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REPORT OF INVESTIGATIONS—NO. 50

SPORES FROM THE HERRIN (NO. 6) COAL BED IN ILLINOIS

BY

JAMES M. SCHOPF

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JAMES M. SCHOPF

INTRODUCTION

This report is concerned with a description and classification of spores found in the commercially important Herrin (No. 6) coal bed. The study of these minute and interesting forms of fossil plant life is one phase of the studies being made by the Survey to determine the character of the life environment in the different geological periods. Such studies have fundamental importance because a knowledge of the fossil fauna or flora of the successive geological periods provides the standard basis for determining the relative position of geologic strata. The identification and correlation of individual coal beds or coal horizons is essential for development of our coal and other natural resources and the inventory of coal reserves is utterly dependent on the accuracy of such information. Precise correlation also aids in the discovery of geological structures which often are favorable sites for accumulation of oil and gas.

Spores are of further importance with respect to the constitution of coal itself. They offer an unusual opportunity for obtaining definite information of the plant populations contributing to the various coal beds. Variation of the initial plant constituents is one of the important causes for the origination of different types of coal. Type classification is fundamental in the differentiation of coals, but unfortunately its achievement has been delayed because of imperfect knowledge of the plant components.

The study of fossil spores is a field of investigation heretofore scarcely entered in America. Hence a preliminary foundation of description and classification, such as is represented by the present report, is essential to its development. Additional studies are now in progress which deal with distribution of spores throughout the Pennsylvanian of Illinois.

HISTORY OF INVESTIGATION AND ACKNOWLEDGMENT

The investigation of spores in Illinois coals was begun in 1931 under the supervision of Dr. G. H. Cady. During that year a number of column samples of No. 6 coal were collected in southern Illinois. These columns were prepared in the laboratory for study by the many methods of coal investigation.

The first macerated residues of this coal were prepared by Dr. L. C. McCabe (26)* who reported certain of his findings in a paper presented at the Illinois Academy of Science and in an unpublished dissertation at the University of Illinois (27). Mr. O. J. Henbest later macerated and made preparations from these column samples, which form the essential basis for much of the present paper. The author began a continuation of this work in 1934 through funds made available by the U. S. Civil Works Administration. A grant-in-aid from the National Research Council to Dr. Cady enabled the investigation to proceed from August 1934 to June 1935, with the author as research assistant under Dr. Cady's direction. Since June 1935, the previous support of the Illinois State Geological Survey in materials and facilities has been increased to the entire sponsoring of this investigation.

The assistance provided by the National Research Council is gratefully acknowledged. Members of the Survey staff, particularly Mr. O. J. Henbest and Dr. L. C. McCabe, have aided in council and material assistance. Dr. Cady has, in addition, contributed much in the work incidental to preparation of this paper, and to him in particular the author is greatly indebted. Dr. J. T. Buchholz of the University of Illinois Botany Department has read and commented on portions of the manuscript, and Dr. H. H. Bartlett of the University of Michigan has suggested many improvements in details of style and procedure, a service for which the author is especially grateful. Mr. Revilo Oliver of the Classics Department of the University of Illinois has been most kind in checking constructions of the new scientific names proposed in this paper. However, it is due to the continued interest of Dr. M. M. Leighton, Chief of the Survey, that these investigations are made possible.

SOURCE OF MATERIAL

The material of the present report was derived from four column samples of Herrin (No. 6) coal, which is a member of the Brereton cyclothem (or formation) of Wanless and Weller (53) and is the uppermost bed of the Carbondale formation. This bed is commercially important in two isolated areas in Illinois; one in the northern and the other in the southern part of the State. The present study has been limited to the southern area as shown on the index map in figure 1. Two columns were obtained from the Belleville region at points separated by but a few miles; column 1 from a local mine south of Belleville, and column 3 from a mine along the Mississippi bluff northwest of Belleville. Column 18 was obtained from a mine in Washington County, located more centrally in the southwestern part of the Illinois basin. Another column (No. 31) was taken from the "Southern Illinois" district near Johnston City. There is a notable similarity in the species and distribution of spores in the columns from near Belleville and in the Johnston City column. Fewer species are present in the Washington County column but those present are also found in the other localities.

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* References will be found on pages 53-55.

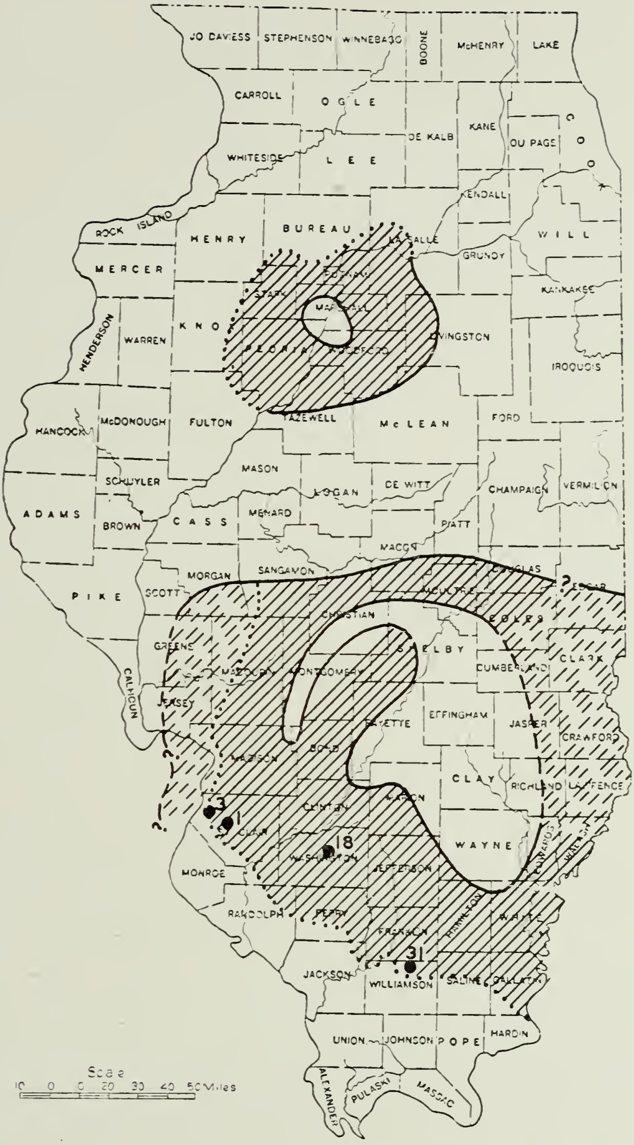

Figure 1.—Localities in southwestern Illinois from which samples were taken. Important areas of Herrin (No. 6) coal cross-lined (inferred where lines are broken).

The Carbondale formation has been considered approximately equivalent to the Allegheny formation of eastern United States and Noé (31) believes that this group of beds "corresponds somewhat to the Westphalian D" of Europe. The spores of Illinois No. 6 coal, when compared with European spores, tend to confirm correlation with the higher Westphalian of western Europe.

PREPARATION PROCEDURE

The four columns were studied in separate vertical units. Columns 1 and 31 were separated arbitrarily into small blocks 2 cm in vertical dimension throughout. Columns 3 and 18 were separated into benches up to 8 inches in vertical extent more or less in accord with what appeared to be natural depositional benches. These benches are not sufficiently definite for extensive stratigraphic comparison except when identified in relation to persistent shale partings; hence most of them seem of very local significance. In comparison of the two methods used in subdividing the columns it was found that use of natural bench divisions was advantageous. Very little additional distributional refinement was evident by study of residues from the arbitrary 2 cm blocks and the much greater number of separate macerations and the added study required is probably not necessary in most instances. The smaller bands and laminae apparently have little influence on distribution of spore varieties.

The spores were liberated from the coal matrix by maceration with the well known Schulze's solution (potassium chlorate, ($KClO_3$), in concentrated nitric acid, (HNO_3)) which oxidizes and partially dissolves the humic matrix. The coal material was prepared for treatment by splitting the individual samples, previously noted, into flakes along the horizontal planes. The residue was washed free of acid and treated with a 10 to 20 per cent solution of ammonium hydroxide (NH_4OH) for 24 hours or more until the humic material was thoroughly dispersed. The dark brown liquid was then decanted or siphoned off and the residue washed several times by repeatedly flooding with water and siphoning off or decanting, allowing time between each operation for the residue to settle.

No fixed procedure can be recommended for various coals. Weathered coal generally macerates more readily than fresh coal and the procedure best suited for each type of sample must be determined by trial.

To facilitate observation under the Greenough type binocular, the washed residues were sized by wet seiving through Tyler standard screens of the following mesh sizes; 20 (833μ opening), 35 (417μ), 65 (208μ), and for some samples 100 mesh (147μ). Four or five differently sized residues were thus obtained and all except the finest were carefully searched for well preserved specimens which were removed for mounting. The finest separation is more conveniently handled by mounting a small amount of the residue in glycerine jelly and studying in the customary method used in pollen analysis of

Quaternary peat. The smallest spores present in the fine separation are not included in the present paper but will be treated at another time. Dissecting needles flattened on the end were found convenient for handling the larger spores and a fine pipette for smaller specimens. The remaining residue was stored in labeled sample bottles in an alcohol-glycerine (2-1) mixture. It was found that *Penicillium* (a common mold fungus) attacked the residues if they were stored merely in water, hence alcohol was used, being less objectionable in handling than formalin. Glycerine was added to counteract the brittleness so often observed in material exposed to alcohol for a considerable time and also to minimize the possibility of the residue drying out during storage.

The specimens to be mounted were sorted—Syracuse watch glasses proved convenient—and transferred to 95 per cent alcohol. Diaphane, a resinous mounting medium somewhat similar to euparal was used. A discussion of this mounting medium has recently been given by J. T. Buchholz in "Stain Technology" (9). Its greatest advantage with our fossil material seems to be its tolerance to moisture, making it possible to proceed directly from 95 per cent alcohol to the commercial "diaphane solvent". Since prolonged action of this solvent causes some material to become more brittle, the specimens were quickly removed from it and arranged in a drop of diaphane on a slide. The slides were set aside to allow the diaphane to partially harden and when the specimens were firmly fixed in position another drop of more concentrated diaphane was applied and the cover glass adjusted. After hardening (over a hot plate or in an oven if desired) the slides are especially suitable for study by means of transmitted light. Leitz Ultropak equipment was used for observation of the spores at higher magnifications by incident light.

COAL MACERATION PROCESSES

Coal maceration dates from 1855, when Franz Schulze (42) published a short paper entitled "Über das Vorkommen wohlerhaltener Zellulose in Braunkohle und Steinkohle", in which coal had been treated with potassium chlorate and nitric acid to make microscopic structure more visible.

Reinsch (35: p. 3) macerated coal using a different method which is given only briefly in the praeloquium of the Micro-Paleophytologia. As reagents he used caustic potash (KOH) and hydrofluoric acid.*

The customary maceration methods in use today have been recently summarized by Jurasky (21). Zetzsche and Kalin (67) have published a slightly different method which is said to minimize injury to spores and cuticles during maceration. This method consists essentially of bromination of these waxy bodies. Zerndt (63: p. 3) and Sahabi (38: p. 14, 18) have used modifications of this sort and report satisfactory results.

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* *"Studio,—per usum methodi dissolutionis elementorum carbonis per ferventem solutionem Kalii Kaustici et per Acidum Hydrofluoricum in elementa solubilia et in elementa insolubilia, successit, ut numerus exhauriens et ad solvendam quaestionem de natura vera Triletum, formarum extantium formae principes acquierentur."*

Other information bearing on the maceration method may be obtained from general treatises on coal such as Stutzer's (50). Although broadened in application and usefulness in recent years, the fundamental process is the same as that originally used by Schulze.

BOTANICAL CONSIDERATIONS

SPORES AND THEIR EQUIVALENTS

The relation of spores to life cycles of their respective plants is a basic consideration in the systematic study of such bodies. For further information pertinent to the subject, the reader is referred to discussions given by Bower (8) and by Eames (11) and others which discuss the gametophyte generation. The present section deals principally with the different kinds of spores and equivalent structures which may be isolated from coal.

The term spore is used in the present paper to designate those propagative bodies which consist essentially of the gametophyte (derived from a single cell) enclosed and protected by a more or less waxy noncellular layer or membrane, the spore coat. In coal ordinarily the spore coat alone is distinguishable although in some cases the gametophyte may also be present as a carbonized lamina.

The kinds of spores differ according to the type of plant reproduction and may best be discussed from that standpoint. The two major reproductive types which concern us are the free-sporing and the seed-bearing. The former are more primitive; some plants of this organization show diversification in the sexual specialization of their spores. The spores or spore equivalents of seed plants are always highly differentiated with respect to the sexes.

Free-sporing plants are those in which the spores are liberated from the sporangia which produced them and continue development, under favorable conditions, separately from their parent sporophyte. Seed-bearing plants retain and nourish the female gametophyte (spore equivalent) within the sporangium during growth and the male spore is generally transported to it *via* the air after being shed in the usual way. Such a reproductive method is much more complex than that found in free-sporing plants. The latter, however, were much more abundant in the ancient flora than they are at present, although the free-sporing habit is still found in our common ferns and other present day Pteridophytes.

Sexual differentiation among spores of the primitive free-sporing type may be recognized by differences in spore size but not all sex differentiation involves size. Examples of this sort occur among modern heterothallic bryophytes but these plants have not been recognized in the Paleozoic. Plants showing spore size differentiation are said to be heterosporous, the male spores being generally small and easily dispersed by air, the female spores relatively large. Free-sporing plants whose spores are not thus differentiated are said to be isosporous or homosporous. The spores of isosporous plants are all the same size, generally small, serve both male and female functions, and are termed isospores. Only the small male spores of heterosporous free-sporing plants are true microspores; the larger female spores are called megaspores. The larger size of the megaspore is presumably an adaptation for the storage of food which nourishes the embryo arising later.

Since the isospores of homosporous plants and the microspores of heterosporous plants are much alike in size and form, discrimination between the two is usually difficult for isolated specimens. On the other hand, since in many specific instances representatives of each type are distinctive, there is reason to believe that many forms may eventually be assigned correctly through inference from similar spores being identified in known fructifications. The practice generally followed by coal microscopists of calling all smaller varieties of spores "microspores" should therefore be avoided, since it will tend toward confusion when more precise information becomes available. The author suggests that, where there is doubt, spores of the isospore and microspore types should be referred to merely as small spores.

As was stated, the seed-bearing mode of reproduction is characterized throughout by marked male and female sexual differentiation of the spore structures. Since these structures are often found in maceration residues along with spores of free-sporing plants they must be accorded some consideration particularly in regard to the terminology employed.

Thompson (51) has pointed out that sexual differentiation in seed plants is expressed to a considerable degree through modification of the sporangia, the manifestation of which he calls heterangy. He does not believe that size differentiation of spores, i. e., heterospory, *necessarily* preceded the seed habit in the course of evolution. Consequently some caution must be exercised in calling the male and female spore structures of seed plants microspores and megaspores respectively. Further discussion relative to this question may be found in the article cited above and in a later paper by Thompson (52) referring to a note published in 'Nature' by Scott (44).

At least one group of plants is known, however, in which there is no question that seeds contained true megaspores. These are the isolated spores described herein as new genus, *Cystosporites* known to be allied with *Lepidocarpon,* a seed belonging to the lycopod order. *Lepidocarpon* shows a minimum of heterangy and in a great many particulars agrees favorably with the fructifications of heterosporous but free-sporing lycopods. It is well established that we are justified in speaking of the large spore within this and similar seeds as seed megaspores. The male spores of *Lepidocarpon* are cryptogamic in character and no doubt are truly microspores.

In several cases gymnospermic seeds have likewise been isolated from coal and in addition to the female spore membrane show adhering remnants of integumentary cuticle. Although these are not described in the present paper it is convenient to mention them here. Gymnosperms are markedly heterangious and attained the seed habit wholly independently of *Lepidocarpon.* It seems that these large gymnospermic female spores ought also to be called seed megaspores. However, since no free-sporing heterosporous ancestry is *known* to have preceded the seed habit in the gymnosperm line complete justification for this designation is lacking. In some primitive gymnosperms the male spores show considerable advance in organization beyond the cryptogamic microspore and yet lack some significant features of modern pollen. For these it is proposed to apply Renault's term "prepollen". A more detailed discussion of prepollen is given on pages 14-15.

For completeness the spore equivalents of modern gymnosperms and angiosperms should be mentioned although no angiosperm ancestors are recognized in the Paleozoic flora. The male spore equivalents in these are fairly similar in organization and are called pollen. Modern pollen is especially characterized by the formation of a pollen tube. The female gametophytes of modern gymnosperms appear to resemble the fossil forms of the Paleozoic in all significant characteristics of spore organization. The female gametophytes of angiosperms on the other hand show little to aid in comparison. There is no suggestion of a spore coat and the gametophyte as a whole is so extremely reduced that spore homologies pertinent to the above discussion cannot be confidently drawn.

The accompanying table 1 shows in a condensed form the general relationship of spores in vascular plants and summarizes the preceding discussion.

CONFIGURATIONS AND ORIENTATION OF SPORES

Two main types of spore configurations are prevalent due to differences in the process of spore formation from the preexisting spore mother cells. The first division of the spore mother cell nucleus may be followed immediately by bipartition of the protoplasm. A second nuclear division (resulting in formation of the individual spore nuclei) is again followed by partitioning of the two halves by walls. Thus there are two successive times at which partition is effected. Resultant spores are bilateral, more or less elongate and somewhat wedge shaped. In the contrasting mode of spore formation no bipartition of the protoplasm immediately follows the first nuclear division. Instead, the second nuclear division soon takes place and the four nuclei thus formed take positions in the single protoplasmic mass equidistant from one another. Walls, enclosing the nuclei to constitute four young spores, are then formed simultaneously. When wall formation is simultaneous the individual spores are tetrahedral in form. Lycopod megaspores are illustrative of this mode of formation.

TABLE 1

Type of Reproduction	Kinds of Spores or Spore Equivalents[1]
A. Free-Sporing Mode of Reproduction: 1. Spores not distinguishable as to sex; Plants *Homosporous* or *Isosporous*	For both sexes *Isopore* (=homospore)
2. Spores distinguishable according to sex; Plants *Heterosporous*	Male *Microspore* Female *Megaspore*
B. Seed-Bearing Mode of Reproduction: Always distinguishable as to sex: not necessarily heterosporous in the sense given above. Plants *Heterangious* 1. Primitive Seed Plants	Male *Microspore* *Prepollen* or *Pollen* (?) Female *Gametophyte of Primitive Seed.* (May, or may not, be properly called a *seed megaspore,* depending on whether plants are Heterosporous as well as Heterangious.)
2. Modern Seed Plants	Male *Pollen* (produces pollen tubes) Female *Gametophyte of Modern Seed*

[1] Megaspores are easily distinguishable by their relatively large size in most cases. Spores which can not be assigned to the isospore, microspore, prepollen or pollen categories will be merely termed small spores.

