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I hereby recommend that the thesis prepared under my supervision by Aureal T. Cross

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be accepted as fulfilling this part of the requirements for the degree of Doctor of Philosophy

Approved by: John H. Hoskins

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OBSERVATIONS ON PALEOZOIC PLANTS
FROM MIDDLE-WESTERN UNITED STATES

Parts I - V

A dissertation submitted to the

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of the University of Cincinnati

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by

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OBSERVATIONS ON PALEOZOIC PLANTS FROM MIDDLE-WESTERN UNITED STATES

Parts I - V

by

Aureal T. Cross

Table of Contents

Preface.. 3

Part I. GENERAL CONSIDERATIONS....................... 5

1. The nature and occurrence of coal balls..... 5

2. Preparation of the material for study....... 9

3. References................................ 17

Part II. FURTHER STUDIES ON THE COAL BALL FLORA OF IOWA.. 19

1. Collections.................................. 19

2. Flora.. 22

3. Tabulation of species....................... 23

4. References................................... 27

Part III. REVISION OF THE PALEOZOIC CONE GENUS BOWMANITES (SPHENOPHYLLALES)..................... 28

1. Introduction................................. 28

2. The Structure and Affinities of a New Species of Bowmanites from Iowa............. 32

a. Material, Preparation and Procedure...... 32

b. General Morphology...................... 34

c. Axis.................................... 36

d. Sporophylls............................. 38

e. Sporangiophores......................... 42

f. Sporangia................................ 50

g. Spores.................................. 56

h. Affinities.............................. 59

3. Discussion.............................. 60

4. Taxonomic Treatment..................... 70

a. Bowmanites (Binney) emend............... 70

b. Sections Simplices, Jugati, and

Conferti................................ 74

c. Key to the Species of Bowmanites........ 75

d. Description of Species.................. 78

1. Bowmanites simplex, spec. nov....... 78

2. B. trichomatosus (Stur), comb. nov.. 80

3. B. angustifolius (Germ), comb. nov.. 81

4. B. Scottii, spec. nov............... 82

5. B. tenerrimus (Ett.), comb. nov..... 84

6. B. gracilis (Crépin), comb. nov..... 85

7. B. Dawsoni (Will.) Weiss............ 87

8. B. cuneifolius (Sternb.), comb. nov. 90

9. B. verticillatus (Schloth.), comb.

nov................................. 92

10. B. charaeformis (Jongmans), comb.

nov................................. 93

11. B. trisporangiatus, spec. nov....... 94

12. B. cambrensis Binney................ 96

13. _B._ _Römeri_ Solms-Laubach............. 98

14. _B._ _laxus_ Halle....................... 100

15. _B._ _fertilis_ (Scott), comb. nov...... 101

16. _B._ _Kidstoni_ (Hem.), comb. nov....... 103

17. _B._ _major_ (Bronn), comb. nov......... 105

18. _B._ _tenuissimus_ (Kidston), comb. nov. 106

5. References.................................. 108

Part IV. A CONSIDERATION OF THE STRUCTURE OF LEPIDOCARPON SCOTT BASED ON A NEW STROBILUS FROM IOWA (abstract) 118

1. Introduction................................ 118

2. Material.................................... 119

3. _Lepidocarpon_ _ioense_, sp. nov................ 124

a. Strobilus................................ 124

b. Axis..................................... 124

c. Sporophyll............................... 124

d. Ligule................................... 126

e. Sporangium............................... 126

f. Spores................................... 128

g. Location, Horizon and Material........... 128

h. Name of type............................. 129

4. Discussion.................................. 130

5. Summary..................................... 138

6. References.................................. 139

Part V. TWO NEW SPECIES OF LEPIDOSTROBUS FROM THE LOWER POTTSVILLE OF ORANGE COUNTY, INDIANA...... 141

1. Introduction.................................. 141

2. Material...................................... 143

3. Summarized type diagnoses.................. 163

a. *Lepidostrobus imbricatus*, spec. nov..... 163

b. *L. arrectus*, spec. nov.................. 165

4. Summary....................................... 168

5. References.................................... 169

Acknowledgements.................................. 172

Preface

Ancient plants are rarely recovered as complete entities and the discovery of all of the parts necessary to give a complete story of the structure and life history of these plants is rarely accomplished; therefore it is necessary to deal with the available plant parts as organ genera and species. The desirable but virtually unattainable goal is, of course, the eventual understanding of the form, structure, and life history of each plant; its correlation with allied forms and the utilization of this information in the interpretation of the phylogeny and evolution of both ancient and modern plants.

The following investigations and discussions of some of the problems inherent in the study of Paleozoic plants are based on specimens which were collected from the Middle-western United States by Professor John H. Hoskins and the author over a period of several years and now housed at the University of Cincinnati. Since 1939 we have collaborated in a study of certain of these specimens as evidenced by 5 papers and 7 abstracts published, and the presentation of 8 papers before scientific societies. It is almost impossible in the present report, without sacrificing continuity, to delimit the sections which are the result of our collaborations, from those which have been formulated entirely by myself. As unpublished portions of this paper and additional parts which are as yet incomplete will eventually be published under joint authorship, it seems advisable to accept joint responsibility for all new species or combinations herein proposed.

It has seemed desirable to treat general considerations of the floras and each principal plant group discussed herein as separate parts. This organization requires separate conclusions and bibliographies, increasing, I believe, the utility of the paper as a whole.

A. T. Cross

Part I

General Considerations

The nature and occurrence of coal balls

Rounded or irregularly shaped concretions are found in many coal beds. In Britain and America they are usually called "coal-balls" whereas in Germany and other Central European countries they are referred to as "Torfdolomiten", "Torfkalksteine", "Torfsphaerosiderite", etc. These concretionary masses range in size from about one-half centimeter to several meters in diameter. They are often found twinned or in a chain-like series in situ in the coal seam or occasionally in the overlying shales. Usually, however, the concretions in the fire-clays and shales below and above the coal are of a different sort; they may be a) epigenetic, i.e., they were developed in the sediments after they were deposited, as is shown by the transgression of the bedding planes or laminae of the enclosing sediments through them; or b) syngenetic (often diagenetically altered subsequently), which developed by concentric accretion, during sedimentation, about a nucleus. The nucleus may be either an organic fragment such as a leaf, seed or shell, as is the case in the well-known ironstone concretions from Mazon Creek, Illinois, or an inorganic body such as a piece of rock or a mineral crystal. Coal-balls are distributed without much order through the seam of coal and in the roof shales. They normally occur in lenses or pockets and are completely surrounded by coal. The layer of dark shiny coal, called "glance-coal" which immediately surrounds the nodule may be split cleanly away from the fossil plant mass but the exposed surfaces normally do not give any clue as to the contents.

Coal balls consist of dark-brown to yellow-brown, more or less solid masses of dolomitized, calcified or silicified plant remains. Sideritic coal balls are less common than calcareous coal balls. Varying quantities of iron sulfur, aluminum, manganese and other chemicals are present in the forms of inorganic compounds. The coal balls which show the best preservation of the plant material are those which are most nearly pure calcium carbonate or silicon oxide. Most of the coal balls known from deposits in America arc calcified whereas the silicified nodules are equally common in Europe. Those which contain a high percentage of impurities such as various iron sulphides or iron oxide often show little structure in the contained plant fragments.

Coal balls were formed in position and are really concretionary formations of peat. Proof of this in situ formation is evident from the numerous records where single large stems or stigmarian rootlets have been found extending through a unilateral series or chain of coal balls still in position in the coal. That coal balls must have formed in the peat stage is borne out by the fact that the nodules are sometimes considerably larger than the thickness of the entire coal seam. In all cases the coal appears to be compressed as has actually been the case, to less than one-fourth its original vertical dimension. The layers of coal are domed over the coal balls and slope away from them in all directions. The lack of distortion or compression of the nodule would seem to indicate that the processes of fossilization of the masses of plant aggregates had been completed very early in the history of the deposit. Furthermore, coal balls must have been formed before the plant organs had suffered any considerable destruction by decomposition and compression which could only be in the earlier stages of peat formation. Often even the most delicate plant organs can be recognized, though some are in a poorer state of preservation than others.

Distortion or destruction of the tissues is often found when there is considerable accumulation of an iron sulfide, either in the form of marcasite or iron pyrite. In these cases, it seems that the carbonized cell-wall has acted as the locus for the accumulative growth of the pyrite into a crystalline aggregate. The subsequent growth is then toward the center of the cell or into the intercellular spaces. It is only with secondary pyritization (i.e. recrystallization of the pyrite) that the cell walls are crossed and thus destroyed or distorted. During primary pyritization the pyrite replaces the crystals of calcium carbonate in the calcified coal balls. Calcification, dolomitization and silicification do not destroy the tissues. Actually the plant cell walls have not been replaced by minerals and the altered products of the original cells are not carbon but complex organic compounds. Pollen, spores and resin globules are the best preserved of all structures found in coal deposits. Fatty or waxy tissues such as horny seed coats and cuticula are also usually well preserved.

The plant remains enclosed in a coal ball may be seen either 1) by splitting the coal balls in a plane of fracture, which is usually parallel to the short axis, 2) by observation of a cut and polished surface, 3) by the preparation of thin sections, 4) by use of the peel method, or 5) by maceration of the coal ball and the isolation of the plant fragments. These techniques will be discussed subsequently.

Coal balls were found in England as early as 1841. Coal fields of Holland, Belgium, France, Germany, Czechoslovakia, and the Donetz basin in Russia have yielded extensive collections. In the United States they were first found in Illinois by Dr. G. H. Cady who transmitted them to Professor A. C. Noé for study (Schopf, 1941). Since that time they have been found in Iowa, Kansas, Texas, Indiana, western Kentucky, West Virginia, and recently one has been found in the glacial drift in southwestern Ohio, probably from the eastern Kentucky coal fields. Schopf (1941) has given a rather complete account of the occurrence and stratigraphic relationships of the principal coal ball deposits. (See also Plate 13, Part III).

Preparation of the material for study

The success of the study of fossils depends to a considerable extent on the preservation of collections from oxidation and the proper preparation of them for study. Many techniques have been worked out in various paleobotanical laboratories throughout the world, but oftentimes they remain unpublished until later workers have discovered them independently. The techniques which we employed are either essentially unmodified, standard procedures or embody important improvements or they are entirely new. A brief outline of these will suffice.

It is often advisable to prepare casts and molds to preserve a record of the original condition of the material if it is found necessary to section the specimens for proper study. Air-drying, liquid rubber which has recently been developed may be applied to a specimen as paint. After a desirable thickness has been obtained by successive coats of rubber, a backing of cheesecloth may be embedded in an additional coat of rubber, thus giving greater rigidity to the mold, and enabling it to hold its shape permanently. The rubber mold may then be removed by lifting a corner and stripping it off. This mold preserves even the most minute details of the surface configuration including overhangs, and will retain its form indefinitely. It is often advisable to make a plaster cast of the back of the rubber mold in which it may be placed to facilitate making positive casts later.

The rubber mold must be dampened just before pouring the plaster into it in order that the plaster will not be withheld by air bubbles from the minute markings upon the surface. In dampening the mold, it should be first dipped in water and then all the free water should be removed by a gentle stream of air. A fine grade of plaster should be used especially if the specimen shows important surface ornamentation. The rate of setting of the plaster may be slowed (for detailed work) by the use of ice cold water and even further by the use of salt water. Hot water will hasten the time of setting, which is often useful in preparation of large and/or three dimensional casts. Gum arabic or glue dissolved or suspended in water may be added to the wet plaster to make the resulting cast stronger. Water soluble paints of the desired color, i.e., the one most nearly simulating the matrix, may be suspended in the water before mixing it with the plaster. The plaster, when poured, should have the consistency of molasses, i.e., it should be thick but not stiff.

A method of enlarging casts of specimens bearing definite surface configurations or possessing a definite shape has been worked out by several paleontologists. The rubber molds of the original specimen are made in the same way as those already described except that the cheesecloth backing must be omitted. The molds are then placed in kerosene and allowed to remain until they have expanded to about one and a half times their original size. The mold is then carefully lifted out, the excess kerosene is taken up with a blotter, and it is placed in a sand mold. This sand backing is almost necessary, for the rubber has lost much of its tensile strength and would break down under the weight of the plaster if unsupported. A plaster cast is then made in this enlarged rubber mold. From this enlargement another rubber mold may be made. The step may be repeated several times. Expansion is quite uniform throughout the rubber so that distortion in the enlargements is almost non-existent. If the first mold is taken from a plaster cast which has been colored as described above, part of the color will be transferred accurately to several successive steps of enlargement.

Friable or wet impressions or casts of fossils may be preserved in the field in several ways. Rubber molds may be made of large casts or material which may not be moved either because of size or condition. Smaller specimens may be completely embedded in Duco Cement to hold them together. This may be dissolved later with amyl or butyl acetate, thus freeing the material for study. Collodion and cellulose acetate may be used to great advantage in embedding dry material which is very friable. Nitro-cellulose solution or cellulose acetate may be cheaply and adequately made by substituting movie film for guncotton or parlodian as the cellulose ester. The gelatin must first be removed from the film with hot water before dissolving it in amyl acetate. A supersaturated solution of gum sandarac in alcohol may be used to preserve the material either wet or dry. This is the best preservative we have found for all around use and it has the advantages of being simple to prepare and inexpensive. It dries on the specimen into a clear shiny film that is impervious to most acid fumes, water and dust. It does not shrink nor become milky when put on a wet specimen as does cellulose acetate.

Photographing original specimens is sometimes difficult due to surface markings or mineral discoloration. If the rubber mold of the original specimen is shaded uniformly white by the precipitate of the dense fumes given off when ammonium chloride is heated in an ammonium chloride tube, a picture may be made of the mold and these difficulties are overcome. It is best to overexpose and underdevelop both the negative and the prints, for such a procedure increases the shadow and contrast. Often negatives will become covered with fingermarks due to careless or excessive handling. We have been able to remove these in most instances from either surface by washing the film in cold water for five to ten minutes, transferring it to a wet glass plate or ferrotype board, and wiping it firmly with a well-soaked chamois skin.

Cutting and grinding specimens may be done in a number of ways. One method recently improved upon in our laboratories in order to obtain some special sections is the use of a fine wire and some abrasive (Carborundum or Aloxite) powder. A board has been fitted to a vise in the following manner (Fig. 1, pl. I): holes were bored into it to correlate with the position of the shaft of an ordinary commercial vise, the vise is then taken apart and the board inserted over the shaft which is then

Plate I

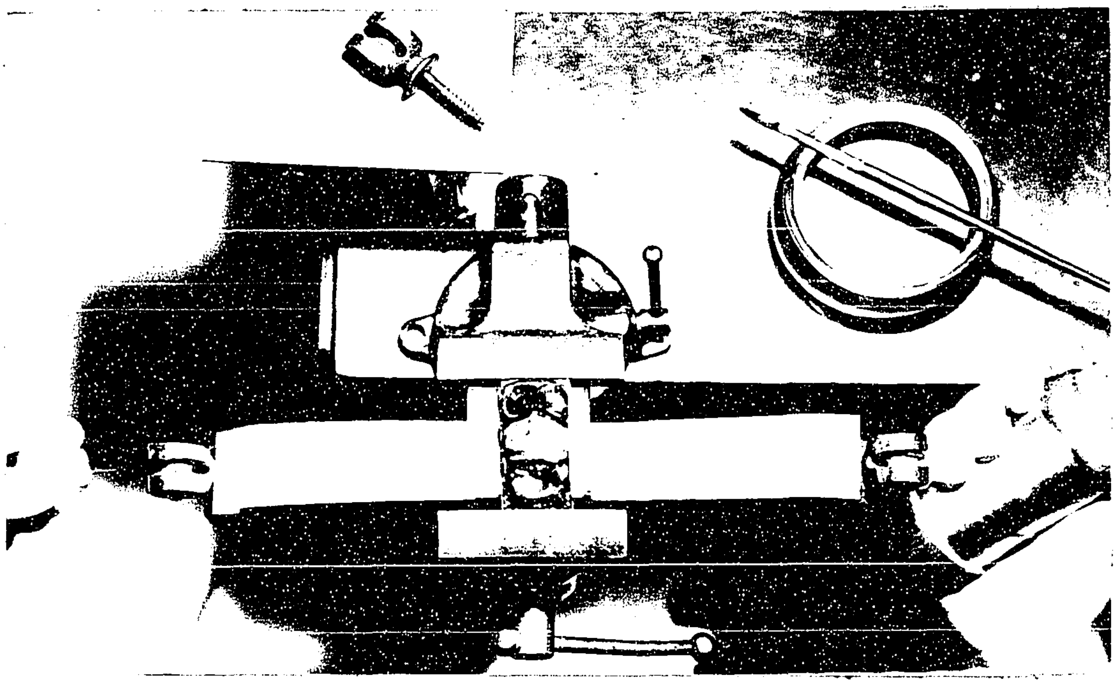

Fig. 1. Apparatus used to facilitate making cuts in fossils with a fine wire and carborundum. A single pulley which acts as one of the two guides when properly fastened to the frame is shown in the upper left hand corner.

reassembled; at each end of the board, which extends about six inches on either side of the vise shaft, a pulley is mounted rigidly, upside down, and the base of the pulley frame is cut out thus exposing the base of the pulley. The specimen to be cut is partially embedded in sealing wax which may be clamped in the vise or fastened to the board. The wire is then drawn over one pulley, across the specimen and over the second pulley. The pulleys act as guides to insure a straight cut. Number 30-36 gauge steel or tinned wire is found to be quite suitable along with number 400 grinding powder as the abrasive. With this simple device, a perfectly straight, almost polished cut may be made with the loss of less than 200 microns of the material.

The method of making peels is so well known that few comments concerning the study and mounting of peels suffice. All peels were first given a preliminary examination. If the specimen contained very little marcasite or pyrite, observation of the rough (lower) surface with direct light proved best. Other peels seemed to show considerably more detail when studied by reflected light with the rough surface of the peel down, i.e., as taken from the coal ball. After a preliminary examination, some of the better or more typical peels were mounted in Canada balsam after having first been cleared with Eycleshymer's solution. Mounted peels may be observed with high magnifications, an oil immersion (1.8 mm.) objective being used for observation of the structure of cell walls and of spore configuration.

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Part II

Further studies on the coal ball flora of Iowa

Collections

Coal balls have been found in nearly all coal producing counties of south-central Iowa. Dr. L. R. Wilson of Coe College, Cedar Rapids, Iowa and several of his students made collections from mines near What Cheer and Des Moines, Iowa, as early as 1937. At about the same time Mr. William C. Darrah of Harvard University (1939) began an extensive collection with the invaluable aid of Mr. Frederick O. Thompson of Des Moines. Collections for the University of Cincinnati were begun in 1939 by Professor John H. Hoskins, Mr. R. M. Kosanke, and the author, and during the following summer, Dr. Th. Just of the University of Notre Dame and Dr. A. H. Blickle of Ohio University joined Dr. Hoskins and the author in a rather extended expedition, a portion of which was devoted to the collection of additional coal balls.

In all, we obtained specimens from 18 mines in 7 counties. Over 2,000 coal balls weighing about three and one-half tons were collected, more than half of which were found in two mines, the Angus and the Atlas from near Oskaloosa, Mahaska County, Iowa. We have sectioned 1,550 of these coal balls and of these about 450 were worthy of careful study.

The Banner Coal Mine, near Indianola, Warren County, Iowa, has yielded 75 coal balls, most of which were poorly preserved. One unusual specimen, containing a single petrified cone was the subject of an extensive investigation, an abstract of which is included here in Part IV. This coal is in the Des Moines Series, as are all the others investigated, and is probably the Lower Coal of Lugn's Lucas County Report (1927), the oldest coal in the Pennsylvanian of Iowa. It correlates favorably with the Lower Carbondale of Illinois.

The second and largest collection to be worked was that of the material from the Angus Mine, a large strip mine, five miles northeast of Oskaloosa, Mahaska County. The coal balls recovered here were found principally in lens or pocket in the upper of the two seams of coal. The lower seam appears to be devoid of coal balls. About 200 specimens were studied from this collection.

The Atlas Coal Mine, another large strip mine, six miles south of Oskaloosa, also yielded large numbers of good specimens. This material occurs indiscriminately throughout the single vein of coal. Though the number of coal balls to be found is far greater than at the Angus Mine, and probably even greater than those originally available at the Shuler Mine, north of Waukee, Dallas County, Iowa, during 1937, 1938 and 1939 when the south wing of that mine was being extensively worked, the degree of preservation is less, and secondary pyritization has destroyed the plant material completely in a majority of the coal balls.

The Angus and the Atlas Mines have furnished most of the plant specimens to be reported in this paper. Our collection from the Shuler Mine has not been worked, but Darrah(1939, 1941) has published rather complete lists of the flora which he has found there. Only occasional specimens from the 14 other collections have been examined, and in these selected coal balls no additional species have yet been encountered.

Exact stratigraphic correlations have not been made for any but the coal seam exposed in the strip-mining operations at the Banner Coal Mine as already discussed. Local mining engineers consider both the Atlas and Angus coal seams to be the same. On the basis of plant content of the coal balls we question this correlation at the present time. Without doubt both seams are in the upper part of the Des Moines Series, but, as we will show directly, the flora of the two mines does not correspond as closely as it should, considering the fact that the mines are only about nine miles apart.

Flora

The conspicuous plant assemblage from the Angus Coal Mine specimens is principally the Cordaitales-Pteridospermae-Filicales type, with lesser numbers of Sphenophyllales, Calamitales and Lepidodendrales, in that order of abundance. This corresponds closely to the florule set up for the Shuler Mine near Des Moines, and a few others of lesser importance, by Darrah (1939).

On the other hand, the Atlas Mine appears to have had a more abundant assemblage of Calamites, Sphenophyllales, and Lepidodendrales, in that order of occurrence numerically, with respectively fewer numbers of Cordaitales, Pteridospermae, and Filicales species.

Disregarding the unequal numerical occurrence of the more conspicuous species, the flora from the two mines is essentially homotaxial, which correlates very closely with that recorded from Illinois, Kansas and Texas. The whole aspect is somewhat similar to that of the Westphalian C and Stephanian floras of Europe.

Tabulation of Species

It is impossible at this time to give more than an incomplete and generalized list of the species of fossil plants found in the Iowa coal balls. Some have been positively identified to species; others only tentatively. A large number of the specimens recovered must, for the present, remain tabulated under generic designation until new material is recovered, or until additional sections reveal critical structures. It may be possible to establish specific identification for some, only after a complete reinvestigation has been accomplished of the material previously reported, as has been the case in Part III of this report.

The tentative tabulation submitted here corresponds in general to lists published by Darrah which have been previously cited. He has recorded several species which have not as yet been found in our material, and likewise, we have encountered an even greater number which has apparently not recovered.

Lycopodiales

Lepidodendron Veltheimii Sternberg.
L. selaginoides Sternberg
Lepidodendron sp.
Lepidodendron spp. (3) (leaves)

Lepidostrobus fuliginosus Leclercq
Lepidostrobus spp. (2)

Lepidophloios sp. (stem)
Lepidophloios spp. (2) (leaves)

Bothrodendron sp. (mundum ?)

Bothrostrobus mundus Williamson
Bothrostrobus spp. (2)

Lepidocarpon Lomaxi Scott
Lepidocarpon ioense Hoskins and Cross

Lepidophyllum sp.

Sigillaria sp. (stem)
Sigillaria sp. (leaves)

Stigmaria ficoides Brongniart
Stigmaria sp.

Articulatales

Sphenophyllum plurifoliatum Williamson
Sphenophyllum insigne Williamson

Bowmanites trisporangiatus n. sp.

Calamites suckowi Brongniart

Arthrodendron (?) sp.

Asterophyllites sp.

Annularia sp.

Calamostachys sp.
Paleostachya sp.

Filicales

Stauropteris sp. (Oldhamia?)

Zygopteris (?) sp.

Etapteris Scotti P. Bertrand
Etapteris sp. (diupsylon?)
Etapteris sp.

Ankyropteris (?) sp.

Botryopteris tridentata (Felix) Posthumus
B. forensis Renault
B. americana Graham
B. Renaulti C.E. Bertrand and K. Cornaille
B. cylindrica Williamson
B. radiata Darrah

Anachoropteris involuta Hoskins
Anachoropteris sp. (Williamsoni?)

Psaronius sp.

Asterotheca sp.

Scolecopteris sp.

Ptychocarpus (?) sp.

Pteridospermae

Heterangium sp.

Conostoma oblongum Williamson

Lagenostoma sp. (ovoides?)

Medullosa sp. (Noei?)

Alethopteris sp.

Neuropteris sp.

Triginocarpus spp. (3)

Pachytesta gigantea Ad. Brongniart

Rhabdocarpus sp.

Carpolithes sp.

Cordaitales

Cordaites spp. (2) (stems)
Cordaites spp. (2) (leaves)

Mesoxylon sp.

