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PTERIDOSPERM MALE FRUCTIFICATIONS: AMERICAN SPECIES OF *DOLEROTHECA,* WITH NOTES REGARDING CERTAIN ALLIED FORMS

BY

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PTERIDOSPERM MALE FRUCTIFICATIONS: AMERICAN SPECIES OF *DOLEROTHECA*, WITH NOTES REGARDING CERTAIN ALLIED FORMS

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ABSTRACT—*Dolerotheca* includes a group of pteridosperms (Medullosaceae) characterized by very large and unusual pollen-bearing organs. Their botanical pertinence to plant microfossil studies and to phyletic theories, as well as their rarity in good preservation, lends considerable interest to these fossils. The morphology of the polleniferous organs, or male fructifications, is reviewed preliminary to taxonomic treatment of the new American material. Three new species are described in considerable detail both as to general external form and internal organization—a result possible only because of preservation in the limestone concretions in coal beds known as coal balls. The species of *Dolerotheca* are assembled in a new sub-tribe called the Dolerothecinae. The evidence for relating these forms with other coalball fossils known as *Myeloxylon*, and, in turn, with *Medullosa*, is discussed with particular reference to one species where the peduncular organ of attachment seems to be preserved. Notes are also included regarding a specimen of *Dolerotheca* preserved in surface imprint in an ironstone concretion, and regarding the allied Whittleseyinean group classed as *Codonotheca*. The relationships and comparative anatomy of *Dolerotheca* with other pteridosperm groups that present homologous features are discussed and a tentative evolutionary interpretation presented. *Heterotheca* of the Lower Carboniferous appears to represent a plausible ancestral type, combining features of both the lyginopterid and medullosan lines of descent. The morphology of *Dolerotheca* suggests, however, that evolutionary modification has been by elaboration and septation of a single telomic structure rather than by adnation and concrescence of many.

INTRODUCTION

THE male fructifications of pteridosperms are less well understood than most of the other organs pertaining to this large group of ancient plants. The fact that a considerable number of the Paleozoic fernlike plants bore seeds and hence were not true ferns, in spite of their highly dissected or pinnatifid leaves, became established about 45 years ago. Since then a number of pteridosperm seed types have become well known; on the other hand an equivalent amount of information has not been obtained about the male fructifications despite the fact they must have been numerous. Some of the first recognized pteridosperms seemed to have male fructifications resembling the synangia of ferns. These organs were presumed to be conservative and little modified in the evolutionary transition from the free-sporing to the seed habit. However it has become clear during the last fifteen years that certain other groups of pteridosperms possessed male fructifications that differ radically from organs known in ferns. A more complete understanding of the characteristics and the nature of the diversity of male fructifications in pteridosperms will have important influence on ideas of phylogeny and relationship among this large, chiefly Paleozoic, plant alliance.

Among the pteridosperms the plants classified as *Dolerotheca* display conspicuous differences with regard to their male fructifications. Such fructifications of *Dolerotheca* have not been commonly reported, and up to the time specimens here described were discovered, only a single fragment was known which showed well preserved tissue structures. A few surface impressions and coalified compressions of similar fructifications have been recognized, but these are difficult to interpret and naturally afforded much less conclusive information about their structural organization than do the specimens described below.

These new fossils from coal balls have the cells preserved in almost perfect detail. Coal

A

38.5 mm

B

C

9.5mm

D

4mm

2mm

E

3mm
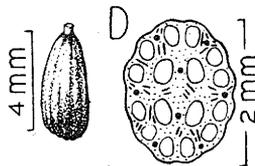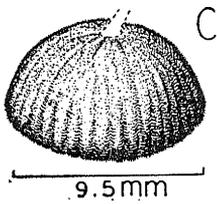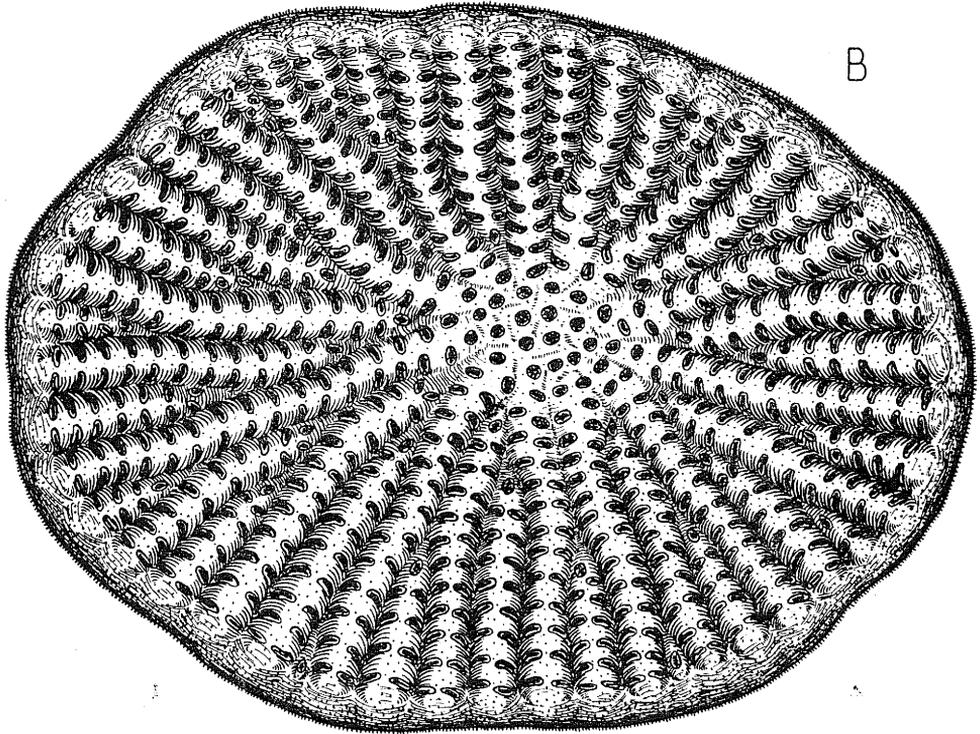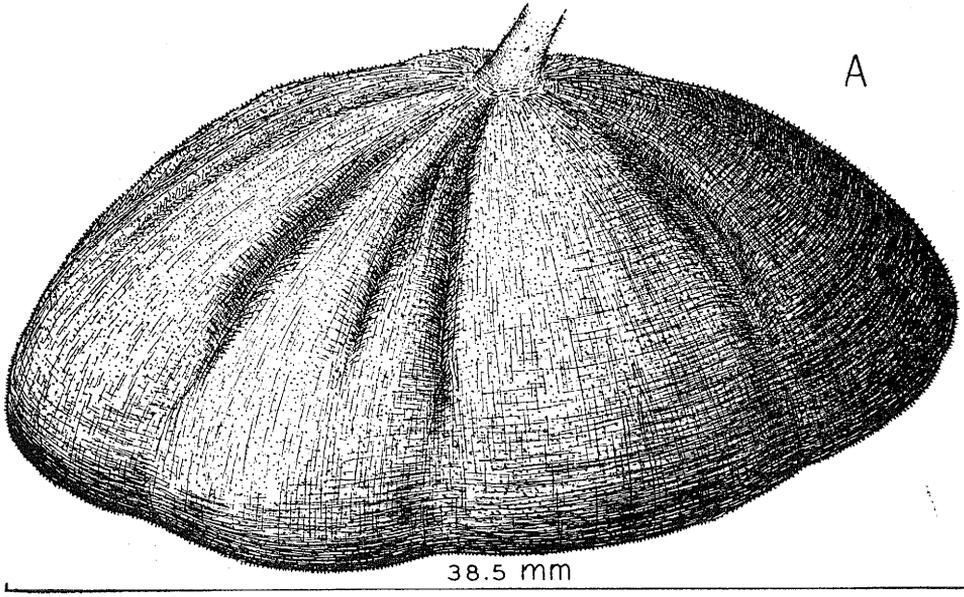
balls are calcareous, siliceous, or dolomitic concretions that formed in some Carboniferous peat beds, in which mineral matter solidly infiltrated, enclosed, and preserved plant organs and other peaty materials with remarkable perfection. The enclosed plant materials were protected from subsequent alteration, whereas the adjacent unmineralized peat became much compressed and was transformed to coal. Consequently it is possible to describe the *Dolerotheca* fructifications found in coal balls in considerable detail and to compare their anatomical and tissue structure with that of more conventional organs of spore or pollen production.

This new information permits more adequate comparison with the fructifications of other pteridospermous plants than was previously possible and thus assists in interpretation of relationships and phylogeny. Because only a few of the fossils that can be compared with *Dolerotheca* are as amply described, and because the organization of *Dolerotheca* fructifications is relatively novel, the writer's present phylogenetic interpretation is tentative, a working hypothesis that later discoveries may or may not confirm. A full appreciation of the significance of *Dolerotheca* may be impossible for some considerable time.

These descriptions of fossil fructifications should also help to clarify the relationship of certain common types of plant microfossils that are abundant in coal. The value of isolated spore and pollen types in identifying and tracing individual coal beds is a matter of current investigation. Their effective use depends not only on knowledge of their stratigraphic distribution but also on a knowledge of the natural groups of plants which they represent. From such knowledge it may be possible to attribute certain varieties of coal material to certain kinds or to various associations of plants. Spores and pollens actually found in their parent fructifications indicate affinities of at least some of the similar spores and pollens isolated from coal and thus facilitate a more accurate biologic classification of the abundant microfossils. Isolated spores of the type borne by *Dolerotheca* are usually identified with the genus *Monoletes*, in part, unless their more precise affinity can be established (Schopf, Wilson, and Bentall, 1944). At present, when subsidiary information about the organs that bore them is lacking, the isolated spores cannot be assigned to a less generalized group.

Dolerotheca is believed to be allied with the Medullosaceae as broadly defined. The writer believes that the Medullosaceae includes the genera *Alethopteris, Callipteris, Myeloxylon, Medullosa, Rotodontiospermum, Trigonocarpus* (at least in part) and some other allied genera typified by their seeds. *Neuropteris*, and some other genera typified by characteristics shown by leaves and fronds, may possibly be allied with this family, in spite of the fact that their relationship to the type genus, *Medullosa*, has not been indicated by recent studies.[1]

The comparison of *Dolerotheca* with fructifications of the Whittleseyineae tends to confirm the alliance of this subtribe within the medullosan family.

Halle's brilliant research (1933) on the structure of the Whittleseyinean types was based largely on coalified compression specimens. With some hesitation he included

[1] Schopf (1937), Steidtmann (1944) and Andrews (1945) all present evidence of alliance between *Medullosa* and *Alethopteris*.

Dolerotheca as a member of the Whittlesey-inean subtribe. The structure of *Dolerotheca* is now shown to be sufficiently different so that its separation as another subtribe seems advisable; the alliance of the new subtribe Dolerothecineae (here proposed; see p. 687) with the Whittleseyineae can scarcely be doubted and only the taxonomic decision as to how this relationship should most appropriately be expressed can involve any difference of opinion. In this regard the writer has followed Halle in utilizing the subtribal category because he believes the Dolerothecinean group merits recognition on a par with the Whittleseyinean group.

The Medullosaceae is an important family which includes several genera having extensive distribution in the Euro-American floral province of the Carboniferous and Permian, with some species of special stratigraphic value. It therefore seems remarkable that so little has been known in general about the male fructifications of these plants. Undoubtedly they were actually much more common than would appear from scattered references in the present literature. They may not have been recognized in some instances because they appear to have been deciduous shortly past maturity and they may have disintegrated readily after they dropped from their attachment on the plant. Furthermore, in their more common preservation as compressions, the male fructifications frequently do not show very distinctive megascopic features and the char-

acteristics they do show have in the past been difficult to interpret. The data to be presented relative to their organization and microscopic characteristics may aid considerably in facilitating recognition of such organs in various states of fossil preservation. Additional records and observations are needed to establish their use in stratigraphic paleontology.

SUMMARY OF MORPHOLOGY AND ORGANIZATION OF DOLEROTHECA

Detailed information about the plants classified as *Dolerotheca* is lacking for all parts except the male fructification, and characteristics of such fertile parts provide the only basis for identification. Evidence of histology and association point to the very great likelihood that the fructifications were borne on fronds of the same type as *Myeloxylon* and *Alethopteris*. The manner in which the male organs were connected to the plant is not precisely known, and only in *Dolerotheca reedana* has a probable connective organ (described as a peduncle (?), c.f., p. 710) been observed. However, the peduncle (?) is not in actual attachment. The evidence at hand suggests that the organs were shed from their connection with the plant soon after maturity, and that their early abscission left a very inconspicuous scar, both on the parent axis and on the fructification itself.

The male fructifications of *Dolerotheca* are broadly bell-shaped and include numer-

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EXPLANATION OF PLATE 104

FIG. *1*—*Dolerotheca formosa*, longitudinal section—fructification is enclosed in a dense mat of *Alethopteris* leaves. From coal ball 219 B1 (t 1).

2—Same as above, section from opposite side of saw kerf. From coal ball 291 Cl (b 1).

3—*D. formosa*, transverse section (peel) of fructification across the irregular distal (dehiscence) surface. From coal ball 129 A (t 7).

4—*D. formosa*, transverse section of fructification taken at a higher level than figure *3*, intersecting dehiscence tissue only on the left. From coal ball 129 A (t 22), scale same as figure *3*.

5—Same as above, section taken at a higher plane. From coal ball 129 A (t 25), scale same as for figures *3* and *4*.

6—Same as above, section at the top of fructification. The fragment of "sparganum" cortex shown in the upper center does not seem to be attached. Note horizontal sections of *Alethopteris* leaves showing venation. From coal ball 129 A (t 38), magnification same as figures *3* and *4*.

7—*D. formosa*, transverse section of a different fructification at level of dehiscence tissue with associated *Alethopteris* leaves. From coal ball 129 A (t 38), same scale as figures *3* and *4*.

8—*Dolerotheca fertilis* (Renault) Halle, longitudinal section of sporangium and spores, o. d, spores; b, intersporangial tissue; c, sporangial membrane (?); f, lysigenous tube ?. Copeid for comparison from Renault (fig. 1, Pl. XIII, 1902).
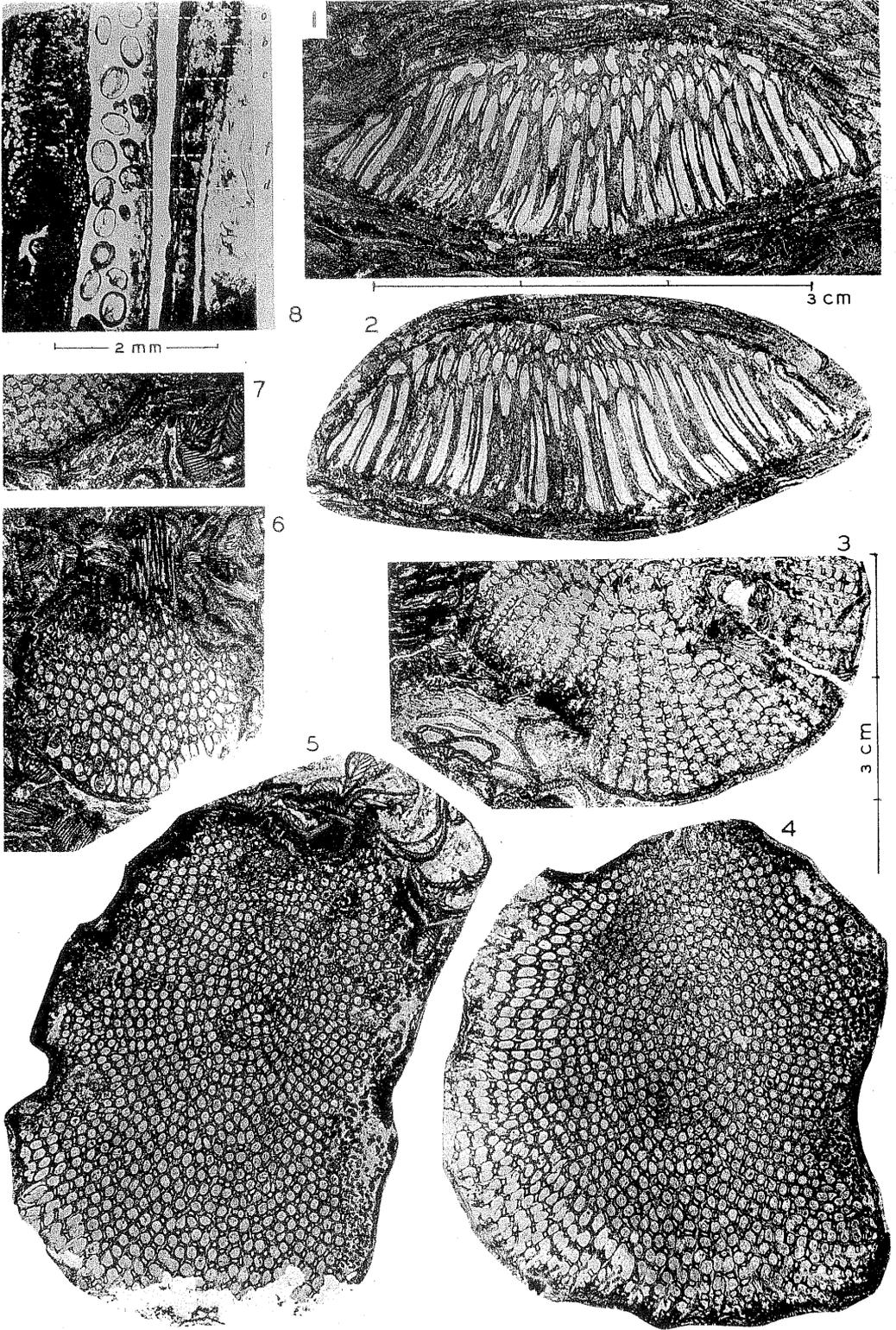
Schopf, *Dolerotheca formosa* n.sp., *D. fertilis* Halle
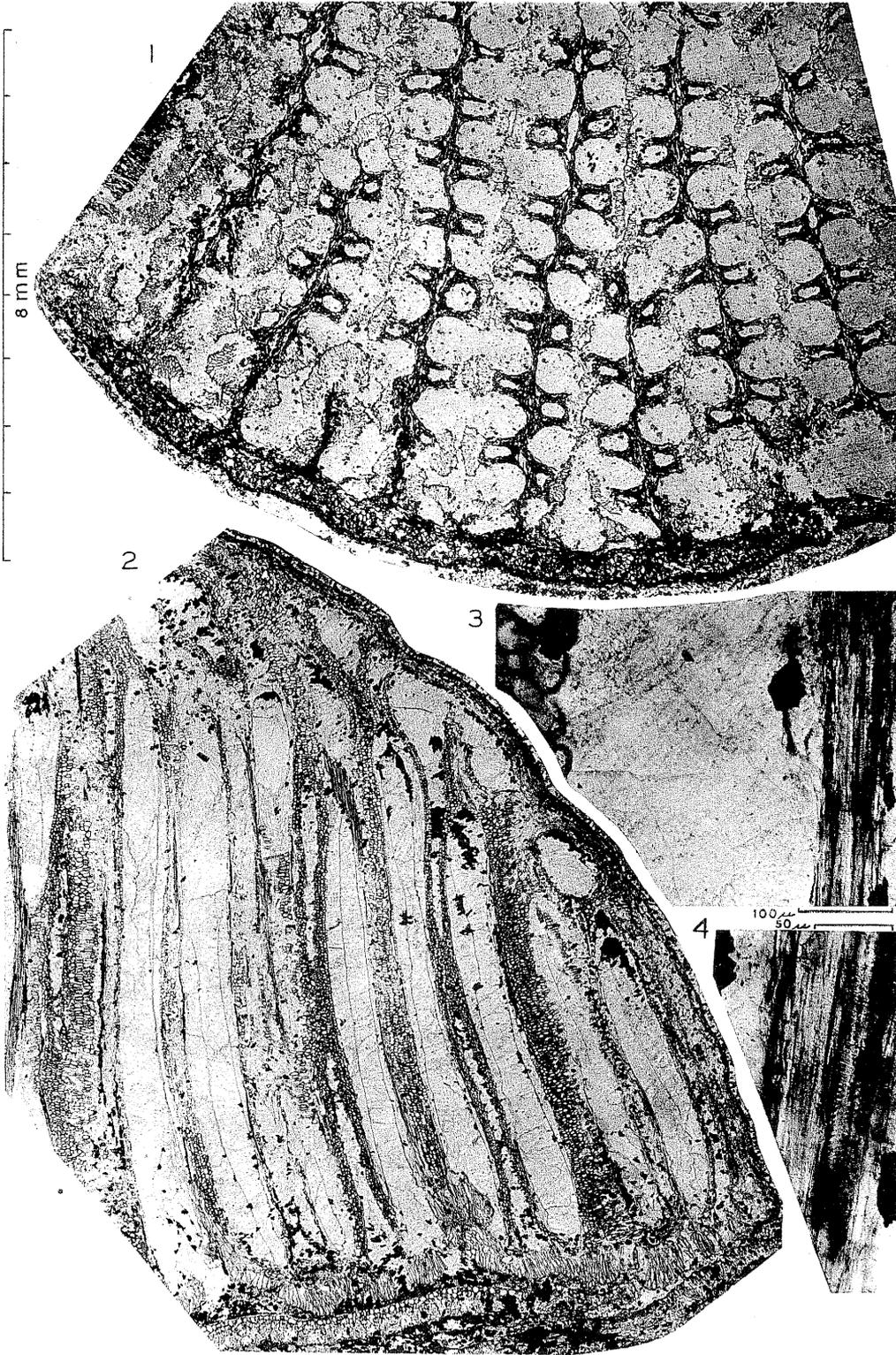
Schopf, *Dolerotheca formosa* n.sp.

ous long tubular sporangia immersed completely in tissue. The structure is large and massive and quite unlike any of the conventional types of polleniferous structures (see, for example, the discussion presented by Wilson, 1937). Because of the difficulties of homologous comparison, the male fructification of *Dolerotheca* may conveniently be referred to by a noncommittal morphologic term as a *campanulum*.[2] Essential features of such a *campanulum* are diagrammatically sketched in text figure 1. The external aspects of *Dolerotheca* fructifications have been reconstructed as shown in the frontispiece illustrations A, B, and C.

Dorsally, that is, on the side of attachment, the organ is enclosed by a differentiated layer here called the campanulary cover; the distal surface is evidently adapted to permit emission of spores from the sporangia. The distal side is covered by a tissue zone, here called the dehiscence layer, although no kinetic mode of sporangial dehiscence has been recognized. The dehiscence layer is more or less radially grooved and each ripened sporangium opens by a slit or pore into the grooves of the distal surface. There is evidently no analogue of the prismatic epidermal cells so common in sporangia of cryptogamic plants which frequently are specialized to provide for expulsion of spores.

The dehiscence layer probably is perforated when the campanulum dries at maturity. It may be that radial tensions are set up at that time to cause rupture of this layer at the distal ends of sporangia. In any event although the sporangia are completely immersed in parenchymatous and sclerotic

[2] Refering to the external form; *campanula*, L., a little bell.

intrasporangial tissue, the tips are effectively opened to shed the spores. No instance has been observed where an isolated sporangium has failed to open so that the full normal and mature complement of spores was still retained. In the *Dolerotheca* campanulas described by earlier authors, more numer-
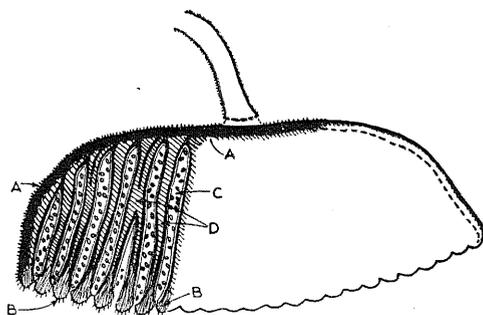

FIG. 1—The campanulum of *Dolerotheca*. Median longitudinal aspect: Diagrammatic
A. Campanulary cover layer
B. Dehiscence layer
C. Tubular sporangia
D. Inter-sporangial tissue: ground parenchyma, secretory elements, sclerenchyma, vascular strands.

ous spores apparently were retained in the sporangia, but their specimens were so incomplete or unfavorably preserved that dehiscence details could not be reported.

The sporangia are in paired rows radiating from the center of the fructification, with their long axes approximately parallel to the organic axis of the campanulum. New double rows of sporangia are intercalated towards the periphery of the solid bell-shaped structure.

Glandular pubescence is a common attribute of many pteridosperms and has been

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EXPLANATION OF PLATE 105

FIG. 1—*Dolerotheca formosa*, transverse section of fructification at level of dehiscence tissue. From coal ball 129 A (t 7).

2—*D. formosa*, longitudinal section of fructification showing shorter sporangia at margin; note slight sigmoid curvature of longer sporangia. A transverse section of *Alethopteris* leaf is shown at the bottom below dehiscence tissue. From coal ball C 1 B 1 (b 18 c), magnification same as figure *1*.

3—Vascular strand from section shown in figure 2. Tissues around it are poorly preserved; at the left is tissue bounding a sporangium.