There have been attempts to interpret these two modes of spore formation phylogenetically as primitive and more advanced types, but there does not seem to be any present unanimity of opinion as to which is the more primitive. The two types are apparently not of far reaching significance because in the modern genus *Isoetes,* the megaspores are tetrahedral and the microspores bilateral. In groups of higher plants one form or other may be characteristic, but numbers of exceptions seem to show that the change from one type to the other may take place in fairly restricted circles of plant relationship and hence no great reliance may be placed on these characters by themselves for extensive phylogenetic use. Among the lower plants perhaps the tetrahedral or simultaneous type of spore is more common; however the bilateral or successive types are also encountered. Similarly prepollen of both kinds is known but the more common species of prepollen now recognized are typically bilateral.

In orienting spores or spore equivalents for precise description the relations established in the original tetrad are referred to. The side of the spore which is internal in the original four spore tetrad grouping is said to be proximal. The side of the individual spores which was external in the tetrad grouping is distal. The proximal side in the spores of lower plants is marked by a triradiate (trilete) or a linear (monolete) suture at which point the spore coat becomes ruptured during growth of the gametophyte within. Modern pollen generally undergoes a great deal more modification and growth within the sporangium after the separation of the spore from the tetrad groupings than occurs in cryptogamic spores. Consequently the tetrad markings are much less distinct or altogether eliminated in the mature pollen and it is much more difficult to establish the original tetrad relationship. Orientation of gymnospermic pollen grains is made possible by location of prothallial cells on the proximal wall. Wodehouse (57) mentions orientation of angiosperm pollen in several places in his recent text. The germ pores of these provide the best clew to the original tetrad relations when the mode of origin of the pores has been demonstrated.

PREPOLLEN

The term *prepollen* was used by Renault (36: p. 270) in describing the large monolete pteridosperm spores found in *Dolerophyllum* (now *Dolerotheca* (15)) fructifications and also spores of the same type found in the pollen chambers of some pteridospermic seeds. The cellular organization in these is very different from that of cryptogamic spores. For reasons given below it is believed that a satisfactory distinction may be made between them and other spores or spore equivalents found in maceration residues of coal. Because the points of distinction seem to be botanically significant, prepollen is used as a category coordinate with pollen. Prepollen is considerably more primitive in type of organization but it may represent the Paleozoic equivalent of certain types of modern pollen, in the same way that pteridosperms are considered ancestral to the Cycadales. Most authors have designated these spores as "pollen". It is believed, however, that revival of Renault's term will facilitate more precise discussion of such fossils.

A distinction of fundamental importance serving to distinguish prepollen from modern pollen is the point of germinal exit. The term germinal exit is used to indicate rupture of the spore coat for normal exposure of the gametophytic product whether this be spermatozoids, a pollen tube, or vegetative gametophytic tissue. The existence of pollen tubes in plants of the Paleozoic is still open to question since they have yet to be demonstrated. Germinal exit in prepollen is probably proximal but in modern pollen typically distal. Germinal exit in cryptogamic spores is so far as known, always proximal. The process of exit (commonly spoken of as germination) is a common feature in all spore bodies and it is physiologically significant since the sport coat, which was previously the dominant feature of the gametophytic environment, is essentially dispensed with at this stage. In the species of prepollen described (pp. 42-49) features indicative of proximal germinal exit are found.

Cryptogamic spores are similar to prepollen in having proximal exit and it is chiefly due to this similarity that prepollen is considered as primitive among the male spores of seed plants. It seems likely that originally the postulated cryptogamic ancestors of modern seed plants also were proximal in germinal exit and that at some stage of evolution rather abrupt change in the exit position occurred. In the Paleozoic prepollen figured by Zerndt (59: pl. 8, figs. 42-49) as "Pollen of *Dolerophyllum* sp." there seems to be distal infolding of the coat similar to that seen in cycad and some angiosperm pollen when dry. Such spores as this may represent a transitional stage in the process whereby distal exit finally became established. How ever this may have occurred, the prevalence of proximal exit among the primitive land plants shows that this condition is probably a fundamental feature of spore organization and hence it is a point of significance when this condition is indicated in the male spores of ancient seed plants.

TAXONOMIC TREATMENT

Although various authors have proposed a multiplicity of classification schemes for Paleozoic spores none of these are wholly adopted in the present work. Study of the different systems has shown that although differing in details, such as the manner of spore designation and grouping, they are fundamentally similar, each author having more or less arbitrarily proposed a series of "types" or names with little regard for fundamental botanical considerations. The few authors who are exceptions to this analysis have been disregarded by the majority of workers in this field.

The classification of spores admittedly presents many difficulties. When an attempt is made to classify spores in accordance with the standard taxonomy apparently inconsistent situations arise. In part this is because taxonomy of higher plants is almost entirely based on structures of the sporophyte, whereas spores belong to the gametophyte generation. The fact that Paleozoic plant genera are extinct further complicates the problem so that this treatment must necessarily be different from that used by students of Cenozoic and Recent spores or pollen.

One taxonomic difficulty arises from the presence of isolated microspores and megaspores of heterosporous plants. Although the occurrence of one type of spore implies the presence of the other, it has not thus far been found practical to use the same nomenclature for the two because definite proof of their correlation is lacking. The species characters of the megaspores and microspores are not the same and do not correspond even when produced by the same plant. It is altogether improbable that evolutionary changes in species characters of the two kinds of spores occurred at the same time. Thus, even if fortunate circumstances enable us to make a precise correlation of both kinds of spores at one horizon there still would be serious doubt of a similarly precise correlation holding good higher or lower in the geologic section. The most conservative practice and one leading to least confusion seems to be the separate classification of microspores and megaspores. While this requires the use of different names it tends to reduce the possibilities of error. The use of multiple names (the so called "organ genera") is not new to paleobotanists, and the inherent difficulties in correlating one part of a plant showing certain specific characters with another make it necessary. This applies equally to botanical correlation of the species of megaspores, their microspores, or either of these with the parent sporophyte. However, it is possible to correlate botanically many groups of spore species with higher taxonomic categories (based on vegetative sporophyte structures), and for nearly all botanical purposes this degree of correlation is sufficient.

These are among the considerations that have governed the work presented here. Genera have been defined on the basis of larger natural taxonomic categories and in this sense they are thought to represent a natural classification. The spore genera are artificial in that they correspond, not to normal sporophyte genera, but to categories approximating a family or suborder in the standard taxonomic scheme. It is of course desirable to restrict the generic groupings in spore classification to as small a natural category as discriminating study will allow. To this end it will probably be necessary to further restrict the present genera in some cases and to propose other new genera later on. Consequently the present study cannot in any way be regarded as final. The emended genus *Sporites* is an exception to the above remarks since it is recognized as a form genus in the widest sense used for terminologic convenience in cataloging spores of doubtful affinity.

Since it is deemed desirable to use separate specific and generic nomenclature for each of the different morphologic types of spores, e.g., megaspores, microspores, prepollen, etc., these morphologic categories serve as convenient subheadings. They of course have no status as taxonomic divisions.

SYSTEMATIC DESCRIPTIONS

SPORE VARIETIES

In table 2 are listed the spore varieties to be described. Their general frequency of occurrence and the category to which they belong is given in adjoining columns, but as previously mentioned, small spores found in the fine residues of this coal are not included in the present paper.

Table 2

Genus	Species	Frequency of Occurrence[1]	Spore Category
TRILETES			
(Sections)			
Aphanozonati	T. reinschi	(g)	Megaspore
	T. brevispiculus	(e)	"
Lagenicula	T. translucens	(g)	"
	T. (?) rugosus	(c)	"
	T. (?) nudus	(a)	"
Auriculati	T. spp.	(b)	"
Triangulati	T. triangulatus	(f)	"
	T. gymnozonatus	(c)	"
CYSTOSPORITES	C. breretonensis	(e)	Seed megaspore
MONOLETES	M. ovatus	(g)	Prepollen
	M. ellipsoides	(a)	"
	M. aureolus	(c)	"
PARASPORITES	P. maccabei	(d)	"
Fern sporangial masses[2]		(e)	Isospores
Calamite sporangial masses[2]		(c)	Megaspores?
SPORITES	S. plicatus	(d)	
(*incertae sedis*)	S. fumosus	(c)	

[1] Occurrence Key: a. Very infrequent; b. Local and infrequent; c. General but infrequent; d. Local but moderately abundant, esp. in certain benches; e. Moderate abundance especially in certain benches; f. Well represented but not abundant; g. Abundant.

[2] In a more adequate consideration of these interesting fossils it will be necessary to utilize generic and specific nomenclature.

DESCRIPTIONS OF MEGASPORES

Genus Triletes Reinsch emend. Schopf

Fossil megaspores, radially symmetrical, exhibiting definite proximal and distal aspects according to relationships established in the original spore tetrad. The proximal side is marked by three sutures (comprising the essential trilete structures) radiating equally or nearly so from the center of the proximal side. The proximal side is often set off from the distal by arcuate ridges or more elaborate equivalent structures, arising at the extreme margin of contact between sister spores of the original tetrad. Distal surfaces are smooth or variously ornamented; the proximal areas likewise, but usually less profusely so than the distal portions.

The natural symmetry of the spore body is of importance. In the section *Lagenicula* the axis is more elongated than the transverse diameter; in other sections of the genus the reverse is generally the case. In favorable specimens the same layers of the spore coat may be seen as are shown by megaspores of present day *Selaginella* and *Isoetes,* and in fact all the essential features of the spore morphology in these modern genera are likewise found in *Triletes* spores of the Paleozoic. Spore size is variable within certain limits but *Triletes* is on the whole abnormally large in comparison with spores of present day plants. No well established species of the genus are less than 300μ in diameter and several are larger than 2 mm. These larger megaspores are probably to be correlated with the large arborescent lycopods. All megaspores here included in *Triletes* are considered on the basis of their morphology to belong to the heterosporous free-sporing lycopods; in this sense the paleobotanic genus *Triletes* is taken to represent a natural plant group somewhat comparable to a suborder in the normal classification. The megaspores of lycopods allied with *Lepidocarpon* which attained seed habit organization have been segregated in a new genus discussed later on in this paper (p. 38).

Type Species.—Triletes reinschi (Ibrahim) (=*Triletes* I Bennie and Kidston) probably should be considered the genotype. Although Reinsch gave a diagnosis of *Triletes* he named no species but merely assigned numerals to the various forms. Many of his forms are based on characters induced through preservation or maceration and cannot easily be reduced to species in the present sense. *Triletes reinschi* was the first form designated by Bennie and Kidston (as *Triletes* I) and has some claim as genotype since it is the earliest described species which is now treated under binomial nomenclature. A further practical consideration is that it is widespread and shows the essential features of Paleozoic lycopod megaspores very well.

Thus far Bartlett (3) is the only author to give much consideration to the generic status of *Triletes* although many authors have used the name for spores recognized as lycopodiaceous. Reinsch applied the name to spores illustrated in Plate XI, figures 1-10, 15, and 16 of his *"Neue Untersuchungen Über d. Mikrostruktur der Steinkohle"* published in 1811 but the publication in 1883 of *"Über Algenähnliche und einzellige Körper in der Karbonkohle Central-Russlands"* (in Flora, vol. 4) more generally is accepted as the date of origin. The more ample and satisfactory diagnosis published independently in 1884 in the *"Micro-Paleophytologia"* probably should be taken as correctly expressing Reinsch's views on these fossils. He states that *Triletes* applies to *"Entia vegetabilica adhuc ignota natura ac adhuc extincta."* Reinsch, as Bartlett says, had apparently "never seen a megaspore of *Selaginella"* and although he compared his *Triletes* with the microspores and isospores of other cryptogams they were still considered to be fossil *Algae*. This opinion has long been discredited; but Reinsch's diagnosis is the first systematic attempt at classification which was sufficiently explicit and well enough illustrated to be of scientific value for this type of fossil.

Bennie and Kidston in 1886 (4) corrected Reinsch's erroneous attribution of the organisms. They regarded *Triletes* only as a name. (presumably a form genus) for all kinds of spores, pointing out that spores of many orders possess a "triradiate ridge." However, the large spores which they described were "with little reason to doubt—referable to some of the extinct *Lycopodiaceae*". Although Kidston never attempted to delimit lycopod spores separately he applied the name *"Triletes"* only to spores of this kind. Three new varieties, *Triletes* XIX (later described by Zerndt as *Triletes tuberculatus*), *T.* XX and *T.* XXI, were added in 1890 (22) to the eighteen types previously described. This procedure of numbering spores has been followed by several later authors.

David White (54) referred the megaspores of *Lepidophyllum* to *Triletes* (p. 216 and 218) and rejected (p. 251-2) a suggestion of Lesquereux that such spores were borne by *Taeniophyllum*, a presumed pteridosperm.

Seward (46: p. 215) stated that "The designation *Triletes* is applied to isolated spores of *Sigillaria* or to those of *Lepidodendron*."

Mrs. D. H. Scott (45) in 1906 described some megaspores which were found within sectioned sporangia of *Lepidostrobus foliaceus*. She tentatively named them *Triletes diabolicus*. Since there are available only isolated cross-sections of this species, the morphology is still rather uncertain.

Bartlett (2) isolated lycopod spores from weathered coal in glacial drift at Ann Arbor, Michigan almost 20 years ago. He obtained three well defined species of spores which were assigned to Reinsch's genus after careful study of the literature. From his review and discussion of the Micro-Paleophytologia it seems clear what the taxonomic status of *Triletes* should be. Other authors have been slow to accept his interpretation, possibly because he did not give a generic diagnosis redefining the genus. This is unfortunate, because in the last few years there have been a number of separate individual systems of classification proposed which are all different and contrary to the best usage of biological nomenclature.

Hirmer (19: p. 231) defined *Triletes* thus: "einzelne Megasporen von Lepidostroben und anderen heterosporen Blütenzapfen von Lycopodiales-verwandshaft."

Zerndt in 1930 (59) applied the name *Triletes* to large spores isolated from the "Stephanian" of Libiaz Poland, stating that he was merely following the system used by Bennie and Kidston. He did however follow Bartlett in applying regular binomial designations. In 1931, Zerndt (61) enumerated 31 "Types" of which 24 were assigned to *Triletes,* 4 to *Lagenicula,* 2 questionable varieties and one (type 31) as pollen of *Dolerophyllum.* Some of the spores which he had previously named were treated as synonymous with or included with other forms in the same type. The confusing part in this treatment (aside from the fact that it uselessly duplicated spore designations) is that Zerndt's types are altogether different from those of Bennie and Kidston, although twenty-one of them have the same numbers. In 1934, Zerndt (63) provided names for several of his spores previously designated only as "Types". He has continued these practices in several of his later publications (32, 64, 65, 66) until his "Types" now number 46 including about thirty named species or subspecies of *Triletes.* These were apparently used synonymously with the numbered types in some, but not in all, cases. Zerndt was not very explicit about delimitation of his "Types", so one can not be certain of the degree of coordination intended between them and the species. There is of course no real need to continue the numerical designations since most of his forms now are satisfactorily named. However, most of the data he presents relative to stratigraphic distribution is given in terms of his poorly defined "Type" numerals. It is apparent from Zerndt's more recent works that, notwithstanding the convenience of type numerals for tabular summarizing as seen especially in his earlier publications, the double method of designation is now becoming cumbersome. He included no adequate diagnosis of *Triletes* in these papers but the author believes the majority of his species rightfully belong to this genus. However, his *Triletes giganteus* is considered to belong in the Lepidocarpaceae and consequently has been segregated to a new genus described on page 38. Two others of Zerndt's species, T. *gracilis* and *T. karczewskii,* probably do not belong in *Triletes* in the redefined sense. Whether or not they happen to be microspores as he suggests, at any rate neither agree well in morphology with spores of known lycopod origin. Consequently, on two counts at least, these spores should be released from *Triletes* for the present and assigned to the more generalized *Sporites* group. Zerndt's species of *Lagenicula* are thought to be more correctly placed as a section within *Triletes* than separate from it. This is discussed more fully below.

In spite of these criticisms of Zerndt's works, it must be emphasized that he has provided the most ample source of information now available on many of the species included in the genus *Triletes* redefined. His publications are abundantly and excellently illustrated (albeit only by reflected light for most species), and his recordings of numerous measurements add greatly to our knowledge of spore variation.

In his doctor's dissertation published in 1933, Ibrahim (20) proposed a new artificial system for classifying spores in which *Triletes* is used for all spores with trilete structure; but as used, the name does not form the substantive in a bi- or trinomial nomenclature. Hyphenated subgroup names supersede *"Triletes"* in performing this function. However, the chief criticism of Ibrahim's system is that it places together in hopeless confusion the spores of totally unrelated groups of plants. His cumbersome terminology actually tells no more than was apparent when all spores were grouped under the name *"Sporites"* of H. Potonié. *Triletes,* as used in the sense of Ibrahim, loses the meaning it had acquired through use since Bennie and Kidston and is of no more paleobotanical value than at the time Reinsch proposed it.

Loose (24) followed the same system as Ibrahim. Wicher (55) also followed the same artificial divisions but retains *Sporites* of H. Potonié as a generic designation. Wicher reduced *Triletes* as used by Zerndt, to synonymy in several instances.

T. M. Harris (16) in 1935 used *Triletes* as a form-genus for isolated megaspores of probable lycopod affinity, and considered that the genus was emended thus by Bennie and Kidston. This may be the more correct systematic interpretation although no one else seems to have made the same deduction. Harris proposed that the spores described under *Selaginellites* by Miner (28), also be included in *Triletes* since as Harris says (p. 155) "There is no evidence that they belong to *Selaginellites*—(rather than to *Isoetes* or any other heterosporous lycopod that then existed)".

Sahabi in 1936 (38) used *Triletes* only as a synonym, in part, of some of his spore types, which are once again classified differently from any other author, although the artificial subdivisions instituted by Bennie and Kidston are still used and to some extent amplified. Zerndt (66) has recently discussed the identity and stratigraphic distribution of Sahabi's spores.

The spores sometimes known as *Lagenicula* have been included in the present treatment as a section within the genus *Triletes. Lagenicula* was instituted by Bennie and Kidston (4: p. 114, 115). Their diagnosis proceeds as follows: *"Lagenicula* (New group). Macrospores of oval or circular outline (when compressed) and provided with a neck-like projection which eventually splits into 3 subtriangular segments. Outer surface smooth or bearing bristle-like hairs."

Scott (43: p. 166) in his "Studies in Fossil Botany" refigures *Lagenicula* I of Bennie and Kidston stating that it is "probably of *Lepidostrobus Veltheimianus*". Certainly there is no reason to doubt that species of *Lagenicula* were also produced by heterosporous lycopods.

