

***Calamophyton* is not a Sphenopsid**

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In 1960 an extremely productive fossil locality of Middle Devonian plant remains was encountered in a quarry near Lindlar (Rhineland). The beds in which they occurred are Middle Eifelian in age.

Among the plant fossils were numerous remains of *Calamophyton primaevum* Kräusel and Weyland, including several stems of young plants. The habit of the stems and of the larger fronds closely resembles that of *PSEUDOSPOROCHNUS*. This gave rise to the suspicion that *CALAMOPHYTON* may not be a protoarticate but rather a fern. To test this hypothesis a portion of a structurally preserved stem was included in plastic at the laboratory of Professor S. Leclercq. Though the preservation was not particularly good (fig. 4) a rough polystelic structure of the cladoxylalean type could be recognized.

Encouraged by this observation S. Leclercq began to investigate a petrified branch of *Calamophyton bicephalum* Leclercq and Andrews from Goé (Belgium, Lower Givetian). This very well preserved specimen showed unquestionable polystelic structure. Therefore the authors have decided to publish a joined paper on the anatomy of Belgian and German specimens above mentioned. It is the purpose of this preliminary note to give the description of a transversal section taken at two different levels of each specimen: a third order branch (Belgian material); a stem (German material).

A detailed treatment of the anatomy and mode of emission of the vascular bundles of *Calamophyton* will appear later. The reconstruction of the habit of the plant will be given apart in connection with a report on other plant remains from Lindlar.

BELGIAN MATERIAL.

The description of the Goé material serves as starting point in this paper because the selected specimen shows :

- I — the transverse bands generally cited as a characteristic feature of *Calamophyton* preserved from compression ;
- II — a branched lateral organ, not flattened in one plane, but divided into two equal branches directly superimposed as it has been observed on the lateral appendages of *Calamophyton bicephalum* (Leclercq and Andrews 1960).
- III — a not compressed anatomy preserved by iron hydroxide.

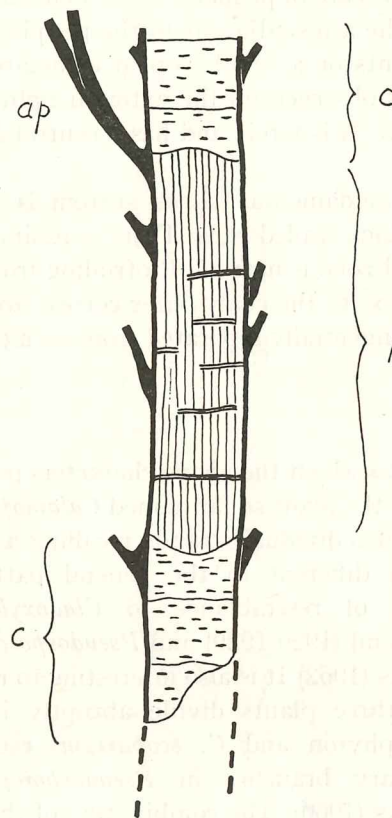
External morphology.

The specimen represents a fragment of an unbranched shoot of the third or fourth order of branching, it is 9,5 cms long and 7,5 mm. wide. Short lengths of the axis are impregnated by iron hydroxide, others are carbonized. The cortical surface of the compression shows minute punctuations and defined transversal lines some of them crossing over the whole diameter. On the petrified areas the transversal lines generally appear like narrow furrows resulting of accidental ruptures of the xylem plates fig. 1. In 1960 (p. 5). Leclercq and Andrews suggested already that :

« the transversal bands are preservation artifacts... that they » are not correlate with any regularity in the distribution of the » lateral appendages and that there is not adequate reason for » comparing them precisely with the characteristic nodal structure of articulate as the calamites and *Equisetum* ».

On the compression the longest lateral appendage has been delicately uncovered. It has revealed a fork in a vertical plane giving two equal segments directly superimposed. This mode of

branching of the lateral organ is a characteristic feature of the leaves and the sporangiophores of *Calamophyton bicephalum* (Leclercq and Andrews 1960).



« *Calamophyton bicephalum* ».

FIG. 1. — Third or fourth order branch preserved from compression and petrifaction showing

transversal lines some crossing over the diameter.

ap — lateral appendages. The uppermost on the left showing an upper and lower segments superimposed.

c — compression ; p — petrified area.

Anatomical structure.

