

PSEUDOSPOROCHNUS NODOSUS SP. NOV., A MIDDLE DEVONIAN PLANT WITH CLADOXYLALEAN AFFINITIES

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WITH PLATE 1-10 AND 7 FIGURES IN THE TEXT AND ON 2 FOLDERS



Contents

	Page
I. Abstract	2
II. Introduction	2
III. Previous records and interpretations	3
IV. Stratigraphy and material	5
V. Description of the external morphology	7
1. Terminology	7
2. Branches of the first order (formerly called stem)	9
3. Stems (new)	9
4. Crown of stem (new)	10
5. Roots (new)	10
6. Branches of the second and third order	11
7. Fronds-vegetative	13
8. Fronds-fertile	13
VI. Summary of external morphology and reconstruction of the plant	14
VII. Description of anatomical structure	14
1. Gross appearance of petrified specimens	15
2. Technique	15
3. Detailed description of anatomical structure	15
a. Gross configuration	17
b. Details of xylem structure — branch of second order	18
c. Mode of emission of a leaf trace	20
d. Details of xylem structure — branch of third order	20
e. Details of xylem structure — branch of first order	21
f. Cortical structure	21
g. Longitudinal sections	21
h. Stem	21
i. Root	21

	Page
VIII. Diagnosis	21
IX. Discussion	22
1. General comments	22
2. Comparison of <i>P. nodosus</i> with other species on the basis of external morphology	24
3. Comparison with other genera on the basis of anatomy	25
4. Affinities of <i>Pseudosporochnus</i>	28
X. Summary	29
XI. Literature Cited	30
XII. Explanation of plates	31

I. Abstract

This paper reports a large collection of *Pseudosporochnus* from the Middle Devonian at Goé, Belgium. New information on roots and trunk indicate that the plant probably grew as a much-branched, small tree. Detailed descriptions are given for the ultimate appendages (fronds), both sterile and fertile, which are bilaterally symmetrical. Anatomical structure is shown to be cladoxylalean. *Pseudosporochnus* can no longer be regarded as a psilophyte. *P. nodosus* sp. nov. is proposed for the Belgian fossils.

II. Introduction

The present investigation is designed to give a fuller account than has hitherto been possible of the external morphology, anatomy and fructifications of *Pseudosporochnus*. Further we propose to review and discuss the suggestions that have been made concerning the phylogenetic position of this interesting Middle Devonian plant in monographs and in standard textbooks of Plant Morphology and Paleobotany.

The study is made possible by a large collection of more than 534 specimens collected from a single outcrop in Belgium.

Special interest in this collection is provided by the discovery, for the first time, of petrifications that disclose anatomical features indicative of affinity with the Cladoxylales.

We are indebted to the "Fonds National de la Recherche Scientifique de Belgique" for financial support for the two field trips (1949 and 1952) conducted by LECLERCQ during which the collections were made.

We want to thank the "Conseil d'Administration de l'Université de Liège" for valuable assistance, especially with regard to the photographic and microscopic equipment: the Linhof "Cardan" camera (18 × 24 cm) particularly useful for large specimens, and the Leitz "Ortholux" for microscopic observations and photography under strong reflected light.

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We wish to express our gratitude to Mr. MAURICE DISCRY, Chief Preparator in the Laboratory of Paleontology of the University of Liège, for his skilled and devoted assistance during the course of this study; also to Mr. JOSÉ LEWALLE, Assistant in the same Laboratory, for his enthusiastic help. To M. JEAN DAMBLON, Hortonom in the Institute of Botany of the University of Liège, we express warm thanks for his reconstruction of a branch of the second order with fertile and sterile fronds and his reconstruction of the entire plant.

III. Previous Records and Interpretations

KREJCI (1881) described briefly some fossil plants from central Bohemia as an alga, *Chondrites verticillatus*. STUR (1881) wrote a splendid description of the same plants, placing them in the genus of living algae *Sporochnus*, as *S. Krejci* STUR. STUR stated that the ultimate ramifications (side branches) were irregularly arranged on the branches that bore them (p. 14). He noted longitudinal costulations on the larger axes and small elevations or depressions on all axes. He considered that because of its abundant branching, the plant reached a large size (p. 16). POTONIÉ and BERNARD (1904, p. 34) found evidence of tracheids in specimens of *S. Krejci*. They therefore transferred the fossils to the vascular plants and erected a new genus, *Pseudosporochnus*, to receive them. The name then became *P. Krejci* (STUR) P. & B. On the basis of their longest specimen, between 1.5 and 2 meters in length and 20 cm wide at its bulbous base, they considered *Pseudosporochnus* to have been a small tree (pp. 27, 28). All branching in the plant seemed to them to be basically dichotomous and they regarded *Pseudosporochnus* as a possible ancestral form of Psilotaceae. They did, however, realize that the ultimate branchlets might be equivalent to leaves and the swollen terminal tips equivalent to sporangia (p. 36). They speculated that if this were true, *Pseudosporochnus* might be related to the ferns (including pteridosperms) rather than to Psilotaceae (p. 36).

LANG (1927) gave a very clear description of a branch from the Stromness beds in Scotland. Although his specimen bore no ultimate ramifications, it did show the digitate branching characteristic of the axes of *Pseudosporochnus* described by POTONIÉ and BERNARD and by STUR.

HIRMER (1927, p. 176) postulated that a restriction of growth of the rhizome of *Rhynia* led to the type of "corm" found in *Horneophyton* and that still further restriction could produce the bulbous base found on many axes of *Pseudosporochnus*. He recognized that the ultimate branchlets were spirally arranged on the branches but speculated that this was merely the result of more profuse branching in *Pseudosporochnus* than in the two simpler genera. For him, *Pseudosporochnus* was an arborescent form standing at the termination of the psilopsid series. He also suggested that the profuse branching of *Pseudosporochnus* might point the way to the arborescent lycopods.

ZIMMERMANN (1930, pp. 110—113) regarded *Pseudosporochnus* as much more differentiated than the Rhyniaceae although his reconstruction (1930, fig. 45) shows only dichotomous branching in the plant. This interpretation is not supported by the published evidence which makes the spiral arrangement of the ultimate branchlets quite clear. ZIMMERMANN considered *Pseudosporochnus* to be intermediate between the primitive psilopsids and the Protoarticulatae and between the psilopsids and the Primofilices, especially *Cladoxylon scoparium*. Finally, he wrote that because the tips of the ultimate branchlets of *Pseudosporochnus* were flattened, they represented the beginning of phylloid formation.

Later ZIMMERMANN (1959) subdivided the Psilophyta into two orders: I Rhyniales (p. 154) and II Pseudosporochnales (p. 163). He recognized two families in the latter, 1) Pseudosporochnaceae and 2) Svalbardiaceae. He regarded Pseudosporochnales as a "connecting link" between psilophyta and pterophyta, omitting his earlier reference to Protoarticulatae. He maintained that weakly differentiated telomes, still present in Pseudosporochnales, constitute the basis for including them among the psilophytes. On the other hand, the beginnings of a stem and fronds were, for him, the evidence of some relationship to primitive ferns like Protopteridales.

In the description of *Pseudosporochnus*, ZIMMERMANN mentioned "schmale Blättchen oder vielleicht auch Sporangien" as the ultimate segments of the "leaves". We believe he is right despite the fact that he had no evidence at his disposal when he wrote. Like some other authors he seems to have understood intuitively the foliar nature of the tips of the ultimate segments of the leaves.

We cannot agree that *Pseudosporochnus* and *Svalbardia* can be placed in the same order. The fructifications of the two plants have nothing in common as will be pointed out in greater detail below. We

also believe that the organs regarded by ZIMMERMANN as roots of *Pseudosporochnus* are probably portions of xylem strands. His application of the term crown to the cluster of branches originating from the stem is one that we consider particularly appropriate.

SEWARD (1931, p. 134 and fig. 45) adopted the concept that *Pseudosporochnus* is a large plant probably over 10 feet in height.

In 1931 (p. 13) HØEG reported a strange specimen from western Norway. He considered it to be a trunk of *Pseudosporochnus* apparently bearing a crown of branches that had broken off (fig. 2, p. 14). Because the specimen was long (65 cm) and wider (14 cm) than any axes described previously, it lent weight to the suggestions by STUR and by POTONIÉ and BERNARD that plants of this genus were small trees. HØEG, like ZIMMERMANN, placed *Pseudosporochnus* in a position intermediate between the simpler psilophytes and the protoarticates. His basis for this decision was the similar but rather uncommon mode of branching observed in the two genera *Calamophyton* and *Pseudosporochnus*. Both plants have a stout axis abruptly divided into several main branches (pp. 14, 15).

KRÄUSEL and WEYLAND (1933) re-investigated the entire flora of the Middle Devonian of Bohemia and reaffirmed the opinion of POTONIÉ and BERNARD (1904, p. 28) that *Pseudosporochnus* is the most common element of the flora. They noticed the small elevations or depressions on the axis that STUR (1881, pp. 16, 17) interpreted as scars of fallen hairs, but the German authors considered them to be cortical structures (p. 12). Like STUR (1881, Taf. II, fig. 4) and POTONIÉ and BERNARD (1904, text fig. 69) had done earlier, they mentioned some large lacerated specimens from which rigid isolated bands, closely packed and arranged more or less parallel fashion, emerged from the end of the axes. These specimens gave the impression of resistant bundles whose surrounding soft tissues had been macerated away (p. 17). KRÄUSEL and WEYLAND believed that neither POTONIÉ and BERNARD's longest branch nor HØEG's (1931) large axis belonged to *Pseudosporochnus*. They therefore adopted the view that *Pseudosporochnus* is not an arborescent plant (pp. 15, 17). They described (p. 15) tiny spores 4—7 μ in diameter isolated from the matrix containing entangled sporangia of *Pseudosporochnus*. If the spores really belong to this genus, they are the first to be described. KRÄUSEL and WEYLAND (p. 17) wondered about the meaning of the ultimate filiform and thickened branchlets: were they leaves or were they ultimate lateral branchlets? In their opinion the kind of branching supported the latter interpretation. The terminal position of the sporangia made an additional reason for them to classify *Pseudosporochnus* as a psilophyte.

EAMES (1936, p. 319) stressed the importance of regarding *Pseudosporochnus* as a plant body, much branched and more differentiated than other psilophytes. He considered the ultimate branchlets to be equivalent to leaves but to be branched in more than one plane and thus to be very different from the "enation" type of outgrowth that is found in simpler psilophytes. The fact that the sporangia had been described as slight enlargements of the axes bearing them was, for EAMES, a strong argument in favor of classifying *Pseudosporochnus* with the psilophytes.

SMITH (1955, p. 164) accepted the concept that *Pseudosporochnus* might be tree-like in habit and perhaps 3 meters tall.

RENIER (1912) and LECLERCQ (1940) reported the presence of *Pseudosporochnus Krejci* (STUR) P. & B. in Belgium. Two impressions were collected by LECLERCQ at Mousset near Pepinster, a locality that is not discussed in the present paper. The two pieces were fragmentary. The first (# MS. 86) reached 114 mm in length and divided in the usual manner into three secondary branches of almost equal widths; the second (# MS. 59) was 90 mm in length and bifurcated (p. 50). Both fragments showed the small, tangentially elongated scars or elevations observed earlier by STUR and by KRÄUSEL and WEYLAND. The author also described isolated "leaves" that were filiform and repeatedly bifurcated. Some "leaves" had thickened terminal tips. One swollen tip yielded, upon maceration, small dark red bodies (? "spores") whose diameter was 6—9 μ (p. 51). LECLERCQ was inclined to consider *Pseudosporochnus* to be a small tree (p. 52).

LECLERCQ has reexamined the collections from Mousset in the light of the abundant new material from Goé. She found that one specimen may show clearly the closely spaced tangentially elongated elevations or if these were not preserved, depressions in their place or, in some places a perfectly smooth surface.

HOEG (1942, pp. 79, 117, and 1937, p. 548) treated *Pseudosporochnus* as a large, much-branched plant lacking flattened and webbed leaves but possessing sporangia that were merely inflated tips of ultimate, fine ramifications comparable to those of the simpler psilophytes. Considering *Pseudosporochnus* to be an advanced psilophyte, he derived from it *Svalbardia*, a primitive fern whose ultimate branchlets were flattened in one plane (p. 177).

EMERGER (1944, pp. 117, 133) followed ZIMMERMANN in regarding *Pseudosporochnus* as an arborescent psilophyte whose ultimate fine ramifications were flattened like leaflets. He believed that the flattened extremities marked a tendency toward the differentiation of leaves by a basipetal invasion of a cauline organ by a foliar structure (p. 170). This interpretation is very similar to ZIMMERMANN's concept of phylloid formation in *Pseudosporochnus*.

GOTHAN and WEYLAND (1954, p. 75) treated *Pseudosporochnus* as a leafless psilophyte with a vigorous stem surmounted by a crown of branches which exhibit a tendency toward the production of a large assimilation surface.

MÄGDEFRAU (1956, pp. 94, 408) considered *Pseudosporochnus* to be intermediate between the psilophytes and ferns and to possess, like *Aneurophyton* and *Protopteridium*, megaphylls or at least ramifications in three dimensions that can be regarded as incipient fronds.

OBRIHEL (1959, p. 386) pointed out that KREJCI's species name *verticillatus* has priority over STUR's name *Krejci*. He therefore erected the new combination *Pseudosporochnus verticillatus* (KREJCI) OBRIHEL 1959 for the plant. This name will be followed in the present paper. In the same paper (p. 385) OBRIHEL erected a new species, *P. chlupaci* for three specimens in the National Museum at Prague that were previously referred to *P. Krejci*.

Even this brief review indicates the desirability of learning more about the anatomy, the habit, the phyllotaxy and mode of branching of ultimate branchlets, the possible flattening of the tips of the branchlets, and the structure of the sporangia of *Pseudosporochnus*. The results may cast new light on the affinities of the genus and may show whether it is an advanced psilophyte, a plant evolved beyond the psilophytes but still ancestral to one or more higher groups, or whether it should be placed in one of the higher groups such as ferns.

