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OBSERVATIONS ON FOSSIL PLANTS
FROM THE DEVONIAN
OF EASTERN NORTH AMERICA
VI. *XENOCLADIA MEDULLOSINA* ARNOLD

BY

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CONTENTS

Introduction	297
Description of new specimen	298
Comparison with other forms	300
Systematic descriptions	303
<i>Xenocladia</i> Arnold, emend.	303
<i>Xenocladia medullosina</i> Arnold	303
Affinities	303
Literature cited	306
Plates	(after) 307

INTRODUCTION

IN 1940 the author founded the genus *Xenocladia* on the basis of petrified plant fragments of unknown affinity from the Middle Devonian Tully pyrite of Erie County, New York. Although anatomical details are preserved with remarkable clarity, the specimens are too small to show the size or form of the original plant. A new specimen submitted in 1950 by Mr. Rudolph Kopf, of Buffalo, New York, does throw light on these characters as well as indicating affinity with the Cladoxylaceae. This specimen came from Cazenovia Creek near the town of Springbrook, in Erie County. It is from the Ludlowville formation of the Hamilton group of the upper Middle Devonian. It is slightly older than the original material from the Tully pyrite; the Tully pyrite is separated from the Ludlowville beds by the Moscow shale which is about fifty feet thick. The exact position within the Ludlowville formation is not on record, but pyritized plant fragments occur throughout the Hamilton of Erie County from the basal Ledyard member of the Ludlowville formation to the Tully pyrite which is at the top.

DESCRIPTION OF NEW SPECIMEN

The new specimen consists of a portion of a stem preserved within a limestone nodule which had become broken in such a manner that the interior of the stem was exposed. The preserved part measures about 1 cm. thick by 5 cm. wide by about 10 cm. long. It is impossible to estimate accurately the original size, but the stem was evidently a large one, for the preserved piece appears to represent mostly tissues that were near the surface. The curvature of the outer surface indicates a diameter of about 10 cm. or more, if the stem were round. There is little evidence of much flattening during preservation, but whether the original form was cylindrical is unknown. There is some reason to suspect that the stem grew in a horizontal position and if it did it was probably not round. If the preserved part represents as much as half of the original, the stem was about 2 by 5 cm. Probabilities are that it was larger. The tissues exposed along the broken surface have been considerably damaged by weathering. Consequently, the outer part, which was protected by the limestone matrix, is better preserved. The epidermis and probably some of the underlying tissues are missing, perhaps having been removed by decay or abrasion before submergence.

Although the specimen appears to have once been completely enclosed within a calcareous matrix, the tissues themselves are infiltrated with iron sulphide (marcasite) and calcium carbonate in about equal amounts. Microscopic examination is difficult except in the calcified parts. Structural details can be observed quite satisfactorily in the calcified parts, but the distribution of the two infiltrated minerals is such that none of the vascular strands is wholly calcified (Pl. I, Fig. 2; Pl. II, Fig. 4). As a result, reflected light must be used to observe whole bundles or larger tissue areas. With transmitted light the parts containing marcasite show only as distracting black regions that effectively camouflage the structural pattern.

Transverse surfaces reveal a polystelic* axis which consists of a peripheral layer of radially elongated vascular strands that flank

*The term "polystelic" applied to *Xenocladia* is used in a purely descriptive sense and does not imply that each strand represents a separate stellar system.

an interior containing strands varying from oblong to round (Fig. 1; Pl. I, Fig. 1). Some of the interior strands are as long as the shortest peripheral strands and appear to be oriented for the most part at right angles to them. This constitutes the evidence, mentioned above, that the axis grew horizontally, but the specimen is too incomplete for it to be conclusive. The smaller of the interior bundles are less than 1 mm. in diameter. The peripheral bundles are larger, some measuring 2 by 7 mm. in cross dimensions. Most are straight or slightly curved, but some are U-, L-, and Y-shaped (Fig. 1). Others are constricted at the inner end, which suggests that the strands divide to form smaller ones in the interior of the stem.

