

FURTHER INVESTIGATION ON THE VASCULAR SYSTEM OF *PSEUDOSPOROCHNUS NODOSUS* LECLERCQ ET BANKS

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AND

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LUCKNOW

WITH PLATES 21-24, 5 FIGURES AND 2 TABLES IN THE TEXT

Abstract

Seven petrified areas scattered on a first order branch of *Pseudosporochnus nodosus* LECLERCQ and BANKS are described. Gradual changes in the pattern of the vascular system are revealed. The growth process of the steles is demonstrated. On the basis of the new anatomical features redefined, the plant is compared with other Cladoxylopsida.

INTRODUCTION

The genus *Pseudosporochnus* is hitherto known by three species: *P. verticillatus* (KREJCI) OBRHEL (1959), the type species originally known from Bohemia; *P. chlupaci* OBRHEL (1959) recorded from Bohemia, and *P. nodosus* LECLERCQ and BANKS (1962) found in the Middle Devonian in Belgium. The type material was reinvestigated by KRÄUSEL and WEYLAND in 1933, while a branch of the first order of *Pseudosporochnus* was described by LANG (1929) from the Stromness beds in Scotland.

The morphological details of the three species and other occurrences of *Pseudosporochnus* have earlier been treated at length by LECLERCQ and BANKS. Of all the species known so far, the Belgian plant *P. nodosus*

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Table 1

Petrified Areas "Nodules"	Location on Branch	Dimension (cm.) length x width	Vertical distance from next higher nodule (cm.)	Width of branch near middle of nodule (cm.)	Macroscopic Features
N° VII.	21.12 cm. from base, covering whole breadth of axis, slightly protruding out of right margin.	1.45 x 1.57		1.57	Subcircular, lower margin flat; considerable thickness of xylem eroded, remains of xylem better seen on right margin; scattered sclereids along left margin and lower right corner.
N° VI.	18.92 cm. from base; along left margin, extending nearly to right margin.	1.5 x 1.4	0.7	1.6	Nearly circular, xylem better seen on right and left side, narrowing in middle, upper and lower parts nearly empty, xylem surface wavy showing depressions left by sclereids; scattered sclereids more visible near periphery and over xylem; nearly whole thickness of nodule preserved but severely compressed.
N° V.	16.07 cm. from base; along right margin, protruding out slightly.	1.15 x 1.41	1.7	1.66	Suboval, elongated along width of axis; xylem preserved in left half, right half with scattered sclereids, xylem colour yellow.
N° IV.	9.87 cm. from base; along left margin.	1.5 x 1.05	4.7	1.9	Nearly rectangular with rounded corners, elongated along length of axis; left margin with a narrow strip of sclereids seen over the xylem; remaining part entirely with xylem showing smooth parallel ribs and intervening paler grooves (? parenchyma).
N° III.	7.35 cm. from base; along right margin.	1.24 x 0.6	1.28	1.93	Nearly oval, elongated along length of axis; only sclereids visible along right margin and in middle, upper and lower parts deeply eroded to the level of rock matrix; some bits of xylem noticeable away from the nodule on the left side over the branch.
N° II.	5.8 cm. from base; along right margin, protruding out slightly.	1.0 x 1.02	0.55	2.15	Subcircular, upper margin flatter, lower end nearly conical; sclereids in right half and along left margin; areas between sclereids showing some xylem.
N° I.	1.45 cm. from base upward and 0.49 cm. from left margin of axis.	2.1 x 1.1	2.25	2.44	Subcircular, corners rounded, elongated along length of axis; surface elevated generally towards right half forming a small hump near right lower corner due to folding of axis; xylem more visible on left half, some sclereids over xylem seen on right half; two obliquely crossing thin veins of mineral matter in middle part.

is the only one which has revealed, in addition to its morphological characters, a considerable amount of evidences regarding the anatomical structure, particularly on the second and third order branches, which were more favourably preserved as compared to the first order branch. The present investigation is confined to the detailed anatomical structure of a first order branch of *P. nodosus*, affording a more satisfactory basis for re-interpreting the vascular structure of *P. nodosus*.

One of us (Doctor K. M. LELE) takes this opportunity to express his deep sense of gratitude to the Ministry of National Education and Culture, Government of Belgium for the grant of a Research Fellowship which made this collaboration possible, as well as to the Commission Administrative du Patrimoine, University of Liège for financial assistance to visit the Palaeobotanical laboratories in England and France.

MATERIAL

The material belongs to the collection of the University of Liège (Palaeobotany Department) made earlier by one of us (Professor S. LECLERCQ) from the Middle Devonian (Lower Givetian) beds near Goé, 30 km. east of Liège, close to the confluence of the rivers La Gileppe and La Vesdre at quarries known as Carrières Brandt.

External features: The rock containing the branch is a rather poorly laminated shaly sandstone. The specimen gently slopes down obliquely towards its distal part in the sediment. It measures 32.8 cms. in length and lacks the apical portion as well as the bulging end (fig. 1). The broken distal end is 1.28 cm. wide. The basal region measures 2.48 cm. wide but was evidently wider as is suggested by a fold in the axis which „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“ (LECLERCQ and BANKS, 1962, p. 7). The two margins of the branch run in a sub-parallel manner, narrowing very gradually from the base upwards.

In general, the branch is preserved as a compression, but there are seven localized areas where the internal vascular structure has been preserved as a petrification by the impregnation of iron hydroxide. The surface of the axis is wrinkled, showing fine to coarse, faint longitudinal ribs which are evidently related to the internal structure of the plant. The rough and pitted appearance of the whole surface is due to the abundance of the sclereid nests which have given the plant its specific name.

Petrified areas "Nodules": The seven petrified areas, which represent parts of "Nodules" are scattered over the branch (fig. 1). Their sizes are variable. Most of them except n° VII and probably n° VI touch either the left or the right margin of the axis, but do not extend fully across it. This indicates that the vascular strand has been displaced due probably to the decayed ground tissue. The basalmost nodule (N° 1) lies largely within the pocket of the fold already mentioned which has favourably protected the vascular structures. The salient macroscopic features of the seven petrified areas or "Nodules" are summarized in Table 1. The inclusions which have revealed the best informations are n° I, IV, VI and VII.

