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CALAMOPHYTON PRIMAEVUM: THE COMPLEX MORPHOLOGY OF ITS FERTILE APPENDAGE[1]

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ABSTRACT

Although holotype material of *Calamophyton primaevum* Kräusel and Weyland has not been available since the Second World War, two fertile specimens of that species are in the personal collection of Professor H. Weyland. The purpose of this paper is to disclose the complexity of the organization of the fertile appendage. Formerly it was believed to consist of one segment that had dichotomized once and that had borne two pendulous sporangia, one at each branch. Numerous degagements of sporangia have revealed a complex morphology, consisting of one main segment divided into two secondary segments. Each supports three recurved side stalks which in turn bear 2 sporangia, a total of 12 sporangia. Each secondary segment terminates in two elongated projections. The morphology of the fertile organs is compared with that of two other species, *C. bicephalum* Leclercq and Andrews and *C. forbesii* Schopf. Great similarity of organization exists between *C. primaevum* and *C. bicephalum*. The possible synonymy of these two species is discussed.

IN 1926 Kräusel and Weyland established the genus *Calamophyton*, with *C. primaevum* as the type species, from material collected in the upper Middle Devonian, Honseler Schichten, at Hardberg and Kirberg, Rhineland, Germany. The habit of the plant was unknown until Schweitzer in Leclercq and Schweitzer (1965) suggested that on the basis of specimens collected at Lindlar, Rhineland, the stems of young plants reached at least 32 cm in height and 2 cm in width, although material usually collected consists of branch systems of sterile and fertile twigs.

The reconstruction of the plant by Kräusel and Weyland in 1926 is reproduced in so many textbooks that it is not described again. This investigation deals with the fertile appendage which they describe (1926, p. 141) as "Sporangien länglich oval und seitlichen ahrenförmig angeordneten gabelig geteilten Trägern." Figure 24 of this paper reproduces Kräusel and Weyland's reconstruction of the fertile appendage (1926, p. 139; Fig. 27). It has a simple morphology consisting of one main segment attached to the axis which bifurcates at the tip into two short stalks, each bearing one pendulous sporangium.

TECHNIQUE—The degaging method used is not new. It has been refined with intensive study of fossil floras. Its objective is to follow through the sediment the delicate connections of deeply embedded fragile organs. This technique has been described in detail (Leclercq, 1960). Steel needles of different size and shape, variously sharpened, are used with a small hammer. During uncovering a few drops of a mixture of alcohol and water (2:1) are applied to the area being studied. Progress of the work is followed under a binocular microscope at different magnifications.

STRATIGRAPHY AND MATERIAL—Two fertile specimens of *Calamophyton primaevum* housed in the Institute of Geology of the University of Köln (Rhineland) were used. They were from the personal collection of Professor H. Weyland and are numbered 173 and 1730. They were collected at Kortzert near Kirberg at the limit between the Honseler and Brandenburg Schichten, upper Middle Devonian, in an outcrop close to those of the type specimens (personal communication, Dr. H. Weyland, 1 September 1963).

The two specimens represent a complex system of second- and third-order axes and are fertile throughout. Both show branches converging loosely toward a missing stouter axis. They are partly preserved as impression and compression. They are not part and counterpart of the same specimen and neither of the two has its counterpart. Without the information usually given by the counterpart, uncovering of many fertile appendages was necessary to cross check fractional observations and to clear up the morphology. Specimen 173 is the better preserved and it has given all of the necessary information; therefore specimen 1730 is not described.

DESCRIPTION—Specimen 173 consists of 16 branches converging toward the lower edge of the plate of shale (Fig. 1). They are from 2 to 8 cm long; their average diameter is from 0.8 to 1.6 mm. Along the sides of the axis numerous appendages are attached; some are also situated on the surface. These appendages are entangled, displaced, broken, or detached from the axis. Sporangia have been shed or broken by the