4—Vascular strand shown in figure *3* but at higher magnification showing scalariform and spiral elements.

discussed by Halle (1929, p. 21–22) relative to seeds, and also was described by him (Halle, 1933) on the male fructifications of *Goldenbergia*. Relatively dense short hairs are present on the campanulary cover of *Dolerotheca*, and more sparse longer hairs on the epidermis of the dehiscence layer. Their function, if they possessed a function, is not apparent, but they seem suitable for use as taxonomic criteria. Hairs also are present on the surface of the *Codonotheca* male fructification, one other genus included in the Whittleseyinae.

The spores produced by the campanulary fructifications of *Dolerotheca* are very large, sometimes longer than half a millimeter, or as much as 10 times the usual dimensions of isospores or microspores of cryptogamic plants. They tend to be considerably larger than the pollen grains known from fossil cycads and conifers. They are, however, more primitive in organization than true pollen grains and it seems evident they are more advanced than cryptogamic microspores. For this reason it seems desirable to refer to the spore bodies of the dispersal stage as prepollen, following the practice long ago adopted by Renault (1893–96).

The size of the prepollen and the organization of the campanulas that bore them, immediately suggests a considerable biologic problem regarding the means of effecting fertilization. Such large heavy prepollen obviously was not well adapted to ordinary wind pollination, as the pollen of many modern plants is. Insects have been suggested as a possible vector agent for fertilization but there is little positive evidence to support this idea beyond the mere presence of glandular pubescence which might have attracted insects. To carry this sort of prepollen effectively the insects should have been of a specialized type.

Plants with this kind of prepollen had a relatively long span of geologic existence. The prepollen grains are commonly found in many Upper Carboniferous coal beds both in America and in Europe.

Thus there is good reason to believe that fertilization actually was accomplished with relative ease, because otherwise the plants could not have been as extensively distributed; at times they were certainly dominant elements of the vegetation. Indeed,

Andrews (1945, p. 332) has inferred from his study of their stem anatomy, that Medullosans may have grown in rather dense stands. The prolific occurrence of *Medullosa* stems and roots, *Myeloxylon* type petioles, *Alethopteris* type foliage, *Rotodontiosperm* seeds, and *Dolerotheca* campanulas at the one locality which provided two of the species described below, tends to support this view. However, no evidence points directly at any one of the modes of fertilization suggested by Halle (1933, p. 51). Certainly *Dolerotheca* has the most massive male fructification of any groups Halle included in the Whittleseyinean subtribe, and if the prepollen was expelled by gusts of wind as a general occurrence in smaller forms such as *Goldenbergia* or *Boulaya*, a gale might have been required to clear the spores from sporangia of the massive campanulas of *Dolerotheca*.

Although a majority of spores evidently had been shed in most specimens observed in this study, a number of prepollen grains persist in some sporangia of most of the specimens. It appears to be a reasonable inference that the emission of spores through the distal sporangial opening was often not complete. In spite of obvious maladaptation for easy spore distribution, the writer is inclined to favor dissemination of prepollen by strong gusty wind as more inherently probable than distribution by insects or similar agents. The prepollen is obviously more protected from contact with small vagrant animals than it would be from the mechanical effects of sporadic air currents. There can be little question that intermittent winds could have dislodged most of the prepollen and carried it a little distance after it left the sporangial openings. Information about the location of campanulas and seeds on the parent plants is not sufficiently clear to formulate any opinion as to how far the fertilizing elements would need to be transported after they left their sporangia in order to effect fertilization.

The more important and demonstrable features discussed above are used to establish a new group, parallel to the Whittleseyinae in nomenclatural status. It is clear that *Dolerotheca* differs in some important features from those shown by the Whittleseyinean group. It is believed that coordinate taxo-

nomic ranking of the Dolerothecinae will assist in unifying information about the various genera typified by diverse fossil specimens, so that they can be brought together more easily into a "normal" familial group. In the future it is hoped demonstrated characteristics of the Medullosaceae will come to compare favorably in all essentials with those of families chiefly based on modern material.

Subtribe DOLEROTHECINAE
Schopf. n. subtr.

Diagnosis.—Plants of Medullosan alliance possessing massive male fructifications enclosing numerous elongate tubular sporangia. Sporangia paired in rows radially disposed, containing exceptionally large spores of the prepollen type. Prepollen grains oval, not quite bilaterally symmetrical, with a linear proximal suture. External surfaces of fructification characteristically pubescent.

Type genus.—*Dolerotheca* Halle.

The Dolerothecinae is distinguished from the Whittleseyinae by the massive campanulum, and the more numerous and differently disposed sporangia. It is distinguished from the Potoniéinae by the character of its prepollen, and possibly by features of the sporangia that are not as clearly defined at the present time. *Heterotheca* of the Lower Carboniferous, which may well represent an allied ancestral group, is to be distinguished by lack of tubular sporangia, by differences in its spores, and its smaller size.

Dolerotheca is at present the only genus assigned to the Dolerothecinae. The material available now enables a more satisfactory generic diagnosis to be presented. Although certain features of the genotype species thus acquire added significance, it does not seem that any change in taxonomic meaning "circumscription" is involved, and therefore, although the diagnostic description of the genus is somewhat amplified, it is not regarded as emended.

Genus DOLEROTHECA Halle.[3]

Amplified Diagnosis.—Plants agreeing with the Dolerothecinae (see above), with

[3] Whether *Dolerotheca* is a valid name or not, is open to some question. One of the results of this study has been to show that the specimen and

male fructifications externally campanulate or broadly campanulate in form, enclosing tubular sporangia completely immersed in the campanulary tissue. Sporangia paired in biseriate rows, with additional double rows of sporangia intercalated toward the margins; order of sporangial maturity probably slightly gradate and trending centrifugally. The cover of the proximal side of the campanulum bearing a glandular pubescence of short hairs; distal dehiscence surface with more sparse and more slender hairs and epidermal papillae.

Type species.—*Dolerotheca fertilis* (Renault) Halle.

Halle restudied as much of Renault's material of this species as could be found in

counterpart Grand 'Eury illustrated and described under two generic assignments in 1890, i.e., *Androstachys* in textual description, *Discostachys* for the plate, is congeneric with the present *Dolerotheca* material. Grand 'Eury's specimen is evidently a reasonably well preserved compression example of the type that may be more commonly recognized now that it is possible to interpret the structure.

Halle in 1933 was unable to be sure of the generic identity of the Grand 'Eury specimen and that shown by Renault's silicified fragment of *Dolerophyllum fertile;* the latter was taken by Halle to be the generotype of *Dolerotheca*. The present material is complete enough to show clearly that the *Androstachys-Discostachys* specimen and the silicified fragment are congeneric. The popular old name "Dolerophyllum," which Renault used in the sense of a combination genus, is of course inapplicable to the fertile specimens that had been included in it, as Halle recognized. But we cannot now regard the *Androstachys-Discostachys* specimen as ambiguous, as Halle suggested. One would suppose that one of the names proposed by Grand 'Eury, either *Androstachys* or *Discostachys*, would have to be applied since both have a clear claim to priority over *Dolerotheca*. White, in fact, anticipated this possibility in 1903 and suggested, with reference to some comparable material that *Androstachys* should be selected "if the generic identity of the sterile leaves (i.e., referring to *Dolerophyllum*, s.s.) and the supposed polleniferous leaves is not established."

The name *Androstachys* is, however, unavailable since Grand 'Eury himself had used the name earlier in reference to a fertile zygopterid frond. Therefore *Androstachys* Grand 'Eury, 1890, is a junior homonym of *Androstachys* Grand 'Eury, 1877, and though now regarded as a synonym, such names cannot be reused according to the express stipulation of Article 61 of the International Rules of Botanical Nomenclature.

1929, and presented the results of his observations and new photomicrographs in 1933. A line tracing from the transverse section Halle studied, showing arrangement of sporangia, is reproduced here in text figure 2.
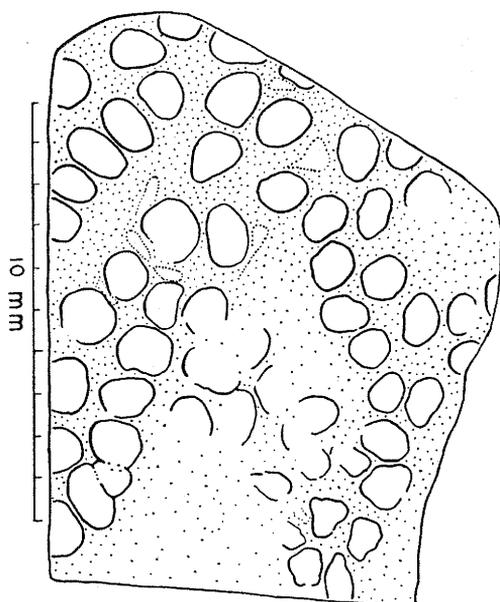

10 mm

FIG. 2—*Dolerotheca fertilis*, transverse section of Renault's holotype. Line tracing from published photograph by Halle (1933, pl. 9, fig. 2), showing about 50 sporangia, most of which are associated in paired rows.

It is evident that it accords with species described below in having radially paired rows of sporangia. This interpretation is more in agreement with Halle's alternative suggestion (Halle, 1933, p. 48) and with the structure shown by the "Mont-Pelé"

There seems no alternative to the conclusion that *Discostachys* Grand 'Eury, 1890, type *D. cebennensis*, as illustrated by that author in plate 7, fig. 2 A and A', in the Gard report, is a name that may be available, with priority over *Dolerotheca* Halle, 1933. If the name had not been confused with *Androstachys* and if a proper description had appeared under the name *Discostachys* no question would exist about the propriety of using it in this connection. Grand 'Eury for inexplicable reasons confused the names he applied to his specimen but the descriptive facts pertinent to it are relatively clear. The chief

compressions of *Dolerotheca*.[4] A photograph of a longitudinal section of *D. fertilis* was illustrated lithographically by Renault in a little known publication in 1902. This figure (Renault, 1902, Pl. 115, fig. 1) has been rephotographed and is presented in pl. 104, fig. 8 for comparison. Three additional figures of prepollen have been copied from this same publication by Renault (1902, pl. 114, fig. 4, pl. 12, figs. 3–4) and are reproduced in pl. 108, figs. 11–13. All the structures are in evident generic agreement with the new forms described below. The most divergent structure is the ground parenchyma, described as aerenchymatous by Renault, but scarcely mentioned by Halle. Sclerenchyma seems to have been lacking in the European forms.

NEW SPECIES OF DOLEROTHECA

Three new species of *Dolerotheca* are de-

problem now is to properly incorporate this information systematically.

So far as factual matters pertaining to identification are concerned, it does not make much difference which name is applied. The nomenclatural types of both names leave much to be desired in the way of completeness and preservation. The writer believes, however, that preference should be given to *Dolerotheca*, although it was proposed later. It is a name now in current use, being mentioned in at least three recent textbooks. *Discostachys* is in complete disuse, apparently has never been cited in a textbook, and was regarded as a dubious and confused synonym by both White and Halle. Hence, in the present paper the writer proposes to retain *Dolerotheca* as Halle introduced it in 1933. In order to clear it of conflict with *Discostachys* G. 'E., 1890, he further proposes that *Discostachys* be regarded as a *nomen confusum* and that *Dolerotheca* be added to the list of officially conserved names, being specifically conserved over *Discostachys* as typified by *D. cebennensis* G. 'E., 1890.

It appears to the writer that this course is the one most likely to promote stability in reference to the group of plants involved. Any other is likely to lead to prolonged nomenclatural confusion that would be profitless in advancing knowledge of these plants or any aspect of paleobotany.

[4] Saporta and Marion (1885, p. 74) also mention that locules of the "Dolerophylleae" (evidently they had the Mont-Pelé specimens described as *D. berthieri* in mind) are distributed in "two contiguous rows."

scribed below. One of them, distinguished as *D. formosa*, is represented by a somewhat indefinite number of specimens. They are rather common in the large coal ball aggregate collected from a coal bed below the Calhoun limestone in southwestern Richland County, Illinois, in 1937. A preliminary note (Schopf, 1938) identified the zone as lower than the La Salle limestone, but it has been learned since that this was in error and that its stratigraphic position is higher. The deposit is in the upper part of the McLeansboro group and has been discussed relative to other coal ball zones in a previous publication describing an unrelated lycopsid form, *Mazocarpon oedipternum*, that was found in the same coal ball aggregate (Schopf, 1943). A considerable number of the *D. formosa* fructifications are quite fragmentary. Study has has been mainly based on three essentially complete specimens. About 15 other specimens in a good state of preservation have been observed incidentally in slices of the Calhoun material, and the general features have been checked from them, both on sawed and etched surfaces and from peel preparations.

Two specimens of a much smaller form, here described as *Dolerotheca villosa*, also were discovered in examination of coal balls from the same deposit.

The third species has been described under the name of *Dolerotheca reedana*, so called in recognition of Fredda D. Reed, Professor at Mt. Holyoke College. Professor Reed discovered this specimen in the course of her investigation of fossil plants in coal balls from the Harrisburg (No. 5) coal bed in Saline County, Illinois. She generously permitted the writer to include it in this study when it was learned that comparable material from the Calhoun locality was being investigated. *D. reedana* thus is from the Carbondale group of the Illinois Pennsylvanian, and of considerably earlier geologic age than the other forms described here. At present it represents the oldest described species of *Dolerotheca*, but future discoveries will probably extend the range of the genus into still lower strata.

The most obvious difference between the three species is in size and character of pubescence, but other differences also can be noted.

DOLEROTHECA FORMOSA Schopf, n. sp.

Frontispiece, figures A, B; plate 104, figures 1–7; plate 105, figures 1–4; plate 106, figures 1, 2; plate 107, figures 1–6; plate 108, figures 1–10; text figures 3a–d, 4–13

External Characters.—Male fructification broadly campanulate, about 40 mm. in diameter and 11–14 mm. thick. Point of attachment somewhat excentric. Proximal (dorsal) side convex, probably of leathery texture, somewhat irregularly indented radially, indentations diminishing toward margin. Proximal surface covered with numerous glandular simple hairs, sometimes capitate tipped. Distal side also slightly convex, with bifurcating radial (dehiscence) grooves 1–2 mm. deep except near the center where they become obsolete or less regular. Sporangia are arranged in double rows between the grooves and open into them by slit-like perforations. Toward the center of the fructification sporangial openings are more pore-like since the grooves are shallower there. Distal surface covered with sparse simple hairs and epidermal papillae; the hairs consist of one to three cells and are more slender and much less glandular appearing than those on the proximal surface.

An accurately scaled reconstruction of these external features is presented in the frontispiece figures A and B. The peduncle only, in fig. A, is hypothetical since no attached specimens have been found. The proportions of these figures have been carefully checked with sections in both planes.

General Anatomy.—The tubular sporangia of *D. formosa* are 0.6 to 1 mm. in diameter and vary from about 4 to 12 mm. in length. In a preliminary note (Schopf, 1938) they were described as "radially related in pairs of rows; sterile locules alternate with the fertile ones in each radial series." This is a fair statement of the arrangement of sporangia and other cavities but the "sterile locules" mentioned should be designated by the more non-committal term, lysigenous tubes, because there is no evidence of their sporogenous nature although this at first seemed probable. The tissue surrounding the lysigenous tubes is ragged on all edges. Aside from miscellaneous tissue frag-

ments none has any contents. They may function as respiratory chambers somewhat as the parichoi of lycopod stems, although there seems to be no special means of communication with the exterior. Renault thought the aerenchymatous tissue of *D. fertilis* would assist the fructification to float in water. Doubtless this suggestion would apply as well to the lysigenous cavities, but the advantage of this structure is not evident unless the plants had the growth habit of pond lilies—a suggestion which for various reasons seems far fetched.

Relations of the sporangia are diagrammatically illustrated in text figure 3. The outer dark shaded zone represents the campanulary cover which in this species is about 400–800 μ thick, and extends over the strongly convex proximal surface as shown in figure 3d. The double rows of sporangia are best shown in cross-section close to the lower dehiscence surface (fig. 3 c). This surface is covered by an epidermis beneath which appears the rather delicate elongate cells of the dehiscence tissue. The dehiscence tissue covers the lower ends of the sporangia and the areas between. It extends deeper inside the fructification along the strong dehiscence grooves as shown in the frontispiece figs. B. Thus a section across this lower part of the fructification (fig. 3 c) shows the free sides of sporangia clothed by the dehiscence tissue which has split opposite each locule to provide egress of spores from sporangia. The lower surface of these fructifications is slightly convex so that the section shown in text figure 3 c is slightly off the main transverse plane, more accurately transected by the section shown in text figure 3 b. Near the margin of this figure the dehiscence tissue and grooves between the sporangial rows again are shown. Centrally the sporangia are tubular and separate except where septae have broken down.

Text figure 3 a, from a section across the middle of the fructification, shows a very similar character although the double rows are not so obvious. A nearly radial longitudinal section is shown in text figure 3 d and the transverse planes corresponding to the sections in figures 3 a–c are approximately indicated.

One of the interesting features in arrangement of sporangia is the way new paired rows are added by intercalation toward the margin. Text figure 3 c shows this best by the course of the dehiscence grooves. Plate 105, figure 1 represents a photograph of part of this same section. In the longitudinal plane the sporangia incline upwards around the margin of the fructification as shown in plate 105, figure 2 until they abut on the dorsal cover layer. Thus they are shorter than sporangia more centrally located. This feature may provide a clue to the mode of growth of these fructifications. It also is worthy of note that many of the sporangia are not actually straight but have a slight sigmoid curvature which is apparent in nearly all of the near-radial sections (text fig. 3 d; plate 104 figs. 1 and 2; plate 105 fig. 2; plate 107, fig. 1).

In regard to growth the chief question is the order of sporangial maturity, whether centripetal or centrifugal. One would expect the sporangia first formed in ontogeny to be the most complete and longest. These evidently are the ones centrally placed in this fructification and so it seems most plausible that the fructification expanded as a capitate head with the central, i.e., the most axial sporogenous tissues maturing first and marginal tissues somewhat later. The course of maturation in this event would be centrifugal or opposite to that in umbels and capitula of modern plants. The number of marginal rows produced and the final diameter attained by the fructifica-

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FIG. 3—*Dolerotheca formosa*, sections of fructification: schematic indication of tissues. Spores are shown black, inter-sporangial tissue (ground parenchyma and sclerenchymatous strands) represented by dashed areas, dehiscence tissue is stippled, campanulary cover dark with white stippling. Drawings prepared by projection of "peel" sections at low magnification, scale of enlargement is indicated. The serial number of preparations is given for each figure.
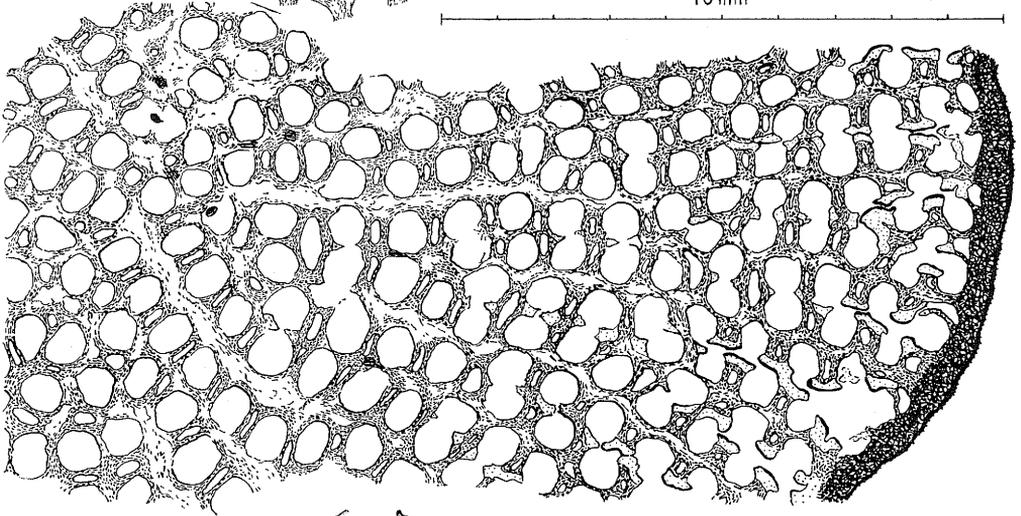
A, B, C.—Transverse sections.

D.—Vertical (slightly tangential) section. Ruled lines (A–A, B–B, C–C) indicate approximate relative levels at which transverse sections for figures A, B, and C were obtained; the transverse series is from a different specimen than section D; both are from coal ball 129.
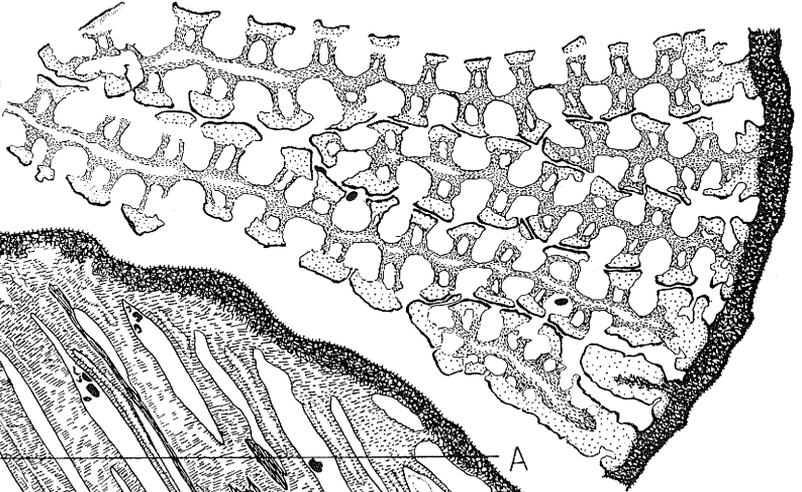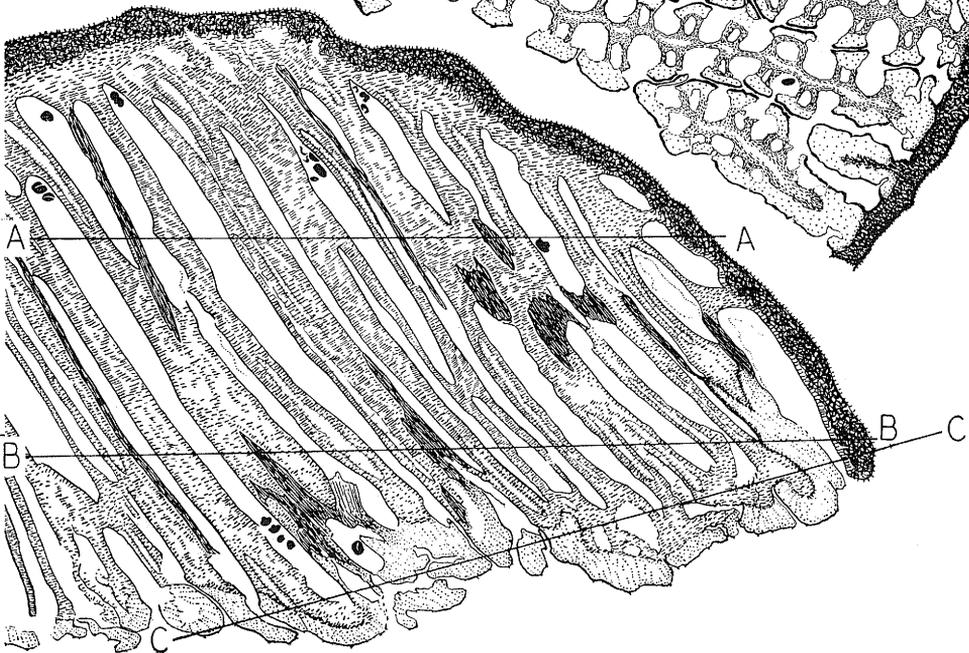
A
129A (T22)

B 129A (T13)

10 mm

C
129A (T6)

D
129B (S4)

A——A

B——B——C

C
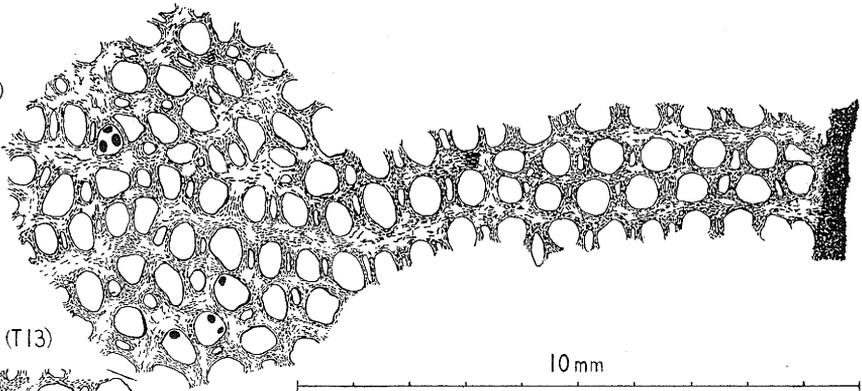
tion was probably dependent to some extent on environmental conditions which favored or retarded growth and reproductive processes in the plant.