In transversal section the vascular system shows a complex polystelic structure. It consists of 14 to 16 separated steles of

varied size and form : oval, straight, slightly curved, U shaped or having four to five arms radially disposed (fig. 2). The number of arms at the periphery is larger than the number of the free steles : it is 19. All the steles are of primary wood. Central steles have no protoxylem, but the arms adjacent to the periphery, have a few protoxylem elements or a small loop in a mesarch position. A single free trace is observed on the external right side of the U shaped stele (fig. 2). It is terete and has a central decayed protoxylem.

An abundant fundamental tissue surrounds the steles. It consists of large thick walled cells. There is no internal sclerotic tissue. The cortical zone is narrow. Protruding from a parenchymatous inner cortex, to the coaly outer cortex, are small groups of sclerotic cells tangentially separated from each other.

Conclusion.

The conclusion to which the above characters point is that the vascular system of the plant so far named *Calamophyton bicephalum* is composed of individual strands recalling a cladoxylalean anatomy. Though different in the general pattern it shows significant points of resemblance to *Cladoxylon scoparium* Kräusel and Weyland (1926-1929) and *Pseudosporochnus nodosus* Leclercq and Banks (1962). It is also interesting to note that main branches of the three plants divide abruptly in a «digitate fashion» (*Calamophyton* and *C. scoparium*) recognized as a crown of secondary branches in *Pseudosporochnus nodosus* Leclercq and Banks (1960). The combination of these characters removes *Calamophyton bicephalum* from the Sphenopsid placing it in the fern-like family Cladoxylaleae.

The misconception of the genus *Calamophyton* Kräusel and Weyland (1926-1929) rests upon the following wrong interpretations :

- I — the transversal bands interpreted as the nodal structure of an articulated plant ;
- II — the organisation of the sporangiophores considered a simple forked appendage bearing one or two sporangia hanging down at each end of the recurved tips ;

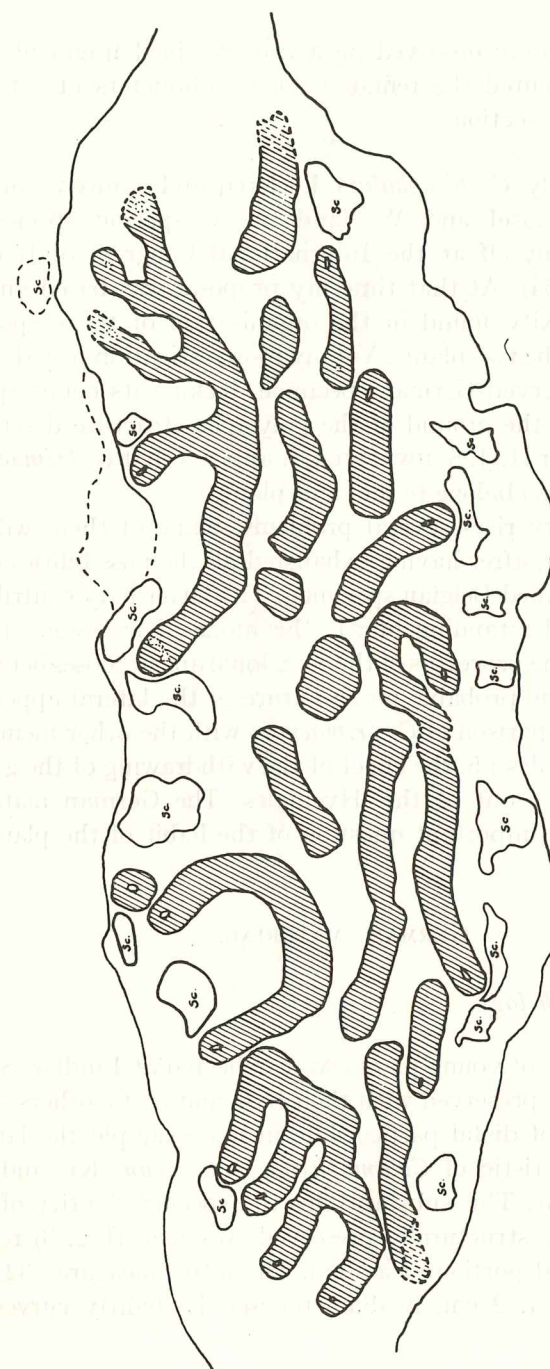


FIG. 2. — Transverse section of a third or fourth order branch of *C. bicephalum* Leclercq and Andrews. The xylem plates are represented, not the ground tissue surrounding them.

