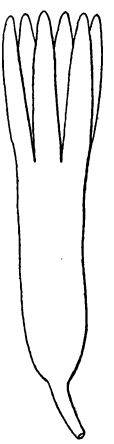
ART. IX. — *Codonotheca, a New Type of Spore-Bearing Organ from the Coal Measures;** by E. H. SELLARDS. (With Plate VIII.)

THE iron-stone nodules of Mazon Creek, Illinois, which have preserved so many interesting fossils, contain not infrequently an isolated, but unique, and as yet undescribed type of fructification. The conditions of preservation in these nodules are such that by careful developing it is possible to make out many of the details of structure of the fossils contained in them. In the present case, the abundance of material at hand, and the unusual organization of the reproductive organ give an especial interest to the study. It is the purpose of the present paper to describe the structure of this peculiar type, in so far as the material at hand will permit, in the hope that a description of the fructification will lead to its recognition in collections from other localities in this and foreign countries, and to the determination of the plant to which it belongs. The collections from the Mazon Creek locality in museums, especially of this country, are generally quite extensive and some of these may be found to contain specimens throwing new light on the relation of this fructification.

The spore-bearing organ is a symmetrical cup- or bell-shaped body, made up of a circle of six equidistant, lamina-like, spore-bearing divisions, arising at a common level, united laterally at the base, free at the tips, thus surrounding a central cavity; each division is traversed on the inner or spore-bearing side by two strong bundles supplied by the dichotomy of six main strands; the union of the laminæ and bundles below forms a cylindrical base, while the whole organ is borne on a slender petiole. The base, which seems to have consisted for the most part of an external envelope of non-resistant fleshy tissue, is usually more or less completely flattened in the fossil condition. It is traversed by lines, often wavy and irregular, lying near the surface and extending along the dorsal side of the spore-bearing divisions, probably representing subepidermal bands of strengthening tissue. The fusion of the six main vascular strands forms a cone-shaped area of resistant tissue at the center of the base, large at the top where it breaks up into strands, pointed below where it is replaced by less resistant tissue. This area occasionally retains its cylindrical shape (figs. 1 and 11, Pl. VIII). The six strands originating at a common level from this central area diverge and dichotomize also at approximately the same level. The twelve bundles formed by this dichotomy pass into the six spore-bearing divisions, which

* Abstracted from a thesis submitted to the Graduate Faculty of Yale University, May, 1903, for the degree of Doctor of Philosophy.

for convenience will be spoken of in this paper as spore-bearing segments, or simple segments. The distribution of the bundles to the segments is characteristic. Each individual segment is supplied not by the two bundles resulting from the dichotomy of a single main strand, but receives one bundle from each of two adjacent strands (compare figs. 1, 4, 11, 15, and the plan of structure, fig. 5, Pl. VIII). This peculiarity in the arrangement of the bundle system can be verified from numerous specimens, and is one of the prominent structural features of the organ of fructification. The free tips of the segments occasionally stand open, thus retaining in part their original shape, owing probably to their having been quickly buried in sediment. By carefully removing the matrix which fills the cone-shaped cavity enclosed by the segments, it is possible to examine the six parts in place. The two figures, 14 and 15, illustrate a specimen worked out in this way, as seen from the two sides. The matrix filling the cavity formed by the expanded segments was removed intact and has the shape of a cone flattened laterally, on which is preserved the impressions of the six spore-bearing segments. On refitting the two parts of the nodule together, there results an elliptical cavity, large at one end corresponding to the top of the organ, and becoming smaller and disappearing toward the crushed base. The shape of the organ is thus partly preserved in this nodule, being simply compressed laterally. On looking into the cavity a very satisfactory idea of the shape and arrangement of the parts, and of the whole organ as it appeared in life is obtained. The outline restoration of this fructification given in the accompanying text figure is based on this and similar specimens. The plan of structure of the organ (fig. 5, Pl. VIII) represents the hollow top as unrolled and the solid base as cut through the center and laid open. The section is made to pass between segments I and VI, hence directly through strand number I. The letter *c* marks the bottom of the cavity enclosed by the segments.



Codonotheca; restoration of the spore-bearing organ. Natural size.