Histology.—The proximal or dorsal side of the fructification is covered by the rather thick more or less coriaceous campanulary cover. It has a definite cuticularized epidermis bearing numerous short glandular appearing hairs. These hairs are 60–90 μ long and about 45 μ broad consisting of from two to five cells, all of which except the terminal cell are broader than long. The terminal cell is variously cone-shaped and sometimes has divided into two cells to become capitate. All the cells have dark contents shrunken away from the cell walls, which gives the hairs a glandular appearance. The dark material does not appear "resinous" and may be the remains of a dense cytoplasm containing tannin derivatives or other materials. Some cells contain rounded central bodies reminiscent of nuclei. Three of the hairs are shown sectioned vertically in text figure 12. A somewhat better idea of the hairs and epidermal pattern is obtained from cuticular fragments prepared by dissolving the calcite matrix in dilute hydrochloric acid. The hairs drawn in outline in text figure 9 a were obtained in this way and the arrangement of cells around the hair bases is shown from a similar preparation in text figure 9 b. Photographs of the same material are shown in plate 107, figures 3–5. Figure 5 was taken at a higher plane of focus than the others to show the upstanding tips of the hairs. These fragments prepared by hydrochloric acid treatment have the advantage of being more translucent than thin sections since much of the dark cell contents has been removed. The epidermal cells proper are irregularly polygonal with contents similar to that of the hairs. The dark contents are not limited to the hairs and epidermis but several layers of deeper cells near the lower margins of the fructification also possess similar inclusions

as shown in text figure 7. From two to four or five cells may adjoin the basal hair cells. No stomates have ever been recognized in the epidermis of the cover although, in view of the spongy tissue lower in this layer, their absence is noteworthy.

Beneath the epidermal tissue is a zone of spongy parenchyma generally not well preserved, with numerous large intercellular spaces. Isolated in this spongy tissue are groups of nearly isodiametric sclerotic or stone cells. These are shown most clearly in the section illustrated in plate 107, figure 6, which was cut obliquely tangential to the cover layer and appears thicker than it actually is for this reason. The groups of stone cells seem comparable in position to the sclerenchyma of the sparganum cortex of *Myeloxylon* petioles and also to cells of the sclerotesta of certain trigonocarp seeds. The cell shapes and the tissue occurrence differs considerably, however, so that the histologic similarities are not very marked. Numerous large secretory canals are also present and possess characteristic opaque contents. The contents often are more broken by calcite intrusions than the resin rodlets[5] of *Myeloxylon* petioles. This may indicate that the contents in the two instances were somewhat different in consistency and perhaps slightly different in composition when mineralization occurred.

The vascular supply of the campanulum of *D. formosa* is not prominent. It has never been possible to demonstrate tracheids in the marginal region. In a few instances delicate strands of small closely spiral, annular or scalariform tracheids have been seen near the top of the fructification. These are generally located internally at a lower histologic level than either the secretory canals or the groups of stone cells and are appar-

[5] The term "resin rodlet" is used herein only in a descriptive sense similar to the usage in coal microscopy. In no case is any particular chemical composition to be inferred from the descriptive use of this term.
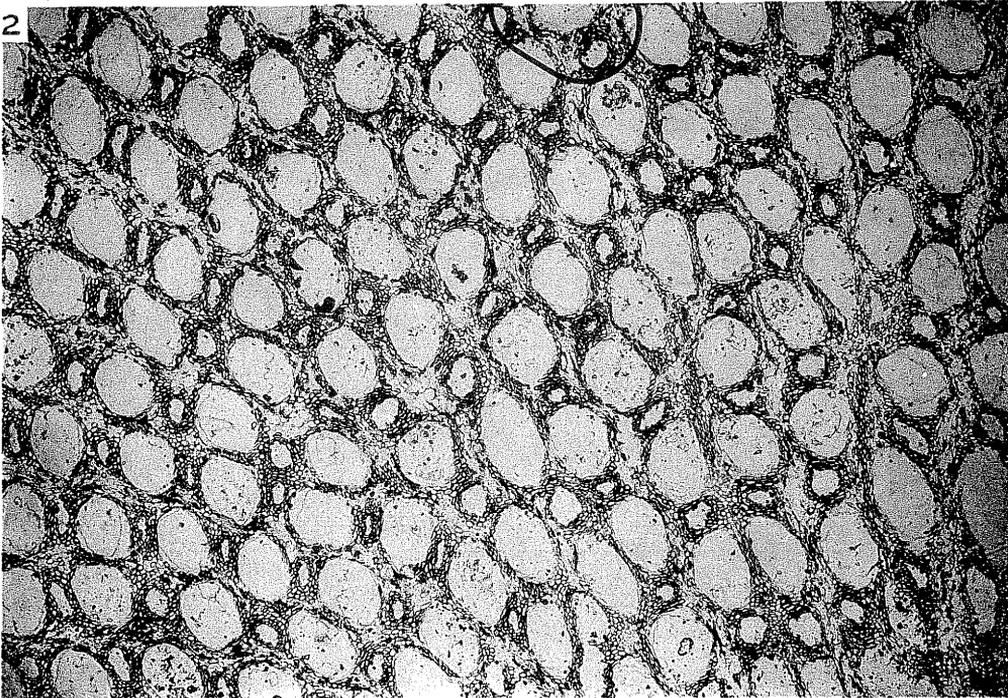

FIG. *1—Dolerotheca formosa*, transverse section near center of fructification about 3 or 4 mm. above level of dehiscence tissue. From coal ball 129 A (t 12).
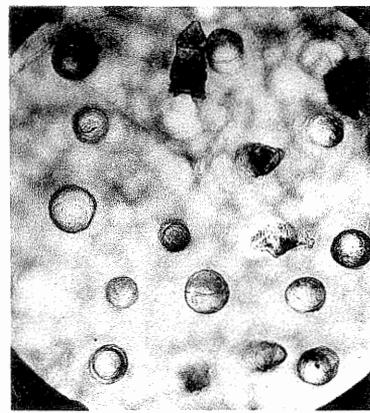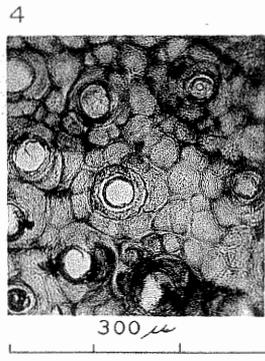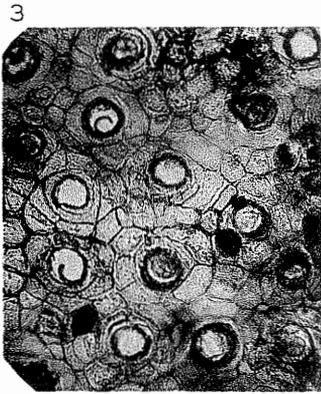
2—Section similar to figure *1* but about 3 mm. higher, showing more compact structure. From coal ball 129 A (t 27), magnification same as figure *1*.
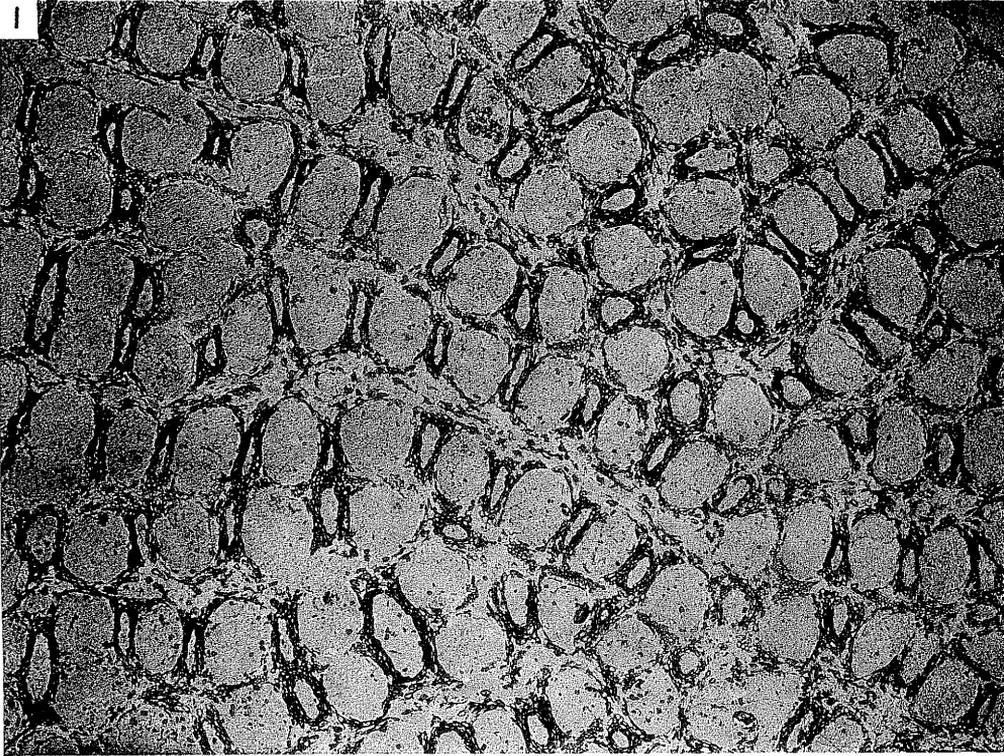
10 mm

Schopf, *Dolerotheca formosa* n.sp.

Schopf, *Dolerotheca formosa* n.sp.

ently unrelated to either in their position. Presumably phloem accompanies them but preservation of the tissue immediately surrounding them is poor and the details are obscure.

The spongy tissue of the cover merges internally with the intersporangial ground parenchyma which is somewhat thicker walled, has larger cells and is generally well preserved. The cells tend to be radially elongated as is apparent in the longitudinal section in text figure 5, and in the transverse sections illustrated. The intersporangial parenchyma is the fundamental groundwork of the fructification, since it chiefly encloses and in fact often seems to constitute the walls of sporangia. A relatively small number of cells, chiefly in the lower part near the dehiscence area, possess secretory contents. The ubiquitous resin rodlets also occur in this ground parenchyma and extend down close to the dehiscence surface (cf. r. r., text fig. 6).

Although ground parenchyma appears to constitute most of the wall of the sporangium without any sort of differentiation, in many sporangia there is a somewhat shrunken membrane which originally enclosed the spores. This membrane is noncellular and does not seem to be of waxy nature like cuticle although it is quite persistent. That it is an organic structure and not a pseudomorph in the calcite is shown by its presence as a definite membrane in nitrocellulose peels. There are at least two possible explanations for this membrane. One is that it represents the remains of a sporangial plasmodium. However it might better be taken to represent the remains of peri-archesporial tissue which has been transformed to a gelatinous or mucilaginous film. The latter is more probable because it seems the ground tissue must have shown some differentiation adjoining the sporangia, at least during the early stages of growth. Since differentiated perisporangial tissue is not otherwise in evidence, the sporangial membrane probably represents a vestige of it.

The dehiscence tissue occurs over the distal ends of sporangia, extending up above the radiating dehiscence grooves. It consists of undulated elongate cells with oblique and tapered end walls. Cells near the distal surface are thin-walled and from three to five times as long as broad (cf. text fig. 9 c). Deeper within the fructification the cells become longer, more tapering at the ends, and their walls thicker and straight. In short, they assume all the characteristics of fibrous sclerenchyma. Although they merge in this manner with the internal sclerenchyma system (described on p. 696) only the thin-walled tissue has contact with sporangial openings. It is not assuredly established that specialized kinetic cells are nowhere present to provide for the opening of sporangia, but they have not been recognized and no dehiscence mechanism is evident.

So far as can now be ascertained, spores are shed through slits or pores produced by mechanical fracture of the dehiscence tissue. It is not altogether clear why the fractures always coincide with the distal ends of sporangia. Since no actually "motivating" cells responsible for the opening of sporangia can be demonstrated, the designation "dehiscence tissue" may not be particularly appropriate; still it appears that this thin-walled tissue is specially modified as a whole to permit shedding of spores. In any

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EXPLANATION OF PLATE 107

FIG. *1—Dolerotheca formosa,* longitudinal section similar to fig. *2,* Pl. 2. Note dark sclerotic strands which merge below with the dehiscence tissue. From coal ball 219 C 1 B 1 (b 9), magnification same as fig. *6.*

2—D. formosa, intersporangial vascular strand. From coal ball 219 C 1 B 1 (b 18).

3, 4—D. formosa, cell patterns of proximal cover epidermis showing frequency and relative position of hairs. From hydrochloric acid maceration of coal ball 229 B 2 C.

5—Same as above, photo at higher plane of focus to show the tips of upstanding hairs. Note hair broken from its base; hairs similar to these are the basis of drawings in text fig. *9* A.

6—D. formosa, longitudinal section at margin of fructification. Note groups of sclerids in the cover layer and hairs shown above it. The hairs appear disconnected because the section is oblique with reference to the surface of the fructification. From coal ball 219 C 1 B 1 (b 44).
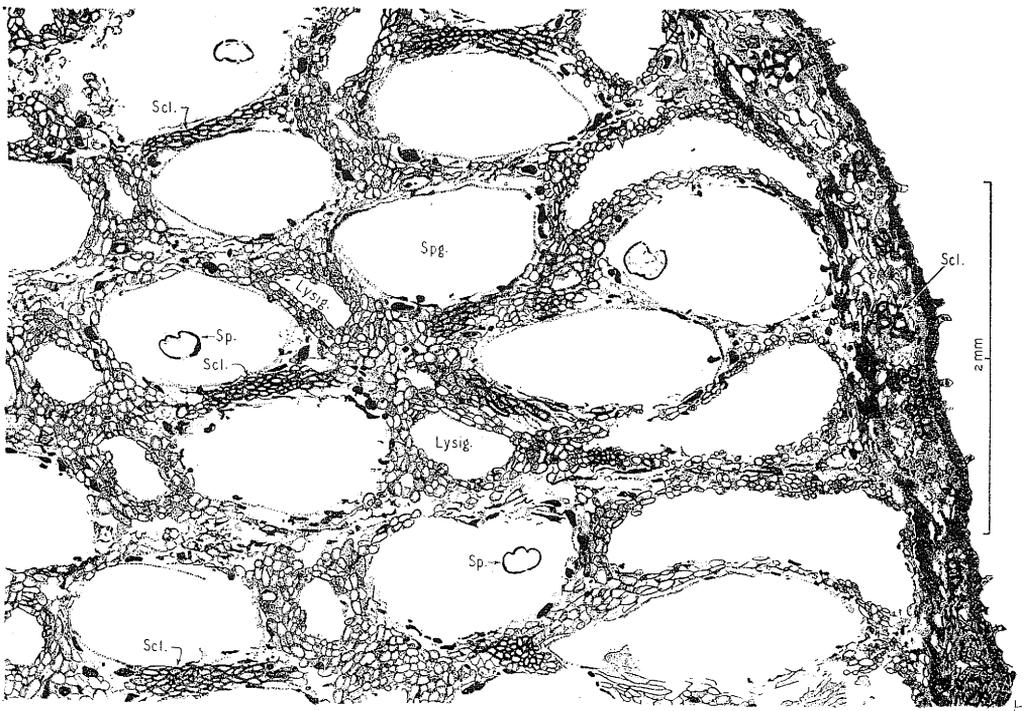
FIG. 4—*Dolerotheca formosa*, transverse section showing spores (Sp.), sporangia (Spg.), lysigenous tubes (Lysig.), Sclerenchyma (Scl.). The character of the inter-sporangial tissue and of the campanulary cover also is shown. From coal ball 129 A (t 37).
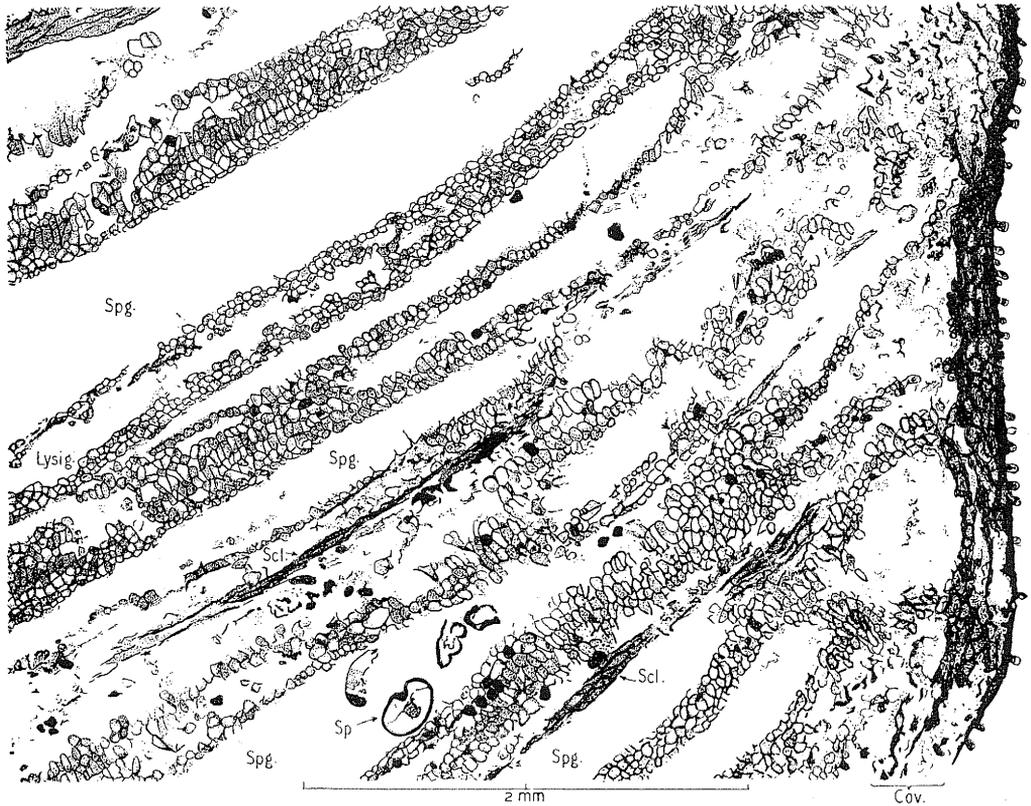

FIG. 5—*Dolerotheca formosa*, longitudinal section for comparison with transverse section shown in text figure 4 (lettering symbols the same; cov. = campanulary cover). From coal ball 129 (B₃).

event this function is the essence of sporangial dehiscence, whether by a kinetic mechanism or not. Sections across the slits in the dehiscence tissue communicating with sporangia are shown in text figs. 7 and 8. The preservation is best in marginal areas such as shown in fig. 7 and this also may indicate that maturation of the fructification proceeded centrifugally. If the central

as the dehiscence tissue opposite the ends of sporangia. No stomates have been observed but it is conceivable that the dehiscence pores are initiated by some sort of modified stomatal apparatus. The hairs are more sparse than on the dorsal cover surfaces, more slender, simple, consist of 1–3 cells, and are less glandular appearing. No capitate tipped hairs have been observed.
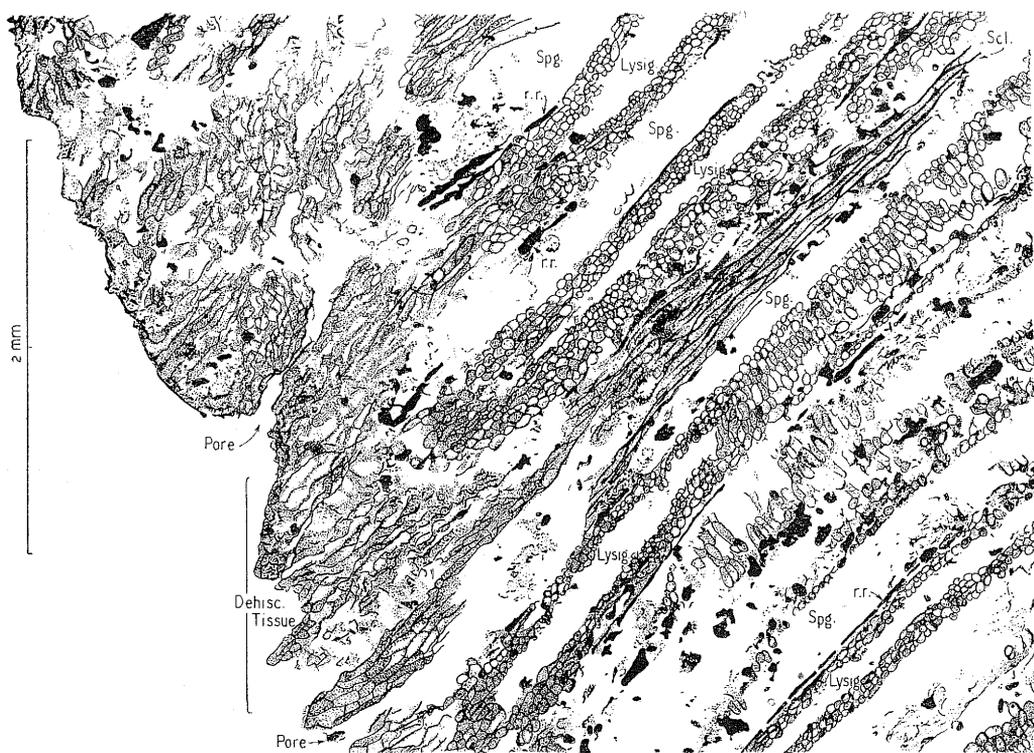

FIG. 6—*Dolerotheca formosa*, longitudinal section of distal part of fructification showing dehiscence tissue, sporangial pores, sporangia (Spg.), lysigenous tubes (Lysig.), sclerenchyma (Scl.), resin rodlets (r.r). From coal ball 129 (b 3).

pores were the first to open, presumably they might become more fragmented before the organ dropped from the plant and had a chance to be petrified.

The definite epidermis of the dehiscence layer is of particular interest since no equivalent of the usual prismatic wall of cryptogamic sporangia is present. This epidermis is composed of somewhat flattened cells often bearing hairs or papillae (cf. text fig. 9 c). It apparently is fractured in the same way

Papillae however are extended to a variable degree on nearly all cells not otherwise acting as hair bases. The relation of the distal epidermis to the dehiscence tissue is shown in text figure 9 c, and the shape of distal trichomes may be contrasted with those of the integument shown in figure 9a at somewhat greater magnification. The distal epidermis apparently is not strongly cutinized and is more irregular and broken by original fractures. Consequently no suit-

able preparations have yet been obtained by dissolving the calcite matrix. All the details reported have been observed in sections.

Aside from the campanulary cover, supporting tissue of the large fleshy male fruc-

bridges between them. Their arrangement is evident in text figures 4 and 6 and they can also be seen in pl. 107, fig. 1, and pl. 105 fig. 2. Two small strands are shown in text figure 10 deeper within the fructifica-
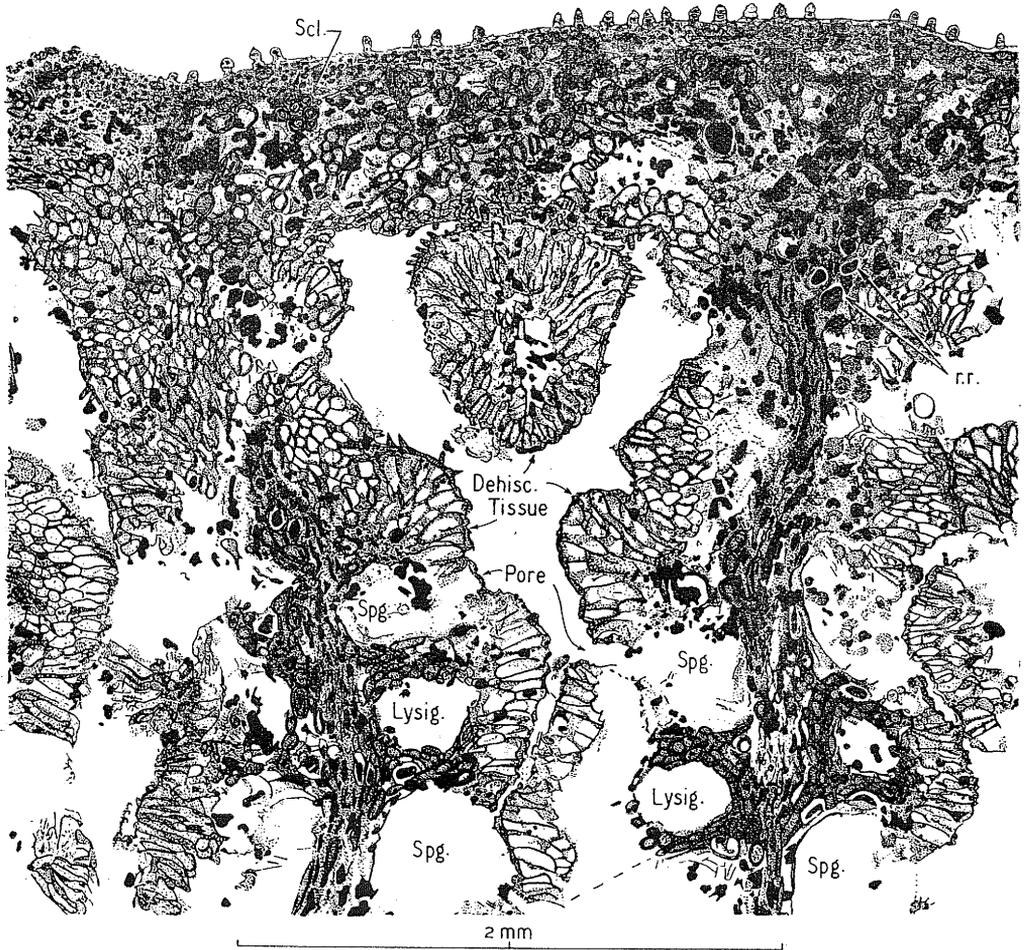

Fig. 7—*Dolerotheca formosa*, transverse section of distal part of fructification showing campanulary cover layer with sclerotic cells (Scl.), dehiscence grooves, dehiscence tissue, sporangia (Spg.), lysigenous tubes (Lysig.) and resin rodlets (r.r.). From coal ball 129 A (t 38).

tification of *D. formosa* is limited to the fibrous sclerenchyma strands developing above the dehiscence grooves. As mentioned, cells of the dehiscence tissue merge with the sclerenchyma in these areas by a gradual transition. Apparently the fibrous strands act as isolated buttresses or "stays" to prevent distortion as there are no sclerotic

tion. A type of cell wall thickening sometimes also occurs in the tangential bars on either side of the lysigenous tubes between sporangia. These cells however are not usually elongate and spindle-shaped like the fibrous strands and probably owe their sclerotic appearance to some other cause. The fibrous strands are somewhat compara-

ble to the sparganum strands of *Myeloxylon* but their distribution is different so that the resemblance may be mostly superficial.