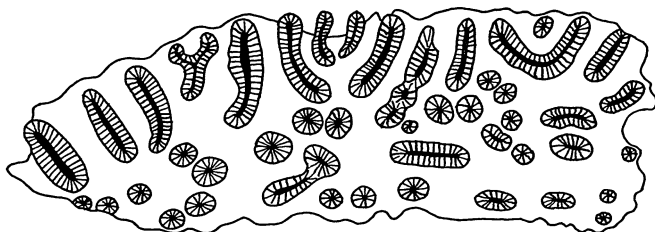


FIG. 1. Diagram of cross section of stem of *Xenocladia medullosina* Arnold, showing form and arrangement of the vascular strands and the approximate extent of the primary and secondary xylem. $\times 2$.

The peripheral strands probably do make up a bundle system, but connections between them are few and on the surface of the stem the strands extend parallel to each other as far as they can be followed (Pl. II, Fig. 3). In this respect they strongly resemble the condition in *Pietzschia*, a polystelic stem, described by Gothan (3) from the Upper Devonian, on which the peripheral bundles produced surface ribs reminiscent of those of a *Calamites* cast. The parenchyma in which the bundles are embedded is preserved in some places and where infiltrated with calcium carbonate can be seen with transmitted light (Pl. II, Fig. 4). This tissue is uniformly constructed and is composed of round or oval thin-walled cells and intercellular spaces filled with dark material. No sclerenchyma has been observed.

Little can be said concerning the structure of the vascular strands

in addition to that given in the original account (Arnold, 1). Each strand is an axis completely invested with secondary wood but without pith. The center is occupied by the primary xylem. In the smallest bundles, such as those described (1), the primary xylem consists of only a few cells without intervening parenchyma and the secondary xylem extends as rows of radially aligned cells almost to the center. In the larger strands the amount of primary xylem is greater; in some of the peripheral ones it consists of an internal strip of tissue which is one-fourth to one-third as wide as the whole strand (Pl. I, Fig. 2; Pl. II, Fig. 1). The number of protoxylem areas appears to vary with the size of the strands. The smallest strands show only one, but the oval and elongate ones seem to have more. The exact number is obscured by the opaque mineral matter that is present in parts of every strand. Each bundle is surrounded by a thin tissue zone that evidently was phloem, but the structure has either become lost by decay or been rendered invisible through mineralization. Wherever preserved, it appears to be a band of thin-walled cells almost one-third of a millimeter wide.

The secondary xylem is a compact tissue of regularly arranged tracheids that range from 20 to 60 microns in diameter (Pl. II, Fig. 1). They average about 40 microns in diameter. There is no visible parenchyma, either as separate cells or in the form of rays. If rays are present in any form, they are very small and rendered obscure by disintegration and mineralization of the cells. Longitudinal sections show that the tracheid walls bear one or two rows of bordered pits, which are alternately arranged when biseriate (Pl. II, Fig. 2). The tracheid-wall complexes, wherever measured between lumina of adjacent cells, are at some places as much as 17 microns thick but at most places thinner.

COMPARISON WITH OTHER FORMS

Polystely is a phenomenon, first appearing in the Devonian, which is exhibited by a number of late Paleozoic genera. It is an ancient character that may have developed among plants not far removed from the psilophytic complex. Paleozoic polystelic stems that bear some resemblance to *Xenocladia* are *Medullosa*, *Cladoxylon*,

Steloxylon, and *Pietzschia*. In the original description *Xenocladia* was compared with *Medullosa*, but the new specimen brings it closer to *Cladoxylon*. Aside from the gross polystelic structure, the only feature that furnishes any basis for comparison between *Xenocladia* and *Medullosa* is the multiseriate pitting on the tracheid walls. In all other respects the differences between them far outweigh the resemblances. Outstanding among the differences are the structure of the primary wood and the leaf bases. There are also important differences in the secondary xylem. In *Xenocladia* the secondary xylem is composed of small compactly placed tracheids and inconspicuous rays. The number of steles in the medullosas, especially in the Pre-Permian examples, is fewer than in *Xenocladia*, there ordinarily being only two or three. Moreover, there is no evidence that *Medullosa* or any of its near relatives was in existence during Devonian times.