Zerndt (59) in 1930, treated *Lagenicula* as a group subordinate to *Triletes* and coordinate with the other three divisions of Bennie and Kidston. However, in his 1931 publication (61) and subsequently, he used it as a genus coordinate with *Triletes.*

Ibrahim (20) believed that *Lagenicula* represented forms which differed from species of *Triletes* only in their mode of preservation, and for this reason disregarded it. Although *Lagenicula* is difficult to define satisfactorily it still may represent a natural subdivision within the heterosporous lycopods if the majority of species which have been included in it are considered.

Zerndt in 1934 (63: p. 25) for the first time discussed what characters he particularly has in mind distinguishing *Lagenicula* as a genus. The author is in substantial agreement with him on most points and believes that this group deserves recognition although not as a separate genus. The differences exhibited by *Lagenicula* are of the same order of magnitude as those exhibited by other sections now to be described within *Triletes,* hence it is more correctly considered as a section of the genus than as a group of equal magnitude. This goes back to the sense in which Zerndt first used the name in 1930. The features which seem important in distinguishing *Lagenicula* are given on page 27.

In the above review are included only those authors who have used *Triletes* and *Lagenicula* in one sense or another. The issue has been further complicated, however, by others who have separately used other "systems" for classifying spores and disregarded earlier work. It is with the hope of clarifying the situation that the generic definition is emended and the history of these names reviewed.

It is noteworthy that no paleobotanist has seriously questioned the lycopod affinity of the spores we are discussing since Bennie and Kidston's paper was published. The evidence that Kidston presented was quite conclusive and should leave little doubt as to its general correctness. Information acquired since that time only serves to emphasize this relationship with the Lycopodiales.

Sections of Triletes.—Kidston (4) divided *Triletes* into three subgroups, the *Laevigati, Apiculati* and *Zonales,* which have been used by several later authors, notably Zerndt and Sahabi. These divisions probably were not intended as a permanent classification since it must have been evident to Kidston that they were based on quite arbitrary and artificial distinctions. Thus the presence or absence of apiculi is certainly a relative character which varies with even a natural genus as was shown by Pfeiffer (33) in her monograph of *Isoetes.* Motelay and Vendryès (29) also illustrate the variation in spore ornamentation found in this genus. Kidston illustrates spores of various *Selaginella* species which would necessarily be separated into his three divisions, *Laevigati, Apiculati,* and *Zonales* if classified with *Triletes.* Consequently it is apparent that no individual features of spore ornamentation, such as his divisions are based on, are sufficient for judging relationship, particularly in so large a natural group as is represented by *Triletes.*

Classification should reproduce the phylogeny and natural plant relationship to the extent of probability indicated by available information. Consequently it is justifiable to dispense with the *Laevigati, Apiculati,* and *Zonales* divisions, largely for the same reasons that the Linnean system of botanical classification has been abandoned. The sections of *Triletes* must be based on broader points of similarity in spore morphology which show a greater likelihood of denoting natural relationship.

The section divisions proposed for *Triletes* are as follows:

1.	*Aphanozonati*	sectio nov.
2.	*Lagenicula*	(B. and K.)
3.	*Auriculati*	sectio nov.
4.	*Triangulati*	sectio nov.

This sectional division of *Triletes* was proposed by the author as early as December 1936 at a meeting of the Paleontological Society of America, in Cincinnati. More recently Zerndt (65: p. 584) has independently suggested the *Auriculati* as a generic subdivision but since he omitted a description the name cannot be credited to him according to botanical rules of nomenclature.

The correlation of these groups with genera now in ordinary paleobotanic use is not possible at present. It is doubtful that it will ever be possible to extend such correlation to the extent that names primarily based on other plant organs will supersede names based primarily on spores. Species characters in the different plant parts do not change concurrently in geologic time, and specific association at one time may not hold at another. This is all the more reason for attempting to classify spores separately according to their natural relations with one another. Certain organs of plants are known to be "conservative" and others are subject to rapid evolutionary alteration. How rapidly the species characters of spores change in the course of time and how these may correlate with other evolutionary changes within the mother plants, can be precisely ascertained, if ever, only by extensive study which will be long in attainment.

It is on the basis of comparative morphology that the sections of *Triletes* are suggested. The author believes that spores assigned to any one of these groups are more closely related to one another than to those of other groups. In so far as this is true such a classification approaches natural phylogeny and leads toward an evolutionary understanding of these fossils. When the lines of relationship become thoroughly established this information will be of direct value for stratigraphic purposes. Consequently the accurate classification of spores is far from being a topic of mere academic interest.

It is believed that the kinds of spores found in association with lycopod cones will contribute materially toward further understanding of the different groups. As proof of the value of spores in lycopod classification we have only to look at the emphasis placed by taxonomists on spores in the modern genera *Isoetes* and *Selaginella*. It is unfortunate that even at the present time, relatively few adequate observations have been recorded of fossil spores found in association with the fructifications which bore them.

Sectio APHANOZONATI sect. nov.

Spores large; round or oval. Zonal appendages lacking; arcuate ridges usually present. Trilete structures moderately proportioned, lacking strong apical prominence, and usually occupying about half of the area of the proximal "hemisphere" (planimetric measurement). Spore coat generally thick. Surface ornamentation variable, sometimes extremely apiculate.

The large size and the moderate development of haptotypic structures on these spores are taken as cardinal points in diagnosis of this group. (Wodehouse (57) defines "haptotypic characters" as "those which are due to internal environment, such as the stimuli received by a developing pollen grain from contacts with its neighbors.") The body wall ornamentation of aphanozonate spores is secondary; ornamentation such as spines, granules, etc. are characters, generally speaking, for specific discrimination but are of no great importance in terms of the larger group discussed here. The name proposed refers to lack of prominent zonal features.

The *Aphanozonati* are the largest and most obvious and consequently have been recorded most often by previous workers. It was spores of this group which misled Carruthers (10) causing him to establish the genus *Flemingites* on the assumption that these spores were sporangia. Binney (5) has given a subsequent discussion correcting Carruthers. Due to constant association with large cones, and the consideration that only cones with large sporangia could have contained such spores, it is probably safe to assume that the *Aphanozonati* belonged to the larger lycopods.

TRILETES REINSCHI (Ibrahim)

Plate 2, figures 2-4; plate 5, figures 8, 9

Spore large, unornamented, ranging in size from 1700 to 2500μ for the majority of specimens. Round to oval, generally flattened axially, with folds occasionally present. The pyramic areas normally occupy 40-45 per cent of the proximal half of the flattened spore by planimetric measurement. Surface naturally smooth, dull textured, dark brown to almost black in color by reflected light. Double thickness of spore coat nearly opaque; single thickness is of a deep red color by transmitted light showing a fine granulose texture. Thickness of spore coat 25 to 35μ.

Trilete structures simple, radii about 450μ long. Arcuate ridges chiefly evident on account of their darker color but sometimes obscure. In all cases however, it is possible to detect a low ridge where the coat is actually thicker than elsewhere. This arcuate thickening is seen in thin-section (pl. 5, fig. 9, A and A_1) on the proximal side adjacent to the recurved extremities. It is the presence of these slight ridges in conjunction with the size, thickness of the spore coat, its presence in a bed where *T. reinschi* has been isolated, and the lack of other species which would be confused with it, which makes possible the identification of this spore from a thin-section.

Isolated spores frequently show the suture split open, producing a characteristic aperture and showing the lip to advantage. The aperture is slightly acuminate at the ends of each ray and the segmental apices also constrict the trilete opening. The lips are narrow, rounded and sometimes glossy. The apex of each segment is slightly thicker than the rest of the spore coat and somewhat darker in color. Infrequently there are a few folds at the segmental apices.

Bocheński (6) has recently illustrated spores indistinguishable from *T. reinschi* derived from a new species of cone, *Sigillariostrobus czarnockii.* His observations are particularly interesting since a great range in megaspore size is shown. The megaspores in apical sporangia (this cone apparently is entirely megasporangiate) were less than half a millimeter in diameter while those in the more basal portions were normal size for *T. reinschi.* It would seem probable that many of the spores in the cone Bocheński describes were not fully developed since it is only in somewhat immature cones that such spores are still found in the sporangia.

Rousseau (37) has obtained some large spores from laminae in shale. His "Types" 1-6 cannot be distinguished from *T. reinschi* although they are from older strata.

Sahabi (38) has apparently confused *T. reinschi* with Type 2 of Zerndt as he gives both of these as synonyms of his Type 1. Two of Sahabi's illustrations, however, are clearly of the *reinschi* type and only superficially similar to Zerndt's Type 2 spores. According to Zerndt these latter belong to *Calamites.* It is impossible to consider *T. reinschi,* however, as belonging to other than a heterosporous lycopod. Thus, although Sahabi's illustrations in his plate 1, figures 1 and 2, are probably *T. reinschi,* his discussion on page 34 seems to show that at least two kinds of spores have been confused in his "Type".

T. reinschi very likely is an aggregate species, i. e., it probably is to be correlated with several different species of cones. The characters of these spores are very generalized (except for their consistently large size). Cone characters probably permit taxonomic subdivision to greater degree than the spores alone do in this instance. Besides, *T. reinschi* is known to be very long ranging stratigraphically. The chief value of *T. reinschi,* then, is an ecologic indicator for certain larger lycopods. Since it is so big it certainly was not ordinarily carried very far from its point of origin.

To bring synonomy of *T. reinschi*, previously given in 1935, (40), up to date the following may be added:

1935 Types 1 to 6 incl. Rousseau, Bull. du Musee Royal d'Histoire Nat. de Belgique, XI (21), p. 3-4, plate 1, figures 1-5. Plate 2, figure 6.

1936 Type I Sahabi (only in part), Dissertation, Lille, p. 34, plate 1, figures 1 and 2.

Triletes reinschi is the most common species of large megaspore found in coal No. 6. It is often abundant in the bed immediately above the blue-band clay parting.

TRILETES BREVISPICULUS sp. nov.

Plate 1, figures 13 a-r; plate 2, figure 6; plate 3, figures 1-4

Spores large, diameter usually slightly less than 2 mm, round or oval, frequently folded. Trilete radii equal one sixth of the total spore diameter. Spore coat 20 to 30μ thick as measured in optical section. Arcuate ridges only slightly thickened. Pyramic areas dotted with small simple spines. Distal surfaces adorned with characteristic short spines of less than 15μ elevation beyond the spore coat; these consist of a broad swollen basal portion with a small but distinct central apiculation.

Triletes brevispiculus resembles *Triletes (Sporites) tuberosus* Ibrahim, and *Triletes* Typ. 14_1 Zerndt in part; one specimen figured by the latter in 1932 (62 : pl. 2, fig. 10) being most like it. Some of the apiculate spores figured by Bailey (1 : pl. 55, figs. 39, 44, 46) compare favorably with this new species but examination of his original material will probably be necessary before a satisfactory comparison can be made. European horizons have furnished a variety of apiculate forms of *Triletes* but this is the second apiculate species described from this country.

Triletes brevispiculus is distinguished chiefly by its apiculi on the distal surfaces as shown in plate 3, figures 2-4. These are very low, of 10 to 12μ elevation as shown in side view by drawings in plate 1, figures 13 a-k, with a clear distinguishable central columella. They are quite apparent on a cleanly macerated spore since the broadly proportioned apiculi are dark brown against the tawny background when viewed by reflected light. A specimen subjected to over maceration in hot concentrated nitric acid furnished additional information as to the structure of these short spines. In plate 3, figures 2 and 3, are shown photographs of this spore coat. The spines are integral with the exospore and more resistant to maceration. The columella penetrates into the exospore and appears as a dark central projection of each spine. The basal portion of each apiculation is tumid, distinctly raised and set off from the spore coat proper. This is well illustrated on a normally macerated spore in plate 3, figure 4. The profile view is seen here and also shown in the line drawings on plate 1, figures 13 a-k. The height seen in profile at the margin of plate 3, figure 4 is about the maximum for the distal apiculi of this species.

Apiculi of a different sort adorn the pyramic areas and this sudden change of apiculation is the most distinctive feature of the arcuate ridges. However it may be ascertained by transmitted light that the spore coat is also somewhat thicker on the arcs, similar to the ridges of *Triletes reinschi.* These proximal apiculi are also illustrated from portions of the over-macerated specimens and in the plate 1, figures 13 l-r. They are more closely spaced than the distal spines and consist of small conical projections taller than broad. In reflected light at low magnifications they appear as small dark colored granules speckling the pyramic surfaces as shown in the crayon drawing, plate 2, figure 6.

The trilete sutures are frequently found open so that the shape of the aperture forms a character of some value in identification of this species. Shape of the aperture is distinct from that illustrated by Bartlett (2) for *Triletes mamillarius.* It is characteristically broader in *Triletes brevispiculus* with the radial termination more abrupt. The lip of *T. brevispiculus* is rounded, frequently glossy, slightly nodular, and quite narrow, as seen in plate 3, figure 1. The portion adjoining the apex of each segment is a little darker and thicker than the rest of the pyramic surfaces but otherwise not distinctive.

The mean diameter of *T. brevispiculus* is about 1900μ, with a maximum of about 2200μ. A greater number of spores fall below the most frequent size rather than above it, which is probably due to the presence of some spores which had not attained full expansion in growth. The spore coat is thinner and hence more translucent than in *T. reinschi.* Trilete radii usually extend for one-half to one-third of the spore radius.

This spore shows characteristic zonal distribution within coal No. 6, the most prominent zone being just above the widely distributed blue-band parting.

Holotype.—Plate 2, figure 6; Illinois Geological Survey Collection; Column 3, Belleville, Illinois.

Sectio LAGENICULA (Bennie and Kidston)

Spores medium-sized, typically bottle shaped; axial dimension longest. Apex prominent and originally somewhat pyramidal. Arcuate ridges generally present; extreme zonal appendages lacking. Spore coat variable in thickness and ornamentation.

The spores of this group are characterized by a unique type of specialization involving chiefly the apical segments of the spore coat. This specialization in its more extreme form consists of an evagination of the apex beginning abruptly about midway on the pyramic surfaces. The structure thus formed consisting of the elongated and upraised apical portions of the three pyramic segments may be termed the vestibule. It is such a definite feature in many of the lageniculate spores that it must have had a definite function. It seems likely that it helped to retain a fertilization droplet which perhaps exuded from the mature archegonia when the egg cells were ready for fertilization. The vestibule is a morphologic feature that is apparently limited to certain lycopod megaspores of the Carboniferous; none of the modern forms known are comparable in this respect. In its more moderate development the vestibule is not set off separately from other apical features. It merges with the pyramic surfaces and is present only as an elongated apical region.

Due to the natural elongated shape of the apex the three segments tend to be more acute than in the other sections of *Triletes* where the ideal 120° angle between the trilete rays is more closely approximated. This peculiarity in the original shape makes *Lagenicula* distinctive in crushed preservation as obtained from ordinary coal residues. The pyramidal apex is not vertically compressible into a single plane without marked distortion. Coupled with this is the fact that the axial dimension of these spores is greater than the radial diameter. These factors combine to favor lateral compression of lageniculate spores in the coal. Likewise, spores of this type are best preserved when laterally compressed. In such cases the pyramic segments often flare apart providing the characteristic appearance. When these spores do chance to be flattened axially the apex is generally considerably contorted and preservation is on the whole less favorable for observation.

The presence of a vestibule by itself may be insufficient as a basis for concluding affinity within the section *Lagenicula.* For example, *Triletes breviaculeatus* Zerndt, 1936, was not placed in this group although Zerndt's illustration seems to indicate a well formed vestibule. On the other hand *Lagenicula splendida* Zerndt, 1937, was included due to its distinct vestibule although from its size and other characteristics it might well have been placed with the *Aphanozonati. Triletes tenuispinosus* Zerndt, 1934, has an apical prominence suggesting an incipient vestibule which might indicate that its closest affinity was with *Lagenicula.* Lageniculate spores of coal No. 6 and all higher horizons in the Eastern Interior Basin thus far examined do not have a well defined vestibule. Spores from some of the lower Pottsville series which are believed to be related to them do have structures similar to those Zerndt has described. Consequently the progressive simplification of this feature of spore morphology during the Carboniferous may be of considerable value in later stratigraphic studies.

TRILETES TRANSLUCENS sp. nov.

Plate 1, figure 12; plate 5, figures 3-5

Body oval, slightly elongated, average length *ca.* 900μ. Spore coat 15-20μ thick and highly translucent. Surface devoid of special ornamentation. Arcuate ridges usually evident, occasionally obscure. Trilete structures simple; rays *ca.* 275μ long as measured along margins of flattened segments.

These spores often are laterally or obliquely compressed so that the trilete structures are located at the end as shown in plate 1, figure 12, and plate 5, figures 4, 5. When vertically compressed, as in plate 5, figure 3, the tips of the pyramic segments are distorted. The lips of the segments are not especially demarcated nor is there any suggestion of an apical vestibule. This species is placed in the *Lagenicula* division of *Triletes* because of its general shape and proportions.

Triletes translucens resembles *Triletes* (*Lagenicula* (sic.)), *tenuimembranosa* Zerndt, 1937 (65: p. 587, pl. 14, figs. 1-2) which he previously designated "Type 25" (61: p. 175, pl. 9, figs. 33-35). No doubt the two species are closely related. However, the spore coat of Zerndt's species is given as hardly 7μ thick—considerably less than *T. translucens*.

Ibrahim (20: pl. 7, fig. 65) illustrates one spore which is apparently very similar to *T. translucens* although no magnification is given and the description is very brief. He assigns this specimen to *T. rugosus,* discussed next, which is probably a separate species.

Two instances have been observed where four *T. translucens* spores were still associated in tetrads.

This species is particularly characteristic of the basal part of Illinois No. 6 coal including one bench directly above the blue band. This distribution was found in all four columns investigated.

Holotype.—Plate 5, figure 4; Illinois Geological Survey Collection; Column 3, Belleville, Illinois.

TRILETES (?) RUGOSUS (Loose)

Plate 5, figure 6

1932 *Sporonites rugosus* Loose, Neues Jahrbuch für Min. Geol. u. Paläont., Beilage Bd. 67 part 2 p. 452, pl. 20, fig. 59.

Spore distinguished from the preceding species by its slightly smaller size, thicker spore coat (20μ+) of coarse surface texture tending to be rugose. The arcuate ridges are less expanded. The general form is more quadrate and the apical structures project less from the general body contour; as in *T. translucens* no vestibule can be detected. The pyramic segments are oftentimes contorted; on this account the segment margins appear darker in figure 6, since this photograph was made by transmitted light. By such illumination the spore is reddish in color; in reflected light a dark brown. Probably the most prominent feature which distinguishes this species from *T. translucens* is the thicker and much less translucent spore coat.