Note 16 free steles, oval, straight, U shaped some having four to five arms radially disposed ; protoxylem missing in the central stele ; protoxylem or small loop near the distal end of the arms adjacent to the periphery ; sc-nest of sclereids.

III — the anatomy observed on a tiny petrified fragment that represented the remaining few millimeters of a transversal section.

Most probably *C. bicephalum* Leclercq and Andrews and *C. primaevum* Kräusel and Weyland are co-specific species as suggested by myself at the International Congress of Botany (Edinburgh 1964). At that time my proposal was based on the similar complexity found in the organisation of the « sporangiophores » of the two plants. Yet my re-investigation rested upon one badly preserved German specimen, lacking its counterpart.

Presently on the ground of the polystelic structure described below by Doctor H. J. SCHWEITZER, it appears that *C. primaevum* and *C. bicephalum* belong to the same plant.

This discovery rises several problems. Some of them will be considered later, after having exhausted all the possibilities offered by the petrified Belgian specimen. The latter may contribute to a better understanding of : 1. the mode of emission of the leaf traces ; 2. the processus of the occasional anastomoses between the steles ; 3. the probable pinna-nature of the lateral appendages ; 4. the comparison of *C. primaevum* with the other members of the Cladoxylales ; 5. the effect of the withdrawing of the genus « *Calamophyton* » out of the Hyeniales. The German material may solved the important question of the habit of the plant.

GERMAN MATERIAL.

External Morphology.

Several stems of young plants were collected at Lindlar. Some of these are still preserved with their base and roots, others show the branching of distal parts, while in one example the lateral organs characteristic of *Calamophyton primaevum* Kr. and W. are even present. This substantiates the specific identity of the stems. The only structurally preserved specimen (Fig. 3) represents the central portion of a stem. The latter measures 32 cm. in length and ca. 2 cm. in diameter and is slightly curved —

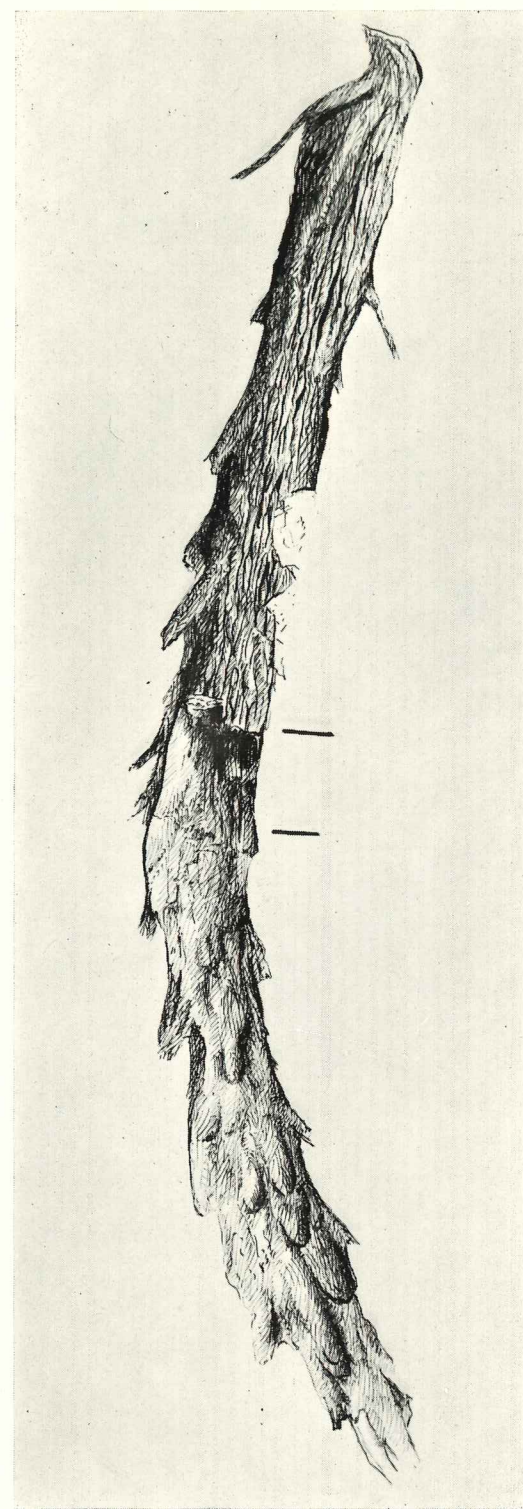


FIG. 3. — Young stem of *Calamophyton primaevum* Kräusel and Weyland preserved from compression. The location of the petrified and embedded piece is between two lines. $\frac{3}{5}$ natural size.

