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CALAMOPHYTON BICEPHALUM, A NEW SPECIES FROM THE MIDDLE DEVONIAN OF BELGIUM

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ABSTRACT

This paper describes five specimens of Calamophyton found in the Middle Devonian of Belgium. Well preserved specimens have revealed the fact that both sterile and fertile appendages branch to form three-dimensional structures which are more complex than was formerly known for the genus. A new species, *Calamophyton* **bicephalum**, is established in which the sporangiophores bore twelve pendulous sporangia when all developed. SUZANNE LECLERCQ, Université de Liège, Laboratoire de Paléontologie Végétale, 7, Place du Vingt-Août, Liège, Belgium; HENRY N. ANDREWS, JR., Henry Shaw School of Botany, Washington University, St. Louis 30, Missouri.

INTRODUCTION

The fossil plant material on which the present study is based was collected by S. Leclercq in 1949 and 1952 from a Middle Devonian horizon in eastern Belgium. The Middle Devonian in Belgium is divided into the Couvinian and the overlying Givetian and our specimens come from the lower part of the latter.

The fossiliferous horizon is well exposed in one of two quarries (the north one) known locally as the "Carrières Brandt". They are situated on the upper part of the western slope of a hill lying 400 meters south of the junction of the rivers "La Gileppe" and "La Vesdre" at the small village of Goé which is in turn located about 30 kilometers east of Liège and 20 kilometers from Germany. The plant-bearing horizon is a lens-shaped deposit of numerous greenish and grey-blue shale layers 0.1 to 1.1 meters thick which are interbedded with arkose strata. It has been shown that the Middle Devonian in this region is a littoral formation deposited in shallow marine conditions (Aderca, 1932, p. 14; Liegeois, 1956, p. 98).

The fossil remains are abundantly distributed through the shales but the quality of preservation varies with the different layers. In most of them large specimens are encountered while in some the material is more fragmentary. The plants are found for the most part as well preserved compressions and occasionally as petrifactions in which the plant tissues are impregnated with iron hydroxide.

The "Goé flora" is a large one and includes many specimens referable to the Protoarticulatae. Some of them are large, splendid specimens representing the

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typical habit of *Calamophyton*; others are more fragmentary and it is problematical as to whether they should be referred to this genus or to *Hyenia*. It is, moreover, very possible that some will prove to lie outside the limits of both genera.

As is often the case in paleobotany our knowledge of these presumed early articulates has accumulated as the result of the work of several investigators and the quality of preservation and relative fragmentary state of the plants dealt with has varied greatly. Due chiefly to faulty preservation previous interpretations are not entirely correct and it seems fair to assert that, in general, the plants are not as well known as some of the published accounts would lead one to believe.

The present investigation was initiated in part from the discovery of the elaborate organization of the sporangiophore of the Upper Devonian sphenopsid cone *Eviostachya hoegi* Stockmans which was described in detail by Leclercq in 1957. The unexpected complexity of the sporangiophore "head" of this plant and the availability of well preserved specimens of the Middle Devonian Protoarticulates suggested the desirability of reinvestigating the latter.

Our study is based on several *Calamophyton* specimens which display the typical habit of that plant and the preservation is such that we have had an opportunity to contribute somewhat to a better understanding of the morphology of the leaves and spore-bearing appendages. The latter have proven to be much more complex than was supposed and we have been able to add appreciably to our knowledge of the branching pattern of the leaves. It is thus necessary to review the previous studies, at least briefly, particularly with reference to the presumed differences between *Calamophyton* and *Hyenia*.

Previous Studies

The genus *Calamophyton* was established in 1926 by Kräusel and Weyland with *C. primaevum* as the type species. It is reconstructed as a plant with an upright main stem which branches initially in a more or less digitate fashion; the primary branches, although predominantly monopodial, may also give rise to nearly equal dichotomies (see their plate 15, fig. 2). The leaves are once or twice forked and apparently less filiform than those of *Hyenia*. In view of our own description that follows it is perhaps significant to emphasize this difference as noted by Kräusel and Weyland (cf. their text figs. 26 of *Calamophyton* and 16a, 16b of *Hyenia*). Somewhat stouter, unforked sterile appendages were borne on the "main stem" and on the basal part of the primary branches. The fertile shoots are similar to those of *Hyenia* but each arm of the bifurcated sporangiophore usually bears but one sporangium (cf. their text fig. 27 of *Calamophyton* and text fig. 22 of *Hyenia*). Additional specimens were described by the same authors in their 1929 contribution.