Zerndt (64 : p. 4) has recently stated that *Sporites rugosus* Loose is identical to *Triletes giganteus* Zerndt (now *Cystosporites giganteus,* see p. 39) but presents no further comment. The author cannot agree with this, at least so far as the material herein described is concerned. It is perhaps possible that abortive forms of *Cystosporites giganteus* lacking the apical cushion may bear some superficial resemblance but the illustrations previously published do not seem to bear this out.

Triletes (?) *rugosus* has been found sparsely represented in several localities from No. 6 coal.

TRILETES (?) NUDUS (Nowak and Zerndt)

Plate 5, figure 7

1936 *Lagenicula nuda* Nowak and Zerndt (also as Type 43) Bull. Int. de l'Acad. Polonaise des Sci. et des Lettres. Serie A; p. 60, pl. 1, fig. 6.

Spore body proximally elongate in the characteristic *Lagenicula* form although the vestibule is not particularly demarcated. Specimens are usually compressed laterally, undoubtedly due to their apical elongation which caused them to come to rest within the deposit lying on their sides. Length of such specimens from apex to base is 700 to 825μ, which is a little less than the dimensions given by Nowak and Zerndt. Maximum body width varies from 600 to about 750μ. Surface of spore is matte to rugose with frequent folds caused by flattening. Arcuate ridges are clearly developed, varying to some degree in their expansion. The spore coat is moderately dense to nearly opaque showing a dark red translucency in transmitted light; it is over 20μ in thickness as seen at the margin of the body. By reflected light the spore is dark brown.

This species is sparsely represented from No. 6 coal of the Belleville area in benches below the blue band. Nowak and Zerndt also indicate a somewhat infrequent occurrence of *T. nudus* in Poland. No other species are known which agree closely with this form.

Sectio AURICULATI sect. nov.

Spores of medium size; form generally subtriangular or trilobate due to expansion of the spore coat opposite the trilete radii. Flange moderately or weakly developed in the interradial areas. Trilete sutures long, extending in most cases from apex to equator. Spore coat relatively thick, in most cases nearly opaque. Surface ornamentation variable.

Zerndt (65: p. 584) has recently suggested that this group include spores of his type 11 and 12 and also, possibly type 5. These forms have been described as *Triletes auritus* (Zerndt (59), its numbered subspecies and *Triletes apendiculatus* which were described by Maślankiewicz (Acta Soc. Bot. Poloniae, 9, pp. 158-164, 1932) and *Triletes auritus* var. *grandis* Zerndt (65). The author believes that *Triletes tuberculatus,* Zerndt's Type 16 (59) =Triletes XIX of Kidston (22: p. 93)) should also be included.

The *Auriculati* illustrate well the artificiality of Kidston's original three divisions of *Triletes.* Although it is certainly a matter of interpretation whether the zonal structure constitutes a true flange or not, Zerndt previously placed his Type 11 and 12 forms in the *Laevigati*: several might as justifiedly have been placed in *Zonales*. He has placed *Triletes tuberculatus* in the *Apiculati* although it is clear that the general morphology of this form is quite comparable to other auriculate species and is not similar to aphanozonate species formerly placed in *Apiculati* with it.

The *Auriculati* are little known in association with the cones which bore them. One probable instance known to the author is that suggested by the small figures given by Schimper in his "Atlas" accompanying the "Paleontologie Vegetale" (pl. 62, figs. 34 and 39) which are said to be derived from *Lepidostrobus ornatus*, Lindley and Hutton. If reliance can be placed on size of spores as an indication of origin, the large size of several representatives, such as *Triletes tuberculatus* Zerndt, for example, is indicative of their association with medium- to rather large-sized strobili.

This group is poorly represented from Illinois No. 6 coal. Thus far only a few specimens have been obtained; these were from the basal part of Column 3 at Belleville, Illinois. Abundant auriculate spores have been obtained from coals both lower and higher in the section which will be described in a later paper. The few specimens in No. 6 coal possibly belong to two species which are briefly described below. Because of the scarcity of well preserved material it is thought best to withhold naming these forms until a later time when the more abundant material has been studied. Both forms seem to be in the upper size range of the *Auriculati*.

TRILETES (AURICULATI) sp. (a)

Plate 2, figure 5

Spores slightly subtriangular, total diameter from one radial extremity 1635μ; diameter of body proper 1221μ. Trilete sutures extending to the equator. Surface rugose laevigate with a few small irregularly placed apiculi which are darker in color than the rest of the spore. Flange thick and tapering abruptly at the margin; only moderate development of the radial prominences.

TRILETES (AURICULATI) sp. (b)

Plate 4, figures 8, 8a

Body less triangular than the preceding and lacking the dark colored apiculi. Radial over-all diameter about 1500μ. Density of the spore coat is similar to that of the preceding form and this together with the extent of the trilete radii and size tend to identify it with the auriculate group although the characteristic "ears" are not well developed.

Sectio TRIANGULATI sect. nov.

Spores of medium size or somewhat smaller. Spore body usually round or oval; zonal appendages, when present, sometimes radially extended lending a triangular appearance. Such zonal appendages usually are somewhat membranous, thinner than the spore coat proper. Arcuate marking or equivalent zonal structures commonly present near the true equator of the spore body. Trilete rays generally long in proportion to body size. Surfaces smooth or variously ornamented by reticulation.

Characteristics of the *Triangulati* are also exhibited by megaspores of *Selaginellites* and those of modern heteroporous lycopods. Some of the spores described by Harris (16) from Scoresby Sound, Greenland, may be placed most appropriately with the *Triangulati* section of *Triletes.* The same is true for the megaspores described somewhat earlier by Miner (28). The presence or absence of a well defined zonal appendage, prominent or moderate ornamentation of various sorts are convenient characters for specific discrimination within this larger spore group; individually none of these characters can be considered diagnostic for a larger natural alliance.

The *Triangulati* are most probably to be correlated with *Selaginellites* or similar forms judging from the works of Zeiller (58: p. 140-142, pls. 40, 41) and Halle (14) which illustrate fertile parts of these herbaceous plants.

Herbaceous lycopods (such as *Selaginellites* or *Lycopodites*) are not generally known from coal balls and on this account are not commonly mentioned as contributors in coal formation. It may be supposed that conditions required for growth by these plants were different from those which immediately precede and accompany formation of coal balls so that the vegetative tissues are not usually preserved for petrification. However, herbaceous lycopods are known from roof shale fossils in a number of localities in this country which renders the association of such plants with this coal forming flora nevertheless quite probable.

TRILETES TRIANGULATUS Zerndt

Plate 1, figures 7, 8; plate 4, figures 1-7; plate 7, figures 5, 6

Over-all dimensions, measured from one radial extremity to the opposite margin, range from about 575 to 800μ. Body diameters are in the neighborhood of half a millimeter (500μ). The body is round to slightly oval or cuneiform. A triangular appearance is imparted in some cases by radial extension of the flange in line with the trilete structures and the trilete apparatus itself imparts something of a triangular aspect due to the corresponding spore coat thickening in these areas. However, the triangular appearance is frequently more apparent than real. There is much variation in the degree of reticulation which has been used by previous authors as the chief means of distinguishing varieties of this species. In color, the body of these spores generally shows brown in reflected light; the flange is yellowish. The general features of the triangulatus type of spore are thus easily described and these spores are readily distinguished from other kinds known at present.

These spores are of the *Selaginella* type differing from modern *Selaginella* in possessing a more strongly developed equatorial flange and slightly exceeding the majority of *Selaginella* spores in size. Spore ornamentation patterns and morphology are in substantial agreement. The similarity is still more striking when comparison is made with spores obtained from certain Paleozoic species of *Selaginellites.* For these reasons it does not seem out of place to suggest that the spores known since 1930 as *Triletes triangulatus* Zerndt, were derived from herbaceous lycopods of the Paleozoic equivalent to certain of the *Selaginellites* species.

A considerable amount of variation in general features exists in the spores of this kind isolated from Illinois coal. These will be discussed under separate headings below, with reference to the separate morphological features. No attempt is made to separate *Triletes triangulatus* into smaller groups at this time although variation within the species is sufficient to indicate that this may be necessary later on. Additional studies of distribution of the forms within other coal beds may indicate that these groups of spore characters are united into several relatively distinct biological entities, each of which is more in harmony with the prevailing concept of a species, than the single group now known as *Triletes triangulatus.*

Reticulation.—In his 1930 publication Zerndt (59) distinguished two forms of *Triletes triangulatus;* the one first given has priority and must be accepted as the typical form of the species. The second may be taken as a variety of the first as Wicher (55) suggests. On the assumption that this variety is valid the synonomy has been compiled. From study of the Illinois forms of *Triletes triangulatus* we are not certain as to the validity of the variety. It is evident, at least, that the previous taxonomic work on this species has not been adequate. Reticulation size which is the basis of the varietal distinction, has not proved to be a very satisfactory criterion to determine the points in question. A large measure of doubt arises from neglect of previous authors to give the location of the reticulation measured, whether proximal or distal, since, as will be shown, both sides are often reticulated and the reticulae on the two sides vary in size. Of the numerous investigators who have illustrated and described forms belonging to *Triletes triangulatus,* Sahabi (38: p. 43) is the only one to make any mention of the bifacial reticulation. Although proximal reticulation may be distinguished in several of the figures accompanying works which contain no mention of it, it is probably correct to assume most of the reticulation measurements given by these authors apply to distal markings since they are generally most obvious. Where study has been made with reflected light the measurements probably are fairly accurate. By transmitted light the proximal and distal reticulae become superimposed and consequently measurements made under such conditions may easily be in error. Judging from their illustrations Zerndt has used reflected light consistently; Ibrahim and Loose have generally used transmitted light. The author believes that in order to properly describe the morphological features of most spores, and of *Triletes triangulatus* particularly, both types of illumination must be used.

To illustrate the present taxonomic status of this group the previous nomenclature of types referred to *Triletes triangulatus* Zerndt, chiefly based on reticulation (distal?) and notations of reticulation measurements as given in each instance have been compiled.

TRILETES TRIANGULATUS Zerndt

1930 Spora 0.5 mm. Zerndt, Ann. de la Soc. Géol. de Pologne, vol. 6, p. 306, 312, pl. 1, figs. 1a, b, c; pl. 2, figs. 1a, b. Species undivided—no measurements for reticulae given.

1930 *Triletes triangulatus* I Zerndt, Bull. Internat. de l'Acad. Polonaise des Sci. et des Lett., Ser. B, p. 51, pl. 7, figs. 19-24. "Meshes" about 50μ.

1932 *Sporonites regalis* Ibrahim, Neues Jahrbuch für Min. Geol. u. Paläont., Beilage Bd. 67, part 2, p. 449, pl. 16, fig. 24. Reticulae 50-80μ.

1933 *Triletes, Zonales—Sporites triangulatus regalis* Ibrahim, Dissertation, Tech. Hochschule, Berlin, p. 29, pl. 3, fig. 24. Reticulae 50-80μ.

1934 *Triletes, Zonales—Sporites regalis* Ibrahim; Loose, Arb. Inst. für Paläobot. u. Petrog. d. Brennsteine, Band 4, p. 149, pl. 7, fig. 34. Reticulae 35-70μ.

1934 *Triletes, Zonales—Sporites, Sporites triangulatus* Zerndt; Wicher, Arb. Inst. für Paläobot. u. Petrog. d. Brennsteine, Band 4, p. 175. Reticulae 50-80μ.

1934 *Triletes triangulatus* Zerndt, Acad. Polonaise des Sci. et des Lett., Com. des pubs. Silésiennes—Trav. Geol. no. 1, p. 19, text fig. 6, pl. 18, figs. 1-24. Species undivided—no measurements for reticulae given.

1936 *Triletes triangulatus* Zerndt; Schopf, Trans. Illinois State Acad. Sci., vol. 28, p. 107, fig. 6. Distal reticulation about 50μ.

1936 Type X, *Triletes triangulatus* Zerndt; Sahabi, Dissertation, Lille, p. 43, fig. 11, pl. 4, figs. 6-11. Both "external" and "faces of contact" reticulated—size not given. No varieties.

1937 *Triletes triangulatus* Zerndt, Acad. Polonaise des Sci. et des Lett., Com. des pubs. Silésiennes—Trav. Geol. no. 3, pl. 5, figs. 1-5. Figures only, no discussion.

TRILETES TRIANGULATUS Zerndt, var. ZONATUS Ibrahim

1930 *Triletes triangulatus* II Zerndt, Bull. Internat. de l'Acad. Polonaise des Sci. et des Lett., Ser. B, p. 53, pl. 7, figs. 25-30. Meshes approximate 36μ.

1932 *Sporonites zonatus* Ibrahim, Neues Jahrbuch für Min. Geol. u. Paläont., Beilage Bd. 67, part 2, p. 448, pl. 16, fig. 23. Reticulae 10-20μ.

1933 *Triletes, Zonals—Sporites triangulatus secundus* Zerndt; Ibrahim, Dissertation, Tech. Hochschule, Berlin, p. 30, pl. 3, fig. 23, pl. 7, fig. 64. Reticulae 10-25μ.

1934 *Triletes, Zonales—Sporites zonatus* Ibrahim; Loose, Arb. Inst. für Paläobot. u. Petrog. d. Brennsteine, Band 4, p. 150, pl. 7, fig. 31. Reticulae 10-20μ.

1934 *Triletes, Zonales — Sporites, Sporites triangulatus* Zerndt, var. *zonatus* Ibrahim; Wicher, Arb. Inst. für Paläobot. u. Petrog. d. Brennsteine, Band 4, p. 176. Reticulation smaller than on *T. triangulatus* Zerndt sp.

Uncertain Variety

1931 *Triletes triangulatus* III Stach & Zerndt, Glückauf, Jahrg. 67, p. 1123, figs. 32, 33. These figures show small proximal and coarse distal reticulation but in text *T. triangulatus* III is said to agree with *T. triangulatus* I in all characteristics except for smaller size.

The features of reticulation on the forms of *Triletes triangulatus* from Illinois are noted below.

Plate 4, figure 5a, and plate 7, figures 5 and 6, show the body reticulation patterns obtained by ordinary use of transmitted light; the proximal and distal reticulations are very difficult to distinguish separately. However, the individual illustrated in plate 1, figure 7, and in plate 4, figure 6, is very favorable for definition of the proximal reticulation pattern by transmitted light because the distal side is not present, having been lost in the maceration process. The proximal reticulation is not always present. It seems absent in most of these spores illustrated by Zerndt (63) in his larger treatise in 1934 but it is probably present in his figures 3 and 7, plate 18. It is likewise shown in plate 7, figure 27, in the Bulletin International Series B 1930 (59), on the specimen figured by Stach and Zerndt in 1931 (49 : fig. 32), and on the specimens figured without discussion in the second part of his "Megaspores of the Polish Coal Basin" (64 : pl. 5, figs. 1-5). Some of the Illinois material is similarly reticulated. However, on the spore illustrated in plate 1, figure 8, no proximal network can be distinguished. The pyramic surfaces are matte textured and show no real pattern. From spores of this sort one may proceed to those showing extremely well-marked reticulae on the pyramic surfaces, most pronounced toward the apex as in plate 4, figures 4, 6, and 7. In these cases the reticulation tends to become more attenuate passing toward the flange where it may join radial flange striations (fig. 4 or 7) or even carry out on the flange as a network there (pl. 4, fig. 2). The average size of these proximal reticulae varies from 21 to 27μ in diameter.

The distal reticulation is fairly uniform over the basal side of the spore. Size of the distal reticulae varies from less than 30μ to as much as 50μ on the tetrad of spores shown in figure 26, also in the case of the specimen figured in an earlier publication (39: p. 109, fig. 6a). In this tetrad one spore shows its accompanying proximal ornamentation. The distal reticulation also continues in varying degree upon the flange.

The range of variation in the proximal ornamentation has been stressed in the preceding description. This cannot be taken to indicate necessarily that we are dealing with variations within a single biological category of species rank. It does indicate that the conjunction of a larger number of characters must be considered for recognition of such categories and that the proximal features are inadequately known at present. Since the European type material in several instances requires additional description we cannot at present assign the Illinois forms in any satisfactory subordination within the group roughly known as *Triletes triangulatus.*

Flange.—Although the presence of the "equatorial" appendage has always been used in distinguishing *Triletes triangulatus,* little detailing its various characteristics has been written. To the writer this appears unfortunate since the flange shows many distinctive features. The fact that it is by a considerable degree the most fragile part of the spore and hence is often imperfect or broken off entirely may in part account for the lack of attention it has received.

The flange seems to reflect the degree of ornamentation present on the spore body. Hence on spores as shown in plate 1, figure 8, the flange is smooth with the exception of the radial folds or fluting which appears. The spores of *Selaginellites suissei* figured by Zeiller (59: pl. 41; figs. 5, 6) seem to show corresponding flange structure. The smooth flanged spores tend to be less reticulate on their proximal surfaces. Other individuals possess a radially striate flange as seen in plate 4, figures 4 and 7. These "striae" are due to radial thickenings. They often appear to connect with the body reticulation pattern as a further development of the tendency toward radial elongation of the reticulae which is noted in plate 1, figure 7, although the flange itself in this instance does not show the radially striate character.

The most common type of flange marking is illustrated in plate 1, figure 7, plate 4, figures 2, 5, and plate 7, figure 6. Here the flange shows a network of anastomosing thickenings of varying size which tend to diminish toward the margin as the flange decreases in thickness. The coarser strands form a pattern about the same texture as that of distal body markings and likely was formed by the same causal influences. The margin may be irregular or it may have a marginal thickening or "bead", as shown in plate 7, figure 6. Several specimens have been noted where the "bead" was located near the middle of the flange as in plate 4, figure 3. Figure 3a shows the same structure photographed with a slightly different illumination. When present, these features are nicely seen in transmitted light but fragmentation of the flange may make it impossible to determine these characteristics in every instance when the material is not favorably preserved.

In cases where the flange shows marked radial extension there is thickening corresponding to the trilete radii. This radial extension does not seem at all constant, varying in considerable degree or as in plate 4, figure 2, being nonexistent. In general the width of the flange is about $100\mu\pm$ in the interradial area and may be more than 150μ broad at the radial extremities.

Trilete apparatus.—As in the other parts of the spores considerable variation is shown by the trilete structures. The only correlation with other features noted at present is that high fluted lips are often associated with well developed proximal reticulation. Prominence of the triradiate structure is dependent on the "height" to which the lips project separately above the spore body. Likewise it is due to the radial persistence of these structures and to their thickness. In "height" the lips sometimes are separate from the body for as much as 50μ. The apex ordinarily shows a slightly more pronounced development than any other part of the trilete structure. In cases where the lips are considerably upraised they often become noticeably sinuous in accord with the reticulation pattern, with which they seem to be associated (pl. 4, fig. 4). Less pronounced structures are shown in plate 1, figure 8 where the radii are of moderate height (10-20μ), and are nearly straight. The lips are quite narrow, appearing broader when relatively low. In any case they appear to become wider toward the apex, due in part to the tendency of the suture between the lips to split at that point.