IV. Stratigraphy and Material

Before considering in detail the plant material on which this research is based, a brief resume of the stratigraphy of the region it comes from is pertinent.

In Belgium, the Middle Devonian is subdivided into the older Couvinian and the younger Givetian. These horizons correspond to the middle of the Erian series of the Devonian sequence in North America (COOPER et al. 1942, Chart No. 4).

Fossil plants are abundant in the Middle Devonian of Belgium. A systematic investigation of the unit called "Synclitorium de la Vesdre" has so far revealed more than one hundred plant localities (LIÉGEAIS 1953—1956). This is primarily due to the shallow Middle Devonian seas that deposited several littoral formations during their Northwest transgressions (FOURMARIER 1954, ADERCA 1932, LIÉGEAIS 1953 to 1956). Three major plant-bearing horizons have been identified (LIÉGEAIS 1956, STOCKMANS 1940) two of which are located in the Couvinian and the third at the basal part of the Givetian (ADERCA 1932, LIÉGEAIS 1956). This latter horizon is the best developed and has yielded the *Pseudosporochnus* material described in this paper.

The plant fossils were collected by LECLERCQ during a trip of six weeks in the summer of 1949 and during a trip of four weeks in 1952.

The quarries in which the plants were found, known locally as "Carrières Brandt", are situated in a hillside 400 meters south of the junction of the rivers "La Gileppe" and "La Vesdre" at Goé, a small village about 20 kilometers from Germany and 30 kilometers east of Liège.

The fossiliferous horizon is exposed in the northern quarry and is composed of a sequence of interstratified beds of arkose, shaly sandstone and shale. The entire deposit is lens-shaped with a thickness of about 10 meters (LIÉGEois 1956, p. 120), resting conformably on the reddish sandstone of the uppermost Couvinian. So far seven plant-bearing zones have been located.

Each plant-bearing zone varies from irregular to lenticular beds 45 centimeters to 1.10 meters in thickness. The beds split readily into thinner layers, along numerous, flat bedding planes. In composition, the layers are formed of greenish or grey-blue shaly sediment.

Plant remains are found throughout the whole deposit but occur most abundantly in beds number VI, IV and III. In each bed, the splitting of the shale gives evidence of a great variety of facies and state of preservation. In many layers large specimens occur with delicate organic connections still retained, indicating a sub-autochthonous deposition in quiet water, while in others the plant fragment appear to be drifted.

An abundant flora is distributed throughout and is preserved as compressions of which some have petrified segments impregnated by iron hydroxide.

It is obvious that as a paleontological unit the Middle Devonian deposit of Goé is unlike any previously recorded formation except, perhaps, in Bohemia "l'Etage H-h, de BARRANDE" that has yielded a similar flora (STUR 1881, POTONIÉ and BERNARD 1904, KRÄUSEL and WEYLAND 1933).

For that reason, one of the authors (S. LECLERCQ) intends to write later a detailed account of the plant associations, the ecology, lithology and sedimentary facies of the Middle Devonian at Goé in relation to the peculiar features of the geology and stratigraphy of the "Synclinorium de la Vesdre" that are particularly significant.

It is well known that similar assemblages of plants have been found in the Middle Devonian of Germany in the Honseler Schichten and Brandenburg Schichten, and their flora has been beautifully described by KRÄUSEL and WEYLAND. It is, however, too early to correlate the Belgian plant horizons with the German ones. Presently German geologists are reviewing the Devonian formation of the "Synclinorium de la Vesdre" that extends into Germany and they still hesitate to establish a correlation with the Devonian of Rhineland. Therefore, at the present time, it seems justified to refrain from long-distance correlations. Nevertheless in the present state of our knowledge it may be suggested that the Honseler Schichten could represent the plant deposit of the basal part of the Belgian Givetian while the Brandenburg Schichten should be referred to the plant-bearing beds of the Middle Couvinian of Belgium (LIÉGEois 1956).

POTONIÉ and BERNARD (1904, p. 28) remarked that *Pseudosporochnus* was by far the most abundant plant in the beds in which it was found in Bohemia. The same is true for collections made in Belgium. Available for the present study were 534 specimens. The majority of these included part and counterpart, hence there were approximately 267 collection numbers. In a series of careful preliminary studies we selected 264 specimens (approximately 132 collection numbers) for further examination.

The shaly sandstone contains occasional fresh water ostracoderm plates (# 587) and crossopterygian fish scales (# 568).

It may be of some interest to mention that in another outcrop located nearby (Eupen Station) and in the same stratigraphical horizon, a crossopterygian scale has been found and identified by Professor ERIK JARVIK of the University of Stockholm. The scale belongs to the genus *Glyptolepis*, a fresh water fish, very common in the upper beds of the Middle Devonian (LECLERCQ, in LIÉGEois 1956, p. 119).

As has been stated, preservation is mainly as compressions (WALTON 1936). Parts of some axes, however, are petrified by iron hydroxide. On these particularly valuable specimens, xylem and cortex are well preserved. Frequently only the cell wall is petrified, the lumen being empty. When dry, these remains are extremely fragile, disintegrating into dust particles unless handled with extreme care.

The problem of preparing them for microscopic examination was solved by the use of an embedding technique in translucent plastic (LECLERCQ and DISCRY 1950, LECLERCQ and NOEL 1953). Small pieces were embedded and then ground and polished. These have given excellent surfaces for microscopic studies under strong reflected light (see Anatomy, p. 15).

V. Description of the External Morphology

1. **Terminology:** — Up to now *Pseudosporochnus* has consisted of axes, bulbous at the base and divided digitate-fashion at the apex. These have been called the stem. The narrower branches arising from the apex of this stem have simply been called branches or possibly pinnae. Appendages (lateral ramifications) borne on these smaller branches have been described variously as leaves, ultimate branchlets, dichotomized ramifications of the branches, pinnules and so on. STUR and later POROMÉ and BERNARD recognized that these ultimate appendages are irregularly or probably spirally arranged.

We propose to include still another, larger, axis as part of the plant body of *Pseudosporochnus* and to call it the main stem (text fig. 7). It is necessary, therefore, to propose a new term for the axes, described above, that have previously been thought to be the stem. The term we suggest is branches of the first order (text fig. 7). The branches that arise digitate-fashion from the apex of branches of the first order will be called branches of the second order (figs. 2, 7, 9, 10; text figs. 3, 7). The branches produced by dichotomous forking of branches of the second order will be called branches of the third order (text fig. 7 and figs. 24, 25). The spirally arranged ultimate appendages will be called fronds (text figs. 1, 2, 3 and figs. 9, 24—30).

2. **Branches of the first order (formerly called stem):** — The most characteristic feature of *Pseudosporochnus* in earlier descriptions is the basal swelling and apical branching of its "stem". We have numerous examples of this axis, some intact, some with either the base or the apex missing (figs. 2, 4, 7, 8, 10, 13, 29). Certainly, however, the axis can be considerably longer. Specimen # 5060/178, for example, is 33.5 cm from its base to the point where it is broken. The break is below the branching and we cannot be sure how much longer the branch was when alive.

Branches of the first order range from 2.2 to 3.6 cm in diameter at the base. It should be emphasized, however, that the basal end of the branch does not necessarily exhibit the bulbous character that has usually been associated with it. Fig. 8 illustrates this point well. Here the margins of the branch are essentially parallel all the way to the point at which the branch was separated from some lower part of the plant. Specimens like fig. 8 also serve to emphasize the variation in shape of bases of branches of the first order. The range is from those with more or less parallel sides through those with a pronounced bulge on one margin or the other to those whose margins simply widen uniformly to a rounded base (figs. 4, 13, 29 and text fig. 7). An interesting feature of some of the bases is an apparent folding of the tissue that may have occurred prior to fossilization. This feature was noted particularly when uncovering bases by chipping away the matrix with fine steel needles (*dégagement*) and a light hammer (LECLERCQ 1960). It is expressed as a double thickness of what is probably cortical tissue. The fold gives the impression that the cortex was softened during its transport in water and then, when covered by sediments, was thrown into a fold rather than flattened smoothly (fig. 8).

The apex of the branches of the first order varies from 1.1 to 1.9 cm in width and divides into 2 to 4 lesser branches. Somewhat similar digitate branching is found in *Cladoxylon scoparium* Ku. & W. and

in *Calamophyton* Ku. & W. Hence supplementary characters that would permit the positive identification of fragmentary specimens of *Pseudosporochnus* are much to be desired.

Characteristic of all our branches of first, second and third order, and ultimate branchlets as well, are round or elliptical or horizontally elongated structures (figs. 2, 4, 6, 8, 9, 12, 24—28) that are always clearly visible on the compressions. They measure 0.4 to 1.0 mm in height by 0.4 to 2.5 mm in width. They are closely spaced and easily recognized. On some specimens where they may have brushed off in handling, their position may be still outlined by fine anastomosing strands of carbonaceous matter (figs. 6, 13). When uncovering fresh surfaces with finely pointed needles, they are sometimes dislodged, but they can be replaced easily in their original position. Even more significant is the fact that on parts of many specimens they are the only tissue of the axis that is preserved. From the regularity of their occurrence and the uniformity with which they are preserved, we were led to the interpretation that they are masses of hard, probably sclerenchymatous, cells in the cortex. Fortunately some specimens were found in which petrifications of the cortical cells enabled us to confirm the presence of nests of sclereids in the cortex (figs. 11, 12). The size of the nests when petrified is larger than when they are merely parts of a compression. On specimens preserved both as a compression and as a petrification the nests of sclereids are 0.4×0.4 mm on the compression part and 0.6×1.0 mm on the petrified part of the specimen. Detailed studies made on petrified sclereids have demonstrated that the apparently great variation in their size and shape as seen on compressions is governed by the manner in which they were preserved. Occasionally, for example, two adjacent nests may be preserved in contact with one another. This results in what appears to be an unusually wide (tangentially elongate) nest and it is the result of the crushing of the intervening parenchyma by the two nests.

A second feature of the lower, larger branches of *Pseudosporochnus* is the frequent appearance of a slight longitudinal ribbing on the surface of compressions. LANG (1927) noted particularly this feature on his specimen and KRÄUSEL and WEYLAND (1933) likewise referred to it. Our suspicion that this ribbing could be correlated with anatomical structure was borne out by our discovery of a similar ribbing on the periphery of the stele in the structurally preserved parts of the axis. This is illustrated rather well on specimen # 631 (fig. 4). This specimen is in part a compression, in part a petrification. The longitudinal ribbing shown on the upper part of the compression is also shown clearly on the petrified xylem tissue that is present approximately in the middle of the specimen and it can also be seen nearer the base of the specimen (fig. 4). Both the ribbing of the xylem and the nests of sclereids are shown at a higher magnification on figs. 5, 11, 12. Further reference will be made to the cause of the ribbing in our description of anatomical structure.

It is probable that branches of the first order bore appendages (fronds) when they were younger although no scars of any sort are to be found on the axes to prove our point. Nevertheless, evidence in support of our statement is provided by specimens like # 4950/722 A (fig. 9) which shows the branching at the apex of a first order branch. Poorly preserved appendages are still attached below the fork. Another specimen (fig. 7), has a dichotomously forking appendage attached near its base and evidence of others along its sides and near its base although none of the latter is any longer in attachment. Originally we interpreted these organs (fig. 7) as hairs or rootlets, but two facts have caused us to change our idea and to consider them as fortuitously preserved remnants of pinnae instead. The first fact is the discovery of specimens like fig. 9 where leaves can clearly be shown to have existed on branches of the first order. The second fact is that small appendages found on other organs such as the stem (see below under stem) are unforked. We therefore now believe that branches of the first order probably bore fronds at an earlier stage in the ontogeny of the plant. The hard, resistant nests of sclereids in the cortex appear to have crushed all evidence of vascular strands to the ultimate appendages (fronds) during preservation, just as they often crush arms of the xylem (fig. 42). In addition, the loss of most of the cortical parenchyma during preservation may help to account for the lack of scars on the branches. Scars are missing from the surface of all younger branches as well.

An extremely interesting mode of preservation of branches of the first order is shown by fig. 6. Here the axis is typical up to the point where a branching is taking place. Only the xylem is preserved in the rest of the specimen where it is represented by narrow, carbonaceous strands. The number of strands corresponds approximately to the number of arms or lobes that are found on structurally preserved xylem as will be shown later in the section on anatomy. This type of preservation suggests strongly that the arms or lobes of xylem were either free from one another or were only slightly attached to one another near the center of the mass of xylem.

The bulbous base of branches of the first order sometimes shows root-like tissue extending from the base out into the rock matrix. Figs. 1, 3, 4 show this condition which is probably similar to the base that was described by POTONIE and BERNARD (1904, figs. 67, 69) as bearing rootlets. We find that these "rootlets" are not confined to the margin at the base of the specimen. Some of them can be traced up on to the surface of the specimen itself where they extend under or over the nests of sclereids depending on which surface of the part or the counterpart of the branch is being viewed. In such cases the strands occupy a position comparable to that of the xylem. Numerous compression specimens show the xylem preserved as strands, as we stated in the preceding paragraph and, as will be shown in the next section, these branches of the first order are supposed by the authors to be borne on stems. We believe therefore that when branches of the first order broke away from the stems, the broken xylem strands sometimes appeared on the base of the branch as a fringe of root-like structures (fig. 1). Our conclusion is that the so-called rootlets of *Pseudosporochnus* are merely fragmentary, flattened, carbonized strips of xylem (fig. 3).

3. **Stems:** — The demonstration that "rootlets" that were previously believed to attach *Pseudosporochnus* to the soil may be only frayed strands of xylem raised again the question of the habit of the plant. The further demonstration of nests of sclereids on axes of *Pseudosporochnus* enabled us to identify certain larger axes that were included in the collection. These larger axes (figs. 16, 17, 20) measure 5—8 cm in diameter, are covered by nests of sclereids identical to those on branches of the first order, and are up to 25 cm long. Neither end of the longest specimen is an apex and the axis does not taper appreciably. We cannot tell how much longer this axis may have been when alive. Along the margins of the axis one finds closely placed, unbranched appendages that represent either aerial rootlets or multicellular hairs (fig. 17). They are less than 0.5 mm wide and over 1.5 cm in length.