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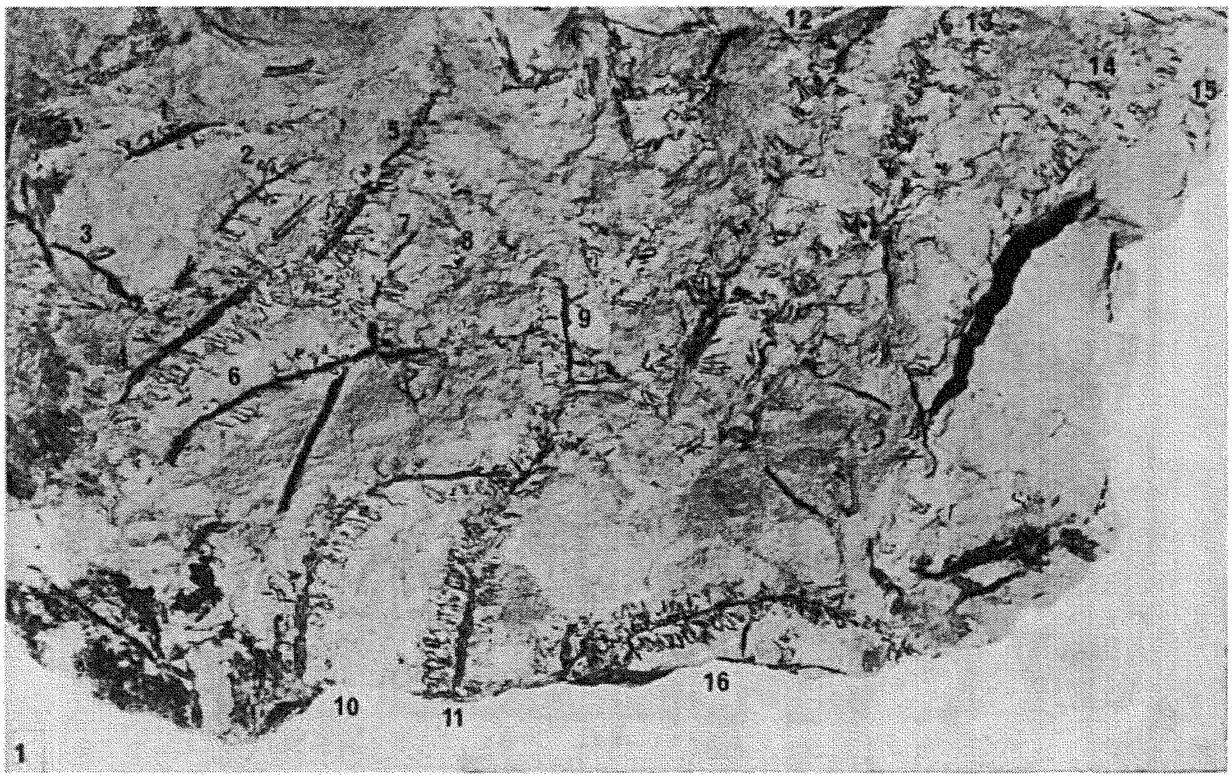


Fig. 1. Specimen 173, showing 16 fertile axes which loosely converge toward a missing stouter axis. × 1.25.

splitting of the shale, or they hang as narrow, empty sacks (Fig. 2–5). This corroborates the suggestion that the specimen represents the slender upper part of a branch system that has been carried along by, or laid down in, running water. At first sight many appendages appear to be simple forked structures divided in one plane, bearing at each end one pendulous sporangium (Fig. 3–5), or occasionally two (Fig. 2, 5), as interpreted by Kräusel and Weyland (Fig. 24). Before uncovering some appendages show more segments, often broken, and pairs of sporangia (Fig. 2–5). Appendages that have helped in understanding the typical branching pattern and that have revealed details of their appearance are described below.

First example (Axis 6, right side. Fig. 6, 14)—One appendage not connected with the axis (Fig. 6) shows an erect rigid segment with an unforked end. It supports laterally two long recurved stalks at a slightly different level. Each stalk bears an empty sporangium 1.6–2.6 mm long and 0.32–0.56 mm wide. This structure recalls the fertile appendage described by Kräusel and Weyland, differing from it by the prolonged distal end of the segment and the extended stalks. Uncovering the proximal end of the appendage revealed its connection with the axis by a broad base that branched. A short length of the branch or second segment was preserved (Fig. 14).

Second example (Axis 16, right side. Fig. 7, 15)—This segment has no distal end. It bears three curved stalks, A, B, C, that converge on it; they are attached at different levels. Note that stalk C is attached on the undersurface of the segment while stalk A is attached on the adaxial surface and is closely compressed. Obviously the stalks are bisporangiate, even if some sporangia overlap or are broken.

Third example (Axis 13, left side. Fig. 9, 16)—The uppermost part of a segment is preserved. Three attached stalks are visible. The end of the segment is rigid and unforked. The stalk at the right is seen almost in its entirety; it deviates slightly from its original straight pendulous position. It bears two overlapping empty sporangia which are not fully preserved. The left-hand stalk curves down and supports two sporangia, one overlying the other. The degagement revealed the curve of a deeply embedded third stalk attached on the undersurface of the segment.