Considerable variation in size is evident in the series of specimens. Those of an average size measure 3 to 5^{cm} from the base to the tips. The width at the top is about $1\frac{1}{3}$^{cm}. The segments above the point where they become free are $1\frac{1}{2}$ to 2^{cm} long and $2\frac{1}{2}$ to 3^{mm} wide. The petiole is incomplete, the longest

observed being a little over 1^{cm}. When well preserved the petiole shows a netlike structure made by strong longitudinal striæ and weaker cross lines, suggesting the structure occasionally seen on the leaves of some *Cordaites* (fig. 16, Pl. VIII).

Spores.—Much interest is attached to the presence of the spores and the position in which they lie. In the best-preserved specimens the spores lie over the segments from the tip to the base, and seem to be confined to a more or less well-marked depression occupying one-half or two-thirds the width of the segment. In such spore-bearing segments as are crushed laterally, at the side of the fossil, the spores are pushed to the inner side, indicating that they were contained in sporangia or chambers near the inner surface, and apparently were not, as might otherwise have been thought possible, held loosely in a central cavity of the segment after the manner of moss sporogonia; in the latter case the spores would appear along the center line of the segment, however crushed. There is no grouping of the spores or other indications of the location of sporangia, which were doubtless more or less completely immersed in the tissue. In order to contain even a few of these large spores the sporangia would necessarily be of large size and if external in position would probably have left definite impressions in the stone, as do the sporangia of most other plants in these nodules. The spores seem to have been scattered somewhat, owing probably to the disappearance of the walls of the sporangia at maturity, so that in the fossil they run together and entirely fill the depression in which they lie.

From the position of the spores, the sporangia appear to have been located along the vascular bundles. Inasmuch as they have not been seen, no attempt is made to represent them in the restoration. The spores are large, elongate-elliptical, 0·29 to 0·31^{mm} long and 0·18 to 0·20^{mm} wide. They are brown in color, somewhat flexible, and section readily on the microtome.* The spore wall consists of an inner, compact layer, and an outer much thicker layer which appears granular in microtome sections seen under a high power. A slit is usually present in the side of the spore, apparently indicating bilateral division from the spore mother-cell. The spores occasionally contain small round grains with dark centers, doubtless representing a part of the original food supply. In size and shape, the spores rather closely resemble those of *Dolerophyllum*, except that there is but a single slit in the side, instead of two furrows as described for that genus. The spores (pollen grains) of *Dol-*

* The spores may be imbedded by the ordinary methods; less time, however, is necessary for dehydrating, and the paraffin bath may be brought to any desired temperature.

erophyllum are contained in a boxlike excavation in the fleshy tissue of the reduced leaf.* There is apparently nothing in the structure of the spore itself, as preserved, to determine whether the plant was homosporous or heterosporous. From their large size the spores might be taken for megaspores. Bilateral megaspores, however, although seemingly occurring rarely, are exceptional among vascular cryptogams. A careful search has been made through all the available material, amounting to about seventy-five specimens (with in most cases their counterparts), many of which have the spores preserved, but no evidence of two kinds of spores has been found. This negative evidence, although hardly conclusive, is entitled to considerable weight. In view of the abundance of material, the chances are very great that if two kinds of spores existed both would be present. The conclusion that the plant was homosporous is, therefore, reasonably certain, unless the second kind of spore proves to have been borne by a differently constructed organ.

The generic name *Codonotheca* is proposed for this type of spore-bearing organ. The type species here described may be known as *Codonotheca caduca.*

Botanical Relations.—The botanical relations of this unusual fructification are as yet very uncertain. The spore-bearing organ seems to have been readily deciduous, and thus far has not been found in connection with the vegetative part of the plant. Two of the fossils lie side by side on one of the nodules in such a way as to indicate that both were probably attached by long petioles to a common stem. At one side and at a slightly lower level is seen a slender striated stem; but the actual connection is not preserved. Three other specimens lie near each other on the same nodule. It has been assumed in the above description that the six parts of the organ are sporangia-bearing divisions. A second hypothesis may perhaps suggest itself, namely, that the parts are themselves enormous sporangia united at the base somewhat after the manner of such genera as *Botryopteris*, *Zygopteris*, and some of the small species referred to *Calymmatotheca.* Their great size and especially the presence of well-developed vascular strands running through them is, however, much against, if not fatal to, such a supposition. Even a slight development of vascular tissue within the walls of a sporangium is unusual, although such may occasionally occur, as shown in a recent paper by Prof. F. W. Oliver.† It seems hardly possible, therefore, that the spore-bearing segments can be individual sporangia, because of their large size and especially the prominence of the vascular

* Renault, Bassin houiller et Permien d'Autun et d'Epinac, p. 266, 1890.