Ordinarily the trilete rays extend at least to the inner margin of the flange. The suture itself does not extend that far however. In plate 1, figure 7, the sutures are shown in asymmetrical development and for the short radius, even the usual thickening out to the flange is lacking.

Internal features.—Under this heading are included those details which are not ordinarily visible on the surface and can best be observed by means of transmitted light.

Density of the spore coat is a character which depends considerably on preservation and the maceration treatment. The body is generally quite dense and it is often impossible to pass sufficient light through for adequate observation unless the condenser diaphram is stopped down to a pin point aperture and the spore body placed directly over this strong beam of light. In many instances accurate observations may thus be made, the marginal wall thickness being brilliantly outlined and the walls horizontal to the view assuming a beautiful deep red color. On the basis of such observations the wall thickness is quite consistently *ca.* 20μ. This measurement probably includes chiefly the exospore. A diffraction line apparently indicates the outer margin of the endospore within.

In several instances a dark "central body" as shown in plate 7, figure 5 was seen. Sometimes it is larger, extending over to one side of the body interior, but however situated this structure seems to be attached along the trilete rays near the apex. It is possible that some of the "nuclei" illustrated by Reinsch in his Micro-Paleophytologia correspond to structures such as this, although most of them undoubtedly correspond to the entire spore body. The "central body" is considered to be a shrunken endosporal membrane which in modern spores maintains connection with the outer layers of the spore coat near the apex. Its presence as a shrunken sac may indicate that the gametophyte in these cases was abortive when the spores were deposited, otherwise the endospore probably would have been distended against the mesospore and exospore.

TRILETES GYMNOZONATUS sp. nov.

Plate 1, figure 9; plate 4, figure 9

Spore essentially round, 500 to 600μ in diameter. Zonal appendages lacking; arcuate ridges obscure. Trilete structures inconspicuous, rays approximately one third of total spore diameter; lips along suture only slightly elevated. Spore coat dense, 25 to 30μ thick. Surface obscurely reticulate to matte textured.

This species is somewhat similar to some individuals of *T. triangulatus* with the very obvious difference that the equatorial flange is absent and also that the reticulation is obscure. Specimens of *T. triangulatus* which have the flange broken off may show superficial resemblance to this species but differences become apparent on closer examination. *T. gymnozonatus* may represent a species of *Selaginellites* which lacked the equatorial appendage as is the the case for *S. primaevus* and *S. elongatus* reported by Halle (14).

Most specimens of this species are obtained flattened vertically or slightly obliquely. This seems to indicate that the spores were originally oval with the axis shorter than other dimensions; otherwise such a preservational preference would not be manifested.

Observation by transmitted light is generally possible only when a tiny beam of strong light is totally intercepted by the spore. Plate 4, figure 9, shows a specimen under these conditions; the spore coat shows brilliantly in optical section around the margins. A shrunken endospore (?) is also visible.

This species is relatively infrequent in coals thus far studied.

Holotype.—Plate 4, figure 9, Illinois Geological Survey Collection; Column 31, Belleville, Illinois.

Genus CYSTOSPORITES gen. nov.

Seed megaspores; fundamental radial symmetry obscure except at proximal extremity. Fertile and abortive forms distinct. Fertile spores very large, elongated, sack like in form. Trilete structures relatively very small. Coat of variable thickness and density; denser in extreme proximal and distal portions, intermediate zone highly translucent. Spore coat composed of interlocking matted fibrils, widely spaced and porous in the intermediate zone. Special ornamentation lacking.

Abortive spores variable in size; form oval to elongate oval. Small individuals frequently remain attached to the fertile member of the tetrad. Specimens over a millimeter long are generally isolated. Trilete features sometimes obscured by a mass of spore coat material which effectively seals the apex. Walls thick, fibrous character obscure; surface smooth or reticulate.

Spores of this character have been identified in several cases within the sporangial cavity of members of the Lepidocarpaceae. A specimen which shows the fibrous coat of a large fertile spore in place is illustrated in plate 8, figures 7 and 8. This specimen and that shown in figure 5 is referred to *Lepidocarpon.* Comparison with spores of other species of the Lepidocarpaceae is more difficult since the majority are coal ball petrifactions and the character of the spores is difficult to establish in the absence of a complete and closely spaced suite of serial sections. The seed megaspores contained in *Illiniocarpon cadyi* Schopf (41) are so far as known at present about the same as those in *Lepidocarpon mazonensis* Schopf when differences in preservation are taken into account.

The new genus *Cystosporites* is established to include primarily *C. breretonensis* sp. nov. designated as genotype, and *Triletes giganteus* Zerndt (60). The discovery that these spores pertain to lycopod seeds makes their segregation highly desirable. Their morphology is in strong contrast to that of *Triletes*. Zerndt suggested their probable affinity in 1930 (60) before conclusive proof was available. The abortive forms of *Cystosporites* were recognized as such by Wicher (56) who designates them as *Sporites varius*. Two abortive forms are described below, both of which have been found in connection with the typical fibrous spore coat of fertile spores.

The complete synonomy of forms which it seems should be included in the genus is listed below with notations as to the type of material described in each case. Complete citations to the various publications are given elsewhere. It is obviously necessary that fertile and abortive megaspores be treated together in classification.

Forms referred to CYSTOSPORITES

1930 *Triletes (Lagenicula) glabratus* Zerndt, Bull. Internat. de l'Acad. Polonaise des Sci. et des Lett., Ser. B, p. 54, pl. 8, figs. 38-41. Small abortive (?) spores lacking apical cushion.

1930 *Triletes giganteus* Zerndt, Bull. Internat. de l'Acad. Polonaise des Sci. et des Lett., Ser. B, p. 71, pls. 9, 10, 11. Fertile spores and abortive spores at apex.

1931 Type 1 Zerndt, Bull. Internat. de l'Acad. Polonaise des Sci. et des Lett., Ser. A, p. 170. Fertile spores.

Type 29 Zerndt, Ibid., p. 175. Probably abortive spores lacking apical cushion.

Type 30 Zerndt, Ibid., p. 175, pl. 8, figs. 26-27. Abortive spores with apical cushion.

1932 Type 30 Zerndt, Jahrbuch für das Berg— und Hüttenwesen in Sachsen, Jahrg. 1932, p. 13A, pl. 1, figs. 1, 2, 3. Abortive spores with apical cushion; one three spored "tetrad".

1934 *Triletes, Laevigati—Sporites, Sporites giganteus* Zerndt; Wicher, Arb. Inst. für Paläobot. u. Petrog. d. Brennsteine, Band 4, p. 172, pl. 8, fig. 9. Fertile spores, often with abortive spores attached.

1934 *Triletes, Laevigati—Sporites, Sporites varius* Wicher, Ibid., p. 173, pl. 8, figs. 3, 4. Abortive spores with apical cushion which Wicher recognizes as pertaining to the previous species.

1934 *Triletes giganteus* Zerndt, Acad. Polonaise des Sci. et des Lett., Com. des pubs. Silésiennes, Trav. Geol. no. 1, p. 13, fig. 2, pls. 1-5. Large fertile spores and small abortive spores lacking apical cushion. (Type 30 spores not mentioned).

1934 *Laevigati—Sporites giganteus* Zerndt; Wicher, Arb. Inst. für Paläobot. u. Petrog. der Brennsteine, Band 5, p. 88, pl. 6, figs. 1, 5. Fertile spores, with or without abortive members.

1934 *Laevigati—Sporites varius* Wicher, Ibid., p. 89, pl. 6, figs. 2, 3, 4, 6. Spores with apical cushion, (sometimes fertile?).

1936 *Triletes* cf. *giganteus* Zerndt; Schopf, Trans. Ill. State Acad. Sci., vol. 28, p. 107, fig. 5, p. 175. The specimen illustrated in this instance consists of a fertile spore with abortive spores. The latter possess the characteristic apical cushions. This specimen is now assigned to *C. breretonensis* n. sp. and designated as the holotype.

CYSTOSPORITES BRERETONENSIS sp. nov.

Plate 1, figures 10, 11; plate 3, figure 5; plate 8, figures 1-4

Fertile spores large; oval, elongate, sack like; dimensions *ca.* 8 mm by mm. Trilete structures relatively small, radial dimension variable; pyramic surfaces depressed in the proximally thickened spore coat, apical prominences lacking. Spore coat fibrous, densely matted and thickest around the arcuate ridges, loose and porous in median portion and more dense at distal end.

Abortive spores somewhat variable in size, remaining attached to the apex of the fertile member of the tetrad when small; largest abortive spores slightly exceed a millimeter in length. Apex generally characterized by a thick rugose apical cushion which obscures the trilete features. Spore coat dense and thick.

Forma ABORTIVUS

Isolated abortive spores which agree with those found in connection with the above species. Surface quite featureless, brown, matte textured in reflected light; sometimes showing slight indication of arcuate ridges expanded beyond the apical cushion when examined by means of a strong transmitted beam of light. Spore coat 20 to 35μ thick.

Forma RETICULATUS

Isolated abortive spores in general morphology similar to the above; spore coat reticulated, reticules usually conspicuous but sometimes obscure; mean diameter of reticulae *ca.* 35μ.

The close relationship of American and European species seems adequately demonstrated. However, no apical elongation occurs in *C. breretonensis* comparable with that illustrated by Zerndt (63: pl. 4, figs. 2-3) and described as characteristic of *Triletes giganteus.* The larger intermediate (and probably abortive) forms, now identified with *T. giganteus* but formerly designated as *Triletes (Lagenicula) glabratus* (then, Type 29) have not been found in our coal. These also differ from abortive forms of *C. breretonensis* in that no apical cushion is present. Bocheński (6: p. 204), and Zerndt (64: p. 4) also, now identify *T. giganteus* with *Lepidostrobus major* (sic.) in the Polish coal field. It has already been suggested (~~39~~41: p. 143) that Bocheński's material may likewise be referable to *Lepidocarpon.* Bocheński further describes an adaxial (distal on the spore) "winglike outgrowth of the exospore" of *T. giganteus* which has not been observed on our material. These differences probably indicate the European and American forms to be specifically distinct. *Lepidostrobus bohdanowiczii* Bocheński is also known to be related, at least so far as the megaspores may indicate. These Bocheński identified with *Sporites varius* Wicher. The type specimens illustrated in Wicher's work are similar to specimens of *C. breretonensis* forma *abortivus* and Wicher had found similar spores attached to forms he identified as

Zerndt's *Triletes giganteus.* Since the fertile spores of *Lepidostrobus bohdanowiczii* are larger, this would seem to indicate that they more probably constitute a distinct species; certain of the abortive forms however may be generalized and indistinguishable for the several species.

In Hirmer's review of Bocheński's work published in Fortschritte der Botanik. vol. 6, pp. 71-72, 1937. he unfortunately mistook Bocheński's first name, Tadeusz, for his last and credited the new plant names accordingly. He has spelled the name *varius* proposed by Wicher (55), "varians," and the spores found in *Sigillariostrobus czarnockii* Bocheński. are reported under a new specific name *(Triletes maius)* credited erroneously to Kidston. These spores are given in Bennie and Kidston's original publication as *Triletes* I and have been treated previously (p. 24) as *Triletes reinschi* (Ibrahim). Hirmer considers that *Lepidostrobus major* (Bgt.) and *L. bohdanowiczii* Bocheński are forms transitional between the free-sporing lepidostrobi and the seed-like *Lepidocarpon.* Hirmer apparently has not considered the appearance of *Lepidocarpon* when preserved as coalified compressions rather than in uncompressed petrifications.

The fibrous coat of *C. breretonensis* is most distinctive. The thinner middle zone renders these spores susceptible to fragmentation so that the more common specimens consist of either proximal or distal halves, or even mere fragments of fibrous spore coat. Since this spore coat is so different from any other material encountered in maceration residues generic identification can be made on this basis alone. In our material the spore coat seems to consist of only a single fibrous layer shown highly magnified in plate 8, figure 3. Wicher, (55: p. 172) however has reported a thin inner (endosporal?) sheath in well preserved specimens of *T. giganteus.* The thin fibrous character of the median region of the spore coat indicates conclusively enough that it did not function in these spores as a protective feature as in free-sporing forms. The loosely matted spore coat in the intermediate zone on the other hand may be considered as an adaptation for food transfer between the sporophyte and the enclosed and retained gametophyte. Although the spores are obtained isolated from other seed structures in maceration residues there is no reason to doubt that the spores were enclosed in seed structures up to the time of maceration. Thin sections of No. 6 coal often show the extremely long and tenuous spores of this genus enclosed by crushed and vitrainized seed coat tissue.

The apex of *Cystosporites breretonensis* frequently shows small abortive sister spores closely appressed to the pyramic areas (pl. 2, fig. 1, and pl. 8, fig. 1) in the original tetrad grouping. Where the abortive spores have been lost the trilete features are seen to be similar in general character to those of *Triletes* (pl. 8, fig. 2). They lack, however, the ornamentation frequently encountered in that group.

Abortive spores which grew to a larger size are more commonly dissociated from the tetrad grouping. These spores are variable in preservation. Those compressed laterally usually seem somewhat less distorted (pl. 8, fig. 4). A more folded specimen is shown in plate 1, figure 10. Reticulate abortive spores occur similarly. The line drawing of a sector of such a spore is shown in plate 1, figure 11, to illustrate the proportional size of reticulae; the adjacent apical cushion outline is shown in solid black.

For some time coal petrographers have described what are known as "tufted megaspores" from coal thin sections. In Illinois No. 6 coal several of these have been identified as abortive forms of *Cystosporites.* The "tuft" is the apical cushion seen on these spores when isolated by maceration.

Larger abortive spores sometimes cling together although separated from the fertile member of the tetrad. Thus far, there has been found no instance where all four spores were equally abortive; invariably it seems one member developed to a much larger size. A three spore cluster of reticulate abortive forms is shown in plate 7, figure 4. Zerndt (62: pl. 1, fig. 1) has previously illustrated a similar 3 spore "tetrad" of abortive forms which is like a few found in our coal associated with *C. breretonensis.*

Cystosporites breretonensis is named for the Brereton cyclothem which contains coal No. 6 and from which the type specimens are derived. The holotype specimen consists of the proximal end of a large fertile megaspore with two complete large abortive megaspores attached. These latter show their characteristic apical cushions; a portion of the apical cushion of the third missing abortive spore is also present.

Cystosporites breretonensis is one of the most common and persistent members of the spore flora known to be associated with Illinois No. 6 coal.

Holotype.—The holotype of this species is that which has been illustrated previously in 1935 (39: p. 109, fig. 5).

DESCRIPTION OF PREPOLLEN

Genus MONOLETES Ibrahim

The status of this genus has been previously discussed by the author in another publication (39) and little has been learned since to alter the opinion expressed there. Although we use the name only for spores of probable pteridosperm origin belonging to the Whittleseyinae (15) we know that *Monoletes,* defined merely as being bilateral in symmetry with a linear striation, does not include spores of pteridosperms either exclusively or inclusively. The spores Kidston (23) isolated from the pteridosperm fructification *Crossotheca,* are of a very definite triradiate type. Halle (15) has isolated triradiate spores from *Potoniea.* We know also that as it was used by Ibrahim, the group included spores probably belonging to eusporangiate ferns, similar to the spore illustrated in plate 6, figure 8. However, the prepollen treated below are thought to belong to peteridosperms. They closely agree with spores Halle isolated from Whittleseyinean fructifications and in general with the spores most frequently found in pollen chambers of Trigonocarp seeds. Other groups of pteridosperms (such as *Crossotheca*) have microspores much like those of certain ferns. As previously stated, within the various groups of plants, spores may be either bilateral or radially symmetric such as shown in plate 6, figures 7 and 8. The inconclusive status of smaller spores of the fern type is perhaps to be expected since the pteridosperm group as a whole is quite indefinite in its boundaries as drawn at the present time. The well known similarity of pteridosperm and eusporangiate fern leaves has called for establishment of form genera of slight phyletic significance and it is not surprising that the same situation is shown by certain of the spores. The significant point presented here is that there is at least one group of pteridosperms, the Whittleseyinae, which can be identified with fair certainty by their prepollen.

We use the generic name *Monoletes* for spores of this group of plants, understanding as we do so, that as yet the smaller spores which seem to possess the same essential characters are not so definitely assignable to any single plant order or necessarily related to the pteridosperms. Any restriction of the name *Monoletes* which could now be presented would have to be based mostly on size. Consequently although the name is herein applied in a restricted sense, formal redefinition is to be undertaken later.

MONOLETES OVATUS Schopf

Plate 1, figures 3-5; plate 6, figures 1-4

Additional observations have served to increase our knowledge of this species since the original publication in 1935. The description has now been amplified by a statistical study of more than a hundred specimens selected at random from several localities. This has provided more accurate information as to range in length and width, thickness of the spore coat and the length and width proportions.

This species may be described as follows: prepollen, oval in general outline, two to four tenths longer than wide, mean length varying from 380 to 430μ, mean width varying from 290 to 340μ. Extremes of length 330 to 495μ; extremes of width 230 and 375μ. It is characterized by one median longitudinal striation (median suture) on the proximal face which is not always straight but often shows a slight angular deviation near the middle. At either end this suture line tends to split and flare laterally in two slight ridges which soon are lost. Encircling the median suture line there appears to be an elliptical ridge with a slightly irregular outline. This ridge crosses the flared ends of the median striation at either end of the spore. The ridge and area enclosed probably aid in some way the exit of the fecundative agent and also possibly may serve as a means of volume accomodation with decrease and increase of water in the spore.

The spore coat is highly translucent and seems to possess a thin inner membrane (the intine or endospore) which ordinarily fits closely within the exine or exospore, but in a few cases draws away from the latter. The exine varys somewhat in thickness in an individual specimen—extreme variations of 12μ have been noted. The mean range of coat thickness for prepollen of this species (taking average values in the cases of individual variation) is 12 to 16μ. The surface appears smooth under low magnification but at higher power it shows dense minute shallow punctae. (The stippling in the drawings which illustrate this species is not to be taken as representing these punctae; they are much finer.)