The vascular bundles are noteworthy for strands, i.e., *between* the paired sporangia. The ground tissue along these radii is generally rather poorly preserved, perhaps due to a slight difference in its character, and dis-
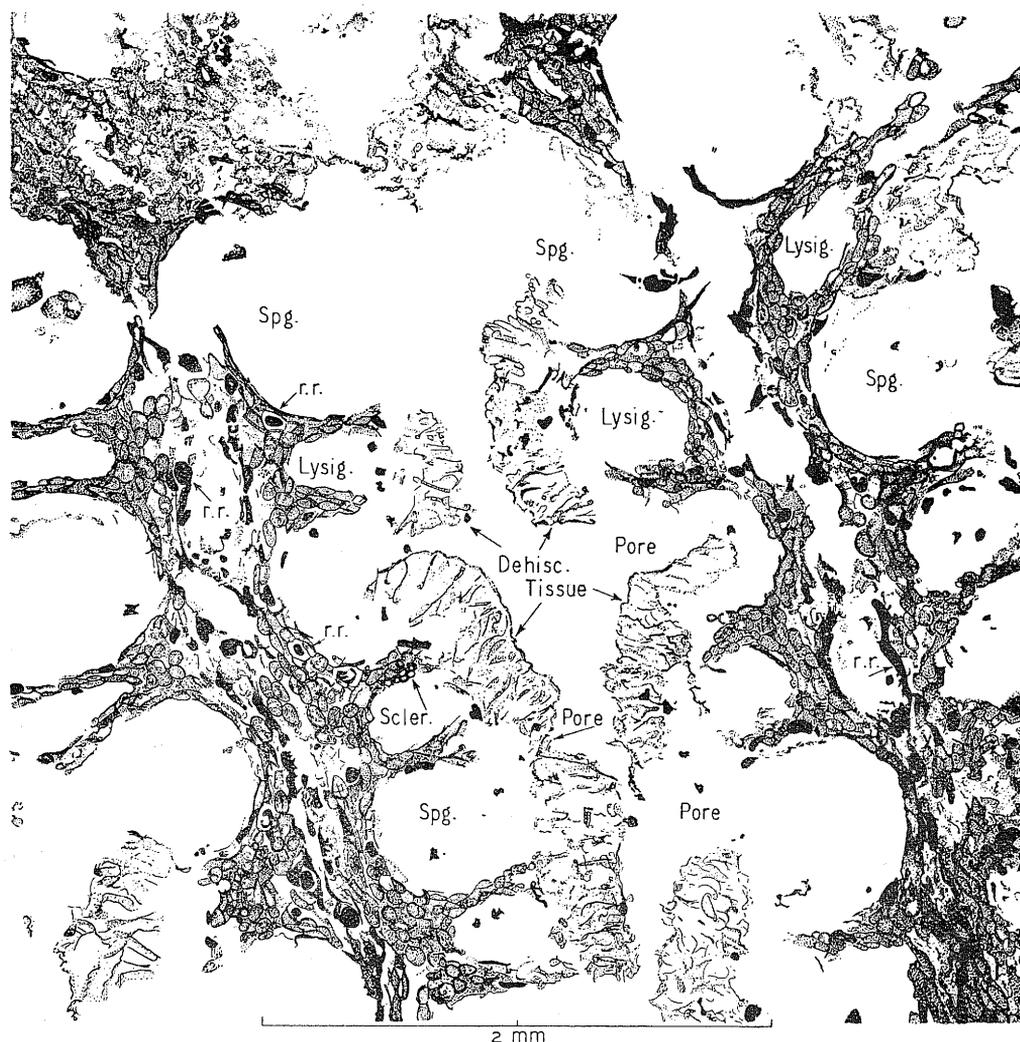

Fig. *8—Dolerotheca formosa,* transverse section of distal part of fructification more centrally located than text figure *6,* (lettering symbols the same). From coal ball 129 A (t 6).

their obscurity. They appear to consist of a few spiral or annular tracheids isolated in the ground parenchyma unassociated with resin rodlets or sclerenchyma; they are not numerous. They seem to be restricted to the radii alternating with the sclerenchymatous organized humic material is present around all the delicate vascular strands that can be found. The tracheids are very small, average about 15μ in diameter, and can be observed chiefly in longitudinal sections where their annulae distinguish them. Figures

showing the vascular strands are shown in text figure 11 and in pl. 107, fig. 2, and pl. 105, figs. 3 and 4.

The vascular bundles are gathered at the top, always situated rather deep within the

lar to those forming the ultimate veinlets in the *Alethopteris* pinnules, which are abundantly associated with this material. Although fructifications of *D. formosa* are the largest of the *Dolerotheca* species known,
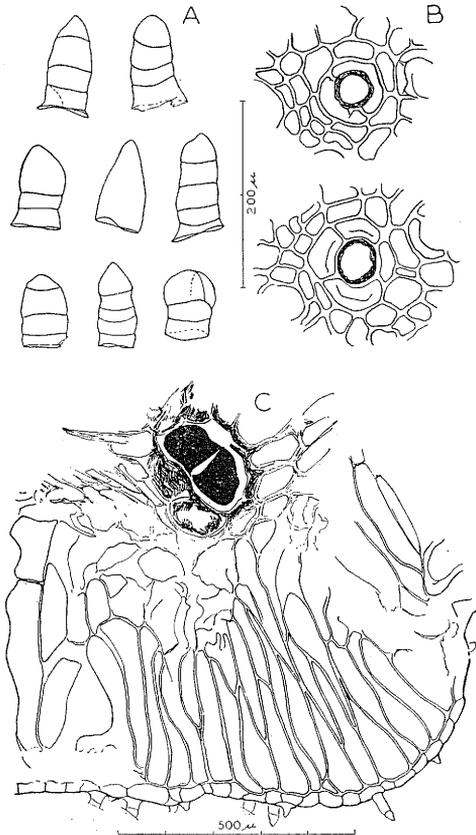

FIG. *9*—A. *Dolerotheca formosa*, hairs of dorsal cover broken from the epidermis after dissolving the calcite matrix.
B. Same, cuticular cell pattern at the base of two of the hairs. Magnification same for A and B.
C. *D. Formosa*, line drawing of dehiscence tissue showing epidermis and hairs. A resin rodlet appears in oblique cross section in the tissue above. From coal ball 219 C 1 b 1 (b 18 c).

FIG. *10*—*Dolerotheca formosa*, transverse section of a septum with a characteristic sclerenchyma strand between sporangia of opposite paired rows (Spg.), also small lysigenous tube (Lysig.). The sporangial membrane (memb.) is continuous in the sporangium on the right; resinous inclusion (r). From coal ball 125 A (t 25).

cover layer, and branch with bundles penetrating downward between the paired locules. These bundles are hardly comparable in size and character of the elements to those in associated *Myeloxylon* petioles. However they appear to contain elements rather simi-
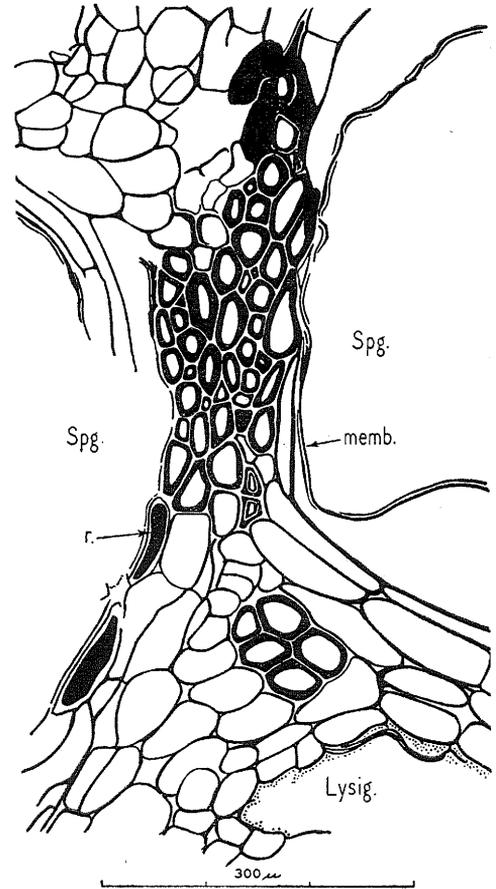
they show considerably less vascular development than either *D. villosa* or *D. reedana* described below.

Spores or Prepollen.—It is important that the difference be recognized between the preservation of spores in coal balls since

these can be dissolved out undistorted by compression, and those which have been flattened and present a somewhat distorted appearance in coal maceration residues. In the latter, only two dimensions may be

Prepollen grains of *D. formosa* are 300–350 μ long and 200–250 μ broad by about 150μ thick. Proximally they are marked by a
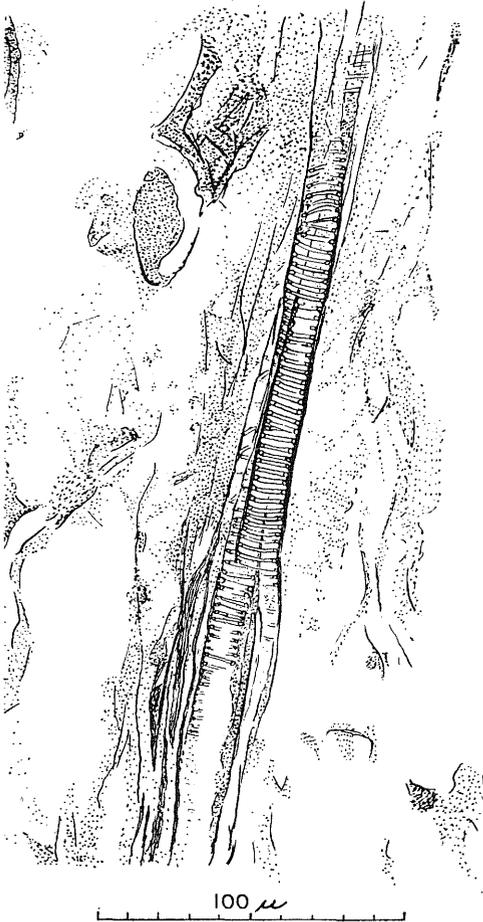
Fig. *11—Dolerotheca formosa*, vascular strand from radius of paired sporangial row, showing spiral or annular thickenings. From coal ball 219 C 1 b (b 18a).

Fig. *12—Dolerotheca formosa*, detailed drawing of dorsal hairs and their contents. From coal ball 129 A (t 38).

accurately observed; the depth dimension must to some extent be reconstructed by inference. In coal ball material all three dimensions may be observed with an accuracy approaching that in living material. Spores of *D. formosa* have been studied isolated after solution of the calcite matrix in addition to those obtained in sections.

monolete suture which in nearly all shows a slight angular deflexion near the middle (pl. 108, fig. 7). To the extent that this suture deviates from a straight line, the spores are asymmetric bilaterally. Distally, the coat has two prominent grooves which approach close together at the two ends but are spread farther apart at the center. An
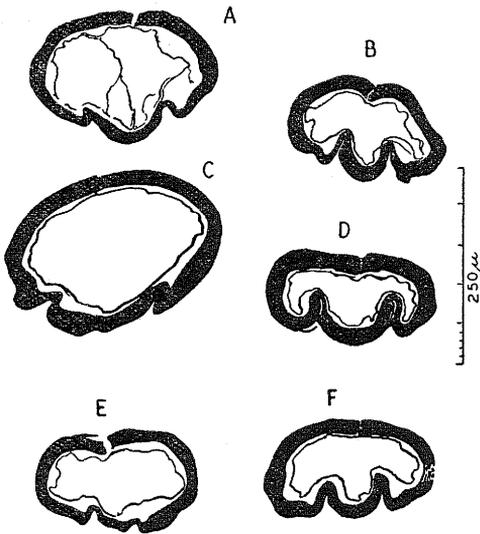
FIG. 13—A–F. Prepollen or spores of *Dolerotheca formosa*. Outline drawings (microprojection) of specimens still within sporangia, in approximately median transverse section; C is most oblique. Proximal suture is uppermost in each, distal grooves and umbo downward. From peel sections of campanulum in coal ball 129.

almost perfect axial section across the short diameter of a prepollen grain is shown in pl. 108, fig. 4. The distal grooves are uppermost in the figure and the proximal suture is marked by a slight indention at the bottom. Shadow outlines of the distal grooves below the plane of focus are evident in an example isolated by solution of the matrix shown in pl. 108, fig. 6, and in fig. 7 the same spore is illustrated at a higher plane of focus showing the characteristic proximal suture. Figures 8 and 9 of plate 108 show examples of other isolated whole grains where the suture has opened. Median sections across the short dimension of grains are shown in outline in text fig. 13. In no case has the umbo between the distal grooves been found separated as a germinal "operculum," or the distal grooves split, except in irrelevant cases where mechanical disturbance, such as may occur in peeling nitrocellulose films, probably had occurred. The shadow of the distal grooves appears on either side and at a lower plane of focus than the open proximal suture in the whole specimen illustrated in pl. 100, fig. 8. For *Dolerotheca fertilis*, Renault

EXPLANATION OF PLATE 108

Magnification same for figs. *1–9*

FIG. *1*—*Dolerotheca formosa*, spore (prepollen) showing collapse of the exospore (pseudomorph shows original outline) and endosporal membrane shows pseudo-cellular structure due to collapse. Section is obliquely longitudinal and intersects only one of the distal grooves on the lower side. From coal ball 129 C (S 7)

2—*D. formosa*, longitudinal section of spore showing original form of exosporal coat and frayed distorted remnants of the endosporal membrane. From coal ball 129 C (S 7)

3—*D. formosa*, oblique longitudinal section of spore similar to fig. *1* showing pseudo-cellular collapse of endosporal membrane. Small cross composed of pyritic crystals is above the indention caused by one of the distal grooves. From coal ball 129 C (S 7)

4—*D. formosa*, transverse section of spore showing typical configuration of layers of the spore coat. Proximal suture (pr. sut.) is at the bottom somewhat obscured by thickness of the section. dist. gr.—distal grooves; endo—endosporal membrane.

5—*D. formosa*, transverse sections of two spores showing distal contour and proximal sutures (pr. sut). The proximal side of the lower spore is slightly collapsed in preservation similar to that shown in fig. *1*. Dist.=distal umbo. From coal ball 129 C (S 7).

6—*D. formosa*, isolated spore showing outline of slightly collapsed endosporal membrane. Note shadow outline of distal grooves. From hydrochloric acid maceration of coal ball 229 B 2 C.

7—Same as above but at a higher focal plane to show the proximal suture.

8—*D.formosa*, isolated spore with proximal suture split open. From hydrochloric acid maceration of coal ball 229 B 2 C.

9—*D.formosa*, spore showing proximal suture open as in fig. *8*. Shadow outlines of distal grooves may also be noted in both figures. From hydrochloric acid maceration of coal ball 229 B 2 C.

10—*D. formosa*, spores in two adjacent sporangia. From coal ball 129 C (S 7).

11—*D.fertilis* (Renault) Halle, sections of two spores probably showing endosporal gametophytic tissue. Details of the spore coat obscure. From Renault (fig. *4*, Pl. XII, 1902).

12—*D. fertilis* (Renault) Halle, spore showing proximal suture—evidently not one of the distal grooves. From Renault (fig. *3*, Pl. XII, 1902).

13—"*Aetheotesta* pollen," showing endosporal gametophyte possibly different from spore (prepollen) of *Dolerotheca*. From Renault (fig. *4*, Pl. XI, 1902).
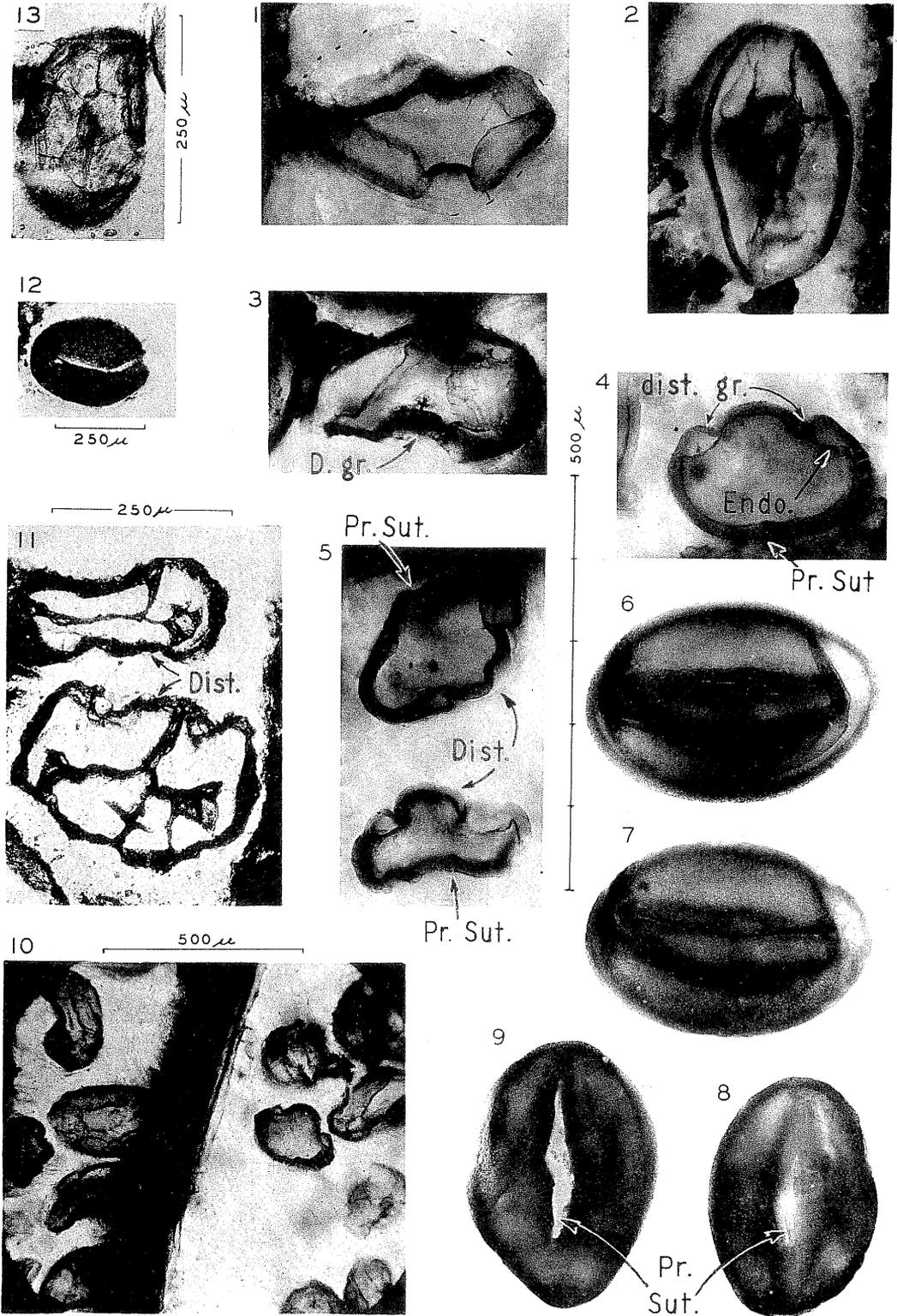
Schopf, *Dolerotheca* spores
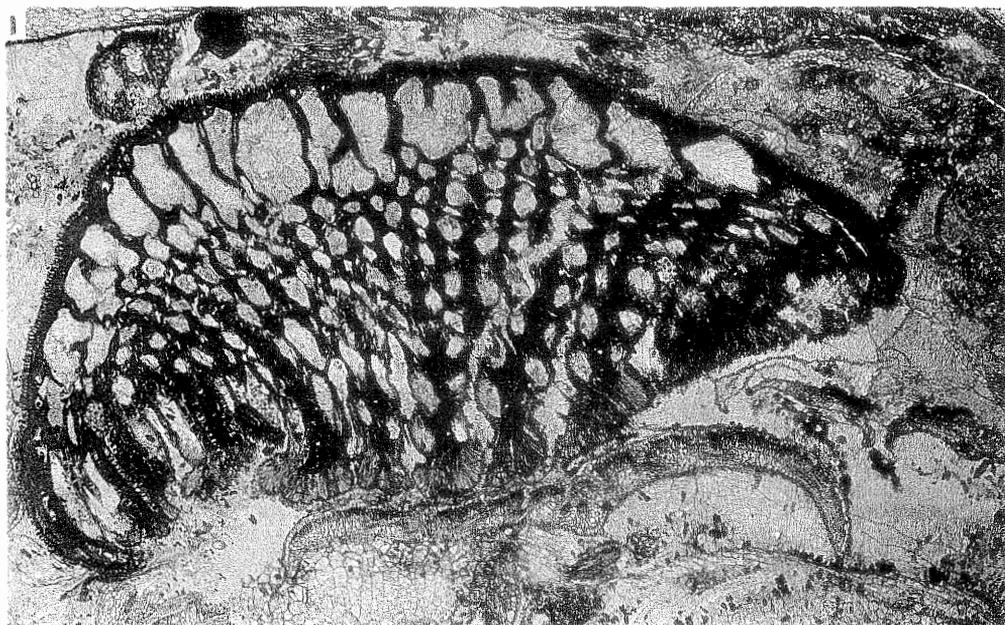
Schopf, *Dolerotheca villosa* n. sp.

(1902) cited the illustration copied here in plate 108 fig. 12, as proof of the opening of the distal umbo as an "operculum." It seems quite clear that this figure illustrates the proximal and not the distal side, and that the slit has occurred normally by way of the proximal suture as in spores of *D. formosa* discussed previously and shown in pl. 108 figs. 8 and 9.

The writer is inclined to attach considerable significance to the angular deflection of the proximal sutute. The sutures of monolete fern spores, e.g. those included in *Laevigato-sporites* (see Schopf, Wilson and Bentall, 1944, pp. 36–37) are not deflected in this manner. The tetrads have not been observed in *Dolerotheca* but the author entertains the possibility they may have shown tetrahedral arrangement and been relatively small. The *Dolerotheca* spores may have enlarged greatly after the tetrad separated and the deflection angle of the suture line may mark the trilete apex and point of departure of the third suture ray that has become obsolete.

The exosporal layer of the prepollen coat varies in thickness from about 8 μ in the trough of the distal grooves, to about 12 μ on the proximal side (cf. text fig. 13, and pl. 108, fig. 4. The exosporal coat also appears thinner at the two ends of the prepollen grains.