Xenocladia resembles some species of *Cladoxylon* in being supplied with a well-defined set of peripheral vascular strands which extend lengthwise in the stem for a considerable distance. In both genera each stele has its own layer of secondary wood that completely surrounds the primary part. The rather pronounced eccentricity of the secondary xylem displayed in most species of *Cladoxylon* is not evident in *Xenocladia*. In *Xenocladia* the secondary xylem is approximately of equal thickness on all sides, except that it appears to be slightly thinner on the extreme outer surface of the peripheral bundles than elsewhere (Plate II, Fig. 1). There are three differences of greater importance between *Xenocladia* and *Cladoxylon*, however, that are believed to be sufficient to keep the two genera completely separate. The first is the difference in tracheid-wall sculpturing, which is scalariform in *Cladoxylon* instead of pitted. The second is that there is no evidence in *Xenocladia* of the type of foliar traces exhibited by *Cladoxylon*, although it must be admitted that the absence of traces in the present material may be due to lack of preservation. The third is the absence in *Xenocladia* of the "peripheral loop" in the primary xylem, an important morphological feature in *Cladoxylon*. The very small primary xylem masses in *Xenocladia* are solid tissues without visible parenchyma. The lack of a peripheral loop in *Xenocladia* is hardly sufficient to exclude the plant from the

Cladoxylon alliance, because its absence might represent a primitive condition, but the compact character of the secondary xylem, which consists mainly of bordered pits, is a sound generic difference.

Less is known of *Steloxylon* and *Pietzschia*, the two remaining genera with which *Xenocladia* can be compared. The name *Steloxylon* was originally applied by Solms-Laubach to material believed to be of Permian age. Bertrand (2) subsequently recognized it in the Saalfeld flora, and Read and Campbell (6) assigned two species from the New Albany shale to this genus. Although Solms-Laubach (8) described *Steloxylon Ludwigii*, the type species, in some detail, it has not been fully figured by anyone. Seward (7) gave a summary of its structure and reproduced Solms-Laubach's figures. In view of the lack of adequate figures of the type species, one questions whether the material from Saalfeld and the New Albany shale, which is considerably older, should be assigned to *Steloxylon*. One hesitates even more to identify anything as old as Middle Devonian with this genus.

Even though existing accounts of *Steloxylon* omit much that is desirable, the small amount of primary xylem and the alternate pitting are points of close resemblance to *Xenocladia*. Both genera differ from *Cladoxylon* in the two characters. A conspicuous difference between *Xenocladia* and *Steloxylon* is the straight and seemingly parallel course of the vascular strands in *Xenocladia*; the complicated anastomosing pattern in *Steloxylon* presents a sharp contrast. Another difference, revealed by the published figures of *Steloxylon*, is the lack of radially elongated peripheral strands; this, in spite of Seward's remarks that some of the strands are bandlike. Even though Seward regarded *Steloxylon* as being closer to *Medullosa* than to any other genus, the only resemblances between them worthy of note are the polystelic character and the bordered pits in the wood. Consequently, the author follows Bertrand (2) in assigning *Steloxylon* to the Cladoxylaceae.

The genus that most closely resembles *Xenocladia* is *Pietzschia*, from the Upper Devonian of Wildenfels, Saxony (Gothan, 3), and from the New Albany shale of Kentucky (Read and Campbell, 6). The resemblance is strong; the main difference is the lack of secondary wood in *Pietzschia*. In both genera the radially elongated peri-

pheral strands produce vertical ribs on the surface of the fossils which resemble those on medullary casts of *Calamites*. A minor difference between *Xenocladia* and *Pietzschia polyupsilon*, the New Albany shale species, is that in *Pietzschia* the interior of the stem does not contain bundles but a few sclerenchyma strands. In the medullary region of *P. Schüllerii* the bundles are less numerous than in *Xenocladia*.

Pietzschia, although it lacks secondary xylem, is certainly the closest of all polystelic genera to *Xenocladia*. Barring a possible difference in trace form the differences are no greater than those that distinguish some of the species of *Lepidodendron*. In light of the present knowledge of the structure of *Pietzschia* and in view of some slight differences that are exhibited, however, it seems desirable to maintain *Xenocladia* as a distinct genus.

SYSTEMATIC DESCRIPTIONS

Xenocladia Arnold, emend.

Plants with polystelic stems some of which attain a diameter of at least 4 cm., with numerous radially elongated peripheral strands and round, oval, or elongated strands occupying the parenchymatous interior; each bundle completely invested with secondary xylem made up of pitted tracheids and a narrow phloem zone; primary xylem solid and small in amount; bundles parallel with each other and straight.