In 1932 Aderca described and figured a fine sterile specimen of *Calamophyton primaevum* which was obtained at the same outcrop from which the new material described herewith was obtained. This specimen will be referred to again but it may be pointed out that it was erroneously determined as *Hyenia elegans* (see

Aderca's pl. 2, fig. 4), although the mistake was corrected by Kräusel (1932, p. 277). In 1940 Leclercq reported *C. primaevum,* as well as a new species, *C. renieri,* from the Middle Devonian of Belgium. She noted (see pp. 18, 33, 35) that most of the leaves in both species were more frequently divided and more filiform than those described for the above mentioned German specimens (cf. Leclercq, 1940, text fig. 9 with Kräusel and Weyland's figures).

The differences between the foliage of *Calamophyton primaevum* and *Hyenia elegans* as indicated by Kräusel and Weyland in the text figures cited above is quite striking; those of *Calamophyton* show a leaf that is narrow, almost wedge-shaped with a notched tip and it is this figure that has been used in textbooks (see, for example, Hirmer, 1927, fig. 400, 401; Arnold, 1947, fig. 55; Walton, 1953, fig. 38; Smith, 1955, p. 241; Magdefrau, 1956, fig. 61). Actually, Kräusel and Weyland's restoration does not bear out this exaggerated difference and in their description the leaves of *Calamophyton* are described as "schmallineal, ein- bis mehrfach gegabelt" (1926, p. 141). Unfortunately their specimens are no longer available for comparison but we shall present additional evidence which suggests that it is very doubtful whether the two genera can be distinguished on the basis of their leaves when only fragmentary specimens are available.

The fertile appendages (sporangiophores) of the two genera were described by Kräusel and Weyland as being very similar. In the case of *Hyenia* each branch of the sporangiophore is said to bear two or three sporangia while only one is found in the corresponding position in *Calamophyton* (cf. their text fig. 22 for *Hyenia* and text fig. 27 for *Calamophyton*). In her 1940 study of certain Belgian protoarticulates Leclercq noted that in *Calamophyton* each branch of the sporangiophore usually bore two sporangia; in the *Hyenia* specimens that she then had available the sporangiophores were noted to have several slender, bifurcating distal appendages. This suggested a greater complexity than was reported for the German fossils and is interesting in the light of our present observations which have been made on specimens of vastly better preservation.

As to the general habit of the plants in the two genera, although Kräusel and Weyland's original restoration of *Hyenia* (1926, pl. 16) shows a plant rather similar to that of *Calamophyton,* it was later recognized that the leafy and fertile shoots of *Hyenia* were borne on a relatively massive rhizome (Kräusel and Weyland, 1932, fig. 3). Studies that confirm this type of habit have been made on *Hyenia* specimens from Norway (Höeg, 1945) and Belgium (Leclercq, 1940) and these authors have both supplied restorations that indicate a conspicuous rhizome with slender upright shoots which are usually unbranched.

In summary it may be said, in the light of our present knowledge, that it is very doubtful whether the upright shoots of *Hyenia* can be differentiated from the distal parts of *Calamophyton* and only the general habit of the two remains as a distinguishing character that may be used with assurance. There is thus some question as to whether the two should be generically separated. It may also be noted that the anatomy of the two is not sufficiently well known to shed much light on the problem.

Materials on Which the Present Study Is Based; Study Technique

It is evident from the above summary that much remains to be learned about these fossil plants and it is particularly necessary that we have better preserved specimens in order to eliminate the doubt that exists concerning the morphology and taxonomy of these presumed early members of the articulate group. Our investigations have not solved all the problems but we have been able to make the following contributions which add to an understanding of the morphology of *Calamophyton*:

1. The sterile appendages (leaves) dichotomize two to four times and it is doubtful whether they can, with certainty, be distinguished from those of *Hyenia.*
2. The sterile appendages are three-dimensional in their branching pattern.
3. The fertile appendages are much more complex than previous accounts indicate.
4. Both fertile and sterile appendages may be borne on the same branch; there is, however, a marked tendency for the fertile appendages to be aggregated together into an apparently specialized branch system, but not into a clearly defined "cone".

The specimens that have been studied and the names assigned to them are as follows:

Calamophyton bicephalum Leclercq and Andrews, sp. nov.: Nos. 5011/609, 5012/337, 5009/588, 5007/346. In all cases the first of each dual number is the permanent one assigned to the fossil and the second is the number originally given in the field).

Calamophyton primaevum Kräusel and Weyland: No. 5006, previously described by Aderca, 1932, pl. 11, fig. 4.

Since the technique that is employed in the investigation of these fossils, although very simple, is perhaps not widely known, a brief description seems appropriate. The plants are preserved as compressions and both fertile and sterile appendages were three dimensional in their branching patterns. Since they also possessed some rigidity a single appendage may extend through several millimeters of sediment, thus it is not possible to apply a transfer technique and remove the entire specimen. What is revealed when the rock is first split gives at best a partial picture of an appendage as we shall point out in some detail in the descriptions. It is thus necessary to follow, through both part and counterpart, a selected appendage in order to determine its three-dimensional form. In the case of the fertile appendages, due to their small size and complex branching pattern, it often becomes necessary to excavate the matrix in terms of fragments only a few microns in diameter. Mechanical vibratory devices are much too coarse for such a delicate degagement and it is accomplished with steel needles and a small, light weight hammer. The size of the needles and the shape of the point will depend on the nature and delicacy of the operation. Invaluable information may thus be obtained with careful, painstaking work and the only costly element involved is the worker's time.