DESCRIPTION OF ANATOMICAL FEATURES

a) Technique for inclusion

In view of the large size of the specimen, the embedding of the petrified areas was carried out in stages. Each of the seven petrified areas was surrounded by plasticine walls, impregnated by styrene and later covered with an appreciably thick coat of bioplastic mixture (100 pts. by weight of Palatal P 4 FI + 2 pts. of catalyser + 0.1 pt. of accelerator + 15 pt. of Styrene). When the mixture became hard enough nearly after two days in room temperature, the branch was cut across at suitable places to isolate the seven petrified areas.

The individual nodules were finally re-embedded completely in plastic, following the method of LECLERCQ and DISCRY (1950). On each block the distal side of the nodule was indicated, and grinding was carried

out from the basal side (proximal). When minute pores, cavities or cracks were found in the surface during grinding, a homogeneous bioplastic mixture (10 gms of bioplastic + 4 drops of catalyser + about 8 drops of accelerator) was poured carefully on the surface and placed under vacuum.

b) Inclusion I

The nodule measures 2.1 cm. in length of which 1.12 cm. was ground from the base upward and the transverse sections were studied in 17 stages to follow the anatomical structure.

General transverse section: The vascular system is polystelic and is distinguishable into an external zone and a central zone of steles (fig. 2). The external zone is composed of more or less straight, separate, clepsydroid arms of different lengths, radially orientated. The central zone consists of circular to oval, separate steles. All the steles are composed of primary xylem and are embedded in a parenchymatous ground tissue (fig. 2, p), generally not preserved, which, however, was most probably well-developed as it will be pointed out later.

The tracheids in the protoxylem of the radial and central steles measure from about 4μ — 8μ in diameter. The metaxylem elements are about 10μ — 40μ . They become progressively larger away from the protoxylem and may again reduce near the periphery of the arm.

The vascular system is surrounded by the cortex, the inner part of which shows a discontinuous ring of sclereid nests ranging from 300μ — 1000μ in average diameter. The sclereids are separated by parenchyma (or ? collenchyma) which occasionally assumes a honeycomb pattern.

Radial steles: Details. The best transverse section (fig. 2) shows nine radial steles of which stele n° R 1, R 3, R 4, R 5, R 6 and R 7, have provided the main information and will be discussed in some detail. The noticeable difference in their size and shape is a result of their mode of growth which is explained below.

Stele n° R 4 is considered as a nearly mature one, because its dimensions ($1470\mu \times 300\mu$) and peripheral loop are identical with the steles found at higher levels (figs. 2, 7 & 16). Though the loop is narrow, it shows within it radially elongated delicate cells (fig. 3).

Stele R 4 shows besides a peripheral loop, another small proxylem point situated near the proximal end (fig. 7). This structure is the result of successive stages of growth that are described below.

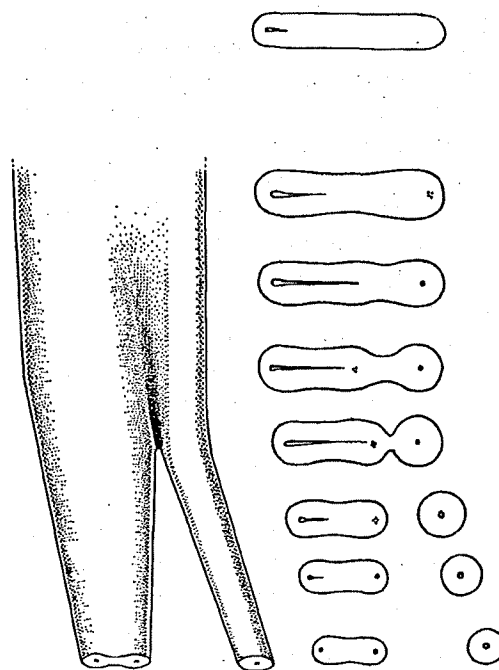
The small stele R 6 ($700\mu \times 300\mu$) (fig. 2) represents an early stage of development of a radial stele in which the two protoxylem groups are differently developed. The peripheral (distal) one is prolonged by a thin median line (fig. 8). The proximal protoxylem is well seen and better developed as compared to that of stele R 4 (fig. 7). On the same radius and facing the proximal end of stele R 6 is a circular stele C 6 (390μ) with a centrarch protoxylem. Higher up in the inclusion, the two would fuse together forming a single arm (Text-fig. 1). This interpretation is based on the successive stages we have followed in the case of stele R 5 ($1540\mu \times 320\mu$).

In figure 7, stele R 5 shows at 'N' (= neck) a noticeable constriction which is not the result of an accident of preservation. Above the constriction one can still recognize what was formerly representing a circular stele similar to C 6 in having retained a centrarch protoxylem. The mesarch appearance of the protoxylem above the constriction is a secondary result of the connection of a central with a radial stele. In earlier stages of stele R 5 (fig. 9) the neck is still shorter and narrower.

Below the 'neck' (fig. 7), one can recognize a radial unit the length (680μ) of which is comparable, though a little longer, to that of stele R 6 (fig. 8). Subsequently the 'neck' increases in width giving the stele a more clepsydroid shape and a size equal to that of stele R 4. Simultaneously the distal loop increases in length, the proximal protoxylem vanishes gradually while the median one (fig. 7) becomes evanescent. Consequently, stele R 5 represents an intermediate stage of development between the two formerly described steles R 4 and R 6 + C 6.

Apparently all steles do not develop a 'neck'. For instance in the case of stele R 3 ($1100\mu \times 310\mu$) (fig. 7), although the protoxylem groups are nearly at the same level of development as in stele R 4 and R 5, its length is shorter by 26μ which is equal to the missing 'neck'. However, one can still make out the circular shape of the

Text-fig. 1. Connection between a radial and a circular stele illustrating the growth process of a radial arm.



central unit that has fused with the radial one. Coming back to the steles R 6 + C 6, the result of the connection of the two will precisely give a total length of 1090μ which is almost equal to stele R 3.

The smallest observed radial stele R 8 ($516\mu \times 200\mu$) is shown in fig. 4. It is clepsydroid in shape and has two protoxylem points connected by a line of small tracheids. The proximal protoxylem point is opened due to compression.