Fourth example (Axis 9. Fig. 8, 17)—Removed from its original position by the turbulence of the water, this segment is almost perpendicular to the branch and is unusually long (7.6 mm). The three stalks and their poorly preserved pairs of sporangia are still connected with the segment. This appendage is particularly interesting as the degagement showed (1) the distance between the

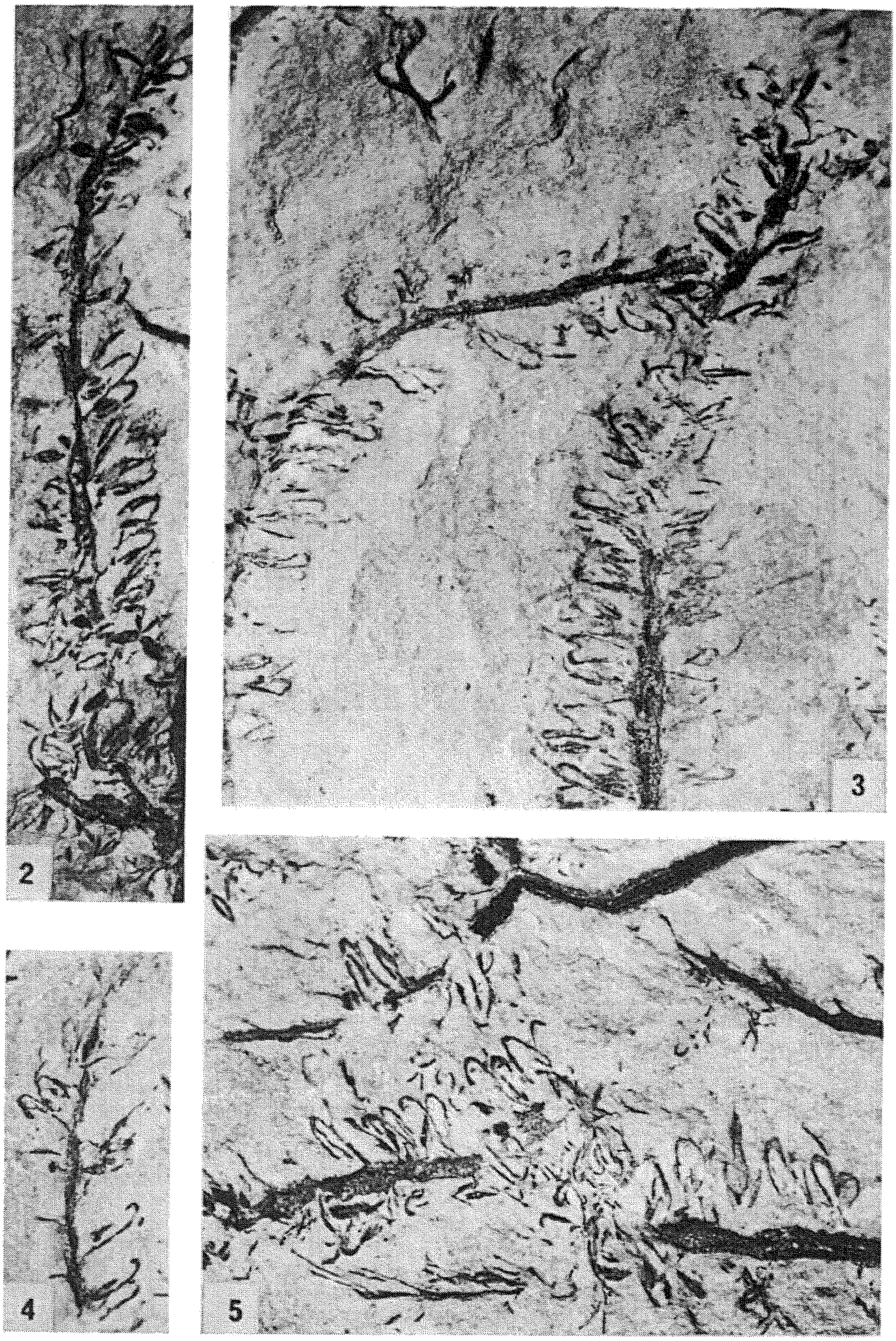


Fig. 2–5. Six axes of Fig. 1.—Fig. 2. Axis 16.—Fig. 3. Axes 10, 11.—Fig. 4. Axis 2.—Fig. 5. Axes 4, 5. All × 3.—Numerous appendages are attached along the sides and a few on the surfaces of the axes. None is complete. Some appendages appear to be composed of a segment with two recurved lateral stalks, each bearing a sporangium. Others show one to three pairs of empty sporangia hanging down and fixed on the segment. Some segments end in an elongated projection.