Xenocladia medullosina Arnold

Peripheral strands about 15, up to 7 mm. long (in radial extent); medullary strands numerous and small, in many instances 1 mm. or less in diameter; primary xylem conforming to shape of bundle, without pith or included parenchyma; secondary xylem without evident rays, consisting of radially aligned, thick-walled tracheids, equally developed on all sides of bundle; ground tissue parenchymatous.

AFFINITIES

Xenocladia is included here as the sixth member of the Cladoxy-laceae as the family has been redefined by Bertrand (2). The other

five are *Cladoxylon*, *Asteropteris Voelkelia*, *Steloxylon*, and *Pietzschia*. *Xenocladia* was originally placed in the "Steloxylaceae" (Arnold, 1), but until more is known about the structure and affinities of the genus *Steloxylon*, utilization of a family name based upon it should be postponed. *Xenocladia* would certainly be out of place in the medullosan family. Assemblage of the six genera named above into the Cladoxylaceae constitutes the most satisfactory grouping possible under present circumstances.

The Cladoxylaceae, as Bertrand has outlined it, consists of very ancient plants with polystelic stems. In transverse section, the vascular system appears to consist of numerous separate strands, each composed of primary xylem completely surrounded by secondary xylem. The central strands are irregular in size and shape and evidently constitute an anastomosing system. The peripheral strands are radially elongate.

The simplicity of the vascular strand in *Xenocladia* is strongly indicative of a psilophytean origin. The general organization of the stem, however, is more complex than in any known psilophyte. The evolution of the polystelic stem probably began with a deeply fluted stele in which peripheral segments became separated from the central part. Further dissolution brought about a complete breakdown of the central part into small separate strands. If a cambium was present at the time the breakup began, the cambium expanded and a portion of it accompanied and surrounded each strand as it became a separate entity. The beginning of such a trend is to be seen in *Schizopodium* (Harris, 4).

In *Schizopodium* the lobes of xylem consist (in part) of serially aligned, pitted tracheids, which are suggestive of secondary wood but reveal no actual evidence of having originated from a cambium. The best-preserved portions of *Schizopodium*, according to Harris, show no cambium, and the explanation given for the orderly sequence of the cells is that they probably resulted from the cell arrangement in the terminal meristem. Such a sequence of cells could only have come about by lateral division, whether it be in a cambium or in the meristem before the formation of cambium as a tissue. If in the meristem, then the cambium may be construed as having originated

from leftover meristem which continued to perform after the adjoining tissues had become fully differentiated. It is possible that cambium and secondary growth may have originated in some such way and that certain vascular plants, as *Schizopodium*, illustrate the initial development. By the time the *Xenocladia* and *Cladoxylon* stages had been reached the cambium was fully developed.

In making comparisons between *Schizopodium* and other ancient vascular plants Harris stressed the points of agreement between *Schizopodium* and early members of the *Cladoxylon* complex. He regarded the Cladoxylaceae as a family of robust plants belonging to the psilophytalean group. If *Asteroxylon* had not been known, he said he would have placed *Schizopodium* in the Cladoxylaceae instead of in the Asteroxylaceae.

The evolutionary series depicting the derivation of a polystelic axis from a simple psilophyte would commence from *Asteroxylon*, with its lobed xylem strand in the aerial shoot and a cylindrical one in the rhizome. In *Schizopodium* the invagination of the xylem was carried to a point where some lobes had become detached, the first step toward polystely. Then, in the two Devonian species *Cladoxylon scoparium* and *C. Dawsoni* (5) the dissection became still more pronounced with more of the lobes having become detached and with a decided tendency toward radial elongation of the bundles. In *Xenocladia*, *Pietzschia*, and *Steloxylon*, and in the early carboniferous species of *Cladoxylon* the separation of the strands had become complete. In some genera of the Cladoxylaceae there is a fairly definite segregation into a set of radially elongated peripheral bundles and rounded or irregular medullary ones. This last stage was achieved by *Xenocladia* in late Middle Devonian time.