Amyelon sp. (radicans?)

Cordaianthus shuleri Darrah
Cordaianthus sp.

Cardiocarpus spinatus
Cardiocarpus sp.

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Part III

Revision of the Paleozoic Cone Genus Bowmanites (Sphenophyllales)

Introduction

Fructifications of Sphenophyllum were known from compressions for many years before casts or fragments of petrified strobili with structure preserved were first studied by Williamson in 1871.

As early as 1838 Presl described a specimen of Sphenophyllum under the name *Rotularia marsileaefolia* Sternberg which showed two laterally developed cones. Germar (1845) figured several species of Sphenophyllum bearing fructifications and in 1855 Geinitz illustrated a rather poorly preserved cone which he attributed to *Sphenophyllum emarginatum*.

A cast of a cone which has since been referred to Sphenophyllum (Zeiller, 1893) was found before 1840 (Binney, 1871) in a nodule of clay-ironstone from near Pontypool, South Wales, by J. E. Bowman. Binney described this specimen as *Bowmanites cambrensis* in 1870 and published Bowman's original unpublished drawings in his memoir of 1871.

Since that time five anatomically different types of cones belonging to Sphenophyllum have been described under the generic names of Volkmannia, Bowmanites, Sphenophyllum and Sphenophyllostachys. Only three of these five general types are known from material with structure preserved. The first of these petrified cones was described by Williamson in 1871 (1876) under the name of Volkmannia Dawsoni from the Lower Coal-measures of England near Oldham. Later Williamson obtained and studied other specimens of the same type from calcareous nodules in the coal seams at Cinder Hills near Halifax, and from Dulesgate.

Another fragment of a cone of this same general type was recorded by Leclercq (1925) which she assigned to Sphenophyllum Dawsoni beta. The specimen occurred in a coal ball from the Bouxharmont beds of Werister. This horizon in Belgium is correlated with the Lower Coal-measures of England.

More recently (Koopmans, 1928) the Dutch Finefrau-Nebenbank horizon, which is also equivalent to the Lower Coal-measures, has yielded a preserved specimen which Koopmans has placed in this group. He suggests that it might belong to forma alpha or beta or even possibly gamma which is more an indication of the confused status of this whole complex than a reflection on either his good work or the condition of the material.

Two other unnamed fragments of silicified Sphenophyllum fructifications were discovered in the Grand 'Croix silcified magmas near Saint Étienne by M. B. Renault. He described and figured one of these in his early investigation upon the structure of Sphenophyllum (Renault, 1877) and later in *Cours de Botanique Fossile* (1882). Zeiller (1893) studied and described the organization of the other as agreeing with *S. cuneifolium* and *S. Dawsoni*. The taxonomic position of these will be reviewed later.

The second general type to be described from a petrifaction was found in the Middle Upper Carboniferous coal seam of Niedzielisko, near Jaworzno (Cracow), Poland and described by Solms-Laubach in 1895 as *Bowmanites Römeri*.

The third general type known as *Sphenophyllum fertile* was first described by Scott in 1905 on the basis of a well preserved fructification from the Lower Coal-measures of Shore Littleborough, in Lancashire. Leclercq (1930) reported the discovery of some additional material of *S. fertile* from the Bouxharmont beds in the coal basin of Liege, Belgium which she later described in great detail (Leclercq, 1935, 1936A, 1936B, 1937).

The only other tangible record of a petrified Sphenophyllum fructification, of which we are aware, appears questionable. Koopmans (1933, pl. II, fig. 21) figured a part of a section taken through a coal ball from the Aegir Horizon (basal Westphalian C or Lower Allegheny) in the province of Limburg (The Netherlands). This photograph, which was made by reflected light from a polished and etched surface, shows an oblique section through the tip of a strobilus which he believes to be a new species of Sphenophyllostachys. The maximum dimensions of this specimen by our measurements based on the photograph are three millimeters in diameter by five millimeters of length. No unquestioned Sphenophyllum cone of such small dimensions has been recorded as far as we can ascertain. It is impossible to find in this illustration any trace of the peculiar elongated sporangiophores which are characteristic of the fertile appendages of Sphenophyllum. In view of the size, appearance, and arrangement of the sporangia and leaves it suggests the fertile tip of a branch of Cordaites (Cordaianthus).

The structure of the petrified strobilus of Sphenophyllum, found in 1941 (Hoskins and Cross, 1941, 1942) in a coal ball from the coal of the Des Moines Series of the Pennsylvania Period in the Angus Mine, near Oskaloosa, Mahaska County, Iowa, enables us to correct the interpretation of certain morphological details of Sphenophyllum cones. These findings together with the distinctive characters of this specimen warrant its description as a new species.

Because of the complex variations which appear in various modes of preservation in species of Sphenophyllum cones reported as compressions or impressions, and because of the difficulties encountered in any attempt to establish diagnostic characters equally applicable to petrified material, compressions, etc., no effort is made at this time to correlate the Iowa specimen with other known American material which has not been carefully studied. Fortunately some of the compression materials from regions other than the United States have been more critically examined so that a comparison with available petrified material is possible. Such specimens are included in the following discussions.

The Structure and Affinities of a New Species of Bowmanites from Iowa.

Material, Preparation and Procedure.

The specimen of a cone of Sphenophyllum in coal-ball No. B-1706 from the Des Moines Series coal, Angus mine, near Oskaloosa, Iowa, which we have noted earlier (Part II) was first exposed by a very oblique transverse section through the middle of the fragment. In the subsequent course of study several additional cuts were made by the wire-cutting technique (Part I) which exposed in all, four true transverse sections, rather regularly spaced, two radial longitudinal sections in the mid-portion of the cone, two obliquely transverse and two obliquely tangential sections. 2-35 peel sections were taken serially from each surface and numbered consecutively. Each of the 20 surfaces is represented by a letter, i. e., 1706a - 1706t inclusive. Representative peels from each series and in several cases, the complete series of specimens from a single surface were mounted in Canada balsam. In all, of approximately 500 peel sections made, over 300 were mounted. Observations were made at various magnifications including the use of an oil immersion objective for the study of cell characteristics and spore sculpturing.

The preservation of the material is excellent throughout the mid-section (3 cm.) of the specimen. Neither the basal nor the apical ends of the cone were present at the time of fossilization and about one centimeter of each of the broken ends (abutting on the edges of the coal ball) is poorly preserved. One side is greatly flattened (Figs. 2, 3) indicating the position in which the cone lay as it fell into the plant litter. This flattening before fossilization clearly emphasizes the fragile nature of this species as well as other fertile shoots of Sphenophyllum in general.

General morphology

The cone is not less than 1.6 centimeters in diameter at any point. There is no evidence of tapering at either end of the 6 cm. fragment in our possession. Several evidences clearly show that this specimen underwent some decay and disorganization before petrification and the decayed ends probably indicate that it was subjected to further deterioration after fossilization, i.e., during the chemical alteration (secondary pyritization) of the coal ball. The distal end of nearly all the horizontal portions (pedicels) of the sterile, dorsal (inferior) segment of the sporophylls is absent. Rarely can a fragment of the upturned portion, the lamina, of a sporophyll be found (Figs. 1, 4, 5). Some of the outermost verticels of sporangia are displaced or entirely missing (Figs. 2, 3) on the unflattened side, and are quite crushed and distorted on the flattened side. Some free sporangia are found elsewhere in the same coal-ball and even some leaf-like fragments which may possibly be those of the missing laminae have been observed.

A radial longitudinal section through the axis parallel to the bedding plane, or flattened side, gives the true appearance of the structure of the cone (Fig. 1). Similar sections taken perpendicular to the bedding plane show excellent organization on one (upper) side only, with an almost unrecognizable tangle

Plate I

Fig. 1. Radial longitudinal section through the cone of Bowmanites trisporangiatus showing general features of the various organs. The vascular elements and the inner cortex of the axis have not been preserved. (Composition from B-1706 R2, 1706 R14, 1706 S2, 1706 S14).

of crushed sporophylls, sporangiophores and sporangia on the other (flattened side.

Axis

The average diameter of the axis based on direct measurement of the four widely separated transverse sections is 4.5 mm. The greatest diameter of about 6 mm. occurs at the nodes. Such a nodal swelling is typical for most of the Articulatales.

The entire central cylinder of the axis is missing as is the surrounding zone of inner cortex, which, on other species, is made up of several layers of very delicate parenchyma cells. The nature of the stele, i.e. whether triarch or hexarch in arrangement of the xylem, is unknown. The exact nature of this character, so important in the distinction between Bowmanites Dawsoni and B. Scottii, may later be found with the recovery of additional material.

The outer cortex of the axis in the Iowa specimen is fairly well preserved. It is composed of rather firm-walled, well-organized parenchyma cells which are sharply reduced in size toward the periphery of the axis. The course and disposition of the centripetal vascular bundles through the outer cortex are clear. They appear to traverse this outer zone in an upward an outward direction in approximately one-third the length of an internode (Figs. 5, 7, 8). There appears to be

Plate II

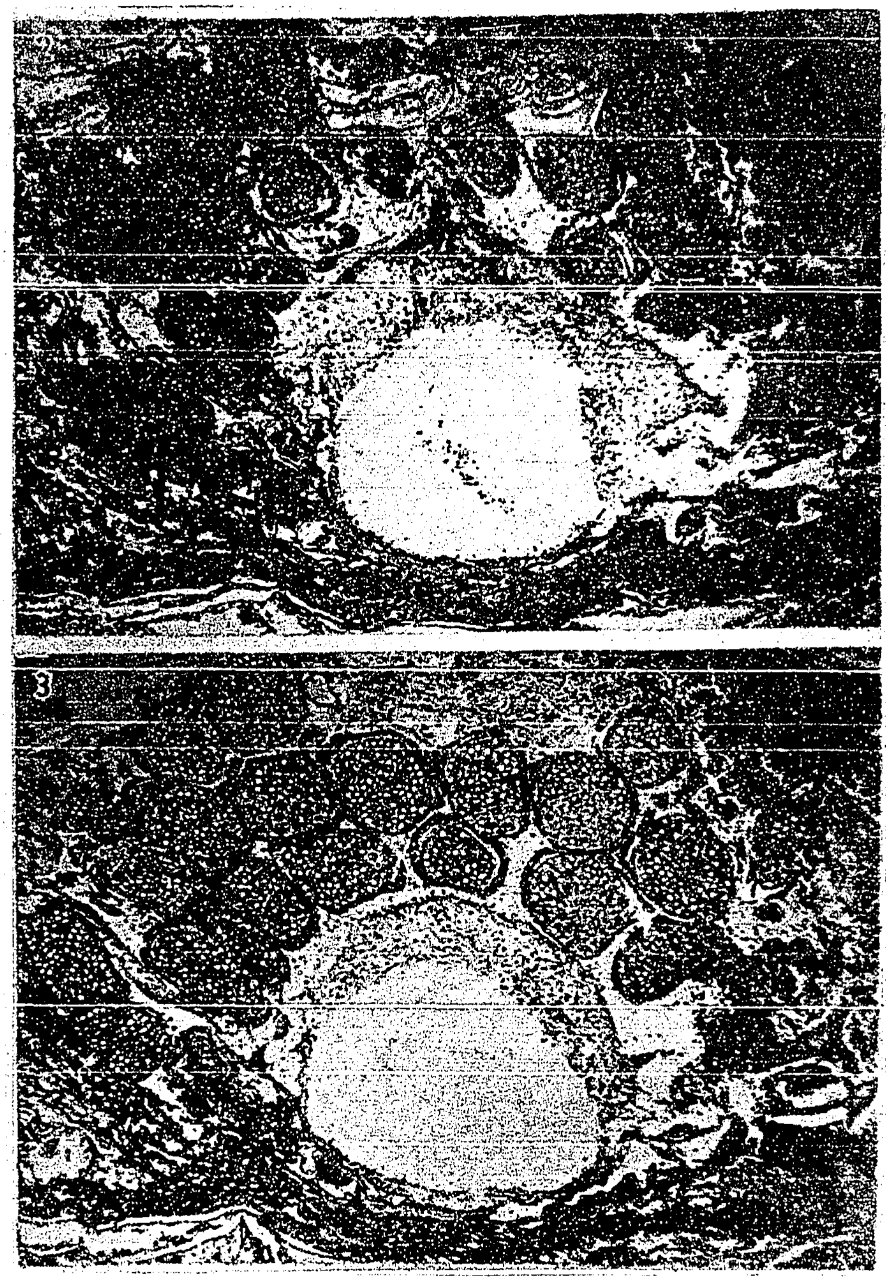


Fig. 2. True transverse section of the cone of Bowmanites trisporangiatus through the region of a node. (Compare with Fig. 3). The increase in thickness of cortical tissue and the decrease in the number of sporangia is typical. (1706 N1)

Fig. 3. Transverse section taken through an internodal region, somewhat lower than the section shown in Fig. 2. Note that the sporangia occur in three concentric verticels and in radially arranged rows from the axis. These rows indicate individual bracts. Microscopic examination of serial sections of the crushed side show it to have about 9 radial rows making a total of 18 bracts and rows of sporangia. (1706 N9)

a serial sequence of bifurcations which result in the single vascular supply for each individual sporangiophore and bract. The problem of the true nature of these bifurcations (Hirmer, 1933; Troll, 1933) will be reviewed later.

The internodes are about 1.5 - 2.0 mm. in length and the greatly thickened bract bases occupy about one-half this distance (Figs. 1, 4, 5).

Several foreign rootlets traverse the hollow central area of the axis (Figs. 1, 2).

Sporophylls

The fertile leaves or leaf-like organs which bear the sporangia in the Sphenophyllaceous plants are called sporophylls or bracts. Morphologically and anatomically these bracts are divided into two principal types of segments. The morphological dorsal segment is inferior to the ventral segment (-s) and the latter appears superficially to be borne upon its upper surface. We may consider the two segments to be a single divided sporophyll arising from the axis at a single node. A common vascular bundle or leaf trace which divides dichotomously in the outer cortex supplies both segments.

We will first consider the dorsal (inferior) segment which is usually referred to independently as the bract or "sporophyll." It is a leaf-like structure comprised of a horizontal portion, the pedicel, and a more or less erect distal portion of varying lengths, the lamina. In most species the point of juncture of these two portions is indiscernable and the lamina curves evenly upward from the pedicel and overlaps the lamina of the superior sporophyll, and in some cases may extend the length of several internodes. The overlapping of the laminae may be definitely imbricate if these free tips of the sporophylls rise more or less vertically from the pedicel, but in many cases the sporophylls are only aristate and divergent, whereas in a few forms they do not overlap at all (B. fertilis, B. trichomatosus, etc.). Occasionally the distal portion of the pedicel is subtended into a heel or spur as in B. angustifolius (Fig. 18).

The bracts of our specimens are arranged in superposed whorls upon the axis. It seems most probable to us that this is a sound generic character. Occasional reports of alternating whorls have been made (Zeiller, 1893, Williamson and Scott, 1894), but distortion during compression may be held responsible in the case of Bowmanites cuneifolium and reinterpretation of Williamson's specimens may be in order. The definite superposition of consecutive whorls of sterile Sphenophyllum leaves justifies the expectation of a similar condition in fructifications. Also those species which do not produce true cones (*B. charaeformis*, *B. major*, etc.) seem to have definite superposition of whorls of fertile leaves.

The number of bracts per whorl is difficult to determine because of their lateral confluence into a collar or disc surrounding the axis, but 18 were counted in four different sections. This number can accurately be determined by a study of oblique tangential sections such as that shown in Fig. 10, where the vascular bundles of the sporophylls are evident, and the free tips of the bracts are exposed as transverse sections. There is always one vascular bundle per bract. The number 18 may have no significance, for the number of bracts per whorl seems to vary from 14-20 in undoubted specimens of *B. Dawsoni*. Transverse sections (Figs. 2, 3) show 18 rows of sporangia above the whorl of bracts which is also indicative of the number of bracts, as we will point out in the discussion of the sporangia. The pedicels are laterally coalescent through about one-third of their length, i.e., for about 2 mm.

The principal body of tissue of the pedicel is a strong

Plate III

Fig. 4. Radial section of cone showing attachment of sporangio-phore to sporangia. A sporangiophore of the third node is shown as it becomes free from the bract in "third position."

parenchyma continuous with and scarcely distinguishable from that of the outer cortex of the axis. Toward the distal end and in the more fragile laminal portion of the bract this parenchyma more nearly approximates the delicate tissue of the inner cortex of the axis. The thickness of the pedicel diminishes, accompanied by a decrease in number of cells from the point of attachment to the axis, where it is about 1 mm. thick, to about 0.5 mm. in thickness distally. One or two rows of smaller cells are immediately subjacent to the epidermis which is a clearly differentiated tissue.

The slender vascular bundle traverses the middle of the bract just below its upper surface. It is composed of but few elements, the smaller spiral members being exterior to the distinctly larger scalariform tracheids. This corroborates the statement made by Williamson and Scott (1894, p. 936) that the xylem of the leaf trace bundle is centripetal. The phloem must have been too delicate to be preserved for we have not been able to observe it.

Sporangiophores

The upper segment of the sporophyll may be divided two or three times and is usually much modified. The sporangiophores arise from the same node as do their counterparts, the bracts.

In our specimen the sporangiophore is a long (2.5-6.0 mm.), slender, stalk-like structure, about 0.1 mm. in diam. for most of its length. Usually the distal end (0.3-0.5 mm.) is gradually enlarged until it is about 0.4 mm. in diam. where it fuses indistinguishably with its sporangium. The sporangiophores in our species are always three times as numerous as the bracts, i.e., there are always three sporangiophores per bract. They arise separately, side-by-side on the bract surface and close to the axis (Fig. 10). In a tangential section through the cone near the axis, they first appear as mounds of tissue, slightly, yet distinctly delimited from the surface of the bract (Fig. 10). In a radial section of the cone, they appear as densely organized, radially elongated, ridges of special tissue which become separated from the bract surface within 0.3 mm. of the axis. This separation occurs in three distinct positions, i.e., axillary, between 0.1-0.15 mm. and 0.15-0.25 mm. for the three laterally adjacent sporangiophores of each bract. We have not been able to ascertain whether the sporangiophore which bears the innermost sporangium always arises in the same position, i.e., between the other two or on the right or left side of the bract base, etc. Neither have we been able to prove that the sporangiophore which first becomes free from the bract surface (Fig. 7) bears the first sporangium; that the sporangiophore arising in "second position" (Fig. 5)

Plate IV

Fig. 5. Radial section showing "third position" sporangiophore arising from the lowest bract, and "second position" on the middle and upper bracts. The fragment of the sporangiophore above the stub of the one on the middle bract belongs to it as is shown by serial sections. The outermost sporangium of the lowest bract has been cut quite obliquely and shows the peculiar nature of its epidermal cells. Dark areas below the point of juncture of the bract with the axis are vascular traces. (1706 R2).

always bears the second sporangium, and that from "third position" (Figs. 4, 5, 8) the outermost sporangium, but in several cases this is known to be true in our material. We have found no cases to the contrary. Due to the flexible nature of the sporangiophores and to the crowded conditions of the sporangia, the sporangiophores follow a tortuous course to their terminations and may therefore be traced only be observation of serial sections. Various accessory hooks and loops occur (Fig. 4). Above the third bract on the righthand side in Fig. 1, the single sporangiophore has been cut through, transversely, 4 times (Serial sections make possible the confirmation of their continuity).

The course of the mature sporangiophores generally extends along the upper surface of the pedicel to a point beyond their respective sporangia, where they rise vertically almost to the lower side of the superior whorl of pedicels, then become noticeably inflated or expanded and sharply recurved toward the axis (Figs. 1, 9). The epidermis, which is strongly differentiated throughout, becomes even more accentuated by an unusual increase in size of the cells and thickness of their walls in the terminal portion of the sporangiophore. These cells also seem to contain considerable organic residue.

In transverse section, the sporangiophores are usually rounded (Fig. 14) but occasional heart-shaped or even invaginated sections are found. These latter occur when two widely separated groups of (or single) epidermal cells seem to enlarge more than the others. The epidermis, which is occasionally more than one cell thick at the distal end of the sporangiophore, surrounds a weak hypodermal tissue which is only imperfectly preserved. Between this and the vascular bundle there is a space marking the former presence of delicate cortical tissue and phloem. The vascular bundle is apparently collateral and consists of several elements. The number of elements increases distally through the course of the sporangiophore until as many as 20 are present at the distal extremity. Most of the elements ~~are~~ have spiral thickenings, but occasional scalariform tracheids are found.

As already noted, the origin and nature of the sporophyll segments, their vascular bundles, and their method of division, has been subject to sharp controversy. Hirmer suggests that the leaf trace divides serially and occasionally collaterally as it enters the bractigerous disc to supply both the sporangiophore and bract, the two principal divisions of the sporophyll. In a series of sections taken from surface 1706a and others of our specimen, we have conclusive evidence that the vascular strand approached the node vertically and outwardly and at a point about 0.5 mm. from the angle formed by the attachment of the bract with the axis, it forked dichotomously, the outer (dorsal) strand passing out of the cortex into the bract without further division and the inner (ventral) portion undergoing two successive dichotomies to result in three equal vascular bundles. Each of the latter is separate and distinct before it emerges from the cortex of the axis. Further it has been possible to prove that the dorsal segment of the second dichotomy, i.e., the first serial division of the ventral strand which supplies the sporangiophores, supplied the sporangiophore which becomes free from the surface of the bract in the "third position" (Fig. 8). The dorsal (outer) segment resulting from the third dichotomy of the leaf trace always supplies that sporangiophore arising from the bract in "second position." The ventral or inner segment of the same serial division supplies the axillary sporangiophore. The sections 1706a 3-7 show this series completely.

The significance of these serial dichotomies is not definite. It will be recalled, however, that we have given evidence to the specificity of each sporangiophore with respect to the sporangia and to the position where it becomes free from the bract, viz. "axillary (first), second, or third position". sporangiophores, supply first, second or third (outermost) sporangia respectively. Such a development does not preclude the morphological interpretation of the origin of sporangiophores in Sphenophyllum as being bifurcations or segments of equal rank with the bracts (ventral segments) of the sporophylls (Hirmer, 1927, Fig. 420). Neither does it exclude the possibility that the most distal sporangium and its sporangiophore developed first from a new primordium and each of the more proximal sporangiophores represented a subsequent and equal development from additional axillary primordia (Troll, 1933, Text-fig. 5).

Troll and Goebel regard the development of sporangiophore arms in the Sphenophyllales as analagous to the development of the androecium of Hypericum sp. In the latter there appears to be a multiplication of the number of primordia rather than the serial division of a single primordium. They also believe that such additional primordia occur during especially favorable growth periods. Bower's term "pleiogeny" (1911, p. 289), which connotes an increase in number of parts beyond the normal or typical, would, according to Troll, be applicable to fructifications of the Sphenophyllales. He believes the theory of serial or collateral fission to be inadequate to explain the origin of sporangiophores, partially on the basis that no comparable living forms (including the Equisetaceae) possess serial division. His study of Equisetum, which served as a basis for such a statement, is of questionable value in view of the several outstanding differences between that genus and Sphenophyllum. Several of the living lycopods show structures which are clearly similar to those found in the sphenophylls. Living Equisetum is, at best, only distantly related to Sphenophyllum, and perhaps scarcely more closely related to it than certain Lycopods. Such an interpretation as Troll's involves the idea that each whorl of sporangiophores as well as the leafy-bracts arise from individual nodes, between which, the suppressed internodes are scarcely evident. This condition is characteristic of several allied genera such as Calamostachys, Paleostachya, etc. The solution of the problem of serial segmentation of leafy organs of plants is beyond the scope of this paper. Scott (1920, p. 94) states that the sporangiophores of Sphenophyllum fructifications are appendages of the bract from which they arise by evidence of both anatomy and position. He is also sure that Cheirostrobus sporophylls were first serially divided in two planes and later collaterally (palmately) segmented (Scott, 1920, p. 104). Hirmer (1933) is a proponent of this interpretation and in an answer to Troll's contention (1933) that serial segmentation is unknown in the plant kingdom but that pleiogeny is of normal occurrence he contends that certain living gymnosperms show serial segmentation.

The course of the vascular bundle and its method of branching, according to Troll (1933), is generally an indication of the nodal character in the above mentioned cones. Later in the same paper, however, he implies that the course of the vascular bundles of the Sphenophyllum cones cannot be used as a basis for argument. Hirmer (1933) remains resolute in his earlier postulation, which agrees with Scott's (1897, 1906), of the serial segmentation of the sporophyll into sporangiophores and bracts. The direct evidence of serial segmentation of the leaf trace in our specimen leads us to conclude, for the present, that the sporangiophores and bracts are derived from the bifurcation of the leaf trace and therefore belong to the same node, a characteristic which we believe to be of generic rank.