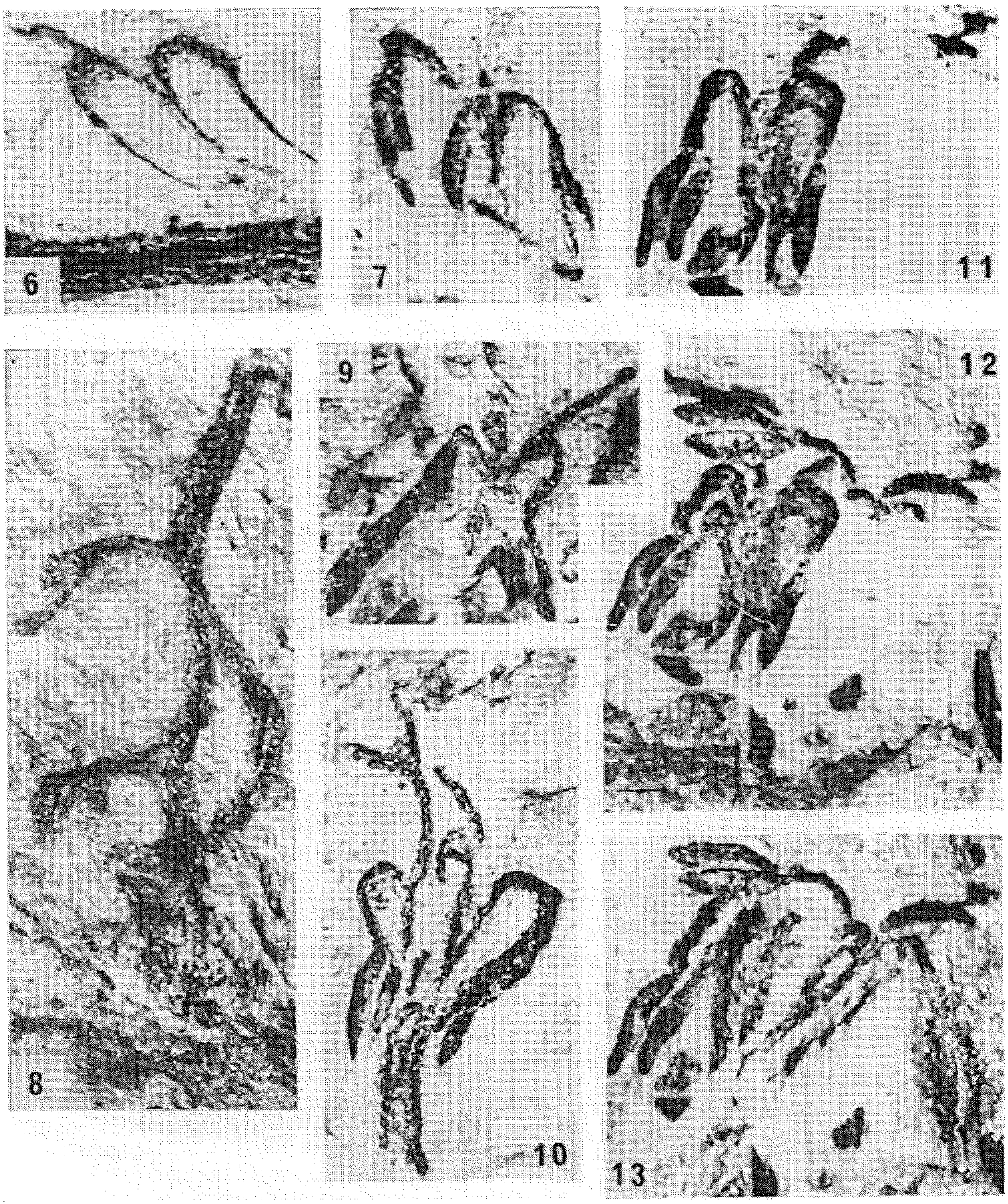


Fig. 6–13.—Fig. 6. An appendage before uncovering. Shown are two recurved stalks and two sporangia. The segment is elongated at the distal end. (See Fig. 14 for same appendage after uncovering.) The state of preservation shown recalls the simple morphology of the fertile appendage of *Calamophyton primaevum* described by Kräusel and Weyland (see Fig. 24, this paper).—Fig. 7. Appendage with three pairs of sporangia in connection with a segment without a distal prolongation.—Fig. 8. An unusually elongated appendage bearing three bisporangiate stalks. Some sporangia are broken or overlap one another. The distal end of the segment is broken at the level of bifurcation. The base is connected with the axis but has almost pulled away from it. (See Fig. 17 where the hatched area indicates the original width of insertion.)—Fig. 9. The uppermost part of an appendage with three recurved stalks. Two are visibly bisporangiate; the third curves behind the segment and has an undivided distal projection.—Fig. 10. A detached appendage with two segments connected at the base. (See Fig. 18, Segment I, which has a preserved bifurcated distal end and two stalks and two connecting stalks; stalk B, on the left, has its two sporangia. The distal end and two stalks of Segment II are broken. Stalk A′ is bisporangiate.)—Fig. 11–13. Three successive stages of degagement of the same appendage. For explanation see p. 777 and Fig. 19–22.—All × 10.

insertion of the stalks, (2) the incipient bifurcation of the distal part of the segment foreshadowing a possible division of the end of the segment, and (3) the proximal end of the segment which is twice as broad as its distal portion and is partly torn from the axis in course of bifurcation. See *first example*, Fig. 14, for similar observation.