There is one slight discrepancy, however, and that is in the appropriateness of making *Schizopodium* a link in the series. The simple breaking up of the *Schizopodium* xylem into separate strands ought to produce a bundle complex with secondary growth limited to the peripheral surfaces. But to develop the *Cladoxylon* type of structure, a lobed stele with secondary growth conforming to the irregular outline is required. In *Schizopodium* the regularly seriated tracheids are confined mostly to the extremities of the lobes. In deriving the

Cladoxylon strand from a *Schizopodium* lobe, it is necessary to assume that when the separation occurred, the cambium or whatever was responsible for the orderly arrangement of the tracheids extended itself completely around the lobe. This may not prove to be an unsurmountable difficulty, even though at present no fossil forms have been described showing this process.

LITERATURE CITED

1. ARNOLD, C. A. 1940. Structure and Relationships of Some Middle Devonian Plants from Western New York. *Amer. Journ. Bot.*, 27: 57-63.
2. BERTRAND, P. 1935. Contributions a l'étude de Cladoxylées de Saalfeld. *Paleont.* 80 (B): 110-90.
3. GÖTTAN, W. 1927. Strukturgebietende Pflanzen aus dem Oberdevon von Wildenfels. *Abh. Säch. Geol. Landes.* 3: 1-12.
4. HARRIS, T. M. 1929. *Schizopodium Davidi* gen. et sp. nov.—a New Type of Stem from the Devonian Rocks of Australia. *Phil. Trans. Roy. Soc. London, B*, 217: 39-410.
5. READ, C. B. 1935. An Occurrence of the Genus *Cladoxylon* Unger in North America. *Journ. Wash. Acad. Sci.*, 25: 493-97.
6. READ, C. B., and G. CAMPBELL. 1939. Preliminary Account of the New Albany Shale Flora. *Amer. Midl. Nat.*, 21: 435-48.
7. SEWARD, A. C. 1917. *Fossil Plants*, Vol. 3. Cambridge Univ. Press.
8. SOLMS-LAUBACH, H. 1910. Über die in dem Kalksteinen des Kulm von Glätzisch-Falkenburg in Schlesien erhalten strukturbietenden Pflanzenreste. IV. *Völkelia refracta*, *Steloxylon Ludwigi*. *Zeitsch. Bot.*, 2: 529-54.

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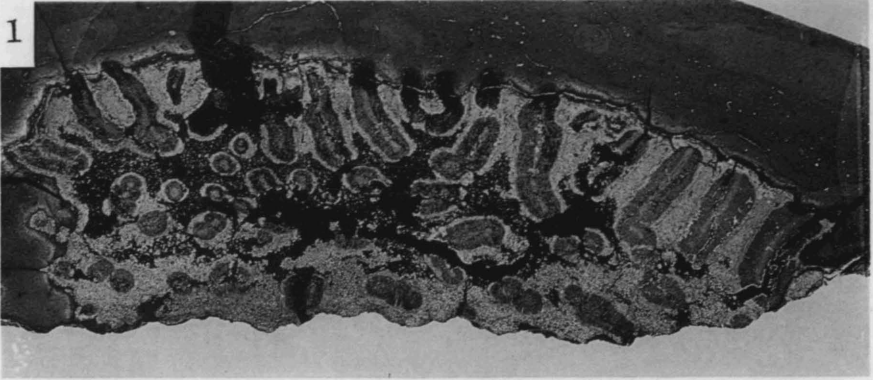
PLATES

EXPLANATION OF PLATE I

	PAGE
<i>Xenocladia medullosina</i> Arnold	303
FIG. 1. Transverse section. Photographed by reflected light. \times 2.	
FIG. 2. Mid-portion of transverse section, the dark part showing the extent of pyrite infiltration. Photographed by transmitted light. \times 10.	