The endosporal membrane is generally present maintaining close contact with the proximal part of the exospore but more or less shrunken away from the distal side and ends. It is out of contact with the exosporal ridges on either side of the distal grooves in pl. 108, figs. 4 and 5 and can be observed shrunken from the exospore at both ends in the isolated grain illustrated in fig. 6. The evident folds in the endosporal membrane shown in fig. 6 are in no way due to compression.
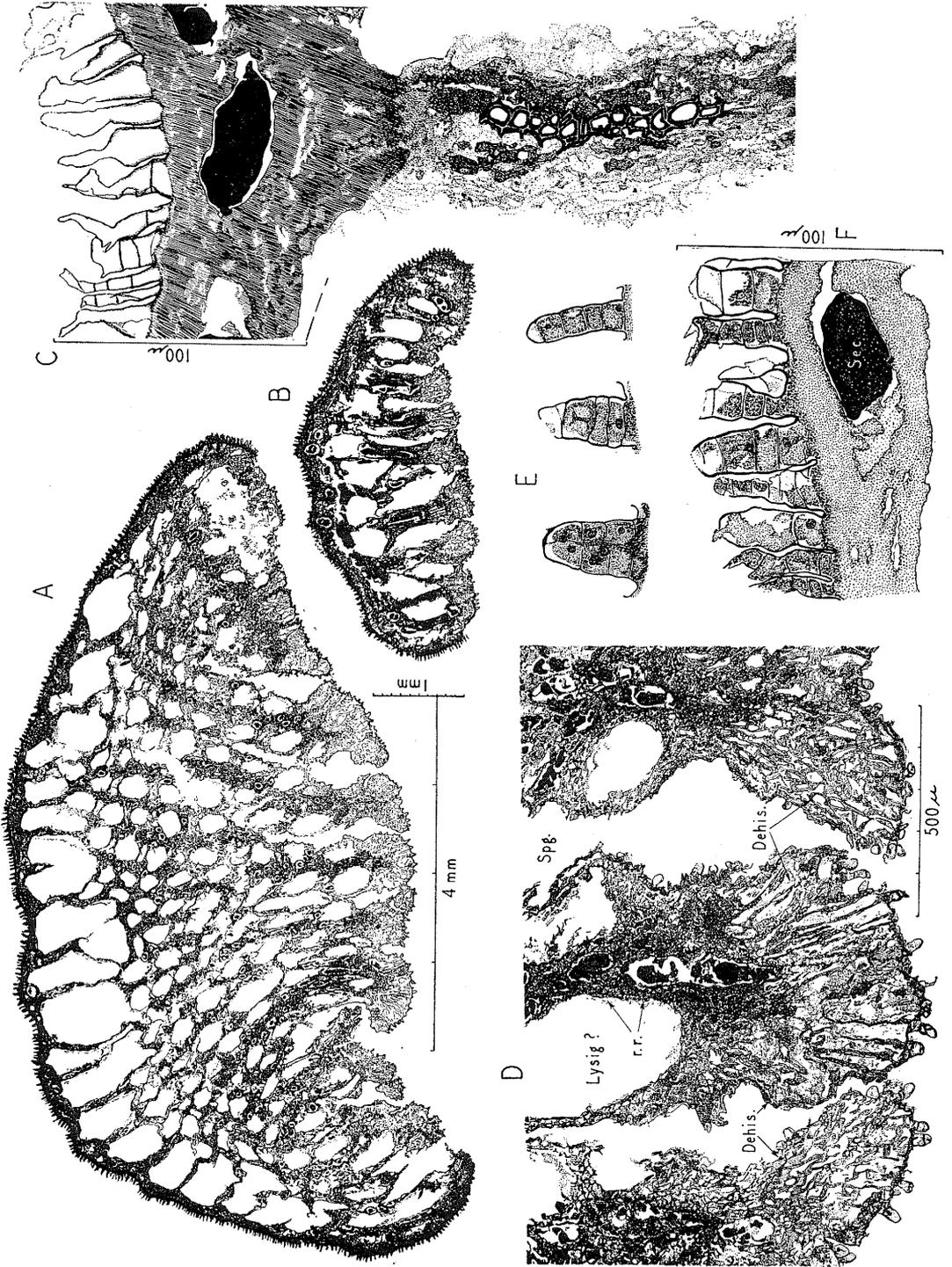
Observations by Renault (1902) and by Florin (1937) have shown beyond doubt that endosporal gametophytes are present in some types of well preserved Paleozoic spores, prepollen and pollen grains. The folded endosporal membrane within some grains of *D. formosa* was at first taken as a remnant of gametophytic tissue, but it seems now that this probably is not the case. Only in the sectioned example shown in text fig. 13 a, is there some question concerning the endosporal interpretation. Instances where the endosporal membrane is folded to simulate gametophytic tissue are shown in pl. 108, figs. 1–3, and may be compared with figs. 11 and 13 of the same plate (which have been copied from Renault) that probably do represent gametophytes. One could be more confident of Renault's interpretation if it were possible to distinguish both layers of the coat (exo- and endospore) as well as vesicular (gametophytic) contents.

Around the spore shown in pl. 108, fig. 1, is a calcite pseudomorph (indicated by the dashed line) which no doubt represents the former outline of the exospore before it partially collapsed during mineralization. Possibly the endosporal membrane also collapsed to its present invaginate outline at the same time. Identification of both layers is certain because the shrunken outer wall shown here resembles the exospore in color and texture and the thin invaginate inner structure is similar to more normally placed endosporal membranes. Plate 108, figure 3, shows an example in which the exospore is somewhat less shrunken, and the collapsed endospore less irregular than in fig. 1. In the lower central part of the figure is a small opaque cross, probably of pyrite crystals. Figure 2 of the same plate shows a spore in which the exospore is unshrunken but the endospore is severely collapsed. In all three instances it is the lack of any other membrane which could represent the endospore that renders a "gametophytic" interpreta-

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tion most questionable. Possibly in fossilized material the walls of gametophytic cells might appear as if fused with the endosporal membrane. But if the membranes interpreted here as endosporal are in reality gametophytic walls, the cellular arrangement of the gametophyte must have been very irregular, to say the least, and the writer can see little definite evidence to support such an interpretation. Probably the gametophyte is the most delicate and least preserved "spore" part. If this tissue is present in any instance, the more resistant spore coat layers should also be accounted for.

Type Material.—The paratypes of *D. formosa* are these illustrated in pl. 104, figs. 1–7 etc. from coal balls 219 and 129 of the Illinois State Geological Survey collection. Should selection of a holotype specimen in any event be required, the writer would prefer to designate the one illustrated in pl. 104, figs. 1 and 2 from coal ball 219. The specimens are from the coal bed just below the Calhoun limestone near the town of Calhoun in Richland County, Illinois. This zone is in the upper part of the McLeansboro group of Illinois.[6]

DOLEROTHECA VILLOSA Schopf, n. sp.

Frontispiece, fig. C; Plate 109, figs. 1–3

Plate 110, figures 1–9, text figures 14, a–b

External Characters.—Male fructification about $\frac{1}{4}$ as large in external dimensions as *D. formosa* and more strongly convex proximally. Proximal surface slightly ridged radially; covered with close set villous hairs.

[6] Age relations of Illinois coal ball horizons are given in a previous publication (Schopf, 1941).

Hairs adorn the lower distal surfaces of dehiscence tissue and are relatively longer and more numerous than in *D. formosa*.

A reconstruction drawn to the same scale as that of *D. formosa* is shown in the frontispiece, fig. C.

General Anatomy.—The tissues are essentially the same as in *D. formosa*. The sporangia are from 300–400 μ in diameter and perhaps as much as 5 or 6 mm. long, or about half as large as in *D. formosa*. Lysigenous cavities also occur as in the other species but they are proportionately smaller and less distinctly preserved. The general relations can be followed in the thin section shown in pl. 109, fig. 1, and text fig. 14 a, as drawn from an adjacent peel section. Plate 109, figure 2 shows peels taken from adjacent surfaces cut at right angles to one another. In pl. 110, fig. 1, and text fig. 14 b, are sections cut progressively more tangentially: The last is far enough out so that, for the short length represented, sporangial locules are cut in fairly good longitudinal alignment. The campanulary cover averages 200–300 μ in thickness and contains large secretory passages. Just below the integument is a row of large pores which seem to have arisen by lysigenous break-down of sporangial septae and other tissues. Each of the persistent septations between these enlarged pores contains an elongate series of tracheids cut transversely. The dehiscence tissue is present in very much the same relationship as in *D. formosa*.

The species is represented by two specimens in the material studied. These are somewhat complementary and afford an adequate basis for diagnosis but nevertheless are less well preserved than those of *D. formosa*. On account of the smaller dimen-

FIG. *14*—A. *Dolerotheca villosa*, oblique median longitudinal section of fructification from coal ball 229 B 1a.

B. *D. villosa*, nearly longitudinal section of same fructification near margin. Magnification, same for A and B.

C. *D. villosa*, section of campanulary cover with hairs, secretory cavity and septum containing vascular strand. From coal ball 229 B 1 a (t 8).

D. *D. villosa*, detail drawing of distal margin of longitudinal section showing epidermal hairs, dehiscence tissue (Dehis.), sporangia (Spg.), Lysigenous tube ? (Lysig.?) and resin rodlets (r.r.), in tissue above. From coal ball 229 B 1 a (t 8).

E. *D. villosa*, hairs from campanulary cover.

F. *D. villosa*, campanulary cover with secretory cavity (Sec.) and hairs with contents. Magnification same for E and F.

sions of *D. villosa* and its rarity it has not been possible to obtain as perfectly oriented sections as in *D. formosa*. Both specimens were cut obliquely. One is complete except that all spores have been shed. The other consists only of the central sporangial tissue and entirely lacks the campanulary cover layer, although the dehiscence layer is well shown. Some of the sporangia in the incomplete example contain a number of flattened and perhaps abortive spores. It seems likely that the cover from this specimen has broken loose from the included sporangia by the disintegration of septae which occur in partial dissolution in the other example.

The only tissues in either specimen which are in fair preservation are the hairs, the dehiscence tissue and the vascular strands. Parenchyma of the cover layer and intersporangial tissue have collapsed into a dark disorganized humic mass preserving only the external outlines and the contents of secretory cavities. The tracheid rows are clear enough but all the adjoining tissues are also reduced to a humic residue without visible cellular organization. It is difficult to account for the fair preservation of original form under these circumstances but there is little or no evidence of distortion.

Histology.—The hairs of the dorsal surface are 4–6 cells long, generally simple but occasionally biseriate. None of them appears to be capitate as are some of those present on *D. formosa;* they are much more closely spaced and differently shaped. The cells are filled with dark material and oftentimes a globular central body is present in each cell. The hairs are set very close to one another forming a villous felt on the proximal surface as much as 60–70 μ deep near the top of the fructification but becoming thinner toward the margin of the campanulum. Individual hairs are shown in text fig. 14 e. Their close arrangement is shown in text fig. 14 c and f; also in pl. 110, fig. 4.

The cover layer has many large secretory ducts with characteristic dark contents, 20–50 μ in diameter. They generally occur in a single series as shown in text fig. 14 c (sec.) and in pl. 110, fig. 4. No vascular strands or stone cells are discernible within the cover layer although this may be due to poor preservation. However it seems likely that the

cover actually is less complex than in *D. formosa*.

Vascular strands seem to be limited to the persistent septae between the large pores located just below the dorsal cover. One of these septae is shown in its relation to the integument in text fig. 14 c. The section here, as in most of the others, is cut obliquely through the hemispheric fructification and is approximately at right angles to the surface of the campanulary cover at this point, which is about the highest in the section. Consequently the tracheid strands which run parallel to the outer surface are cut transversely. About 20 tracheids are shown in this group. Marginal walls of tracheids have broken down also so that probably there were a few more elements in the group originally. Smaller tracheids are seen at several places. Longitudinal sections as shown in pl. 110, figs. 7 and 8, show scalariform elements with the suggestion of an incipient bordered pit here and there in larger cells. The vascular strands seem somewhat more developed and the tracheids somewhat larger in *F. villosa* than in *D. formosa* where only small strands of characteristic spiral and annular tracheids have been observed.

The association of vascular strands with the mid-line of paired sporangial rows is somewhat more evident in *D. villosa* than in *D. formosa*, perhaps due to the collapse of all but the tracheid-bearing septae at the edge of the fructifications. Allowing for bifurcation of vascular strands wherever new sporangial rows are being intercalated toward the margin, it is apparent that the vascularized septae occur regularly along the midline of double series of sporangia, essentially similar to the apparent vascularization of *D. formosa*.

The breakdown of septae just below the cover has not progressed so far in the marginal region but none of the septae near the margin of the fructification contains tracheid strands. Apparently the tracheid bundles radiate only part way down the sides of the fructification. It seems that the vascular strands served for support well as as conduction in this type of fructification, but that the margins were sufficiently rigid that they required no special stiffening. The distance for translocation of materials was not very

great in this smaller fructification and did not require a more extensive vascular supply.

There is no evidence of sclerotic tissue in the fructification of *D. villosa*, although the preservation is not sufficiently good to prove that none existed. Since the hairs and dehiscence tissue, of thin walled cells which are not decay resistant are, nevertheless, well preserved, there is fair presumptive evidence that thicker walled sclerotic tissue was at least not well developed and may have been absent. The preservation does not permit a definite statement.

The intersporangial tissue shows little histologic detail. Large secretory ducts occur here, as in the cover layer, and penetrate down to the dehiscence tissue on the distal side (cf. text fig. 14 d and pl. 110, fig. 5, sec.). There also is a large number of smaller cells with similar contents scattered throughout. It seems that cellular structure was not preserved except where less perishable contents were present to mark more or less accurately the outline of original cell forms.

Dehiscence tissue is in general disposed as in *D. formosa* but it does not extend as deeply along the dehiscence grooves. Since the intersporangial ground tissue is not histologically interpretable, the relation of the dehiscence tissue to internal sclerenchyma strands cannot be made out. There is no evidence of this sclerenchyma, however, and it probably was rudimentary or absent.

Although sometimes obscure, an epidermal layer can be identified covering the distal surfaces as in *D. formosa*. This emphasizes the probability that no prismatic specialization of the epidermis occurs on sporangia of this group of plants. The hairs on the distal epidermis also are more numerous than in *D. formosa*. They are 2 or 3 cells (50–65 μ) long, as shown in text fig. 14 d and in pl. 110, figs. 6 and 9. The terminal cell of each hair is rather abruptly triangular.

Spores or Prepollen.—The specimen constituting the basis for most of the foregoing description has matured and shed all its spores. They are present however in the second more fragmentary specimen, previously mentioned. Prepollen spores are 130 to 150 μ long and 100 to 120 μ broad, with typical proximal sutures and two distal grooves as in *D. formosa*. The spores have collapsed for the most part and no accurate thickness measurement is possible, but the spore coats seem normally thick, and if they are abortive, this occurred in the last stages of growth. The example shown in pl. 110, fig. 2, is from a peel and the distal side has been partially torn away revealing the well defined suture on the proximal side. In figure 3 of pl. 110 a group of more or less collapsed spores is shown inside a sporangial locule. The distal grooves of the large spore at the left are barely distinguishable in the photograph but may be observed in the section at higher magnification by placing it over a concentrated point of light. Thus in structure these spores are typical of *Dolerotheca* but they are the smallest for any species yet reported.

Type Material.—Both specimens used in this description are from the same locality as those of *D. formosa* previously described. There is no question that distinct species are represented for not only do they differ in size and proportions at maturity, but the pubescence and other features are distinctive. The specimen which should be considered as the holotype is from coal ball 229 of the Illinois State Geological Survey collections. The more fragmentary specimen with collapsed prepollen grains is from coal ball 215.

DOLEROTHECA REEDANA Schopf, n. sp.
Plate 111, figures 3, 4; plate 112, figures 2–6; plate 113, figures 1–6; plate 114, figures 1–9, 14, 15; plate 115, figure 9; text figure 15

External Characters.—Male fructification campanulate, slightly more inflated proximally than *D. formosa*. Diameter estimated at 15–20 mm.; central thickness about $7\frac{1}{2}$ mm. Proximal (dorsal) side glandularly pubescent, irregular, covered with verrucosities of varying size and prominence, upon which hairs are particularly numerous. Radial indentions of the integument, if present, are rendered obscure by the surface irregularities. The distal surface is slightly convex, with dehiscence grooves $\frac{1}{2}$ to 1 mm. deep. As in the other species, a definite epidermal layer covers the distal

surface, the cells of which serve as bases for hairs or papillae. Distal hairs lack the dark contents characteristic of those of the proximal cover and are slightly more slender with terminal cells more cone-shaped.

General Anatomy.—The holotype specimen of *D. reedana* is located on the edge of a coal ball so that somewhat less than half of it is preserved; nevertheless enough is present to afford a fairly accurate and complete description. The largest available section is that shown in pl. 111, fig. 4. As shown in that figure the lower central part (lower left) is missing or poorly preserved. The central part of the dorsal cover proper has been destroyed, possibly by intrusion of roots. A much flattened *Psaronius* (?) root is shown at the top of the figure on the left where at least the outer part of the campanulary cover is mising. The unusually thick parenchyma shown just below this foreign root can be followed by a somewhat tenuous but undeniable connection with the more characteristic fructification structure toward the right. The largest vascular strands yet observed in *Dolerotheca* appear in this parenchymal region and one of them is illustrated in pl. 111, fig. 3. Probably the peduncle attachment was close to this point. The presumed peduncle (described later) is not attached but probably belongs to this specimen with which it is closely associated. It is located above the better preserved part of the cover and to the right of the root as shown in pl. 111, fig. 4. It is also illustrated in pl. 112, figs. 2 and 6. The tissues below the peduncle (?) are rather well preserved and one sporangium is cut longitudinally from top to bottom. The more marginal sporangia are also poorly preserved but may be observed in other sections (pl. 112, figs. 2 and 6). The margin of the campanulary cover is everywhere observable on the side of the specimen, notwithstanding spotty preservation of marginal sporangia.

There are two other *Dolerotheca* fragments in the same coal ball which appear to correspond with the type specimen. The fragments show some tissue structure, chiefly in the transverse plane, but the most valuable information they afford is in regard to the spores. Spores in the type specimen are all more or less collapsed.

In addition to the *Dolerotheca* fructification and fragments and the peduncle which probably goes with them, a fragmentary *Myeloxylon* petiole, in part well preserved, is also present in the same coal ball. The possible correlation of these on the basis of histologic structure is discussed later.

The sporangia of *D. reedana* occur in paired rows and presumably they radiate from the center of the fructification as in the other species. However, nearly all the sections available are longitudinal and the characteristics shown best by transverse sections cannot be as accurately established. The sporangia are 350–400μ in diameter and the longest sporangium seen is slightly more than 6 mm. in length; a few sporangia may be slightly longer. The longest sporangia seen are on one side of the center of the fructification and show a slight sigmoid curvature which is somewhat more pronounced in shorter sporangia near the margin.

The lysigenous tubes are clearly shown between sporangia of each radial series. They are relatively large, measuring about 400 by 100–200μ in diameter, with the shorter diameter crowded between the radially adjacent sporangia of the rows. The cells surrounding the tubes have considerably thicker walls than the ground tissue although their dimensions are similar. Possibly the breakdown of tissue inside the cavities has contributed to this appearance.

Dehiscence tissue and fibrous sclerenchyma are present and in general have the same relative position as these tissues in *D. formosa.* Spores were shed through slit-like perforations in the dehiscence tissue as in the other species. No specialized mechanism to produce dehiscence has been noted. Vascular strands are located on the middle radius of paired sporangial rows and alternate with the rows having sclerenchyma strands. In *D. reedana* the vascular strands are more prominent throughout their length, than in the other *Dolerotheca* species. Possibly a combination of fortuitous factors is more responsible than any great biological difference. The radial sections of *D. reedana* are favorable for their observation, and the tracheids of the bundles are larger than in *D. formosa.* Three of the vascular bundles are

cut transversely in some of the sections in the area near the top of the fructification and they probably are only a very short distance from the point at which the peduncle was attached. These bundles are elongated in outline, 300–400μ long and 50–90μ broad (see text fig. 15). Small tracheid
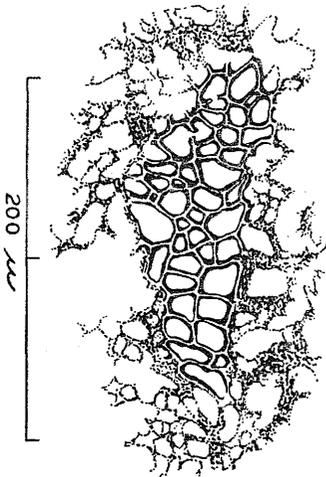

FIG. 15—*Dolerotheca reedana*, transverse section of large vascular strand from campanulary cover close to the probable attachment of peduncle. From coal ball H b 208 B (b 1).

strands branch from the lower edge of the elongate bundles and penetrate downwards between the sporangia (see pl. 111, fig. 3, and pl. 112, fig. 5). The cover layer is vascularized nearly to its periphery by small remnants of the deeply situated plate-like strands.

Histology.—The hairs on the proximal cover are more numerous than in *D. formosa* but they are not as closely set as in *D. villosa*. They range from 40 to 80μ in length and consist of from 3 to 5 cells. Most hairs are peg-like with a round tapering tip but some are clavate or capitate tipped as shown in pl. 113, figs. 1–3. Clusters of hairs cap the warty protuberances of the surface; sometimes this gives the illusory appearance that the hairs branch at the base, as for example, those at the right of pl. 113, fig. 1. Dark shrunken remnants of the cell contents are nearly always evident and sometimes dark nucleus-like bodies are present like those shown in both cells of the short capitate hair in fig. 3.

The epidermis of the campanulary cover consists of small rather thick-walled, nearly isodiametric cells with dark contents (cf. pl. 113, fig. 3). Subdermal tissues also are secretory in appearance though also more definitely parenchymatous. A slightly denser zone of less well preserved cells appears at a variable depth below the dermal layer. In general this zone appears more regular in outline than the surface, due to the presence of the verrucose protuberances of the latter. In some respects the dark layer appears as if it were an incipient pellogen although no clearly distinguished secondary tissue has been produced.

Below the dark layer is a zone of spongy parenchyma. Intercellular spaces are evident as shown in pl. 113, figs. 1 and 2. Secretory cells and resin rodlets are interspersed in the spongy parenchyma as in *D. villosa* but they are less abundant. Sclerids, isolated or in groups, also occur in the spongy tissue. Vascular strands are located near the interior of the spongy zone as shown in pl. 113, figs. 1 and 2, and may mark the internal limit of the cover layer. The tissue internal to the bundle zone of the spongy parenchyma is of the characteristic type which also surrounds the sporangia, i.e., the ground tissue of the fructification. The cover layer thus defined has a thickness of $\frac{1}{2}$–1 mm. depending on whether the end of a sporangium is adjacent (causing it to be a little thinner) or whether measurement includes the thickness of one of the external verrucosities.

The intersporangial ground tissue in *D. reedana* is generally similar to that in *D. formosa*. Secretory cells and resin rodlets are present in the ground tissue as in the other species; they are less abundant in *D. reedana* than in *D. villosa* although individually the secretory cells and rodlets are slightly larger.

As in the other two species, the tissue directly surrounding sporangia is not well preserved. Plate 113, fig. 6, shows a segment of sporangium in longitudinal section with remnants of the original sporangial wall best shown on the left side. The dark membrane is composed of two layers and apparently represents the remains of cells whose end walls have disintegrated. Probably this also indicates the mode of origin of a sporangial

membrane such as described within sporangia of *D. formosa*.

The dehiscence layer is essentially similar to that of the other species. The cells appear shorter however with less oblique end walls. Plate 113, fig. 4, shows the appearance of this tissue; a large resin rodlet of the ground parenchyma appears at the upper left of the figure.

The distal epidermis also is clearly shown in pl. 113, fig. 4. Cell contents are present and the walls appear somewhat thickened although this may have been caused by mineralization. There is no distinction between "thickening" of periclinal and anticlinal walls of the epidermis, and no close comparison can be made with the prismatic layer of cryptogamic sporangia. Nearly every cell serves as a hair base or has a strong central papilla as shown in pl. 113, fig. 5, from a section parallel to the epidermis along a dehiscence groove. Only a few hairs are visible in fig. 4 taken at right angles to a similar surface.

The dehiscence tissue merges with strands of fibrous sclerenchyma as in *D. formosa*. Relative to the size of the fructification the sclerenchyma seems a little more developed in *D. reedana*, but in the absence of good transverse sections this is not certain.

The vascular tissues of *D. reedana* can be followed more adequately than in either of the other species despite the rather fragmentary condition of the available specimens. The fragments of tissue shown in the upper left in pl. 111, fig. 4, show vascular bundles 300–400μ long and 50–90μ broad which must not be far removed from the peduncle attachment. These are also illustrated in text fig. 15, pl. 111, fig. 3, pl. 112 figs. 3 and 5, and pl. 115 fig. 9. The elongate form of these bundles is most characteristic and similar to those of *D. villosa*. Small elements centrally located in the bundles may represent protoxylem. Preservation is not good enough to show definitely the location of phloem although possibly a few phloem elements were present on both sides. Small vascular strands which penetrate the radii between sporangia are evidently given off from the lower edge of the elongate bundles as shown in pl. 112, fig. 5. The main bundles of the cover layer continue nearly to the margin of the fructification although there they are considerably diminished in size. One of the larger bundles near the center of the fructification has been twisted before mineralization so that the pitting can be observed. Part of this bundle is shown at higher magnification in pl. 112, fig. 3, to illustrate the characteristic scalariform and reticulate thickenings. The tracheids are broader than those of *D. formosa* and commonly exceed 20μ in diameter. The vascular strands between sporangia are composed of tracheids of more uniform size than those in the cover itself, and possess similar pitting as shown in pl. 112, fig. 4.

Spores or Prepollen.—The holotype of *D. reedana* contains numerous spores of the prepollen type which are nearly all collapsed. It is evident that this is not the result of petrifaction but was induced earlier, possibly even before this particular fructification was

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EXPLANATION OF PLATE 110

FIG. 1—*Dolerotheca villosa*, oblique longitudinal section of fructification about half way from the center to the margin. From coal ball 229 B 1a (12), scale of magnification indicated below figure (12.5×).

2—*D. villosa*, spore (prepollen) from peel section showing the proximal suture. The distal side of the spore has torn away from the peel. From coal ball 215 C (B 1), (172×).

3—*D. villosa*, sporangial locule full of partially collapsed spores. From coal ball 215 C (B 1), (172×).

4—*D. villosa*, section of cover layer showing close-set hairs above, secretory chambers (Sec.), and persistent septae with vascular bundles (V.B.) cut transversely. From coal ball 299 B 1a (t 6), scale of magnification indicated at right (85×).

5—*D. villosa*, section of dehiscence tissue showing epidermal hairs, sporangial pores, and secretory canals (Sec.) in tissue above. From coal ball 229 B 1a (t 23), magnification same as fig. 4.

6—*D. villosa*, oblique section across edge of dehiscence tissue showing epidermal hairs. From coal ball 229 B1 a 1 (t 6), magnification same as fig. 3 (172×).

7, 8—*D. villosa*, longitudinal sections of vascular bundles showing irregular type of scalariform elements. From coal ball 229 B 2 a (S & B 2) & (S 5), magnification same as fig. 4 (85×).