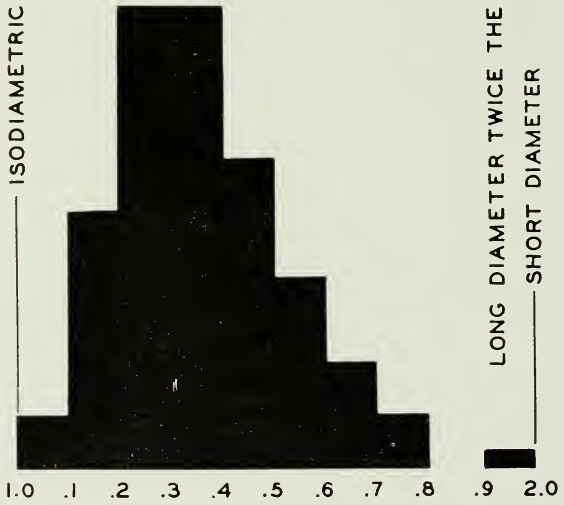

FIGURE 2.—Length-breadth proportions of *Monoletes ovatus.*

In the accompanying histogram (fig. 2) an attempt has been made to characterize the shape of these spores. In analyzing the shape, length was divided by width of each individual and the resulting figures plotted by tenths. The resulting distribution is slightly skew, there being more spores tending beyond the mean, toward elongate than toward isodiametric proportions. This is an obvious expression of the tendency to form longitudinal folds which increase the proportionate length of the specimens for measurements. Spores showing moderate and characteristic folding are illustrated in plate 1, figure 4, and plate 6, figure 1. The other spores illustrated have been selected to show structures which are often obscured by the folds induced through compression.

In an earlier publication (39: p. 108) it was thought that the encircling ridge was a haptotypic structure causally connected with the median suture. It is now considered as a distinct feature, probably formed later during growth of the spore. It customarily appears symmetrically placed around the median striation (pl. 6, fig. 2); however additional study has shown that this is not always the case as on the specimen shown in plate 1, figure 3.

Sometimes *Monoletes ovatus* is found in sporangial masses indicating in these instances that the spore bearing structure was included in the peat before the spores had been shed. An example of this sort is shown in plate 6, figure 4. The linear impressions are a feature common to most of the spore masses of this type. The inside diameter of the sporangium must have been about 900μ. The constituent spores are approximately 250 by 440μ.

MONOLETES ELLIPSOIDES (Ibrahim)

Plate 1, figure 14; plate 6, figures 5, 6

1932 *Sporonites ellipsoides* Ibrahim, Neues Jahrbuch f. Min. etc. Beil. Bd. 67, p. 449, pl. 17, fig. 29.
1933 *Monoletes, Laevigato-sporites ellipsoides* Ibrahim, Diss. Tech. Hochschule Berlin, p. 40, pl. 4, fig. 29.
1934 *Monoletes, Punctato-sporites ellipsoides* Ibrahim, Loose Arbeiten aus dem Inst. f. Paläobot. etc., Bd. 4, p. 158, pl. 7, fig. 35.
1934 *Monoletes Laevigato-sporites; Sporites ellipsoides* Ibrahim, Wicher Arbeiten aus dem Inst. f. Paläobot. etc., Bd. 4, p. 185.

Prepollen with the same general size and form as the preceding species. Distinguished from it chiefly by lack of an encircling ridge around the median suture. Suture well defined. Germinal exit was probably by means of the suture as seems indicated in the example shown in plate 1, figure 14. This species is infrequent in Illinois coal No. 6 but probably is more abundant in certain other beds in this country.

MONOLETES AUREOLUS sp. nov.

Plate 1, figures 1, 2

Spore broadly oval, encircled by an equatorial bladder; inclusive length varies from *ca.* 200 to 340μ. Body marked by a median suture which traverses the length of the spore body nearly to the bladder then bifurcates at both ends to continue out upon the bladder as two divergent ridges. A lateral striation parallels the median suture on either side about midway from the lateral margins of the spore body. Lateral striae extend beyond the body at either end until they join the flared end ridges of the median suture. Bladder wall thin and membranous; body wall dense, *ca.* 20μ thick.

M. aureolus is a spore type which is at present quite unknown in connection with other plant remains. It is most comparable to pteridosperm prepollen because the median striation agrees with this structure as seen in *M. ellipsoides* and *M. ovatus*. Although somewhat smaller than these species it is well above the usual size range of microspores or isospores. The equatorial bladder suggests abnormally large Cordaitalean pollen as it would appear compressed in the proximo-distal plane but Cordaitalean pollen has been shown by Florin (13) to be derived from a tetrahedral tetrad and have vestiges of the trilete sutures somewhat similar to the trilete imprint which Wodehouse has seen on pollen of *Abies.*

The only record of a similar spore known to the author is that of *Monoletes, (Zonalo-sporites) vittatus* briefly described by Ibrahim (20: p. 41). The information given there does not permit a satisfactory comparison with our material although these spores are certainly closely related. *Monoletes vittatus* is given as 240μ in length with a narrower marginal appendage and apparently lacking the accessory proximal striae found in *Monoletes aureolus.*

The greatly contrasting density of spore body and bladder make this form particularly difficult to photograph. Figures 1 and 2 of plate 1 have been traced from such photographs as could be obtained and the structural interpretation checked during tracing by observation both by transmitted light and reflected illumination by means of the Ultropak. The marginal bladder is shown to be such in places where torn, as in figure 1, and also by the marginal halo shown by transmitted light. No inner reticulation pattern such as is common for the bladders of coniferous pollen can be discerned.

Both the median and lateral striations appear to be haptotypic in origin and hence they serve to define the proximal side. The median striation characteristically shows a slight angular deviation in the middle similar to that sometimes present on *M. ovatus* and likewise indicated by Ibrahim (20: pl. 6, fig. 45) for *M. vittatus.* The lateral striae are also not absolutely straight but curve somewhat in accord with the outer contour of the spore as shown in the two illustrations.

Monoletes aureolus has been observed in maceration residues of No. 6 coal from several localities but never in abundance.

Holotype.—Plate 1, figure 1.

Genus PARASPORITES gen. nov.

Spores with two lateral bladders in superficial appearance resembling winged pollen of modern conifers. Distal harmomegathic* mechanism lacking; proximal germination apparatus consists of a modified trilete structure. Body round or oval. Spore coat of moderate and uniform thickness; except in the region of the germination apparatus. The outer spore coat layer (perine?) continuous over spore body and expanded to form the bladders.

Although the general aspect of these spores is coniferous we cannot be sure of this affinity until comparable spores are described which have been isolated from fructifications. If these spores are related to the Coniferales

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* See Wodehouse R. P. (53, pp. 155-157, 542) for discussion of this term, which refers to the volume-change accomodating mechanism seen in modern pollen; e. g., when alternately wet and dry.

they constitute one of the oldest records of this group of plants. On the other hand they may be pteridospermic and more closely related to species of *Monoletes* previously described.

Pityosporites Seward (47: p. 398) is the only spore genus previously described which seems comparable with *Parasporites*. Seward's designation was suggested for "spores, provided with bladder-like extensions of the exine, agreeing in size and form with those of modern Abieteneous genera." The spores now assigned to *Parasporites* are more than twice the linear dimensions of Seward's spores. He included in *Pityosporites* three spores, two of which, *P. antarcticus* (48: p. 311-13) and *P.* sp. (from Solms-Laubach's Wealden material), are modern in many aspects, having bladders distally inclined, thick proximal walls, etc. He also assigns one of Nathorst's (30: figs. 54-55) larger winged spores (from the Hör clay) to this genus. The bladders of these latter forms are situated opposite one another and the body wall is illustrated lacking any distinctive characteristics. This latter form might conceivably be classed as prepollen and considered related to *Parasporites* if the significant features of the spore body can be ascertained. It is also possible that it is referable to the *Caytoniales*.

Harris (17: pp. 40-46) has recently instituted the genus *Caytonanthus* for pollen bearing fructifications that are referable to the Caytonial order. His *Caytonanthus arberi* and *Caytonanthus* sp. 'A' are represented by pollen only. No doubt his attribution of these spores is correct but we may, perhaps, question the propriety of assigning isolated spores to a genus in which spore characters are not a primary consideration. Harris considers certain smaller spores Nathorst illustrated (30: figs. 56, 58) referable to *Caytonanthus* since he lists these of Nathorst's figures with a query under *C. kochi* Harris. The pollen of *Caytonanthus* is relatively small (20-30μ by 12-20μ), the two bladders are placed with slight asymmetry on the body which is not described as possessing harmomegathic mechanism or tetrad markings. Harris' drawings are not sufficiently detailed to conclusively demonstrate a total lack of these features; in fact his figures A, of *Caythonanthus* sp. 'A', and F of *Caytonanthus arberi* in his text figure 4 do show some suggestion of a vertical striation on the body. Possibly these slight body markings will enable us to form an opinion concerning the position of exit and the tetrad configurations of this material when more completely studied.

The spores illustrated by Lück (25) from clay associated with the Stassfurt salt deposits of Permian age acquire added significance in the light of Harris' work. Lück's spores, (especially his form III, fig. 59), although inadequately described in several essential details, are more comparable to spores of *Caytoniales* than to any others known at present. The two-winged spores of *Ullmania* and *Pityanthus* mentioned by Florin (12) may likewise be significant but as yet we have no basis of comparison for them.

It seems that the Caytonian spores and others of the same sort which are not so easily referred to that order, should be segregated into a separate genus. Whether or not there may be a genetic relationship between them and our older *Parasporites* awaits the addition of more information.

Florin's paper on Cordaitalean pollen (13) shows that *Parasporites* is not directly related to this group. According to Florin the trilete imprint is present to mark the proximal side, but in the mature grains this structure is not located in connection with the body of the mature spores at all. Instead, there is a bladder which has separated and expanded away from the body on all but a small distal area and the small obsolete trilete imprint is located only on the bladder membrane. The small area of contact between the bladder and body must be the point of germinal exit since he shows that prothallial cells line the body cavity except at this point. Proximal location of prothallial cells and distal exit is comparable to the condition in modern conifers. It is anomalous to find the spore coat layers split apart on the proximal side however. In lycopod spores the various layers are in most intimate contact along the trilete (proximal) sutures and in Abietineous pollen the thick proximal cap shows little dissociation in the various layers of the spore wall. At any rate, however, the Cordaitalean pollen studied by Florin is quite different from *Parasporites.* In the latter genus the bladder membrane invests the whole spore and is expanded on the two ends. The line of bladder attachment on the spore body is quite definite, front and back, as can be ascertained by observation in reflected light. The bladders do not intercommunicate as in the *Cordaites* pollen. However, the investing bladder membrane (perine?) with its capacity for expansion away from the spore body seems to be a common feature in *Parasporites,* modern pine pollen, Cordaitalean pollen and probably in some others.

The preceding discussion has touched on most of the older fossil spores known to us which possess two lateral bladders. Spores of this kind promise to be of considerable aid in tracing plant relationships from the Mesozoic back to the Paleozoic but the affinity of *Parasporites* cannot be stated at present. Florin in a recent visit to this laboratory very kindly examined a few of these peculiar spores and expressed the opinion that they were not coniferous and were, more probably, pteridospermic. Future work no doubt will bring enlightening evidence. However this may be, *Parasporites* bears evidence of proximal exit and thus is considered to belong truly in the prepollen category as distinct from later pollen.

PARASPORITES MACCABEI sp. nov.

Plate 1, figure 6; plate 7, figures 1-3

Spore equipped with two lateral bladders, *ca.* 300μ broad inclusively. Body round, *ca.* 240μ in diameter. Bladders crescentic and opposite. Trilete structure asymmetrically developed; the ray vertically disposed between the bladders least developed. The other two "lateral" rays are distinct and connect by an arcuate marking. The single pyramic area thus enclosed may form an adaptation for germinal exit. Body wall dense, 15 to 20μ thick, surface rugose. Bladder membrane translucent, 2 to 3μ thick, externally smooth, internally granulose or obscurely reticulate.

The two bladders are distinct on both sides and do not intercommunicate. They overlap the body in compressed specimens for one-third to one-half of the bladder width as characteristically shown in plate 7, figure 3. Faint internal reticulation may be seen in the bladder as to the right in figure 2. Rugosity of the spore body is reminiscent of *Tsuga* pollen which likewise is enveloped by a membrane over the rugose body surface.

The trilete structure is more clearly visible on some specimens than on others; sometimes it appears to be quite obsolete. The specimen illustrated in plate 1, figure 6, shows the trilete marking to advantage. In others the two lateral rays are much more strongly developed than the vertical one. A single arcuate marking connects the two strong rays. This structure seems of about the same character as the "encircling marking" of *Monoletes ovatus.* It is possible in both cases that the area enclosed acts as an operculum for germinal exit. The specimen shown in plate 7, figure 1, shows this "operculum" to advantage. The vertical ray here is poorly developed. The single pyramic area differentiated seems to be weaker structurally than the rest of the spore coat since folds occur there more often than elsewhere on the spore body (see pl. 7, figs. 2, 3).

The spore body is reddish by transmitted light; by reflected light dark brown. The bladders are yellowish translucent and bronze tinged by reflected illumination.

Parasporites maccabei was first observed in maceration residues by L. C. McCabe of the Illinois Geological Survey. It was one of the miscellaneous spores illustrated by him (26) in 1931. It has therefore been named in his honor.

This species is known from both Illinois coal No. 5 and coal No. 6. The chief source of material studied is from the upper part of one Belleville column where in bench 9b a number of specimens were obtained. They have not, however, been found in any notable abundance.

Holotype.—Plate 7, figure 1, bench 9b (slide 73) of Column 1, Belleville, Illinois.

SPORES OF FERNS AND CALAMITES

SPORES OF TRUE FERNS

Spores of this class of plants have not as yet been thoroughly studied. Mention of them is made for the purpose of illustrating one further advantage of the maceration method and to record the presence of ferns as contributors to the spore flora of coal No. 6 in southwestern Illinois.

Fern spores are known both of bilateral and triradial types (see p. 12). Although extreme heterospory is known in certain specialized present day ferns those of the Paleozoic are generally considered to be isosporous, i. e., produced only one kind of spore which served both male and female gametophytic functions. These isospores are usually quite small, often about 30μ in diameter and variously ornamented. Being so small they are easily dispersed by wind.

In the fine residues these small spores may be found isolated. Obviously these individuals may have been carried a long distance before being deposited and hence they offer small assurance that their mother plants contributed to the local coal. Because of their chance for wind dispersal they may, when better understood, offer superior means of correlation over relatively long distances. Because our studies have thus far been chiefly concerned with the classification of spores of the local coal forming flora, we have not studied these isolated small spores.

Proof that the ferns were locally present may be found in the sporangial masses of spores which often occur in maceration residues. In these cases the fertile fronds must have been embedded in the Carboniferous peat before their spores had been shed. The multitude of spores in each sporangium were subsequently pressed together and still show the internal form of the sporangium when liberated as a mass from coal by maceration. The morphology of the individual spores can often be seen at the thinner margin of the mass; if this is impossible a slight pressure on the aggregate will often liberate individuals suitable for observation.

An individual characteristic variety of sporangial mass is illustrated by the camera lucida tracing shown in plate 6, figure 7. A single spore from this mass (indicated in its position by the black outline) is shown drawn separately at the right and is about 30μ in diameter.

Ferns of the Paleozoic possessed sporangia of a more massive type than those in most common modern ferns and the spores were produced in greater numbers. Spore output per sporangium has a phylogenetic significance as shown by Bower (7: pp. 261-267). It should be possible to devise a means of determining with fair accuracy the approximate numbers of spores present in these masses.

These massive sporangia of the original plants were often grouped in more or less coalesced clusters. Such a group of sporangia is called a synangium. The presence of synangium bearing ferns are shown in maceration residues by definite groups of spore masses which have become stuck together at the margins during incoalation. Such a synangial group composed of four sporangial masses is shown in plate 6, figure 8. The spore variety which composes this mass, *ca.* 30μ in length, is shown drawn separately by the side at higher magnification. The supplementary information such spore masses provide will undoubtedly make the correlation of these small spores with their respective plant groups much easier.

SPORES OF CALAMITES

In the course of these studies a few sporangial masses which probably are derived from *Calamites* were observed. Hartung (18) has provided information on the morphology of some calamite spores by investigating the type material of Weiss, using maceration methods. Some of these which were found in coal No. 6 agree well with spores of *Macrostachya*.

Our calamite spore masses are often paired, each half tapering distally and resembling a bunch of grapes in outline. The sporangial groups slightly exceed a millimeter in length and are less than half as wide at the broader basal end. Individual spores (probably slightly differentiated megaspores) are about 90μ in diameter with a simple unornamented trilete suture. Spores are quite translucent with no emphytic ornament. In some of the masses of this type a considerable admixture of shrunken and presumably abortive spores was seen. Partial abortion of spores has been previously noted in calamite sporangia by Scott (43: p. 50).

SPORES *INCERTAE SEDIS*

Genus Sporites H. Potonié emend. Schopf.

Unassigned spores whose morphology and functional categories are too imperfectly known to be placed in some more satisfactorily characterized group.

This name is recommended for use as a form genus in the broadest sense. In this paper it is used for forms considered worthy of recording but lacking in biological significance. Such forms may nevertheless be of some use in the characterization of geological strata. Robert Potonié and his students have recently revived the name *Sporites* which was suggested in 1893 by Heinrich Potonié (34: p. 185). The name originally was casually given to large megaspores (probably lycopod of the group *Aphanozonati*) which had earlier been called *Sporangites glabra* and *Sporangites papillata*. In their more recent usage *Sporites* has been applied as a "form" name in the broad sense, applying indiscriminately to all kinds of spores. Thus the name was in partial synonomy with *Triletes* and the other genera instituted in this paper.

Zerndt (63: p. 27) has recently used this name in essentially the sense proposed here, without stating any generic diagnosis, however.

For such a group as *Sporites* no genotype is necessary since its value is only in its convenience for designation.

Sporites plicatus sp. nov.

Plate 7, figures 7-9

Elliptical spores, 0.7 to 1.0 millimeter in length and one half to two thirds as wide. Germination apparatus is generally obscure. In certain instances, as shown in plate 7, figure 7, there is a suggestion of arcuate ridges and the three apical flaps placed on the side. Often no such structure is visible but a single triangular piece projects from the side of the specimen as in plate 7, figures 8 and 9. The spore wall is fairly thin (*ca.* 18μ) and translucent, with the surface slightly roughened. Folds are generally conspicuous down the length of the spore.

The general size of the spore and texture of the coat, compare favorably with *Triletes translucens* of the *Lagenicula* section of *Triletes*. Apical structure is obscurely defined and the shape of the body is different. Whereas *Triletes translucens* is clearly of a lycopod type, the spore here described, understood as it is at present, does not yet permit any conclusion as to its affinity. Because it is one of the characteristic forms found in Illinois No. 6 coal at Belleville, it does, however, merit recognition.

Holotype.—Plate 7, figure 8; from Column 3, bench 2, Belleville, Illinois.

SPORITES FUMOSUS sp. nov.