The size of these new axes in relation to the size of branches of the first order indicates that they are stems and that unquestionably *Pseudosporochnus* was a large plant.

4. **Crown of stem:** — We have a specimen (figs. 14, 15) composed of both part and counterpart, whose dimensions are such that it might have terminated an axis like those which we refer to as stem. The identification of this specimen as *Pseudosporochnus* is again based on the nests of sclereid cells that cover its surface. The greatest width of the specimen is 10.5 cm and its length is approximately 5.0 cm. It is terminated by five or six lobes that range from 2.0 to 4.0 cm in width at their apices. The diameter of the apex of each lobe apparently varies with the level at which an appendage broke off the lobe. It is important to note that the diameters of the lobes agree well with the diameters of the bases of branches of the first order that we have described above. It is also noteworthy that the lobes show a certain amount of depth. They are not all preserved in exactly the same plane in the matrix. Thus, although they appear at first sight to be flattened in one plane, the indications are that in life this specimen was three-dimensional with branches of the first order departing from it in several planes. It is our interpretation that this specimen could represent the apex of a stem to which the bases of a group of branches of the first order remain attached (text fig. 7). For convenience it may be called a crown.

The discovery of an apparent crown leads to the interpretation that the terete stem of *Pseudosporochnus* was terminated by a crown of branches of the first order borne in three dimensions. This interpretation can explain Høeg's (1931) peculiar axis that was 65 cm long, up to 14 cm wide and

terminated at one end by some sort of broken appendages. Until now there has been no concrete evidence that Høeg's specimen belonged to the genus *Pseudosporochnus*. Our group of organs, linked by the possession of characteristic masses of sclereids, parallels closely the morphology of the Høeg axis and suggests the identity of the two. It is interesting to note in this connection that KRÄUSEL and WEYLAND (1933, text fig. 13) suggested that branches of the second order were arranged in the form of a three dimensional crown at the apex of branches of the first order. The existence of a second "crown" at a lower level on the plant from which branches of the first order may have fallen would be a logical morphological feature if one accepts the interpretation of KRÄUSEL and WEYLAND. The structure of the crown as we describe it can also explain the variation in size of the bases of the branches of the first order. Their width may vary with the height at which they broke away from the crown (compare figs 1, 4, 7, 8, 13, 29).

5. **Roots:** — There still remains the question of how *Pseudosporochnus* was attached to the soil. Neither Høeg's nor our stems show the true base of the plant. We have, however, found specimens that appear to be main, or possibly prop, roots of the plant. Once again the identification of these organs is based on the presence of nests of sclereids like those on branches of the first order and on the stems. These root-like organs are up to 16 cm in length and 2.5 to 3 cm in width (fig. 18). Along their sides they bear downwardly directed lateral roots that form an acute angle with the main root. The laterals, all of which are incomplete, are up to 2.4 cm in length and 5 to 8 cm in width. From the shape and size of the main roots in relation to the size of the stems we deduce that they may have been attached as circle ("crown") around the base of the stem. One main root possessed a small nodular mass of petrified cells in a groove on the surface of the root in which we found the characteristic anatomical structure of *Pseudosporochnus*: arms of xylem and nests of sclereids (figs. 45, 46).

Roots of this size, studied in addition to the stems, increase greatly the possibility that *Pseudosporochnus* was a rather large plant as POTONIÉ and BERNARD suggested on the basis of large branches of the second order.

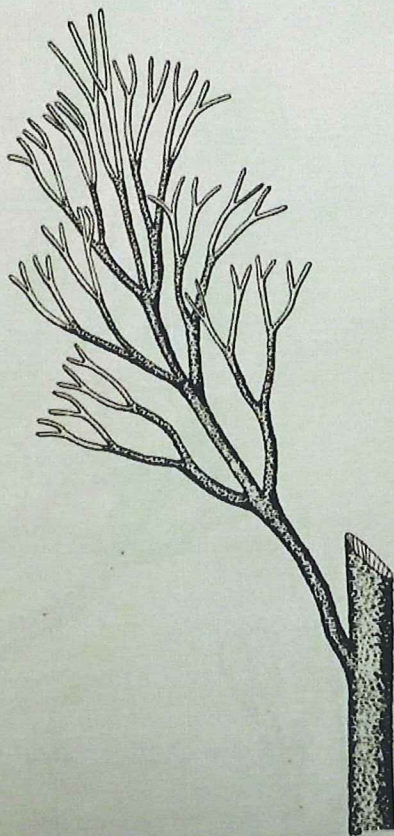
6. **Branches of the second and third order:** — It was remarked above that branches of the first order divide into 2 to 4 or even 5 smaller branches in more or less digitate or palmate fashion. In some specimens the division does appear to be a series of closely spaced dichotomies as POTONIÉ and BERNARD (1904) stated. However, careful observation reveals that occasionally the branches were not all in the same plane (figs. 2, 7, 9, 10). We think it quite possible that at least in some cases these smaller branches were given off from the apex of branches of the first order more or less like a crown. See, for example, the reconstruction by KRÄUSEL and WEYLAND (1933, Abb. 13) who also suggest the possibility that the branches were arranged as a crown.

On some specimens of branches of the first order (figs. 2, 10) evidence of the formation of second order branches appears early as a branching of the stele. Apparently the ramification of a branch of the first order was simple, consisting of a group of branches essentially equal in external size and internal structure as well (figs. 6, 33).

The branches of the second order are preserved in various lengths, our longest being 32 cm of which neither end is complete. Many branches are preserved for 9 to 20 cm. They range from 3 to 12 mm in width at their bases (10 mm is the average) and taper to 1.0 mm and down even to 0.4 mm at their tips when these are preserved. They may or may not branch dichotomously to produce branches of the third order. Both branches of the second order and those of the third order when present end in a pseudovertilcil of delicate, thin fronds, the number of which is approximately five or six. The internodes between these last fronds are very short (figs. 25, 19). All these axes are covered by nests of sclereids identical to those described for the lower parts of the plant. Occasionally the masses of sclereids, arranged in customary fashion, are absolutely the only trace of the axes that is still preserved (figs. 24, 28). This means that not even the margin of the branch or of the frond still remains.

Another interesting type of preservation of branches of the second order and, in fact, branches of the first order in some cases, is illustrated by fig. 7. Here the branches number 2 and 4 are seen as a compression on which the xylem tissue remains as a single broad, flat, carbonized strand. This type of preservation is somewhat similar to that described under branches of the first order on which the xylem is retained as a series of narrow strands, a retted appearance (figs. 3, 6, 10, 29). Perhaps in this second case the xylem was somehow all crushed together before being separated by retting. The result of such a flattening could be a single strand of xylem rather than numerous, narrower, individual strands.

7. **Fronds-vegetative:** — Along the sides of the branches of the second order are numerous appendages whose arrangement, branching, and morphology have been the subject of a wide variety of interpretations. Our material is especially valuable because it enables us to demonstrate unquestionably that these appendages are spirally arranged (figs. 24, 25, 26, 28, 29). The examination of a large number of specimens shows that the fronds are situated both on the surface and at the margins of branches of the second order. It is also possible to chip away the rock matrix using fine needles and a small hammer under a stereoscopic binocular microscope. With this technique one can find fronds arising all over the surface of the branch.



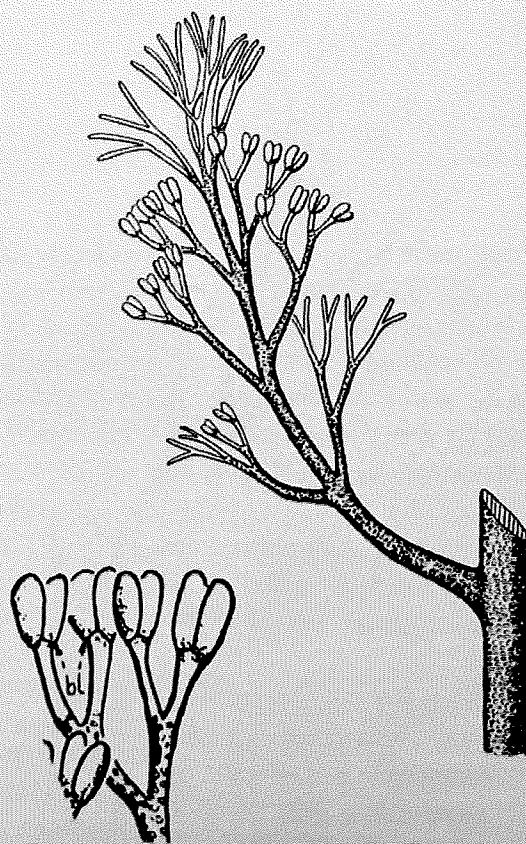
Text fig. 1. Schematic reproduction of a sterile frond, $\times 2$.

The central axis of the frond averages 0.5 mm to 1.0 mm in diameter and usually stands at an acute angle to the branch on which it is borne (figs. 24, 25, 28, 29). At approximately 1.3 cm out from the angle to the branch the frond axis (rachis) divides for the first time, giving rise to two branches of the second or third order. Each of these two pinnae continues on through three successive dichotomies or more or less opposite pinnae.

tomies, ending in eight flat, ultimate segments (text fig. 1 and figs. 26, 27). The central axis continues beyond the first branching and gives off approximately opposite pinnae two more times. As in the case of the first branching, each of the laterals divides dichotomously three times. The rachis itself finally terminates in a dichotomous forking each division of which dichotomizes one or two more times (text fig. 1; figs. 24, 25, 26, 27).

A sterile frond is lanceolate, tapering gradually from the base to the segmented apex. A mature frond supports four levels of pinnae, three of which are given off in a sub-opposite manner. The fourth is represented by the final dichotomy of the rachis. The distance between pinnae decreases from base to apex of frond, from about 1.3 cm to 0.25 cm. The fourth level of pinnae may have 2 or 4 or 8 segments (text fig. 1) depending upon the number of times it dichotomizes. The lower pinnae end in eight terminal segments as a result of three dichotomies. Often a delicate vein is seen in the flat, terminal, limb-like segments. The possibility exists that these segments represent the beginnings of leaves. It is of interest to note in this regard that the rachis of the frond and all divisions of the pinnae except these ultimate segments are covered by minute nests of sclereids.

The fronds average 4 cm in length. Occasionally on the compressions the nests of sclereids are the only tissue that is preserved (figs. 9, 24, 28). Nevertheless, the nests are arranged in the typical manner and the frond is perfectly recognizable. On other specimens only a central vein 0.2 to 0.3 mm in diameter is preserved. Usually it is paralleled by two very fine lines of carbonaceous material that represent the



Text fig. 2. Schematic reproduction of a fertile frond, $\times 2$; detail, $\times 6$.

margins of the axis. When present, these veins dichotomize simultaneously with the divisions of the frond. They constitute additional evidence for considering the entire ultimate appendage as one unit (a frond). The veins are simple. As will be shown below under Anatomy, the vascular tissue of branches



Text fig. 3. Restoration of a branch of second or third order with vegetative and fertile fronds. $\times 2$.

of the second order is in the form of a complex stele. Branches from this stele (? leaf traces) that supply lateral appendages and that have a much simpler form than that of the branch whence they arise, can be interpreted as evidence favoring the frond-like nature of the lateral appendages. In the frond, the trace presumably gives off sub-opposite lateral bundles to the lower pinnae and dichotomizes in the case of the dichotomous branchings.

Toward the end of branches of the second order, or third order if the former have dichotomized, the fronds are closely placed and the whole axis assumes a very bush-like appearance. The end of a branch appears to terminate in a series of divisions that are typical of a *Pseudosporochnus* frond (figs. 25, 19, text fig. 3).

8. **Fronds-fertile:** — The general architecture of a fertile frond is identical to that of a vegetative appendage. Pinnae are given off in a sub-opposite fashion at three or four levels along the central axis. Usually only a portion of the frond is fertile. The basal pinnae may be sterile or partly fertile (text fig. 2 and figs. 29, 30). Pinnae at the second and third levels are wholly fertile, those at the fourth level may be sterile or partly fertile, and the pinna that represents the terminal forking of the rachis is generally sterile (figs. 29, 7).

As a result of three dichotomies, each pinna has eight terminal organs which, here, are sporangia. The upright sporangia are borne in pairs attached to a blunt-pointed surface. Thus they meet at an obtuse angle (text fig. 2 bl. and figs. 22, 30) and they represent the third dichotomy. The fertile pinnae are somewhat smaller than sterile ones because the sporangia are shorter than the flat, ultimate segments of the sterile fronds. The sporangia and the ultimate segments of the vegetative pinnae are homologous organs. Well developed sporangia are 2 mm to 3 mm long and 0.8 mm wide. Occasionally one sporangium of a pair is better developed than the other which has aborted. On some sporangia, there is an appearance of a line of dehiscence on the inner side and the beginnings of a mechanism of dehiscence are visible (fig. 21). In spite of numerous attempts no spores were found within the macerated sporangia though there are spores dispersae in the sediment (LECLERCQ 1960).

A fertile branch of the second or third order supports successive spires of fertile fronds both preceded and followed by vegetative fronds among which one can find some fertile segments bearing pairs of sporangia (figs. 25, 29 and text fig. 3).

VI. Summary of External Morphology and Reconstruction of the Plant

Up to the present, knowledge of the morphology of *Pseudosporochnus* has been confined to compressions of:

- A. an axis, bulbous at its base and hitherto called a stem which, for reasons given above, we now consider as branches of the first order;
- B. branches arising digitate-fashion from the apex of the branches of the first order; we now call these smaller axes branches of the second order;
- C. ultimate appendages, that have been called leaves, branchlets or pinnules; we now call these ultimate appendages fronds.

We propose to include as probable parts of the plant body of *Pseudosporochnus* some larger axes:

- D. an axis up to 25 cm long and 8 cm wide that we are inclined to call the main stem or trunk;
- E. a terminal portion of an axis that we call a crown, characterized by lobes that are presumably the bases of branches of the first order; we presume that this crown was attached to the main stem or trunk.
- F. root-like organs up to 16 cm long and 3 cm wide.