9—*D. villosa*, edge of dehiscence tissue showing epidermal hairs. From coal ball 229 B 1 a 1 (t 6), magnification same as fig. 3 (172×).
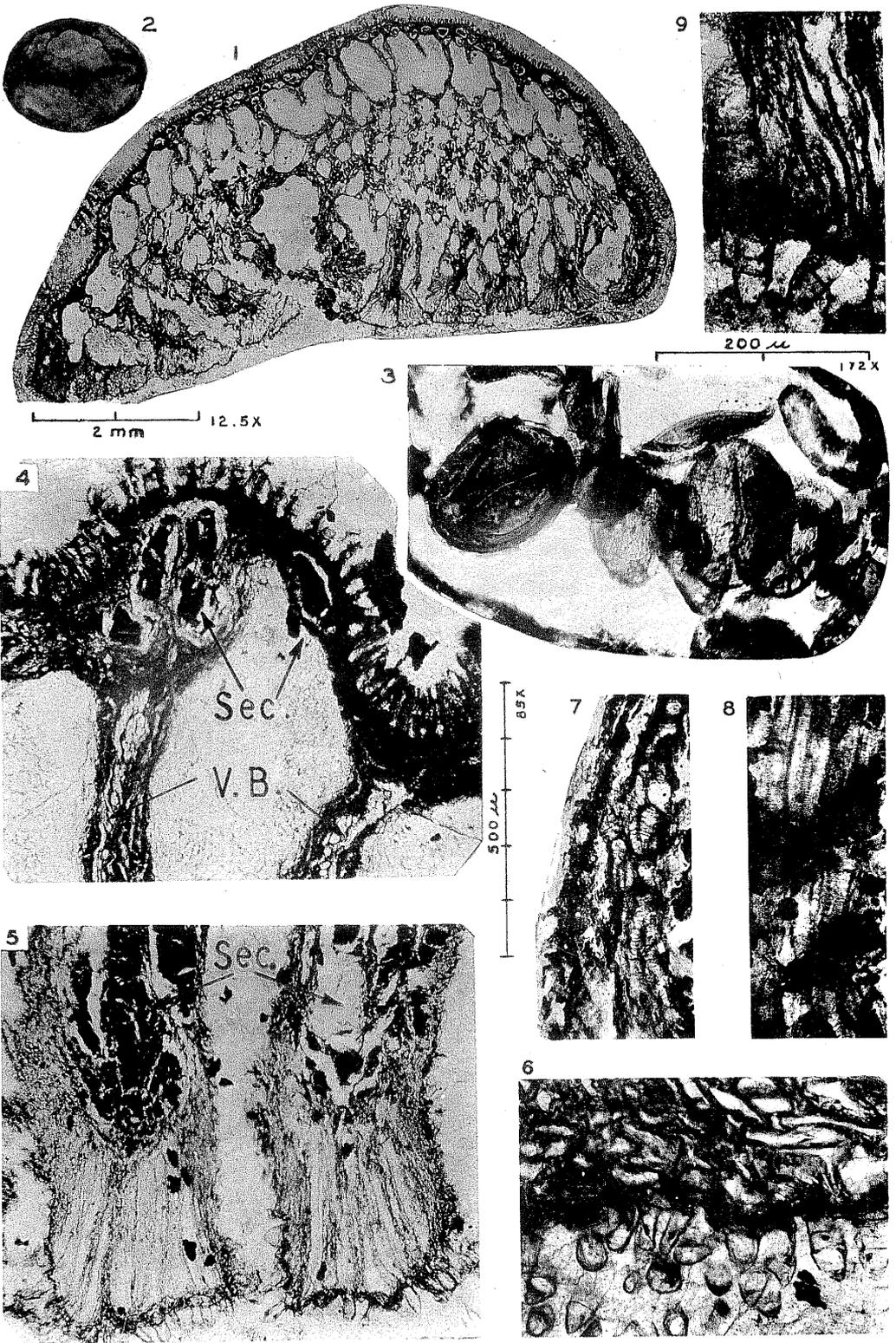
Schopf, *Dolerotheca villosa* n. sp.
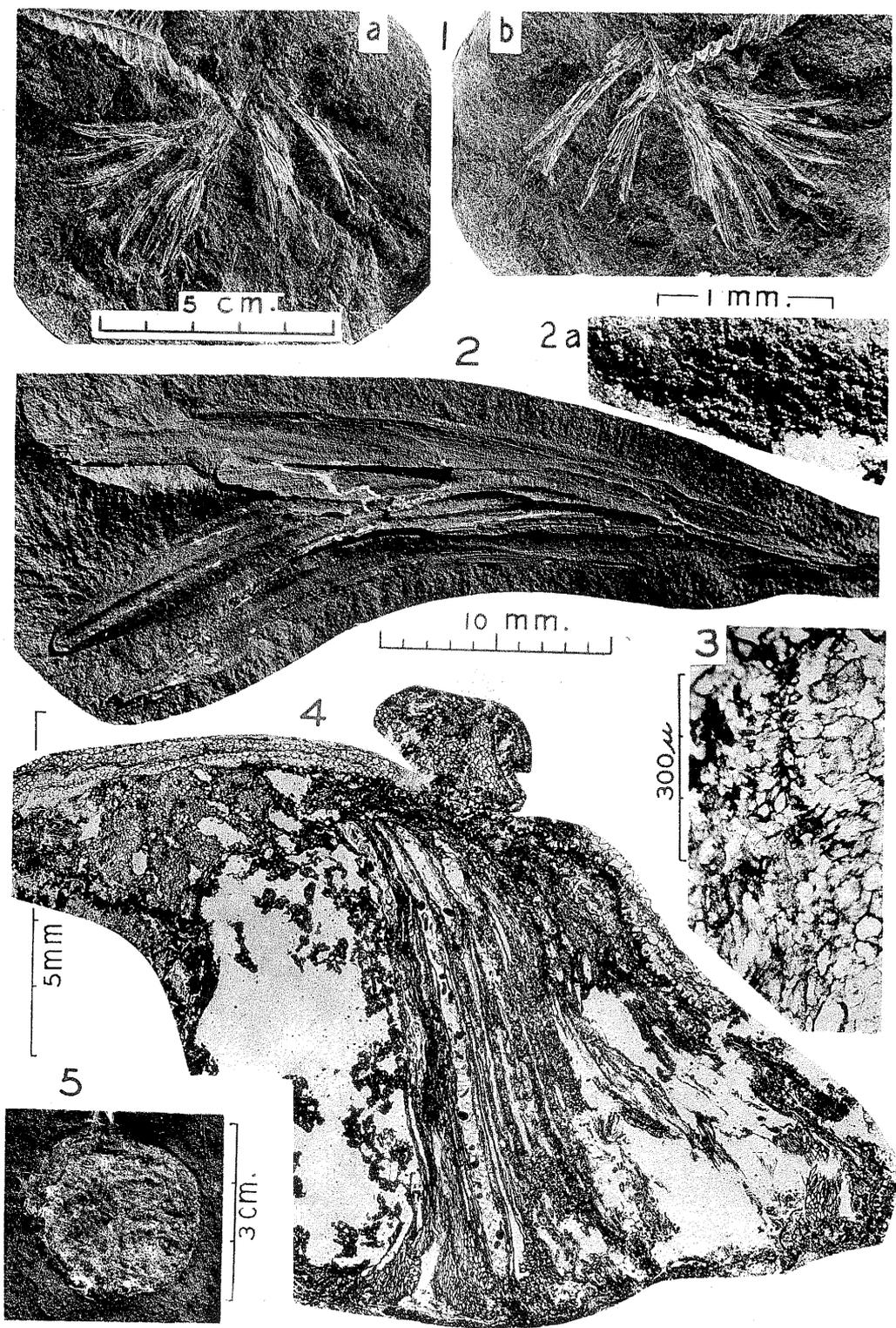
Schopf, *Dolerotheca, Codonotheca*

incorporated in the litter of the peat swamp. The two other *Dolerotheca* fragments present in the same coal ball contain normal spores which are numerous both within and outside of sporangia. The ordinary course of events may have involved general fragmentation of the fructification after the spores matured and fragmentary campanulas like these associated with the uncollapsed spores may be typical. The description of the spores has been drawn chiefly from those in the more fragmentary specimens and not from the collapsed spores in the holotype fructification shown in pl. 113, fig. 6. There can be little doubt that they are specifically identical because, aside from preservation, all the significant characters agree. Many of the normal and uncollapsed spores were isolated by breaking off a fragment containing a portion of a fructification and dissolving the calcite matrix in dilute hydrochloric acid, as was done in the case of *D. formosa*.

The spores of *D. reedana* are very similar to those of *D. formosa* and isolated specimens would be very difficult to distinguish in ordinary coal maceration residues. Individual isolated spores from both of these species would probably be classified as *Monoletes ovatus* (see Schopf, Wilson and Bentall, 1944, p. 38) if no other information was available. Slight differences in size and shape are detectable when spores are uncompressed as these are of *Dolerotheca*, but such slight differences probably cannot be relied upon to separate them if they have previously been compressed.

The prepollen spores of *D. reedana* range from 260 to 325μ long and from 165 to 250μ broad. Although in size they overlap the lower size range of *D. formosa* spores, in general they appear more broadly ovate. The proximal suture is distinct and generally marked by an angular deflection near the center as seen in pl. 114, figs. 1–4. This deflection of the proximal suture seems a trifle more pronounced than in *D. formosa*. The two distal grooves are very prominent but never appear to be split open by natural dehiscence. The spore coat is 5 to 6μ thick at the bottom of the grooves as shown in pl. 114, fig. 5 (Dist. gr.), and each groove is marked by a definite narrow furrow in the coat as shown in fig. 8 of the same plate. The thickness of the spore coat increases to 7 or 8μ outside the furrow near the axis of each groove and then thickens gradually to about 12μ on the distal umbo and to as much as 18μ on the thicker proximal region. The distinction between the proximal suture and distal grooves is evident by the fact that in cross section the suture shows a line of parting extending through the spore coat. The spore shown in median cross section in pl. 114, fig. 15, has split open along this proximal suture line.

Spore surfaces are ornamented only by very fine granulose punctation. In section the coats seem to show obscure radiating striation which may possibly be due to a type of micellar organization.

The endosporal membrane is well shown in many spores dissolved out of the calcite matrix wherever it shrunk away from the

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EXPLANATION OF PLATE 111

FIG. *1a, b*—*Codonotheca caduca*, group of four fructifications attached to a common fertile branch. The two fructifications best shown appear naturally bilaterally symmetrical. Both halves of a specimen from Mazon area, Will and Grundy Counties, Northern Illinois (Carbondale formation, Shale above Illinois No. 2 coal); Ill. State Museum Catalog No. 14326. Slightly reduced.

2—*Codonotheca caduca*, fructification showing surface striation and pubescence (punctate surface due to hair bases). *2a*, Surface of specimen at greater magnification. Specimen from Mazon area, Ill. State Museum Catalog No. 3001.

3—*Dolerotheca reedana*, transverse section of elongate bundle near top of fructification, with smaller vascular strands diverging from it below. From coal ball Hb 208 B (b 4).

4—*D. reedana*, longitudinal section of fructification, with peduncle (?) above. Spores appear as dark spots or lines in the one sporangium cut in good longitudinal alignment. From coal ball Hb 208 B (b 4).

5—*Dolerotheca* sp. Compression from specimen, surface slightly concave. From a "Mazon type" nodule from Carterville, Williamson County, Southern Illinois, from basal McLeansboro shale above the Herrin (No. 6) coal. Ill. Geol. Surv. Catalog No. S B 79, nearly natural size.

outer wall (cf. pl. 114, fig. 5). It is distinctly seen in pl. 114, figs. 14 and 15, but appears to be discontinuous. This discontinuity is probably an artifact induced when the nitrocellulose peels were being prepared. The spores of *D. reedana* thus far have not shown any of the pseudo-cellular (?) endosporal configurations which are prominent in some of the spores of *D. formosa.* If this is at all significant it probably is due to slight differences in the manner of mineralization.

Type Material.—The holotype of *D. reedana* is from Harrisburg (HB) coal ball No. 208, collected for the Illinois State Geological Survey by A. C. Noé, from Harrisburg (No. 5) coal, O'Gara No. 9 mine (open pit), located near the southeast corner of section 21, T. 9 S., R. 6 E., just south of the city of Harrisburg, in Saline County, Illinois. This coal bed lies stratigraphically somewhat above the middle of the Carbondale group of Illinois.

NOTES ON RELATED FOSSILS

The same coal ball in which *D. reedana* was discovered contains a *Myeloxylon* petiole and a small poorly preserved structure which probably is the peduncle of the *Dolerotheca* fructification. This presumed peduncle is described first and evidence bearing on its possible correlation with the species of *Myeloxylon* follows. An impression specimen of *Dolerotheca* preserved in an ironstone concretion is described and discussed and some recent observations on the Whittleseyinean genus *Codonotheca* are presented.

DOLEROTHECA REEDANA peduncle (?)
Plate 111, figure 4; plate 112, figures 1, 2, 6; plate 115, figures 6–8; text figure 16

This is a small (about 2 mm. in diameter) originally triangular (?) structure which extends about 5 or 6 mm. along the top of the *D. reedana* holotype. It is badly fragmented for most of its length so that it cannot be described very satisfactorily. Although it occurs in the closest possible association with this *Dolerotheca* specimen, there is no actual proof of its immediate connection. Its suggested function as the peduncle of *Dolerotheca* is chiefly based on

the structure of epidermal hairs which are well preserved, in part, and correspond closely with those of the dorsal cover of the *Dolerotheca* fructification.

The close association of this peduncular structure is shown in pl. 111, fig. 4 and pl. 112, figs. 2 and 6. A line diagram of the peduncle, text fig. 16, shows its epidermal hairs
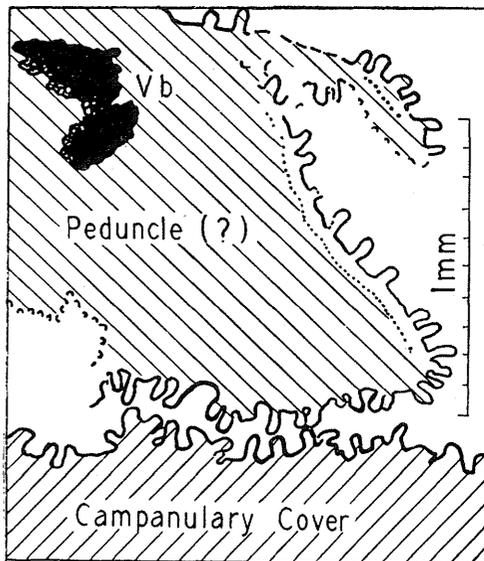

Fig. *16*—Sector of *Dolerotheca reedana* campanulum and probable peduncle, showing the intimacy of association in coal ball H b 208 B. Photo tracing from section (b 6).

to be nearly interlocking with those of the campanulary cover of the fructification below, and their similarity is obvious. Another more fragmented portion which shows the hairs well is illustrated in pl. 112, fig. 1, and at higher magnification in pl. 115, fig. 6. The description of hairs of the dorsal cover layer of *D. reedana* applies equally well to these. The only difference noted is in their arrangement on the epidermis. The hairs of the peduncle are not situated on tubercular outgrowths as they commonly are on the fructification. Some are very close together but in general they are fewer and less closely spaced.

The epidermis of the peduncle is quite distinct and shows no evidence of any irregular cell divisions. The epidermal cells contain

dark contents but are not obscure on this account, as are many of the dorsal epidermal cells of the campanulas. There is no indication of any sclerotic tissues in the peduncle. The ground tissue is parenchymatous and includes a few resin rodlets as shown in pl. 112, fig. 1 (R) and pl. 115, fig. 6.

It has not been possible to ascertain the nature of the entire vascular complement of this specimen because at least half of it is poorly preserved throughout its length. The vascular bundles differ considerably in form from those in the proximal part of the *Dolerotheca* fructification as may be seen by comparing fig. 8 (peduncle) and fig. 9 (fructification) shown at the same magnification on plate 115. There is considerable similarity in size of the elements of both and in the pitting. Vascular bundles of both are chiefly composed of scalariform tracheids. The peduncle bundles seem probably mesarc and may be concentric, but phloem is too obscure to be confidently identified. The outline of the most evident bundles is shown in text fig. 16 (V.B.). Perhaps the chief vascular bundle in pl. 115, fig. 8, and other figures may be in process of dichotomizing, but if so, the fission requires a distance of several millimeters for completion. The pattern of vascularization of the petiole is not clear because two or possibly three other bundles which belonged to it are disconnected and variously distorted. One of these appears at the lower left in pl. 115, fig. 8. Because of this distortion it is not certain that this peduncle was essentially radial in its symmetry rather than dorso-ventral.

The close agreement between epidermal hairs of *D. reedana* and this peduncle, the great similarity of elements of the vascular bundles and the conjunction of other factors, although individually merely suggestive, when taken together furnish rather convincing indication that the peduncle pertains to that species.

MYELOXYLON, cf. M. AMERICANUM
(Hoskins)[7]

Plate 115, figures 1–5

A segment of a petiole probably referable to *Myeloxylon americanum* is present in the

[7] Originally described as *Angiospermophyton americanum* (Bot. Gaz. vol. 75, p. 390, 1923),

same coal ball that contains the holotype of *D. reedana*. Its identification with Hoskins' species is not immediately evident by comparison with figures published with the original description. However, comparison with the original slides showed that *M. americanum* is more variable than suggested by Hoskins and that the specimen under consideration agrees with it in many features. Some of Hoskins' slides show a heavy zone of radially elongated subdermal sclerenchyma extending nearly continuously around the margin on one side. In other places, these sclerenchyma strands are tangentially elongated and less prominent. Adjacent to the thick marginal sclerenchyma, the sclerotic "caps" accompanying vascular bundles and secretory canals are very heavy, but they become progressively thinner toward the center of the petiole where there is almost no sclerotic bundle sheath. Sclerotic caps of moderate development are irregular in marginal outline as seen in transverse section. Resin rodlets are fairly numerous and possess no distinct epithelial layer of cells. Cells of varying size, averaging slightly smaller than those of the ground parenchyma, enclose the secretory ducts. Thin tangentially elongated epithelial cells such as those present in the Nashville myeloxyla associated with *Medullosa distelica* (cf. Schopf, 1939) do not occur. Petiolar secretory canals in Nashville specimens are all about the same diameter. In *Myeloxylon americanum* there is a wide variation in the size of the canals, many of them are large and contain typical resin rodlets but others are much smaller and some are similar in size to large parenchyma cells of the ground tissue. In fact, numerous evenly distributed parenchyma cells also appear to have secretory contents. The gradation seems to be complete between ducts of the two extremes in size.

The *Myeloxylon* fragment in the *Dolerotheca* nodule from Harrisburg does not have the extremely heavy sclerenchyma present

this species is referable to *Myeloxylon*. The author has personally consulted the types which are part of the collection of the Illinois Geological Survey, and verified the opinion originally expressed by Seward (1923). The species seems to be well represented in the Harrisburg coal balls.

in parts of the type specimen of *M. americanum*. It appears to agree in most particulars with less sclerotic portions of that species, however, and probably cannot be distinguished from it.

One small area of the specimen associated with *D. reedana* seems to lack subdermal sclerotic tissues entirely, even in the proximity of marginal secretory canals. A portion of this area is shown in pl. 115, fig. 1. The marginal vascular bundles all possess a definite sclerotic bundle sheath, however, and the one shown in pl. 115, fig. 2, is typical. The phloem of this bundle (Ph) is excellently preserved and unusual in this respect. Generally phloem tissue is lacking as in the bundle shown in plate 115, fig. 3. The presence of a secretory duct adjacent to the xylem and enclosed by the sclerotic bundle sheath in fig. 3 is exceptional. Protoxylem as identified by small tracheids is chiefly concentrated next to the phloem as in the type of *M. americanum*. Some small tracheids also occur which are not in proximity of the phloem but it is questionable whether these are actually protoxylem elements. They may be merely small cells of the metaxylem which were late in development and failed to enlarge fully. It is also possible that they represent only the tapering ends of normal metaxylem elements. The large metaxylem elements shown in pl. 115, fig. 3, are gathered in two groups, possibly preparatory to bifurcation.

A large characteristic secretory canal and resin rodlet with sclerotic tissues somewhat separated is shown in pl. 115, fig. 4. Two smaller canals with less sclerotic development but situated in about the same relative position in the petiole are shown in fig. 5.

BIOLOGIC CORRELATION OF THE PEDUNCLE(?) OF DOLEROTHECA REEDANA AND MYELOXYLON AMERICANUM

The evidence for concluding that the hirsute peduncle described above belongs to *D. reedana* has been presented. It is desirable also to consider further the histologic evidence which supports the correlation of this structure with *Myeloxylon*, since some such relationship may fairly be presumed to have existed.

Although it seems probable that *Medullosa*, *Myeloxylon*, *Dolerotheca* and others are correlative genera in Pennsylvanian strata (and possibly through most of this system) there is as yet no evidence to show how, i.e., on what particular part of the plants, the male fructifications were borne. They may have been attached to the ultimate rachides of an *Alethopteris* type frond. Some evidence now indicates that seeds were borne in this manner (Halle, 1927, Arnold, 1937). It is equally plausible that the male fructifications may have been borne on special fertile branches somewhat as suggested by the specimen of *Codonotheca* illustrated by Darrah (1938) and by the specimen shown in Pl. 111, fig. 1 (no. 14326 of the Langford collection in the Illinois State Museum, Springfield). A similar fruiting habit has recently been described for *Lacoea seriata* by Read (1946) and a comparable occurrence is shown by *Goldenbergia glomerata* (Halle 1933). It is also conceivable that the male fructification was attached directly to the main axis, arising in the axil of a leaf base near the tip of the stem, or, if the fruit bud was dormant for a time, its position might have been farther down the trunk. Un-

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EXPLANATION OF PLATE 112

Fig. *1*—Peduncle (?) probably of *Dolerotheca reedana*, showing resin rodlet (R) and epidermal hairs. From coal ball Hb A (t 4).

    2—*Dolerotheca reedana*, longitudinal section at margin of fructification with peduncle (?) above. Distal (dehiscence) surface is irregular because the section is obliquely transverse to the dehiscence grooves. From coal ball Hb 208 B (t 3).

    3—*D. reedana*, longitudinal section of vascular bundle near top of fructification showing irregularly reticulated and scalariform elements. From coal ball Hb 208 B (B 4).

    4—*D. reedana*, longitudinal section of vascular strand near margin of fructification. From coal ball Hb 208 B (b 2).

    5—*D. reedana*, transverse section of vascular bundle near top of fructification showing small strands (v) given off below. From coal ball Hb 208 (b 2), magnification same as fig. 4.

