ART. XXII.—*On the Fertile Fronds of Crossotheca and Myriotheca, and on the Spores of other Carboniferous Ferns, from Mazon Creek, Illinois;* by E. H. SELLARDS. (With Plate VII.)

INFORMATION in regard to the spore-bearing organs of Carboniferous ferns has accumulated slowly and with difficulty. The parts of the plants are usually disconnected, and more or less fragmentary. Dimorphic genera are not uncommon, and specimens connecting the fertile and sterile segments or fronds are rare. It is usually difficult to correlate genera described from microscopic structure with others based on plant impressions. And yet, a satisfactory knowledge of a considerable number of genera and species has resulted from the work of the various investigators who have taken up this subject since the time of Brongniart. These investigations indicate that ferns with the annulus absent or but slightly developed, and having other Marattiaceous characters, predominated in the Carboniferous, and included a much greater range of form and structure than is seen in the living representatives of the family. Besides the numerous exannulate ferns, others are known with a well-developed annulus, and are, therefore, presumably Leptosporangiate. The reference of these fossils to their respective families of living ferns is attended with more or less doubt. The Hymenophyllaceæ, Gleicheniaceæ, Schizæaceæ, and Osmundaceæ have been recognized with some degree of certainty.

Prof. Renault, of the Museum of Natural History of Paris, has recently described *Parkerioidea* Renault, a genus from the Coal Measures of Grand' Croix, near St. Étienne. The character of the annulus, the form of the spores, and the ornamentation of the exospore have led him to refer this form to the Parkeriaceæ. Certain of the spores show sculpturing, while others are smooth and have three radiating lines at the apex. The former are interpreted as microspores, the latter as megaspores.*

The same writer had previously detected what he believed to be indications of heterospory in *Pecopteris*, one of the Marattiaceous ferns,† as well as in an extinct family of ferns, the Botryopterideæ.‡ The evidence of heterospory in the Botryopterideæ has not been fully accepted.§ The papers on *Pecopteris* and *Parkerioidea* are mentioned more fully later in the present article, where, in connection with the descrip-

* Comptes Rendus de l'Academie des Sciences, March 10, 1891.
† Ibid., October 21, 1891. ‡ Bull. Soc. Hist. Nat., Autun., iv, 1891.
§ See Scott, Studies in Fossil Botany, p. 289 ; Zeiller, Éléments de Paléobotanique, p. 74.

tion of the spores of some Carboniferous ferns, it is pointed out that, as far as the radiating lines ("lines of dehiscence") at the apex are concerned, they cannot be considered characteristic of megaspores.

The fructification of several genera of Carboniferous ferns is well shown in an exceptionally large and complete collection from Mazon Creek, Illinois, in the Yale Museum. The sporangia are often preserved, and in many cases the spores are found in place, and can be removed and studied. In the present paper the Mazon Creek representatives of two interesting genera, *Crossotheca* and *Myriotheca*, will be described, together with the spores of some other species.

In the earlier American literature many of the fertile ferns were grouped together without sufficient regard to their true generic separation. *Sorocladus*, as established by Lesquereux,* was so broadly defined as to include more than one natural genus. *S. stellatus* was the first of the five species described under the genus. Four of the species referred in the "Coal Flora" to *Sorocladus* had been previously placed by Lesquereux in the Tertiary *Staphylopteris* Presl. It was probably Schimper's objection to considering these forms under Presl's genus that led Lesquereux to create a separate genus for them.†

One of the five original species of *Sorocladus*, *S. ophioglossoides*, has been referred by David White to *Crossotheca*, and *S. sagittatus* was recognized as falling naturally within the same genus.‡

Crossotheca.

Zeiller, Ann. Sci. Nat. (Bot.), ser. 6, vol. xvi, 1883.

Crossotheca is a genus of more than ordinary interest, because of its dimorphic fronds, its large marginal sporangia, and large spores. Several species are known in Europe, all of Coal Measure and Permian age. Besides the two species just mentioned from this country, a third is added in the present paper.

Crossotheca sagittata.

Plate VII, figures 1–3*c*, 8.

Staphylopteris sagittatus Lesq., Geol. Surv. Ill., vol. iv, p. 407, pl. xiv, figs. 4–6, 1870.

Pecopteris abbreviata Brongn. ? Lesq., Geol. Surv. Ill., vol. iv, p. 403, 1870; Second Geol. Surv. Penn., Description of the Coal Flora, vol. i, p. 248, pl. xlvi, figs. 4–6*a*, 1880.

