 2), and have lengths that range from 88 to 165 μ (text-fig. 1) and breadths from 44 to 121 μ. The percentage size distribution is shown in the text-figure. Average dimensions are 135 μ long by 81 μ broad (based upon 250 grains). The walls of the pollen grains are relatively thick (approximately 8–9 μ) and are essentially devoid of ornamentation although a few grains have an extremely faint punctation. In the dispersed form similar pollen would be assigned to the genus *Monoletes* Schopf, Wilson, and Bentall 1944.

Discussion. Information concerning published species is restricted to features of individual synangia although we can now suggest certain other features of fertile regions of *A. iowensis*. Of these species, *A. elongata* and *A. hemingwayi* have the most completely known synangia. In these forms the number of sporangia (8–9 in *A. elongata*, 9 in *A. hemingwayi*) and range of pollen dimensions are fairly well established.

Aulacotheca is extremely rare in occurrence in North America. Initially described under the name *Whittleseya campbelli* by White (1900) on the basis of material from several horizons within the Pottsville of the Appalachian region, North American material has subsequently been assigned to *Aulacotheca campbelli* (Arnold 1947, 1949) in most instances; however, Jongmans assigned material from the Pocahontas and New River Beds of West Virginia to *A. elongata* and *A. hemingwayi* (Jongmans 1937). Material from Eastwood, Michigan described under the name *A. campbelli* (Arnold 1949) is fairly well known and in this instance the number of sporangia per synangium is 6. Additional material described by Arnold from the Sewell Formation of West Virginia as *A. campbelli*, and the material originally studied by White has not been shown to have spores present nor has the number of sporangia per synangium been determined, although it appears that Arnold's estimate of 6 is probably correct in comparison with the better preserved material from Michigan. The number of sporangia is also not

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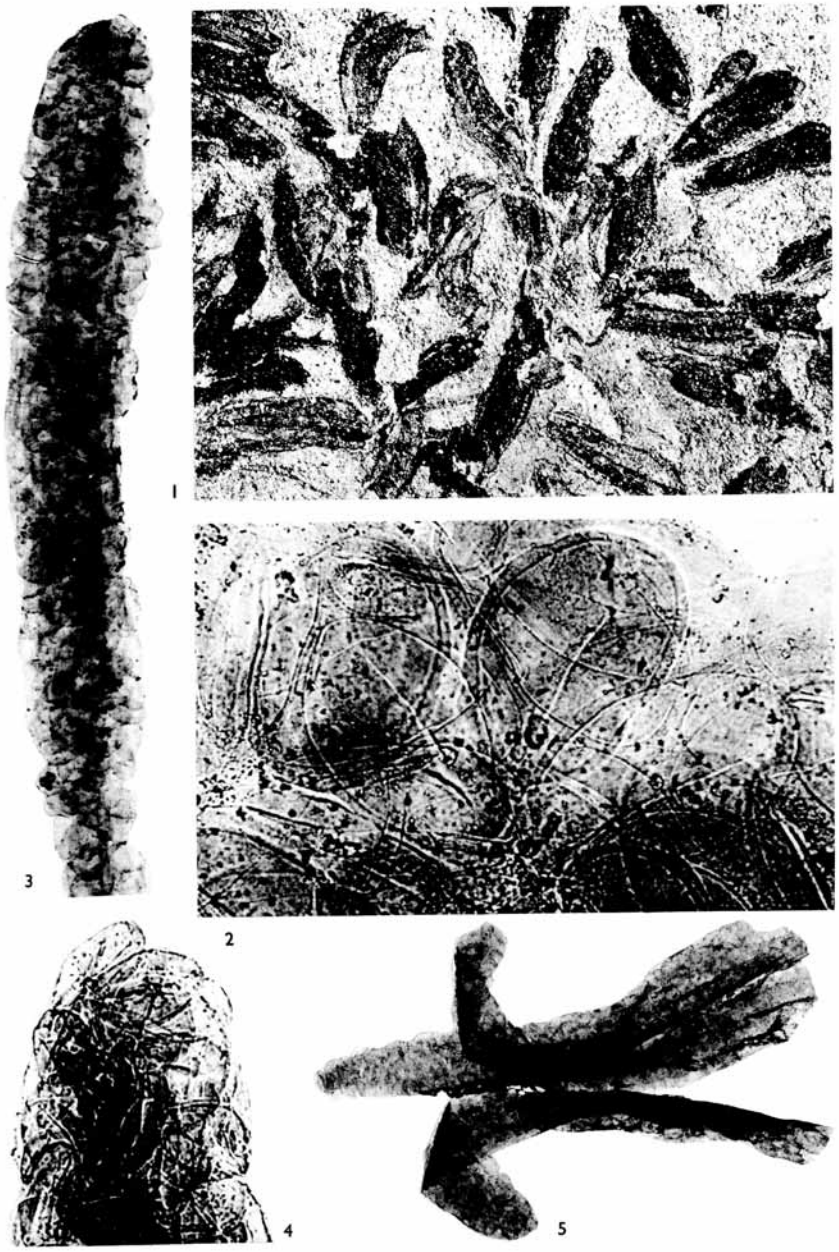
Figs. 1–5. *Aulacotheca iowensis* sp. nov. 1, Portion of specimen showing numerous representative synangia; 1324a, ×5·5. 2, Portion of pollen mass showing detail of individual grains; Slide 2928, ×300. 3, Individual pollen mass after treatment with dilute Clorox; Slide 2928, ×43. 4, Portion of pollen mass showing disposition of grains that suggests the tubular form of the pollen sac; Slide 2928, ×120. 5, Individual synangium having three pollen sacs partially separated; Slide 2926, ×22.