Plate 5, figures 1, 2

Spore round, 350 to 500μ in diameter, trisymmetric, lacking any noteworthy ornamentation or appendages. The trilete rays are linear slits in the spore coat, varying in length from one fourth to one third of the spore diameter. Lips are sometimes slightly raised but otherwise not separately distinguishable from the spore body. Arcuate ridges lacking. The character of the spore coat is the most distinctive feature. As seen by transmitted light it is variegated, being dark brown or yellow grading into areas of lighter shade. This effect is to a considerable extent due to the maceration process. Under advanced maceration treatment there is a tendency for the darker areas to become pitted, the lighter areas becoming quite membranous. Plate 5, figure 2 shows this effect. The normal appearance is given in plate 5, figure 1a by transmitted light and in figure 1b by reflected light.

The morphologic features exhibited by *Sporites fumosus* are quite generalized aside from the distinctive smoky translucency of the coat. This character may later allow correlation with some group of plants; the heterosporous calamites or the selaginellaceous lycopods at present seem the most likely.

Sporites fumosus is recorded from all localities of No. 6 coal which have been studied thoroughly, although nowhere in any notable abundance.

Paratypes.—Plate 5, figures 1, 2, Illinois Geological Survey Collection; from Belleville, Illinois, Column 3, benches 6 and 14.

SUMMARY

In this paper special attention has been paid to the classification of spores. The genus *Triletes* has been emended and subdivided into four sections, each of which includes a group of closely related lycopod spore species. The artificial division of *Triletes* used by Bennie and Kidston has been discontinued. New genera, *Cystosporites* for seed megaspores allied with the Lepidocarpaceae and *Parasporites* of uncertain alliance, have been proposed. *Monoletes* has been continued in use for microspores of whittleseyinean pteridosperms. *Sporites* has been emended to apply only to spores otherwise unassignable.

The spores here classified under *Monoletes* and under *Parasporites* are thought to merit botanical distinction as prepollen.

The plant groups and their spore representatives as isolated from No. 6 coal are listed below:

Lycopods	*Cystosporites*
	Triletes, Sectio *Aphanozonati* (from large plants)
	Triletes, Sectio *Lagenicula*
	Triletes, Sectio *Auriculati*
	Triletes, Sectio *Triangulati* (from small, probably herbaceous plants)
Whittleseyinean pteridosperms	*Monoletes*
Uncertain affinity	*Parasporites*
True Ferns and Calamites	Unnamed sporangial spore masses.

Twenty varieties of spores, in all, are dealt with, eight of which have been described as new species.

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DESCRIPTION OF PLATES

Foreword.—Owing to the diverse sizes of the different spores and the varying photographic character of points to be illustrated it has been necessary to use a variable scale of magnification in preparing these plates. It is felt that some of the disadvantages inherent in this practice have been overcome by giving many actual measurements in the plate descriptions as well as the ratio of magnification. Likewise are included notations as to the type of illumination used in obtaining any particular figure. To the author this seems quite important since it is only by knowing the manner of illumination that one may correctly interpret the structure shown by photographs of these semitranslucent fossil bodies.

Certain of these illustrations have been retouched where, in the author's opinion, such retouching served to bring out the true structure otherwise imperfectly represented due to halation or some other defect inherent in photographic illustration.

PLATE I

Fig. 1. *Monoletes aureolus* (x 115). Length 342μ. Photo tracing, transmitted light. Column 3, bench 6.

2. *Monoletes aureolus* (x 127). Length 288μ. Photo tracing, transmitted and reflected light. Column 3, bench 12.

3. *Monoletes ovatus* (x 110). Length 392μ. Camera lucida drawing, transmitted light. Colchester No. 2 coal, Atkinson Mine. Miscl. slide 74.

4. *Monoletes ovatus* (x 73). 473μ x 320μ. Photo tracing, transmitted light. Column 31, sect. 5.

5. *Monoletes ovatus*. Length 490μ. Photo tracing, transmitted light. Column 31, sect. 56.

6. *Parasporites maccabei* (x 110). Breadth 288μ, height 249μ. Bladders at broadest point 56μ and 43μ. Photo tracing, transmitted light. Shows trilete structure and "operculum". Column 1, sect. 73.

7. *Triletes triangulatus* (x 43). Maximum diameter 853μ. Average diameter of proximal reticulae 27μ. Photo tracing, transmitted light. Distal side is absent from this specimen.

8. *Triletes triangulatus* (x 43). "Radial" diameter 831μ. Photo tracing, reflected light. Column 3, sect. 15.

9. *Triletes gymnozonatus* (x 65). Diameter 550μ. Camera lucida drawing, reflected light. Column 3, sect. 27.

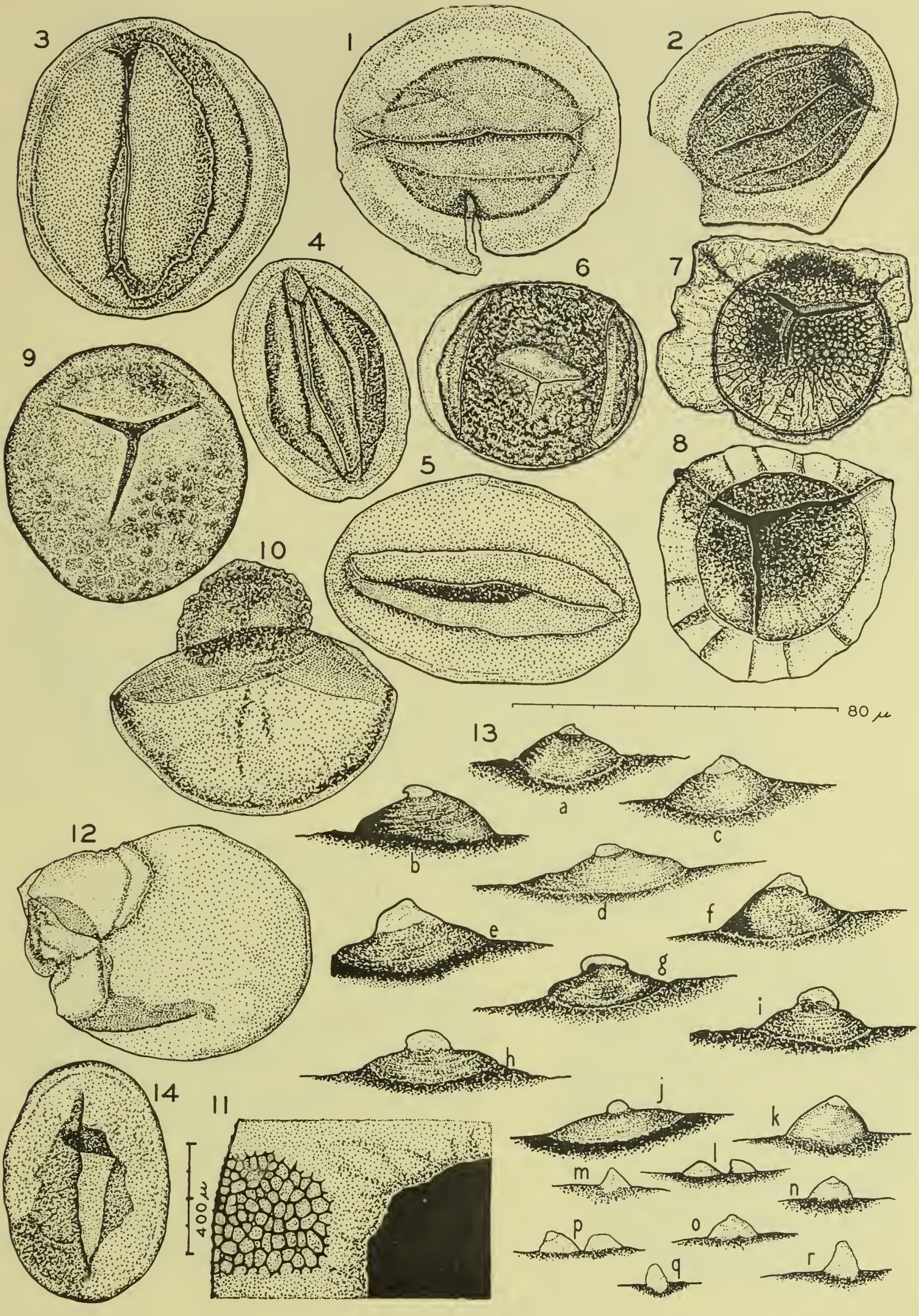
10. *Cystosporites breretonensis* forma *abortivus* (x 43). 950μ x 850μ. Camera lucida drawing, transmitted light. Column 31, sect. 21.

11. *Cystosporites breretonensis* forma *reticulatus* (scale given). Camera lucida drawing, reflected light. Portion of spore showing reticulation. Column 31, sect. 52.

12. *Triletes translucens* (x 43). 985μ x 765μ. Camera lucida drawing, transmitted light. Column 31, sect. 20.

13. a-r *Triletes brevispiculus* apiculae (x 570). Camera lucida drawings, transmitted light. In profile at edge of the spore; the lower examples are from the pyramic areas, the others from distal surfaces. Column 31, sections 42 and 43.

14. *Monoletes ellipsoides*. 442μ x 300μ. Photo tracing, transmitted light. Column 31, section 52.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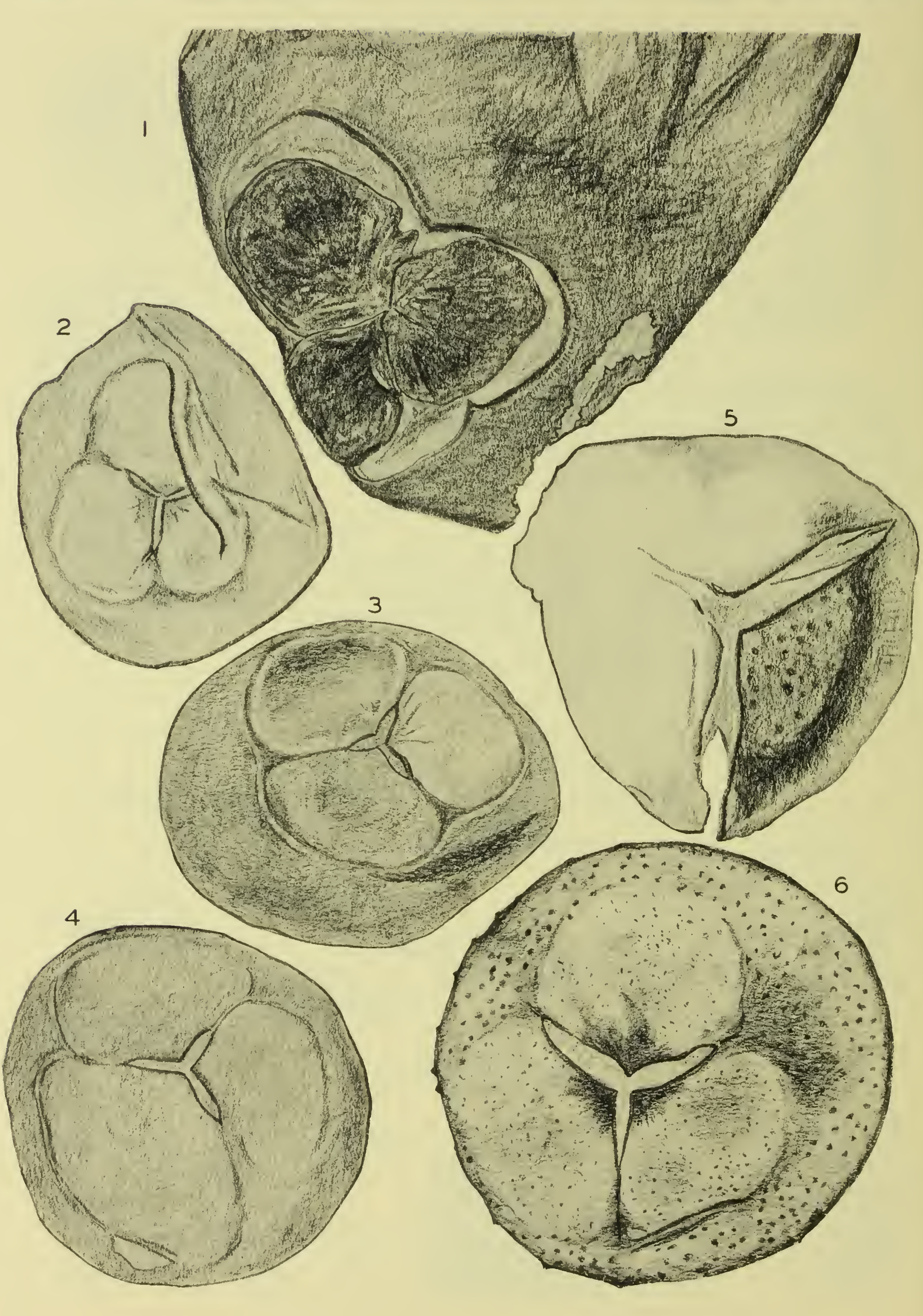
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PLATE 2

Fig. 1. *Cystosporites breretonensis* (x 30). Camera lucida drawing, reflected light. Crayon drawing of apex with three small abortive spores. Column 3, sections 19-20.

2. *Triletes reinschi* (x 20). Diameter 2130μ. Camera lucida crayon drawing, reflected light. Column 3, section 27.

3. *Triletes reinschi* (x 20). Largest diameter 2625μ. Camera lucida crayon drawing, reflected light. Arcuate ridges and radii are prominent because of dark color. Column 3, section 57.

4. *Triletes reinschi* (x 20). Diameter 2580μ. Camera lucida crayon drawing, reflected light. Column 3, sections 53-54.

5. *Triletes (Auriculati)* sp. (*a*) (x 33). Radial diameter 1535μ. Camera lucida crayon drawing, reflected light. Proximal side of spore. Column 3, bench 1.

6. *Triletes brevispiculus* (x 27). Diameter 1885μ. Crayon drawing, reflected light. Column 3, sections 17-18.

PLATE 3

Fig. 1. *Triletes brevispiculus* (x 45). Diameter 1520μ. Reflected light, some transmitted light. Column 3, bench 2.

2, 3. *Triletes brevispiculus* highly magnified. Transmitted light. Supermacerated coat showing structure of apiculi. Basal part of Belleville No. 6 coal.

4. *Triletes brevispiculus* (x 90). Reflected light. Sector of spore at higher magnitude to show spines. Column 31, section 1.

5. *Cystosporites breretonensis* (x 10). Reflected light. Very large and almost complete specimen; small portion at apex missing. Column 31, section 30.

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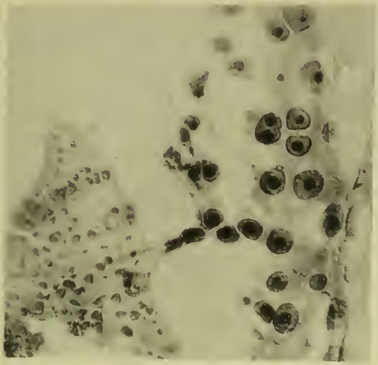

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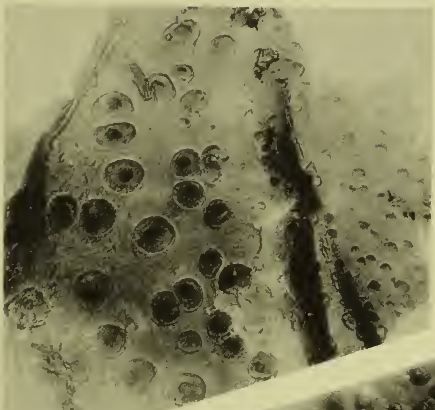

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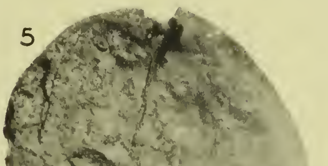

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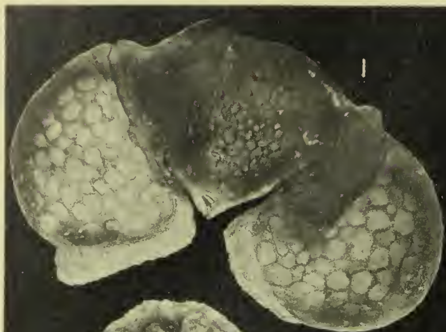
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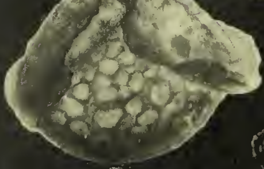

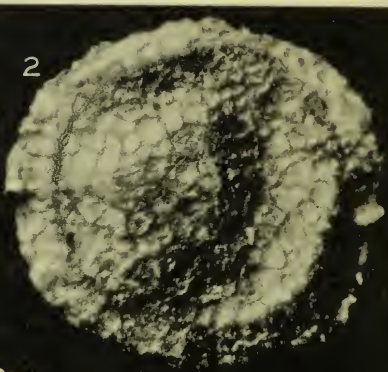
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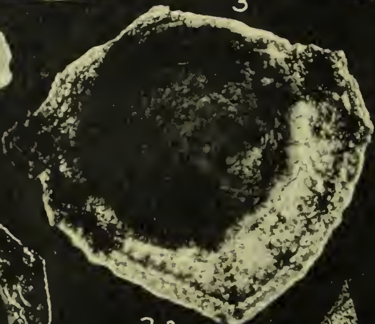
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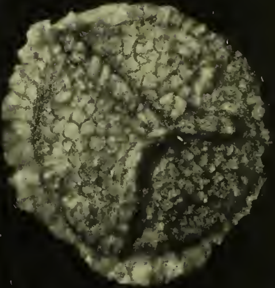
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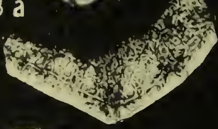
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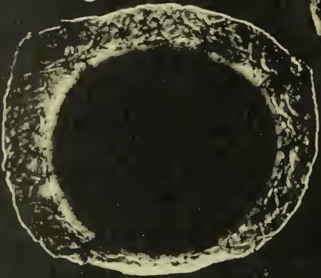
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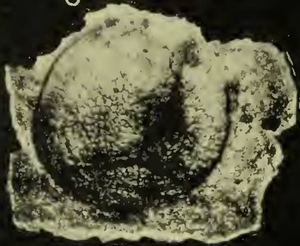
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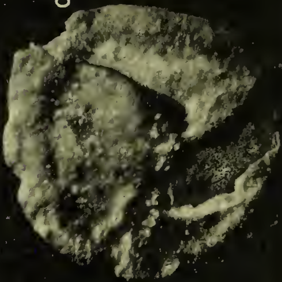
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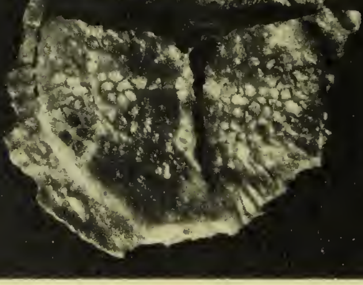
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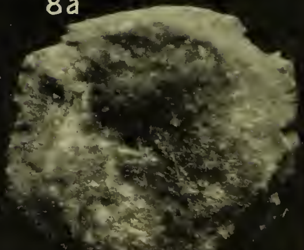
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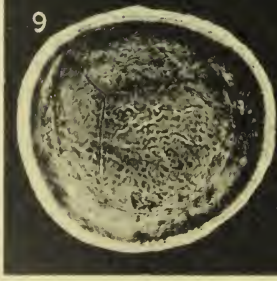
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PLATE 4

Fig. 1. *Triletes triangulatus* (x 43). Reflected light. Tetrad; the middle spore at the top shows proximal reticulae on pyramic areas, others show distal reticulation. Column 31, section 80.