PLATE I

1



2

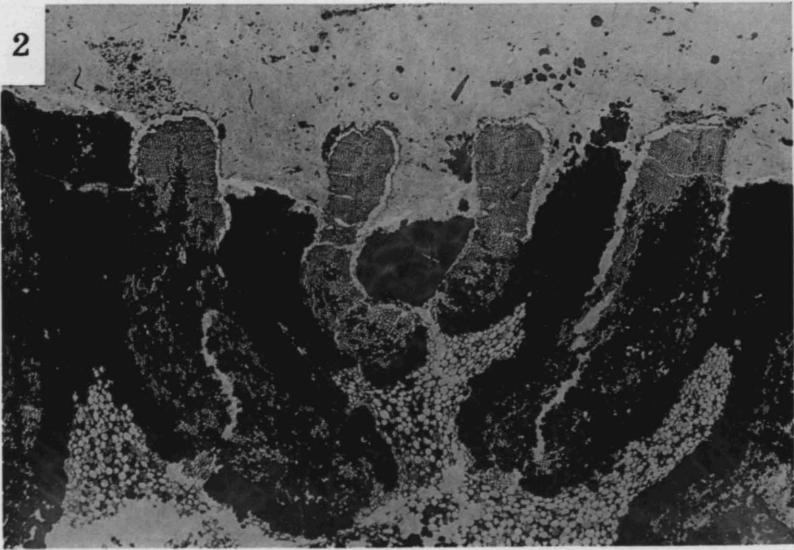
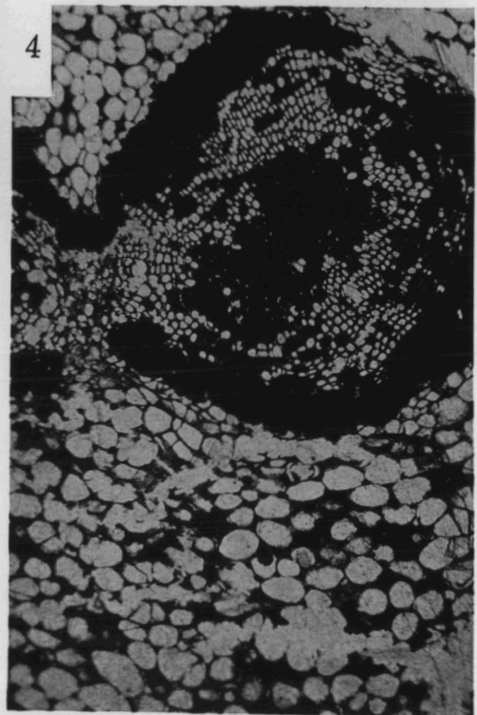
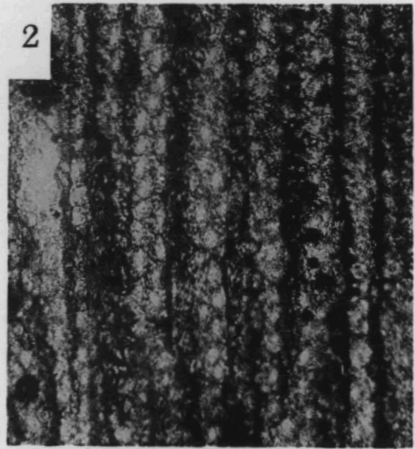
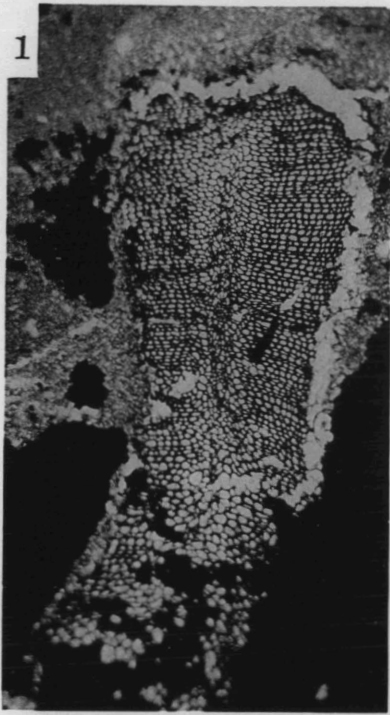


PLATE II



EXPLANATION OF PLATE II

	PAGE
<i>Xenocladia medullosina</i> Arnold	303

FIG. 1. Outer part of peripheral strand, showing thin strip of primary xylem and secondary xylem developed almost equally on both sides but thinner on outer extremity. The opaque portions represent pyrite infiltrated tissue. Areas showing cell structure are calcified. Photographed by transmitted light. $\times 33$.

FIG. 2. Radial longitudinal section of strand (tangential to main axis), showing remnants of biseriate pitting on tracheid walls. Photographed by transmitted light. $\times 110$.

FIG. 3. Part of outer surface of stem exposed by breaking away the limestone matrix, showing the parallel course of the peripheral strands. Natural size.

FIG. 4. Bundle of interior, showing partial pyritization of the tissues. Photographed by transmitted light. $\times 33$.

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