† On a Vascular Sporangium from the Stephanian of Grand Croix, The New Phytologist, vol. i, p. 60, March, 1902.

strands running through them. On the contrary, the organ appears to be made up of six lamina-like fertile divisions, united in a circle at the base so as to enclose a central cavity, the sporangia being borne on the inner side and probably partly or entirely immersed in the fleshy tissue.

It seems wholly improbable that *Codonotheca* can have any direct or close connection with the mosses or other plants lower in the scale of development than the vascular cryptogams. It is true that a water-conducting tissue is rather well developed in the stem of some mosses, and to some extent in the sporogonia of a few genera, but a well-developed vascular system, such as this organ possesses, is at present entirely unknown in any plant below the Pteridophytes. On the other hand, the unusual structure of the reproductive organ makes it difficult to determine the systematic position of the genus among the vascular plants. The spore-bearing region of the known Paleozoic and recent Equisetales is typically a cone formed by the shortening of the internodes of the main axis, or of the axis of a branch. The cone is made up of several to many nodes and internodes. Each node may bear a whorl of fertile sporophylls, or fertile and sterile whorls may alternate or be variously modified according to the genus. In the extinct Sphenophyllales, the cone is also formed by a shortening of the internodes of the axis, and the fertile sporophylls are borne in whorls at the nodes. The sporangia of the Lycopodiales are borne at the base of the sporophylls, which usually form a cone. The ferns, although a more varied class, seem to include no type whose fundamental structure is comparable to that of *Codonotheca*. Some species of *Schizæa*, as *S. pennula*, have a cluster of similarly shaped sporangia-bearing divisions, but these have external dorsal sporangia with a ring of thick-walled cells at the top, and lack entirely the unusual cyclic arrangement and the fleshy petiolate base characteristic of *Codonotheca*. It is also evident that this new type can have no connection with such ferns as the Hymenophyllaceæ, in which the elongated receptacle, bearing the sporangia, is surrounded by an indusium-like outgrowth of the lamina. The extinct fernlike genera *Botryopteris* and *Zygopteris*, which have sporangia clustered at the ends of slender peduncles, do not seem to admit of comparison with *Codonotheca* except on the hypothesis, which appears to me untenable, that the six divisions of the organ are so many large sporangia.

For many years numerous plants have been known from the Paleozoic, having a stem structure resembling that of the ferns on the one hand, and the cycads on the other, but so different in many ways from both as to be with difficulty included in either. Since 1899* these plants have been united to form an

* Potonié, Lehrbuch der Pflanzenpalaeontologie, p. 160.

intermediate group, the Cycadofilices, the more generalized divisions of which are believed to form, to some extent at least, a connecting series between the ferns and cycads. The stem structure indicates considerable diversity among the several divisions of the group. Unfortunately hardly anything is known of the fructification. Certain sporangia of the *Calymmatotheca* type have been found so closely associated with one genus of the Cycadofilices, *Lyginodendron*, as to make their connection probable.* *Lyginodendron* has finely divided foliage, and is one of the more fernlike of its class. The small species of *Calymmatotheca* found in association with *Lyginodendron* have large sporangia grouped in a cluster at the end of a petiole, free at their tips, free or united at their bases, and borne on dimorphic fronds. A number of other plants of various structure have been referred to *Calymmatotheca*. The largest of these and also the first described species of the genus, *C. Schimperi* Stur, is an imperfectly known fossil. According to Stur† the plant consists of six parts, 18^{mm} long, united at the base by threes, and is apparently entirely different from many of the smaller species which have been referred to the genus.

Aphlebiocarpus Stur is another imperfectly understood genus of unknown affinity.‡ This remarkable fructification consists of about five foliar parts, more or less deeply lobed or fringed, arranged in an involucre-like whorl. According to Stur, the sporangia are small, solitary, and deep set, and are placed thickly over the upper or inner surface of the "involucre." The spores are not described, and the vegetative part of the plant, except for the branching axis, is unknown.