Sorocladus sagittatus Lesq., Coal Flora, vol. i, p. 329, 1880; Atlas, pl. xlviii, figs. 10–10*b*, 1879; vol. iii, p. 761, pl. C, figs. 4–5, 1884.

Pecopteris Fontainei, Lesley's Dict. of the Fossils of Penn., p. 606, 1889 text figure. See, also, Lesquereux, unpublished manuscript.

* Second Geol. Surv. Penn., Description of the Coal Flora, vol. i, p. 327, 1880.

† Paléont. végét., vol. iii, p. 512.

‡ Mon. U. S. Geol. Surv., No. 37, Flora of the Lower Coal Measures of Missouri, pp. 60–64, 1899.

Crossotheca sagittata preserves the details of fructification much better than the other American species, and illustrates well the characters of the genus. The large fertile pinnules are expanded at the base in the form of an arrow, thus allowing greater area for the attachment of the sporangia. The small pinnules are slightly or not at all enlarged at the base. The upper surface of the pinnule is flat with a distinct median line, and with the lateral veins obscured. The sporangia are unusually large, measuring $2\frac{1}{2}$ to 4^{mm} in length and $\frac{1}{2}$ to $\frac{3}{4}^{mm}$ wide. They are placed as seen in figures 1, 2, and 3, in a single row around the entire border of the pinnule, free nearly or quite to the base, and are often seen filled with spores.

Figure 2 gives a side view of the pinnule as partly freed from the matrix, and showing the full length of the sporangia.

From a study of the type of the genus, Prof. Zeiller thought it probable that the sporangia were united in little clusters at the ends of the nerves. The specimens figured and others in the Yale collection indicate that in the case of *C. sagittata*, at least, the sporangia are attached side by side in a single row, without any tendency toward grouping. The same specimens confirm the statements of Zeiller that these are individual sporangia, since, in the specimens at hand, they are often filled with spores, in contradistinction to Stur's interpretation of the fringed pinnules as dehisced sporocarps.*

Some of the best preserved sporangia show a slit on the outer side, as seen in figure 3*a*, which probably indicates the place of dehiscence.

The sterile part of the frond is very different from the fertile, so much so that if not found in direct connection their relation would hardly be suspected. The pinnules are small, rounded, close, oblique, connate, and decurrent at the base, the smaller entire, the larger becoming lobate. The ultimate pinnæ are broadly linear-lanceolate, alternate, oblique, and close, often touching. The rachis is large and round. The midrib of the pinnule is broad, shallow, and decurrent. The lateral veins curve regularly to the border, and fork once, twice, or three times, according to the size of the pinnule. The surface is rough, appearing minutely scaly. Some of the veins are heavier than others, giving the venation an irregular appearance.

The extreme apex of the frond is often sterile, the fertile pinnules and pinnæ appearing at some distance below. This is not always the case, however, since in the frond figured by Lesquereux ("Coal Flora," volume iii, pl. C, figure 4) the entire apical part is fertile. It is not possible to state, on any evi-

* Abhandl. d. k. k. Geol. Reichsanstalt, Wien, 1885–87, Flora der Schatzlaren Schichten, Part I, pp. 273–275.

dence at hand, whether the entire frond below the apex was fertile, or only a few of its segments. There is no indication of sterile segments below the fertile ones, although some of the incomplete fronds reach a length of 15 or 16^{cm}. It is probable that some of the fronds were entirely sterile, and that others were mostly sporangia-bearing, the apical part only being, in most cases, sterile.

The spores of this species are large, from ·056 to ·060^{mm}, round, and marked at the apex by three distinct radiating lines. The exospore is thick, resistant, brownish, and marked by minute warty thickenings.

The sterile fronds were at first doubtfully referred by Lesquereux in the "Coal Flora" to *Pecopteris abbreviata* Brongn.* In volume iii of the same work, however, a small part of the sterile apex is figured in connection with the fertile frond, and David White states that Lesquereux's unpublished manuscript contains descriptions and figures of the two parts in connection.† In the Yale collection the fertile and sterile parts are shown in direct connection in no less than nine instances. (See figure 8.)

Crossotheca trisecta sp. n.

PLATE VII, figures 4–4*c*, 9.

A second and apparently new species is present in the material from Mazon Creek. The sterile part of the frond is much like that of *C. sagittata*, but the fertile pinnules are entirely different. The latter are usually trisectate. The central lobe is elongate-ovate, or nearly round, and borne at the end of a slender stalk. The lateral lobes are smaller, round, and borne on short lateral stalks. A second pair is sometimes borne by the larger pinnules. Lateral lobes may be lacking in one or two pinnules near the apex of the pinna. The sporangia are probably smaller than those of *C. sagittata*, and are not distinctly preserved on either of the two fertile fronds in the present collection. The sporangia-bearing lobes have a form much like that of the type of the genus *C. Crépini*, but the type species lacks the trilobate appearance of the pinnules, and has more finely divided sterile fronds having a different type of venation.‡ *C. ophioglossoides* from Clinton, Missouri, has narrower and longer fertile pinnules.