An early stage of development of a radial stele is seen in the stele R 2 (fig. 5) measuring $560\mu \times 400\mu$. Its oval shape, with two very close protoxylem groups, give the impression that it represents an intermediate stage between a circular stele, of which the protoxylem has just divided, and a radial stele. This opinion is confirmed higher up (fig. 2) where that stele has increased in length and the two protoxylem groups, in mesarch position are connected by a thin line. We are, therefore, inclined to consider that the stele R 2 has been displaced from its original position in the outer zone, between the steles R 1 and R 3, as a consequence of the lateral compression resulting from the 'fold'.

Central steles: Details. The transverse section in figure 2 shows several central steles which are noticeably distinct from the radial ones in being mostly circular with a centrarch protoxylem point. Steles C 3 and C 10 which are cut somewhat obliquely in the above section were circular in other stages (figs. 7 & 13).

In the central part of the inclusion, where the steles are unprotected due to lack of sediment, several steles have successively appeared (stages 9, 10) during course of grinding, then disappeared. In this way a total of 12 steles has been observed. In this section (fig. 2) the missing steles are indicated by a cross.

Like the radial steles, all the centrals are not at the same stage of development, nor have they identical behaviour. We have already explained the peculiar trend of the stele C 6 which is orientated towards the growth of the radial stele R 6.

In the case of stele C 4 + C 5, two central circular steles have fused. In the earliest stage 2 despite the bad state of preservation, two ill-defined circular steles (C 4 and C 5) were noticeable close to each other (fig. 10). In one of them, the centrarch protoxylem is still observable. For a certain distance, the units could not be clearly followed up but in stage 9, their metaxylems were fully connected together. In stage 11, the oval shape is already reached and the stele measures $780\mu \times 380\mu$. The former centrarch protoxylems

which have remained permanently independent, now appear in a mesarch position but without a definite median line between them, unlike the case of a radial stele (fig. 11).

If correctly interpreted, the starting points of the growth of a radial and central stele were slightly different. In the case of an oval central stele, most probably two circular steles have fused their metaxylems together, their protoxylems remaining independent. Conversely, in the radial steles, though the very starting point has not been observed, the information obtained from the stele R 2 (fig. 5) (described above) indicates that one circular stele, by the dichotomy of the centrarch protoxylem, followed by the elongation of the metaxylem, could result in a radial stele.

Ground tissue: We have mentioned above the "fold" in which the favourably preserved steles were found. In fact the good state of preservation of the vascular system is not due to the fold which could have caused a severe squeezing of the whole structure. It is more likely that the amount of parenchymatous tissue which surrounded the steles could have acted as a cushion against the forces of compression. This inclines us to believe that a wide development of parenchyma occurred in the basal part of a first order branch.

c) Inclusion IV

The nodule measures 1.5 cm. long and 1.05 cm. wide, of which about 7.6 mm. thickness was ground from base upwards. The first complete transverse section was revealed at about 4.5 mm. above the base. A total of ten stages were followed up.

General transverse section: The cross-section (fig. 15) represents more than half of the diameter of the axis. It is obvious that the vascular organization is more compact and more developed than that of inclusion I. It consists of about 13—14 radial steles and a reduced number (3—5) of elongated central steles. The ground tissue is poorly developed and there is the usual ring of sclereid nests.

Radial steles: Details. As a result of compression, which in this nodule has been perpendicular to the lying axis, the steles have been distorted, fractured and their parts variously juxtaposed or overlapped.

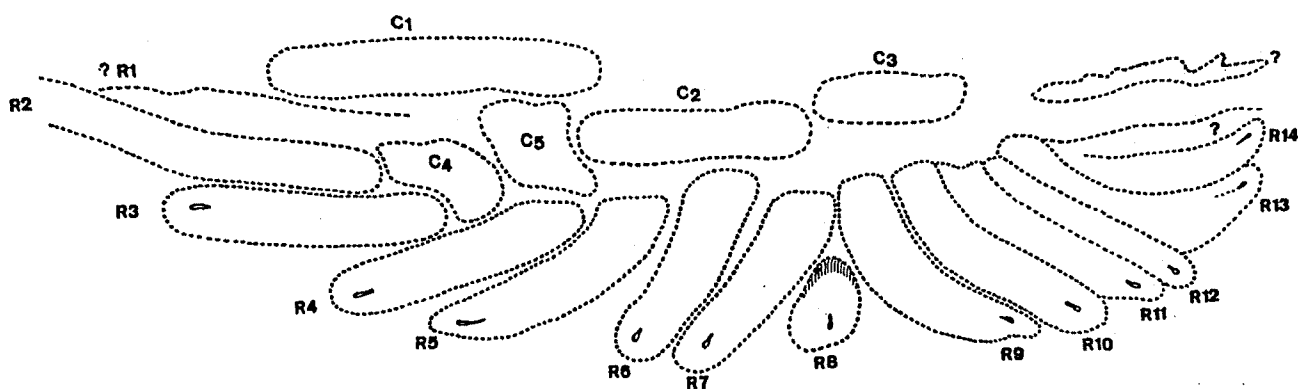
In the median part the steles are overshortened and over-widened whereas at the two extreme ends they are over-elongated and laminated, so that the intermediate steles afford the best sizes for comparison. Considering this, it appears that the arms were originally more or less equal in length. Their estimated size, about $1270\mu \times 300\mu$, is nearly comparable to the longest mature radial stele of inclusion I (steles R 1, R 4, R 5 and R 7). The steles are straight, separate, more or less clepsydroid, with a distal peripheral loop. No proximal protoxylem has been observed. The stele R 8 (fig. 15), badly compressed and squeezed between steles R 7 and R 9, is reduced to its distal end which shows, in fig. 19, a narrow peripheral loop. Text-fig. 2 is a semi-diagrammatic general view of the cross-section reconstructed from the various best preserved stages of each arm.

Central steles: Details. The five central elongated steles seen in the Text-fig. 2 have not been encountered at the same level. Consequently, in the fig. 15 representing stage 1, stele C 2 ($1200\mu \times 240\mu$) and the broken stele C 3 ($760\mu \times 240\mu$) are observable while stele C 1 only shows its outline through the plastic. It appears in stage 8 where it measures $1700\mu \times 280\mu$. Apparently two more central steles (C 4 and C 5) have been wedged in between. None of the steles have shown any protoxylem.

We consider that the central elongated steles in the inclusion IV represent the mature stage of the oval steles noted in the central zone of the inclusion I.

The main changes of the vascular system in its ascending course are the preponderance of the radial steles over the centrals, the decreasing number of circular steles and the diminution in the amount of protoxylem elements reduced to the peripheral loop.