Gross Morphology of the Branch System

Reference will be made first to figure 1 (No. 5012/337) which is the largest and most complete specimen insofar as the branch system as a whole is concerned. This consists of a major axis two cm. in diameter which divides repeatedly; since it is shown natural size in the figure it does not seem necessary to cite measurements for the various branch orders. It should be noted that the ultimate basal part of the plant is not preserved nor has this been identified in any other specimens. We shall, however, as a matter of convenience in description, refer to this basal part *of the specimen* as the *main stem,* and the first division members as the *primary branches.*

Although the initial branching of the main stem in a more or less digitate fashion seems to be highly characteristic of *Calamophyton* there is some variation in the organization of this cluster of primary branches. In figure 1 the main stem divides to form two unequal branches and the latter continue to dichotomize more or less equally throughout the length of the specimen. In the specimen shown at the upper left of figure 7 the main stem produces, almost simultaneously, seven primary branches of nearly equal diameter; the main stem of the specimen in the lower right of this figure starts with an equal dichotomy and the primary branches quickly divide again. In figure 14 the main stem produces three primary branches, although it might be interpreted as an initial unequal dichotomy in which the larger branch to the right dichotomizes again about two mm. above the initial division. The rather broad diagonal white band running through the upper part of the main stem represents a slight fault in the rock.

It is important to note that the main stem in fig. 1, and to a lesser degree the basal portion of the primary branches, shows the transverse bands which have been cited as a characteristic feature of *Calamophyton.* Several of these striations are preservation artifacts although some suggest an internal structure possibly comparable with the higher articulates; they are not evident in the upper branches of the specimen. Less clearly defined bands are present in the larger specimen (upper left) of fig. 7; we have not observed the transverse bands in the other specimens at our disposal. It also seems significant that in the basal part of this specimen (fig. 1) the striations are not correlated with any regularity in the distribution of the sterile appendages; thus if it is assumed that the transverse striations indicate nodes the leaves are scattered irregularly through the internodal region. Therefore we do not feel that there is sufficient evidence to regard this character as distinctive of *Calamophyton* and there is not adequate reason for comparing them precisely with the characteristic nodal structure of articulates such as the calamites and *Equisetum.*

THE STERILE APPENDAGES (LEAVES)

A. ON THE MAIN STEM

The sterile appendages or leaves on the main stem are somewhat more robust than those borne higher up on the plant. Some *appear* as simple unforked structures, others are branched while some represent only the basal portions of branched leaves. The best preserved examples were found on specimens Nos. 5012/337 (fig. 1) and No. 5011/609 (part and counterpart, figs. 20 and 21). Some leaves of

No. 5012/337 are reproduced at a magnification of ×5 on plate 1; they represent the appendages shown in fig. 1 at points *a* (fig. 2), *b* (fig. 3), *c* (fig. 4) and *d* (fig. 5). It will be noted that the most profusely branched leaf reached four orders of divisions and was found higher up on the stem than the other examples cited.

One leaf was found on the main stem of the right hand specimen shown in figure 7 (point *a*) which contained a clearly defined vascular strand which could be followed almost to the tip. This leaf is shown enlarged in fig. 11 and a portion of the vascular strand is shown in fig. 10; the tracheids are apparently of the annular type.

In specimen No. 5011/609 (fig. 20) the leaves display a tendency toward a whorled arrangement but it seems significant to note that the transverse bands, previously considered as characteristic of *Calamophyton*, are not evident here and, as we have noted above, the transverse bands in the stem in fig. 1 are not correlated with any regular arrangement of the leaves.