In addition we have demonstrated:

- G. the spiral arrangement of the fronds on the branches;
- H. the pattern of branching of the fronds and their pinnae, and the bilateral symmetry of the frond;
- I. the identical morphology of sterile and fertile fronds;
- J. the existence of obvious, distinct pairs of sporangia borne terminally on the forked ultimate segments of a frond.

Direct evidence of organic connection proves that A-B-C-G-H-I-J are parts of one plant. Evidence that D-E-F are part of the same plant is strong but still lacks the positive proof of organic connection.

With the facts at our disposal we can attempt a reconstruction. We picture *Pseudosporochnus* as a small tree (textfig. 7). The "trunk" arose from a circle ("crown") of roots to an approximate height of one to several feet where it gave rise to a crown of first order branches. This first branching took place in three planes. The branches tapered very gradually for a considerable distance to a point where rather abruptly they again divided into a crown of branches of the second order. This branching too was three dimensional. Branches of the second order forked dichotomously into branches of the third order. Both the last two orders of branches were densely covered by spirally arranged fronds. Probably all branches bore fronds at one time but because they were deciduous, they were preserved chiefly on branches of second and third order. The branches terminated in an ultimate spiral of six to eight thin, delicate fronds. Fronds were of two types, all vegetative and partly vegetative, partly fertile. Fronds were lanceolate, bilaterally symmetrical structures tapering gradually from the base to the forked, flattened, ultimate segments. A mature frond bore four or five levels of pinnae. Pinnae were given off the rachis in sub-opposite fashion and forked three times terminating a) in a vegetative frond in eight flat, linear segments which may have functioned as leaves and b) in a fertile frond, in eight sporangia borne in upright pairs.

Apparently the system of ramification consisted of two kinds of branching: a close spiral or "crown" in the branching of the trunk, the branches of the first order and the insertion of the fronds; bifurcations or dichotomies in the forking of the branches of the second order and pinnae. However, as regards the internal structure of the axis, the similarity that existed between the anatomy of the axes of three different orders disclosed an obvious primitive feature in a plant whose morphology had reached a high level of differentiation.

The reconstruction attempted in text fig. 7 is necessarily diagrammatic and provisional. We must await the discovery of new facts to prove positively the attachment of the crown of the stem, the trunk and the root to the rest of the plant.

VII. Description of Anatomical Structure

1. **Gross appearance of petrified specimens:** — Short lengths of various parts of our specimens have been petrified by impregnation of the cell walls and sometimes the lumen of the cells by iron hydroxide. The xylem in numerous specimens occupies more than half the width of the axis. Splitting of the fossiliferous sediment has usually stripped the cortex away from the xylem. The study of these specimens at low magnification, under a stereoscopic binocular microscope, provided much preliminary information.

The most conspicuous feature of the petrified axes is a longitudinal ribbing of the surface of the xylem. This is well illustrated on a branch of the first order at normal size (fig. 4) and enlarged $\times 5$ on figure 5. Between two ridges of xylem is a vertically elongated furrow or band of more delicate tissue, probably parenchymatous, whose color is slightly paler than that of the xylem. Remains of parenchymatous cells are observed on the transverse section around the tips of the xylem arms (= ridges) (figs. 33, 41, 43) where they assume a honeycomb appearance when only the walls of these cells have been preserved.

The xylem ridges seem to be uniform in structure, composed chiefly of scalariform tracheids, though a few reticulate or pitted tracheids may be observed at a higher magnification. The ribs appear clearly to have been the cause of the longitudinal costulations that have frequently been mentioned in the literature, and in this paper on p. 8 and figs. 1, 2, 4, 10, 29, as being present on the surface of the compressions. The surface of the xylem ribs is frequently undulating. That is, instead of being long, smooth, continuous ridges, they seem to be depressed at close intervals. The cause of this appearance is the pressure exerted by nests of sclereids (figs. 11, 12).

The sheathing of the xylem complex by nests of sclereids is a second characteristic feature of the petrifications. The nests are round to elliptical and three-dimensional. Their dimensions average 0.6 mm high by 1.0 mm wide. They are located in the inner cortex and are arranged in a more or less alternate manner, forming both horizontal and oblique rows (figs. 6, 10, 11, 28, 29) as seen in tangential view. They represent a strong mechanical construction. The cells of the nests as seen in the inclusions in plastic (figs. 38, 42, 48, 60) are thick-walled and essentially isodiametric.

The width of petrified specimens is usually greater than that of corresponding unpetrified parts (fig. 8). Specimen # 635, for example, is 1.6 cm wide where it is petrified but only 1.2 cm wide above and below that area. Specimen # 546 is 1.4 cm wide where petrified and 1.0 cm wide on the compression above and below the petrified part. From such observations it appears that the diameters of the specimen in life may have been greater than we have been led to believe when measuring compressions only.

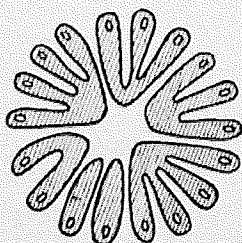
2. Technique: — It has been possible to imbed pieces of these petrifications in plastic (fig. 36) by means of the technique described by LECLERCQ and DISCRY (1950) and by LECLERCQ and NOËL (1953). The pieces embedded are 17 in number. Nine are from a branch of the first order (# 650/A/1 to 650/A/6 and 540/A/1 to 540/A/3); 4 belong to a branch of the second order (# 546/A/1, A/3, A/2 a and A/2 b); 3 from a branch of the third order (# 466/1 to 466/3); one comes from a nodule on the root. The procedure has been to polish a surface, to study it under strong reflected light, to draw it with the aid of a camera lucida, and then photograph the surface and finally to grind it further, repolish and repeat the observations. By this means we have been able to observe 36 levels of transverse sections and to record the changes seen in the equivalent of serial sections. Longitudinal sections have yielded information on the ornamentation of the tracheids and on the sclereid cells of the cortex.

3. Detailed description of anatomical structure: — The description of the internal structure of the branches of the first, second and third order serves as our starting point in the study of the anatomy of *Pseudosporochnus* because of the positive data they provide.

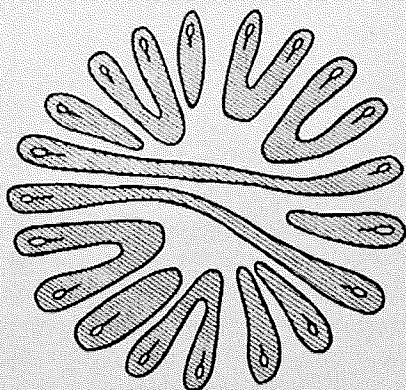
a. Gross configuration: — The three orders of branches show similar complexity in structure. In transverse section, despite severe flattening, one finds that the stele consists of numerous (16–21) arms or plates of xylem elongated in a radial direction (figs. 35, 37, 31). All of this xylem is primary, there being no evidence whatsoever of secondary activity (figs. 37–55). A narrow loop containing protoxylem elements is located near the distal end of the arm (figs. 33, 47, 51). Occasionally the loop was prolonged proximally for a short distance by a narrow band of small elements (figs. 47, 52). Apparently little parenchymatous tissue surrounded and separated the arms which are 16–21 in number in all three orders of branching. A difference that does appear is in the length of the free part of the arms which is greatest in first order branches (1.3 mm, fig. 31), less in second order branches (from 1140 μ long by 180 μ wide to 1165 μ long by 237 μ wide; fig. 33), and least in third order branches (570 μ long by 190 μ wide; figs. 34, 35, 37).

The nests of sclereids present in the inner cortex have crushed the xylem tissue so severely during fossilization that the xylem arms are almost completely pushed together in the center of the stem. It is, therefore, difficult to determine whether the original configuration of the xylem was a protostele with radiating arms, a polystele structure with groups of arms, or a series of free and variously

anastomosing bundles. However, a feature observed on several compressions, such as figures 1 and 3 and particularly 6, points to the existence of numerous strands of xylem that are free from one another at least at their distal ends although some strands may be connected in the center. On figure 6 the xylem is seen to be stripped of all outer tissues over a distance of 10 cm. It shows the remnants of two steles that represent two halves of a dichotomy. The remnants are a group of rigid, closely packed, parallel strands of xylem. It is barely possible that if they had not been joined to a certain extent in the center of the axis they would be separated more widely in specimen # 4972/121. STUR (1881) and POTONÉ and BERNARD (1904) have mentioned a similar state of preservation on their material.



Assumed transversal section of the stele of a branch of third order.



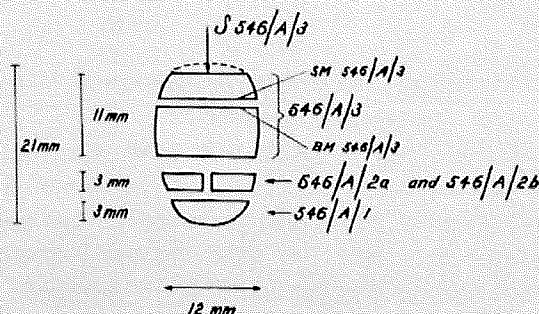
Assumed transversal section of the stele of a branch of first order.

Text fig. 4.

If we cannot remove all doubt about the arrangement of the arms in the xylem of *Pseudosporochnus* without additional material, nevertheless a comparison of our material with parallel and almost parallel conditions of fossilization in closely related material permits us to suggest that *Pseudosporochnus* did possess individual bundles variously anastomosed (text fig. 4). This condition is characteristic of *Cladoxylon radiatum* (BERTRAND 1935, e. g. text fig. 24 and Plate 37, figs. 124, 127) and *C. scoparium* (KRÄUSEL & WEYLAND 1926, e. g. text figs. 40—44). It seems to us at least possible that further flattening of the stems illustrated by these authors would have resulted in the kind of structure illustrated by our figs. 31, 32, 34, 35, 37, 33. Similar evidence is provided by specimens of *Cladoxylon* from basal Upper Devonian in New York State. Dr. F. M. HUEBER, working at Cornell University, has collected stems of *Cladoxylon* preserved by iron pyrite. Some specimens are flattened as badly as our Belgian material. Others are preserved with little or no crushing. In the latter, the xylem is preserved as many, variously lobed bundles that anastomose in various ways as one takes sections at different levels along an elongate axis (HUEBER 1960). HUEBER's material shows conclusively that *Cladoxylon* stems can be compressed to the point where it is almost impossible to know that the bundles were distinct from each other when the plant was living. A second feature of his material is that some specimens possess and some lack thick-walled, non-vascular cells between the arms of xylem. The effect of severe compression is always more pronounced in those axes that lack the thick-walled cells.

Our inability to prove that the xylem in *Pseudosporochnus* is composed of individual strands detracts in no way from its general cladoxylalean aspect as is seen in the fuller analysis below.

b. Details of xylem structure in a branch of the second order: — Specimen 546/3 is taken from a branch of the second order. It is our most interesting specimen because it has retained the cortical zone, some well-preserved xylem arms, and two leaf bundles (fig. 33). It also appears that the xylem consisted of two masses such as might be produced below a dichotomy. The petrification was a compact yellow nodule of iron hydroxide 21 mm long and 12 mm wide including the entire width of the branch (fig. 36). The external surface of the nodule was structureless and gave no indication whether or not preserved tissue would be found. It was also too fragile to be removed without preliminary treatment which involved strengthening the nodule by means of drops of translucent liquid plastic. As the plastic penetrated the specimen it began to polymerize making it possible to cut the nodule from the rock without damage. Subsequently the nodule was embedded in a block of plastic (fig. 36).



Text fig. 5. Profil diagram of the inclusion 546 A with plane of sectioning.
S = Summit surface, SM = Summit-middle surface, BM = Base-middle surface.

A profile diagram of the nodule is given on text fig. 5 together with the plan adopted for sectioning. Its orientation was determined by the presence on the compression of a lateral appendage, probably a frond. Two saw cuts were made near the base and the surfaces obtained were ground and polished. The first transverse surface (546/A/3/1) is reproduced on fig. 33. Further grinding and polishing on that surface have provided 21 successive levels for study. Subsequently the summit of the nodule was cut, ground and polished in order to check the changes that had occurred as a result of the branching of the xylem. In the hope of obtaining supplementary information, the nodule was cut again in its middle region, giving the new surfaces S. M. 546/A/3 and B. M. 546/A/3. The investigation of these surfaces has confirmed the general pattern revealed by the other cuts. Pieces 546/A/2 a and 546/A/2 b have provided radial and other longitudinal sections.

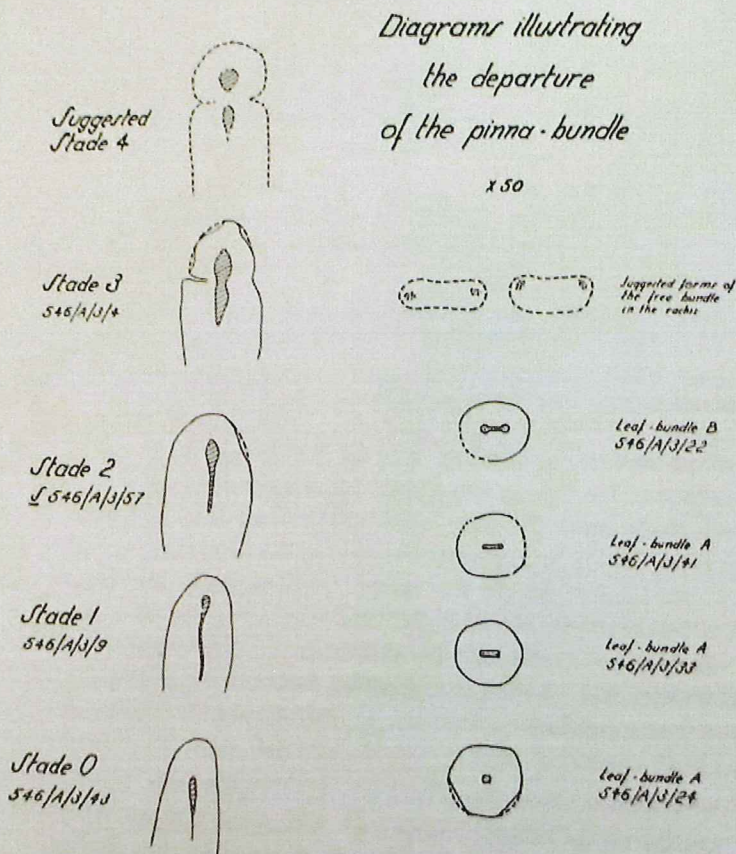
Fig. 33 is a compressed axis whose diameters are 12 and 4.9 mm, including the cortical tissue. The xylem is unequally elongated at its lateral margins. On the left side a few arms are well preserved; on the right side the mass of xylem appears to be stretched tangentially. A wide zone of cortex surrounds the vascular system. The arms on the left are the best that we have found and they reveal critical details of xylem structure (fig. 47). For convenience we have numbered these arms 1 to 6 (fig. 33). At the tip of each arm there is a small, narrow peripheral loop provided with protoxylem elements (fig. 47, 51, 52) and surrounded by metaxylem. All of the arms show primary xylem only and the order of maturation is clearly mesarch.