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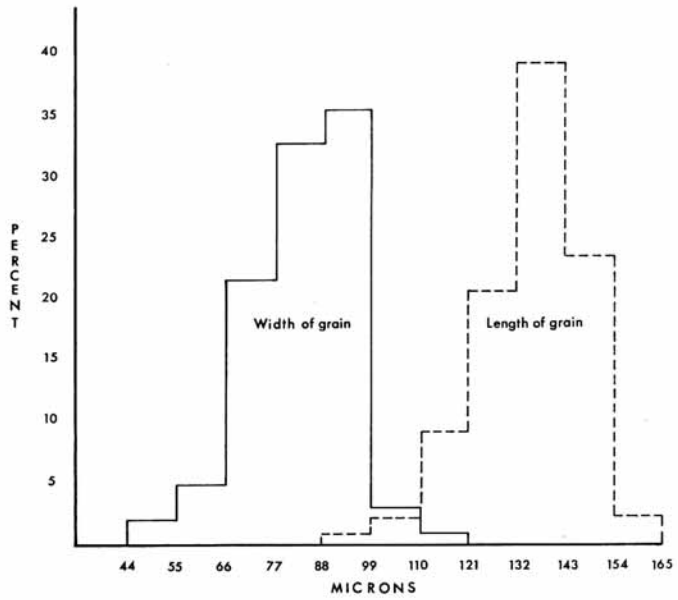
known in *A. dixiana* and *A. hallei*. Hemingway (1941) suggested that *A. Hallei* had 6 'loculi', but apparently believed them to be synangia rather than individual sporangia. *A. iowensis* with 3 to 4 sporangia per synangium has a lower sporangial number than any other species for which this number is well established. Evidence for either the presence or absence of a central hollow region is totally lacking, in so far as we can



TEXT-FIG. 1. *Aulacotheca iowensis* sp. nov. Histogram illustrating range and percentage distribution of pollen grain dimensions; based on a sample of 250 grains.