It is contended that the vascular organization seen in the inclusion IV represents the mature structure of the branch. At this level the polystelic structure is for the first time clearly distinct on more than half of the diameter. Consequently it may be suggested that a whole transverse section of the branch consisted of about 20 to 24 radial steles surrounding a small central group of nearly 3 to 6 tangentially elongated steles, giving approximately a total number of 23 to 30 steles. The radial steles have the privilege to have the protoxylem elements included in a peripheral loop.



Text-fig. 2. A semi-diagrammatic cross section of the axis in inclusion IV (see figs. 1 and 15).

d) Inclusion VI

This nodule (1.5 cm. x 1.4 cm.), situated very high on the branch, revealed a severely compressed structure in the cross-section as was suspected from external observations. The nodule was ground up to 8 mm. above its base before some structure could be recognized. In the middle part, the radial and central steles are entirely pushed together under the pressure of the sclereids and consequently no more distinguishable from each other. On the lateral sides, the flattening being less severe, a number of radially over-elongated and overlapping steles are seen, some of them possessing a distal loop. This state of preservation reproduces identically the appearance of the xylem observed by LECLERCQ and BANKS (1962, figs. 33 and 47) in a branch of second order of *Pseudosporochnus nodosus*. In view of the high location of the nodule VI on the branch, the striking general similarity of its internal structure with the anatomy of a second order branch could well be expected.

The severe pressure that has obscured the xylem structure of the central part of the branch raises the question of the presence or extinction of central steles at that level. This question will be restated in the light of the reinvestigation of the material studied by LECLERCQ and BANKS and dealt with in the comparison.

e) Inclusion VII

In view of the small thickness of the xylem preserved in this inclusion (1.45 cm. x 1.57 cm.), it was utilized for the purpose of longitudinal sections.

As reported earlier by LECLERCQ and BANKS, the tracheids are commonly scalariform; the spiral or reticulate elements were not recognizable. The scalariform thickenings are horizontal to somewhat oblique (fig. 25). Associated with them are a kind of tracheids, not yet noticed in *P. nodosus*. These are pitted elements about 2μ — 5μ in diameter with circular to oblique pits, and usually arranged in a single row (figs. 6 & 14). The pits may be close but commonly they are separated by a variable distance up to 7μ . In some cases the pits show what appears like a border (fig. 6). A sort of transition from pitted to scalariform elements has been occasionally noticed. In general, the tracheids vary in their diameter from about 12μ — 35μ which compares with the sizes taken from a cross-section of the tracheids in the inclusion I.

Main results

1. The polystelic structure of *Pseudosporochnus nodosus* is confirmed.
2. Cross-sections have revealed an outer ring of radial steles and a central zone of circular to oval steles. All are composed of primary xylem. The vascular system is embedded in a parenchymatous tissue more or less well-developed according to location, and surrounded by a discontinuous ring of sclereid nests.

3. In the basal most inclusion (N° I), the outer zone consists of straight, unconnected, nearly clepsydroid steles, each having two mesarch protoxylem points, one at either end. The steles are unequal in length according to their mode of growth.

The increase in length is the result of a subsequent fusion between a radial and a circular stele (Text-fig. 1). Simultaneously, with the increase in length, the protoxylem elements are differently developed: while the peripheral protoxylem becomes a small loop, the others vanish successively.

The central zone consists of a majority of circular steles, typically centrarch and a few oval steles which apparently are the result of the fusion of two circulars.

In the fused unit, the two centrarch protoxylems remain independent but reach a mesarch position as a consequence of a lateral elongation, and higher up vanish. It is interesting to note that at that level the central steles are more numerous than the radials.

4. In contrast to inclusion I, the organization at the level of inclusion IV (8.7 cm. above) is more compact as a result of the greater preponderance of the radial steles over the centrals. The radial steles are more or less equal in length. Their average size is comparable with the longest radial stele of inclusion I. No other protoxylem is observed except a small peripheral loop.

The number of central steles is reduced to 4—6. They are laterally elongated, without recognizable protoxylem and seemingly represent the ultimate stage of the oval steles of inclusion I. No circular stele has been observed.

At this stage, the vascular system appears to represent the mature development which is found higher up.

5. The structure observed in inclusion VI, located at 17.5 cm. above the inclusion I is identical with that of the second order branch described by LECLERCQ and BANKS (1962, p. 17).
6. Scalariform tracheids are more common but pitted and bordered pitted elements have also been observed.
7. The reconstructions in the Text-figs. 3 & 4 represent, in an uncompressed state, an ideal transverse section through the basal and the middle part of a branch.

DIAGNOSIS

Pseudosporochnus nodosus LECLERCQ and BANKS, 1962

The original diagnosis given by LECLERCQ and BANKS (1962, pp. 21—22) is subdivided into (A) External morphology and (B) Internal structure. The diagnosis of the external morphology is retained. The internal structure is redefined.

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 x 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: Emended diagnosis. Up to the third order branches, xylem consists of two zones: an outer and a central. The outer zone consists of about 18 to 24 radial steles, straight, clepsydroid, unconnected and more or less unequal in length in the first and second order branches. In third order branches, steles are laterally connected in groups. Growth of the steles results from the fusion between a radial and a central stele. Protoxylem mesarch, one to three groups may occur according to the stage of the growth of the stele; a small peripheral loop in mature steles only.

Central zone consists of circular, oval and elongated steles, their number varies according to location on branch; central zone well-developed towards base consisting of about 20 steles which are circular and cen-

trarch or oval with two mesarch protoxylem groups, one at each extremity. Central steles decrease in number higher up (5 to 8), elongated central steles without recognizable protoxylem. All xylem primary.

Tracheids chiefly scalariform but annular, spiral and even bordered pitted elements also present. Parenchyma in the center and between the steles well-developed near base but reducing higher up. Inner cortex consists of nearly isodiametric nests of sclereids in a discontinuous ring, nests separated by parenchyma.

Holotype: N° 4996/354 B.

Paratypes (LECLERCQ and BANKS): Compressions, Nos. 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.

Specimen studied by LECLERCQ and LELE: N° 5060/178.

Inclusions (LECLERCQ and BANKS): Nos. 650 A/6 — 650 A/5 — 546 A/3 — 546/2b — 466/1/19 — 466/2 — 466/3 — 168/1.