The mass of xylem on the right seems to represent the beginning of a branching or an unequal dichotomy (fig. 33). It is noteworthy that the two masses of xylem each appear to consist of 16 to 21 arms, the same number that is found in the single xylem mass of an unbranched stem. To test the hypothesis that branching is seen here, a cut was made near the apex of the petrification (text fig. 5).

On the resulting polished surface there is a main group of arms and a smaller mass clearly separated from it although the two are still included in a common cortex.

c. Mode of emission of a leaf trace: — In our material it has not been possible to follow the complete outward progress of a leaf trace because the trace appears to be quite oblique and the heavy concentration of nests of sclereids in the inner cortex apparently crushed and destroyed the bundles soon after they became separate from the xylem. Nevertheless, by grinding and observing successive surfaces we secured the following data that are summarized in text fig. 6.

Each arm of the xylem has a single, short and narrow peripheral loop near its distal end. Occasionally the protoxylem is well preserved in the loop (fig. 51). The loop is prolonged for a short distance toward the inner extremity of the arm by a narrow line of small elements. This is referred to as Stage Zero of the emission of a trace (text fig. 6 and fig. 51).



Text fig. 6.

- Stade 1: the loop apparently increases slightly in both length and width (fig. 52, arm # 2; text fig. 6).
- Stade 2: the distal part of the loop is extended laterally and becomes more or less triangular. Simultaneously the tip of the arm enlarges slightly and files of metaxylem tracheids converge around the distal part of the loop (fig. 53; text fig. 6).
- Stade 3: the greatly enlarged loop is constricted in the middle and filled with protoxylem elements and delicate parenchyma (fig. 54); the increasing metaxylem closes the loop. It happens that both tissues have been destroyed and that the loop appears as a large constricted lacuna (fig. 55).

Stade 4: the exact manner of detachment of the trace from the arm has not been observed. On text fig. 6, therefore, the probable appearance of Stade IV is merely suggested. The peripheral loop seems to remain closed as the metaxylem is constricted and "pinches off" the trace. The traces themselves are terete in sectional view. Fortunately two of them, A and B, were preserved on the left hand side of the petrification and appeared in the first transverse section (fig. 33). They have been followed a short distance out from the arm into the cortex where they soon become altered in form and structure by the action of nests of sclereids during fossilization (figs. 47—50 and 56—60).

Stade 5: the free bundle has a more or less circular form and is composed of metaxylem surrounding a small (or two?) central protoxylem point (fig. 56; text fig. 6).

Stade 6: the protoxylem mass elongates tangentially and there are now two distinct protoxylem points located close together (figs. 57, 58, 59 and text fig. 6).

Beyond Stade 6 the traces are crushed by the sclereid masses of the inner cortex (fig. 60). This leaves us in the unfortunate position of being unable to prove how many traces enter one frond or whether the two protoxylems were arranged symmetrically or were displaced toward the abaxial or adaxial surface as one compression (fig. 24) suggests.

There is evidence that the frond probably received only one bundle. First, we have shown that the vegetative and fertile fronds of *Pseudosporochnus* are bilaterally symmetrical appendages with pinnae arranged suboppositely. This mode of branching foreshadows a bundle of oval or rectangular clepsy-droid form that gives off pinna traces alternately from the two ends (text fig. 6). As a matter of fact, this is a common type of petiole bundle in many Paleozoic ferns. In this connection we do know that bundles A and B (figs. 57 and 59) had two symmetrically arranged protoxylems long before they reached the base of a frond. It is also observable on bundle A that a few rows of metaxylem converge toward the two poles.

Second, we have compared the diameter of bundle A which was about 250 μ with the compression of a bundle preserved on some fronds. At the base of the frond (specimens 286 A and 354 B) the diameter of the bundle is 250 μ and 350 μ . Probably in the latter case the bundle had reached its fullest development in the base of the frond. It is interesting to note here that KRÄUSEL and WEYLAND (1926, p. 146) described a terete bundle in *Cladoxylon scoparium*. It appeared in two successive slides, first opposite one arm of xylem and then in the cortex (figs. 42 and 43).

By analogy with cladoxylaleans from Europe and North America we should expect more than one trace to supply each frond. However, P. BERTRAND (1935) mentioned (p. 145) a single bundle "F" given off by a few arms (see his text figs. 17, 20, 22 and Plate XXVIII, figs. 71, 72, 74). He believes that this may be a true foliar trace. Similarly he reported bundles associated with *C. radiatum* which he believed supplied aphlebiae or petiolules (see p. 150 *C. radiatum* and text fig. 25). On Plate XXXI, fig. 85 at F he indicates a supposed foliar trace in this same species. About the petiolules BERTRAND wrote (p. 150): "Le stipe de *Cl. radiatum* est entouré d'une multitude de petits rachis qui lui appartiennent manifestement. Nous figurons plusieurs de ces organes (figs. 120, 121, 123 on Plate XXXVI and Plate XXXIX). On voit que normalement ils n'ont qu'un seul faisceau en forme d'anneau aplati rempli par un parenchyme à parois minces, entouré de parenchyme libérien. Mais ce faisceau est constamment en voie de division et c'est pourquoi il n'est pas rare de trouver deux faisceaux à l'intérieur de la même section indice certain d'une division prochaine (fig. 127)." ... "Si certaines de ces ramifications (les petiolules) sont sans nul doute des aphlébies, on peut se demander si quelques-unes au moins ne prennent pas directement naissance sur le stipe principal." ... "Chaque pétiole a un plan de symétrie principal et une structure dorsiventrale accusée, bien que nous n'ayons pas trouvé trace de limbe."

The petiolules described by BERTRAND for *C. radiatum* remind us of the frond and pinnae of *Pseudosporochnus*. BERTRAND declares that the petiolule is undoubtedly aphlebiae but is his case proved? The petiolules are borne directly on the stem. They are numerous and have a single bundle given off by

one arm. The bundle is bilaterally symmetrical and it divides frequently, apparently by dichotomy, as in the pinnae of *Pseudosporochnus*.

Although we have been unable to follow our traces continuously from their origin into a frond, we believe that there is little doubt that our bundles are the traces to the fronds. Their size and their possession of two symmetrically disposed protoxylems correspond precisely with the arrangement of the pinnae observed on compressions of fronds. We, therefore, believe that in *Pseudosporochnus nodosus* the traces are not multiple and that an arm gives rise to a single bundle at its tip. Text figure 6 provides an hypothetical interpretation of the origin and development of the frond-bundle.

The affinities of *Pseudosporochnus nodosus* will be discussed below. However, from the preceeding description a close relationship between *Pseudosporochnus* and the Cladoxylaceae, particularly *Cladoxylon radiatum*, emerges clearly. Our plant is more simple in its general structure and in its emission of traces to fronds. It lacks the "en chapelet" arrangement of protoxylems that is found in *Cladoxylon mirabile*. By contrast we never find more than two protoxylems, one permanent in the arm and one that moves into the trace.

d. Details of xylem structure in a branch of the third order: — Our inclusion # 466 comes from a smaller axis, probably a branch of the third order produced by a dichotomy of a branch of the second order (figs. 34, 35, 37). On the transverse section one finds approximately 19 arms. It is not possible to count all 19 on any one section because a single nest of cortical sclereids may crush three or four arms of xylem (fig. 37). Only after several surfaces have been prepared and the area of the sclereid passed do the arms reappear (figs. 34, 35). An analysis of several surfaces, however, provides the necessary data for counting the complete number of arms.

Most noticeable in a branch of the third order is that the free ends of the xylem arms are shorter than in branches of the second order (figs. 33, 34, 35) and lateral connections between some of the arms are perfectly clear (figs. 38, 40, 43). The center of the mass of xylem in # 466/2 is badly crushed (fig. 37). Through the mass are narrow strands of mineralized debris showing no cellular remains. These strands may represent the remnants of crushed parenchymatous tissue that, in life, separated the plates of xylem. Similar strands can be seen in the xylem of second (fig. 33) and first (fig. 31) order branches where they may represent the same parenchymatous tissue. It is not possible to determine the extent of this supposed parenchymatous tissue so we are proposing only that some, possibly many, of the xylem arms or plates were separated by strips of parenchyma. We are not suggesting that a large pith-like tissue necessarily occupied the center of the stem.

It is also suggested that at its apex the anatomy of a branch of the third order is simpler than at lower levels because of the repeated emission of fronds. On compression specimens this ultimate part of the branch terminated in a pseudo-verticil of six or eight fronds (fig. 25). Thus a transverse section of this apex might show a ring of free bundles embedded in a parenchymatous ground tissue or even, possibly, a more or less stellate siphonostele that will break up into bundles similar to the frond traces A and B observed in the inclusion 546/A/3 to 546/A/3/51.

e. Details of xylem of a branch of the first order: — Specimen # 650 was taken from a branch of the first order measuring 19.5 cm in length, 2.5 cm wide at its base and 1.5 cm wide at its apex. Several bits of xylem were embedded for study. It should be pointed out that the petrifaction did not cover the entire width of the axis of the compression. The two lateral margins of the xylem tissue are missing. As a result the longer diameter of the xylem mass was greater when alive than it is now. This fact is in conformity with the expected width of a branch of the first order. Similarly the mass of xylem on specimen # 650 (figs. 31, 32) is greater than on inclusion # 546/A/3 (fig. 33). This also is in conformity with the larger size of a first order branch.

Like branches of the second and third order, the xylem is all primary and is composed 18 to 20 arms tightly compressed together. Peripheral loops, protoxylem position and other details are similar to those found in branches of the second and third order.

f. **Cortical structure:** — In addition to xylem, some cortical tissue is preserved in all three stems. Its total radial diameter is approximately 2.3 mm (fig. 36). No epidermis can be defined. The outer 1.3 mm is an orange-yellow zone in which cells are preserved only occasionally. Next inside is a dark red, continuous zone that is composed entirely of parenchymatous cells. It is about 200 μ in diameter. The inner 0.8 mm of the cortex is composed of nests of sclereids whose tangential dimension is 1 mm. The nests of sclereids are separated tangentially by parenchyma cells so that they form a discontinuous ring around the stele (fig. 33). There is no evidence of sclereids between the xylem arms. In fact, the extent of the crushing of the xylem strand implies that the tissue between the arms was probably parenchymatous.

g. **Longitudinal sections:** — For evidence that the thick-walled cells of the cortex are isodiametric, it is necessary to refer to longitudinal sections. All three stems illustrate the sclereids of the cortex but figure 42 is the most convincing. The same figure also illustrates beautifully the manner in which the nests of sclereids sometimes pinch the xylem bundles. It is the frequent occurrence of this crushing effect that has led us to the belief that leaf traces on all our specimens have probably been destroyed by the sclereid masses during preservation.

In longitudinal section one can also see the vertically elongate, thin-walled parenchyma cells of the cortex.

Xylem cells in longitudinal section are chiefly scalariform as is shown by figures 42 and 44. In some places we can find spiral elements (fig. 44). In other spots there appear to be annular elements (figs. 44 and 42). We have also observed, but not succeeded in photographing, elements that are apparently reticulate. The infrequency and the difficulty of demonstrating all these other types of elements emphasize that scalariform is the most common.

h. **The stem:** — On this organ we were unfortunately unable to find any petrified structure. Only the nests of sclereids on the compressions remain to confirm our assignment of the specimens to *Pseudosporochnus*. It is possible, however, to see longitudinal striations (figs. 17 and 16) where the cortical tissue has disappeared. These longitudinal strands are similar in size and rigidity to some of the bundles seen on specimen # 4972/121 (fig. 6) and they may represent arms or plates of xylem.

i. **The root:** — The main root, figure 18, bears petrified cells that occur in the form of a nodular mass that filled a small geode on the compression. These were removed and embedded in plastic. Although poorly preserved this mass has revealed in transverse section the extremities of six plates of xylem disposed in parallel fashion and elongated radially (figs. 45, 46). The plates are composed chiefly of metaxylem. Neither peripheral loops nor secondary xylem can be seen. In the nodule, the petrified xylem showed parallel longitudinal ribs and closely spaced nests of sclereids. Though fragmentary, this information appears to justify our assignment of the organ in figure 18 to *Pseudosporochnus nodosus*.

On the basis of the evidence presented in this section on anatomy, there can be little doubt that *Pseudosporochnus* shows a real affinity for the Cladoxylaleae. *Pseudosporochnus* is clearly a representative of a primitive stock as demonstrated by the similarity of the anatomical structure in each of its orders of branching except the frond, by its simple mode of emission of frond traces and by the simple structure of the frond trace.