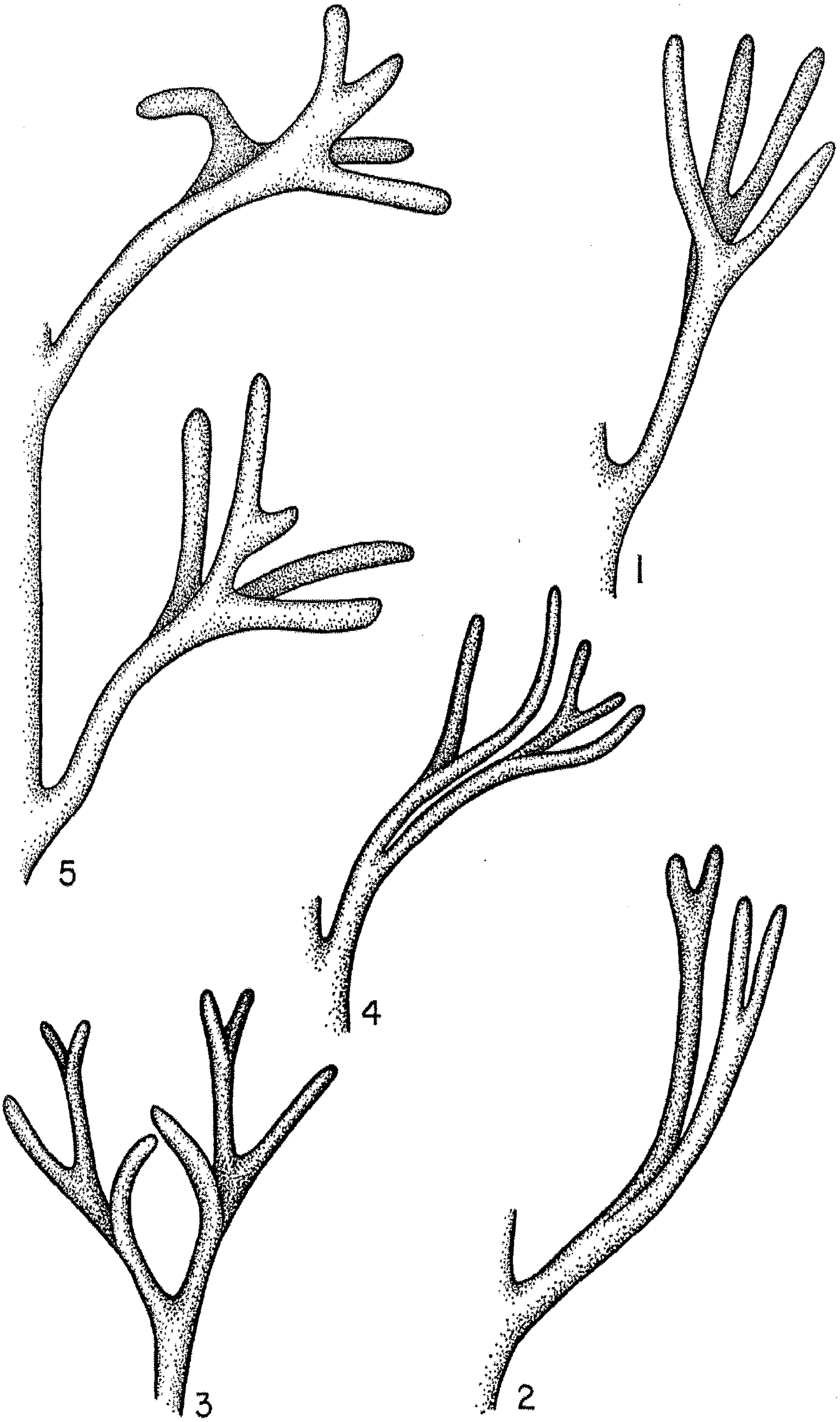
B. ON THE BRANCH SYSTEM ABOVE THE MAIN STEM

It is important to note that, prior to degagement, specimens give a misleading picture of the leaves since only about half of the appendage is exposed by the initial split of the rock specimen; this has been noted for other Devonian fossils in previous studies by Leclercq (1940, 1957). Consequently a considerable number of leaves were degaged or excavated with a small hammer and fine steel needles. Leaves were selected for detailed study that appeared to be well preserved and that were clearly identifiable on both part and counterpart. The leaf was degaged away, starting at the distal end, and followed toward the point of attachment to the stem until a branch was encountered. When this was done to both part and counterpart no question remained as to whether the entire leaf had been revealed. This resulted in the partial destruction of some leaves but the results obtained fully justified the procedure.

In several instances we were fortunate in obtaining the desired information without destruction of the leaf. Figure 8 shows a leaf from specimen No. 5009/588 (fig. 7, *b*) which appeared initially with the Y-shaped terminal portion (*a*) attached at point *b*. Due to a fortunate cleavage of the rock it was possible to remove this terminal portion intact and a comparable branch *c* was revealed directly underneath. The chip was glued in position as shown in the photo, thus preserving the entire leaf. In summary then, we are dealing with a leaf that forked at point *b* to form two equal branches (*a* and *c*) and the latter in turn dichotomize *at right angles* to the first dichotomy. A restoration of the leaf is shown in text fig. 1. Several other fortunate excavations of this sort revealed the same three-dimensional branching pattern without destruction of the leaf.

Several other examples, also taken from specimen No. 5009/588, will be mentioned to record variations in the gross morphology of these leaves:

Text figs. 1–5. 1. Restoration of leaf shown in fig 8. 2. Restoration of leaf shown in fig. 7 at *e*. 3. Restoration of upper leaf in fig. 13. 4. Restoration of leaf shown in fig. 12. 5. Restoration of leaves from specimen No. 5006 shown in figs. 15, 16.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Text figure 2 shows another leaf from the right hand specimen in figure 7 (*e*); this is similar to the preceding example but the initial dichotomy takes place closer to the proximal end and the secondary forking results in shorter branches.