The lines on the upper surface of the pinnule, present on other species of the genus, are much more distinct than on *C.*

* Second Geol. Surv. of Penn., Description of the Coal Flora, vol. i, p. 348; Atlas, pl. 46, figs. 4-6, 1880.

† Mr. White informs the writer that the name *Pecopteris Fontainei*, sp. nov., is given to the sterile fronds of this species in Lesquereux's manuscript.

‡ See the figures of *C. Crépini* given by Zeiller, Ann. Sci. Nat. (Bot.), ser. 6, vol. xvi, 1883, and by Stur under the name of *Sorotheca Crépini*, Flora der Schatzlaren Schichten, pl. xxxv, figs. 3, 4.

sagittata, and sometimes branch. The figured specimen is 15^{cm} long; the first 5 or 6^{cm} are sterile, the remaining pinnæ being partly or entirely fertile. When detached and in fragments the sterile part of the frond is distinguished with difficulty from that of *C. sagittata*. The pinnules are perhaps more finely lobate.

The spores are smaller than those of *C. sagittata*, measuring from ·030 to ·036^{mm}. They are somewhat triangular, with a smooth, thin exospore.

The name *Crossotheca trisecta* is suggested for the species.

Myriotheca.

Zeiller, Ann. Sci. Nat. (Bot.), ser. 6, vol. xvi, 1883.

Myriotheca has numerous independent, sessile, round or egg-shaped sporangia, covering the entire lower surface of the pinnule. The genus is represented at Mazon Creek by a single species, which apparently is the fern described by Lesquereux from Morris, Ill., as *Sphenopteris scaberrima*,* although the rachis is smooth or striate, not punctate as given for that species. The round sporangia are very numerous, close, or almost contiguous, half immersed in the leaf substance, and cover the entire lower surface without any kind of regularity of arrangement or grouping. The spores are of medium size, measuring from ·036 to ·040^{mm}, triangular, with the sides sometimes slightly concave. The genus is a rare one both in Europe and in America. No other species has been reported from this country. The genus was founded by Zeiller on a single fragment from the Coal Measures of France. The European specimen representing the type species, *M. Desaillyi*, has smaller pinnules with a tendency to become lobate. The sporangia of the American species are nearly round, and larger than those of the European species, measuring ·40 to ·50^{mm}.

Because of the absence of any indication of an annulus, Prof. Zeiller included both *Crossotheca* and *Myriotheca* with the Marattiaceæ. The large size of the spores and comparatively small output to the sporangium are, however, characters not met with in the living representatives of that group. The position of the sporangia, marginal in *Crossotheca*, and covering the whole lower surface of *Myriotheca*, is unusual for Marattiaceous ferns.

Spores of other Ferns from the same Locality.

At least four other species of ferns in the Yale collection have the spores preserved. All retain their natural brown color, and something of their food contents, and, as far as appearances are concerned, might be spores from living plants.

* Geol. Surv. of Illinois, vol. iv, p. 408, pl. xv, figs. 1 and 2, 1870.

Some of the larger spores have granular bodies within or clinging to them, which show a dark spot at the center and something of the structure of concentric starch grains.

The spores from a large number of fronds of two species have been examined in order to find whether or not there were indications of more than one kind of spores. The species studied were *Pecopteris* (*Ptychocarpus*) *unita* Brongn., and the form referred doubtfully by Lesquereux to *P. villosa* Brongn.,* which probably belongs to the *Asterotheca* division of *Pecopteris*. Both species are extremely abundant at Mazon Creek, and the sporangia-bearing fronds numerous. The spores of *P. villosa* are small, measuring only ·013 to ·016^{mm}, smooth and spherical. The exospore is very thin. The spores of the European examples of *P. unita* have already been made known by Renault.† The spores of the specimens at hand are ·016 to ·018^{mm} long, and ·010 to ·011 wide, being elongate or bean-shaped when seen from the side. The exospore is thick and smooth. The three radiating lines at the apex can be seen on some spores. As in other Marattiaceous ferns, the spore output to the sporangium in both species was evidently very great. The spores from many specimens of both species and from various parts of the same specimen present no differences in structure, size, or sculpturing, that could be interpreted as indicating two kinds of spores. It is, therefore, practically certain that both were homosporous, and this is exactly what might be expected in typically Marattiaceous ferns. The fact is of interest in connection with Renault's paper referred to above, in which unusual conditions are observed in one of the European species of *Pecopteris*. The fern described by Renault, which is of the *Asterotheca* division or sub-genus of *Pecopteris*, has one set of spores which are smooth and marked at the apex by three radiating lines. These are considered megaspores. In the same sorus, and possibly in the same sporangium, are other spores of about the same size, thought to be microspores, which lack the lines at the apex and show structures interpreted as the mother cells of antherozoids.