Sporangia

Three sporangia are borne linearly above each bract member of the whorl. They are not less than 1.7 mm. in shortest diameter and some are at least 2.4 mm. The sporangia are borne at the enlarged tips of the sporangiophores which bear the same relationship to them as the funiculus does to an anatropous ovule (Figs. 4,9). The sporangium rests directly on the surface of the bract below and reaches the base of the bract above. This condition shows clearly in true median

Plate V

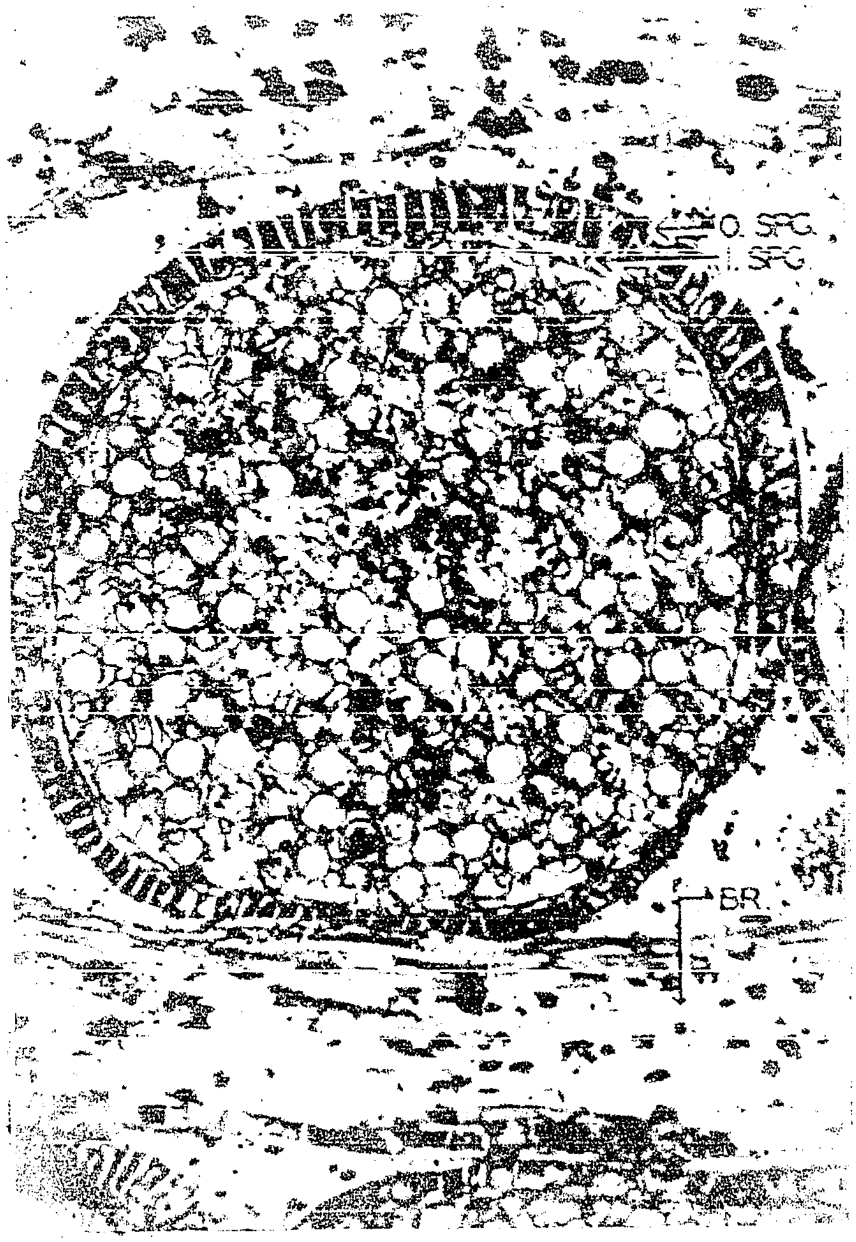


Fig. 6. Single sporangium shown in true median section. Note that it rests on the bract (BR) below and almost touches the one above. The crushed, delicate inner sporangial wall (I. SPG) is clearly visible. The general, gradual decrease in the size of the much-thickened cells of the outer sporangial wall (O. SPG) from the upper distal side to the lower and axial side is quite evident. (1706 R14).

section (Fig. 6) and in oblique tangential section (Fig. 10). The sporangiophore passes to one side or the other, sometimes causing a slight furrow (Fig. 10) on the lower side of the sporangium, and attaches to one side or the other of the top but never directly in the middle. The sporangia are crowded closely together and very rarely (Fig. 3) one of the sporangia in the inner of the three concentric verticels does not develop. In such a case, there are but two sporangia per individual bract. This spatial relationship results in a densely crowded cycle of sporangia nearest the axis, and the second and third verticels are successively less crowded. A comparison of Figs. 1 and 2 with Fig. 10 shows this character rather conclusively.

There is no justification, according to the general picture given by our material, for such an hypothetical areal distribution of sporangia as proposed by Hirmer (1927, Figs. 417, 419, 421). These figures are basically unsound and unfortunately misleading. In the first place, material figured by Binney (1871), Williamson (1874, 1876, 1890), Williamson and Scott (1894), Solms-Laubach (1896), Leclercq (1925), Koopmans (1928), and others shows a rather densely crowded organization and the resultant distortion which normally accompanies such crowding. Those figures show further that the space between the whorls of bracts is more or less

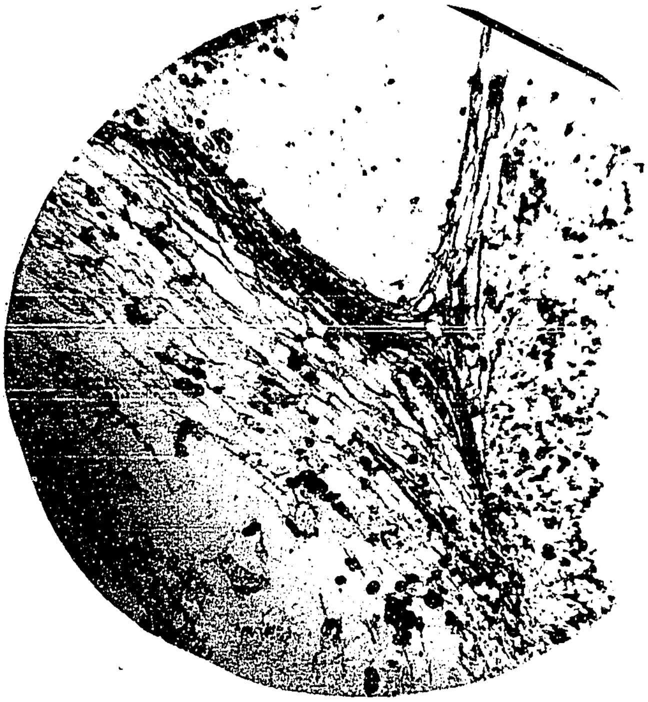
Plate VI

Fig. 7. Enlarged section showing attachment of bract to axis of the strobilus. The vascular bundle supplying the sporangiophore of "first position" (axillary) is not shown. The vascular bundle which seems to lead to it is shown in other sections to supply a sporangiophore which arises from the bract surface in "third position". Note the point of bifurcation of the bundle, one half of which supplies the bract. (1706 R16).

completely filled with sporangia. To attempt to project sporangia of normal size on the sporangiophores as shown in Hirmer's above mentioned figures would result immediately in the necessity of placing some above or below the others. Our figures as well as several of the figures already cited from other sources show this is not the case, but rather the sporangia are usually borne in a single plane above the bract. Exception to this is found in Bowmanites fertilis and perhaps B. Römeri.

The sporangial wall is made up of two principal layers. The outer, or epidermis, is comprised of large, greatly thickened cells. They are as large as, and continuous with those of the epidermis of the distal end of the sporangiophore, and are indistinguishable from them. There appears to be a gradual diminution in size of the cells of the sporangium in all directions from this point of attachment. The thickening is occasionally irregular and gives the superficial appearance of an annulus. Though such a structure has been suggested (Zeiller, 1893; Williamson and Scott, 1894), and is within the realm of possibility, serial sections of our material tend to show that the thin place in the sporangial wall (Fig. 14) is a groove apparently resulting from the proximal position of the sporangiophore as it circumscribes the distal side of the sporangium.

Plate VII



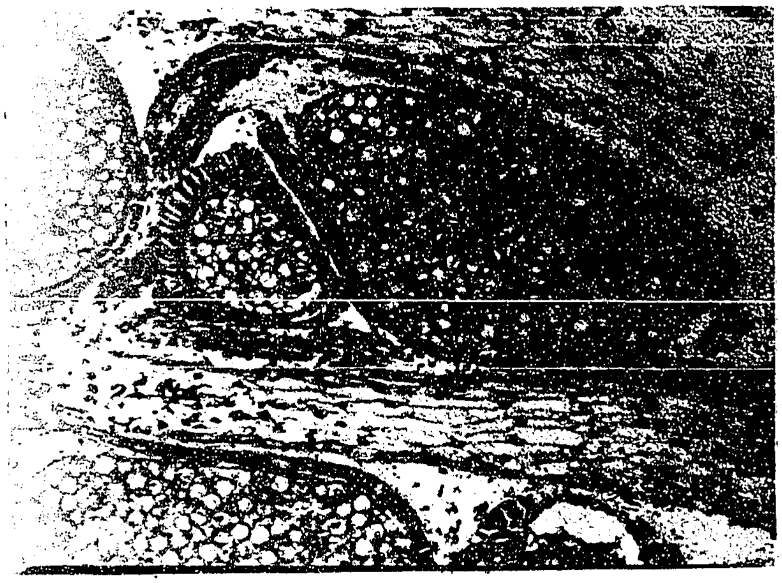


Fig. 8. The sporangiophore which is given off the bract (left) in third position is shown here to be supplied by a vascular bundle which is the adaxial (inner) segment of the division of the leaf trace (lower right).

Fig. 9. Enlarged sporangium showing increase in size of the sporangiophore as it rises from its bract component and extends to the base of the bract above and there bears the sporangium in an anatropous fashion. Due to the nature of the section, the sporangium appears pyriform. This is due to the attachment of the sporangiophore to one side or the other of the sporangium rather than directly in the middle of the distal side.

Fig. 10. Enlarged section of Fig. 15. Coalesced bract bases (collar) (at top of picture) show the fused sporangiophores as humps of tissue in this oblique section. In the lower whorl of bracts, (bottom) some separation is shown (lower right) into individual bracts. See discussion in text, pp. 40, 43, and 52.

The inner sporangial wall is made up of 2-4 layers of very weak, thin-walled, parenchyma cells which are usually collapsed. These are much smaller than the epidermal cells (Figs. 4, 6, 7, 9, 14) and are apparently continuous with and indistinguishable from the delicate inner tissue of the sporangiophore (Figs. 4, 9). The vascular bundle of the latter organ is terminated abruptly just before reaching the inner margin of the fragile hypodermal tissue. The termination of the vascular bundle is probably the only distinguishing point which marks the end of the sporangiophore.

The sporangia are densely packed with conspicuous spores which will be discussed in the following paragraphs.

Spores

Spores of Sphenophyllum fructifications have been figured by several authors. The highly characteristic ornamentation of the spore wall has been more or less confused. Williamson and Scott (1894, p. 939) state that "their cell-wall possesses a highly characteristic ornamentation, consisting of prominent spines, which are connected together on the external surface of the exosporium, by a reticulum of elevated ridges." Knox (1938, Fig. 120) shows a single spore taken from Bowmanites Dawsoni as having much enlarged, prominent spines, connected by lesser ridges. According to our material, from which

Plate VIII

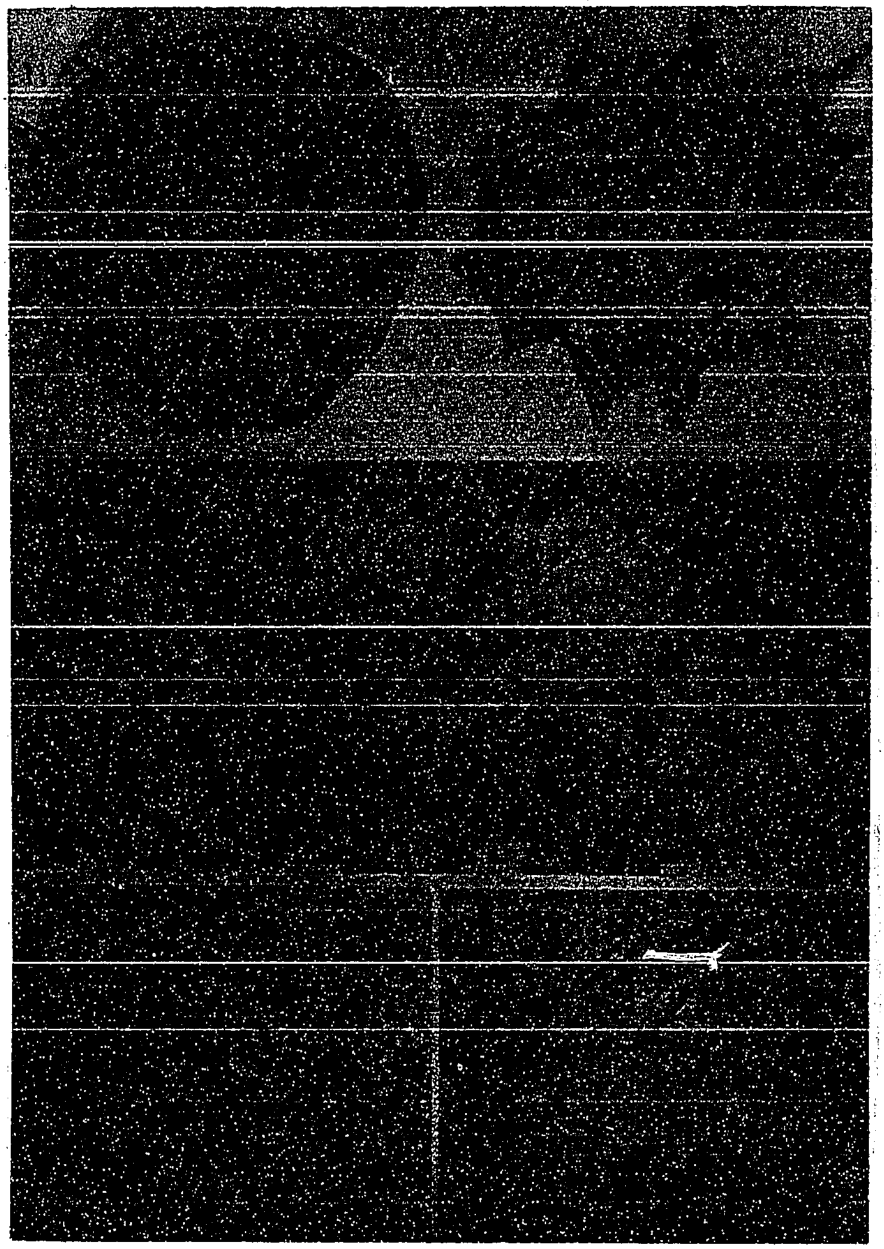


Fig. 11. Enlarged spore showing pustulose wall with good tetrad scar.
Fig. 12. Spore with falsely "spinose" appearance. Caused by a portion of the spore mother cell membrane persisting on its wall.
Fig. 13. Habit showing several types of spores in one small area. The spore to the left is very similar to that shown in Fig. 11 and the spore to the lower right corresponds to Fig. 12.
Fig. 14. Section showing difference in size of sporangiophores, depending on the proximity to point of attachment to sporangia.
Fig. 15. Oblique longitudinal section showing fusion of bracts into a collar at left. Note the deformity of the bract bases on the crushed side. Parts of three whorls of bracts are shown.

figures have been obtained (Fig. 13), that are almost identical with those shown by Williamson (1890, Figs. 17, 18) and those figured by Knox, this is not the case. Maceration of the sporangia and isolation of the spores show, rather, a continuous network of heavy ridges with a sort of bipolar orientation on the exine. The large "false spines" which are shown well in Fig. 12, which was taken from a thin section, appear to be fragments of the spore mother cell membrane. These prominences or bits of tissue are lost in maceration which further substantiates our interpretation. A definite tetrahedral dehiscence scar is usually present (Figs. 11, 13) on the intine as well as on the exine. The intine has a pustulose or granular configuration on its surface.

There is no evidence of heterospory in our specimen. The spores do have a variation in size form 95 μ to 124 μ exclusive of the ridges and "spines" in the same sporangium, i.e., as shown in Fig. 11. These ridges usually are not more than 15 high thus giving an overall diameter of about 130-140 μ to the spores. Renault's reported heterospory (1877) is known to be a misinterpretation. He considered a peculiar tangential section through a sporangium to be a section through a megaspore. Zobel's report of heterospory (1910) has been generally disproven. It is readily conceivable that some of the spore mother cells or even some of the individual members of the tetrad developed less completely than others, or were even completely abortive in a sporangium so tightly packed with spores.

Affinities

With all these characters in mind we feel that our specimen is distinct from previously reported fructifications. We therefore designate it as a new species.

In an attempt to name, classify and correlate it with other Sphenophyllum fructifications we became aware of serious discrepancies and conflicts in previous reports. Further we were unable to discover the consistent use of clearly distinctive characteristics in previous descriptions of new species. In order to positively place our specimen on record it then became necessary to investigate all the previous reports of fertile shoots of Sphenophyllum, and to show the more evident discrepancies and points of confusion. The following discussion will give adequate justification to our contentions and make possible the revision of the entire genus. Following that revision, as complete a description as possible is given of all previously reported species, and the type description and name of our new species is there included.

Discussion

In the attempt to classify our specimen as a species of the fructifications of Sphenophyllum we encountered great difficulties because of the present confused status of the classification of these fossils. To begin with, the name Sphenophyllostachys as applied to the cones of the genus Sphenophyllum only recently gained favor among leading paleobotanists (Hirmer, Zimmerman, Walton). This name, though recognized at its inception by Seward (1898) as a sesquipedalian one, would normally be acceptable because of its basic meaning, i.e., designating the cones or strobili of the Sphenophyllales. Unfortunately, for reasons of priority, the validity of the name is questionable.

According to the present rules of botanical nomenclature, and more especially those pertaining to paleobotany, we are obliged to use the first name applied to a plant or group of plants since 1820, the date selected for absolute priority of fossils, as long as this name has been validly published, unless strong evidence is submitted that any change of a name well established by long and consistent usage would create serious confusion. In such a case steps could be taken to have that name retained as a *nomen conservandum*.

For reasons well known to all who work with the fragmentary remains of fossil plants, it is necessary to set forth generic designations for various plant organs as well as for entire plants. Obviously this necessity poses additional taxonomic complications but in reality is a convenient simplification of the task of assigning organs or fragments of organs to the plants which bore them. Although organic connection is the only proof of definite relationship, evidence of an organic connection between two plant fragments in one case may not be regarded as proof of the fact that all similar specimens must bear identical relationship. The reason for this awkward situation is the necessity of considering the time relationship in addition to the geographic and structural relationships. However, we do not doubt that the cones considered in this paper represent the well known and important Paleozoic cone genus belonging to Sphenophyllum.

In his excellent memoir (1893) Zeiller claimed that certain previously described fructifications were undoubtedly those of Sphenophyllum and that the Bowmanites Dawsoni Williamson cones as well as certain others, except two, known only from impression material were, like some leaf remains, referable to Sphenophyllum cuneifolium. This interpretation was generally considered sound and was subsequently adopted in principle by various authors (Williamson and Scott, 1894; Seward, 1898;

Kidston, 1901; Scott, 1905, et al.). The statement that all similar specimens from horizons widely separated geologically and geographically are similarly related is untenable. Recognizing this difficulty, Seward (1898) proposed the distinct organ genus Sphenophyllostachys for the cones assignable morphologically and/or anatomically to the genus Sphenophyllum, but whose organic relations with the plants could not be shown. However, at least two other generic names had been created earlier than Seward's for cones now known to have sphenophyllaceous affinities.

Volkmannia Sternberg (1825), one of these early cone genera, included elongated, distichous cones arranged either on lateral branches or at the tips of stems. Most of the diverse specimens included in this heterogeneous group were correlated with vegetative remains of Asterophyllites, others with Calamites and a few Sphenophyllales. The first species described, V. distachya Sternberg (1825), was later (1833) referred by the same author to V. arborescens, which has since been transferred to Calamites arborescens. Later Geinitz (1855) and Feistmantel (1869) called it the fructification of Asterophyllites foliosus and finally the latter author (1872) believed it to be identical with Macrostachya gracilis Stur. The second species of Volkmannia originally described by Sternberg was V. polystachya. Apparently it is now referable to Calamostachys polystachya, although it has also been considered as the fructification of Asterophyllites rigidus and classified under the generic designations of Bruckmannia, Calamites, Paracalamostachys, Asterophyllites, and Palaeostachya.

Under the present rules of nomenclature Volkmannia, then, should be applied to the cones of the type which were originally described when this generic name was proposed. Calamostachys, which was created by Schimper (1869) for a portion of Volkmannia, and which is now known to include Sternberg's original type material, should rightfully be reduced to synonymy. There is no justification for retaining a name of the basis of "euphony" (Seward, 1898, p. 351) nor on the basis of clarity as suggested by Schimper (1869). However, the long acceptance and present widespread, uniform application of the name Calamostachys, and the obvious implications of the relationship of this organ genus to Calamites are probably sufficient grounds for recommending the retention of this name. In such a case, other forms which were erroneously included under the name Volkmannia may not retain the name, even after the complex assemblage of unrelated forms has been transferred elsewhere. Once the type material is removed from a genus, there is no further basis for retaining the name and it should then be considered a nomen rejiciendum. Therefore the inclusion under the name Volkmannia of various species now recognized as fructifications of Sphenophyllum, such as V. Dawsoni, cannot justify the retention of the name as valid for Sphenophyllum fructifications.

Taxonomic Treatment

Bowmanites (Binney) Hoskins and Cross, emend.

1871 Bowmanites Binney, Paleont. Soc. 1870:59-60, pl. XII, figs. 1, 1a, 1b, 1c, 2, 3.

1822 Sphenophyllites Brongniart, Class. d. végét. foss.: 9, 34;(pro parte).

1823 Rotularia Sternberg, Essai flora monde prim. 1(2):34, 37; 1(4):32;(pro parte).

1825 Volkmannia Sternberg, Vers. ein. geogn.-bot. Darst. d. Flora d. Vorwelt. Fasc. IV. I, 4:42. Tentamen p. XXIX. (pro parte).

1828 Sphenophyllum Brongniart, Prodrome. p. 68. (pro parte).

1898 Sphenophyllostachys Seward, Fossil Plants 1:401-402.

1909 Monosphenophyllum Lotsy - Vorl. ü. Bot. Stammesgesch. 2:525, fig. 349, III.

1909 Disphenophyllum Lotsy - Ibid. 2:525, fig. 349, IV.

1909 Difurcosphenophyllum Lotsy - Ibid. 2:525, fig. 350, II 1, 2.

1909 Tetrasphenophyllum Lotsy - Ibid. 2:525-526, fig. 350, III.

Sporophylls verticillate, either arranged in true cones or in a series of loose whorls alternating with vegetative leaves, borne terminally or on lateral branches, usually less than 2.5 cm. in diam. and 10 cm. in length, homosporous; compactly organized or lax, usually covered with the overlapping laminae of successive whorls of sporophylls or sometimes only by peltate expansions of sporangiophores (B. fertilis, B. Römeri ?); axis small with small hexarch or triarch xylem surrounded by a weak parenchyma and a stronger outer cortex. Single vascular strands are given off at each point of the xylem which divide as they traverse the cortex in an upward direction to supply each leaf member of the whorl. Before entering the leaf the vascular bundle divides into an inferior (dorsal) strand which passes into the sterile bract and extends distally at least to its lamina (if present), and a superior (ventral) strand which may divide (probably dichotomously) once or twice to give rise to the individual vascular bundle which traverses the entire length of each sporangiophore and terminates abruptly at the point of attachment to the sporangium.

Sporophylls usually much modified, though some are indistinguishable from vegetative leaves, usually superimposed, always consisting of a sterile dorsal (inferior) segment and one to several, branched or unbranched, ventral (superior) segment or segments, the sporangiophores, which bear distally small (0.5-3.0 mm.), elongate-ovoid (often distorted) sporangia, either singly or in pairs, from infundibuliform or peltate expansions. Bases of sporophylls (bracts) fused into a collar-like disc; tips free. Sporangiophores, though anatomically distinct when they emerge from axis, arise from the superior surface of the disc (fused bract bases) near the axis and bear their sporangia in one plane in one to several concentric cycles above each node (except B. fertilis).