VIII. Diagnosis

Pseudosporochnus nodosus sp. nov.

a) **External morphology:** plant believed to consist of a crown of roots at the base of a trunk which produces a crown of branches at its apex. The branches give rise in turn to a crown of second order branches that fork only by dichotomy. Branches are densely covered by spirally arranged fronds

approximately 4 cm in length. Fronds give off sub-opposite pinnae 2 to 4 times. Pinnae dichotomize three times, terminating in flattened segments or in pairs of sessile sporangia 2 to 3 mm long $\times$ 0.8 mm wide. Rachis of frond beyond the sub-opposite pinnae terminates in a series of one to three dichotomies. All organs of the plant are characterized by the presence of elliptical structures approximately 0.4 to 1.0 mm high by 0.4 to 2.5 mm wide that represent nests of sclereids in the cortex. The plant had a minimum height of 2 or 3 meters.

b) Internal structure: xylem consists of an equal number of radiating arms (16 to 21) of primary xylem in branches of first, second and third order; probably some arms extend across the diameter of the axis and others are free or join to make U- or V-shaped strands. Peripheral loop occurs near the extremity of each arm and probably remains closed as simple, terete frond traces are pinched off the tip of the arm. The order of maturation is mesarch. Traces soon develop two protoxylems which lie in the tangential plane as a prelude to the formation of elliptical, clepsydroid traces, one of which is believed to enter each frond. Tracheids are chiefly scalariform, but annular, spiral and reticulate are also present. Tissue between xylem arms is parenchymatous; outer cortex is parenchymatous and well separated laterally by parenchyma.

Holotype: No. 4996/354 B.

Paratypes: Compressions, No. 5062/TP — 4968/694 — 4962/TP — 5059/631 — 4972/121 — 4967/21 — 5060/178 — 4950/722 A — 4993/619 — 4997/540 — 5061/583 — 4956/462 — 4955/114 A — 4955/114 B — 4954/173 — 5051/57 — 4961/168 A — 4960/599 — 4969/654 — 5054/286 — 5055/456 — 4981/55 A — 5055/455 — 4981/55 B — 4951/161.

Inclusions, No 650 A/6 — 650 A/5 — 546 A/3 — 546/2 b — 466/1/19 — 466/2 — 466/3 — 168/1.

Species name: Refers to the characteristic nests of sclereids in the cortex.

Horizon: Middle Devonian; Lower Givetian.

Material: 534 specimens, majority represent part and counterpart. Deposited in the Paleobotanical Collections, Laboratoire de Paléontologie Végétale, University of Liège.

Locality: Goé, 30 km east of Liège, close to the confluence of the rivers La Gileppe and La Vesdre at quarries known as Carrières Brandt.

Borrowed, for comparison, *Pseudosporochnus verticillatus*, Compression No. 36, from the Collection of Professor H. WEYLAND, Geologisches Institut, Universität Köln, Germany.

IX. Discussion

1. General Comments:

Pseudosporochnus has received a great deal of attention on the part of phylogenetic morphologists because it seemed at first to be a rather oversized psilophyte from which, by various processes such as reduction, fusion, flattening or webbing, one might hypothesize the origin of other groups of plants. Some of the numerous suggestions appear at various places in this paper and need not be repeated. The probability is that *Pseudosporochnus* will be less useful in theoretical discussion of evolutionary intermediates as a result of our new information. However, in pointing out what we can learn about the genus when abundant, well-preserved material is available, it is interesting to note the far-seeing character of some early observations.

STUR (1881), for example, used what he called scars of hair bases as a criterion for uniting isolated parts of the plant. KRÄUSEL and WEYLAND (1933) commented that these scars seemed more likely to be cortical structures. We have found that cortical sclereids, whose true nature is revealed in our petrifactions, are extremely valuable in demonstrating the unity of unattached specimens. The work of both of the earlier authors is thereby shown to be useful and is corroborated.

POTONIÉ and BERNARD (1904) believed the plant to be a small tree. KRÄUSEL and WEYLAND (1933) were less convinced because they considered the longest specimens of POTONIÉ and BERNARD to be truly indeterminable and, therefore, not valid for establishing the habit of the plant. HØEG (1931) added a possible stem (trunk) to the material available. On this stem, at one extremity, the bases of branches were still attached in the form of a crown but the lack of other convincing characters left the identity of the specimen uncertain. Our discovery of probable roots, crown, and trunks of *Pseudosporochnus* tends to confirm both POTONIÉ and BERNARD and HØEG.

Throughout the literature on *Pseudosporochnus* there has been uncertainty over the morphology of the ultimate ramifications. The major question was whether they simply continued the supposed dichotomous branching of the entire plant body into successively smaller units or whether they were true appendages (fronds, leaves or other) of the branches. POTONIÉ and BERNARD (1904) foreshadowed the sub-opposite branching of the rachis of the frond that we have described by their emphasis on the closeness of the dichotomies in the frond. We believe they saw a rachis just as we have seen it but perhaps not quite so well preserved and perhaps with a slight bias in favor of dichotomy. KRÄUSEL and WEYLAND (1933) also came very close to the truth when they indicated that the "frond" retains a central axis despite the fact that it looks as though it forked merely into a mass of fine branches. This is exactly what our material shows to be a certainty. Now that we are able to show that the vascular supply to this frond was a trace that is completely different from the xylem strand of the branch, it becomes perfectly clear that the appendages are not mere continuations of an axis but are true lateral organs or leaves. The bilateral symmetry of these organs is simply another confirming piece of evidence. The result of course is a major change so far as morphological concepts are concerned. It means that *Pseudosporochnus* no longer has anything whatsoever to do with psilophytes.

Another vexing problem for the earlier workers was the apparently club-shaped terminal ending of some segments of the fronds. KRÄUSEL and WEYLAND (1933) were the only investigators to produce concrete evidence that the bodies were sporangia. These authors macerated spores 4 to 7 μ in diameter from organs presumed to be sporangia of *Pseudosporochnus*. Our material confirms the existence of well defined terminal organs that must be called sporangia despite our inability to obtain spores from them. The question of greatest significance still remains unsolved. Both KRÄUSEL and WEYLAND and we ourselves have seemed to demonstrate the presence of sporangia. Does the considerable discrepancy in size and morphology of these bodies on the two species amount only to a species difference or does it foreshadow the ultimate discovery of heterospory in *Pseudosporochnus*?

The mode of branching of *Pseudosporochnus* has raised doubts too. It was the apparent consistency of dichotomy in the plant that caused morphologists to consider the genus psilophytic. The possibility of other interpretations have appeared from time to time. POTONIÉ and BERNARD's (1904) recognition of dichotomies very close together on the leaves, ZIMMERMANN's application of the term crown to the branches of second order arising from the apex of the branches of the first order and KRÄUSEL and WEYLAND's splendid reconstruction (1933, text fig. 13) showing clearly a three-dimensional "crown" are examples. It is not all surprising, therefore, that with better material we are able to suggest the existence of a "crown" of roots, a "crown" of branches of the first order, and a "crown" of branches of the second order. If these crowns represent some sort of a compressed spiral, the fronds illustrate the density of the uncompressed spiral that is retained in some organs because the fronds are certainly closely and tightly packed on second and third order branches. They are also just as close on that portion of first order branch on which we have found a few fronds remaining attached. The spiral arrangement of the parts so far mentioned serves to set the fronds aside even further as truly lateral appendages. They fork in sub-opposite and dichotomous fashion, a manner quite distinct from that found elsewhere in the plant except of course in the dichotomies of the branches of second order.

Our observations support the possibility that SIVA (1881) may actually have seen some scars of hairs on the stems. Our probable trunk seems to have been covered by short hairs 0.3 to 0.4 mm in

width. We have not observed scars left by these hairs nor have we seen them on lesser orders of branch. However, as we have pointed out elsewhere the cortical sclereids could have destroyed scars of hairs and scars of fronds just as rapidly as they destroyed leaf traces, crushed arms of xylem, and even compressed against one another to make larger nests.

It will come as no surprise to some morphologists, for example, ZIMMERMANN (1959) and EMBERGER (1944), that the anatomy of *Pseudosporochnus* is, as we have shown, much more complex than that of psilophytes. Both authors suggested that the anatomy seemed more complicated than in simple psilophytes but neither could do any more than speculate about this. Perhaps, of course, the complex structure that we have revealed goes further in the direction of evolutionary advance than either had visualized.

KRÄUSEL and WEYLAND (1933), admitting that information on the xylem was lacking, speculated that *Pseudosporochnus* might have been an herb without secondary xylem. Again our new information confirms their thinking in respect to the xylem although our new organs indicate that the plant had the habit of a small tree.

On the whole, it is our proof that *Pseudosporochnus* possessed spirally arranged, bilaterally symmetrical, complex-branching fronds supplied by a distinctive leaf trace that removes this genus from any connection with psilophytes. It is the complicated arrangement of the xylem in plates or arms radially disposed and the possession of a bilaterally symmetrical frond that relate the genus to the fern-like plants, specifically Cladoxylales. It is this combination of characters that removes *Pseudosporochnus* from further consideration as an evolutionary intermediate between any major groups of plants. It is, therefore, unnecessary to review the numerous debates over the role of *Pseudosporochnus* in the evolution of one or another group because the plant as we now know it is not at all the same organism about which the speculation was raised.

2. Comparison of *Pseudosporochnus nodosus* with other species on the basis of external morphology:

Our new species is closely related to *P. verticillatus* (KREJCI) OBRHEL 1959. The general morphological structure of branches of the first, second and third order and of the fronds is essentially the same. Differences are discussed below.

The trunk and the roots assigned to *P. nodosus* are as yet unknown for *P. verticillatus*. Therefore, the habit of the two plants may be different.

Cortical sclereids, arranged in nests, are a prominent feature of all organs of *P. nodosus* and complete details of their morphology and anatomy have been given. STUR (1881, p. 16, 17) described scars of hairs on the branches of *P. verticillatus* and KRÄUSEL and WEYLAND (1933, p. 12) considered that the "scars" might be caused by groups of cells in the cortex. If *P. verticillatus* possessed sclereids in the cortex, they were not prominent and we have no details of their structure. For the present, therefore, the large, conspicuous masses of cortical sclereids in *P. nodosus* constitute a striking difference between the two species.

The anatomical structure of *P. nodosus* likewise distinguishes it from *P. verticillatus* whose internal structure is still unknown. However, we do think that *P. verticillatus* may have the structure of a cladoxylalean. The longitudinal ribbing on some of its branches and the longitudinal strips of tissue (tissue that we interpret as xylem) that are seen on decorticated specimens (see STUR 1881, Taf. II, fig. 4, and POTONIE and BERNARD 1904, text fig. 69) both indicate that the xylem occurred in the form of separate strands or long arms as in *P. nodosus*. Nevertheless the lack of petrified axes of *P. verticillatus* and the great range of variation among cladoxylaleans as shown by BERTRAND (1935) compell us to regard the Belgian material as a distinct species.

The most positive distinction between the two species is the fructification. Both species bear sporangia in terminal pairs. Those of *P. verticillatus* (fig. 23) are smaller, measuring 1.2 mm long by 350 μ wide. Those of *P. nodosus* are considerably larger, 2 to 3 mm in length by 700 μ wide. Sporangia of *P. nodosus* are sessile and two sporangia are inserted on a blunt-pointed segment of the frond. Spor-

angia of *P. verticillatus* are borne singly on a sort of pedicel whose length is 0.8 to 1.1 mm. Two "pedicels" occur side by side and join at their base. We are indebted to Professor WEYLAND for the loan of a specimen of *P. verticillatus* on which some sporangia are compressions and others are petrifications. On the latter a distinct break in continuity between sporangium and "pedicel" is clearly visible (fig. 23). In both species the sporangia represent the ultimate segments of fronds. They are, therefore, homologous organs.

The differences between the Belgian material and the earlier described *P. verticillatus* seem to us sufficient to justify the erection of a new species.

It is interesting to speculate on the possibility of heterospory in *Pseudosporochnus*. One would have to demonstrate first that the two species represent only one plant and also that the two sizes of sporangia occur on this one plant. If this were done, the contrast between the smaller and the larger sporangia would be sharper than between the presumably heterosporous sporangia of *Archaeopteris latifolia* ARNOLD (1939) where the smaller are 0.3×2.0 mm and the larger are 0.5×2.0 mm. The possibility of heterospory is just one of several that must be left for future investigations.

P. nodosus is also clearly distinct from OBRHEL's new species, *P. chlupaci*. The outline of a single frond of *P. chlupaci* is triangular and the base of the triangle forms the apex of the frond. The outline of the frond of *P. nodosus* is lanceolate (p. 12). A mature frond of *P. chlupaci* appears to have 3 pinnae that arise close together on the rachis. The rachis of *P. nodosus* produces pinnae in sub-opposite fashion 2 to 3 times and a fourth time as a result of a final dichotomy. Pinnae of *P. chlupaci* appear to dichotomize 4 times whereas those of *P. nodosus* fork 3 times. Illustrations of the ultimate tips of *P. chlupaci* show little evidence sporangia but if the thickened tips do represent fertile organs, they are more like those of *P. verticillatus* than those of *P. nodosus*. A striking and unique feature of *P. chlupaci* is the thickening of the pinna at each dichotomy. Above and below the dichotomy the pinna is distinctly narrowed. *P. nodosus* shows no sign of this feature. Finally, in *P. chlupaci* the segments of each dichotomy depart from one another at a rather wide angle giving an appearance of stiffness to the frond as a whole. In contrast the angle of the dichotomy in *P. nodosus* is narrower and the frond is more lax in appearance.

3. Comparison of *Pseudosporochnus* with other genera on the basis of anatomy:

The closest affinity of *Pseudosporochnus* seems to be with the Cladoxyleae. Specifically it shows significant points of resemblance to the genus *Cladoxylon* so far as anatomy is concerned. In both *C. mirabile* (BERTRAND 1935, Plate 29, fig. 75; Plate 31, fig. 83) and *C. radiatum* (BERTRAND 1935, Plate 36, figs. 118, 122) the xylem consists of radially elongate, narrow arms of xylem some of which anastomose in various patterns toward the center of the stem. In both species there is a well defined peripheral loop near the extremity of each arm. Both they and *Pseudosporochnus* show 12 to 21 arms of xylem. In the two species of *Cladoxylon* there are traces that BERTRAND interprets as foliar traces (or aphlebiae or petiolules). These traces appear to fork, often dichotomously, and call to mind the foliar traces we find in *Pseudosporochnus*.