The second paper by the same author describes somewhat similar appearances in *Parkerioidea*. The megaspores are smooth and show the triradiate lines at the apex. The microspores, found in the same sporangium, lack the lines, and are sculptured with a polygonal network.

The three radiating lines are seen on the spores of all the ferns examined by the writer, when viewed from the apex, and

* According to Mr. Robert Kidston, Fossil Flora of the Radstock Series, Trans. Roy. Soc. Edinburgh, vol. xxxiii, Part II, 1886-7, p. 37, *P. villosa* has a doubtful existence, having been established in all probability on a villous specimen of *P. oreopteridia* or a closely related species.

† Bassin Houiller et Permien d'Autun et d'Epinoe, Pt. II, p. 10.

on both micro- and megaspores of *Selaginella*, and the Carboniferous Lycopods, as well as on such heterosporous living ferns as *Marsilea*. The tetrahedral division of the spore mother cell, of which the three radiating lines are indicative, is well known to be extremely constant, not only for the Pteridophytes, but for all those plants commonly grouped under the Archegoniateæ, and for the microspores of most of the flowering plants.*

The lines, therefore, cannot be considered characteristic of, or in any way distinguishing megaspores. Their absence in some cases may be due to imperfect preservation, or they may be obscured by the view of the spore presented. In the case of *Parkerioidea*, there is some doubt as to whether it is not possible that the spores when seen from the apex present the lines and a smooth face, and when seen from the base are sculptured, the lines being obscured by the thickness of the spore.

The recent studies of Prof. Bower† have directed attention to the importance of the size of the spores and the number to the sporangium. Bower's investigations show that among living ferns an increase in the size of the spores, correlated with a decrease in the output to the sporangium, accompanies, in a general way, the advance in development and specialization from the Marattiaceæ through the various families of the Leptosporangiate ferns. The little that is definitely known of the spores of fossil ferns supports Bower's conclusions. It is a question, however, how far the size and number of the spores may be relied upon to separate Marattiaceous from non-Marattiaceous ferns.

The spores of *Pecopteris villosa* are smaller than those of such living Marattiaceæ as *Angiopteris evecta*, *Kaulfussia*, *Marattia Douglassii*, or *Danæa moritziana*. *Crossotheca* and *Myriotheca* have much larger spores, comparable in size to many of the Leptosporangiate ferns. It is hardly possible, with fossil ferns, to count the number of spores to the sporangium, but it is evident that in the case of *Pecopteris unita* and *P. villosa*, the output to the sporangium was very great, while that of *Crossotheca* and *Myriotheca* was comparatively small.

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* See Campbell, University Text-book of Botany, 1902, pp. 199 and 323.

† Studies in the Morphology of Spore-Producing Members, Parts III and IV, Phil. Trans. Roy. Soc., vol. clxxxix, 1897, pp. 35–81 ; vol. cxcii, 1899, pp. 29–138.

EXPLANATION OF PLATE VII.

FIGURE 1.—*Crossotheca sagittata;* part of a fertile frond. The lower and the upper pinnules on the right hand side show the expanded base. The second pinnule from the base on the same side gives the full length of the sporangia. × 1½.

FIGURE 2.—Same species; a pinnule with the matrix removed to show the full length of the sporangia. × 2.

FIGURE 3.—Same species; a medium sized pinnule seen from the base and side. × 2.

FIGURE 3*a*.—A single sporangium. × 4.

FIGURE 3*b*.—Spores of the same species. × 240.

FIGURE 3*c*.—Cross section of a fertile pinnule with sporangia. × 2.

FIGURE 4.—*Crossotheca trisecta* sp. n.; fertile and sterile parts of frond. × ½.

FIGURES 4*a*, 4*b*.—Fertile pinnules of *C. trisecta*.

FIGURE 4*c*.—Spore of *C. trisecta*. × 240.

FIGURE 5.—*Myriotheca scaberrima;* fertile pinnules. × 2.