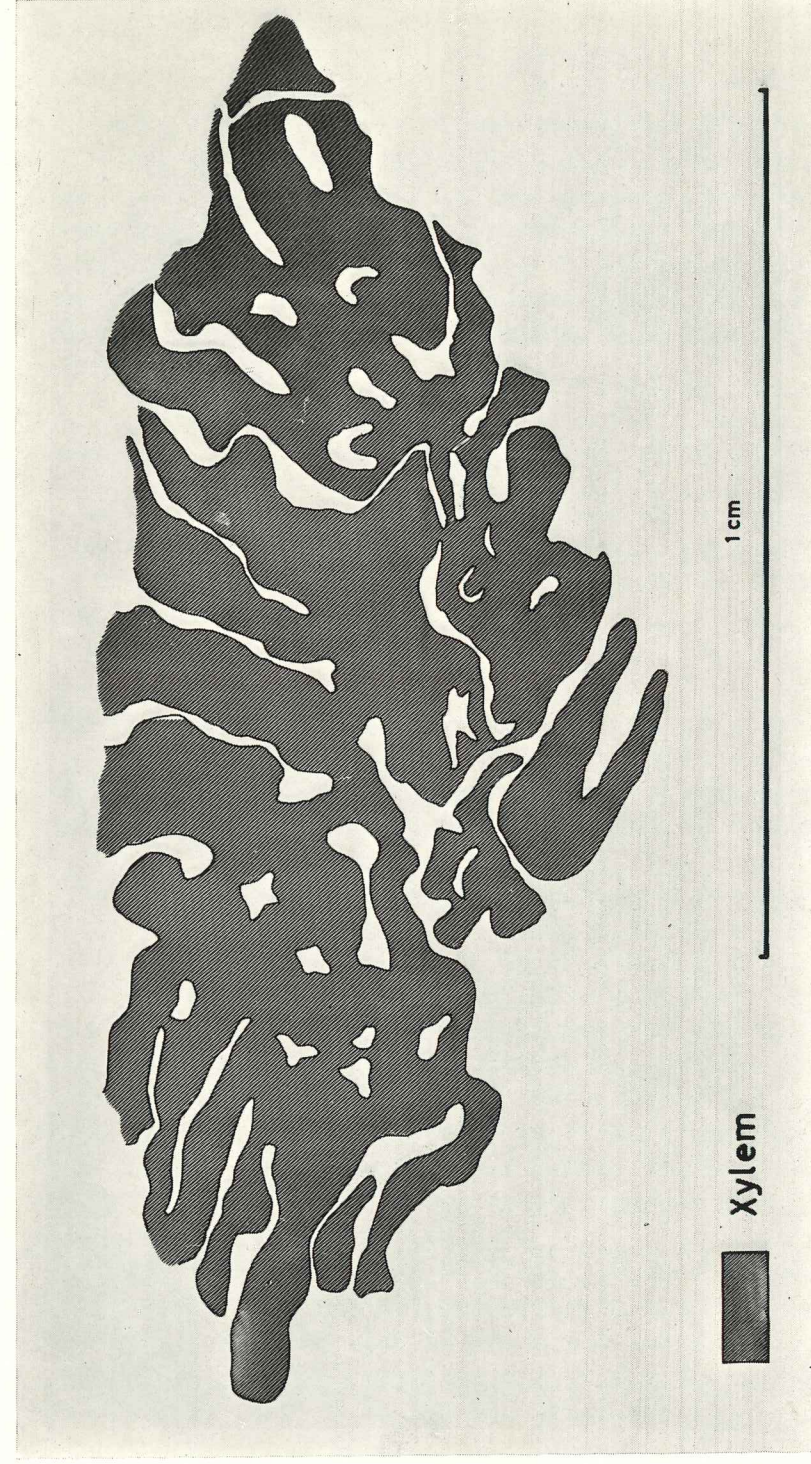


FIG. 4. — Transverse section of the stem. Xylem plates in cross — hatched area ; white areas — parenchymatous ground tissue.

probably a secondary feature. It bears branches, usually about 0,4 cm. thick, which are arranged in an irregular spiral, but of which only the basal portions are still preserved. The tissue visible in the lower half of the stem exhibits a wrinkled texture which does not correspond, however, to the morphology of the stem surface, for the stem broke apart lengthwise during the splitting of the rock. Thus one is looking at the surface of fracture i.e. at structures of the interior.