Fifth example (Fig. 10, 18)—An almost complete detached appendage floats apart from its branch between axes 11, 12. It consists of a main broad segment that branches into two narrow segments. Although the middle part of the appendage has been damaged by the splitting of the shale, it is evident that the whole segment consisted of the erect segments I and II. The segment on the left gives new information; its tip is distinctly bifurcated. The curving stalk B is preserved with its pair of sporangia. Stalk A is broken in the middle of its length. Segment II, right, has an unforked tip; this appearance is the result of a break just below the fragile distal bifurcation of the segment. Degagement uncovered the curved part, B′ and C′, of two other stalks which overlap one another. B′ shows its connection with the segment. Both have lost their sporangia. Stalk A′ is seen in full with its hanging pair of sporangia.

Sixth example (Axis 12, left side)—This appendage, more deeply embedded in sediment than the others, offered the possibility of three successive stages of degagement. (Fig. 11–13, 19–21.)

Stage 1 (Fig. 11, 19)—The structure is confused in the middle of the appendage. Especially in this case is it unfortunate that the counterpart is missing. The segment supports two stalks, with the one on the left giving the impression of bearing two connected sporangia; however, if one connection is certain, the other is doubtful. The slightly widened end of the straight segment probably indicates that the tip was initially bifurcated as shown in *example 5*, Fig. 18. Note the small isolated bifurcated carbonaceous area seen further on the right.

Stage 2 (Fig. 12, 20)—The recurved stalk C, which was overlain by stalk A, has been uncovered. Stalk C is shown as inserted on the undersurface of segment I. The sporangium assigned with some doubt to stalk A is seen in organic connection with stalk C and is the second sporangium of the pair. Stalk A has lost a sporangium whose point of insertion is still visible (Fig. 12, 20). Working from the carbonaceous area noted above, the uppermost part of a segment with a forked tip was uncovered. It was under segment I with which it appears to converge. Stalks A′, B′, and C′ became visible. In order to expose stalk A′ fully the terminal part of segment I was removed.

Stage 3—After stalk B was completely removed the point of insertion of stalk A′ was discovered low down on segment II (Fig. 13, 21). Segment II was followed very close to its point of junction with segment I. Stalk B′ which overlay segment A′ is broken just below its curve. The third stalk, C′, has been fully uncovered; it has shifted to the right and bears a pair of poorly preserved sporangia which give a weathered impression.

Observations reached in the course of successive degagements are summed up in Fig. 22 which represents the superimposed stages of uncovering. It shows in position of fossilization the displaced stalks and entangled sporangia of a whole fertile appendage. From this reconstruction the original morphology can be visualized.

The fertile appendage was a rigid and erect organ with an average height of 5.2–6 mm. It was adaxially inclined and attached to the branch axis by a main segment that divided into two secondary segments equal in length and having prolonged forked tips. Each secondary segment supported three side stalks which curved downward; they were seemingly spirally disposed, with each bearing two pendulous sporangia—a total of 12 sporangia when none were detached or aborted.

The six appendages described in detail have been selected to form a sequence of increasing complexity which leads to a correct interpretation. Similar structures can be recognized on the axes of Fig. 2–5. The state of preservation of the appendages indicates that prior to fossilization the plant had partially decayed and had been deposited in an allochthonous plant-bearing bed.

Discussion—Obviously the morphology of the fertile appendages here described differs sharply from those of *Calamophyton primaevum* as understood by Kräusel and Weyland (our Fig. 24; Boureau, 1964). It must be recalled that in 1926 and 1929 when these authors were studying their material, techniques of degagement had not reached the degree of refinement now possible. Also their specimens were poorly preserved and, as demonstrated by their illustrations, quite fragmentary. This study demonstrates that it is necessary to follow carefully the tiny organs deeply embedded in the sediment.

In 1960 H. Andrews and I used the degaging technique in the study of the new species *C. bicephalum* that we established for well-preserved material that I had collected in the Middle Devonian of Belgium. At that time the general organization of the sterile and fertile branch systems in the two species was alike, but a sharp difference existed between their fertile appendages (Fig. 23, 24). This difference was so great that we wrote (Leclercq and Andrews, 1960, p. 17): "In the light of what has now been found in *C. bicephalum* it may be desirable to rework with the degaging technique the available material of the other two species (*C. primaevum* and *C. renieri* Leclercq [1940]) to try to determine the real value of the three specific epithets."

In our diagnosis (Leclercq and Andrews, 1960) we reported the following structure: . . . "a fertile appendage consisted of a basal stalk which divided into an upper and lower segment; each segment bore three short side branches which terminate in a slight bifurcation with a pendulous sporangium attached to each, resulting in a total of 12 sporangia; each of the two main segments terminates in a short dichotomy. Sporangia are cylindrical, pointed at the distal end, 2.0–2.7 mm long by 0.5–0.7 mm in diam, with possibly a line of dehiscence on the ventral side." Undoubtedly this diagnosis is true for the fertile appendage of *C. primaevum* and for the genus.