Codonotheca suggests at first sight a possible resemblance to the male flowers of some gymnosperms. *Tumboa (Welwitschia)* has microsporophylls united in a circle at the base. The microsporophylls of the Mesozoic Bennettitaceæ, also, as Wieland has shown, are fused in a circle at the base. But the relation to these genera is probably not close, since the Bennettitaceæ, as well as *Tumboa*, seem to have an abortive, seed-bearing cone at the center.§

While the genus may find its place as an aberrant type among one of the well-known classes of Pteridophytes or even gymnosperms of Cordaitalean affinity, it may on the other hand

*Scott, Studies in Fossil Botany, pp. 334–336; Benson, Ann. Bot., vol. xvi, pp. 575–576, 1902.

†Die Culm-Flora der Ostrauer und Waldenburger Schichten, Abhandl. der k. k. geol. Reichsanst. zu Wien, vol. viii, p. 149, 1877.

‡Ibid., p. 304, pl. 37, 1877; Die Carbon-Flora der Schatzlaren Schichten, ibid., vol. xi, Abth. I, p. 15, 1885.

§Wieland, A Study of Some American Fossil Cycads, pt. iv, This Journal, vol. xi, p. 424, 1901.

prove to fall within the comparatively varied but less well-known Cycadofilices, as representative of a specialized division at present included in that group and which has suffered extinction. The plants to which the *Codonotheca* type of fructification belongs, as far as the arrangement of their spore-bearing organs is concerned, seem to have reached a comparatively specialized condition as early as the Upper Carboniferous. There are present in the Coal Measures and at the Mazon Creek locality several genera or groups of plants, the fructification of which is either unknown or but imperfectly understood. Conspicuous among these, both from its large size and great abundance, is *Neuropteris*, especially the large species, *N. decipiens* Lesqx. Renault* and others have shown that the petiole of *Neuropteris* as well as that of *Alethopteris*, possesses the *Myeloxylon* type of stem structure. The Meduloseæ to which *Myeloxylon* belongs are regarded as a divergent branch of the Cycadofilices.† The only information regarding the fructification is that obtained by Kidston from a specimen of *N. heterophylla*, a species of the small-pinnuled division of the group.‡ Kidston's material was unfortunately poorly preserved, but served to indicate that the fronds were dimorphic, and that the spore-bearing organs were grouped in clusters at the ends of the slender petioles. There is reason for believing that the entire Neuropterid group was dimorphic. As a rule, those plants having the sporangia on the under side of the fronds, after the manner of ordinary ferns, not infrequently preserve impressions of the sporangia and sori. *Neuropteris* is abundant throughout the Coal Measures, and very large collections of Neuropterid fronds have been examined by various paleontologists without finding evidence of sporangia. The large fronds of *Neuropteris* would doubtless supply a considerable number of detached pinnules as compared with the number of fertile spore-bearing parts, however these may have been arranged. In the Yale University Museum collection, the proportion between *Codonotheca caduca* and *Neuropteris decipiens* is approximately one of the former to ten of the latter.§ Nevertheless, the fact should not be lost sight of that there are a number of other plants in the Coal Measures to any one of

* Renault, Affinités botaniques du genre *Neuropteris*, Comptes rendus, vol. lxxxiii, pp. 399–401, 1876.

† Scott, Studies in Fossil Botany, pp. 394–396. Compare also Solms-Laubach, Über *Medulosa Leuckarti*, Bot. Zeitung, Bd. lv, Heft x, pp. 175–202, 1897.

‡ Trans. Roy. Soc. Edinburgh, vol. xxxiii, pt. i, p. 150, pl. viii, fig. 7, 1887.

§ The relative proportion, as here given, is based on the Yale collection from Mazon Creek, which contains 75 specimens of *Codonotheca* to some 1,200 of *Neuropteris*, 750–800 of which are *Neuropteris decipiens*.

which the fructification here described may belong, or that it may represent an entirely new plant.

My thanks are due Dr. Alexander W. Evans for references to recent botanical literature, and to Dr. David White and Dr. G. R. Wieland, as well as to Dr. Evans, for suggestions on the text and illustrations. Dr. E. R. Cumings has very kindly made most of the drawings. The material on which the study is based is contained in the fossil plant collection of Yale University Museum, made accessible to me through the kindness of Professor C. E. Beecher.