Pseudosporochnus differs from *C. mirabile* in its smaller, narrower peripheral loop and lacks the organization "en chapelet" that characterizes the loops of *C. mirabile*. Also *Pseudosporochnus* lacks secondary xylem and lacks any sclereids in the center of the stem and between the arms of xylem. It has nests of sclereids in the cortex whereas *C. mirabile* has an almost continuous zone of sclereids in the cortex. The latter species also has peculiar large cells in the position of pericycle surrounding each arm (BERTRAND 1935, Plate 29, fig. 75). These are lacking in *Pseudosporochnus* as now known.

Pseudosporochnus has more in common with *Cladoxylon radiatum*. Both plants have a small, narrow peripheral loop, lack secondary xylem and give rise to simple foliar traces by pinching off the tip of an arm. To date both lack *Hierogramma* and *Syncardia* branches although *C. radiatum* does give rise to branches that contain numerous simple, more or less terete bundles. Such branches have not

been found in *Pseudosporochnus*. Further, the cortical sclereids of *Pseudosporochnus* produce a marked distinction from *C. radiatum* which lacks sclereids.

There appears to be no close relationship between *Pseudosporochnus* and the other species of *Cladoxylon* described by BERTRAND (1935).

Clearly the generic distinction between *Pseudosporochnus* and the species of *Cladoxylon* that it resembles most closely must be maintained, if only because the habit and fructifications are known for *Pseudosporochnus* whereas nothing whatsoever is known of these characters in the Carboniferous *cladoxylons*.

Pseudosporochnus must also be compared with Devonian species of *Cladoxylon*. *Pseudosporochnus* is undoubtedly closely related to *Cladoxylon scoparium* KRÄUSEL and WEYLAND (1926) from Germany on the basis of similarities in both morphology and anatomy. The mode of branching of the main branch and the densely spaced, spirally arranged, lateral appendages are pretty much the same in the two plants. Anatomically both have well-defined xylem strands that are elongated radially and that possess a peripheral loop near their extremity. Both have terete bundles that presumably supply the fronds or leaves (KRÄUSEL and WEYLAND 1926, text fig. 43 and p. 145). Cortex was thick and well developed in both species.

KRÄUSEL and WEYLAND (1926, Plate 12), in successive transverse sections, showed an axis 2 to 3 mm in diameter (text figs. 40—43) and another 5 mm in diameter (text fig. 44). The authors wrote (p. 149) that the number of arms increased in older axes where they tended to form a more or less solid mass of xylem. *Pseudosporochnus* appears to show a somewhat similar relationship. The amount of xylem in a branch of the first order is about twice that in a branch of the second order which in turn has about twice that in a branch of the third order. This reduction in amount of xylem is reached less by a diminution of the number of arms than by a shortening and narrowing of the arms. At the same time the xylem mass appears to be more discontinuous in the younger branches. We have not observed xylem in a branch as narrow as 3 mm. It may be that in such an axis the xylem is reduced to a few arms. The number cannot, however, be less than 6 because on a compression the branches terminate in 6 to 8 ultimate fronds disposed in a close spiral (fig. 25).

C. scoparium differs from *Pseudosporochnus* 1) by having small, irregularly segmented leaves whose outline is wedge-shaped (KRÄUSEL and WEYLAND 1926, text figs. 30—37); 2) by lacking nests of sclereids in the cortex; 3) by having a fructification composed of a fan-shaped cluster of sporangia located terminally in a depression in the segments (or stalks) that bear them (KRÄUSEL and WEYLAND 1926, text fig. 38 and Plate 17); 4) by having a central sclerenchymatous pith; 5) by having groups of xylem arms whose number increases rapidly as sections are taken lower down on the axis (i. e. in older branches); 6) by having some secondary xylem (KRÄUSEL and WEYLAND 1929). The differences between the two plants seem to be sufficient to keep them apart in separate genera.

Additional representatives of *Cladoxylon* have been found in Upper Devonian (Frasnian) rocks in New York State. *Cladoxylon dawsoni* READ 1935 was described originally by DAWSON from marine strata in central New York. It is characterized by 18 arms of xylem that tend to radiate from the center of the axis. Some of the arms are joined into Y-shaped or V-shaped strands. Others are free. Peripheral loops are distinct and terete traces are apparently pinched off the ends of the arms. A limited amount of "secondary" xylem is found along the side of a few arms. The cortex is wide and parenchymatous. It appears to have radially arranged groups of slightly thicker-walled parenchyma that converge toward the outer edge of the cortex, resulting in a somewhat ribbed appearance. It is entirely possible that the xylem of *Pseudosporochnus* resembled that of *C. dawsoni* in arrangement prior to being crushed during fossilization. The sclereids in the cortex of *Pseudosporochnus*, the secondary xylem of *C. dawsoni*, and the lack of information on the morphology of the latter preclude the use of this name for our plant.

From continental strata of lowest Frasnian age in the Catskill Mountains of eastern New York, HUEBER (1959, 1960) has collected two kinds of petrified axes of *Cladoxylon* and also compression specimens of branches assignable to *Pseudosporochnus*.

One type of *Cladoxylon* (Hensonville, New York) has sclereids among the arms of xylem as well as in the cortex and is, therefore, distinct from our *Pseudosporochnus*. The other type (E. Ashland, New York) is likewise different for several reasons. It has over 40 arms of xylem at the larger end of the specimen, approximately half this number distal to a dichotomy, and it seems to lack obvious peripheral loops. Three traces, produced by three adjacent xylem arms, appear to enter each appendage. The central trace becomes clepsydroid, the two laterals remain terete. No morphology is known and no physical connection to the specimens labeled *Pseudosporochnus* sp. has yet been established. Thus the New York material must remain distinct from the Belgian *Pseudosporochnus*.

Pietzschia GOTHAN (1927) is known from the Upper Devonian of Wildenfels, Saxony and from the New Albany shale of Kentucky (READ and CAMPBELL 1939) where it is either Upper Devonian or Mississippian in age. The characters common to the two genera are the radially elongate arms of xylem and the lack of secondary xylem. The differences are the large central area in *Pietzschia* in which numerous small, circular bundles are located. Each has a central protoxylem point. In addition the peripheral bundles of *Pietzschia* are not connected in any way and each has two protoxylem points, one at either extremity (GOTHAN 1927, p. 6). Also *Pietzschia* may lack peripheral loops. The differences are sufficient to keep the two genera apart.

Xenocladia medullosina ARNOLD 1940 (emended ARNOLD 1952) comes from Middle and Upper Devonian strata in New York State. Like *Pietzschia* it has central, terete and radially aligned, peripheral bundles. Unlike *Pietzschia*, bundles of both types have secondary xylem. Apparently the two genera are more closely related to *Cladoxylon taeniatum* than to *Pseudosporochnus*. *C. taeniatum*, however, shows large peripheral loops, *Xenocladia* has none and *Pietzschia* may also have none.

Steloxylon SOLMS-LAUBACH (1910) was found near Semipalatinsk in Western Siberia in deposits of doubtful geologic age that are probably Permian or older (SCOTT 1923, Vol. II). In transverse section the large stem (5 inches in diameter) consists of a large number of xylem strands of two types, circular and radially elongated. None possess a loop, all have very little primary xylem and well developed secondary xylem. The bundles anastomose and form a complex network of tracheary tissue. Many small petioles are arranged spirally around the stem. They receive two or more traces from the external bundles of the stem and, as in the cladoxylons, they retain a stelar structure. The vascular system of the leaf bases is chiefly secondary. Pitting on the tracheids is multiseriate bordered and the rays widen toward the center of the stele as in the Medulloseae. The only points of resemblance to *Pseudosporochnus* are the radially elongated xylem arms and the dense covering of small leaf bases that recall the numerous fronds of the branches of *Pseudosporochnus*.

P. BERTRAND (1935, p. 111) saw a similarity between *Steloxylon* and *Cladoxylon dubium*. If this were confirmed, the age of the former genus would be carried back to Lower Carboniferous. BERTRAND in the same paper suggested that *Steloxylon* might be a subterranean organ of some cladoxylean found at Saalfeld. The abundant emission of petiole bases on the Siberian species makes this interpretation doubtful.

It is hardly necessary to compare *Pseudosporochnus* with *Völkelia* SOLMS-LAUBACH (1910) another genus from Saalfeld that is included in the Cladoxyleae. *Völkelia* has large, ovate-angular and smaller terete steles with tracheids that are pitted on all walls. The xylem mass is much more complex than that of *Pseudosporochnus*.

Asteropteris noveboracensis DAWSON 1880 is another plant with which *Pseudosporochnus* must be compared. It was found in marine beds of Frasnian age at Milo, New York. BERTRAND (1914) restudied DAWSON's original material and added several details to the description. HUEBER (1959, 1960) has found new specimens in deposits of lowest Frasnian age in eastern New York but has been unable to locate

either Dawson's type specimen or slides made from it. The plant has a central mass of xylem with 11 to 13 slender, radiating arms that unite in the center of the axis forming a star-shaped mass or that unite into two main groups of arms. Peripheral loops are present near the extremity of each arm and all of the xylem is primary. A thick cortical zone consists of polygonal sclerenchymatous cells (BERTRAND 1914, p. 913). Leaf traces are present in the cortex, each lying opposite an arm of the xylem from which it is probably pinched off in the same manner as in *Pseudosporochnus*. Apparently single traces supplied the appendages. While still in the cortex, each trace became at first bipolar and then quadripolar as it moved further out from an arm. *Pseudosporochnus* differs from *Asteropteris* by its nests of sclereids in the cortex, by the more massive character of its xylem arms, by the possession of a considerably greater number of xylem arms and by the fact that its xylem probably included a number of completely separate arms of xylem. Even more significant is the probability that the trace to its frond is clepsydroid and not quadripolar as that of *Asteropteris* is believed to be.

4. Affinities of *Pseudosporochnus*:

If, as the evidence suggests, *Pseudosporochnus* is a member of Cladoxylaceae, it becomes the seventh genus in the family. The Belgian species is the second to illustrate characters of external morphology. *Cladoxylon scoparium*, which should perhaps be placed in a distinct genus, is the other species whose external morphology is known.

The complexity reached in the development of varying patterns of xylem arrangement in the Cladoxylaceae has been interpreted in many different ways and various authors have discussed the affinities of the family with the pteridosperms (SCOTT 1923, Vol. 2), with the Equisetineae (EMBERGER 1944, p. 212), with the Ferns, and with the Psilophytales.

BERTRAND (1935, p. 116) regarded the Cladoxylaceae as a group of primitive ferns with affinities to the Zygopteridaceae. Plants that he referred to the genus *Cladoxylon* showed little distinction between stems and petioles and had petioles of a clepsydroid shape. BERTRAND may be correct in his assumptions but it is most unfortunate that so far the organic connection of *Hierogramma* or *Syncardia* (BERTRAND 1935, p. 110) or *Clepsydropsis* to the stems of *Cladoxylon* (ibid: p. 113) has not been established.

WALTON (1953, p. 94) included the Cladoxylaceae in the Coenopteridineae. He discussed only two genera *Asteropteris* and *Cladoxylon*. We emphasize a distinction made by WALTON that two types of lateral branches were produced, those that retained radial symmetry in their vascular system and those with bilateral symmetry. Both types have been found in *Pseudosporochnus*, the stele of branches of first, second and third order shows unquestioned radial symmetry whereas the frond is supplied by a trace that developed two protoxylems soon after its origin — a bilateral symmetry. "This type of leaf trace", says WALTON, p. 96, "is characteristic of the petiole bases of many undoubted ferns of Paleozoic age."

HARRIS (1929) considered Cladoxylales to be a group of vigorous plants that arose from psilophytalean stock.

EMBERGER (1944) treated Cladoxylales as an offshoot of Psilophytales which evolved in an independent line toward the primitive ferns and which were related to the Stauropteridales, though more differentiated than the latter.

ARNOLD (1952, p. 305) in his paper on *Xenocladia medullosina*, suggested a possible trend in evolution starting from a monostelic, lobed xylem strand like that of *Asteroxylon*. A pronounced invagination might have produced free lobes as in *Schizopodium*. An increasing dissection of the xylem mass could lead to the situation in *Cladoxylon scoparium* and *C. dawsoni* (READ 1935) in which anastomoses still existed and the xylem arms were elongated radially. The separation of xylem strands culminated in *Xenocladia*, *Pietzschia* and *Steloxylon*. This is an interesting view.

ZIMMERMANN (1959, pp. 155—165) included five orders in his class Primofilices, one of which is Cladoxylales. He assigns this order to a place intermediate between Psilophytales and Ferns. *Pseudosporochnus* and *Svalbardia* are placed in the families Pseudosporochnaceae and Svalbardiaceae. The two families constitute the order Pseudosporochnales in the division Psilophyta. We, of course, remove

Pseudosporochnus to the Cladoxylales because of its leaves and its anatomical structure. Further the manner of bearing sporangia terminally in pairs on highly organized fronds in *Pseudosporochnus* is sharply distinct from the location of sporangia in clusters on the upper side of a variously forked lateral appendage of *Svalbardia*. The differences impress us as sufficient to keep these two genera in separate orders.

PICHI-SERMOLLI (1958, p. 84) omits *Cladoxylon* and several other Devonian fern-like plants from his class Filicopsida and interprets them rather as "forerunners of the Pteridospermopsida". Some authors place *Cladoxylon* and its relatives in a class by themselves, the Cladoxylopsida (e. g. see PICHI-SERMOLLI 1959, pp. 451, 453). This procedure emphasizes their unique combination of characters and permits different authors to place them near one or another group depending upon the author's preference.

From the above brief survey Cladoxylaceae emerge as either a more or less isolated family among ferns that shows affinities to Psilophytales and to Zygopteridaceae or as an even more isolated family that may be in the line of evolution toward seedplants.

Originally *Pseudosporochnus* was classed in Psilophytales. Now it must be placed in Cladoxylales. Whereas its sporangial position may be considered to be a retention of a primitive feature, the complex morphology of its frond is clearly an advanced character as is its stelar anatomy. Similarly its habit is indicative of a relatively advanced condition if all the parts we believe we have assembled into one plant are interpreted correctly. Its leaf trace is produced in the manner well known in simple types of Zygopterideae. It is vexing to be uncertain whether or not *Pseudosporochnus* has reached heterospory. Were *P. verticillatus* and *P. nodosus* two different homosporous species or were they parts of one heterosporous plant? Only the discovery of new material can solve this problem.