Inclusions (LECLERCQ and LELE): Nos. 5060/178/I, 5060/178/IV, 5060/178/VI, and 5060/178/VII.

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, Université de Liège, Belgium.

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.

COMPARISON AND DISCUSSION

In 1962, LECLERCQ and BANKS have given a detailed review of the previous records and an interpretation concerning plants related to or supposed to be related with the Cladoxylopsida. It is not necessary to repeat it here. The researches of these authors on *Pseudosporochnus nodosus* have caused the plant to appear in a new light, as it has been removed from the Psilophyta to a systematic position close to the Cladoxylopsida. They have in great details worked out the external and internal morphology of the new species. Although they (p. 22) could accurately demonstrate the polystelic structure, they could not clear up completely the organization of the vascular system due to the compressed state of the petrified central areas of the axis. Therefore, they suggested that some xylem plates (or steles) in the first order branch extended across the diameter of the axis and some others were free or joined to make U or V-shaped strands.

We are in general agreement with these authors as to the gross features of the vascular system. However, our observations bring three major points of difference. First, there is no lateral anastomosing between the radial steles, no steles crossing over the diameter of the axis in the first and second order branches. Secondly, there is a permanent group of central steles throughout the whole branching. A third point of interest is the discovery of the process of growth of the radial and central steles.

In relation with the second point stated above, a reinvestigation of the material of LECLERCQ and BANKS has permitted a better view of the central part of the third order branch. Four central steles could be observed, two being nearly circular and one of them apparently with a centrarch protoxylem (figs. 20, 21) while the other two steles are laterally elongated (fig. 22). The exact number of central steles remains unknown as the left part of the axis is badly compressed. The average number of central steles was presumably 7—8. Most probably the central steles were scattered in the central parenchyma. These observations furnish the evidence that a central group of steles persists from the first order branch to the third order.

The lack of lateral connections and secondary xylem as well as the existence of central circular steles point the affinity of *P. nodosus* closest to *Pietzschia* GOTHAN than any other genus of the Cladoxylopsida. Two species have been described: *P. schülleri* (GOTHAN, 1927) from the Upper Devonian of Wildenfels Saxony, and *P. polyupsilon* READ and CAMPBELL (1939) either from Upper Devonian or Mississippian of the New Al-

bany shale of Kentucky. Both are established on short fragments of petrified axis lacking branching, root, leaf or fructification.

As regards the anatomy, *Pseudosporochnus nodosus* has much in common with *P. schülleri*. Both plants have a distinct outer zone consisting of radially elongated, unconnected xylem plates, unequal in length and straight with two protoxylem points, one at either extremity; a group of central steles either circular and centarch or oval with two mesarch protoxylem. As seen in his illustration reproduced in our fig. 24 (GOTHAN, 1927; Pl. 1 fig. 4), GOTHAN (1927, Pl. 6 and 10) interprets the oval stele as the possible result of the fusion of two circular steles. In addition, he believes that circular steles join a radial stele towards its inner extremity (1927, Pl. 2 fig. 5; pp. 7 and 10). We have reproduced this important stage in fig. 23.

The differences between *P. nodosus* and *Pietzschia schülleri* are in the development of the sclerenchyma, the parenchyma and the number of steles. *Pietzschia schülleri* is distinguishable by its strong construction made of triangular sclerenchymatous strands running straight between the xylem arms (fig. 24) and in having developed a large inner parenchymatous groundmass. Other differences are: 1 — the lack of a loop in *P. schülleri*, but we have seen in *Pseudosporochnus nodosus* that the development of a loop can be a postponed formation, closely related with the growth of the steles; 2 — the high number of steles, over 34 radial steles and certainly more than 40 central steles. The steles have been counted on the original Pl. 1, fig. 3 of GOTHAN, as the author did not give any information on the total number of the stelar strands.

We are inclined to consider that the differences in the anatomy of the two plants are minor as compared with the important features represented by the general organization of the vascular system and the mode of growth of the steles which seems comparable.

Pseudosporochnus nodosus differs from *Pietzschia polyupselon* READ and CAMPBELL (1939, p. 444) in many points. The Kentucky plant has 54 vascular bundles (in the type specimen); occasional lateral branching of the bundles; abundant sclerenchymatous formation: sclereid strands in the central parenchyma and radially elongated sclereids between the vascular bundles; leaf traces in pairs and of ultimate upsilon shape.

Mention must be made here of a possible new member of the Cladoxylopsida: *Calamophyton bicephalum* LECLERCQ and ANDREWS (1960) formerly considered as a Protoarticulatae. In 1965, LECLERCQ (in LECLERCQ and SCHWEITZER) has revealed the polystelic structure of a branch of third or fourth order. It consists of a total of 16 steles, all of primary formation. The peripheral steles are curved having two to five connected arms, radially disposed with a mesarch protoxylem group or loop at each end. The central steles are more or less circular, straight or sinuous. They lack protoxylem elements. A ring of small sclereid nests surrounds the vascular system. The ground tissue is abundant. A free terete trace with a central protoxylem has been observed.

The two plants *C. bicephalum* and *P. nodosus* have in common a group of central steles that lack protoxylem, no secondary formation, terete trace and the sclereids nests in the cortex. As regards external morphology, the two plants have comparable branching of the axis in a palmate or crown-manner, dissected appendages, spirally disposed. They differ in respect of the three dimensional pattern of the sterile and fertile appendages in *C. bicephalum* on which the rigid fertile appendage is divided into an upper and a lower segment, each supporting three pairs of side stalked sporangia that are pendulous. In *P. nodosus* erected sporangia are borne terminally on forked pinnae. So far as we know, the differences are sufficient to keep the two plants apart in separate genera.

In 1962, LECLERCQ and BANKS have discussed thoroughly (pp. 25—26) the common characters and the differences of the external and internal morphology between *Cladoxylon scoparium* KRÄUSEL and WEYLAND and *Pseudosporochnus nodosus*. However, a special mention of the behaviour of the vascular system in both plants needs to be made here as it falls within the special scope of this paper.

KRÄUSEL and WEYLAND (1926) have reported that on a short vertical distance of narrow axis (2 to 5 mm. in diameter) of *Cladoxylon scoparium* rapid changes in the anatomy are observed.