The morphology of the fertile appendage of *C. primaevum* as revealed in this study is almost identical. The differences between the two are minor; the fertile appendage of *C. bicephalum* is twice as large (8–10 mm in height) as that of *C. primaevum* (5–6 mm) (cf. Fig. 23, × 5, and Fig. 14–22, × 10, with Fig. 22–27 in Leclercq and Andrews, 1960). The whole plant of *C. bicephalum* is more robust (diam of the fertile axis is 2.8–4 mm) than *C. primaevum* (diam 9.8–1.6 mm). (Cf. Fig. 1, this paper, with the type specimen of *C. bicephalum*, Fig. 1 in Leclercq and Andrews, 1960.) The matter of size is not by itself, however, an absolute basis for differentiating two species.

Leclercq and Andrews (1960) also pointed out that the fertile and sterile appendages of *C. bicephalum* were three-dimensional in their branching pattern; this is to say that leaves and fertile appendages were not flattened in one plane but branched vertically into upper and lower segments and that the latter were terete. This feature could not be observed on specimen 173 as the quality of its preservation is too poor. Concerning the impressions and compressions, *C. bicephalum* Leclercq and Andrews and *C. primaevum* Kräusel and Weyland are probably conspecific species as Leclercq suggested in 1964. Recently, on the basis of the polystelic anatomy found in a third-order branch of *C. bicephalum* (Leclercq, in Leclercq and Schweitzer, 1965) and in the stem of a large specimen assigned to *C. primaevum* (Schweitzer, in Leclercq and Schweitzer, 1965), the genus *Calamophyton* has been removed from the Sphenopsida and placed in the Cladoxylopsida.

The shifting of *Calamophyton* to the Cladoxylopsida raises the question of the misconception of the genus by Kräusel and Weyland. This rests upon three wrong interpretations. The first is that the transverse bands observed on the main branch and the axis of higher order are interpreted as the nodal structure of an articulated plant. In fact, as written by Leclercq and Andrews (1960, p. 5) ". . . the transversal bands are preservation artifacts; they are not correlated with any regularity in the distribution of the lateral appendages. . . . There is no adequate reason for comparing them precisely with the characteristic nodal structure of articulates such as the calamites and *Equisetum*." This interpretation was confirmed by Leclercq (in Leclercq and Schweitzer, 1965, p. 1396) on a petrified specimen that demonstrates the transverse lines to be the result of accidental shrinkages of the vascular system in the course of embedding and a fill-in by a mineral substance.

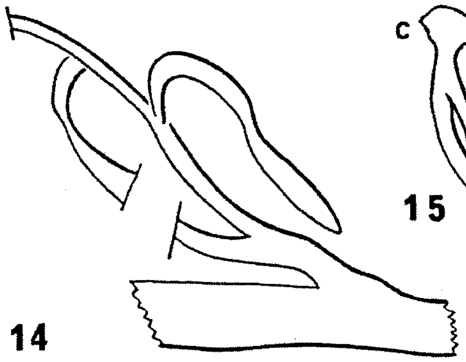
Secondly, the organization of the fertile appendage was defined as a "sporangiophore" with a simple morphology representing an initial type that may have evolved later toward the peltate sporangiophore of the Articulatae that flourished during the Carbonaceous period.

Third, the anatomy of a tiny petrified area of a transverse section was interpreted as an opened sinuous siphonostele.

As a consequence of the above information, debate over the role of *Calamophyton* in the evolution of the Sphenopsida has become useless, as it is not at all the same plant about which the speculation was raised. On the other hand, withdrawing the genus from the Protoarticulatae raises several problems, among them the taxonomic position of *Hyenia*, a genus which so far has appeared to be closely related to it (Banks, 1961; Leclercq, 1961).

The genus *Calamophyton* appears to have a limited stratigraphical extension as it has been collected only in the Middle Devonian (Couvinian and Givetian). On the other hand it has a wide geographical range. Abundant in Europe, particularly in the Rhineland and Belgium, it has been found recently in North America. In 1964 Schopf collected fragmentary material in the Mapleton Sandstone of northern Maine. Among his material is a fertile ascending divided shoot system (1964, Fig. 4) that has pairs of sporangia close to the axis but not connected with it. He points out that the symmetrical position of the sporangia suggests that the arms (stalks) of the fertile appendages were recurved and might have a greater complexity of morphology than can be immediately determined (p. D47). The spores

Fig. 14–24.—Fig. 14–21. Sequence of appendages with increasing complexity of the morphology. (See corresponding figures, 6–13.)—Fig. 22. Restoration of the fertile appendage of *Calamophyton primaevum* produced by superimposing the stages of uncovering shown in Fig. 19–21. For explanation see text p. 777.—All × 10.—Fig. 23. Restoration of the fertile appendage of *C. bicephalum.* × 5.—Fig. 24. Restoration of *C. primaevum* as understood by Kräusel and Weyland.