    6—*D. reedana*, longitudinal section at margin of fructification with peduncle above. From coal ball Hb 208 B (b 10).
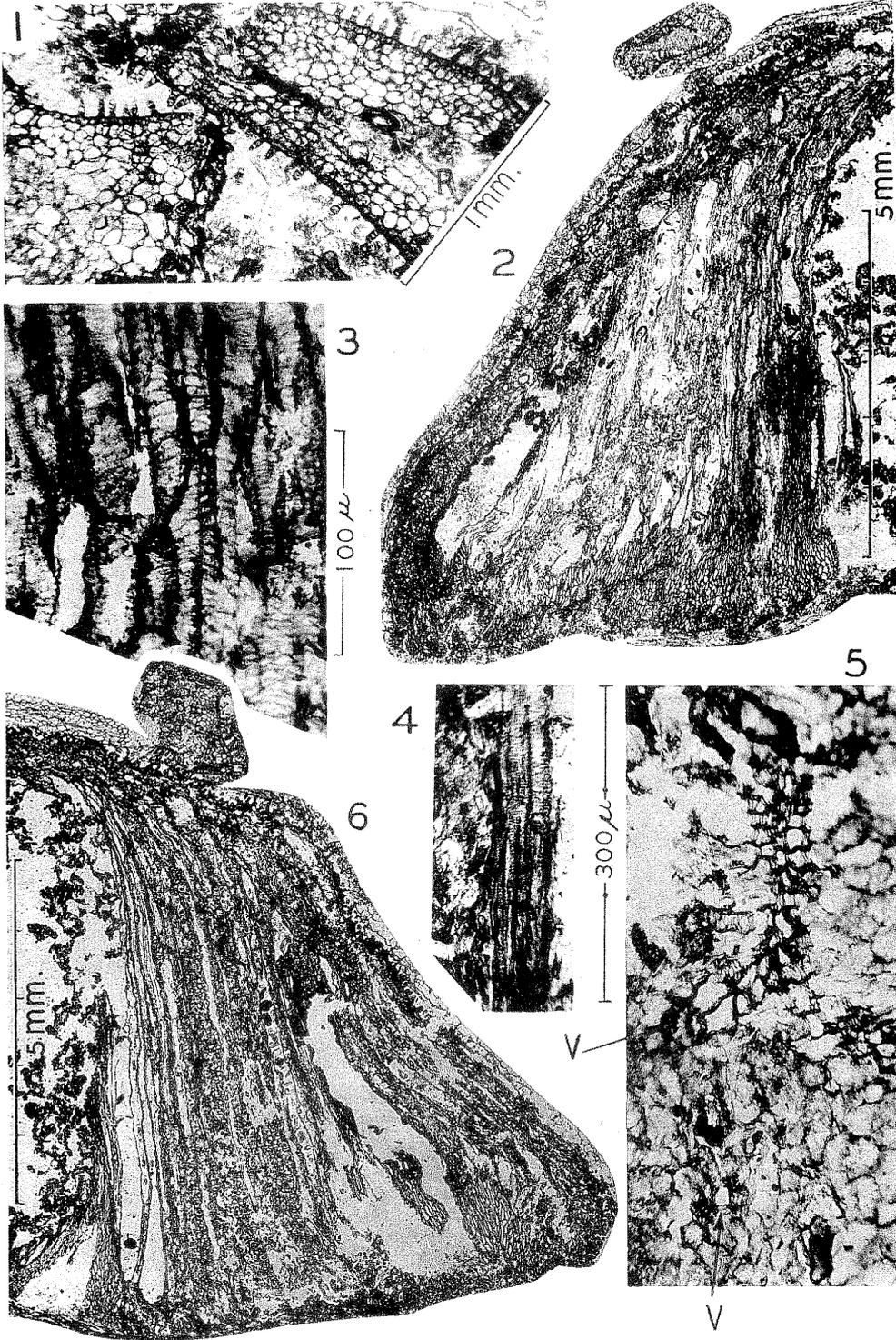
Schopf, *Dolerotheca reedana* n.sp.
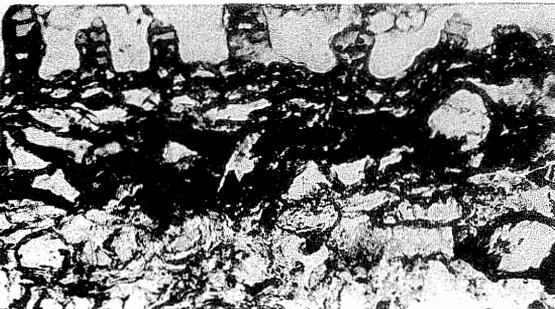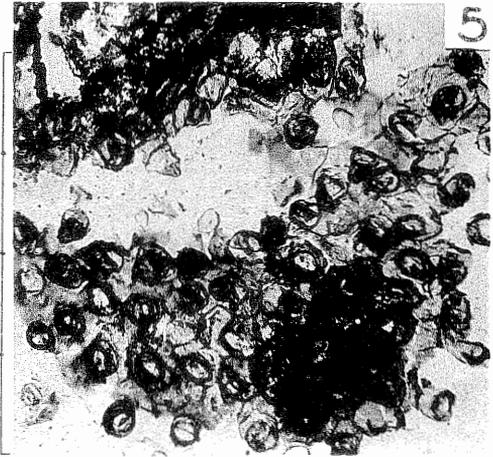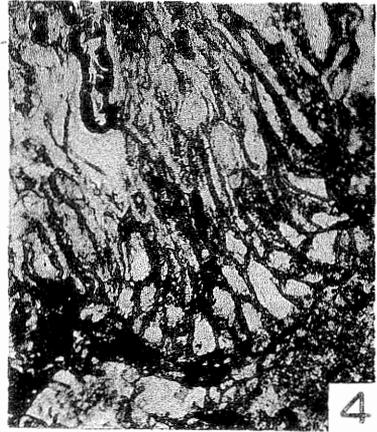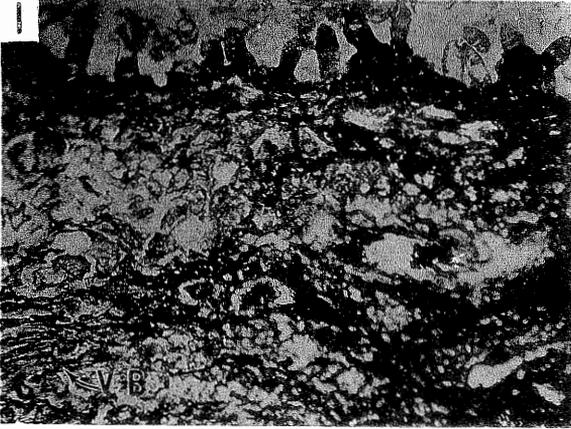
Schopf, *Dolerotheca reedana* n.sp

fortunately there is no evidence directly bearing on the condition in *Dolerotheca.*

The extent of agreement or disagreement between structures of the *Dolerotheca* peduncle and large *Myeloxylon* petioles possibly should not be emphasized. There is no known reason to assume that these structures should be very similar, even if they were parts of the same plant. They are functionally diverse organs of long standing no matter what the structural similarities or dissimilarities may be.

Plate 115, figures 1–7, shows portions of the *D. reedana* peduncle (figs. 6–7) and of *Myeloxylon* cf. *M. americanum* (figs. 1–5) at the same magnification for comparison. *M. americanum* has no epidermal hairs so far as known although associated and probably correlated pinnules of *Alethopteris* are hirsute on the lower surface and some hairs are also present on minor divisions of the rachis. The foliar hairs are more slender and less glandular than these of the peduncle and present no particularly convincing points of similarity although all of them appear to be uniseriate.

Aside from the absence of hairs the *Myeloxylon* epidermis agrees fairly well with that of the peduncle. The epidermal cells of the petiole are darker due to greater deposits of secretory (?) material than in the peduncle, as may be seen by comparing figs. 1 and 6 of Pl. 115. The petiole also has a distinct cuticle which is separated slightly from epidermal cells in the portion shown in fig. 1. These epidermal differences might be disregarded as due to differences in ontogenetic age. The peduncle probably grew quickly and persisted only a short time whereas it seems likely that the large petioles were at least as permanent on these plants as the petioles are in living cycads.

Plate 115, figure 1 shows an area where the subdermal sclerenchyma is essentially absent. This condition is probably not unusual in *Myeloxylon.* It seems clear that the development of sclerenchyma is variable to a considerable extent and that much of the variation has not yet been systematically described. The normal variation due to relative position in the petiole, i.e., whether ultimate, penultimate, or main divisions of the rachis, has not been accurately ascertained for most species and until this is done specific identifications of *Myeloxylon* specimens will be of doubtful value except where precise homologies can be established for comparison. Thus it is not entirely clear what emphasis should be placed on the very subordinate development of sclerenchyma in the small section represented in fig. 1 except that it is rather comparable in appearance to the subdermal tissue of the *Dolerotheca* peduncle.

Although the vascular strands of the fructification and peduncle of *Dolerotheca* offer some strong points for comparison, neither shows much similarity to the collateral bundles of the *Myeloxylon.* The peduncle vascular strand shows no clear distinction between protoxylem and metaxylem as in the petiolar bundles and there are considerable differences in the size of elements (compare fig. 7 with figs. 2 and 3 of pl. 115 which are reproduced at the same magnification). The largest cells of the

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EXPLANATION OF PLATE 113

Fig. 1—*Dolerotheca reedana,* section of cover layer showing hairs mounted on small verrucose protuberances. Note position of vascular bundle (V. B.). From coal ball Hb 208 B (b 4).

2—*D. reedana,* section similar to fig. 1 but somewhat better preserved. Note the numerous secretory cells (R. R.) below and in the vicinity of the vascular bundle (V. B.). From coal ball Hb 208 A (t 4).

3—*D. reedana,* section of outer part of cover layer showing hairs, one of which is capitate, epidermis and dark incipient phellogen (?) layer below. From coal ball Hb 208 B (t 3).

4—*D. reedana,* section of lobe of dehiscence tissue showing epidermis and hairs, secretory canals in tissue above. From coal ball Hb 208 b (B 18), magnification same as fig. 1.

5—*D. reedana,* section in part parallel to lobe of dehiscence tissue showing number and arrangement of epidermal hairs. From coal ball Hb 208 C' (t 2).

6—*D. reedana,* section of a sporangium containing collapsed spores. The row of cells bounding the sporangial locule on the left is more delicate than the rest of the intersporangial tissue and may indicate the nature of the sporangial membrane seen in *D. formosa.* From coal ball Hb 208 B (B 18).

peduncle bundles are about the size of protoxylem elements in the *Myeloxylon*. Whether small ultimate divisions of the rachis would show more similarity to the peduncle in vascularization cannot be stated now although it is known that the vascular elements are smaller in the ultimate petiolar branches.

The peduncle of *Dolerotheca* is similar to the *Myeloxylon* petiole in that both possess similar secretory canals. In fig. 6, a resin rodlet is situated in the ground parenchyma similar to the one shown in fig. 1. Although they are fewer in the peduncle both have very similar ground parenchyma.

Such similarities probably are insufficient evidence for biologic correlation, but the differences also are inconclusive because dissimilar organs are being compared. A more pertinent comparison might be possible between ultimate divisions of the *Myeloxylon* rachis and the peduncle.

DOLEROTHECA IMPRESSION

An interesting specimen of *Dolerotheca* was collected by the writer in 1938 from near Carterville, Williamson County, Illinois. It was found upon splitting one of the ironstone concretions of the Mazon Creek type which occur there in grey shale overlying the Herrin (No. 6) coal. This coal bed is accepted arbitrarily as the top member of the Carbondale formation, hence the fossil is from the lowermost McLeansboro. Although plant preservation is similar, this zone is considerably younger than the classical one at Mazon Creek. Anatomical features being absent, it seems inadvisable now to apply a specific designation to this specimen although it probably is distinct from the other species. The chief point worthy of note is the generic identification of the form, a point which seems reasonably established in spite of the differences in preservation existing between this and the other *Dolerotheca* specimens. This occurrence gives some basis for hope that the geologic record of *Dolerotheca* and allied genera will be further augmented by compression and impression specimens. Coal ball petrifactions can be counted on to provide a basis for anatomical interpretation but such specimens are relatively scarce and, therefore, usually do not constitute a main source for information

desired in stratigraphic problems. This additional specimen of *Dolerotheca* suggests that the genus may not be as rare in the Pennsylvanian beds of America as the scant literature indicates.

Description of the three American species of *Dolerotheca* has shown that the vascular strands are located rather deeply within the dorsal cover layer. This may well afford a good basis for distinguishing *Dolerotheca* from seemingly perfoliate cyclopterid leaf impressions which may superficially correspond in outline. The cyclopterids show venation clearly whereas it may be doubted that *Dolerotheca* ever does (also see Florin, 1926). An obscure radial alignment of sporangial impressions appears to be most characteristic of impressions and compression specimens of *Dolerotheca* (cf. Halle, 1933, pl. 9, figs. 5 and 6).

DOLEROTHECA sp.
Plate 111, figure 5; plate 114, figure 10

Fructification nearly circular in outline, about 28 mm. in diameter; the campanulary cover is indicated by the rim 2–3 mm. wide around the margin. Sporangial rows are shown by more or less definite protuberances radiating from center. Prepollen grains are large, about 450μ in their longest dimension and about 390μ in the shortest; proximal suture and distal grooves of the prepollen are evident; the prepollen coat is finely granulose. Anatomical details unknown.

The specimen has suffered considerable compression and most of its original carbonaceous content is gone. The cavity formerly occupied by compressed tissues has been partly replaced by a friable film of calcite and kaolinite in which some carbonaceous fragments still are present (pl. 111, fig. 5). A few prepollen grains are present in this friable semi-mineralized layer and may be observed under a Greenough-type microscope. They show no definite arrangement to indicate the form of sporangia and it is evident that they had mostly been shed before fossilization. One of the spores remaining is shown in pl. 114, fig. 10. Twenty or more spores, all of the same kind, have been observed and this seems sufficient evidence to indicate that these examples are not foreign to the specimen.

The characteristic spores and the nearly

circular form of the fructification with no indication of lobes or appendages make the generic identification of this fossil certain. It may, however, be distinct from other species because its spores are somewhat larger and more broadly oval. In size the fructification is intermediate between *D. reedana* and *D. formosa.* With the exception of its larger spores, this form seems intermediate between these well characterized species.

Other compression specimens which may be congeneric are those described as *Daubreeia* (in part) (White, 1903, p. 107; Sellards, 1908, pp. 430–433),[8] *Doleropteris pennsylvanicum* (Dawson 1890, p. 7), and possibly, judging from White's (1903, p. 107) discussion, also the *Plinthiotheca angularis* of Lesquereux. It should be stressed that the presence of prepollen or other proof of sporogenous nature is of critical importance in identifying any of these with *Dolerotheca.* Thus far this has not been shown, but it may be if reinvestigation is undertaken using modern improved methods. However, the specimen illustrated as *Daubreeia* (?) by Sellards (1908) in pl. 56, fig. 5 of Vol. 9 of the Kansas Survey is particularly suggestive of *Dolerotheca.* It is about $21\frac{1}{2}$ by 25 mm. in diameter and seems to show radiating sporangial rows with additional rows intercalated toward the margin. It was collected from the LeRoy shale near Blue Mound in Kansas.

CODONOTHECA

Codonotheca is one of the genera included by Halle in the Whittleseyineae. It has been definitely identified chiefly in nodules from the Mazon Creek area in Grundy and Will Counties of Northern Illinois. Some observations have been made on a few specimens which are of interest in the present connection.

CODONOTHECA CADUCA Sellards
Plate 111, figures 1, 2; plate 114, figures 11-13

The specimens are all much flattened. In part this may be attributed to pressure

[8] Specimens of *Daubreeia* in the U. S. National Museum, including three of those studied and illustrated by Sellards, show clearly that they are not fertile organs comparable to the *Dolerotheca campanulas.* They appear, at least superficially, more like *Dolerophyllum* (see Florin, 1925).

resulting from burial but the author believes that a good deal of the asymmetry in cross section is original, since the Mazon nodules often preserve surficial form without much distortion. According to this interpretation the *Codonotheca* fructification consists of a single loosely paired row of tubular sporangia. Free ends of the sporangia penetrate the matrix so that it is difficult to accurately ascertain the number but it seems there were commonly six and may sometimes have been eight in all. Sellards (1903) and subsequent authors have all considered the *Codonotheca* fructification to be radially symmetrical. If *Codonotheca* and other Whittleseyineans were bilaterally instead of radially symmetrical and composed essentially of a single double series of tubular sporangia, they would seem to show greater correspondence with the structure of *Dolerotheca.*

The author is not yet prepared to accept fully Halle's conclusion as to the uniseriate whorled arrangement of sporangia and the hollow interior of the Whittleseyinean forms. The lamina-like form of *Whittleseya* was accepted without controversy by students of fossil plants for many years and further evidence is needed before the view long held is completely discarded. A bilateral interpretation of *Codonotheca* at any rate, would seem equally acceptable.

A further character of *Codonotheca* which seems to have escaped particular notice is the pubescence of the outer surfaces. Sellards (1903) mentioned longitudinal striae and weaker cross lines which no doubt represent the impressions of epidermal cells and in the description of his fig. 15, pl. 8, he stated that fig. 17 shows the "minutely roughened or pitted surface". The pits mentioned are acutally hair bases which appear to be more or less glandular and closely set. In distribution at least, they are similar to those of *Goldenbergia* and *Dolerotheca.* It is not unusual for the ironstone matrix of Mazon concretions to preserve such surface features faithfully and the specimen shown at slight enlargement in Pl. 111, fig. 2 shows the "punctate" surface characteristically. In fig. 2a of this plate, a densely pitted surface of the same specimen is shown at greater magnification. The bases of hairs can be seen penetrating the matrix surrounding *Codonotheca* but the shape of

the hair itself is not commonly exhibited. In a few instances they appear relatively long and tapering; more so than the hairs of *Goldenbergia* shown by Halle (1933, pl. 2, figs. 18-19). The *Codonotheca* surfaces are best observed by reflected illumination with the Greenough type microscope when the specimens are flooded with xylol. The author regards the occurrence of these hairs as further confirmation of Halle's assignment of *Codonotheca* to the Whittleseyineae, and as additional evidence linking the Dolerothecan and Whittleseyinean subtribes.

The recognition of a definite pubescence on *Codonotheca* is useful and aids in the identification of fragmentary or otherwise questionable specimens. For example, examination of the originals of illustrations labeled *Codonotheca cadua* in pl. 43, figs. 1 and 2, of Bull. 52 of the Illinois Survey are shown by this criterion to be wrongly identified. The original of fig. 1 is more likely a tuft of lycopod leaves similar to the *Lepidodendron rigens* of Lesquereux. That shown in fig. 2 is probably a whorl of inflate *Annularia* leaves which were originally deposited somewhat distorted from their usual position. On

the other hand the specimen in fig. 3 of the same plate shows the characteristic pubescence near the basal part and is no doubt correctly identified even though no spores are visible in the three sporangia exposed. Erroneous identification of specimens as *Codonotheca* is by no means rare in collections from the Mazon beds of northern Illinois.

*Spores or Prepollen.*—The folds shown on spores of *Codonotheca caduca* by Darrah, and thought by him to be similar to the distal grooves and umbo of other Dolerosporeae, were considered by Florin (1937) to be a "single long and broad germinal furrow." According to the present author's interpretation this "germinal furrow" is only a chance structure caused by incidental collapse or folding. Only one spore out of the fifteen or more illustrated by Darrah shows folds definitely enough to support the possibility of distal specialization. Since this one spore appears to be unique even in the original figures, the writer is inclined to question whether it has any special significance. Spores of *Codonotheca* are illustrated in pl. 114, figs. 11-13 and these show nothing that can be interpreted either as distal


EXPLANATION OF PLATE 114

Magnification same for figs. *1-13*, scale indicated.

FIG. *1*—*Dolerotheca reedana*, spore (prepollen) showing strongly bent proximal suture. Spore isolated from fructification by solution of calcite matrix in hydrochloric acid. From coal ball Hb 208.

2—*D. reedana*, isolated spore showing proximal suture. From coal ball Hb 208.

3—*D. reedana*, isolated spore showing very moderate deflexion of proximal suture. From coal ball Hb 208.

4—*D. reedana*, isolated spore similar to fig. *2*, proximal suture appears under different illumination due to the presence of a bubble of CO_2 inside the spore coat.

5—*D. reedana*, isolated spore showing endosporal membrane in plane of focus. From coal ball Hb 208.

6, 7—*D. reedana*, spores showing umbo and distal grooves. From coal ball Hb 208.

8—*D. reedana*, spore tilted to one side showing thin area at bottom of one of the distal grooves. From coal ball Hb 208.

9—*D. reedana*, spore photographed to show proximal suture (*9a*) and at a lower plane of focus to show distal grooves (*9b*). From coal ball Hb 208.

10—*Dolerotheca* sp., large spore from compression specimen shown in Pl. 111 fig. *5*. P.S.—Proximal suture, D. gr.—distal grooves. Ill. Geol. Survey Catalog No. S B 79.

11-13—*Codonotheca caduca*, spores showing proximal suture only. Photographed at the same magnification and other conditions as those shown in figs. *1-10*. From specimen from Mazon area, Ill. Geol. Surv. Catalog No. S B 1006.

14—*Dolerotheca reedana*, peel section including (above) the tip of one spore cut transversely, distal side up, and spore sectioned longitudinally (below), one of the distal grooves (Dist.) cut obliquely at the right. From coal ball Hb 208 D (B 1), magnification indicated above figure.

15—*D. reedana*, median transverse section of spore showing distal umbo and grooves above and spore coat split open below along the proximal suture. Dist. gr.—distal groove; Exo—exospore layer; End—endosporal membrane; Prox.—proximal side. From coal ball Hb 208 D (B 1), magnification same as fig. *14*.
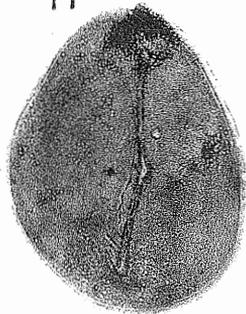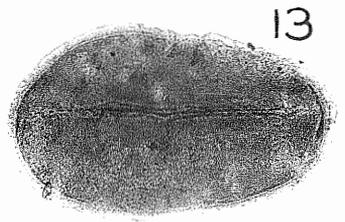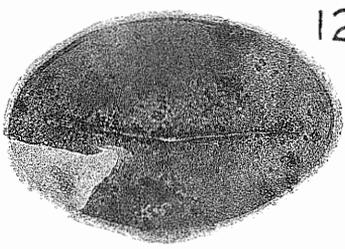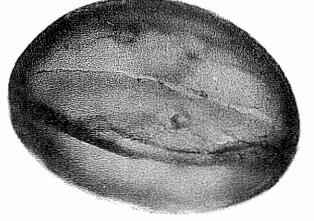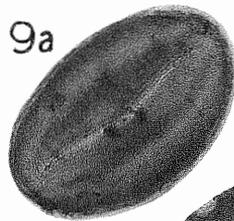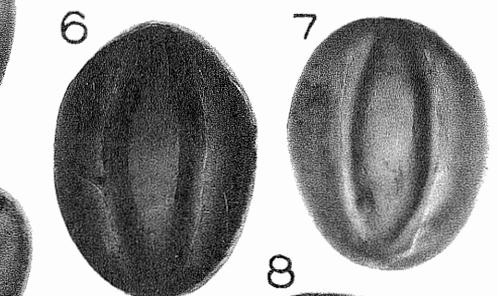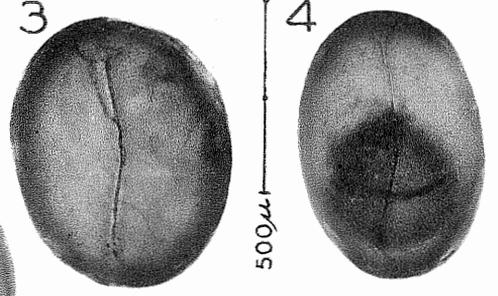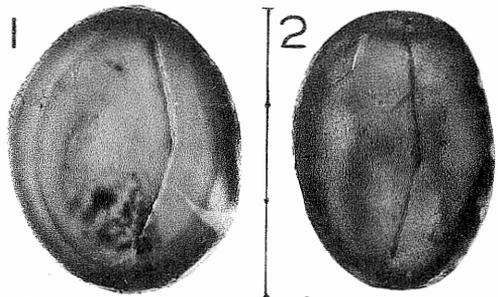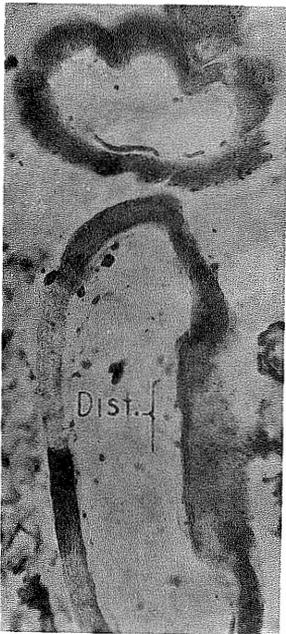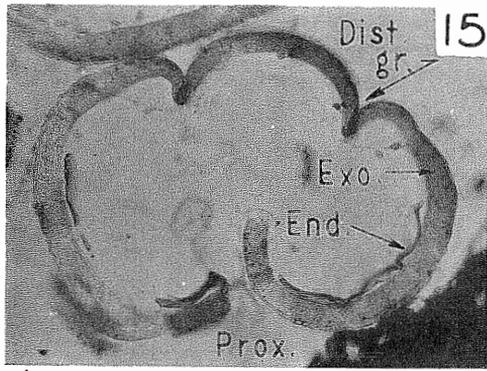
Schopf, *Dolerotheca, Codonotheca* spores
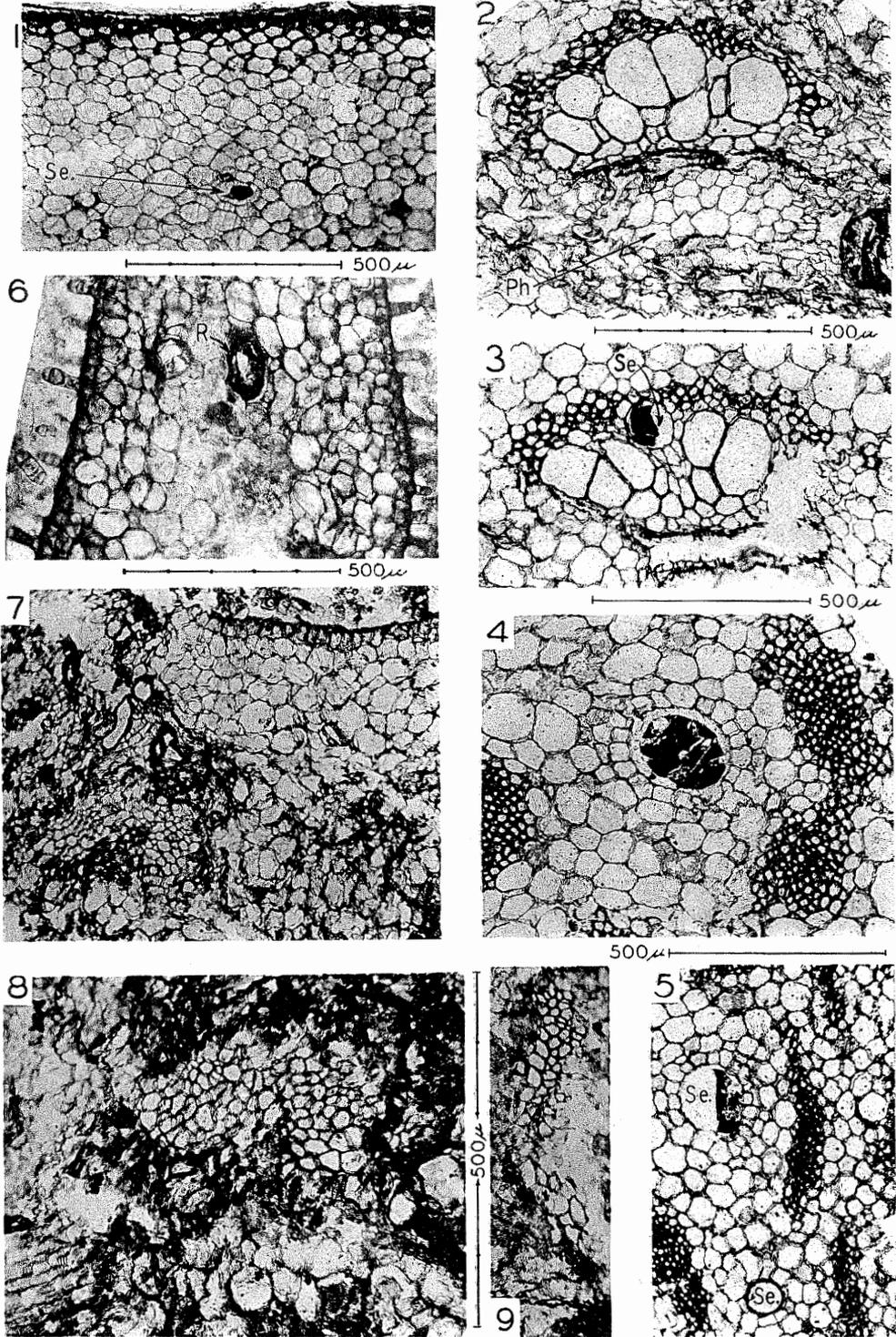
Schopf, *Myeloxylon americanum* and *Dolerotheca peduncle* (?)

grooves or a "germinal furrow." In these spores the proximal suture and granulose surface texture are the only distinctive features. Their shape and size correspond with other members of this pteridosperm alliance. It is true that incidental folds sometimes are present, but, according to the writer's interpretation, *Codonotheca* spores lack any discernible vestige of distal apparatus. If specimens occur which have distal specialization they probably should not be identified with Sellards' *Codonotheca caduca* because his description obviously is accurate for those of the Mazon specimens this writer has examined. The similarity of material examined in connection with the present study to Sellards' original description shows that *C. caduca* is an accurately defined species.