In a cross section, gross features consist of a group of steles radially elongated, most of them abundantly anastomosed, and sharply curved. Each arm has a mesarch peripheral loop. At the narrower diameter of younger parts of axis, there are about two small groups of steles lying in an abundant ground tissue of which the central area is sclerenchymatous. Lower down the groups increase in number and in complexity to such

extent that the xylem becomes a mass of connected arms, closely packed, dominating over the parenchymatous cells. Apparently a terete trace is given off and a small development of secondary xylem occasionally occurs.

As pointed out by the German authors, the number of xylem arms increases rapidly as sections are taken lower down on axis even of narrow diameter (5 mm.); so rapidly that they wonder which pattern of vascular system could be expected in main branches. They hypothesize that the increase in diameter of larger axes might be reached by the addition of secondary formation i. e. secondary xylem, or by the simple augmentation in size and separation of steles in new ones.

They write (1926, p. 147): "Sicher ist jedenfalls, dass die Zahl des Stelen mit dem Alter zunimmt, bis sich schon in verhältnismässig dünnen Achsen ein geschlossener Pseudoholzkörper bildet. Dickere Achsen konnten nicht untersucht werden. Es ist daher unbekannt, ob in ihnen Sekundärzuwachs auftritt oder ob das Dickenwachstum auch weiterhin, etwa mit dem der Monokotyledonen vergleichbar, lediglich durch Ausbildung und Auseinanderdrängung neuer Stelenzweige zustande kommt."

In other words, the increase in diameter by the development of secondary xylem should result in a robust axis where xylem dominated on parenchyma. On the contrary, the increasing in diameter reached by the development and division of steles should result in a large number of small steles scattered in a wide parenchymatous tissue; the axis would be fleshy.

Precisely in the case of *P. nodosus* the vascular system in a lower part of a branch of first order points to second process (Text-fig. 3). This fact inclines us to consider that the peculiar swollen bulbous part could have been particularly fleshy. Such a structure could explain the ease with which the branches of the first order were broken away.

According to that hypothesis we have taken the diameter of marginal and central strands still observable on some impressions of *P. nodosus*. The selected specimens were main stems or trunks, crown of stem and first order branches (figs. 1, 3, 6, 15 and 17 of LECLERCQ and BANKS, 1962). The measurements are given below.

Table 2

Vascular strands on compression	Stem N° 5051/57 fig. 17	Crown of Stem N° 4955/114 B. fig. 15	First order branches		
			N° 4972/121 fig. 6	No 4962/TP. fig. 3	N° 5062/TP. fig. 1
Range in diameter in μ	200—700	200—500	300—1100	100—400	200—500
Common Size in μ	300	? 500	400	200	200
Size-range of steles in Inclusion I (first order branch)	Mature radial steles		1100 μ —1540 μ		
	Small radial steles		516 μ — 700 μ		
	Circular to oval central steles		380 μ — 780 μ		

They show three sizes comparable to the diameter of petrified radial, circular and oval steles. Interesting is the fact that the smallest diameters are dominating on the main stem and the crown of stem as if small radial oval and circular steles were more numerous in these parts of the plant than the mature steles of the higher levels. Yet one must not forget that a few strands only could be seen on the compressions, and that the width of petrified specimens is usually greater than that of corresponding unpetrified parts.

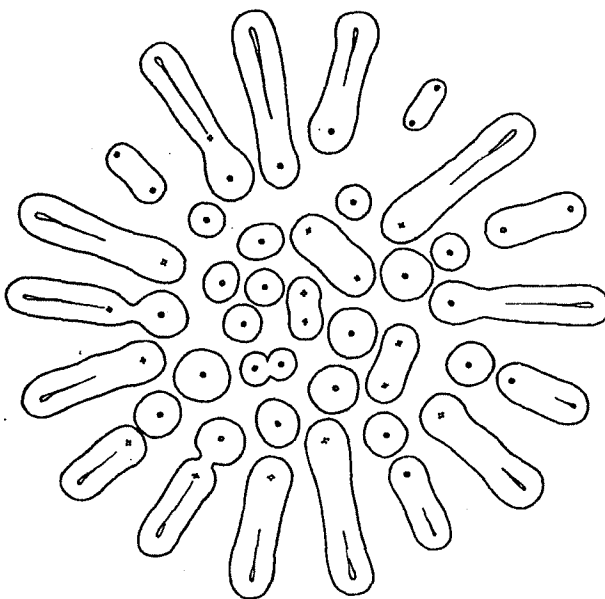
From the above informations and measurements, one may hypothesize that the swollen base of a first order branch could have had an intermediate anatomy between the structure of the higher level branches and

the lower main stem. It may be contended that the fleshy bulbous region should have consisted of a large number of small steles, radials and centrals, scattered in a dominating parenchyma.

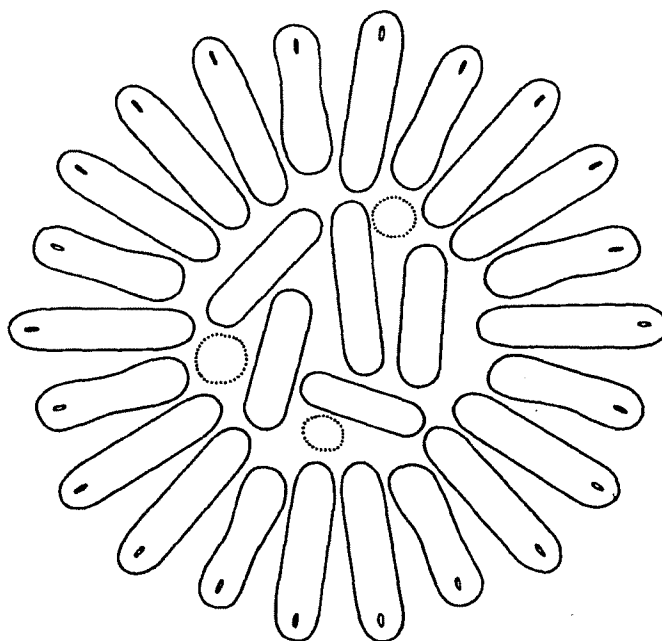
Pseudosporochnus nodosus, as we understand it now, reveals a great plasticity in the organization of the vascular system. It appears that the distinction between radial and central (circular) steles is one of comportment and is principally determined by their upward behaviour after having left the bulbous region.