Figure 12 shows a leaf attached at point *c* in figure 7. This was revealed initially, partly in side view and partly in surface view, and no further excavation was conducted. The leaf divides first at *a*, and then both branches divide at right angles to the first division at *b*. At the upper of the *b* divisions one of the two secondary branches was lost but this is indicated in the restoration drawing given in text fig. 4.

The upper portion of figure 13 shows another leaf from the same specimen (fig. 7, *d*). In this case the entire leaf was exposed initially and it is included to illustrate an example in which four orders of branching are evident; it is shown in text fig. 3 as an aid in interpretation. This represents the maximum degree of branching that we have observed in the leaves of *Calamophyton.*

Other leaves with four orders of branching have been carefully uncovered on the part and counterpart of specimen No. 5009/588 (figs. 9, 19). When well preserved they appear similar to the one shown in fig. 13 and text fig. 3. Another example (fig. 5) of one with four orders of branching is shown in the fertile specimen No. 5012/337 at point *d*. It is important to note that the leaves inserted in a similar position on a sterile branch system were small and wedge-shaped.

Many other examples could be cited but they would only duplicate the results obtained from those cited above. The ones chosen reveal the typical branching pattern and the variations that are encountered with reference to the number of orders of branching. There are numerous examples of the type shown in figure 8 and occasional variants from this pattern reveal a lack of forking of the secondary branches but the examples shown in figures 9, 12, 13 and 19 with three or four orders of branching seem to be most typical.

It is pertinent next to summarize the evidence that indicates the leaves are three-dimensional structures. In most cases it could be observed that the first dichotomy resulted in two branches that were directly superimposed; this is well shown in figure 8 where branch *a* was directly above branch *c*. In the second division, however, the resultant two segments lie apparently in the same bedding plane. In most cases where two or more orders of branching were present we are virtually certain that the orientation of successive branchings was at right angles, except possibly the fourth order. Additional evidence comes from examples such as the one in figure 12 (text fig. 4) in which irregular fracturing of the rock revealed a leaf initially in side and surface view.

There is next the question of the cross-sectional shape of these appendages; they are shown in the restorations as having been terete and we feel that there is substantial evidence to indicate that this was the case.

First, the leaves must have had considerable rigidity to have retained their three-dimensional form during fossilization. As many degagements reveal, one primary segment pushed down into the accumulating sediments so that the leaf as a whole was not flattened into one plane. It seems most unlikely that this would have been possible if the leaves had been thin, laminate structures.

Second, in well preserved specimens the thickness of the carbonaceous film is somewhat greater than might be expected if the leaves were laminate.

Third, for whatever correlation purposes it may be worth, it may be noted that several early land plants that are known in the petrified state (*Rhynia, Horneophyton,* at least some Coenopterids) possessed a shoot system in which the ultimate branches are terete.

THE FERTILE APPENDAGES (SPORANGIOPHORES)

The quality of preservation of the fertile appendages varies considerably and this is due in part to their relative state of maturity at the time of fossilization. Our most significant evidence has come from specimen No. 5011/609 in which the preservation is excellent and the sporangiophores retain most or all of their sporangia. In contrast to this, specimen No. 5012/337 seems to be one in which dehiscence took place some time prior to fossilization; most of the sporangia are shriveled, fragmentary or missing.

Our basic description will, therefore, deal with a well preserved and apparently complete appendage from No. 5011/609. This is supplemented with a description of a second appendage of this specimen as well as several from No. 5012/337, partly to illustrate minor variations in the morphology of the fertile appendage and differences that result from the preservation of specimens at different states of maturity.

SPECIMEN NO. 5011/609

The fertile branch system as a whole is shown natural size in figure 21, the general morphology of the specimen being essentially the same as that found in the specimens shown in figs. 1, 7 and 14. It consists of an upright main axis of about 7 mm. in diameter which, at the top, divides into three primary branches which are of about the same size. One of the branches is dichotomized. The ultimate basal and terminal portions of the specimen are not preserved.

Below the point of division the main axis bears sterile, rigid appendages. These represent for the most part only the basal portion of the whole appendage; some are more complete and display a part of the more distal, divided portion. These organs are similar to the "basal leaves" found on the main axis of specimen No. 5012/337 (fig. 1).

The primary branches of the specimen are fertile throughout the portion that is preserved (fig. 29). They bear many whorls of sporangiophores only, there being no associated bracts. It has not been possible to determine the number of sporangiophores in a whorl; there are at least three and possibly as many as six. It was also difficult to decide whether, in successive whorls, the appendages were superimposed or alternate, though it is more probable that they were superimposed.