FIGURES 5*a*–5*c*.—Spores of the same species. × 240.

FIGURES 5*d*, 5*e*.—Starch grains from the spores of the same species. × 240.

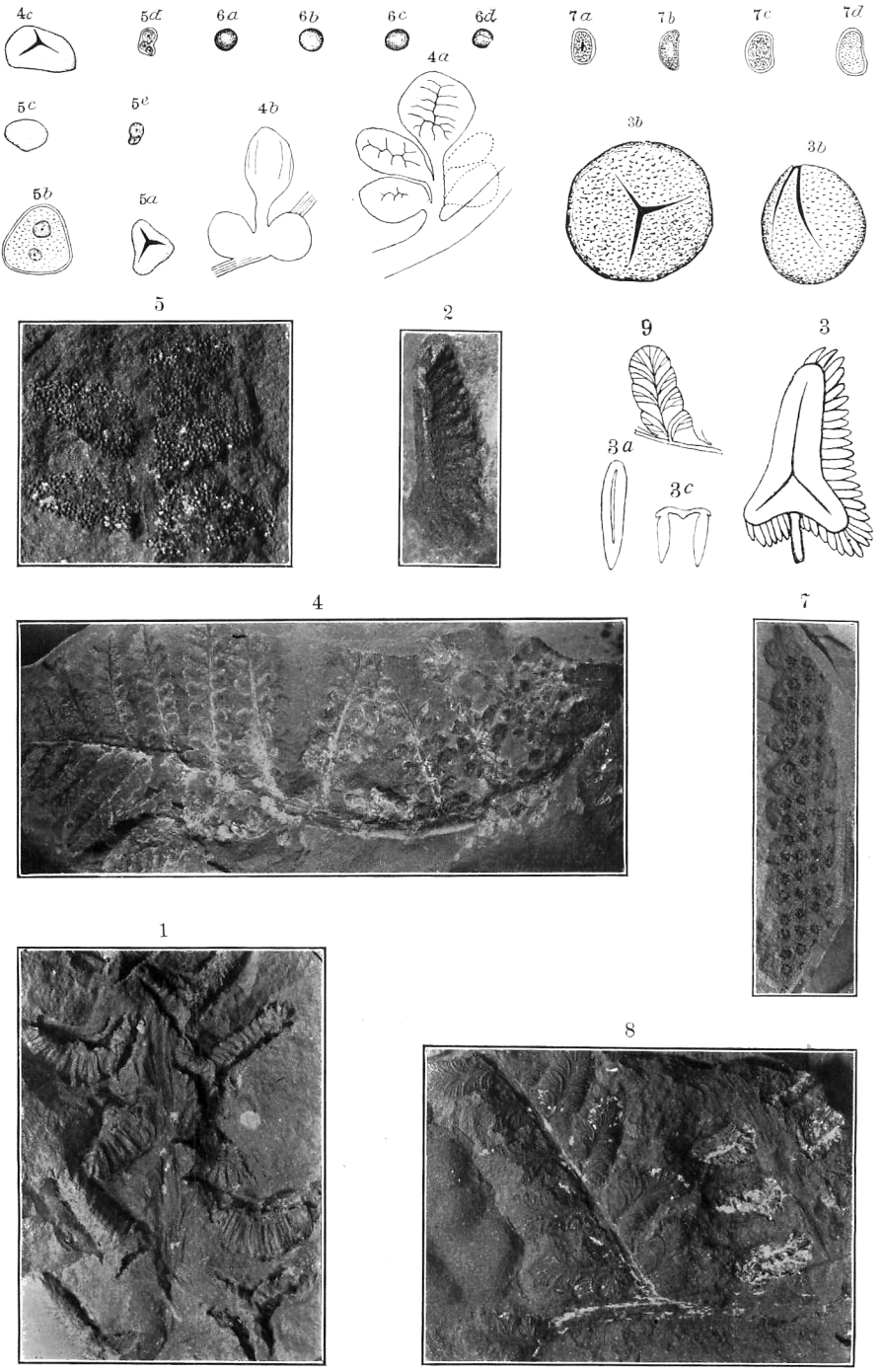
FIGURES 6*a*–6*d*.—Spores of *Pecopteris villosa*. × 240.

FIGURE 7.—*Pecopteris unita;* fertile pinna. × 2.

FIGURES 7*a*–7*d*.—Spores of the same species. × 240.

FIGURE 8.—*Crossotheca sagittata;* fertile and sterile parts in connection.

FIGURE 9.—*Crossotheca trisecta;* sterile pinnule. × 2. [× 1½.



Carboniferous Ferns.