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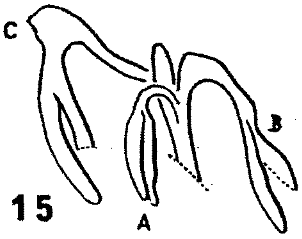

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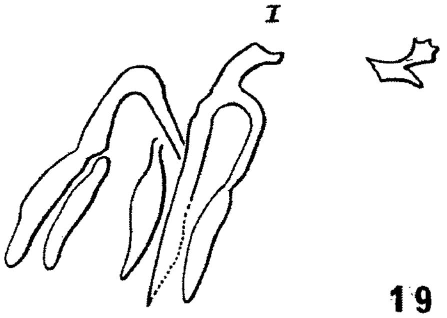

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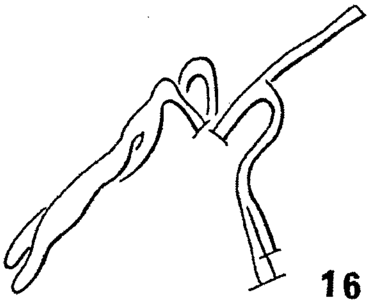

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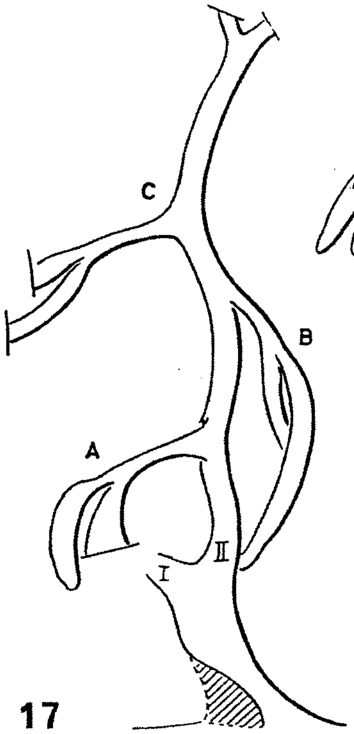

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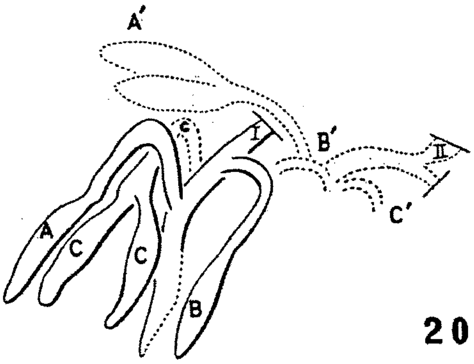

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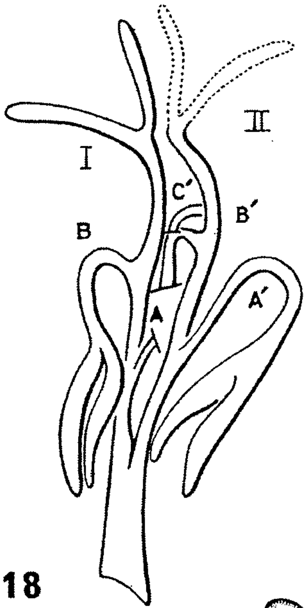

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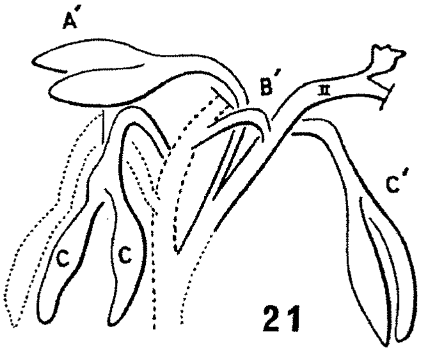

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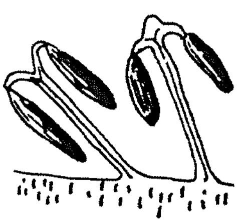

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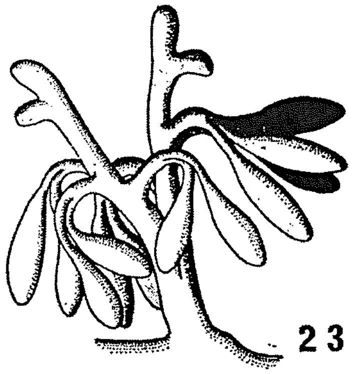