Sporangial wall of two layers, the outer with large cells greatly thickened on their inner and lateral walls, the inner layer of two to four rows of delicate cells which appear to be continuous with the parenchyma of the sporangiophore. Sporangia densely packed with large numbers of isosporous spores which may vary slightly in size in the same species. Spores usually with a ridged (falsely spinose) exine and a more delicate intine with triradiate tetrad scar often present.

At present 18 species are recognized as valid; borne on plants known by leaf impressions or stem anatomy as Sphenophyllum.

The outstanding characters which delimit this genus from other allied genera (Calamostachys, Cheirostrobus, Cingularia, Paleostachya, et al.) are its homospory, the division of fertile bracts into a sterile dorsal sporophyll and a fertile, ventral sporangiophore(-s), the pedicellate or stalked nature of the sporangia, the configuration of the spores and the triarch or hexarch nature of the xylem of the axis.

Known as compressions, casts and petrifactions from North America, Europe, Asia and the East Indies.

Bower and others (Bower, 1935, pp. 151-152; Seward, 1910, p. 7; Walton, 1940, p. 70) suggested that the organ genus for fertile shoots related to Sphenophyllum is heterogenous and that certain forms should be removed from it in view of their apparent morphological differences. But after a careful investigation of most of the records of fertile shoots of Sphenophyllum and an analysis of the group as a whole, we concluded that Bowmanites is a homogeneous organ genus and prepared the above generic description in accordance with this interpretation.

Further, on the basis of the number of sporangia borne on every sporangiophore, the species here included in the genus Bowmanites can be placed in the following three distinct sections, i.e., Simplices, Jugati and Conferti. Descriptions of these sections are given below and are followed by a key to the valid species, each of which is then described as fully as possible.

Section *Simplices* Hoskins and Cross

Sporophylls arranged in distinct cones or alternating with sterile bracts from which they may or may not be distinguishable. Always one sporangium borne (often in an anatropous fashion) at the enlarged distal end of a more or less elongated sporangiophore; one to five sporangia per bract arranged in as many concentric verticels in one plane above each whorl of sporophylls.

Section *Jugati* Hoskins and Cross

Sporophylls morphologically different from sterile leaves and always arranged in distinct cones. Sporangia borne in pairs on a distal, peltate expansion of the branched or unbranched sporangiophore. Two to thirty-four sporangia per sporophyll, often not arranged in a single plane but densely packed between two successive whorls of sporophylls.

Section *Conferti* Hoskins and Cross

Sporophylls never arranged in distinct cones and often indistinguishable from sterile leaves. Sporangia borne in clusters of four on a terminal disc-like expansion of the sporangiophore. Four to eight sporangia (one or two clusters) per sporophyll arranged in a single plane above the sterile pedicel.

Key to the species of Bowmanites

I Sporangia borne singly on sporangiophores --- Section Simplices

a Mostly one or two (rarely three) sporangiophores per bract.

b Always one sporangiophore per bract and one whorl of sporangia per node.

c Sporangia borne on elongate sporangiophore

--- B. simplex (1)

cc Sporangiophore very short; sporangia appearing sessile.

d Sporangia borne axially; sporophylls moderately curved and short.

--- B. trichomatosus (2)

dd Sporangia borne somewhat distally on pedicel. Lamina of sporophyll vertical to pedicel and extended below it to form a spur or heel.

--- B. angustifolius (3)

bb Usually two sporangiophores per bract (sometimes one or three).

c Two (rarely one) whorls of sporangia per node. Cone small. Stele triarch in petrified specimens.

d Petrifactions; sporangiophores greatly elongated. --- B. Scottii (4)

dd Compressions; sporangiophores short.

e Cones small, compact; sporophylls much dissected.

--- B. tenerrimus (5)

ee Cones 5-8 cm. long, lax; sporophylls not dissected. --- B. gracilis (6)

cc Two, whorls of sporangia per node (sometimes three whorls on the same cone). Cones large, if present; stele hexarch in petrified specimens.

d Fertile bracts arranged in definite cones

e Petrifactions --- B. Dawsoni (7)

ee Compressions

f Westphalian A, B, and perhaps C. --- B. cuneifolius (8)

ff Stephanian or Westphalian D

--- B. verticillatus (9)

dd Fertile bracts not arranged in definite cones. --- B. charaeformis (10)

aa Always three or more sporangiophores per bract. Sporangia always in three or more verticels in one plane per node.

b Three concentric verticels of sporangia per node.

--- B. trisporangiatus (11)

bb Four or more concentric verticels of sporangia per node --- *B. cambrensis* (12)

II Two or more sporangia borne on each sporangiophore.

a Sporangia borne in pairs on sporangiophores --- Section *Jugati*

b Sporangiophores unbranched;

c Usually 3 per sporophyll --- *B. Römeri* (13)

cc Usually 1 per sporophyll --- *B. laxus* (14)

bb Sporangiophores much branched; 14-18 per sporophyll. --- *B. fertilis* (15)

aa Sporangia borne in clusters of four on each sporangiophore --- Section *Conferti*

b One sporangiophore per bract terminated by a large (one cm.) disc which bears the sporangia. --- *B. Kidstoni* (16)

bb Two sporangiophores per bract terminated by a much reduced disc (sometimes only a point of coalescence of sporangia bases).

c Sporangiophores and groups of sporangia in two concentric whorls per node; arising serially on undivided bracts --- *B. major* (17)

cc Sporangiophores arising singly on adjacent halves of each bract forming one concentric whorl of sporangiophores. --- *B. tenuissimus* (18)

Description of Species

(1) Bowmanites simplex Hoskins and Cross, spec. nov.

1877 Sphenophyllum sp. Renault, Ann. Sci. Nat. Bot., sér. 6, 4:303-304, pl. 9, figs. 9-11.

1882 Sphenophyllum sp. Renault, Cours Bot. Fos. 2:102-103, pl. 15, figs. 7-8, pl. 16, figs. 3.

1893 Sphenophyllum sp. Zeiller, Mem. Soc. Géol. France, Paleont. Mem. 11:28-30, pl. V, figs. 5, 5A, 5B, 5C, 5D.

1893 Sphenophyllum sp. Zeiller, Ibid:34-36.

Cones very small, 11 mm. long x 3-5 mm. diameter. Subglobose sporangium borne singly on short sporangiophore which is attached to it as in B. Dawsoni; one per bract borne a short distance from axis. Spores very small; configuration unknown. Sporophylls inserted on the axis at an angle of 90°. Pedicels of sporophylls about 1 mm. in length and laminae arise vertically for about 2 millimeters.

One concentric whorl of sporangia above each whorl of bracts, the small size, and the prominent insertion of the sporophylls at right angles are the distinguishing features. These specimens also occur much later geologically, i.e., Upper Carb. (Stefanian), than B. Scottii and B. Dawsoni.

Plate IX

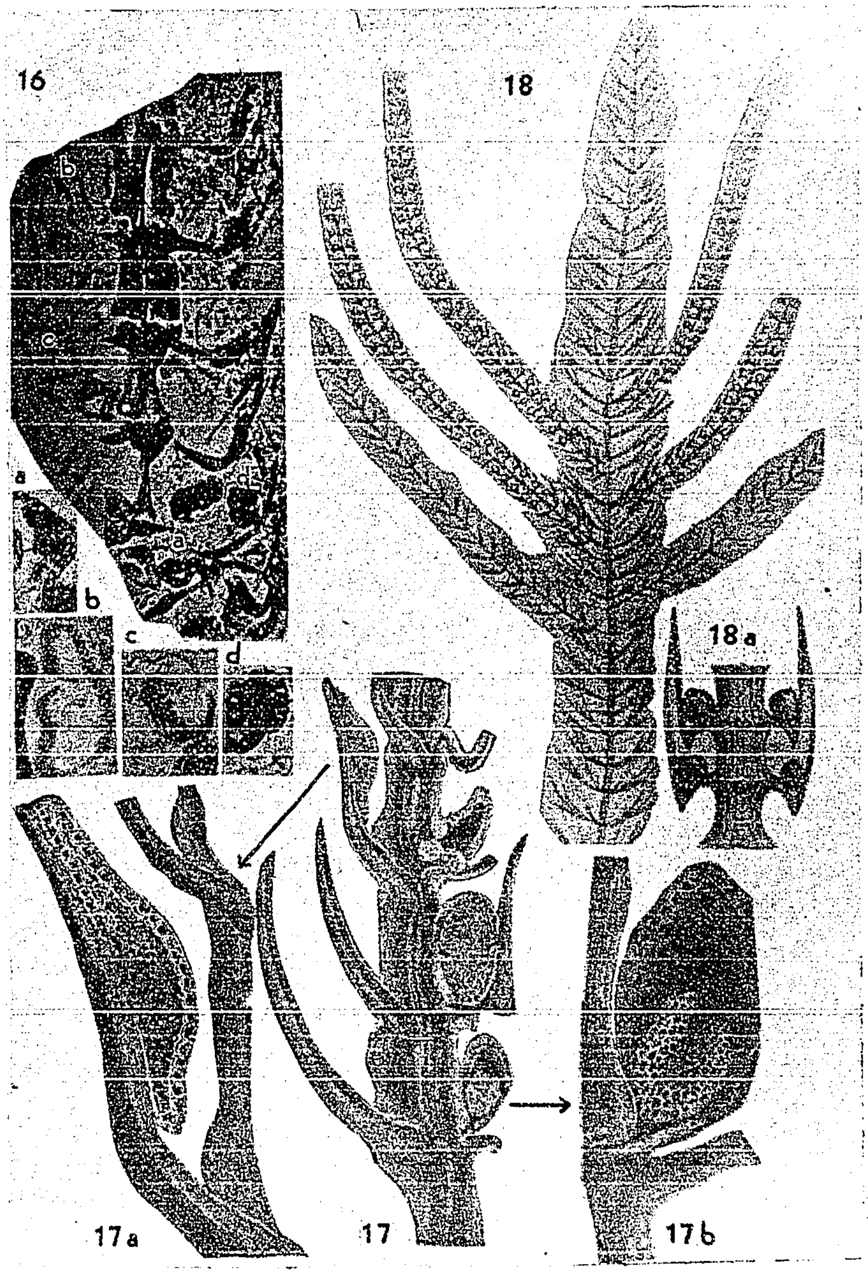


Fig. 16. Longitudinal (near radial) section of Bowmanites simplex. (After Zeiller, 1893). a, b, c, and d, are sections of the much broken and distorted sporangia. Cotype.
Fig. 17. Cotype of B. simplex (After Renault 1877). 17a shows a much flattened sporangium and a bract. 17b was interpreted by Renault as a megaspore. The peculiar epidermal cells of the sporangium often present such a picture (see Fig. 5). Both these specimens were found by Renault though Zeiller studied the one figured in Fig. 16.
Fig. 18. Bowmanites angustifolius (After Schimper, 1874). Note the heel at the end of the pedicel and the base of the lamina.

Stefanian (Grand Croix); silicified magmas near Saint-Étienne, France.

Petrifactions (Only two specimens known.)

(2) Bowmanites trichomatosus (Stur) Hoskins and Cross, comb. nov.

1882 Sphenophyllum tenerrimum Weiss, Aus. Steink.: 12, pl. X, fig. 63; not Ett.

1884 Sphenophyllum tenerrimum Weiss emend., Abhandl. geol. Specialk. v. Preussen u. d. Thüringischen Staaten. 5(2):199, pl. XVI, figs. 4-5.

1887 Asterophyllites trichomatosus Stur, Abh. k. k. Geol. Reichsanst. Wien 11(2):202, pl. 15, figs. 1-4.

1887 Sphenophyllum trichomatosum Stur, ibid

True cones formed. Sporangia ovoid, borne singly and nearly sessile (probably borne on short sporangiophore) one per sporophyll, a short distance from the axis. Bracts or sporophylls not sharply bent up at distal extremities but rather gently curved from horizontal portion (pedicel). Usually considered to be sessile but better material may show sporangiophores present, a characteristic of the genus.

Carboniferous; Karwin, Karlsflötz; Dombrau. f. 2, 3.; Austria.

Yorkian (M. Coal-measures); Cooper's pit, Worsbro' Dale, Barnsley, Yorkshire. Shale and rock over Barnsley "Thick Coal" (Kidston's material).

Westphalian B; South Wales.

Suchaer (U. Westphal A); Ostrau-Kerwnir, etc.

Compressions.

(3) Bowmanites angustifolius (Germ.) Hoskins and Cross. comb. nov.

1848 Sphenophyllites angustifolius Germar, Verstein. Steink. Wettin u. Löbejün: 18, pl. VII, figs. 4-7.

1850 Sphenophyllum angustifolium Unger, Gen. et Sp. Plant. Foss.: 71.

1864 Sphenophyllum angustifolium (Ung.) Coem. and Kx. emend., Monographie Sphen.: 26, pl. I, figs. 7, 7A, 7B.

1869 Sphenophyllum angustifolium (Germ.) Schimper, Traité Paléont. Végét. 1:343-44, Atlas: pl. 25, figs. 1-4.

1882 Sphenophyllum angustifolium Germar, in Renault, Cours Bot. Fos.: 88-89, pl. 13, figs. 19-23.

Cones definite, lax, elongated (10 cm. ±), slender, borne as fertile lateral branches of indeterminate growth. One subglobose sporangium per bract borne probably on a short sporangiophore which is attached to the upper surface of the bract near the axis. (Possibly in older specimens the sporangiophore as well as the bract elongated and thus the sporangium itself is not borne in an axillary position but, rather, distally upon the pedicel). Distal portion of sporophyll pedicel appears cupped, having (externally) the appearance of a heel. Probably 6 bracts per whorl.

U. U., Carb. or Permian (Stephanian or Rothliegendes); South Wales, Germany.

Compressions.

(4) Bowmanites Scottii Hoskins and Cross, spec. nov.

1895 Sphenophyllum Dawsoni (Will.) Will. and Scott, Phil. Trans. Roy. Soc. London. B. 185:933-959, pls. LXXVI and LXXXV, figs. 26 and 54.

1898 Sphenophyllostachys Dawsoni (Will.) Seward, Fossil Plants 1:401; (ex parte).

1908 Sphenophyllum Dawsoni (Will.) Will. and Scott, forma beta Scott. Studies in Foss. Bot., 2nd ed., 1:100, 102-106, fig. 42.

1909 Monosphenophyllum Dawsoni (Will.) Lotsy, Vorl. über Bot. Stammesgesch. 2:525, fig. 349, III. (pro parte).

1920 Sphenophyllum Dawsoni (Will.) Will. and Scott, forma beta Scott. Studies in Foss. Bot., 3rd ed., 1:89, 92, 94, fig. 91.

1925 Sphenophyllum Dawsoni β. Will., in Leclercq, Mém. Soc. Géol. Belgique:34.

1925 Sphenophyllum Dawsoni β. Schimp., in Leclercq, ibid. pl. VII, figs. 5, 5a.

1927 Sphenophyllostachys Dawsoni (Will.) Seward, forma β. Scott, in Hirmer, Handb. Paläobot. 1:356-57, not Sph. Dawsoni β of fig. 416.

Definite cones small, over 15 mm. long x 5.5 to 6.5 mm. in diam. Globose (sometimes distorted) sporangia (about 0.5-1.0 mm. in diam.) borne singly on elongated sporangiophores, 2 per bract (rarely one) in 2 concentric verticels between each two whorls of sporophylls. Sporangiophores slender (0.15 mm. in diam.) where they arise from the superior surface of sporophylls near the axis; inflated or swollen (0.4 mm. diam.) where they join the sporangia. Sporiangium suspended like an anatropous ovule in regard to its funiculus. Spores spherical, 65-85 μ in diam.

including anastomosing ridges of exosporium which give a false spinose appearance. Sporophylls about 15 per whorl, elongated, curving gently upwards distally and overlapping laminae of several superior verticels; fused at base into narrow collar and inserted on the axis at the nodes at an angle of about 45°; about 5 whorls per centimeter of the axis. Associated with Sphenophyllum plurifoliatum Will. (= S. myriophyllum Crépin).

This species essentially similar in anatomy to Bowmanites Dawsoni (Will.) Weiss except for its triarch xylem (instead of hexarch), its smaller number of sporangia between each 2 whorls of bracts, and its generally smaller size.

L. Coal-measures; Halifax, England.

Bouxharmont beds; Werister, Belgium.

Petrifactions.

(5) Bowmanites tenerrimus (Ett.) Hoskins and Cross, comb. nov.

1854 Sphenophyllum tenerrimum Ettingshausen, Abh. k. k. Geolog. Reichsanst. 2(3):30-31; (pro parte).

1874 Sphenophyllum tenerrimum (Ett.) Helmhacker, Berg - und hüttenm. Jahrb. 22(1):50-53, pl. III, figs. 14, 15.

1877 Sphenophyllum tenerrimum (Ett.) Stur, Abh. k. k. Geol. Reichsanst. 8(2):108 (214), pl. VII. figs. 12-14.

Cones compact, very small, terminal. Sporangia, probably on short pedicels, arranged in one or two concentric verticels per whorl of bracts; axillary in position. Essentially similar (though smaller) to Bowmanites cuneifolius but for one outstanding feature, i.e., the leaves are greatly dissected and ultimate segments are linear and ribbon-like. A ridge or fold on the dorsal and distal side of the pear-shaped sporangia indicates position of sporangiophore.

U. U. Carboniferous; (Kulm) Austria.

L. Namurian (A); Silesia.

Compressions.

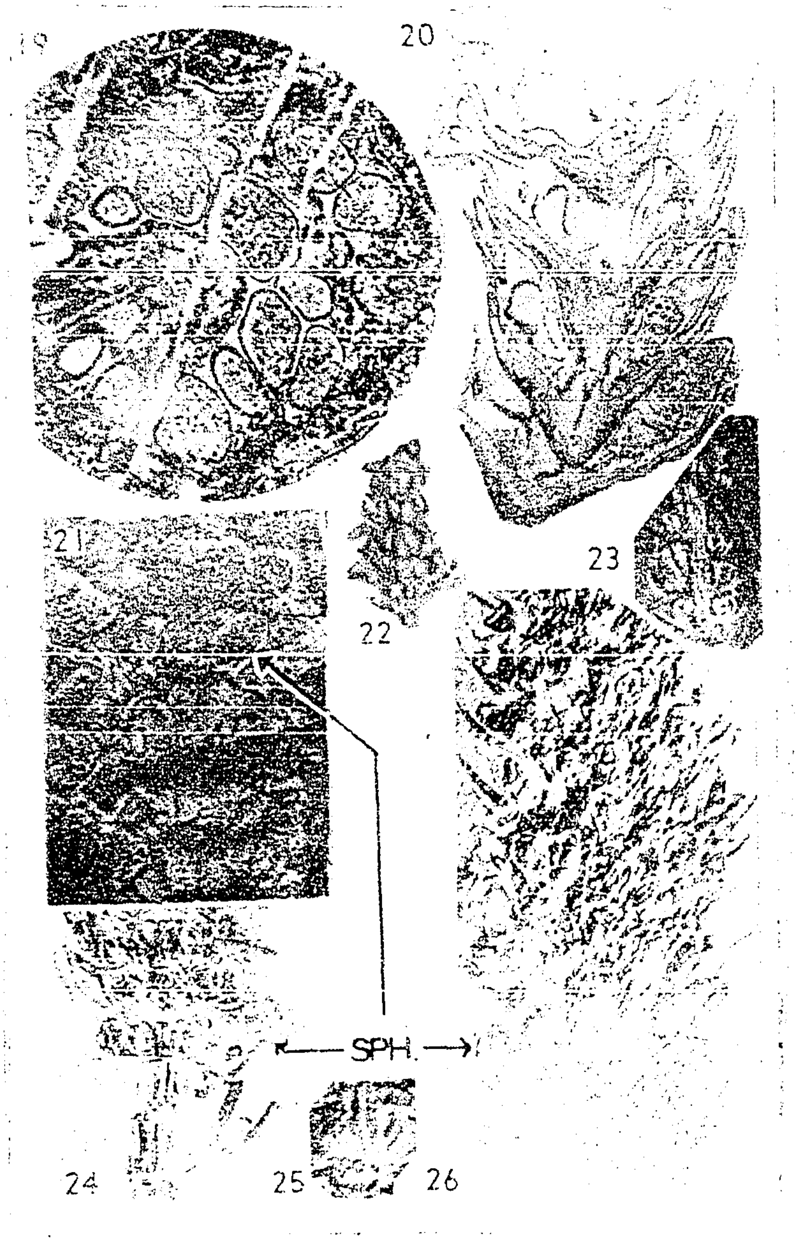
(6) Bowmanites gracilis (Crépin) Hoskins and Cross, comb. nov.

1880 Sphenophyllum gracile Crépin, Bull. Soc. Roy. Bot. Belgique, sér. 2, 19:8-10.

1893 Sphenophyllum gracile (Crépin) Zeiller, emend. Mém. Soc. Géol. France, Paleont. Mém. 11, 4:25-26. Text-fig. H.

Cones, known only from impressions, lax, 5-8 cm. long, 3-5 mm. wide, probably covered with overlapping laminae. Ovoid sporangia

Plate X



Figs. 19, 20. Obliquely transverse and longitudinal sections of B. Scottii after Williamson and Scott, 1894.
Fig. 21. Bowmanites gracilis. Note sporangiophore (SPH) bearing sporangia in typical fashion. (After Zeiller, 1893.).
Fig. 22. B. tennerimus according to Stur. (After Renault, 1882).
Fig. 23. Bowmanites sp. Kawasaki (1931, Fig. 20). Possibly B. simplex or B. trichomatosus, but certainly a member of the Simplices.
Figs. 24-26. Bowmanites cuneifolius after Zeiller, 1893. The sporangiophores (SPH) and sporangia in two's on each bract shows clearly. Fig. 25. shows a single whorl of bracts with sporangia removed showing cup-like fusion of the several bracts into a collar.

borne singly on short, thick sporangiophores, probably 2 (sometimes 1) per bract in one or two concentric verticels between two whorls of 6 leaves each, per node. Morphologically these cones resemble those of Bowmanites Scottii and even the dimensions of the comparable structures of the two agree fairly well with one another. The specimens studied by Zeiller seem to indicate that at least some of them were immature.

Carboniferous (Charbonnages des Produits); Belgium

Compressions.

(7) Bowmanites Dawsoni (Will.) Weiss, Abhandl. geol. Specialk. v. Preussen u. d. Thüringischen Staaten 5(2):200-202. 1884.

1871 (1876) Volkmannia Dawsoni Williamson, Mem. Lit. and Phil. Soc. Manchester, ser. 3, 5:28-40, pl. I-III, figs. 1-7.

1893 Sphenophyllum cuneifolium Zeiller, Mém. Soc. Géol. France, Paléont. Mém. 11, 4:1-39, pl. II, figs. 1-3, pl. III, figs. 1, 2; (pro parte).

1895 Sphenophyllum Dawsoni (Will.) Will. and Scott, Phil. Trans. Roy. Soc. London B 185:933-959, pl. LXXVI, fig. 25; pl. LXXXV, figs. 55-58, (pro parte).

1898 Sphenophyllostachys Dawsoni (Will.) Seward, Fossil Plants 1. 401; (pro parte).

1901 Sphenophyllum cuneifolium (Sternb.) Kidston, Trans. Nat. Hist. Soc. Glasgow. 6(1):124-27, fig. 23; (pro parte).

1908 Sphenophyllum Dawsoni (Will.) forma α. Scott, Studies in Foss. Bot., 2nd ed. 1:100, 102-106, fig. 43.

1909 Monosphenophyllum Dawsoni (Will.) Lotsy, Vorl. ü. Bot. Stammesgesch. 2:525, fig. 349, III; (pro parte).

1914 Bowmanites Dawsoni Will., in Pelourdé, Paléont. Végét.: 70.

1920 Sphenophyllum Dawsoni (Will.) forma Scott, Studies in Foss. Bot., 3rd ed., 1:92-96, fig. 46.

1927 Sphenophyllostachys Dawsoni (Will.) Seward forma α Scott et forma β Scott, in Hirmer, Handb. Paläobot. 1:355-56, figs. 416-418; not Sph. Dawsoni (Will.) Seward forma β Scott, ibid.:356, line 15 to end of page.

1940 Sphenophyllum (Sphenophyllostachys) Dawsoni (Will) Will. and Scott, in Walton, Fossil Plants:70-72, fig. 47.

Cones large, 10-12 mm. or more in diam., several cm. long; axis 2.5 mm. diam.; hexarch xylem characteristic. Subglobose sporangia (sometimes distorted) borne singly, in an anatropous fashion (i.e. pendant and suspended on the sporangiophore from its adaxial side), usually 2, sometimes three per bract, disposed in two (or occasionally three) concentric verticels above each whorl of bracts; 1-2 mm. in diam. (±). Sporangiophores long, slender, 0.15 mm. in diam. where they become free from surface of bract and inflated (or infundibuliform) to about 0.4 mm. in diam. where they fuse with the wall of sporangia which is apparently one layer of cells thick. Spores, 75-100 μ in diam. (average for 12 specimens) including ridged exosporium, appear spinous in cross section and possess a tetrahedral scar on endosporium. Sporophylls (bracts) 14-20 per whorl fused into a collar at their bases, inserted at an angle of about 30° and curving gently upward; laminae overlapping several superior whorls; bundle divides upon entering collar of fused bracts giving rise to a strand for its respective bract and another strand which bifurcates again and supplies the two sporangiophores. Associated indirectly but rather conclusively with vegetative remains of *Sphenophyllum cuneifolium*.