PHYLOGENETIC CONNECTIONS

Up to the present time *Dolerotheca* has occupied a somewhat isolated systematic position because it was not known in sufficient detail to permit accurate comparison. It is hoped this deficiency has been largely overcome by the material that has been described above. In the paragraphs below the writer suggests a relationship for *Dolerotheca* with other pteridosperms. Unless one adopts the view that the seed habit associated with pteridosperms arose spontaneously in several independent phyletic lines, and therefore that the group as known today is a highly polyphyletic and unnatural one,

some hypothesis of mutual relationship is called for, even though it may be held tentatively and by no means regarded as proved in detail.

The writer believes there is ample evidence to indicate the lygenopterid and meddullosan pteridosperms are monophyletically related, that is, derived ancestrally from a single common stock, and the following discussion is based on this assumption. These two groups include the pteridosperms best known and they constitute the nuclear material of reference for the pteridosperm group as a whole in the consideration of all modern authors.

Since 1930, Zimmerman's telomic concept of organization of higher plants has been used comparatively because of its simplicity, and because of its recognition of fertile organs as fundamental units in the make-up of plants, a view that has long been advocated by F. O. Bower and others concerned with fundamental interpretation of botany. Complex fructifications may arise by the aggregation of fertile telomic units so that the result is a synangium in the strict sense. Probably they also may arise by enlargement and elaboration of a single fertile telome. The structure of the *Dolerotheca* campanulum seems to be more readily explained by the latter evolutionary process, and the sort of elaboration it prominently displays is regarded by the writer as most easily explained by a process of septation.

Any elaborated fructification of this type

EXPLANATION OF PLATE 115

Magnification same for figs. *1–7*, scales indicated.

FIG. *1*—*Myeloxylon* cf. *M. americanum*, non-sclerotic margin of petiole. Note cuticle and secretory duct (Se). From coal ball Hb 208 B (B 18).

2—*M.* cf. *M. americanum*, vascular bundle with sclerenchyma sheath moderately developed. Note phloem (Ph.) which is well preserved. From coal ball Hb 208 C (t 2).

3—Bundle similar to that in fig. *2* but lacking the preservation of phloem—a secretory duct (Se) is located next to the xylem within the sclerotic sheath.

4—*M.* cf. *M. americanum*, resin rodlet and sclerenchyma strands moderately developed. From coal ball Hb 208 C (t 2).

5—*M.* cf. *M. americanum*, area near margin of petiole showing a moderate development of sclerenchyma strands and small secretory canals (Se). From coal ball Hb 208 C (t 2)

6—Peduncle (?) probably of *Dolerotheca reedana*, for comparison with fig. *1*. R—hollow resin rodlet. From coal ball Hb 208 A (t 4).

7—Peduncle (?) probably of *D. reedana*, showing vascular bundles. From coal ball Hb 208 B (B 4)

8—Vascular bundles shown in fig. *7*, at higher magnification. Scale indicated at right.

9—*D. reedana*, bundle from near top of fructification for comparison with fig. *8*. From coal ball Hb 208 B (B 2), magnification same as fig. *8*.

derived by a process of telomic septation may conveniently be called a septangium. This and other self explanatory terms have been used in indicating possible lines of

it be granted that the lygenopterid and medullosan pteridosperms, at least, have a common phyletic derivation and that the male fructifications in one or several of the
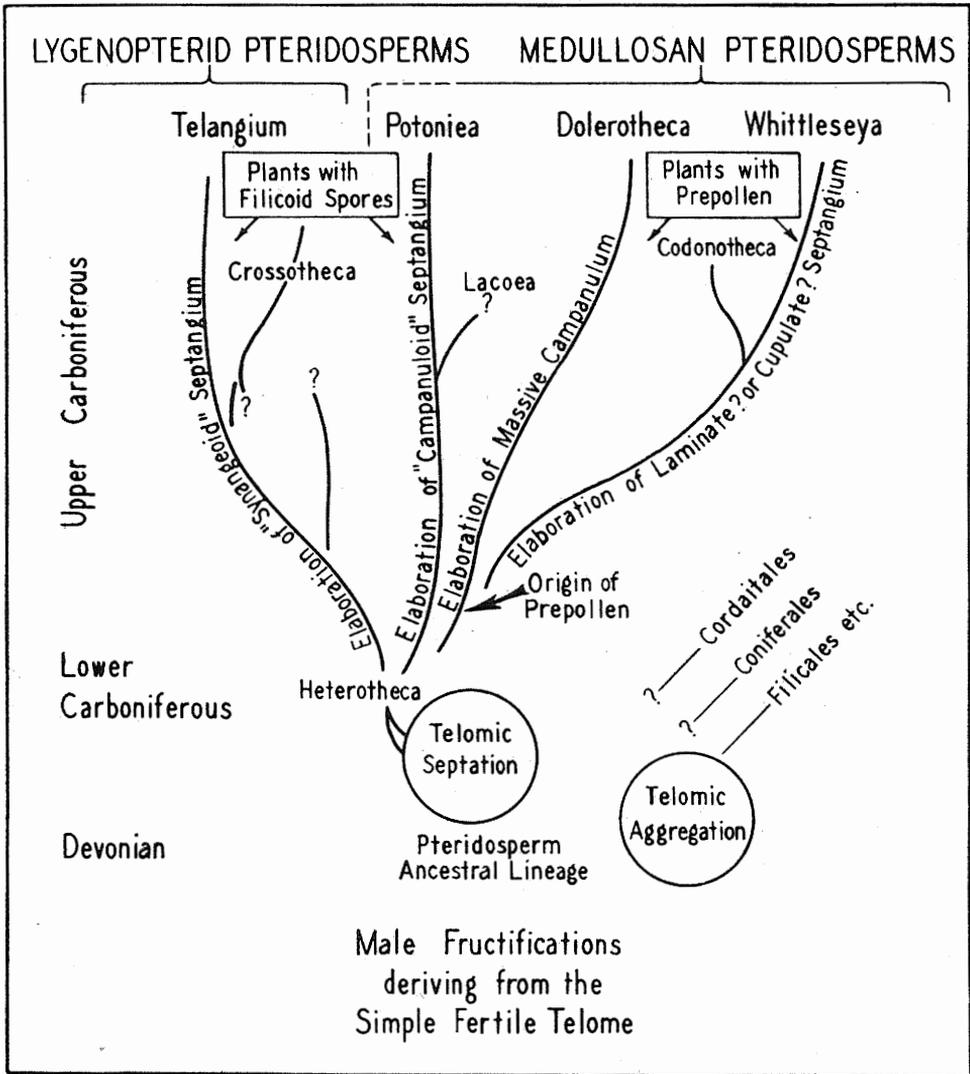
FIG. 17—Hypothetical pteridosperm relationships according to septangial interpretation of male fructifications.

evolutionary morphologic modification in the chart given in text fig. 17.

The general problem posed in this connection may be briefly stated as follows: if

constituent groups of this alliance had evolved by septangial modification, the possibility would be presented for extending the inference of telomic septation to the inter-

pretation of complicated sporangia in all of the pteridospermic groups. Although this question is highly theoretical, it could be of considerable importance in definition of the pteridosperm group as a whole. The suggestion of elaboration of pteridosperm male fructifications by the process of septation is not new, since Miss Benson recognized the distinct probability of its occurrence in at least two other important genera, as discussed below. The writer believes the septation hypothesis deserves more serious consideration than it has frequently been accorded in morphologic interpretation of the pteridosperm polleniferous structures.

The most surprising result of the present study, from the standpoint of comparative anatomy, is that *Dolerotheca* shows *no evidence of cyclic organization or derivation.* The radial arrangement of paired rows of sporangia is the dominating feature. Toward the margin new double rows of sporangia are intercalated; the new rows do not appear at any uniform distance from either center or periphery, but are inserted at various positions as the divergence between preexisting double rows affords space for their accommodation. Hence the symmetry of the *Dolerotheca* campanulum is decidedly radial in character and not cyclic. The symmetry is not very definite and the central focus of rows is not necessarily the center of the fructification.

In view of the fundamental importance which Dr. Halle has attached to cyclic arrangement in the Whittleseyinae, and the indisputable relationship between the Dolerothecineans and the Whittleseyineans, the morphology and morphogenetic derivation of the large pteridosperm fructifications may require reconsideration. To the writer, Dr. Halle's alternative suggestion, stated in the footnote on p. 57 of his important contribution on the spore bearing organs of pteridosperms, seems most easily reconciled with the present array of facts. He stated (Halle, 1933, p. 57 footnote), "It is perhaps also possible to imagine septation of a single sporangium of the remarkably large type found in some of the Psilophytales; the "sporangia" of *Sporogonites* have a certain superficial resemblance to the *Aulacotheca* type in shape, in their comparatively large size, and in their longitudinal furrows."

A synangial interpretation of *Dolerotheca* is difficult because *a pair* of tubular sporangia, rather than a single one that could be directly derived from a fertile telome, seems to be the fundamental unit of structure, and because the sporangial units, single or double, permit no easy comparative derivation from a telomic branch system (see Zimmerman, 1930). It would seem more plausible that the campanulum has been derived by septation or "septangy" and that *the whole fructification is comparable to a single telome*, much modified, rather than to a synangial aggregation of fertile telomes in the manner which was more strongly favored by Halle in 1933 and which he summarized in 1937. The process of sporangial septation is no more improbable, biologically, than the process of aggregation (synangy) in the case of fertile members. A basic evolutionary difference, involving synangy in ferns and septangy in pteridosperms, might, in fact, be called on to explain why the seed habit, with its various interconnected modifications, was so early attained by the latter group. The gymnospermic ovule represents an elaboration of a fertile telome also, and some degree of linkage is to be expected in male and female characteristics of the same plants.

It probably is not necessary to search as far back as the Devonian to find a primitive type of male fructification with plausible ancestral relationship to the Whittleseyas, Dolerothecas, and Potonieas, but the primitive type of telome is closely approximated in some of the Devonian plants. In the writer's opinion, the type of male fructification borne by *Heterotheca grievi* Benson, may serve very well to illustrate a plausible ancestor for *Potoniea, Whittleseya* and allied forms, and *Dolerotheca*.

Heterotheca was regarded as in biologic correlation (i.e., supposed to be a part of the same plant) with *Heterangium*, a genus identified by anatomical characteristics of the stem. Primitive species of *Heterangium* are about the proper geologic age and morphologic type to be close to the direct ancestry of both the Lyginopterid and Medullosan lines of pteridosperm specialization. Both *Heterangium* and *Heterotheca* are of Lower Carboniferous age from the Calciferous Sandstone in Scotland, and this fact

makes ancestral consideration feasible in relation to more specialized Upper Carboniferous (Pennsylvanian) forms.

The structure of *Heterotheca* is most readily interpreted as a product of sporangial septation (see Benson 1922, pp. 128–129). The fruiting body is slightly flattened, half-fusiform, and $3\frac{1}{2}$ to 4 mm. long. It contains numerous sporangia, 16 of which may be seen in cross-section; 12 sporangia at the level shown in the cross section diagram, D, of the frontispiece, are peripheral and 4 central in position. The spores are small (20–30μ in diameter) with a trilete suture. A surface reconstruction of *Heterotheca* is also shown in fig. D of the frontispiece, drawn at the same scale as the *Dolerotheca* figures. The diagrammatic cross-section is drawn to a larger scale to indicate the relative locations of vascular bundles and sclerotic tissue.[9]

From such a structure as the *Heterotheca* fructification, it is possible to suggest several lines of evolutionary specialization, as is indicated in the schematic diagram in text fig. 17. No attempt has been made to present a complete pteridosperm synopsis in this chart, and gymnosperms other than pteridosperms are not included.

As to the possibility of complex fructifications arising by septation of simpler fertile structures, as well as by aggregation, Bower stated (Origin of a Land Flora, 1908, p. 111) "in each case of a synangium, it may be a question whether the structure results from septation or from fusion." Possibly nowhere in the plant kingdom does homoplasty play a more important part than in the development of the male fructifications of pteridosperms, and if the pteridosperms are truly one of the several large monophyletic

[9] Information about *Heterotheca* has been drawn entirely from Dr. Benson's publication of 1922. Reproductions of her original photographs illustrating this form do not offer very convincing support for the description or interpretation. Recently Dr. T. G. Halle, in a personal communication, has emphasized the need for further information about it. The writer sincerely agrees that a more definitive study, if possible with the aid of modern peel preparations, should be undertaken. Until this is done the accuracy of the original interpretation cannot be confirmed and opinions about the relationship of *Heterotheca* will have to be reserved to the extent, at least, of uncertainty about the photographic illustrations.

plant groups the septate derivation of their male fructifications in general (in contrast to the aggregation interpretation of fern synangia) needs to be considered. Since it seems most essential to regard *Heterotheca* and *Dolerotheca* fructifications in this light, other genera definitely linked with Pteridosperms, such as *Crossotheca* and *Telangium*, also should be considered in the same fashion even though they more successfully simulate the synangia of ferns. Miss Benson has presented evidence for septate origin, both in her paper on *Telangium* (1904) and in her discussion of *Heterotheca* (1923).

In *Heterotheca* the internal sporangia are poorly placed for the shedding of spores; the development of elongate sporangia free of one another at the distal ends appears a likely evolutionary trend which is plausibly exemplified by *Telangium*. The frontispiece illustration, fig. E, shows a reconstruction of the *Telangium* fructification drawn at the same scale as the other figures. Other modifications of *Telangium* as contrasted with *Heterotheca* also are evident, but it seems necessary to call attention only to the contraction and simplification of the cover layer in *Telangium*, and to the elongation and reduction in number of characteristically *paired* sporangia.

In the derivation of *Potoniea* from a type like *Heterotheca*, it is evident that sporangia have been modified to tubular form and the fructification expanded. Whether they are anatomically paired or not, cannot be determined from the evidence at hand. The cover layer has been elaborated (rather than contracted as in *Telangium*) and evidently serves as a sporangial receptacle. The sporangia apparently are free of one another, at least for a considerable part of their length. This would represent a considerable improvement over the *Heterotheca* condition insofar as dispersal of spores is concerned. The great size elaboration of the *Potoniea* fructification is a significant feature.

Dolerotheca and *Whittleseya* and their closer relatives are distinguished from the pteridosperms previously mentioned in this connection, in having prepollen rather than fern-like types of spores. The suggestion has been made that these advanced spores may possess a vestigial third trilete ray; if so, they were derived from a tetrahedral tetrad

and thus may not differ as much as they would seem to at first glance, from the types of pteridosperms with fern-like microspores. Regardless of this, prepollen is sufficiently different from the matured androspores of the lygenopterid pteridosperms that an important biological difference is indicated. We are not in a position to interpret the full significance of prepollen as yet. A special pollenation mechanism seems to be implied, but at least the wide-spread occurrence of prepollen in the upper Paleozoic is well established.

Except for the important difference in spores, *Dolerotheca* and *Potoniea* show a similar tendency in elaboration of sporangia, and, to some extent, in enlargment of the campanulum as a whole. This structure in *Lacoea* is larger than in *Potoniea*, and compares more favorably in this respect.

Ground tissue completely enclosing *Dolerotheca* sporangia, and sclerotic tissue in the campanulary cover, are both quite plausibly derivative from the type of structure in *Heterotheca*. *Dolerotheca* shows more adequate provision for dispersal of spores.

The morphologic comparison of *Dolerotheca* and *Whittleseya* is clouded by what the writer believes must be a misinterpretation of the structure and organization in the latter. The previous ideas are reviewed briefly in order to clarify the present position.

Newberry (1853) adopted the view that the broad shovel-shaped organs (of which he had seen some thousands) were leaves of uncertain affinity. He evidently did not question their morphologic identity as leaves, but he was at a loss to relate them or place them systematically. Other authors substantially followed Newberry, more or less tentatively suggesting a gymnospermic alliance, until it became clear that these were fertile, rather than vegetative organs. Kidston may have been the first to suspect that they were the male organs of pteridosperms. A statement to this effect, somewhat unsatisfactory in details, was made by Seward (1917, p. 129) who illustrated prepollen Kidston had obtained from *Whittleseya elegans*. However, prior to Halle's study (1933), the tubular form of the sporangia, a most important characteristic, was unrecognized. Furthermore, Halle demonstrated that *two* rows of sporangia are present across the width of the *Whittleseya* "lamina."

Halle regarded the "lamina" essentially as a tube, containing "loculi . . . arranged in a uniseriate whorl," that owed its laminate form to compression. With this view the present writer is unable to agree.

The first occasion for doubting the cyclic arrangement of locules in *Whittleseya* fructifications came in the realization that it was entirely at variance with the radial organization shown by *Dolerotheca*. In other particulars it seemed possible to reasonably reconcile the new information on *Dolerotheca* with what was known about *Whittleseya*. It seemed strange that *Dolerotheca* should have sporangia radially arranged in paired rows, while in *Whittleseya*, very similar sporangia with similar spores, are arranged according to a wholly different unseriate cyclic pattern.

Further study and review of this matter have convinced the writer that the *Whittleseya* male fructification was never hollow, or campanuloid in form, but in truth is a laminar structure as it was first interpreted. He believes that it consists essentially of a single *paired* row of sporangia that is the morphological equivalent of one of the numerous paired sporangial rows so definitely established for *Dolerotheca*.

Such an interpretation appears to explain adequately all the features observed in Halle's excellent sections (new sections could hardly bear more definitely on this point because, as Halle stated, loc. cit., p. 22, "the median carbonized zone shows no natural longitudinal rupture nor any other indication that it has been formed by compression of two layers originally separated by a central cavity") and it likewise is in full accord with the extensive observations of Whittlesey (1849), Newberry (1853), White (1901) and others. Most of the specimens have been preserved in fine grained matrix that surely would have filled any hollow central cavity in some instances, had such a cavity ever existed. The very thin intervening shale layer Halle demonstrated at the distal edge of the lamina is not at all commensurate with the hollow cavity he postulated, and possibly it may be related to a dehiscence groove similar to those of *Dolerotheca*. There is no specimen known to the writer, nor any that has been described,

in which such a central filling is a prominent feature. A quotation from Whittlesey's little-cited original description (1849) of the *Whittleseya elegans* fructification is still most pertinent to the discussion:

It was first observed by my brother, the Rev. S. H. Whittlesey, about four years ago in the falling roof of the "Chestnut Ridge" coal mine, discovered and opened by us in 1845, and which is situated one mile and a quarter northwest by north from the centre of Tallmadge, Summit County, Ohio.

It is there called "the flower," and has a striking general resemblance to one, but has no botanical resemblance to flowers or other parts of fructification.

If this was originally an *open pod* whether a flower or not, there should have been seen among several hundred specimens that I have examined, evidences of a circular or oval opening at the edge or apex of the figure. These edges could not always have been pressed together symmetrically so as exactly to cover each other, and if there were two surfaces with interior organs between them, it must have occasionally appeared in that light. But in no instance is there such a separation of the serrated edges, there being but one line across the apex, which is generally straight or slightly curving, as in the drawing.

. . . The very fine but distinct curved lines or striae, extend with great regularity, converging to a point at the base where the stem unites. Its space in the rock is represented by a *very thin* scale of coal, the raised lines on one face of the specimen corresponding to depressed lines on the counterpart, showing it to be a single thickness and not double.

. . . On some of them may be seen fine cross marking like nerves of reticulation, but in the finest specimens these are wanting, and are probably due to wrinkles of compression. The teeth at the edge are not uniform in number. I have counted from eighteen to twenty-six. The light, slender, but well defined stem is generally wanting. It is never seen longer than represented in the sketch, and seldom more than half an inch in length, where it terminates abruptly as though it were broken off. There are minute straight lines like fibres in this stem.

(The fossils) . . . exist in the ordinary bluish gray, soft argillo-siliceous shale of the coal series, and in spots are seen in immense numbers, from one to one and half feet above the coal. The shale is charged with myriads of coal plants, but the only hint I have met with showing any relation between this and the other plants, is the fact that where the *Pecopteris lonchitica* is most abundant, this is seen in greatest numbers.

. . . The *Carpolithus* is abundant in the roof of the same mine.

It will be noted that the most striking feature of Halle's reconstruction (loc. cit., text fig. 5, p. 24), viz., the duplicate distal margin of the hollow bell, is the feature

Whittlesey stated is never seen although he quite evidently looked carefully for such an indication. In several respects Whittlesey's discussion is more astute than that of later authors; he certainly was impressed with the possiblity that the organs might be fertile structures. Halle's modern study has fully confirmed Whittlesey's suspicion as to the nature of the organs, but is not reconciled with the general evidence as to their morphology. All facts known now appear in reasonable agreement if the view expressed regarding the paired sporangial row is adopted; further information on sporangial dehiscence and tissue structure is not likely to be obtained until petrified specimens are found.

The morphology of these organs naturally has important bearing on their phyletic morphogenesis. For the same reasons that the writer questions the cyclic arrangement of *Whittleseya* sporangia, he also questions that such organs can be derived from "a whorl of fertile telomes fused tangentially" (cf. Halle, 1937, p. 231).

Although the *Whittleseya* fructification is not nearly as massive as that of *Dolerotheca*, the probable correspondence in plan of organization argues about as strongly for a septangial interpretation of one as the other. It appears that the cover layer of *Whittleseya* has been persistent, but that the fructification has enlarged along two radii only, instead of many. Neither the radial nor bilateral symmetry of *Dolerotheca* is exact, but the *Whittleseya* fructification may be more nearly symmetrical bilaterally. The fact that *Heterotheca* fructifications are not perfectly half-fusiform, but show a bilateral tendency in transverse outline, suggests the possibility of deriving a more strictly bilateral fructification from it as well as a more massive radial type. There is little question that significant differences of long standing exist between *Dolerotheca* and *Whittleseya*, and it is supposed that the parent stocks diverged at a fairly early date, after prepollen was an established feature, as indicated in text figure 17.

In *Codonotheca* the cover layer appears to have become contracted to expose the free ends of sporangia. Such development would seem a parallelism of that which took place earlier and more directly in the ancestry of

Telangium. It is interesting that *Codono-theca* is of large size and that no reversion to the fern-simulating septangial type has occurred.

The writer believes that although the phyletic relationships and postulated structural modifications are highly speculative, they have greater likelihood of substantiation, in part at least, than may frequently be the case in a "Merkmals Phylogenie" (see Zimmerman, 1930). This belief is based on convergence of evidence supplied by the probable biologically correlative fossils (stems, leaves, seeds) which can not be discussed in this paper. Many of the relationships, of course, are not likely to be satisfactorily established for many years.

It appears that such matters of phylogenetic relationship as have been suggested may have an importance beyond their inherent theoretic interest. The elaboration of the male fructifications very probably occurred as a gradual evolutionary process in many linked characteristics. If a "key" can be supplied to gradational evolutionary series in geologic time, it provides a most convenient tool for the stratigraphic paleontologist wherever such fossils are encountered. The evolutionary hypotheses embodied in the foregoing discussion should be tested wherever possible by comparison with other better known fossils, to indicate more objectively their value in stratigraphic definition. Their value as time indices will be more evident as discernible stages of evolutionary development are keyed with definite stratigraphic zones. The male organs discussed here have the advantage (from the paleontologic standpoint) of a fairly determinate type of growth, so that in normal course of fossil preservation, typical specimens should be mature and therefore fairly comparable ontogenetically.

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