2. *Triletes triangulatus*, distal aspect (x 83). Average diameter 624μ; average diameter of reticulae 33μ. Reflected light. Column 3, bench 4.

3. *Triletes triangulatus* (x 55). Extreme diameter 900μ. Transmitted light, strong illumination. 3*a* weaker illumination. Column 31, section 75.

4. *Triletes triangulatus*, proximal aspect (x 85). Diameter 440μ; average diameter of reticulae 21μ. Reflected light. Column 3, bench 4.

5. *Triletes triangulatus* (x 55). Radial diameter 769μ. Strong transmitted light. Flange structure. 5*a* Body reticulation. Column 31, section 75.

6. *Triletes triangulatus* (x 45). Maximum diameter 853μ; average diameter of proximal reticulae 27μ. Transmitted light. Distal side is missing from this specimen. Column 1, section 34.

7. *Triletes triangulatus* (x 65). Body diameter 565μ; reticulation *ca.* 28μ average. Reflected light. Column 3, section 25.

8. *Triletes (Auriculati)* sp. (*b*) (x 27). Radial diameter 1380μ. Reflected light. Proximal side. 8*a* Distal side. Column 3, bench 1.

9. *Triletes gymnozonatus* (x 55). Diameter 566μ. Transmitted light; strong beam intercepted by spore. Column 31, section 75.

PLATE 5

Fig. 1. *Sporites fumosus* (x 80). Diameter 455μ. Transmitted light. 1a Reflected light. Column 3, bench 14.

2. *Sporites fumosus* (x 110). Diameter 400μ. Transmitted light. Photo shows the characteristic pitting developed, probably by overmaceration. Column 3, bench 6.

3. *Triletes translucens* (x 60). Longest diameter 822μ. Photo, transmitted light. Column 3, bench 3.

4. *Triletes translucens* (x 65). 822μ x 675μ. Photo, transmitted light. Column 3, bench 2.

5. *Triletes translucens* (x 60). 820μ x 875μ. Photo, transmitted light. Column 18, bone coal, bench 0.1.

6. *Triletes* (?) *rugosus* (x 80). 533μ x 488μ. Photo, strong transmitted light. Column 3, bench 4.

7. *Triletes* (?) *nudus* (x 45). 814μ x 748μ. Reflected light. Column 3, bench 4 (section 25).

8. *Triletes reinschi* (x 20). Maximum diameter 2232μ. Photo, reflected light. Column 31, section 32.

9. *Triletes reinschi*, in thin section of coal (x 75). Length 1643μ. Transmitted light. Large spore showing layers in spore coat. Column 18, bench 3 (section 12).

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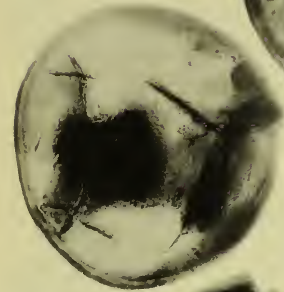
a



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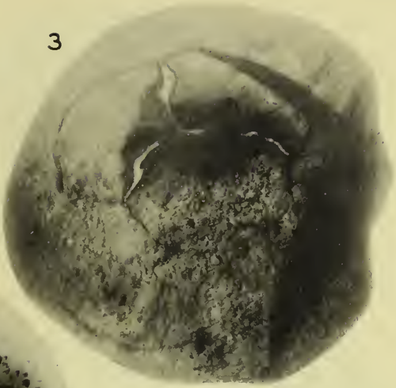

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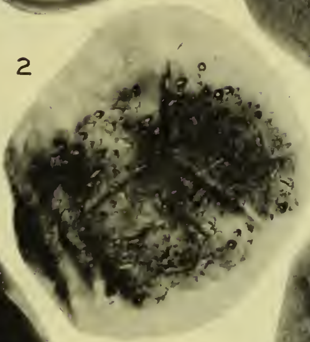

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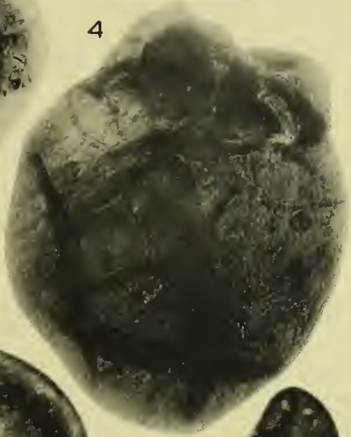

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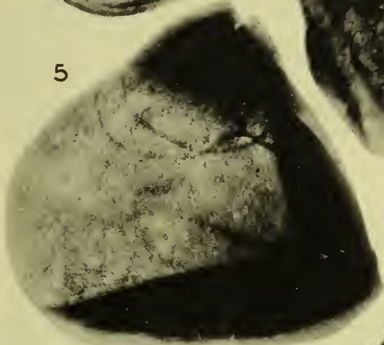

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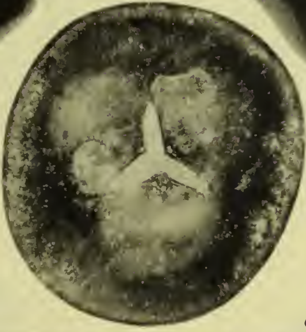

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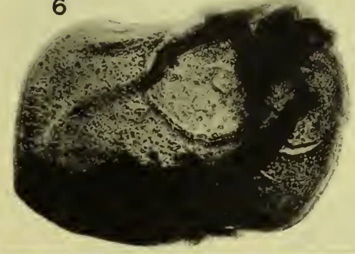

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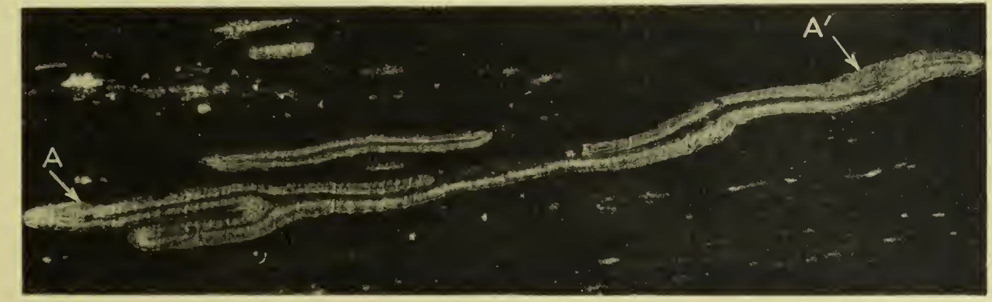

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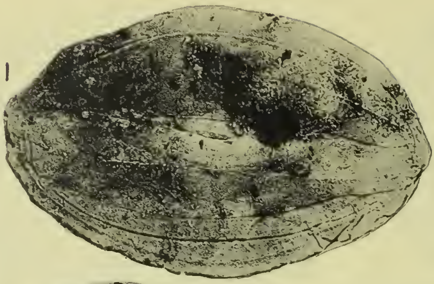

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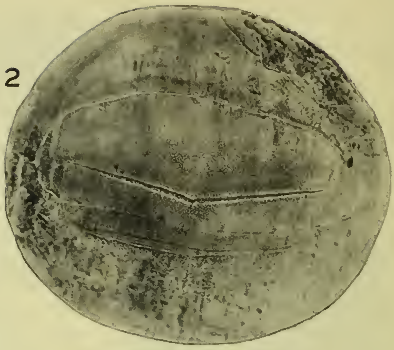

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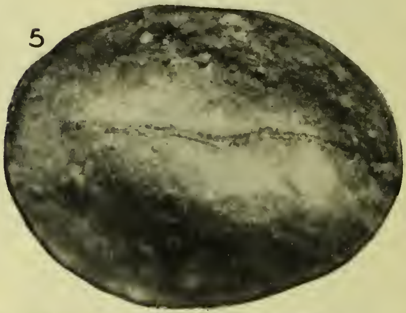

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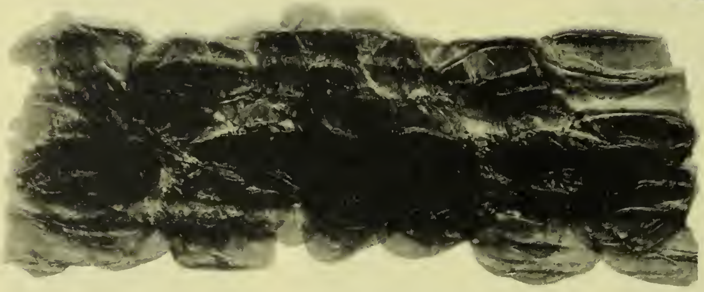

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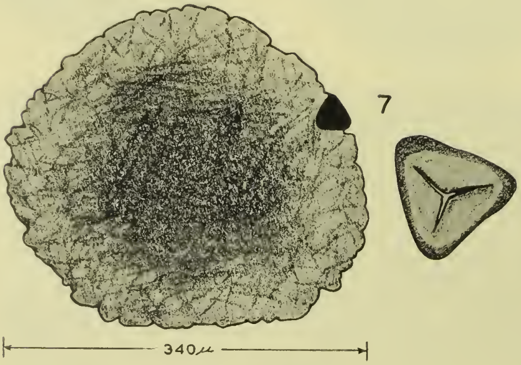

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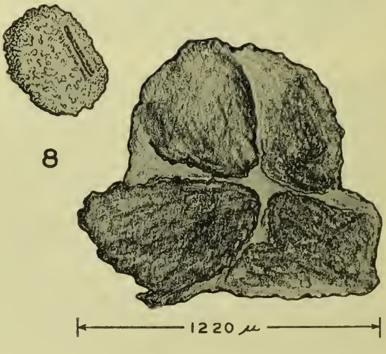

PLATE 6

Fig. 1. *Monoletes ovatus* (x 120). 465μ x 302μ. Transmitted light. Photo by L. C. McCabe. Column 18, section 30A, bench 6a.

2. *Monoletes ovatus* (x 112). 441μ x 387μ. Transmitted light. Column 31, section 57.

3. *Monoletes ovatus* (x 120). Transmitted light. Column 18, section 30A, bench 6a.

4. *Monoletes ovatus* (spore mass) (x 40). Spores approximately 250μ x 440μ; internal width of sporangium *ca.* 900μ. Transmitted light. Column 3, bench 1.

5. *Monoletes ellipsoides* (x 115). 448μ x 348μ. Reflected light. Column 31, section 4.

6. *Monoletes ellipsoides* (x 140). 285μ x 205μ. Photo, transmitted light. Maceration 60 Indiana Va coal.

7. Fern spores: Isolated sporangial mass. Enlarged spore *ca.* 30μ in diameter. Dimension of mass given on plate. Camera lucida drawing, transmitted light. Column 31, section 57.

8. Fern spores: Synangial mass derived from four sporangia. Dimensions of mass given on plate. Enlarged spore *ca.* 30μ in length. Camera lucida drawings, transmitted light. Column 31, section 34.

PLATE 7

Fig. 1. *Parasporites maccabei* (x 235). 278μ x 227μ. Transmitted light. Photo by L. C. McCabe. Column 1, section 73, bench 9b.

2. *Parasporites maccabei* (x 185). 340μ x 280μ. Transmitted light. Column 1, section 85. Indication of reticulation shown on one bladder.

3. *Parasporites maccabei* (x 145). 323μ x 287μ. Transmitted light. Photo by L. C. McCabe. Column 1, sections 71-72, bench 9b.

4. *Cystosporites breretonensis* forma *reticulatus* (x 63). Transmitted light. Three spore "tetrad", apical cushions opaque. Photo by L. C. McCabe. Column 1, section 70.

5. *Triletes triangulatus* (x 90). Extreme diameter 555μ. Transmitted light. Shows central body, presumably shrunken endospore. Colchester No. 2 coal, Atkinson Strip Mine, Miscl. slide 74.

6. *Triletes triangulatus* (x 53). Extreme diameter 912μ. Transmitted light. Column 31, section 32.

7. *Sporites plicatus* (x 55). Long diameter 822μ. Transmitted light. Column 3, bench 2.

8. *Sporites plicatus* (x 50). 955μ x 670μ. Transmitted light. Column 3, bench 2.

9. *Sporites plicatus* (x 50). 955μ x 550μ. Transmitted light. Column 3, bench 2.

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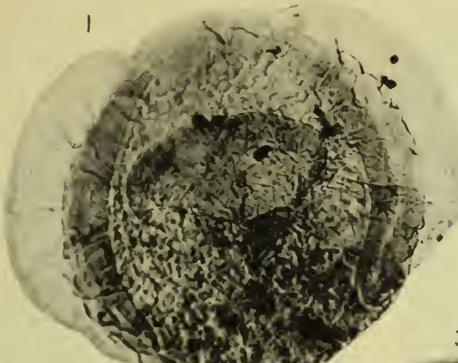

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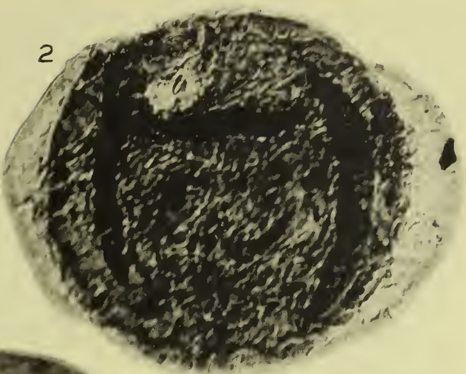

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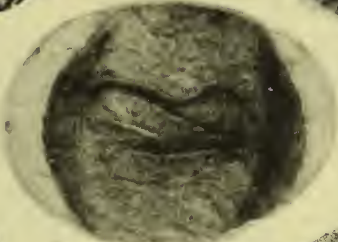

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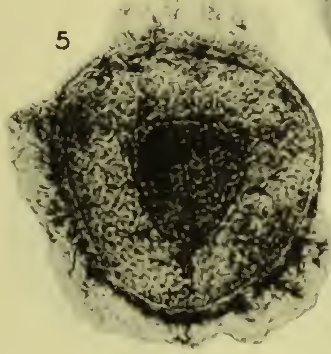

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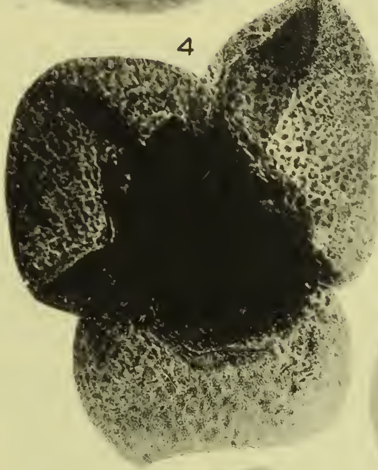

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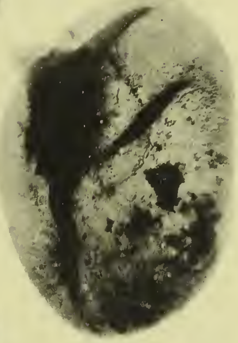

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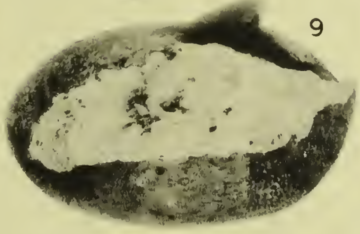

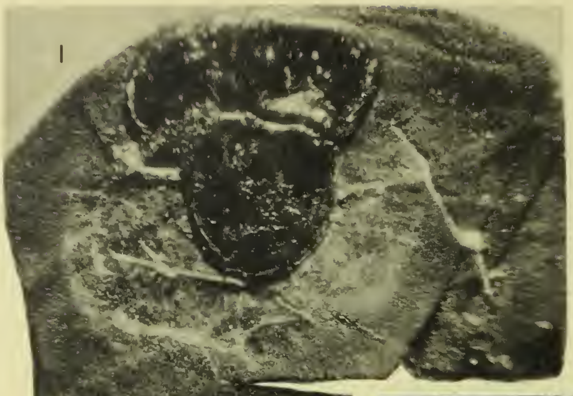
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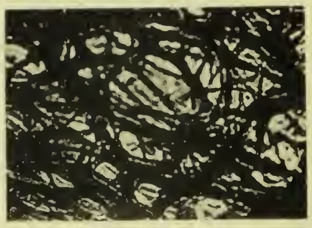
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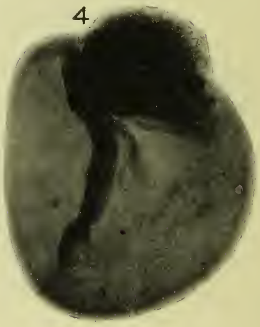
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PLATE 8

Fig. 1. *Cystosporites breretonensis* (x 115). Length of trilete radii *ca.* 800μ. Reflected light. Spore apex with 3 abortive spores covering the pyramic areas. Column 3, section 25.

2. *Cystosporites breretonensis* (x 50). Length of trilete radii *ca.* 200-300μ. Transmitted light. Apical portion of fertile spore showing trilete structures. Column 1, section 72.

3. *Cystosporites* spore coat highly magnified. Transmitted light. Column 1, section 89.

4. *Cystosporites breretonensis* forma *abortivus* (x 75). Length 970μ. Transmitted light. Column 31, section 53.

5. *Lepidocarpon mazonensis* (x 1.5). Sporophyll broken vertically. The right half shows the point of attachment. Nodule from shale above Colchester (No. 2) coal strip area 2 miles west of Wilmington, Ill.

6. Texture of spore coat from *Lepidocarpon* sp. seed megaspore highly magnified. From specimen shown in figs. 7 and 8. Reflected light. Compare the fibrous texture shown here with that in figure 3.

7. *Lepidocarpon sp.* (x 3.9). Sporangium somewhat compressed, broken vertically showing a well preserved seed megaspore. Nodule from shale above Colchester (No. 2) coal strip area 2 miles west of Wilmington, Ill.

8. *Lepidocarpon* sp. (x 8.9). Sporangial structures of figure 7 more highly magnified. Apex of spore is covered with iron carbonate; the patches of white mineral are calcite. A splinter, presumably of the cone axis, is shown at the right.