The special features of this species are the large size of its cones, the presence in most cases of two sporangiophores per bract, and the hexarch xylem. By comparison *B. Scottii* has smaller cones and a triarch xylem, whereas *B. trisporangiatus* is generally larger and has ordinarily three whorls of sporangia per node.

L. Coal-measures; Halifax, Oldham, Shore, Stalybridge and Bacup, Great Britain.

Finefrau-Nebenbank; Netherlands.

Petrifactions.

(8) Bowmanites cuneifolius (Sternb.) Hoskins and Cross, comb. nov.

1823 Rotularia cuneifolia Sternberg, Versuch I. Fasc. II:33, pl. XXVI, figs. 4a and 4b.

1880 Sphenophyllum cuneifolium (Sternb.) Zeiller, Végét. foss. du terr. houil. de la France:30, pl. CLXI, figs. 1, 2. (pro parte).

1884 Bowmanites germanicus Weiss, Abhandl. geol. Specialk. Preussen u. d. Thüringischen. 2:201 (287), pl. XXI, fig. 12.

1893 Sphenophyllum cuneifolium (Sternb.) Zeiller, Mém. Soc. Géol. France, Paléont. Mém. 11, 4:1-39, pl. I, pl. II, figs. 1-3, pl. III, figs. 1-2.

1911 Bowmanites germanicus Jongmans, Meded. Ryks. Ops. van Delfs 3:417, fig. 391.

Cones definite, lax, more than 1 cm. in diam. and up to 10 cm.

in length. Known as impressions from essentially the same horizons as B. Dawsoni and probably identical with it. Two (sometimes three) concentric whorls of sporangia borne on elongated pedicels which arise from the superior surfaces of the 14-20 bracts which are fused into a collar or cup at their bases, and are extended vertically, their linear lanceolate tips overlapping several superior whorls.

The specimens of Weiss and Jongmans, i.e., B. germanicus Weiss, are somewhat smaller than the cones usually found on undoubted Sphenophyllum cuneifolium stems and the sporangia are markedly smaller but they are possibly immature. Because the petrified specimens of undoubted B. Dawsoni have not been found in connection with vegetative parts of Sphenophyllum cuneifolium Sternb., it is best not to combine here that species with Bowmanites cuneifolius.

M. and L. Coal-measures; Great Britain.

Westphalian A; French and Belgian coalfields.

M. U. Carboniferous; Germany.

Compressions.

(9) Bowmanites verticillatus (Schloth.) Hoskins and Cross, comb. nov.

1804 Sphenophyllum verticillatum Schlotheim, Flora d. Vorwelt: 57, pl. 2, fig. 24.

1837 Sphenophyllites Schlotheimii Germar, Isis: 425, pl. 2, fig. 1, a, b.

1855 Sphenophyllum emarginatum Brongt., in Geinitz, Die Verst. der Steink. form in Sachsen: 12, pl. 20, fig. 7.

1883 Sphenophyllum emarginatum Brongt, in Schenk, Pflanz. Verst. Richt. "China" 4:220, pl. XXXVIII, fig. 1.

1910 Sphenophyllum verticillatum Schloth., in Zobel, in Potonié, Abb. und Beschr. No. 138: 1-10, figs. 1-7.

Two types of cones postulated; if actually present, this species would be the only established heterosporous member of the genus. Female cones similar in structure to the cones of Bowmanites cuneifolius (scarcely distinguishable from the immature specimens of the latter). Male cones with numerous sporangia (0.5 mm. in diam.) crowded in several axillary verticels at each node. The spores of these are supposedly round and without ornamentation. The other (female?) sporangia are elongated, axillary, 1 mm. in diameter, and equal in number to that of the subtending bracts, and contain macrospores (No spores have been illustrated).

We believe that further investigation will reveal that the two forms are actually separate species or that the "microsporangiate" cone is very immature. This would account for the smaller size, and the unornamented (immature) spores, but not the extra whorls of sporangia which are more difficult to explain.

Though tentatively separated this species seems to belong, at least in part, to B. cuneifolius ("microsporangiate" cones), whereas the remainder belongs possibly to B. trichomatosus ("macrosporangiate" cones) or an unknown similar form.

U. U. Carboniferous; Lititz near Pilsen, Bohemia.

Stephanian or Westfalian D; Germany, Russia, et al.

Compressions.

(10) Bowmanites charaeformis (Jongmans) Hoskins and Cross, comb. nov.

1912 Sphenophyllum charaeforme Jongmans, Ann. k. k. Nat. Hofmus. Wien 1912: 449-450, pl. 6.

No definite cones present. Sporangia borne in anatropous fashion, singly, at the slightly enlarged tip of slender sporangiophores. 2 sporangiophores or more arise from the ventral (adaxial) surface of each bract near the axis. Fertile leaves or bracts similar in appearance to sterile leaves and of same number (9?) per whorl. Vegetative stems are slender, 1-2 mm. in diam., with long (3 cm. ±) internodes; lateral branches, with internodes 2 cm. long, bear fertile leaves at their nodes.

Jongmans noted a longitudinal ridge on the surface of several sporangia which suggested to him a possibility that a fused pair of sporangia instead of a single one were borne terminally on each sporangiophore. Unless this condition is definitely established, *B. charaeformis* must be placed in the section *Simplices*.

L. U. Carboniferous, Franziska vein, Ostrau section; Hruschau, Lower Silesia.

Compressions.

(11) *Bowmanites trisporangiatus* Hoskins and Cross, spec. nov.

Definite cone larger than those of *B. simplex*, *B. Scottii*, and *B. Dawsoni*; not less than 16 mm. diam. and several (6+) cm. long. Axis over 4.5 mm. in diam. Vascular cylinder of axis unknown. Three, essentially spherical, large (1.7 - 2.4 mm. diam.) sporangia borne singly in an anatropous manner above each of the 18 bracts of each whorl, always appearing as three concentric series or verticels of sporangia above each whorl of sporophylls.

Sporangial wall two-layered with an outer single layer of large cells and an inner multicellular layer of delicate cells. Spores large, 100 - 130 μ including irregular exosporium of anastomosing ridges with bipolar orientation (central body of sphere 80 - 115 μ). Spores densely packed in sporangia; intine with prominent tri-radiate tetrad scar. Sporangiophores slender (250 μ) greatly elongated, separated at their bases, arising in three distinct positions near the axis from the surface of the collarette formed by the laterally fused bases of the bracts; infundibuliform at distal end from which sporangium is suspended. Sporophylls inserted at an angle of about 20°; laminae turned abruptly upward at distal end of pedicels and overlapping several (?) whorls above. Single bundle bifurcates in outer cortex, the dorsal (inferior) strand supplying the bract and the ventral (superior) strand giving rise to three branches, in two simultaneous divisions, which are separate and surrounded by parenchymatous tissue and appear as ridges fused to the surface of the bract at the point of emergence from the outer cortex.

The characteristic and constant occurrence of three sporangia per bract in three concentric whorls per node in any section, in addition to the larger size of spores and cone in general, are the principal features which distinguish this species. The known geologic occurrence is markedly later than that of _B. Dawsoni_, _B. Scottii_, _B. cuneifolius_, but somewhat earlier than that of

B. simplex.

U. Carboniferous, Des Moines Series (= L. Carbondale of Illinois = L. Allegheny of Eastern U. S. = u. Westphalian C of Europe); Oskaloosa, Mahaska County, Iowa.

Petrifaction.

(12) Bowmanites cambrensis Binney, Paleont. Soc.: 59. pl. XII, figs. 1, 1a, 1b, 1c, 2, 3. 1871

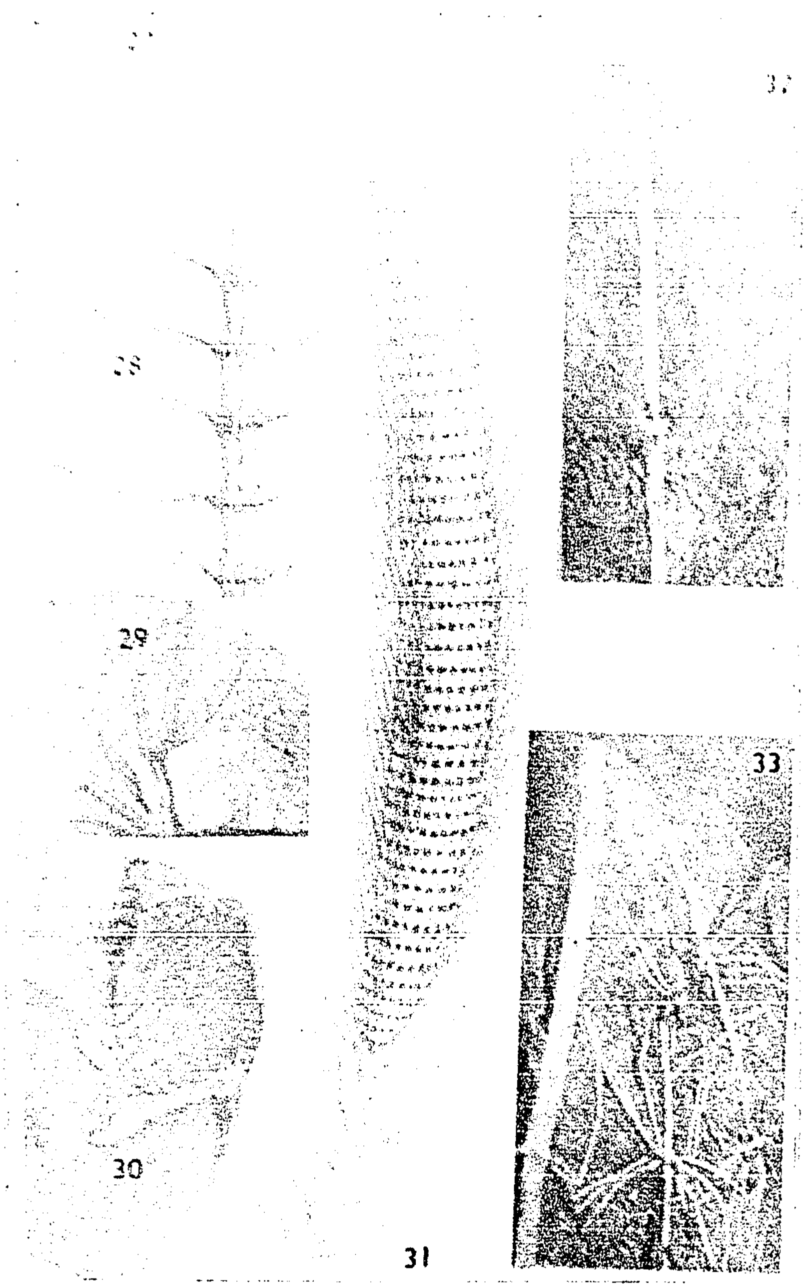
1888 Bowmanites cambrensis (Binney) Howse, Cat., Nat. Hist. Trans. of Northumberland, etc. 10:38, fig. 2.

1893 Sphenophyllum cuneifolium (Sternb.) Zeiller, Mém. Soc. Géol. France, Paléont. Mém. 11, 4:3-39. (pro parte).

1927 Sphenophyllostachys Dawsoni (Will.) Seward, forma gamma Hirmer, Handb. Paläobot. 1:357. figs. 419, 420.

Large cones about 10 cm. long and 1-2 cm. in diam., borne at tips of lateral branches. Essentially similar in structure to B. Dawsoni but with 4-5 pedicellated sporangia per bract and consequently 4-5 concentric whorls of sporangia between each internode. Probably all sporangia borne linearly upon the bract and not in alternating groups of one and two as postulated by

Plate XI



Figs. 27-31. Reproductions of Binney's figures (1871) of Bowmanites cambrensis. Fig. 27. The sporangia in this figure were interpreted as spores by Binney. Fig. 30 shows a photo of a mold of the base of the cone and Fig. 31 is a reproduction of a drawing made by Mr. Bowman when he had all the fragments of the cone at hand. Figs. 32-33. Bowmanites charaeformis Jongmans (1912) showing lax nature of vegetative branch and the long, unmodified leaves which bore the sporangia in their axils.

Hirmer. Sometimes displaced to the one or the other side of the bract if not in linear arrangement.

About 24 bracts per whorl whose attenuated laminae overlap characteristically the superior whorls forming a bristly sheath as in nearly all cones of Sphenophyllum.

L. Coal-measures; near Pontypool, S. Wales, and Bensham Seam; Jarrow.

Casts and compressions.

(13) Bowmanites Römeri Solms-Laubach, Jahrb. d. k. k. Geol. Reichsanst. Wien 45(2):225, pl. IX. figs. 1-4, pl. X, figs. 1-10. 1895.

1898 Sphenophyllostachys Römeri (Solms-Laub.) Seward, Fossil Plants 1:405, figs. 107c, 107d.

1901 Sphenophyllum Römeri (Solms-Laub.) Kidston, Trans. Nat. Hist. Soc. Glasgow, n.s., 6(1):127-8. fig. 24.

1909 Disphenophyllum Römerii (Solms-Laub.) Lotsy, Vorl. ü. Bot. Stammesgesch. 2:525, fig. 349, IV.

1920 Bowmanites Römeri Solms-Laub., in Scott, Studies in Foss. Bot., 3rd ed., 1:96-99, figs. 48, 49.

1927 Sphenophyllostachys (Bowmanites) Roemeri (Solms-Laub.)
Seward, in Hirmer Handb. Paläobot.: 357. figs. 421-23.

1940 Bowmanites Römeri Solms-Laub., in Walton, Study of Foss. Plants: 73.

Well developed cones, approx. 1 cm. in diam.; length several cm. (indefinite); axis unknown. Sporangia elongate-ovoid, 1-2 mm. long with wall several cells in thickness, attached in pairs by their abaxial side to the peltate tips of the slender, elongated sporangiophores; 6 per bract on 3 unbranched sporangiophores (appearing as 3 concentric verticels of sporangia per whorl of bracts in radial sect. of the cone as in B. trisporangiatus). All 3 sporangiophores arise from surface of the bract, probably from a point near the axis. Spores nearly spherical, 100 μ in diam., densely crowded, with two walls, the intine membranous and often folded, the exine thick and bearing numerous anastomosing ridges. Sporophylls separate almost to base (number per whorl unknown); arranged in superposed whorls with the narrow tips overlapping several whorls above.

M. U. Carboniferous; Niedzielisko, near Cracow, Poland.

Petrifaction (only one specimen known.)

(14) *Bowmanites laxus* Halle, Paleont. Sinica A. 2(1):52-54, pl. 11, figs. 1-4. 1927.

Well developed cones, over one cm. in diam., more than 5 cm. long; axis thick (4 mm. in diam.); prominent ridges, opposed at the nodes, i.e., not alternating; internodes less than 3 mm. in length. Sporangia sub-globose, 1.0-1.5 mm. in diam., attached in pairs by their abaxial side to the peltate tip of the slender, elongated (2.5 mm.) sporangiophore; 2 (rarely 4) per bract on 1(2) unbranched sporangiophores (usually appearing as one verticel of sporangia per whorl of bracts in a radial section of the cone. Sporangiophore appears to arise from the surface of each bract in an almost axillary position. This condition plus the peltate, bisporangiate tip, recall *Cingularia*. Spores unknown. Sporophylls or bracts confluent for about half their length (forming the characteristic disc) which is about twice the diameter of the length of the internodes. Tips of individual bracts free, subulate, and often perpendicular to the axis; only occasionally recurved and nearly parallel with it, and rarely ascending to the base of the superior whorl of bracts.

Several cones borne on the thick axis (possibly that of *Sphenophyllum Thonii*) as lateral appendages at each node.

The single verticel of paired sporangia per bract, and the lack of overlapping of the shorter sporophylls which are also more broadly fused laterally, differentiate this species from B. Römeri. Additional material from China collected in a slightly younger stratum (M. Shihhotse Series, Bed 31) and figured by Halle (1927, pp. 54-55, pl. 11, figs. 5-8) appears to belong to this species but careful study of the original material would be necessary to establish this relationship.

L. Permian (L. Shihhotse Series); Chenchiayu,(East section: plant bearing bed 14).

Compressions.

(15) Bowmanites fertilis (Scott) Hoskins and Cross, comb. nov.

1906 Sphenophyllum fertile Scott, Phil. Trans. Roy. Soc. London B 198:17-40, pls. III-V, text-figs. 1-3.

1909 Difurcosphenophyllum fertile (Scott) Lotsy, Vorl. ü. Bot. Stammesgesch. 2:525, fig. 350, II 1, 2.

1927 Sphenophyllostachys fertilis (Scott) Hirmer, Handb. Paläobot. 1:357, 359, figs. 424-25.

1936 Sphenophyllum fertile (Scott) Leclercq emend., Ann. Soc. Géol. Belgique 59:222-248. pls. I-X.

1936 *Sphenophyllostachys fertile* (Scott) Hirmer, in Leclercq
Proc. Sixth Int. Bot. Cong. 1:234, 239.

1937 *Sphenophyllum fertile* (Scott) Leclercq, Ann. Soc. Géol.
Belgique 60:170-172, figs. 1-4.

Definite compact cones present; at least 6 cm. long by 1-2.5 cm. in diam., not covered by sporophyll laminae. Sporangia ellipsoidal, 1.5-2.5 x 1.-1.5 mm., surrounded by a single layer of cells with radially thickened walls; 2 per sporangiophore branch (bisporangiate) and 22-34 per sporophyll, densely crowded. Spores ellipsoidal, 90-96 x 65-70μ, without heavily ridged exospore. Each node bears 6 sporophylls divided into 18 bracts, which are slightly fused at their bases; 6 of them ventral (adaxial), fertile and forked; 12 dorsal (abaxial), sterile, unbranched and lacking upturned portions; 14-18 sporangiophores inserted on the superior face of each fertile bract; each sporangiophore bearing terminally a more or less peltate expansion; some are sterile. Whorls of sporophylls superposed and partially covered externally by peltate sporangiophore tips.

L. Coal-measures; Shore Littleborough, Lancashire.
Bouxharmont Beds; Assise de Châtelet, Belgium.

Petrifactions.

(16) Bowmanites Kidstoni (Hem.) Hoskins and Cross, comb. nov.

1914 Sphenophyllum sp. Kidston, Trans. Roy. Soc. Edinburgh 1(1):131, pl. X, figs. 5, 5a.

1931 Sphenophyllum Kidstoni Hem., Ann. Bot. 45(177):41-44, pls. II, III, figs. 1-8, 17, text-fig. 2.

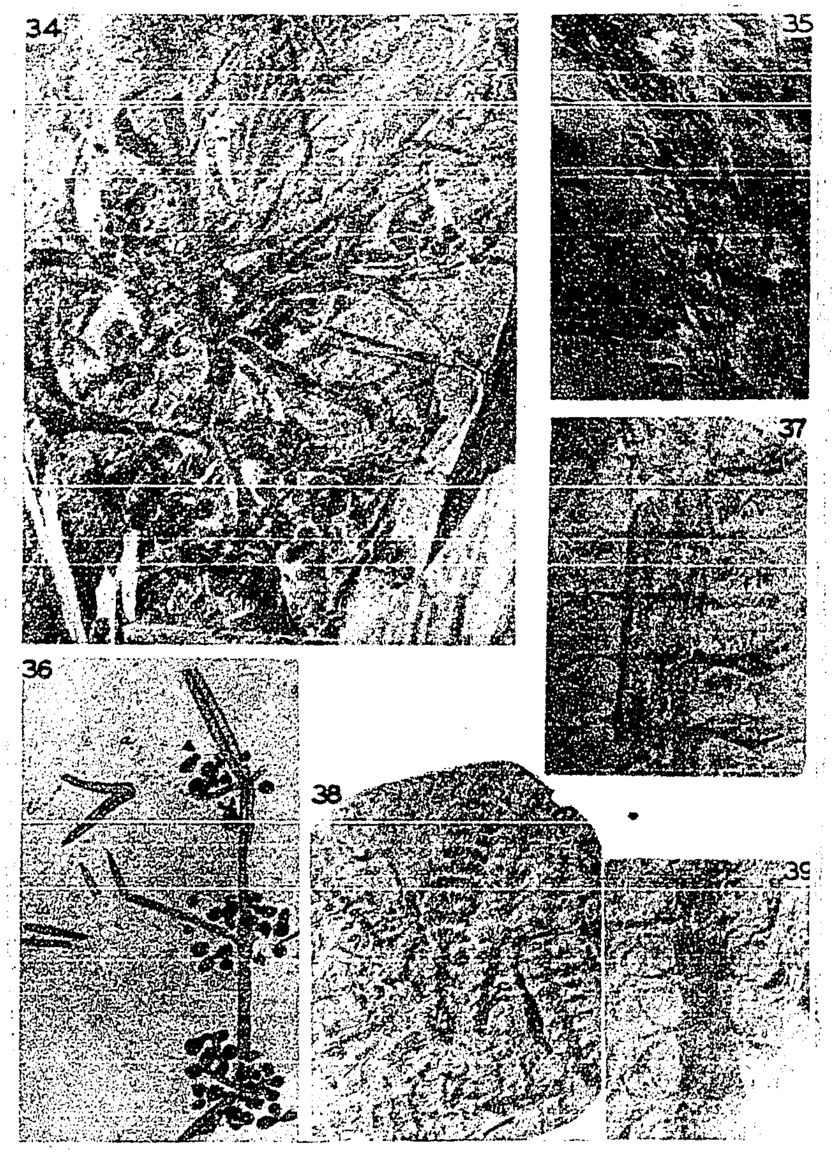
Definite cones absent. Sporangia occur in fours (tetrasporangia) irregularly among foliage in one whorl per node. Sporangia 1.1 mm. in diam., oval or "fig-shaped," i.e., broader than long and flattened at apex. Sporangiophore very short, attached to underside of broad (1.0 mm) disc, which bears sporangia, and arising from collarette near axis (not clearly seen). 6 leaves per node, very deeply dissected (4-7 teeth).

Smaller than B. major and larger than B. tenussimus.

Mid Yorkian Series (Barnsley Coal, "Monckton Rock,"); Royston, near Barnsley. Yorkshire Coal Field (also Staffordshire coal field). Spec. nos. WH 2154, WH 2155, WH 2158, etc.

Compressions.

Plate XII



Figs. 34-35. Bowmanites major showing rather clearly the grouping of sporangia in two groups of four each per bract. (After Kidston.)
Figs. 36. B. tenuissimus. A much smaller plant than B. major. Note the broken group of four sporangia at "a". (After Kidston, 1916).
Figs. 37-39. B. laxus Halle. Figs. 37 and 39 show rather clearly one sporangiophore bearing two sporangia per bract.

(17) Bowmanites major (Bronn) Hoskins and Cross, comb. nov.

1828 Rotularia major Bronn, in Bischoff, Die Kryptogamischen Gewächse 2:139, pl. XIII, fig. 2a, 2b.

1835 Sphenophyllum majus Bronn, Lethoea Geol. 1:32, pl. VIII, figs. 9a, 9b.

1909 Tetrasphenophyllum majus (Kidston) Lotsy, Vorl. ü. Bot. Stammesgesch. 2:525-26, fig. 350, III.

1931 Sphenophyllum majus (Bronn) Hem. emend., Ann. Bot. 45: 39-40, pl. III, figs. 16, 16a, and text-figs. 1, A, B, and C.

No definite cones developed. Sporangia occur in fours (tetrasporangia) irregularly on leaf bracts, the whorls of which may alternate with similar whorls of sterile leaves. Sporangia about 1.5 mm. in diam., pyriform, attached to a much reduced central disc (sometimes only a point) or place of confluence of their attachment to the long slender sporangiophore which arises on the free surface of the fused collar (formed by lateral confluence of bract bases) near the axis. Two sporangiophores and two groups of four sporangia per bract form 2 concentric rings of sporangial groups per whorl, but may often be much displaced. The plant is larger than

Bowmanites Kidstoni which it resembles closely.

Mid-Yorkian Series. (Shale over Barnsley Thick Coal); near Barnsley. Yorkshire coalfield. Spec. Nos. WH 855, WH 2172, etc.

Compressions.