It is important to note that here, as in the case of the sterile appendages, the initial exposure of the specimen gives a misleading picture of the general morphology of the sporangiophore. The latter is a three-dimensional structure and half or more of it may be covered by the rock matrix. In order to be sure of arriving at a correct understanding of the sporangiophore many of them were carefully uncovered under a binocular microscope using needles and a light weight hammer as described above.

Successive stages in the degagement of a selected sporangiophore are illustrated in figures 23 to 27. Figure 22 represents the counterpart (specimen No. 5011/609B) of the initial stage shown in fig. 23. As an introduction to the detailed description it may assist the reader to note briefly the over-all branch pattern: the fertile appendage divides into two segments or "heads" (referred to as upper and lower), each of which bore three short side stalks and each of these in turn terminates in a pair of sporangia; the distal tip of each of the two segments is usually bifurcated but not always so. Thus the sporangiophore as a whole, composed of two similar heads, supports twelve sporangia if all develop.

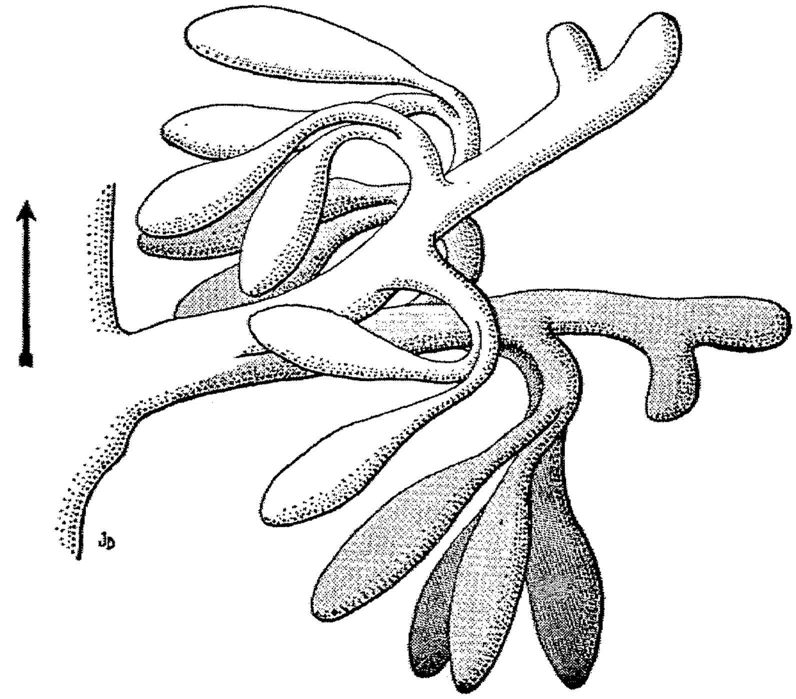
In figures 22 and 23 the upper segment (I) is shown from its base up to the ultimate preserved tip. This segment supports two side stalks, A and B, which are attached on either side at slightly different levels; two sporangia are borne on each stalk (fig. 23 and text fig. 6). Figure 24 reveals the third stalk, C, of the upper segment and one of its sporangia is visible; the second one is still overlain by stalk B although its distal part appears beside the two sporangia of the B stalk. Text figure 6 shows this upper segment or head with the three bifurcated stalks and their six sporangia in the position in which they were preserved.

In figure 24 a portion of the lower segment or head may be seen behind the upper one. Figure 25 shows the lower segment (II) in connection with segment I as well as the three stalks A, B, and C, which are borne by it (segment II); this is also shown in text figure 7. Stalk A has two sporangia in connection; stalk B appears with one sporangium attached and the second lies under segment I; stalk C is just coming into view at this level. In figures 25, 26 and 27 the second sporangium of stalk B has been revealed by removing parts of segment I. Stalk C, which was recurved under segment II, has been uncovered by destroying parts of the latter; it is now clearly revealed and has one sporangium suspended in an anatropous position on each of its two divisions or pedicels. Text figure 7 shows this lower segment (II) with its three bifurcated stalks and their six sporangia.

Text figures 6 and 7 when superimposed show the entangled stalks and sporangia of the entire sporangiophore as it was embedded in the sediment; text figure 8 is a reconstruction of the sporangiophore as we believe it appeared before fossilization and in natural position.

Thus, in summary, the sporangiophore was a small, adaxially inclined appendage attached to the branch axis. At a point about one third of the way from its proximal end the sporangiophore branched into an upper and lower segment. Each segment was erect and rigid and supported three short side stalks fixed at two different levels; the first stalk was given off at a different level than the two others which appear generally to be given off simultaneously. Each of the three stalks is slightly bifurcated at its tip with a sporangium attached to each bifurcation. Usually the distal, rigid portion of each segment of the sporangiophore terminates in an irregular dichotomy.