Paleontological Laboratory, Yale University Museum,
New Haven, Conn., April 2, 1902.

EXPLANATION OF PLATE.

PLATE VIII.

Codonòtheca caduca gen. et sp. nov.

FIGURE 1.—The fleshy covering has disappeared from this specimen by maceration, allowing the resistant area at the center, which still retains its cylindrical shape, to stand out prominently. Strands I to III and VI are visible, IV and V being hidden on the opposite side. Figure 11 is a photographic reproduction of a part of the same specimen with the covering removed, exposing strands IV and V. ×2.

FIGURES 2–3.—Obverse and reverse sides of a small specimen. The very numerous large spores lie in a depressed channel along the segments from the tip to the base. The cavity formed by the united bases of the segments ends at *c*. A part of the upper side of the covering is broken away near the bottom, allowing the spores to be seen within. The base of this specimen, as preserved, is comparatively slender and is traversed by wavy lines. A considerable part of the long slender petiole is preserved. Natural size.

FIGURE 4.—The two bundles supplying the segment, and their origin from two adjacent main strands below, are very well shown in this specimen. Natural size.

FIGURE 5.—Plan of structure of the spore-bearing organ. The top is represented as cut open and unrolled, the base as split down the center and laid open. The cut is represented as passing between segments I and VI, hence directly through strand number I. The end of the cavity is marked at *c*. The cylindrical area at the base first breaks up into six main strands (I to VI) which dichotomize and supply the twelve bundles to the spore-bearing divisions. Natural size.

FIGURE 6.—A group of spores imbedded in sphalerite, and having the surface ornamentation well preserved. ×28.

FIGURE 7.—Spores taken from the surface of the specimen illustrated in figure 2. ×28.

FIGURE 8.—A single spore; showing the slit in the side, indicating probably the bilateral division of the spore mother-cell. Several dark bodies, apparently representing stored food supply, are contained within the spore. ×85.

FIGURE 9.—Section through the spore wall; showing a thick granular outer, and a thin compact inner layer. ×200.

FIGURE 10.—The specimen illustrated by this figure has suffered lateral crushing, and the bundles are partly displaced. A few spores are still clinging to the surface. Natural size.

FIGURE 11.—Same specimen as figure 1. ×2.

FIGURE 12.—Photograph of a small specimen. The first segment on the right is seen from the dorsal surface, showing the parallel striæ. The next segment is seen from the ventral (inner) side. The two strong bundles traversing this segment can be traced in the photograph. The origin of these two strands from alternate strands below, which can be distinguished only by close scrutiny in the photograph, is very evident in the specimen. The outline of the resistant area formed by the union of the bundles below can be followed by its white micaceous coating such as often covers the fossils in these nodules. Natural size.