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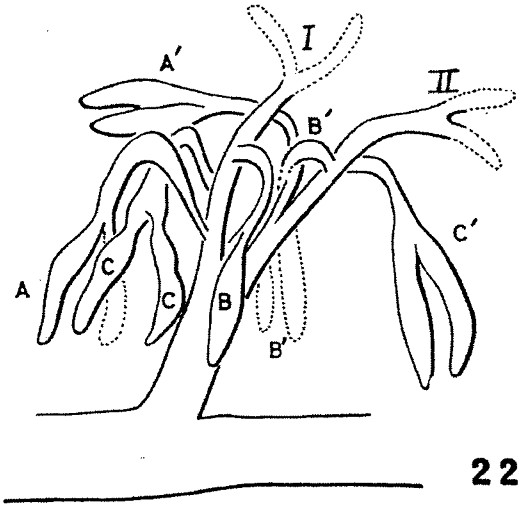

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although reported were not figured. Though fragmentary, the specimens described by Schopf indicate their relationship with the genus *Calamophyton* and a better conformity with the fertile appendages of *C. bicephalum* than with *C. primaevum*. However, it is questionable if the new species, *C. forbesii*, established on poorly preserved material on which no degagement has been made, will be recognized as valid in the future.

In 1966 Bonamo and Banks described sterile and fertile specimens that they assigned to *C. bicephalum*. Their material came from the Ashokan Sandstone (Couvinian) of Ulster County, New York. The allochthonous material consists of poorly preserved axis segments which had been uncovered with such care that the true morphology could be disclosed. The authors observed (p. 783) that the short axis of the fertile appendage forks into an upper portion, segment I, and a lower portion, segment II. Each segment bears three short, recurved laterals bearing two sporangia, and both segments support a sterile elongation of the main axis. Thus there are 12 sporangia per "sporangiophore" or fertile appendage. The sporangia are elongated, oval, and bluntly pointed with a line of dehiscence on the ventral side. They occur in pairs and vary from 2 to 3.5 mm in length and from 0.5 to 0.8 mm in width. The authors described and illustrated well-preserved spores found within the sporangia (p. 783; Fig. 25–30). Moreover, on the specimen from New York state the successive dichotomies of the leaf occur at right angles to each other resulting in a three-dimensional appendage. The organs described by Bonamo and Banks (1966) are identical with the complex morphology of the sterile and fertile appendages of *C. bicephalum* and with the fertile appendages of *C. primaevum* as reported in this account.

Our knowledge of paleobotany progresses at a slow rate by successive accumulations of results resting most of the time on fragmentary material in various states of preservation. The genus *Calamophyton* can be cited as an example. Recognition of the fundamental features of the branching system is ascribed to Kräusel and Weyland (1926, 1929); the three-dimensional mode of segmentation of the sterile and fertile appendages has been cleared up by Leclercq and Andrews (1960); the anatomy has been disclosed by Leclercq and Schweitzer (1965); and the spores have been illustrated by Bonamo and Banks (1966). This information is valid for *C. bicephalum*, but not for *C. primaevum*.

The spores of *C. primaevum* are still unknown. The knowledge of its internal structure rests upon a large specimen interpreted as its stem by Schweitzer (in Leclercq and Schweitzer, 1965), poorly preserved because of one leaf, apparently connected with a branch of the stem. The polystelic anatomy found in a third-order branch of *C. bicephalum* and in the stem (?) of *C. primaevum* is very different. So far no intermediate stage of the internal structure between the stem and branch of a much higher order is known.

Recently Leclerq and Lele (1968), in a study on *Pseudosporochnus nodosus* Leclercq and Banks (1962), had the opportunity to focus attention on the gradual changes of pattern of the vascular system encountered from base to top in a branch of the first order, and then in a branch of the third order. In my opinion as long as the anatomy of the branching system of *C. primaevum* and the internal structure of the stem of *C. bicephalum* remain unknown, doubt will persist as to the synonymy of the two species, in spite of the close similarities of the mode of branching and the morphology of the appendages. Therefore I suggest maintaining provisionally the two species. This is suggested also because *C. bicephalum* has the merit of having been established on abundant and well-preserved material which is still available.

EMENDED DIAGNOSIS OF CALAMOPHYTON—Main branch divides in a digitate fashion or crown into several branches; these branches in turn divide in more or less equal dichotomies. Artifact transverse lines are occasionally present on the branches. Shoot system above the main branch is predominantly fertile or sterile. Sterile leaves and fertile appendages are three-dimensional and terete, most probably spirally disposed. Leaves dichotomize one to four times. Fertile appendages aggregate to form a specialized branch but not in definite cones. Fertile appendages divide in an upper and a lower segment elongated at the distal end; each segment bears lateral recurved stalks that support pairs of hanging sporangia. Sporangia are cylindrical and pointed at the distal end. Dehiscence is ventral. Spores are spherical, trilete, and thin-walled with major folds and have variable types of tiny ornamentations; diam 80–166 μ. Anatomy polystelic.

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