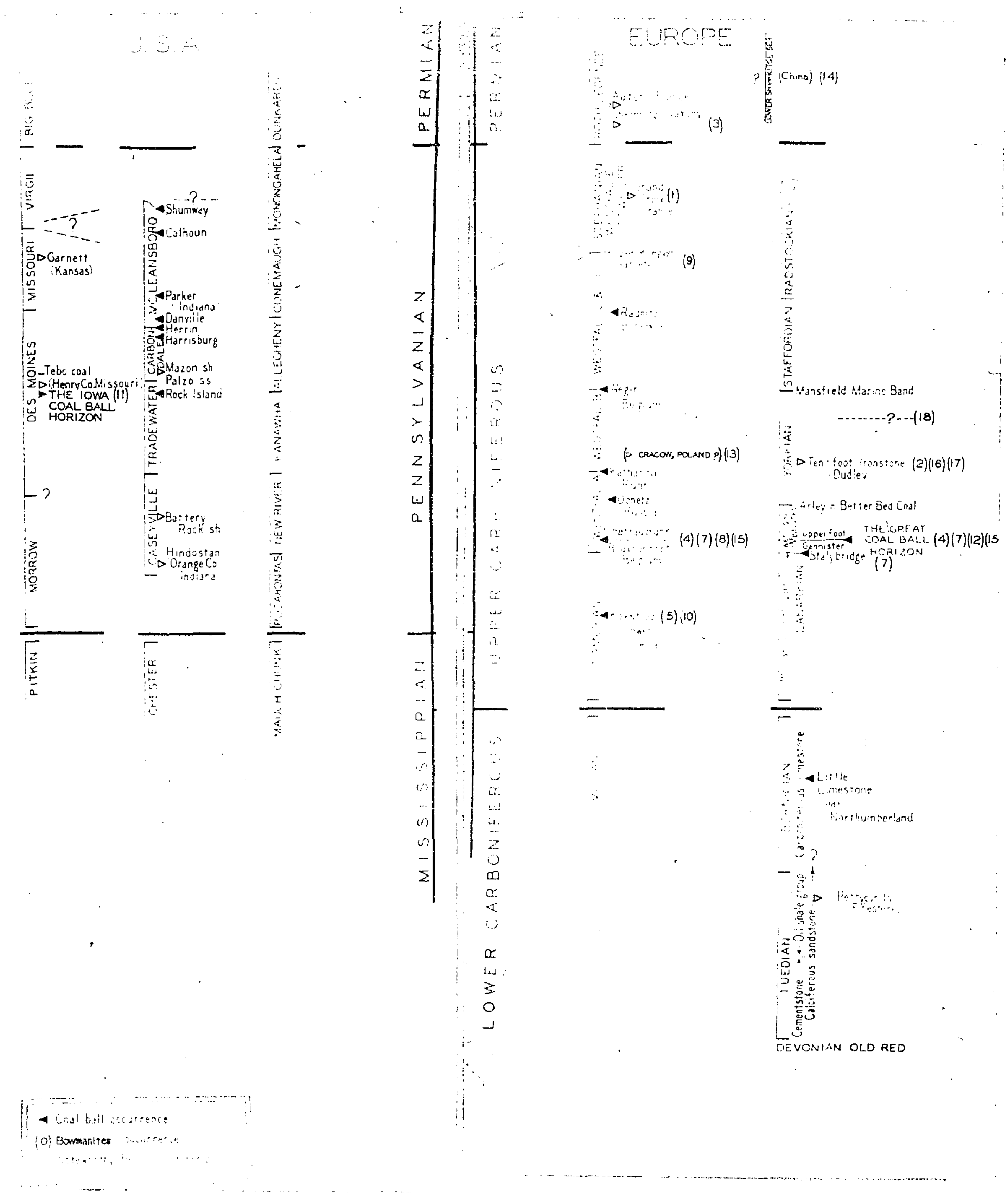
(18) *Bowmanites tenuissimus* (Kidston) Hoskins and Cross, comb. nov.

1914 *Sphenophyllum tenuissimum* Kidston, Trans. Roy. Soc. Edinburgh 50:129, pl XVI, figs. 3, 4, 4a, 5, text-fig. 6.

Definite cones absent. A sporangiophore arises from each half of the divided fertile leaves which are morphologically similar to sterile leaves. Four small (less than 1 mm. including basal stalk) pyriform sporangia are borne on the disc-like terminal end of the sporangiophore. The disc is reduced almost to a point in this species. (The disc may be formed from the confluence of the much shortened, stalk-like attachments of the sporangia.) The portion of the plant bearing the fertile leaves is very slender (stalk, 1 mm. in diam.), several centimeters long and has long (7 mm.) internodes.

M. U. Carboniferous (Westphalian Series); Cosely near Dudley, Clayscroft, England.

Compressions.


EUROPE
BIG BLUE
VIRGIL
MISSOURI
DES MOINES
MORROW
PITKIN
Shumway
Calhoun
Garnett
(Kansas)
MC LEANSBORO
CARBONDALE
TRADEWATER
CASEYVILLE
CHESTER
Parker
Indiana
Danville
Herrin
Harrisburg
Mazon sh
Palzo ss
Rock Island
Tebo coal
(Henry Co. Missouri)
THE IOWA (11)
COAL BALL
HORIZON
Battery
Rock sh
Hindostan
Orange Co
Indiana
DUNKARD
MONONGAHELA
CONEMAUGH
ALLEGHENY
KANAWHA
NEW RIVER
POCAHONTAS
MAUCH CHUNK
PERMIAN
PENNSYLVANIAN
MISSISSIPPIAN
UPPER CARBONIFEROUS
LOWER CARBONIFEROUS
(China) (14)
(3)
(1)
(9)
(CRACOW, POLAND ?) (13)
(4)(7)(8)(15)
(5)(10)
STAFFORDIAN
RADSTOCKIAN
Mansfield Marine Band
--------?---(18)
YORKIAN
Ten foot Ironstone (2)(16)(17)
Dudley
Arley = Better Bed Coal
Upper Foot
Gannister
Stalybridge
THE GREAT
COAL BALL
HORIZON
(4)(7)(12)(15
(7)
LANCASHIAN
Little
Limestone
Northumberland
TUEDIAN
Cementstone
Oil shale group
Calciferous sandstone
DEVONIAN OLD RED
Coal ball occurrence
(0) Bowmanites

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----------1922--Equisetales VI. Loc. cit. Pars 9.

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Part IV

A Consideration of the Structure of Lepidocarpon Scott Based on a New Strobilus from Iowa (Abstract)[1]

Introduction

Paleozoic lycopodiaceous strobili and their isolated parts have been the subject of intensive study by paleobotanists for over one hundred years. The criteria originally given as diagnostic for certain of these genera, and their modifications by later workers through the addition of new characteristics or the change in interpretation of established characteristics, present a confused picture of generic limitations. In this paper we will point out the intergradation and overlapping particularly of Lepidocarpon and Lepidostrobus, arising from modifications of original descriptions, both by direct statement and, indirectly, by assigning to one genus or the other,

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[1] Presented, in part, in partial fulfillment of the requirements for the degree of Master of Arts, to the Graduate School of Arts and Sciences, University of Cincinnati. Published May, 1941. Amer. Midl. Nat.

specimens which possess characteristics of both.

The main objective of this paper is to consider the diagnostic criteria of the genus Lepidocarpon as originally described by Scott (1900, 1901), and to illustrate the characteristics of the genus with new material. The contributions of more recent workers, Arnold, Bochenski, Darrah, Reed and Schopf will be considered insofar as their material concerns ours. It is not the purpose of this paper to approach a monographic study of the lycopodiaceous cone genera.

Material

The material on which this paper is based was collected by the authors as an isolated specimen in the Banner Coal Company's large strip mine about six miles north of Indianola, Warren County, Iowa, just east of U. S. Highway 65-69. Here the vein of coal is three to four feet thick and lies about fifty feet below the surface. It is in the Des Moines Series of the Pennsylvanian Period. The exact age has not been stated but Cline believes it is the same as the Lower Coal of Lugn's Lucas County report.[2] Coulter and Land (1911, 1921) and Matthews (1940) described some strobili of Lepidostrobus Coulteri Jongmans, from the same vicinity.

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[2] Cline, L. M., Iowa State College, Geol. Dept.--Personal Communication.

The specimen consists of a wedge-shaped fragment of a strobilus. From its external appearance we may be certain that we have the entire portion which was preserved. The specimen is carbonized over its entire surface. The preservation of the body of the specimen is excellent to within a few millimeters of the surface. It is calcified with a trace of pyritization. Distortion due to mineralization is negligible. A crystallization pattern occurs which may be sufficiently conspicuous to interfere with critical identification of structures when polished surfaces are studied by reflected light. The use of mounted peels in which all trace of rock matrix has been removed eliminates this problem.

The maximum dimensions of the specimen as found were about six and one-half centimeters high (parallel with the axis), five centimeters in radius (perpendicular to the axis), and three centimeters in width at the circumference (tangential to the strobilus as a whole). This latter dimension tapered evenly to the axis of the strobilus and the specimen thus presents a wedge-shaped surface when viewed from the top.

Significant measurements at the lower part of the specimen were distinctly less than at the upper; i.e., the strobilus tapered toward the base. Neither the apex nor the base of the original strobilus is present but the tapering of our specimen

Plate I

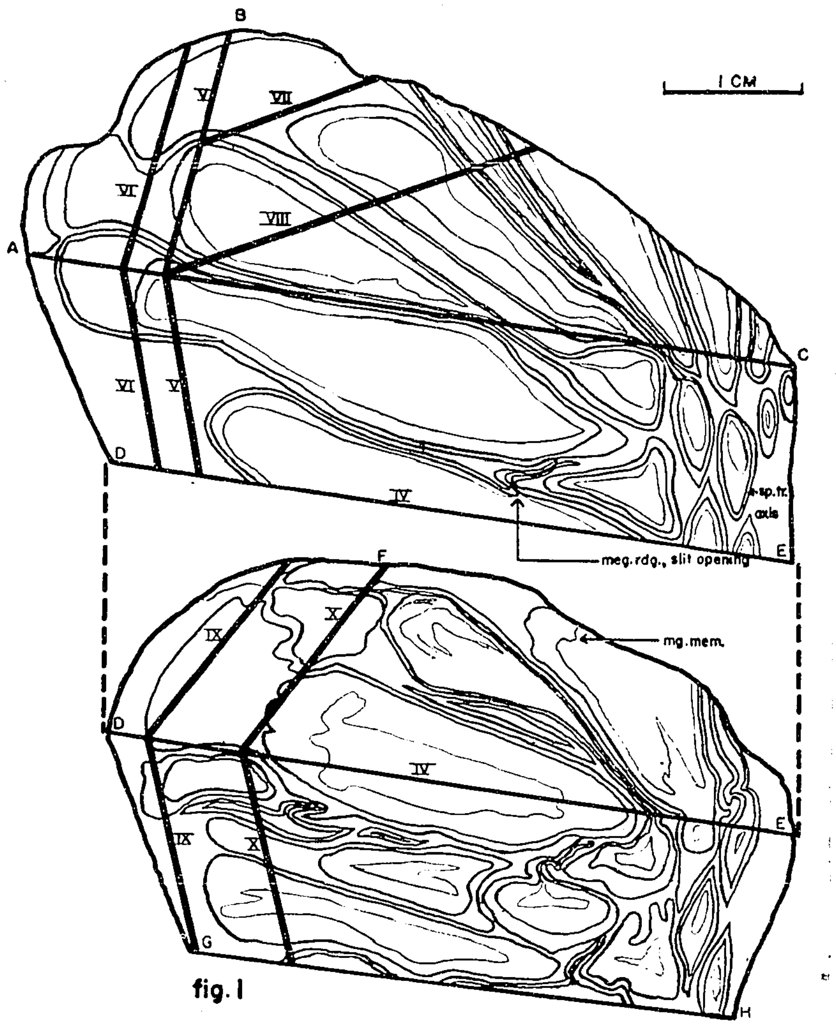


Fig. 1. Superimposed sketch of the upper and lower parts of the specimen of *Lepidocarpon ioense* after being separated by cut no. IV, showing surface features and position of cuts made in the study of the specimen. The axis of the strobilus is at the extreme right. Two transverse surfaces (to the strobilus) are lettered ABC and DFE. ABC was exposed by cut no. I and is near the top of the original specimen. The surface ACHG originally exposed by the obliquely radial cut no. II has been halved at DE by cut no. IV. The surface shown is in a plane intermediate between radial and tangential, and at the right passes through the outer cortex of the axis.

indicates that we have a portion of the lower half of the entire strobilus. According to our observations this fragment contained parts or all of at least twenty-four sporophylls and a portion of the axis. Probably this part was broken free from the rest of the cone before fossilization.

The measurements indicate that the strobilus was at least ten centimeters in maximum diameter and probably more than fourteen centimeters long. Even after a radial and two horizontal surfaces (top and bottom of the fragment) were exposed by cutting off irregularities and poorly preserved portions of the specimen the fragment measured over three centimeters high, with a radius of about five centimeters (Fig. 1). We know of no other specimen of Lepidocarpon as large. Even the large isolated "seeds" which have been abundantly collected, do not attain the over-all dimensions of thirty millimeters long by twelve millimeters high by fifteen millimeters wide as is found in many of our sporophyll invested sporangia.

The eleven pieces of the specimen remaining after sectioning carry the University of Cincinnati Paleobotanical Museum serial numbers: 640 A-K. The slides are numbered according to section and surface numbers I-a, b--X-a, b and serial peels on each surface are numbered in order 1-28 or less. The sections are housed in the University of Cincinnati Paleobotanical Museum, Botany Department, where they are available for study. Several typical slides of the series are in the collections of the Illinois Geological Survey, the University of Notre Dame, and Dr. L. R. Wilson, Coe College, Cedar Rapids, Iowa.

Lepidocarpon ioense sp. nov.

Strobilus

Large, more than ten centimeters in diameter, at least fourteen centimeters long and probably much longer, tapering toward the base.

Axis

Outer cortex, showing spiral arrangement of sporophylls, only part of axis preserved. Sporophyll trace typical, vascular bundle collateral, surrounded by zone of parenchyma and sheath.

Sporophyll

Megasporophylls crowded, arranged in a close spiral, attached nearly at right angles and elongated vertically to the axis for two and one-half to three and one-half centimeters to the up-turned distal lamina. Tips of distal laminae regularly lacking after approximately two and one-half centimeters. Pedicel extended abaxially to form a conspicuous keel throughout, merging with the heel of the distal lamina. An unbranched collateral vascular bundle, traversing the outer cortex, enters the base of the sporophyll and continues throughout its known length. Lateral laminae extend around and above the sporangium, and together with the distal lamina, form an investing structure.

Plate II

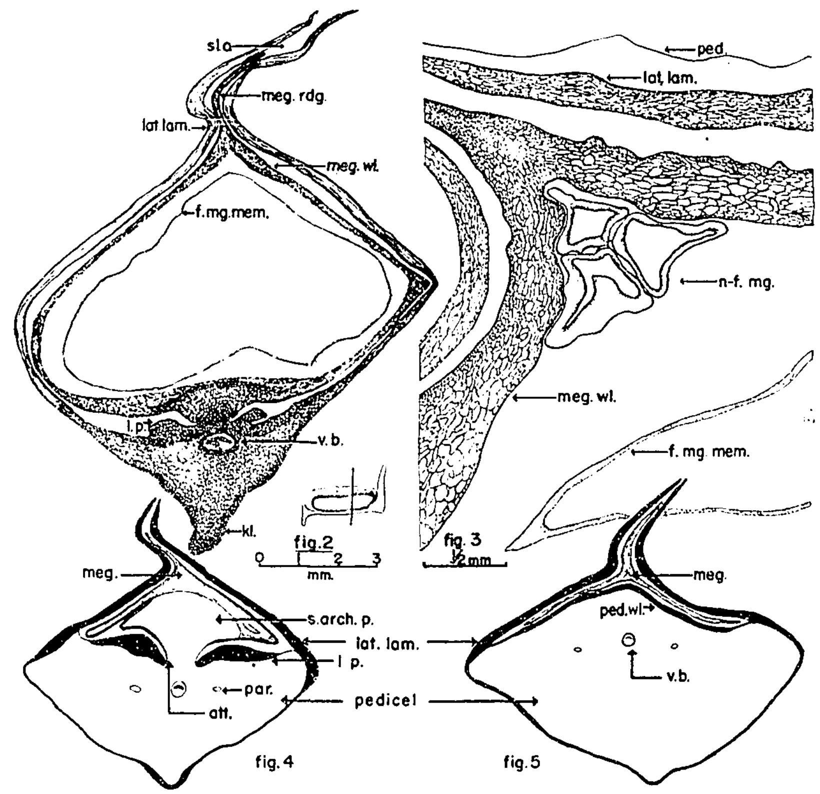


Fig. 2. Sketch showing typical tissue arrangements, parts and structures of a single megasporophyll and sporangium as seen in a section tangential to the strobilus. Position and plane of cut are indicated by inset. sl.o., slit-like opening; meg. rdg., megasporangial ridge; lat. lam., lateral lamina; meg. wl., megasporangium wall; f. mg. mem., functional megaspore membrane; s. arch. pad, sub-archesporial pad; l.p., lateral pad; v.b., vascular bundle; par., parichnos area; ped., pedicel; kl., keel.

Fig. 3. Camera lucida drawing of a tangential section through distal end of megasporangium. The characteristic appearance and position of the three non-functional megaspores (n-f. mg.) of the tetrad are indicated in relation to the functional megaspore wall (f-meg. mem.). Slide no. 640-Vb-2.

Fig. 4. Diagram of transverse section of sporophyll near distal end of sporangium. Basal tissue of sporangium fills much of cavity (meg.) which here is reduced to a narrow three-lobed structure. The origin of the lateral laminae (lat. lam.) is clearly at the lateral margins of the pedicel.

Fig. 5. Diagram of a section of sporophyll beyond that shown in Fig. 4 and distal to the sporangial attachment to pedicel. The free tip of the sporangium (meg.) extends for a short distance in an extremely trilobed form, the inner sporangial wall apparently closing the sporangium cavity. All traces of the basal tissues of the sporangium are lost. The superior face of the pedicel (ped. wl.) extends upward into the space between two of the sporangium lobes. The lateral laminae become free high on the superior face of the pedicel, but their origin from the lateral edges of the pedicel is apparent.

Lateral laminae, in tangential section, extend about twelve millimeters from their attachment on the pedicel, approximately five of which extend above the sporangial cavity, exceeding the sporangial ridge in height by some two millimeters. Lateral laminae, proximally, in close contact with sporophyll base; distally they merge with distal lamina.

Ligule

Ligule present on adaxial surface of sporophyll immediately distal to sporangium; about 450 microns in greatest width and over one millimeter in length.

Sporangium

Megasporangium large, two and one-fourth to three centimeters long, sporangial cavity approximately seven millimeters high, the sporangial wall extending vertically for about two and one-half millimeters forming the megasporangial ridge; sporangium attached for approximately its entire length along the adaxial surface of the sporophyll pedicel, either stalked or essentially sessile, resting on "lateral pads"; sub-archesporial pad increasingly conspicuous distally; distal end of sporangium extends beyond attachment in a characteristic three-lobed extremity, the megasporangial ridge forming one lobe, the other two initiated by extensive development of sub-archesporial pad.

Plate III

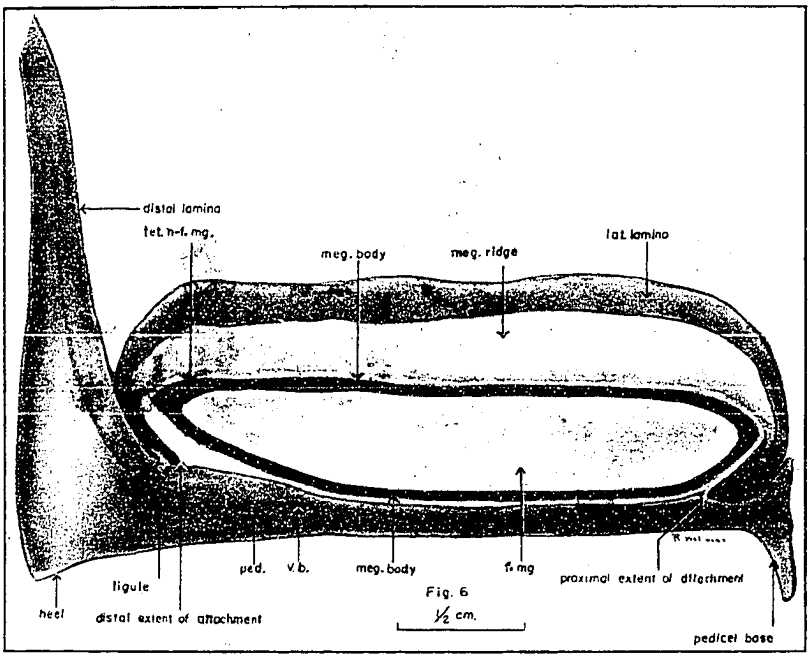


Fig. 6. Reconstruction of a radial section through the sporophyll and sporangium of *Lepidocarpon ioense*. The lateral lamina is shown overlapping the sporangial ridge. The large functional megaspore (f. mg.) in the slightly larger megasporangium (meg. body) and the three non-functional members of the tetrad (n-f. mg) appear in their correct position at the upper distal end of the megasporangium cavity. The ligule is distal to sporangial attachment.

Spores

Four megaspores are present in each megasporium resulting from the divisions of a single functional megaspore mother-cell. Three of these are non-functional, 750-1000 microns in diameter, regularly occurring in the upper part of the sporangial cavity at its distal end; at first remaining in contact in typical tetrad formation, later becoming dispersed. One functional megaspore, very large, nearly filling the sporangial cavity; wall thin and uniform.

Gametophyte tissue

Evidences of gametophyte tissue present in most megaspores, apparently more strongly developed toward distal extremity.

Location and horizon

From coal of Des Moines Series, Pennsylvanian Period, six miles north of Indianola, Warren County, Iowa; Banner Coal Company strip mine.

Material

One calcified specimen, a wedge-shaped section of the lower part of a strobilus, cut into eleven parts from which about 200 peels were taken; housed in Paleobotanical Collection, Botany Department, University of Cincinnati.

Name of type

Lepidocarpon ioense, indicating the geographical source of the material.

Discussion

Lepidocarpon was established as a genus (Scott 1900) to include some previously misinterpreted cone material. (Williamson 1877). Scott's generic diagnosis was revised (Scott 1901) to read as follows:

"Lepidocarpon, gen. nov. (Scott)

"Strobili, with the characters of Lepidostrobus, but each megasporangium inclosed, when mature, in an integument, growing up from the superior face of the sporophyll pedicel.

"Integument, together with the lamina of the sporophyll, completely enveloping the megasporangium, or nucellus, leaving only an elongated, slit-like micropyle above. A single functional megaspore or embryo-sac developed in each megasporangium and occupying almost the whole of its cavity.

"Megaspore ultimately filled by the prothallus or endosperm.

"Sporophyll, together with integumented megasporangium and its contents detached entire from the axis of the strobilus, the whole forming a closed, seed-like, reproductive body.

"Seed-like organ horizontally elongated, in the direction of the sporophyll pedicel, to which the micropylar crevice is parallel."

Scott, in the same work, also says:

"The comparison of specimens in the two conditions"--(immature, lacking the enclosing lateral laminae, and mature with the laminae) "has shown the relation of the seed-like organ of Lepidocarpon to the ordinary megasporangium of a Lepidostrobus. The former differs from the latter in two principal respects: -

"(1) It contains only one functional megaspore, which like the embryo-sac of an ovule or seed, occupies almost the whole interior of the megasporangium, but is accompanied by the three other spores of the tetrad in an abortive condition.

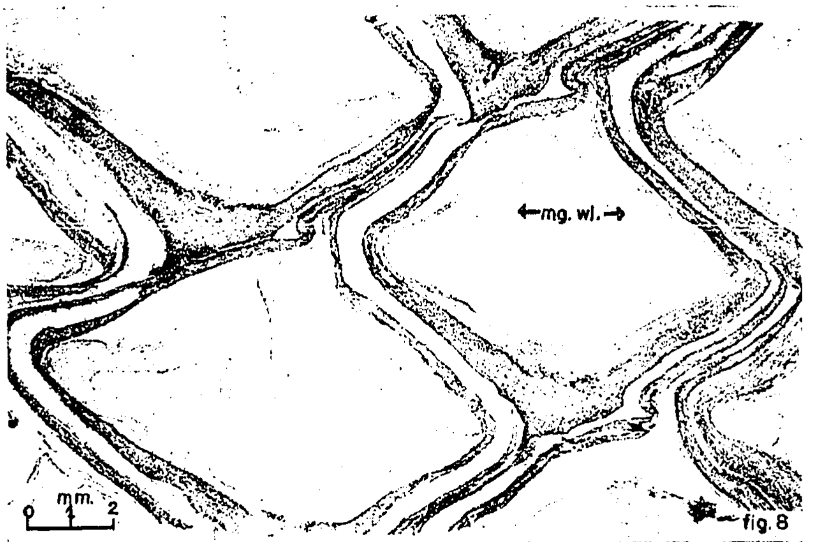
"(2) When mature, the megasporangium of Lepidocarpon is enclosed by an integument, which is a new formation, growing up from the tissue of the sporophyll, and forming, together with the latter, a complete envelope to the sporangium, only open by a narrow micropylar crevice along the top."