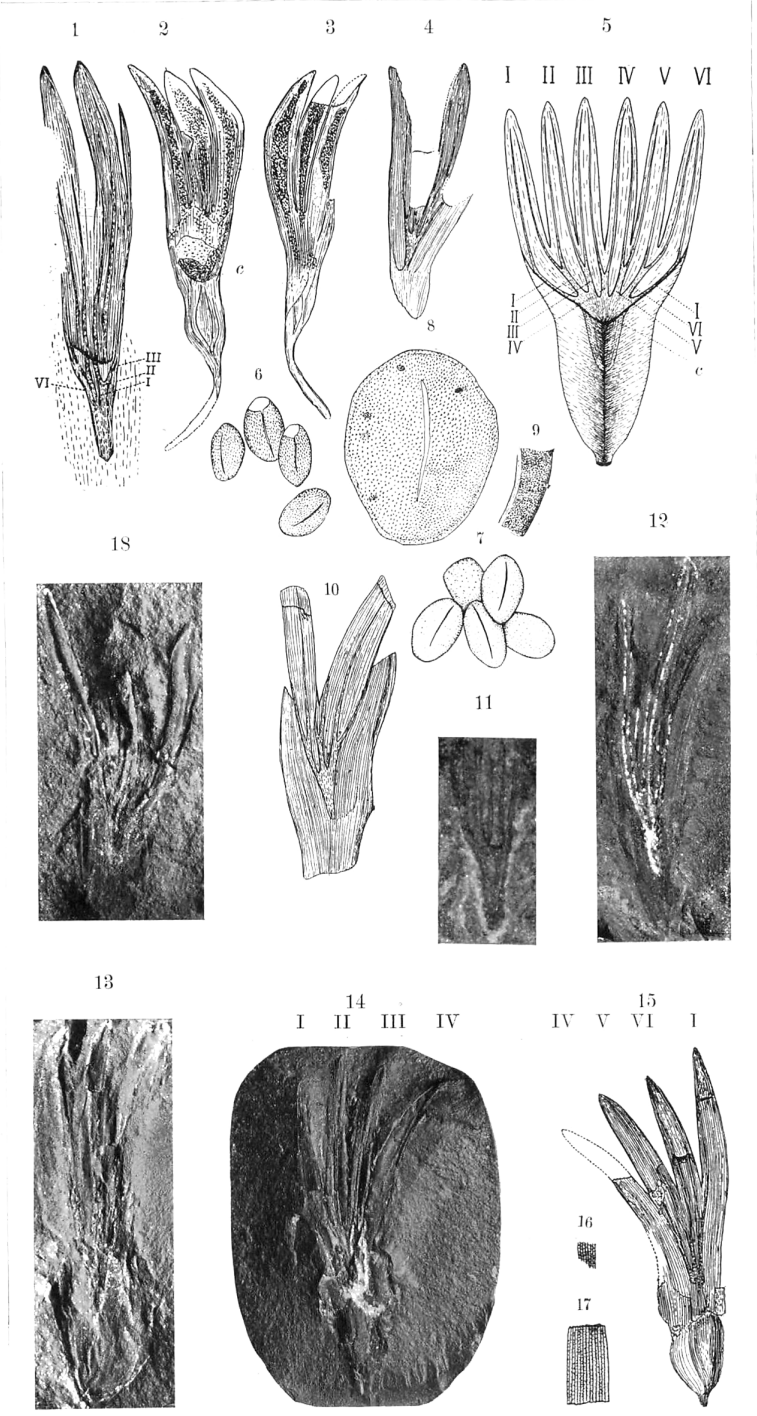
FIGURE 13.—The large base is here flattened. The striæ of the base are more or less disarranged and have a wavy course. Some of them seem to divide, and all converge to the point of attachment. The photograph also shows the cone-shaped resistant area at the center, which is large above where it breaks up into strands; pointed below. The first spore-bearing segment on the left is crushed, giving it an unnatural width. At the top of the next one is seen the dorsal surface marked by fine striæ. Farther down the segment is removed, leaving the impression of the ventral (inner) surface on which the two bundles supplying the segment are seen. At one point about half-way down, the break extends through to the opposite side of the organ and a few spores are seen in place on the opposite surface. Natural size.

FIGURES 14–15.—A specimen worked out so as to expose both sides of the organ. The base of this specimen is not entirely flattened, having partly retained its shape. The side illustrated in the pen drawing, figure 15, shows for the most part the impression (mold) of the outside surface. In places, however, the substance of the plant has clung to the mold. This is true of a part of the vascular system, and the tips of segments VI and I, giving an instructive view of the ventral (inner) surface. The two bundles are distinct, lie near the surface, and are rather widely separated. The segments have considerable thickness as seen in the break, being perhaps half as thick as wide. The impression made by the dorsal surface is longitudinally striate, as seen in the other segments of this and other specimens. The dorsal surface of the segment itself is represented in figure 17, showing the parallel striæ, and the minutely roughened or pitted surface. The photograph of the opposite side as it lies in the nodule, figure 14, gives a partial dorsal view of segments I and IV, which are crushed laterally and distorted. Segments II and III have retained their shape and are seen from the ventral (inner) view. The cone-shaped portion of matrix which originally filled the center of the organ is preserved in the Yale collection, and shows on one side, corresponding to the side from which the photograph was made, the impressions of the ventral side of the segments; while on the other side, that from which the mold serving as the basis of figure 15 came, the dorsal surface of the segments (except the tips of VI and I) are seen. Natural size.

FIGURE 16.—Enlarged detail of the petiole; showing the strong striæ and weaker cross lines. ×3.

FIGURE 17.—Enlarged detail of dorsal surface of the segment. ×3.

FIGURE 18.—An average specimen. Natural size.



CODONOTHECA, A NEW TYPE OF SPORE-BEARING ORGAN.