It has been demonstrated that the circular steles are involved in the process of growth of both radial and elongated central steles. Therefore, we are inclined to consider the central steles as representing a cauline system the members of which play higher up an active role in edifying the gross organization of the vascular system. Most probably the cauline steles never contributed directly to leaf-trace emission, this function being confined to the radial steles that have the privilege of the loop. Precisely, LECLERCQ and BANKS (1962, p. 18) have followed different stages of the outward progress of a leaf-trace, seemingly starting from a radial stele.

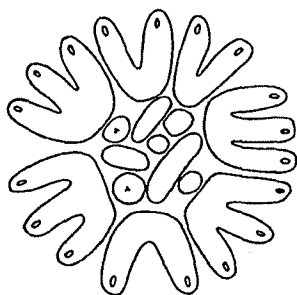
So far our research has revealed three patterns of the vascular system in *Pseudosporochnus nodosus*, two fairly different ones came from a branch of the first order, the other from a branch of the third order. Three ideal cross sections are schematized in the text-figures 3, 4 and 5. Text-fig. 3 represents a section through the basal portion of the branch; it consists of a total of steles approaching 38, arranged in an outer and a central zone fairly equal in development. The outer zone consists of a ring of approximately 18 radial steles, more or



Text-fig. 3. Assumed transverse section of the vascular system of the basal region of a first order branch.



Text-fig. 4. Assumed transverse section of the vascular system in the middle region of a first order branch.



Text-fig. 5. Assumed transverse section of the vascular system in a branch of third order.

less clepsydroid, unequal in length, free and straight with 2 to 3 protoxylem groups distributed on the same radius. The longest steles have a peripheral loop. The central zone is supposed to have about 20 steles scattered in a well developed ground tissue, some being circular and centrarch, others being oval with two mesarch protoxylem.

Text-fig. 4 represents a cross section through the median part of the branch. The presumed total of the steles is close to 27. The radial steles prevail on the centrals. The outer zone consists of a ring of clepsydroid steles more or less equal in length when not compressed, straight, each with a peripheral loop, and without supplementary protoxylem. In the central zone we have observed no more than 4 to 5 elongated steles, apparently lacking protoxylem. However, in the reconstruction we have included three circular steles represented in dotted lines, for we assume that they possibly existed at that level as they still persist up to the third order branch. The ground tissue is much reduced.

Text-fig. 5 reproduces a transverse section of a third order branch. The outer zone is composed of 18 arms, shorter than those of lower orders. They form several groups of two to three connected steles, radially disposed, widened at the base, resulting in a more or less continuous ring. Each arm has one peripheral loop. The central steles, 6 to 8 in number, are circular and centrarch, or tangentially elongated without recognizable protoxylem point. Apparently the ground tissue was poorly developed. It is conceivable that the structures represented in text-figures 3, 4 and 5, if found in separate short petrified fragments, could have been placed in different genera.

The great variability in stelar shape, size, number free or connected steles, lack or presence of a loop, that may exist within an individual axis raises the question of the validity in the diagnostic value of these characters, taken separately, in establishing new genera when short fragments of axis are the only material available.

The small number of fairly complete specimens which can be used as bases for comparison in the Cladoxylopsida, is a major factor contributing to different interpretations, opinions and suggestions of the relationship among the members of this perplexing group.

In this connection it is particularly vexing that the two contemporary Devonian cladoxyloids of which large parts of the external morphology are known, and the anatomy observed at different levels of the axis, give us puzzling information as to the contrasting manner in which their older axes are supposed to have increased in diameter. *Cladoxylon scoparium* advances, with increasing anastomoses of the steles, towards a more or less solid though dissected vascular system, in the downward direction (older axes). On the contrary, in *Pseudosporochnus nodosus* we have seen that a decreasing compactness of the xylem seems to occur in the downward direction, parallel to an increasingly larger development of the ground tissue.

Does the behaviour of the vascular system of the two plants represent two different trends among the Cladoxylopsida, or does it just reflect two different habits? In our present limited knowledge many points still need corroboration to express a valid opinion.

The polystelic structure of *Pseudosporochnus nodosus* is remarkably simple. The straight steles (plates) in their longitudinal course do not fuse with one another for long distances after having reached their full shape and diameter in the lower region of a branch of first order. However, it may be expected that at certain levels a profuse increase of circular steles might have occurred, for instance, below the branching in the crown of the main stem and the first order branch, in order to provide the necessary vascular supply to the new branches.

By that way a vascular system could be established in which a great variability in stelar number would be located in regions of important branching, and followed in between by a numerically more static stage of the stelar system.

In this connection it may be interesting to note that the lateral fusion of steles that leads to a discontinuous ring of xylem, is observed in the third order branch where precisely the simple dichotomizing mode of branching occurs.

This fact could also suggest that the polystelic structure of *P. nodosus* might not be of the same nature as that of the cladoxylaleae of the Lower Carboniferous. At that point of reflection it is safe to recall that the plants, hitherto known, which exhibit the peculiar cladoxylean polystely are few in number and incomplete.

They most probably give us a very imperfect and partial idea of the true taxonomic value which can be assigned to the range of internal structures brought together in the perplexing group of the Cladoxylopsida.

SUMMARY

1. A branch of first order (32.8 cm. long) of which the two extremities are missing have shown seven petri-fied areas scattered over the whole length. Their study has provided new information concerning the arrangement, shape, size of the xylem plates (steles) and the growth process of the steles.
2. The polystelic structure of *Pseudosporochnus nodosus* LECLERCQ and BANKS is confirmed and more accurately defined.
3. The new evidence demonstrates that: (1) In the first and second order branches there is no lateral anastomosing between the radial steles, no steles crossing over the diameter of the axis; (2) there is a permanent group of central steles through the whole branching; (3) the growth process of the radial and elongated central steles is related to the behaviour of the circular central steles.
4. Central steles are considered as a cauline system playing an important role in the building up of the vascular system. The radial steles which have the loop assumed the function of the leaf-trace emission.
5. The xylem is of primary formation. The tracheids show different types of ornamentation: spiral, scalariform (predominant), pitted, and even a few bordered pitted elements.
6. The anatomical part of the diagnosis of *Pseudosporochnus nodosus* LECLERCQ AND BANKS is emended.
7. Comparisons are made with *Pietzschia* GOTHAN, *Calamophyton* KRÄUSEL and WEYLAND and *Cladoxylon scoparium* KRÄUSEL and WEYLAND. Anatomical structure indicates closest affinity with *Pietzschia schüllerii* than with any other member of Cladoxylopsida.
8. It is suggested that the bulbous part of a branch of first order was a fleshy region consisting of a dominant parenchymatous tissue in which numerous small radial and central steles were scattered.
9. The two hypotheses suggested by KRÄUSEL and WEYLAND concerning the possible increase in diameter of the main stem in *Cladoxylon scoparium*: development of secondary xylem, or augmentation in size and division of steles are discussed in the light of the new informations revealed by *Pseudosporochnus nodosus*.