The sporangia were cylindrical sacs 2.0–2.7 mm. long and 0.5–0.7 mm. in



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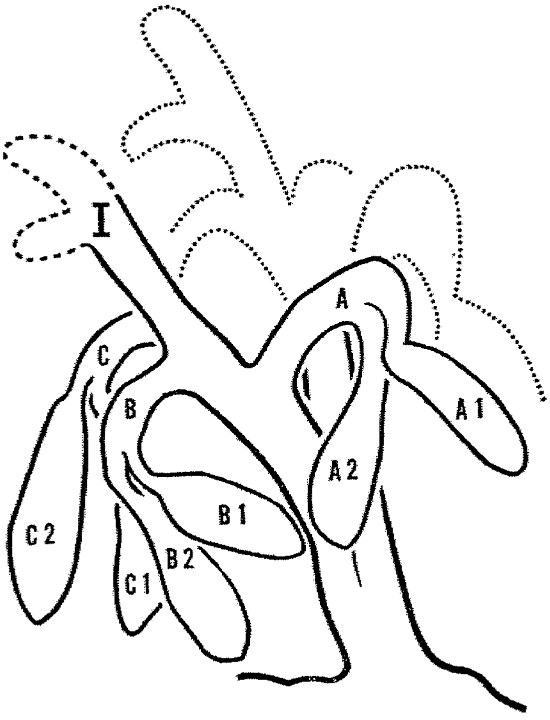

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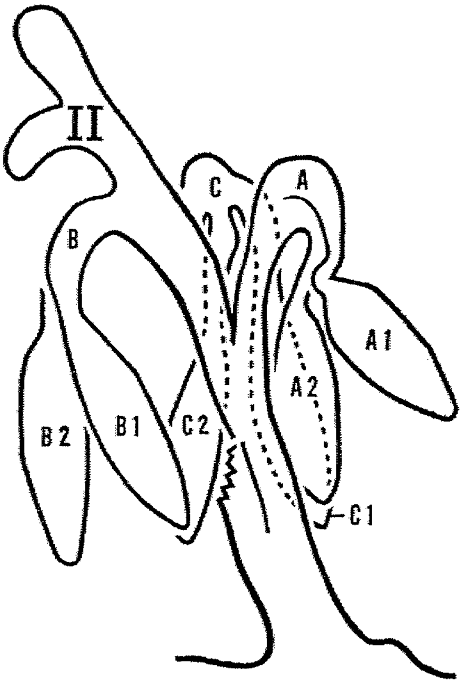

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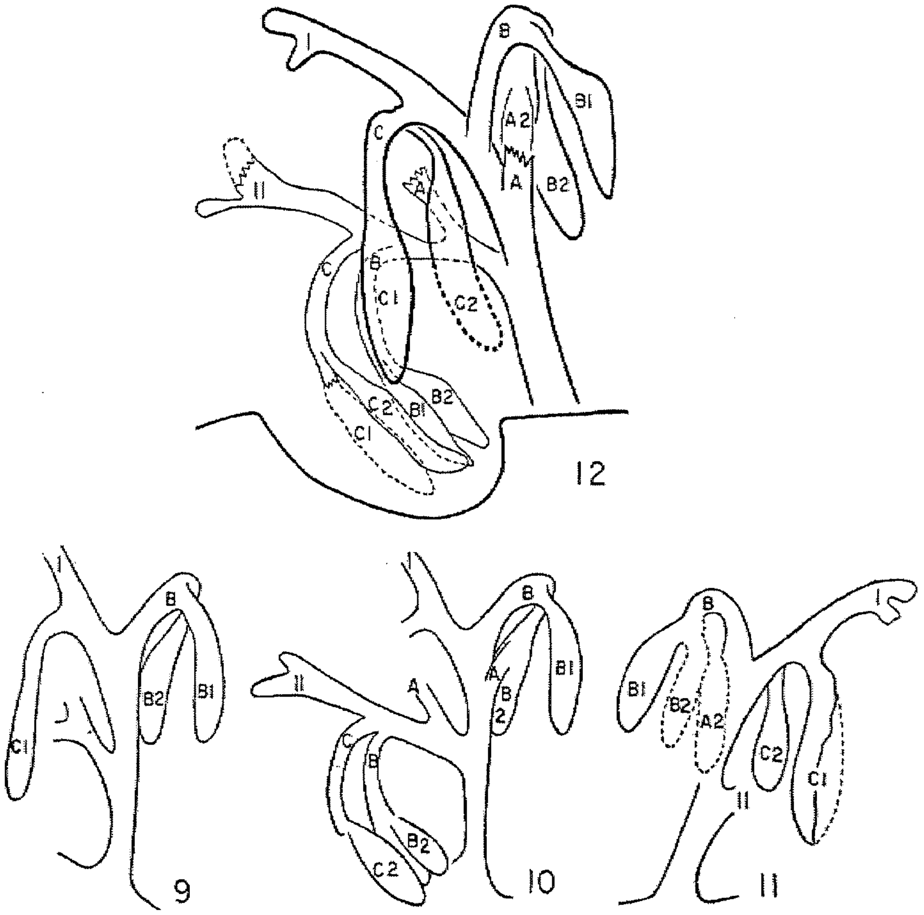
Text figs. 6–8. 6. Upper segment of sporangiophore (I) shown in figs. 23, 24 (specimen No. 5011/609. 7. Lower segment of same sporangiophore (II); see figs. 25–27. 8. Restoration of same sporangiophore. Arrow points toward apex of specimen as a whole.