If plants of the structural complexity of *Pseudosporochnus* and *Cladoxylon scoparium* flourished as early as Middle Devonian time, it becomes increasingly likely that a number of ancestors had preceded them in time. It may be that in their remote past the Cladoxylaleae passed through a stage comparable to the true Psilophytales but it is scarcely safe at present to argue that Cladoxylaleae arose from psilophytes that lived contemporaneously with them.

It is unfortunate that no decision on the taxonomic affinities of the family Cladoxylaceae can be made. The uncertainty is caused in part by the fact that most genera in the family are known only from their anatomical structure. External form is known only for *Pseudosporochnus* and for *Cladoxylon scoparium*. Some characters in the family point toward psilophytes, for example the terminal sporangia. Other characters such as the frond trace are more fern-like. Finally the complex steles of some species have suggested a relationship to the pteridosperms. The family may have been an offshoot of the psilophyte complex or of the early fern complex that flourished as a distinct, but dead-end, evolutionary line. During its span it seems to have developed a considerable range of anatomical and morphological features.

X. Summary

A new species, *Pseudosporochnus nodosus* sp. nov., is proposed for an extensive collection of compressions and petrifications from the Lower Givetian (Middle Devonian) at Goé in Belgium. Evidence is presented to show that the plant was a small tree consisting of a trunk, large roots, and three orders of branching. Bilaterally symmetrical fronds were arranged in a dense spiral on the branches. Their rachis gave rise to pinnae in sub-opposite fashion 2 to 4 times. The pinnae terminated in three successive dichotomies. Fertile fronds differed only in having pairs of sessile, elliptical sporangia replace the ultimate segments of the sterile fronds. Spores were not found within the sporangia. Petrifications revealed internal anatomy characteristic of Cladoxylales. All parts of the plant were characterized by the presence of nests of sclereids in the cortex, hence the choice of species name. The genus is now clearly distinct from the psilophytes and is placed in the Cladoxylales.

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XII. Explanation of Plates

Plate 1

- Fig. 1. Branch of first order; fragment showing at the base remains of xylem strand formerly interpreted as being rootlets. xylem strands = x st, sc = nests of sclereids.
× 1 (specimen No 5062/TP).
- Fig. 2. Branch of first order divided into four branches of second order. The third branch lies at a lower level than the three others. sc = nests of sclereids, x st = xylem strands.
× 3/4 (specimen No 4968/694).
- Fig. 3. Fragment of a branch of first order. The xylem has been stripped of the cortical tissues and appears as a tight bundle of xylem strands = x st.
× 1 (specimen No 4962/TP).
- Fig. 4. Branch of first order preserved from compression = co and petrification = p. Note the swollen base, with nests of sclereids = sc and a fringe of xylem strands = x st.
× 1 (specimen No 5059/631).
- Fig. 5. Petrified part of Fig. 4 (p). Note the parallel ribbing of the xylem.
× 5 (specimen No 5059/631).
- Fig. 6. Branch of first order, forked. The cortex being destroyed on the upper part, the two steles appear as a bunch of xylem strands = x st., sc = nests of sclereids.
× 1 (specimen No 4972/121).

Plate 2

- Fig. 7. Branch of first order divided into four branches of second order. The third branch is behind the others. Nests of sclereids are spread all over the surface of the axis. F = base of a frond in anatomical connection. Fr F = fertile frond in anatomical connection and detached. Pl = a pinna.
× 3/4 (specimen No 4967/21).

- Fig. 8. Branch of first order with six petrified areas = p. The basal part is not bulbous, but has been folded = Fo.
 $\times 1/2$ (specimen No 5060/178).
- Fig. 9. Branch of first order: apical branching. Above and below the fork are fronds in organic connection. Note the closely spaced nests of sclereids covering the axis and the fronds.
 $\times 1$ (specimen No 4950/722 A).
- Fig. 10. Branch of first order divided into four branches of second order. Branches number 2 and 3 with xylem ribbing = x st., sc = nests of sclereids.
 $\times 1$ (specimen No 4993/619).
- Fig. 11. Piece of petrified xylem covered with nests of sclereids = sc.
 $\times 2$ (specimen No 4997/540).
- Fig. 12. Petrified xylem of a branch of first order. On the right the ribbing is regular. On the left the ribs have an undulating surface, due to the pressure exerted by the nests of sclereids. sc = well petrified nests of sclereids.
 $\times 5$ (specimen No 5061/583 A).
- Fig. 13. Branch of first order with the usual swollen base. The whole surface of the axis is covered with nests of sclereids.
 $\times 1$ (specimen No 4956/462).

Plate 3

- Fig. 14. Crown of stem with six lobes or bases of broken branches of first order. The fourth lobe is inserted at a lower level than the other lobes. sc = nests of sclereids.
 $\times 1$ (specimen No 4955/114 A).
- Fig. 15. Counter-part of Fig. 14. The fourth lobe is prolonged by a fragment of axis. The lobes are covered with nests of sclereids = sc.
 $\times 1$ (specimen No 4955/114 B).
- Fig. 16. Fragment of stem covered with nests of sclereids = sc. All over the surface is a slight longitudinal ribbing.
 $\times 1$ (specimen No 4954/173).
- Fig. 17. Fragment of stem: sc = nests of sclereids, ap = lateral appendages, x st = xylem strands.
 $\times 1$ (specimen No 5051/57).

Plate 4

- Fig. 18. Root-like organ: sc = nests of sclereids, r = downwardly directed lateral root-like appendages, p = petrified area.
 $\times 1$ (specimen No 4961/168 A).
- Fig. 19. Branch of third order terminating in a pseudo-verticil of delicate thin vegetative fronds.
 $\times 1$ (specimen No 4960/599).
- Fig. 20. Fragment of stem covered with closely spaced nests of sclereids = sc.
 $\times 1$ (specimen No 4969/654).
- Fig. 21. Pair of sporangia, with a dehiscence line = d.
 $\times 6$ (specimen No 5054/286).
- Fig. 22. Fertile pinnae with well-developed pairs of sporangia. bl = blunt pointed surface of attachment.
 $\times 4$ (specimen No 5055/456).
- Fig. 23. *Pseudosporochnus verticillatus* KREJCI. Pairs of sporangia. d = proximal end of the sporangium.
 $\times 10$ (specimen No 36 from the Collection of Professor Dr. H. WEYLAND, Department of Geology, University of Cologne, Germany).

Plate 5

- Fig. 24. Branch of third order with vegetative fronds spirally arranged.
 $\times 1$ (specimen No 4981/55 B).
- Fig. 25. Branch of third order ending in a pseudo-verticil of delicate thin fronds. Fr F = fertile fronds, V F = vegetative frond. Note the nests of sclereids that cover the axis and the rachides.
 $\times 1$ (specimen No 5055/455).
- Fig. 26. Counter-part of the vegetative frond reproduced in Fig. 27, l s = limb-like segment, sc = nests of sclereids.
 $\times 2$ (specimen No 4981/55 A).
- Fig. 27. Detail of a vegetative frond of the specimen reproduced in Fig. 24. Note the closely spiral arrangement of the fronds and the flat appearance of the ultimate limb-like segments of the pinnae = l s. sc = nests of sclereids.
 $\times 2$ (specimen No 4981/55 B).

Plate 6

- Fig. 28. Branch of second or third order with vegetative fronds spirally arranged.
 $\times 1$ (specimen No 4951/161).

- Fig. 29. A branch of third order with vegetative and fertile fronds spirally arranged. Branch of first order with a bulbous end. sc = nests of sclereids, x st = xylem strands, V F = vegetative frond, Fr F = fertile frond.
 × 1 (specimen N° 4996/354 B).
- Fig. 30. Detail of a fertile frond of Fig. 29, showing the pinnae given off in sub-opposite fashion, the successive dichotomies of a fertile pinna and the upright pairs of sporangia. Fr p = fertile pinna, V p = vegetative pinna, bl = blunt pointed surface of attachment.
 × 4 (specimen N° 4996/354 B).

Plate 7

- Fig. 31. Transverse section of a branch of first order that shows the general stellate structure of the stele.
 × 17 (inclusion N° 650/A/6/3).
- Fig. 32. Transverse section of a branch of first order.
 × 17 (inclusion N° 650/A/5/1).
- Fig. 33. Transverse section of a branch of second order. On the left side six xylem arms well preserved: A 1 to A 6. On the right side there is a beginning of branching = Br. sc = nest of sclereids.
 × 17 (inclusion N° 546/A/3/1).
- Fig. 34. Transverse section of a branch of third order: nineteen xylem arms: A 1 to A 19. Arms 6 and 7 crushed by nests of sclereids while arm 8 which is shown crushed on Fig. 35, is well seen here. Arms 15 to 19 badly preserved.
 × 17 (inclusion N° 466/2/22).
- Fig. 35. Transverse section of a branch of third order: nineteen xylem arms, variously crushed: A 1 to A 19 = arms. sc = nest of sclereids. Arms 6 and 7 well seen, while arm 8 is crushed. Arms 15 to 19 well preserved.
 × 17 (inclusion N° 466/2/16).
- Fig. 36. Petrified axis of a branch of second order embedded in plastic. The nodular form of the iron-hydroxide petrification is seen through the plastic. co = compression, p = petrification, ps = polished surface of the petrified axis reproduced in figure 33, c = cortex.
 × 3 (inclusion N° 546/A/3).

Plate 8

- Fig. 37. Transverse section of a branch of third order with nineteen xylem arms: A 1 to A 19. Compare the sharp apex of the arms with the round apex of the arms of figures 41 and 43 which are still protected by the cortical tissues. sc = nest of sclereids.
 × 34 (inclusion N° 466/2/24).
- Fig. 38. Detail of figure 35. Arm 6 has the protoxylem elements filling the loop. In arm 7, protoxylem elements of the loop are destroyed. sc = nest of sclereids.
 × 65 (inclusion N° 466/2/15).
- Fig. 39. Detail of figure 35. Arms 17, 18, 19.
 × 65 (inclusion N° 466/2/20).
- Fig. 40. Detail of figure 37. Arms 8 and 9 have the protoxylem elements preserved in the loop (= Lo). A 8 to A 16: position of the arms.
 × 65 (inclusion N° 466/2/24).
- Fig. 41. Transverse section of a branch of third order with cortical cells that have protected the round apex of the arms.
 × 17 (inclusion N° 466/1/18).
- Fig. 42. Longitudinal section showing a xylem arm pinched between nests of sclereids.
 × 65 (inclusion N° 546/II b/3).
- Fig. 43. Detail of figure 41: two arms with round apex. Lo = Loop, cc = cortical cells.
 × 65 (inclusion N° 466/1/19).

Plate 9

- Fig. 44. Longitudinal section through the apex of an arm of a branch of third order. Annular and scalariform tracheids. sc = nest of sclereids.
 × 130 (inclusion N° 466/3/3).
- Fig. 45. Root: Upper transverse section of six fragmentary xylem plates, disposed in parallel and radially elongated: A 1 to A 6. sc = nests of sclereids.
 × 65 (inclusion N° 168/1/14).
- Fig. 46. Root: Lower transverse section with five fragmentary xylem arms disposed in parallel and radially elongated: A 1 to A 5.
 × 65 (inclusion N° 168/L 1/5).

Fig. 47 to Fig. 50. A series of transverse sections through the arms 2, 3, 4 of figure 33, B. A. = Leaf bundle, B. B. = Leaf bundle, both badly crushed. sc = nest of sclereids.

× 65 (inclusion No 546/A/3/3).

Fig. 48. The two leaf-bundles B. A., B. B., and arm 4 are crushed by a nest of sclereids = sc. A 2 = Arm 2 with a narrow loop filled with protoxylem elements. A 3 = Arm 3 with a large empty loop. sc = nest of sclereids.

× 65 (inclusion No 546/A/3/10).

Fig. 49. Leaf bundles B. A. and B. B. are better preserved. A 3 = Arm 3; A 4 = Arm 4; A 5 = Arm 5; sc = nest of sclereids.

× 65 (inclusion No 546/A/3/19).

Fig. 50. Leaf bundles B. A. and B. B. are well seen. Compare the state of preservation of Arm 4 in the series represented by figures 47 to 50.

Plate 10

Fig. 51. Stade zero of the emission of a trace. M = Metaxylem, Lo = Narrow loop filled with protoxylem.

× 130 (inclusion No 546/A/3/43, arm 5).

Fig. 52. Stade 1. The loop increases slightly in length and width. Lo = Loop, l = line of small cells.

× 130 (inclusion No 546/A/3/9, arm 2).

Fig. 53. Stade 2. The loop becomes triangular and the files of metaxylem converge around the loop (lo).

× 130 (inclusion No S 546/A/3/57).

Fig. 54. Stade 3. The loop has increased and is constricted in the middle. Protoxylem elements fill the loop (lo).

× 130 (inclusion No 546/A/3/4, arm 3).

Fig. 55. Stade 3. The protoxylem cells are destroyed; the loop appears as a lacuna constricted in the middle of its length. Lo = Loop.

× 130 (inclusion No 546/A/3/10, arm 3).

Fig. 56. Stade 5. Free bundle B. A. with a circular form and one protoxylem point: px.

× 130 (inclusion No 546/A/3/24).

Fig. 57. Stade 6. Free bundle B. A., slightly elongated tangentially. There are two distinct protoxylem points symmetrically disposed.

× 130 (inclusion No 546/A/3/33).

Fig. 58. Stade 6. Free bundle B. A. higher up. The two protoxylem points are distinct.

× 130 (inclusion No 546/A/3/41).

Fig. 59. Free bundles B. A. and B. B. The leaf-bundle B. B. that has been given off earlier than B. A. is tangentially elongated and has two protoxylem points more distantly located than on the bundle B. A. of the figures 57 and 58.

× 130 (inclusion No 546/A/3/22).

Fig. 60. Free bundle B. A. compressed by the nests of sclereids, and altered in its form.

× 130 (inclusion No 546/A/3/51).