judge, for all of the species except *A. elongata*. In the latter Halle (1933) inferred a centrally placed hollow on the basis of the disposition of the spore masses after compression and on the lack of evidence of any relatively thick carbonized area in the centre of the synangium. In some instances, a longitudinal splitting of the flattened synangia into two halves has been used to suggest the presence of the central hollow area, and Halle seems to have been impressed with this feature of the material since it allowed a close comparison to be made with *Whittleseya*, in which a ring of fused sporangia surrounded a large central hollow area and made up a cup-shaped pollen organ that was open at the distal end. In cases where synangia have relatively large numbers of sporangia it can be argued from their disposition, as Halle did, that the sporangia originally formed a ring about a central sterile region, either hollow or of solid tissue. However, in forms such as *A. iowensis* where 3 or 4 sporangia are present, compression results in a disposition of the sporangia which does not permit determination of the exact nature of the central part of the synangium. Thus, largely through limitations of the material, most of the described species of *Aulacotheca* cannot be shown to exhibit

the full complement of features assigned to this genus by Halle in the original diagnosis (Halle 1933, p. 40). In practice, however, most material assigned to the genus shows a similar external form, evidence of slight longitudinal ribbing, and most often a toothed or lobed distal end. In this respect, material assigned to *Aulacotheca* is more or less indistinguishable from that placed in the genus *Boulaya* Carpentier (Carpentier 1925) the most complete study of which was published by Halle (1933). In Halle's study, the genus *Boulaya* is characterized by having relatively fine vertical striations but lacking evidence of any external ribs. In other respects, the genera *Boulaya* and *Aulacotheca* are indistinguishable on the basis of external features. The internal structure of *Boulaya* has never been satisfactorily determined, although Halle believed it to have a central hollow region surrounded by a ring-shaped sporangial region which may or may not have been subdivided into individual sporangia. We have assigned the present material from Iowa to *Aulacotheca* largely on the presence of shallow external ribbing and the clear presence of several individual sporangia within each synangium.

In 1932 Dix suggested that synangia of the *Aulacotheca* type may have been attached to *Neuropteris schlehani*, but, this appears to be an instance of close association in the matrix. Thus, at present, nothing is known of the source plants which produced pollen organs such as *Aulacotheca*. Relationships with the Medullosaceae are deduced from the type of pollen and general organization of the pollen organs, which compare favourably with some better-known pollen organs such as *Dolerotheca* which are almost certainly of medullosan origin. However, the general organization of *Aulacotheca* is not very different from that occurring in some pollen organs believed to have been produced by members of the Lyginopteridaceae. For example, both *Telangium* and *Heterotheca* Benson (1904, 1922) are synangiate and the central portion of *Telangium* was hollow. Fusion of the sporangia apparently extended throughout their lengths in both *Aulacotheca* and *Heterotheca* while in *Telangium* the sporangia were free except near their bases. The genus *Telangium*, is, in turn, questionably distinct from some forms of *Crossotheca* and Kidston believed that the two genera were probably the same (Kidston 1906). Thus, although general accounts of these genera of pollen organs generally assume that the forms are distinct types such is not the case and a great deal of continued research is needed to properly determine the detailed structure of these presumed pteridosperm pollen organs.

A few remarks should be made concerning features of the fertile frond or frond regions of *A. iowensis*. Whether the synangia occurred on separate fertile fronds or merely occupied portions of the same fronds having sterile foliar areas cannot be determined. It is of interest to note that present evidence indicates that *Aulacotheca* pollen organs were borne on pinnate fronds with unequal branching of the frond axes rather than on fronds with equal dichotomous branching. Also, the fertile regions of *Aulacotheca* lacked sterile foliar structures and were apparently 3-dimensional in the distal regions where the pollen organs were borne all around the ultimate axes. In this respect, *Aulacotheca* is reminiscent of several Devonian genera such as *Archaeopteris* and *Tetraxylopteris* (Carluccio, Hueber, and Banks 1966, Bonamo and Banks 1967), and, in view of several studies by Long on Lower Carboniferous pteridosperm fronds and structures such as cupules borne on fronds, illustrates that the frond of Palaeozoic seed ferns was much more 3-dimensional and branch-like than has been supposed.

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