The essential features upon which this generic diagnosis was based have been largely substantiated by our observations. It may be expected that the designation of any form genus will be elastic enough to receive a few irregular species. In recent works, however, first one and then another exception has been taken until, in culmination, if these exceptions are to be followed, significant diagnostic characters of this genus scarcely exist.

Darrah (1941B), in his new species, Lepidocarpon glabrum, which occurs abundantly as isolated seed-like bodies in the coal ball flora of Iowa and Kansas (Darrah 1941A), has cited an instance in which a mature sporangium is shed free of its sporophyll. In general external appearance he describes these bodies as being "smooth and lustrous" and without any prominent scars or markings. He has shown that, structurally, this type is essentially a sporangium with a wall of thickened cells, with no apparent mechanism for dehiscence. He has also shown that these sporangial bodies conform in general character to the portion of Lesquereux's genus Lepidocystis (Lesquereux 1880) represented by L. vescicularis Lesquereux. This type has a bladder-like, oval or squarish, sporangium containing a large spore as contrasted to the type of L. fraxiniformis Lesquereux which has a sporangium containing many spores.

It is Darrah's contention that this species, Lepidocarpon glabrum Darrah, represents a "more mature condition of the seed body than is usually observed in the familiar Lepidocarpon" (Darrah 1941B). In discussing these sporangial bodies from

Plate IV



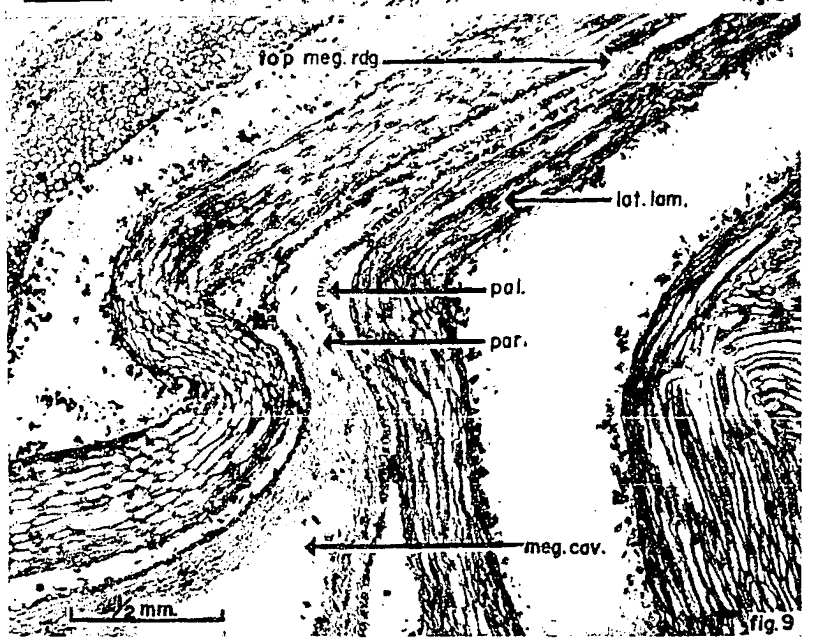


Fig. 8. Section tangential to strobilus showing essentially transverse sections of several megasporophylls and megasporangia about midway between distal and proximal ends. Slide 640-VIII A 3.

Fig. 9. An enlarged detail from Fig. 8; lat. lam., lateral lamina; pal., the palisade-like outer layer of the megasporangium wall; par., the inner parenchymatous wall layer; meg. cav., megasporangial cavity; the unbroken character of the sporangial wall throughout the megasporangial ridge is evident (top meg. rdg.)

the Iowa coal balls he states that only the smaller and more immature forms are recognized as typical and that "all of the seeds attaining a maximal or near maximal size are found isolated." He substantiates this latter statement by observations that the sporangial bodies of L. Lomaxi which are attached to a strobilus in his possession are are approximately four and one-half millimeters in length are immature rather than ripened, while those which have been shed average nearly six millimeters in length. Darrah believes that he is entirely within the bounds of the genus Lepidocarpon in his assignment since these "seed bodies" are merely more mature seeds. We have no basis for questioning his conclusions.

It should be pointed out, however, that this species, L. glabrum, which is shed free of the sporophyll upon maturity, does not conform to one of the major characteristics of the genus as recognized by Scott and already pointed out above, i.e., "when mature the megasporangium of Lepidocarpon is enclosed by an integument - growing up from the tissue of the sporophyll" and the "sporophyll, together with the integumented megasporangium and its contents, is detached entire from the axis of the strobilus."

Arnold (1938) has described as Lepidostrobus braidwoodensis, a lepidophyte strobilus from Braidwood, Illinois, having large megasporangia, each containing a single functional megaspore about two millimeters in largest diameter. Appressed to the triradiate apex of this spore are three non-functional megaspores measuring about one-half millimeter in diameter. There are no investing laminae. He assigns these megaspores to the Lagenicula group of the form genus Triletes. Spores of the Lagenicula group are generally conceded to be of uncertain affinity, but some have been assigned to species of Lepidostrobus. Arnold believes these spores to be indicative of the distinct evolutionary trend among the Paleozoic lycopods in the reduction in number of functional spores and the increase in the size of the functional one. He recognizes Lepidocarpon as representing the highest attainment in this line.

Bočhenski (1936) made a similar report on two species of Lepidostrobus, _L. major_, with a mature functional spore nearly a centimeter long, and _L. Bohdanowiczii_, with a smaller megaspore. In both these species the other members of the tetrad are present in the megasporangium as non-functional spores. Bočhenski believes there is no integument present but records the occurrence of a likely tissue as a remnant of the prothallus. Schopf (1938A) questions this interpretation.

The occurrence of a single functional megaspore essentially filling the sporangial cavity, in association with the non-

Plate V

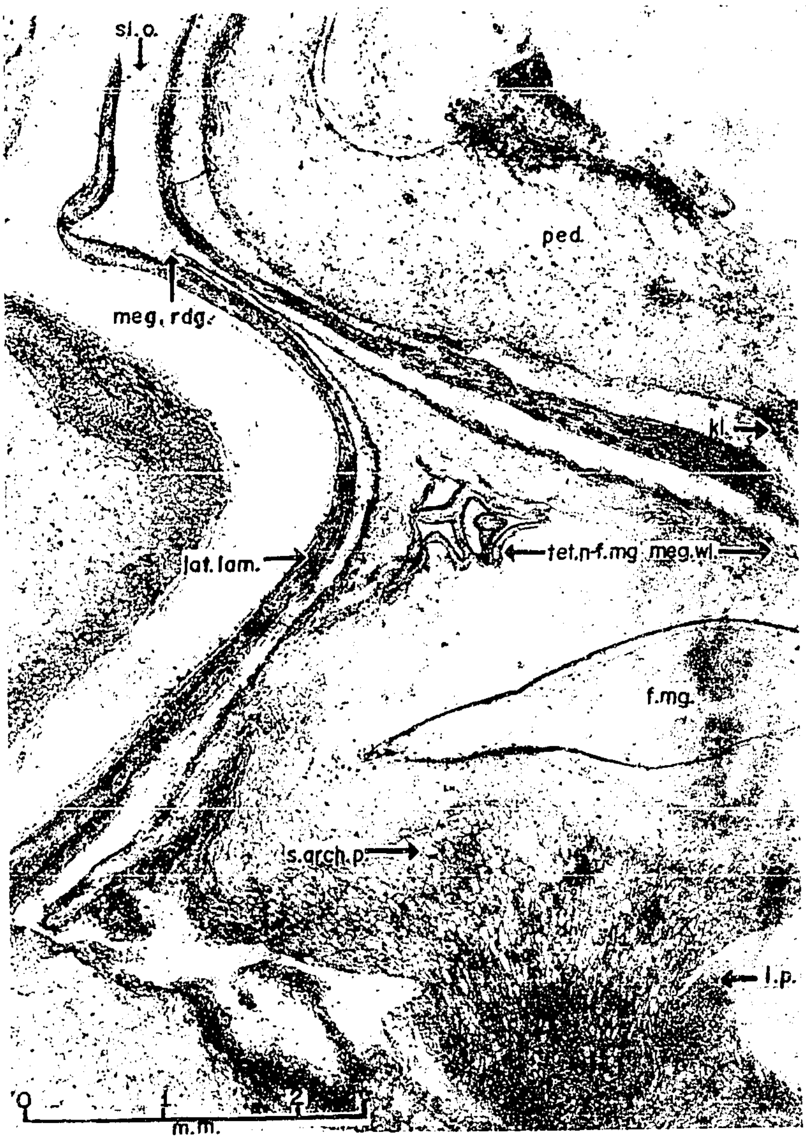


Fig. 10. Section nearly tangential to axis near the distal end of the sporangium. The "saddle-bags" or trilobed appearance of the distal end of the sporangium is just beginning to appear. l.p., lateral pads; s. arch. p., sub-archesporial pad; lat. lam., lateral lamina; f. mg., functional megaspore; tet. nf. mg., non-functional megaspores in tetrad formation; meg. rdg., megasporangial ridge; sl.o., slit-like opening between lateral laminae; kl., and ped., keel and pedicel of adjacent sporophyll. Slide no. 640-Vb 3.

functional members of the tetrad are characteristics which agree with those given by Scott as being diagnostic and of major importance for Lepidocarpon. Apparently the absence of well developed lateral laminae closely investing the sporangium is considered by Bochenski to be of sufficient importance that the distinction between Lepidostrobus and Lepidocarpon may be based on their occurrence or absence. The poor state of preservation of Arnold's material makes further conjecture regarding it difficult. The much larger relative size of the non-functional spores to the functional one, than is known to occur in Lepidocarpon, may be considered indicative of the transitional nature of the species Lepidostrobus braidwoodensis. In our material, the non-functional spores have a much larger actual size but are smaller proportionally when considering the size of the functional megaspore.

It is obvious that the problem raised by the inclusion within the genus Lepidocarpon of L. glabrum Darrah in which the significance of the investing laminae is minimized and the inclusion within the genus of Lepidostrobus of species which possess but a single functional megaspore, thus involving the two significant criteria of Scott's original diagnosis of Lepidocarpon, is one which must receive further serious consideration as to the generic limitations of these and related Paleozoic lycopodiaceous strobiloid forms.

Summary

A portion of a calcified strobilus is recorded from the Des Moines series of Iowa and is here described as a new species, Lepidocarpon ioense Hoskins and Cross.

A detailed description of the structure is correlated with the original generic designations of D. H. Scott.

A review of some recently described species of Paleozoic lycopodiaceous strobili suggests the need for further consideration of the generic limitation of Lepidocarpon and allied genera.

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Part V

TWO NEW SPECIES OF LEPIDOSTROBUS FROM THE LOWER POTTSVILLE OF ORANGE COUNTY, INDIANA[1]

Introduction

Strobili of Paleozoic lycopods are generally abundant and well preserved in the calcareous nodules and coal balls from Europe. American workers have also found considerable *Lepidostrobus* material, but most of these specimens are preserved only as flattened impressions in shales and coal.

Coulter and Land (1911) described a petrified specimen found in a coal pocket in Warren County, Iowa. This specimen was reconsidered with additional material found in the same locality later, and described as a homosporous *Lepidostrobus* (Coulter and Land, 1921). The name *L. Coulteri* was applied to the material by Jongmans (1930A), a fact which Arnold (1935) has brought to attention. The definite horizon of the coal pocket from which the material was taken was not discussed.

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1 Printed in "The American Midland Naturalist," Vol. 24, No. 2, pp. 421-436, September, 1940.

Scott and Jeffrey (1914) described a fragment of a petrified cone from the base of the Waverly Shale in Boyle County, Kentucky. Arnold (1935) points out that the Waverly Shale is Lower Mississippian in age rather than the suggested Upper Devonian. The name Lepidostrobus Fischeri was not valid because of the priority of the application of the name to some French material by Renault. Scott (1915) renamed the specimen L. kentuckiensis.

A partially preserved but complete lycopod strobilus from the Pottsville series of Michigan was named Lepidostrobus Bartletti by Arnold (1930) in order to place it on record. He suggests possible affinities to previously described European cones. In 1932 Arnold (1933) described a lycopodiaceous strobilus from the Pocono sandstone (Upper Devonian) of Pennsylvania as having Sigillarian affinities on the basis of the whorled arrangement of the sporophylls. Later (1935) he referred this specimen to the lepidostroboid group and named it L. Gallowayi.

Graham (1935) has discussed the occurrence of several lycopodiaceous strobili in coal balls from the McLeansboro horizon of Illinois. Complete description was impossible due to imperfect state of preservation. The relationships found between our material and the casts and petrifactions mentioned above will be discussed shortly.

Material

The plant material to be considered here was found in the Hindostan sandstone rocks of the Pocahontas group (Lower Pottsville) of Orange County, Indiana. The presence of plant fragments from the western part of that state has long been noted. Lesquereux (1884) lists ten species including seven ferns and three Lepidodendra. David White (1895) records and discusses 19 specimens of leaf and wood impressions from four quarries in the northwest part of Orange County. Coulter and Land (1921) reported the possession of some stem fragments but no cones from the sandstones of western Indiana. Weller[2] states that extensive collections have been made from the Lower Pottsville (Pocahontas) Series and are described in a manuscript by the late David White. The three larger cone specimens which we have were obtained a number of years ago. The remainder of our material with the exception of an extremely fine cast of a branch tip of Lepidodendron (aculeatum) was collected recently. The entire collection was found in the several Chailleaux and Whetstone quarries about 6 miles northwest of Orleans, Indiana. The sandstone is in two stages and varies from fine to medium grain.

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[2] Weller, J. Marvin, Ill. Geol. Surv. - Personal communication.

The upper of the two stages is the main massive body of sandstone. It is overlain by a thin underclay. In this rock the plants are rather poorly preserved and not as numerous as in the thinly bedded sandstones below. Several large fragments of fair sized trees were found. One of especial note is lying prostrate along a bedding plane and one of the branches of the first dichotomy forks four more times successively. At the second dichotomy, one branch penetrates about three feet of sandstone in an almost vertical position. Over twenty feet of the cast of this tree was exposed in relief by quarrying operations. Kindle (1896) mentions the similar occurrence of a fossil tree in a quarry of this region.

Directly beneath this massive layer, a lesser zone of thinly bedded, very fine, shaly sandstone occurs. It is underlain by a thin coal. Wanless[3] suggests that this is the coal called No. 1 in the Orange County report (Elrod and McIntire, 1876). Kindle (1896) has described the whetstone rocks in some detail.

The age of this deposit of plant material at the base of the Pottsville Series is important. The plants are dissimilar to those known to occur in Indiana, Illinois and western Kentucky, and are possibly the oldest in the interior coal basin.

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[3] Wanless, Harold R., Univ. of Ill. - Personal communication.

Plate I

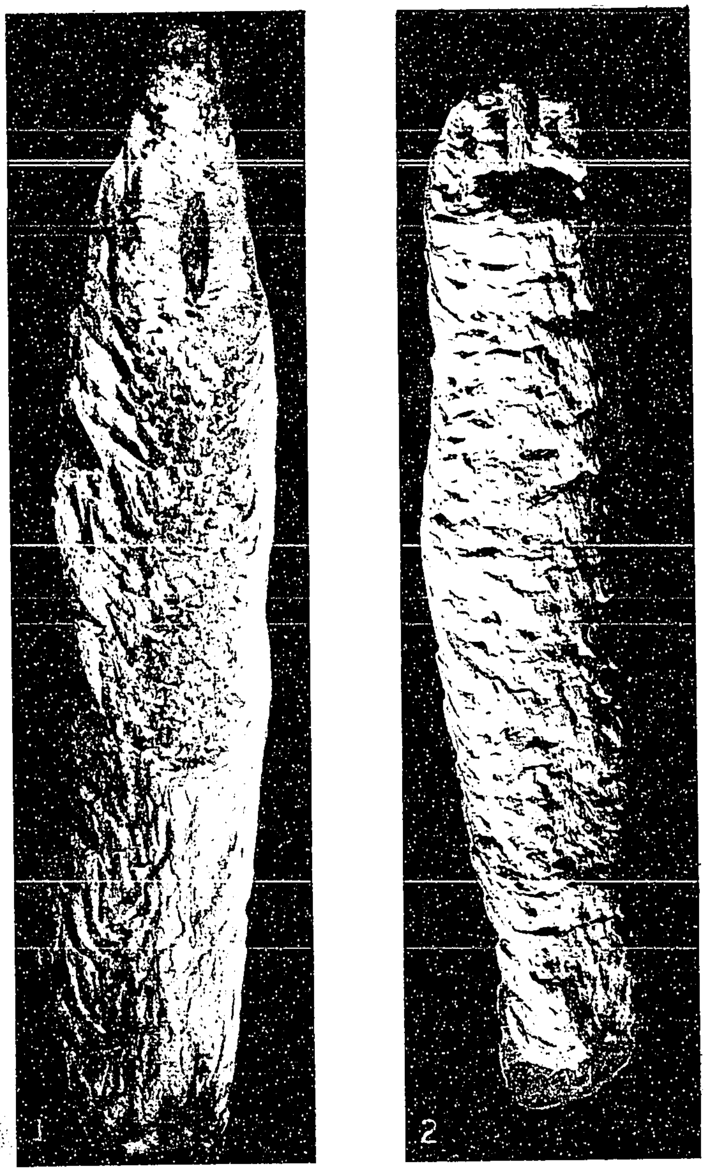


Fig. 1. Holotype specimen of *Lepidostrobus imbricatus*. Base complete and tip missing. ×1⅛.

Fig. 2. Hypotype specimen of *L. imbricatus*. Distal end complete, except for portion broken out to show tip of axis. ×1¼.

These beds have been correlated with the Stalybridge deposits of the Lower Coal-measures of Great Britain and the Bouxharmont beds of Belgium (pl. XIII, Part II).

The five specimens of Lepidostrobus which we have prepared for study may be divided into two rather obvious types.

Four of the specimens are of the first type. The largest and best example of the first type was only partially exposed along one side when found. Careful work with hammer and chisels in the laboratory have exposed an excellent cigar-shaped cone, about 13.5 cm. long and 2.5 cm. in diameter at the base. The tip is missing. The cellular detail has been lost through imperfect preservation as a cast, but all the external morphological features are well shown. After pictures, rubber molds and plaster casts had been made of the entire specimen, a section was cut through the cone 1.5 cm. from the base. A fortunate accident resulted in the breaking of a portion out of this lower section. This exposed some interesting structure which might only have been conjectured otherwise. The axis at the basal point of attachment is about 5 mm. in diameter. It tapers abruptly so that within 5 mm. of the base, the diameter is reduced to about 3 mm. In cross section at the base, at a point 5 mm. above the base, and at the broken tip of the specimen, the axis has

13 ridges visible which are the old sporophyll bases. The significance of this number is not known, but a similar condition is found in L. Bartletti and in the description given by Bower (1893) of L. Brownii. Certain other species have only 11 of these sporophyll bases or less, but there is, apparently, a rather constant number for each species.

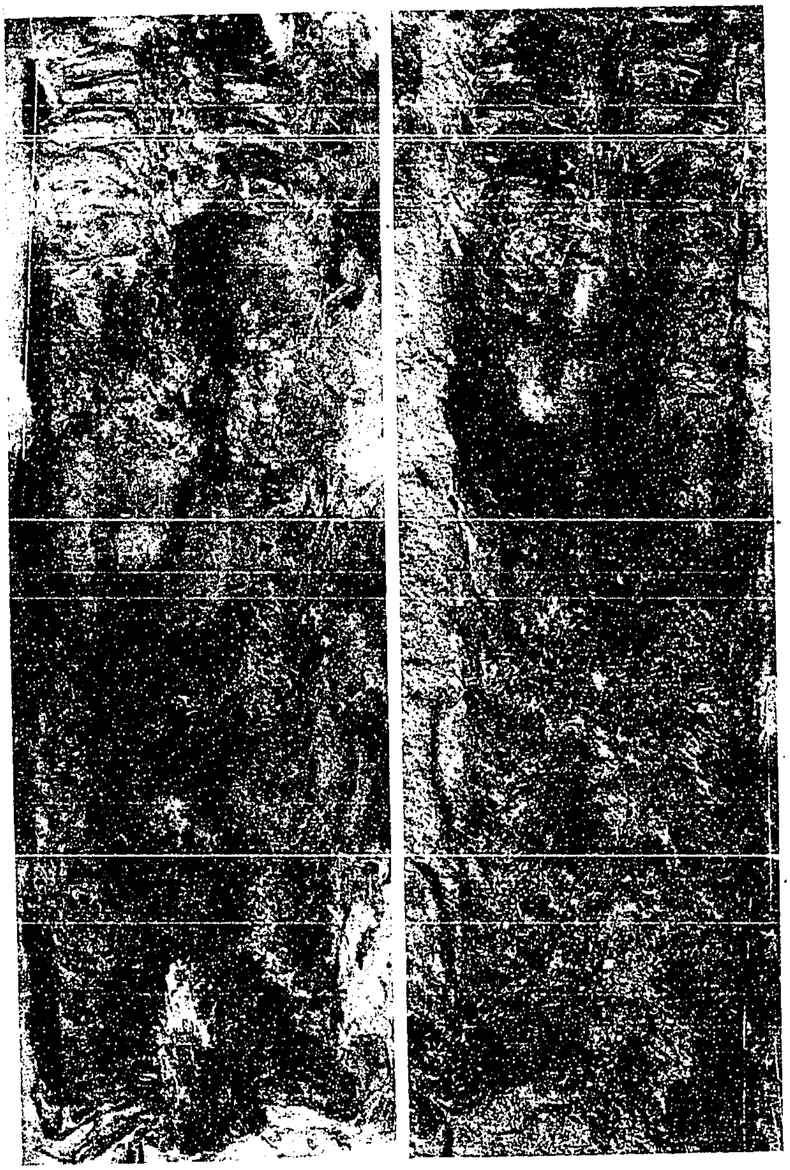
There are, then, normally 13 sporophylls in each spiral revolution about the axis and in a longitudinal section through the cone there are between 95 and 100 such revolutions, in the known 13.5 cm. Such a number of sporangia would indicate their small size.

As in L. Coulteri, L. Bartletti, L. Gallowayi, and the specimens discussed by Graham (1935), the sporophylls are borne approximately at right angles to the cone axis. The sporangia are radially elongated as is characteristic of the lepidostrobus type of lycopod cone. They are borne adaxially on a pedicel, i.e., the portion of the sporophyll which is horizontal. The distal end of the sporophyll, called the lamina by Scott (1920), turns up and overlaps the ends of the next several sporangia. These laminae are rather narrow at their bases, not over 1.5 mm. wide, and are usually less than 2 cm. long. They are closely appressed throughout their length and are imbricate in appearance. Two specimens of this type of cone show the imbricate condition very well. An outstanding feature of the sporophyll is the apparent lack of any portion subtended below the horizontal plane of the pedicel. Hirmer (1927) states that a subtended portion is usually present as does Scott (1920) who adds that the form of the whole sporophyll is somewhat peltate as a result. When this condition exists, as it does in our second type of cone, a portion of the lamina is not only subtended but this part as well as the distal end of the pedicel is usually strongly thickened. The lack of the subtended portion of the lamina is not peculiar alone to our specimen. Graham (1935) discovered a similar situation in his material and states, "The lax nature of the cone and the absence of a downward projection of the lamina distinguish this from previously described species." Such a condition may exist in other species which have been described, but if so, it is neither discussed nor pictured clearly. A median nerve is very prominent on the lamina.

The sporangia, which are about eight mm. in length and slightly over one mm. in height are roughly wedge-shaped in top view. The end nearest the axis is very narrow and is generally wedge-shaped in cross-section. The distal end is rather broad and flattened. The sporangia are so crowded together both laterally and vertically that their sides are fluted by the pressure from adjoining sporangia. Due to the small size of the sporangia and the deformation present we are unable to ascertain the amount, position and mechanics of the attachment to the sporophyll. The presence of a ligule has not been proven for this type in our collections. A cross-section through the entire cone shows well the laterally compact nature of the sporangia and the vertical distortion.