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Explanation of plates

(In the reference code of the figures, the numbers indicate: Collection N° / Field N° / Inclusion N° / Stage)

Plate 21

Pseudosporochnus nodosus LECL. and BANKS

- Fig. 1. Branch of the first order with seven petrified areas over the surface (Nodules I—VII). Nat. Size.
Fig. 2. Transverse section of inclusion I showing outline of the nodule, the radial steles R 1 to R 8, the central steles C 1—C 10, the discontinuous ring of the nests of sclereids (Sc.) and the parenchyma (p). Note predominance of the centrale steles over the radiales. The steles indicated by a cross: C 7—C 9—C 11 are missing on this section. X 30. (5060/178/I/13).
Fig. 3. Radial stele R 4 shows the distal loop with an inner lining of delicate cells. X 150. (5060/178/I/13).
Fig. 4. The smallest known radial stele R 8 shows two equally developed mesarch protoxylem points connected by a median line of smaller tracheids. X 60. (5060/178/I/7).
Fig. 5. Early stage of development of a radial stele R 2. Note its sub-oval shape and the two protoxylem points very close to each other. X 60. (5060/178/I/10).
Fig. 6. Longitudinal section showing a row of closely spaced bordered pits (Bp) in a tracheid. X 200. (5060/178/VI).

Plate 22

Pseudosporochnus nodosus LECL. and BANKS

- Fig. 7. Details of radial steles R 3, R 4, and R 5. Stele R 5 shows a radial and circular steles connected together by a narrow area (N = neck) of metaxylem. Note the three differently developed proxylem points (px). R 3 and R 4 are mature radial steles of different length, (L = loop). The central stele C 3 is typically circular with a centrarch protoxylem. X 60. (5060/178/I/11).
Fig. 8. The radial stele R 6 is in course of fusion with a centrarch circular stele C 6. Note the two differently developed protoxylem points (px) in the radial stele. Stele R 7 is at the same stage of development as R 3 in Fig. 7 but has been compressed by large sclereid nests. Therefore, its proximal protoxylem has got a false appearance of a loop. X 60. (5060/178/I/11).
Fig. 9. Stele R 5 at an earlier stage of growth than in Fig. 7. It shows the beginning of the fusion with a centrarch circular stele (px) by means of one row of tracheids at N. X 60. (5060/178/I/8).
Fig. 10. Two badly preserved centrarch circular steles C 4 and C 5 seen very close to each other before fusion. px = protoxylem. X 60. (5060/178/I/2).
Fig. 11. Same steles as above after fusion. They have increased in size and the two protoxylem points (px) are in mesarch position. X 60. (5060/178/I/15).
Fig. 12. Central stele C 3 with a centrarch proxylem (px), seen at a later stage than in Fig. 7. It has slightly increased in size. Its oval outline is the result of oblique sectioning. X 60. (5060/178/I/13).
Fig. 13. Detail of central stele C 10, typically circular and with a centrarch protoxylem (px). X 60. (5060/178/I/14).
Fig. 14. Longitudinal section showing tracheids with circular to oblique bordered pits (Bp). X 200. (5060/178/VI).

Plate 23

Pseudosporochnus nodosus LECL. and BANKS

- Fig. 15. Transverse section of inclusion IV showing, at different states of preservation, the radial steles R 1 to R 14, some with a loop (L), the central elongated steles C 1 to C 5 and the discontinuous ring of sclereid nests (Sc). In this stage stele C 1 is shown by dotted line as seen through the plastic. C 4 and C 5 are badly crushed. Note the predominance of radial steles over the centrals. X 30. (5060/178/IV/1). (On the right R 3 means R 13.)
Fig. 16. Details of radial steles R 3 and R 4 showing a peripheral loop (L), at the distal end, which is not preserved in the stage represented in Fig. 15. X 60. (5060/178/IV/8).
Fig. 17. Details of steles R 6 and R 7 showing the small peripheral loop (L). They are over-shortened by perpendicular compression. The discontinuity of the metaxylem is accidental. The central elongated stele C 2 is closely pressed against the proximal part of these two steles. X 60. (5060/178/IV/1).
Fig. 18. Central elongated stele C 1. It is over-elongated by perpendicular compression, and fractured. X 60. (5060/178/IV/8).
Fig. 19. Details of radial stele R 8 which has been squeezed by the neighbouring steles R 7 and R 9 and reduced to its distal end which shows a loop (L). Compare the same in Fig. 15. X 60. (5060/178/IV/8).

Plate 24

Pseudosporochmus nodosus LECL. and BANKS

- Fig. 20. Transverse section from a branch of third order (earlier investigated by LECLERCQ and BANKS, 1962; Pl. 8, fig. 37) showing the connected radial steles (R. St.) and a central group of four subcircular to elongated steles C 1 to C 4. Sc = sclereid nest. X 30. (466/2).
- Fig. 21. dto. Details of fig. 20 showing central steles C 1 to C 3. C 1 and C 2 circular; C 3 elongated. C 2 has apparently a centrarch protoxylem (px). X 60.
- Fig. 22. dto. Details of fig. 20 showing central elongated steles C 3 and C 4. Note the lateral connection between the radial steles. X 60.
- Fig. 23. *Pietzschia schüllerii* GOTHAN. Reproduced from GOTHAN (1927; Pl. 2, fig. 5). It shows the process of fusion between two circular central steles (C. St.), both having a centrarch protoxylem point. They are facing the proximal end of a radial stele (R. St.) to which GOTHAN presumed they could be later connected. X 40.
- Fig. 24. *Pietzschia schüllerii* GOTHAN. Reproduced from GOTHAN (1927; Pl. 1, fig. 4). It shows the massive development of the triangular sclerenchyma plates (Sc. p.) between the radial steles (R. St.). Some of the latter have two protoxylem points, one at each extremity. X 10.