Anatomy.

For the purpose of investigation of the stem anatomy a portion of the stem tissue has been removed from the location indicated. But not even in this case are the most peripheral layers of the stem preserved.

The anatomical structure is rather poorly preserved. The outlines of various kinds of tissue can frequently be recognized only on the basis of difference in colour. These again may be rather transitional in many places. It should therefore be emphasized that the cross section given in Fig. 4 constitutes an interpretation rather than a representation of the original anatomy of the stem.

Two types of tissue are apparently involved, one which appears yellow in section (cross-hatched area in Fig. 4), the other coloured more or less black (white area in Fig. 4). Assuming the same condition as in the specimen from Goé the former would represent the xylem and the latter the parenchymatous ground tissue. In neither case, however, can cellular structure be recognized. The xylem forming the bulk of the stem tissue is considerably dissected. There possibly exists a more or less central compact zone from which numerous branches depart radially. The lower half Fig. 4 shows that several branches already separated from the central zone and form independant steles. 1/3

A U-shaped stele both ends of which point towards the abaxial side (as in the steles of the Goé specimen) can be seen at the bottom of Fig. 4 in an area near the periphery of the stem.

Despite the poor preservation of the anatomical features one can confidently state that the stem of *C. primaevum* is polystelic

in structure. But apparently, the xylem is not as completely dissected into individual steles as it is in the branches. In addition the xylem dominates over the (parenchymatous ?) ground tissue.

EMENDED DIAGNOSIS CALAMOPHYTON PRIMAEVUM KRÄUSEL AND WEYLAND.

Synonymy *C. bicephalum* Leclercq and Andrews 1960.

Main branch divides in a digitate fashion or a crown, into several branches which in turn divide in a digitate fashion or in more or less dichotomies. Artifact transverse lines occasionally present. Main branch predominantly fertile or sterile, these lateral appendages most probably spirally disposed. Sterile appendages dichotomize one to four times in a three-dimensional pattern, attaining a length of about one centimeter. Fertile appendages rigid divide in a vertical plane into an upper and lower segment; each segment supporting three short side stalks fixed at slightly different levels; tip of the stalks slightly bifurcated bearing one pendulous sporangium at each bifurcation; total number of sporangium on a fertile appendage: twelve. Sporangia cylindrical pointed at the distal end, 2,0-2,7 mm long by 0,5-0,7 mm wide, with possibly a line of dehiscence on the ventral side. Spores round, trilete with closely aggregated spinae ⁽¹⁾.

Anatomy polystelic in structure in stem and in branches. Xylem of the stem consisting predominantly of large and wide plates radially disposed joined (?) in the center, some plates being U shaped and free. Fundamental tissue poorly developed. Xylem of the branches of third or fourth order consisting of about 16 free steles, of various size and form: oval, straight, slightly curved U shaped, or having four to five arms radially disposed; steles of primary wood; protoxylem missing in central steles; protoxylem and narrow loop in a mesarch position in arms adjacent to the periphery; free trace terete with a central protoxylem. Abundant fundamental tissue of lack thick walled

⁽¹⁾ Spores of *Calamophyton* have just been discovered from Ashokan Sandstone of the lower Middle Devonian of New York State by P. Bonamo and H. P. Banks (1965).

cells surrounding the steles. Cortex narrow with small sclereid nests protruding from the parenchymatous inner cortex to the coaly outer cortex.

Belgian holotype: N° 5063 /601 A and B.

Belgian inclusion: N° 11 601 A 8

Horizon: Lower Givetian (Middle Devonian).

Locality: Carrière Brandt (North quarry) Goé, Belgium.

Belgian material preserved in the Department of Paleobotany of the University of Liège, Belgium.

German inclusion: N° L 1.

Horizon: Middle Eifelian (Lower Devonian).

Locality: Lindlar, Rhineland.

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