A specimen which we recently acquired from the type locality is a well preserved sandstone cast. Only a small portion of the tip of the cone was visible originally, but in our preparation of the material for study we have exposed its entire length and thickness. It is slightly flattened, parallel with the bedding planes of the sandstone matrix. The strobilus is appreciably smaller in all dimensions than the three original specimens and the numerous traces of molds and casts which we found while making our collections. It agrees in all essential details with the holotype. The axis is slightly less than two mm. in diameter constantly throughout its length except for about six mm. of its distal end which tapers very slightly to about one and one-half mm. in diameter. It is bluntly terminated about three mm. from the actual tip of the strobilus (Fig. 2). The sporophylls are spirally arranged, thirteen per revolution about the axis, and the adaxially borne sporangia are densely crowded and distorted. The sporophylls and sporangia

PLATE 2



Figs. 3 and 4. *Lepidostrobus arrectus* as split from rock. ×1¼.

are progressively reduced in size throughout the distal cm. of the cone, and the actual bluntly rounded tip of the axis bears extremely shortened and immature sporangia radiating systematically and progressively from the normal position, which is slightly decurrent from horizontal, to a vertical position (i.e. parallel to the cone axis.). In gross external appearance, then, the tip of the strobilus is bluntly conical.

A second type of cone, represented by one of the four specimens, was exposed by splitting open a rather large, cut slab of grey sandstone. The cone split irregularly through the axis and thus we have a single specimen well shown on both slabs. The cone is somewhat flattened but chiseling has revealed that the flattened diameter is about 2 cm. whereas the normal diameter is about 2.7 cm. Both ends of the cone are missing and no tapering is apparent in the 11.5 cm. which we have. Unfortunately, several small concretionary growths have either destroyed or distorted about one-half of the middle section of our specimen. As in the first type of cone already discussed, no cellular detail is visible but the general organization and external morphological features are well shown.

The axis is about 5 mm. in diameter throughout its entire length. In cross-section there are usually eleven

PLATE 3

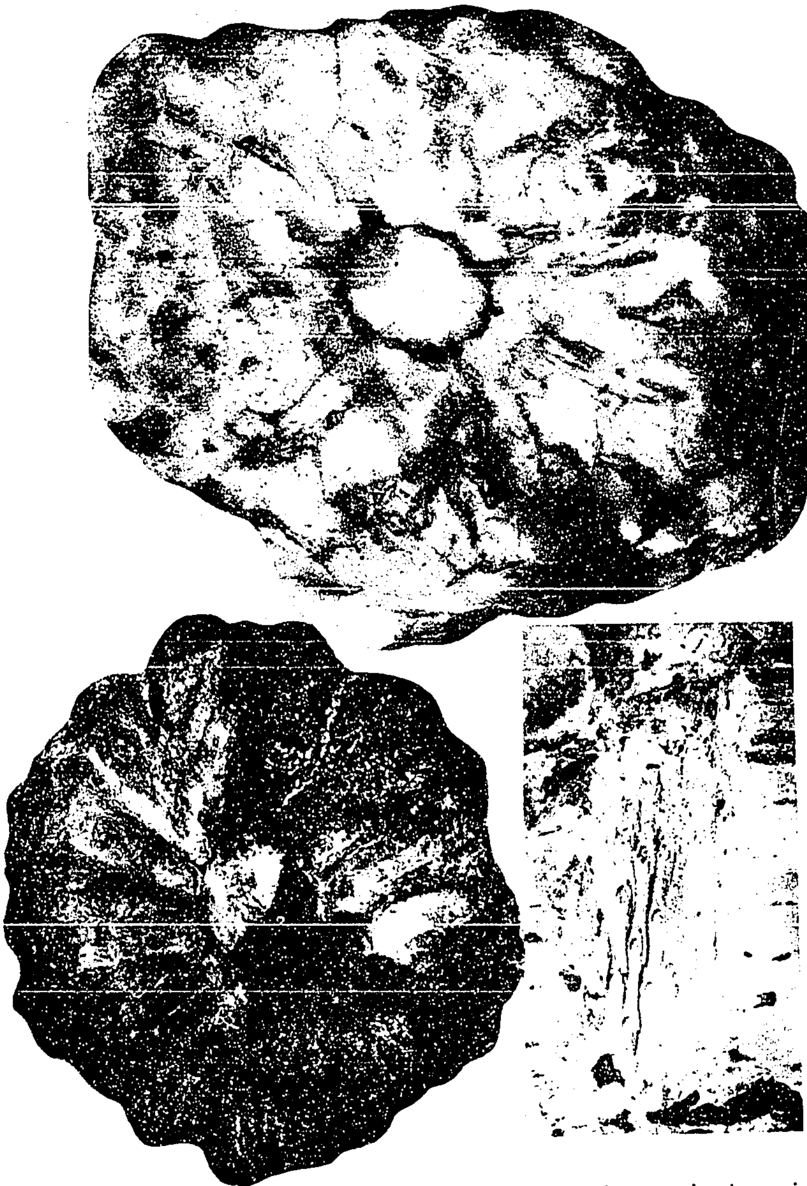


Fig. 5. Cut cross-section near base of *Lepidostrobus imbricatus* showing axis in center, with longitudinal sections through sporangia surrounded by transverse sections of erect laminae of sporophylls of lower insertion. ×4.

Fig. 6. Broken base of same cone showing clearly, the outline of sporangia. ×3

Fig. 7. Central axis of another specimen of *Lepidostrobus imbricatus*. ×7.

sporophyll bases exposed as ridges which indicate the presence of eleven sporophylls for each revolution about the axis in a spiral order. The reconstruction shows 43 such spiral revolutions in the 11.5 cm. This number is less than one-half that found in the first type, although this specimen is only 2 cm. less in length. By computing this average, which agrees quite closely with the measurements taken, the sporangia are slightly more than 2.5 mm. high.

The adaxial angle of the sporophylls to the axis is slightly greater than a right angle, i.e., the distal ends of the sporophylls slope toward the lower end of the cone as much as 93° or 94°. This is accentuated by a prominent, subtended portion of the lamina and a thickened distal end of the pedicel of the sporophyll. The sporophylls at the lower end of the specimen are angled slightly more than this, possibly as a result of the release of the vertical pressure of the compacted sporangia when the lower portion was broken away. The distortion resulting from the concretionary growth in the middle of the specimen is shown by the varying angles of attachment of the sporophylls in the affected area.

The pedicels and sporangia are arched in the middle so that both the axial and distal ends are lower. The distal end is much lower because of the angle of attachment of the

Plate 4

Fig. 8. Greatly enlarged section of tip of axis of type specimen of *Lepidostrobus imbricatus* showing attachment of sporophylls. ×7.

Fig. 9. Broken section of base of same specimen showing abruptly tapering axis. ×5.

sporophyll to the axis. None of the descriptions of casts or petrified American cones records either the arching or the downward slanting pedicels and sporangia. Text discussions and figures by Hirmer (1927), Figs. 208 and 210 of Lepidostrobus Brownii and L. Oldhamius respectively, Scott (1920), Fig. 77 of L. Veltheimianus, and Solms-Laubach (1891), Fig. 25 of a different specimen of L. Brownii than that shown by Hirmer, indicates that these characters have been noted and considered in the European material.

The sporophyll is extremely important in this second type of cone. The broader, flattened part of the pedicel appears to be attached to the axis by a more typically stalk-like portion which is turned abruptly down along the axis and is fused to it throughout its length of one mm. This might be called a rather enlarged sporophyll base. Such a structure is not discernible in the first type of cone. The pedicel itself, i.e., the horizontal portion of the sporophyll which bears the sporangia on its upper surface, is very narrow. This feature shows well in a number of places. The pedicel is flared out broadly at the distal end and is thickened noticeably. The lamina and the pedicel form a definite subtended portion very similar to that modelled after Lepidostrobus Coulteri (Coulter and Land, 1911). The lamina is 3 to 4 mm. wide at the base and 30 to 40 mm. long. It tapers gradually to a width of 1 mm.

PLATE 5

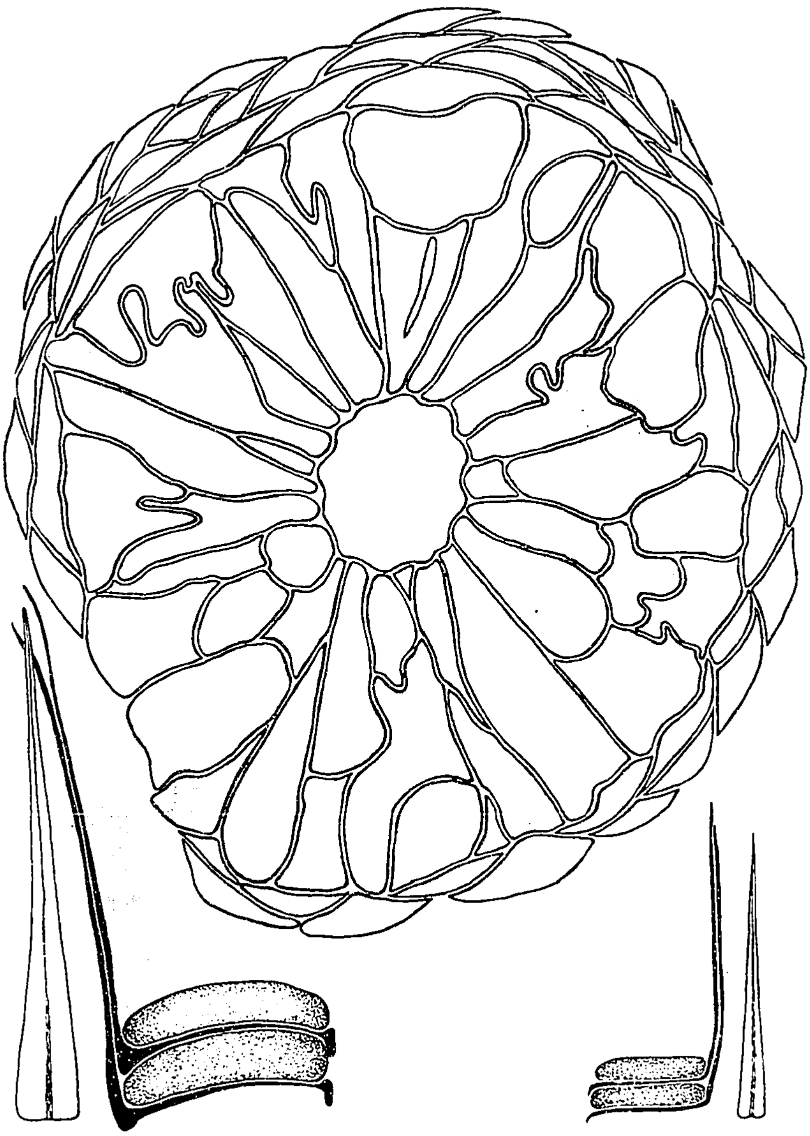


Fig. 10. Reconstruction of cross-section of axis of *Lepidostrobus imbricatus* based on Fig. 5. ×5.

Fig. 11. Enlarged sporophyll and sporangium of *Lepidostrobus imbricatus.* ×2.

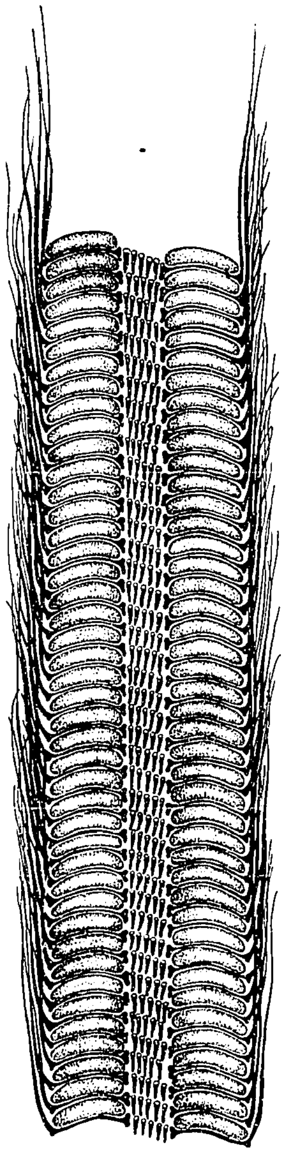
Fig. 12. Enlarged sporophyll and sporangium of *Lepidostrobus ar[illegible]tus.* ×2.

in the first 12 mm. of length, and is characteristically appressed for the lower half. The upper half of the attenuated lamina is slightly divergent and aristate in nature. This is contrasted to the closely overlapping, appressed, imbricate nature of the first type of cone described. A median nerve is definite for the length of the lamina but is not as marked as in the first type. Such a sporophyll seems to be unusual, at least in regard to length. The presence of ligules at the distal ends of the sporangia cannot be definitely shown. Some very confusing markings appear which, if liberally interpreted, may be considered as ligules.

The sporangia are closely crowded both laterally and vertically and are prominently grooved by the adjacent sporangia. In cross-section they differ markedly from those described in the first type. They are narrowed at the axial end but not wedge-shaped. At the distal end they are oblong-ovate in cross-section. The sporangium is rather broad in comparison with the pedicel, and broadly overlaps it. In adaxial view the outline of the sporophyll is generally wedge-shaped. The spores of this cone and of the first type will be discussed together.

The spores of our cones were secured by macerating the sporangia. In our first type of cone only one kind of spore was found. The average diameter of this is about 26-29μ.

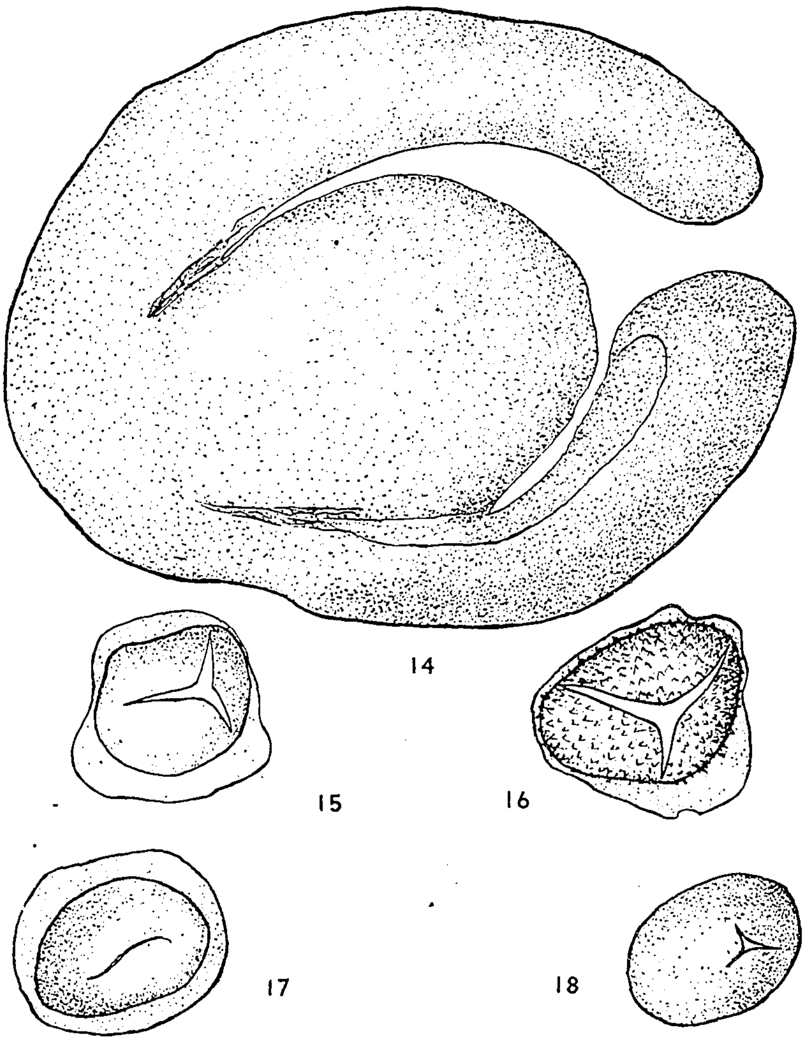
PLATE 6



13. Reconstruction of *Lepidostrobus arrectus.* ×1

A triradiate opening is present in some and absent in others. An equatorial flange is present in a few instances. Whether another type of spore exists and was not found is not known. It would be unsafe to hazard the statement that this specimen is homosporous on the negative basis of not finding larger spores. It is interesting to note that except for its larger size, Lepidostrobus Coulteri is very similar to our species. Spores of but one kind were found in L. Coulteri. The diameter of these spores is comparable to that of the spores of our specimen. Campos (1925) in describing a complete specimen, Lepidostrobus foliaceus, finds only one size of spore, and that measures 32 , which is only slightly larger than our spores. These spores are very similar to ours in general outline and in the nature of the triradiate marking. He states that his specimen is homosporous. However, Mrs. D. H. Scott (1906) had described a megaspore from a different specimen of L. foliaceus. Campos justifies his conclusions by a statement from Berry (1918) that different cones may produce two kinds of spores. However, if two sizes of spores are known to occur in this species, it is certainly difficult to indicate the homosporous nature of any single specimen. Only a complete, well preserved cone such as the specimen described by Campos may be safely called homosporous.

Plate 7



Figs. 14-18. Camera lucida drawings of spores from cones showing relative proportions.

Fig. 14. Megaspore of *Lepidostrobus arrectus*. 165 mu.

Fig. 15. Microspore of *Lepidostrobus arrectus*, showing equatorial flange and triradiate opening. About 29 mu.

Fig. 16. Microspore of *Lepidostrobus arrectus* with roughened exine. 29 mu.

Fig. 17. Microspore of *Lepidostrobus imbricatus* with single slit opening. 26 mu

Fig. 18. Microspore of *Lepidostrobus imbricatus* with trace of triradiate opening. 26 mu.

In studying the spores from our second type of cone, the microspores are found to be practically identical with the spores found in the first type, i.e., 26-29 μ. Most of them have a definite triradiate opening. In addition, a larger spore is found sparingly, at a ratio of about 3 to 100. The size of this larger spore, 160-170 μ, agrees fairly well with the megaspores figured by Arnold (1933) for *Lepidostrobus Gallowayi*, which measure about 150 μ. Certain definite features show clearly that the two cones are of different species. *L. Gallowayi* has whorled sporophylls and is considerably larger.

In order to obtain the spores from our material, several techniques were tried with varying results. Sandstone is normally a poor matrix for the preservation of spores. The spores were not revealed in the sporangia when viewed through a binocular microscope using direct light. Such a condition could be expected, however, so to make sure of the presence of the spores, individual sporangia were chipped from the cones and broken into several small pieces. The most satisfactory procedure found for freeing the spores was first to allow the material to stand for about 15 minutes in hydrofluoric acid. After several washings, Schulze's solution was poured over it and allowed to stand for about an hour. This was followed with several washings in distilled water after which the material was placed in a 30% solution of NaOH (sodium hydroxide). This was allowed to stand from 2-24 hours depending on the amount of organic material present. The NaOH was then poured off and the material washed until neutralized. Without drying, "abopon", a Glyco mounting medium, which is water soluble, was added. The permanent mounts made from this are available for further study.

It is possible that the spores which we obtained were merely washed into or in some manner infiltrated among the sporophylls and sporangia before fossilization. If so, we may not have the original spores at all. This possibility exists in all material preserved as casts. Petrifactions in coal balls and concretions are less likely to be contaminated. It is interesting to note, however, that several fragments of the surrounding matrix were processed in the same manner and the presence of spores from that material could not be definitely established, whereas in the macerated material from the sporangia spores were fairly numerous. The detritus taken from the concretionary growths in the central part of the specimen of our second type of cone was found to have an abundant spore assemblage. This could be expected, since in formation the concretions disrupted the sporangia and then reincorporated them and their contents.

A rough and thickened exine, which should be found on any megaspore unless lost before preservation (Thomson, 1934) is not always evident on the megaspores from our second type of cone. Certain exterior roughenings are present in one or two spores and these resemble somewhat the megaspore figured by Arnold for Lepidostrobus Gallowayi.

With the discussion and criteria in mind, we feel that these cones merit a definite record in paleobotanical literature. While we do not wish to expand this literature with unnecessary new names of species, it seems desirable to give the specimens a name, even though they may lack some of the fundamental characteristics necessary for a complete description. Moreover specimens which are not given a name may easily be overlooked. An attempt has been made to compare critically our specimens with casts and petrifactions of Lepidostrobus which have already been described.

The summarized type diagnoses follow:

Lepidostrobus imbricatus Hoskins and Cross ~~nov.~~ sp.

Strobilus: Medium size, more than 13.5 cm. long by 1.8-2.5 cm. in diameter, essentially cylindrical, base (proximal end) not tapered, tip slightly tapered and bluntly conical. Specimens preserved as fine sandstone casts.

Axis: Approximately 4-5 mm. in diameter at base, tapered abruptly to 2-3 mm. throughout the remainder of length except the distal end which tapers very slightly to the blunt, rounded tip. 13 sporophyll bases prominent when viewed in cross section. No cellular detail observed.

Sporophylls: Arranged spirally, 13 per revolution about the axis and approximately 5 revolutions per cm., progressively reduced in size and maturity at the immediate distal end and so arranged as to form a bluntly-conical tip. Pedicels inserted at right angles to axis and about 6-8 mm. in length to the distal ends where laminae curve evenly upward. No subtended or thickened portion of lamina evident. Laminae 1.5-2.0 cm. long, slender, not over 1.5 mm. wide at base, tapering gradually to sharp point, closely appressed, overlapping many laminae above; imbricate in appearance. Median nerve is prominent.

Ligule: Definite evidence lacking, possibly because of imperfect preservation.

Sporangia: Borne adaxially on sporophyll pedicel. Greatly elongated (6-8 mm.), wedge-shaped in top view, wedge-shaped in cross-section near axis but broadly flattened at distal end and overlapping narrower sporophyll; attachment not distinguishable. Densely crowded vertically and laterally and thus distorted.

Immature at tip.

Spores: Small (26.5μ), triradiate openings in some; obtained only by maceration. No larger spores found in this strobilus.

Location and horizon: Pocahontas sandstone, Lower Pottsville series, Pennsylvanian system. Six miles northwest of Orleans, Orange County, Indiana; Chailleaux quarries.

Number of specimens: Four. One fairly complete strobilus, the holotype specimen, with base intact; one slightly smaller specimen with tip intact, the hypotype specimen; two smaller fragments; several traces of other strobili of probably the same type. Holotype, No. B-620 and hypotype, No. B-1981; Paleobotanical Museum, Botany Department, University of Cincinnati.

Name of species: Lepidostrobus imbricatus, after the imbricate nature and appearance of the laminae of the sporophylls.

Lepidostrobus arrectus nov. sp.[4]

Cone: Medium sized cone, 11.5 x 2.7 cm. Incomplete,

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4 Hoskins, J. H. and A. T. Cross. 1943--Lepidostrobus aristatus Hoskins and Cross, a homonym. Amer. Midl. Nat. 29:542.

both ends missing. Slightly flattened. Preserved as cast in fine sandstone. Middle of specimen distorted by growth of concretions.

Axis: 5 mm. in diameter throughout known length. 11 sporophyll bases on axis when viewed in cross-section. No cellular detail preserved.

Sporophylls: Arranged spirally, about 11 sporophylls per revolution and 43 revolutions. Adaxial angle of pedicel part of sporophylls to axis, slightly greater than right angle. Pedicel 1.1 cm. long. Prominent stalk-like sporophyll bases about 1 mm. long on axis. Laminae very wide at base (3-4 mm.) and 30-40 mm. long. A portion of the lamina is subtended prominently below the horizontal plane of the pedicel and is slightly thickened. Laminae taper rather gradually from wide base to an attenuated tip, are closely appressed for the lower half but slightly divergent above. Aristate in appearance.

Ligules: Presence questionable. Indefinite structure arises from distal end of pedicel.

Sporangia: Borne adaxially on sporophylls, closely crowded. 1 cm. long, wedge-shaped in top view, narrow, but not triangular in cross-section next to the axis, broader and somewhat rectangular-ovate at distal end. Narrower pedicel is broadly overlapped by sporangia. Attachment to sporophyll appears to be throughout length by narrow band of tissue.

Spores: Two sizes of spores have been found by macerating sporangia. The smaller spores are 27μ and the larger are 160-190μ. Triradiate openings are prominent but no bristles are visible, the exine possibly having been destroyed.

Location and horizon: Pocahontas sandstone, Lower Pottsville series, Pennsylvanian system. Six miles northwest of Orleans, Orange County, Indiana; Whetstone quarry.

Number of specimens: One specimen, exposed by splitting sandstone block. Split in half. Paleobotanical Museum, Botany Department, University of Cincinnati.

Name: Lepidostrobus arrectus after the position of the attenuated laminae of the superimposed sporophylls which arise at angles of 70° to 80° from the pedicels. The name arrectus refers to this condition.

SUMMARY

1. Several incomplete *Lepidostrobus* cones have been found along with other plant remains in the Lower Pottsville sandstones of Orange County, Indiana.

2. Diagnostic characteristics of the cone material are given and the two evident types which result are compared with other known casts or petrifactions of *Lepidostrobus*.

3. *Lepidostrobus imbricatus* and *L. arrectus* are the proposed species names for the two types of cones discussed.

4. Summarized type descriptions are given for each species.

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