Text figs. 9, 10. Stages in the excavation of a sporangiophore of specimen No. 5011/609; see also fig. 31. Text fig. 11. Counterpart of same appendage; see also fig. 30. Text fig. 12. Semi-restoration of same sporangiophore. Detailed explanation in text.

diameter and pointed at the distal end. They were apparently strongly constructed for despite the entangled position in which they occur they are often neither broken nor opened. It is possible that the wall of the sporangium was rather thick, perhaps as a result of several layers of cells or having been fossilized when immature; the latter seems most likely.

The mode of dehiscence has not been positively ascertained. Careful examination of the sporangia on the holotype specimen (No. 5011/609) has revealed no distal pore but on a few sporangia a median longitudinal line is found on the ventral side (fig. 28) which may represent the place of dehiscence.

It is evident from the numerous sporangiophores we have studied that their organization was essentially the same throughout; there are, however, some slight variations and in view of the rather surprising complexity of the fertile appendages as contrasted with previous accounts of Calamophytons it seems pertinent to supplement the description given above with somewhat briefer considerations of several other examples.

Text figure 9 is a camera lucida drawing of an appendage (No. 5011/609) prior to any treatment. The sporangiophore stalk divides into the two divisions; a considerable part of I is present but only the basal part of II. Referring to segment I, branch B is shown with its two sporangia B1 and B2 and one sporangium of the C branch is present. In order to expose segment II, which appeared to dip down into the rock, sporangium C1 was degaged away; after working through the sediment underneath sporangium C1 the II segment was revealed as shown in text fig. 10 and fig. 31. Three branches (A, B and C) were found departing from segment II. Branch C terminates in a single sporangium, C1, but judging from its mode of attachment this is one of an original pair; branch B is terminated by one clearly defined sporangium (B2) and there appears to be another beneath it; the third branch (A) could not be followed.

Text figure 11 and fig. 30 show the counterpart of the appendage; only segment I is present. The sporangia B1, B2 and C1 are readily correlated with their position as shown on the other face of the specimen (text fig. 9); there is some question as to the sporangium labeled A1 and a fifth one appears to the right of sporangium B2 whose position on the segment is undetermined.

Text figure 12 brings this information together as a semi-restoration. It may be noted that there were not less than eight sporangia borne by the entire appendage and the number was probably closer to ten or twelve.

Specimen No. 5012/337

Some significant information was obtained from this specimen (fig. 1) concerning the general branching pattern of the fertile appendages but, as noted above, very few sporangia could be identified intact due to the fact that dehiscence had apparently taken place some time prior to fossilization. It should be noted that there is no counterpart of this specimen; when it was found during the quarrying operations an extended search was conducted for the other side but it was apparently completely shattered and lost.

The three sketches shown in text figs. 13–15 show an appendage before and after degagement, and a semi-restoration respectively. The initial appearance was essentially as shown in text figure 13 aside from a slight amount of degagement that was necessary to expose branches B and C. The segment was then degaged away, starting at the distal end and extending down to the point indicated by line ---o. The underlying segment (II) was then detected and when completely excavated it appeared as shown in text fig. 14.

The semi-restoration of this appendage (text fig. 15) thus shows it as consisting of two main branches, I and II; II produces at least two secondary branches and terminates in a forked tip; I produces three secondary branches. All of the sporangia had been shed prior to fossilization.

A second example (fig. 6 and text fig. 16) is included since it gives some interesting information concerning the variation in the general morphology of the fertile appendages and particularly the ultimate terminations. It is virtually certain that the upper portion was attached as indicated by the dotted line but this was not positively demonstrated. The essential features of this appendage seem to be as follows: the main stalk branches into two segments which in turn divide, each giving off several side branches, and terminate in unforked distal tips.

Although specimen No. 5012/337 is the largest one in the collections and the most completely preserved, with reference to the main branch system as a whole, none of the ultimate terminations of the branches are preserved; these probably extended out at least 10 or 15 cm. beyond what is shown in the photo (fig. 1). The ultimate appendages, both sterile and fertile, are for the most part rather poorly preserved and we interpret it as a plant, or portion of a plant, that had shed its spores and undergone partial decay prior to fossilization. Several fertile appendages are sufficiently well preserved as to offer evidence of their relationship with the new species *C. bicephalum.*

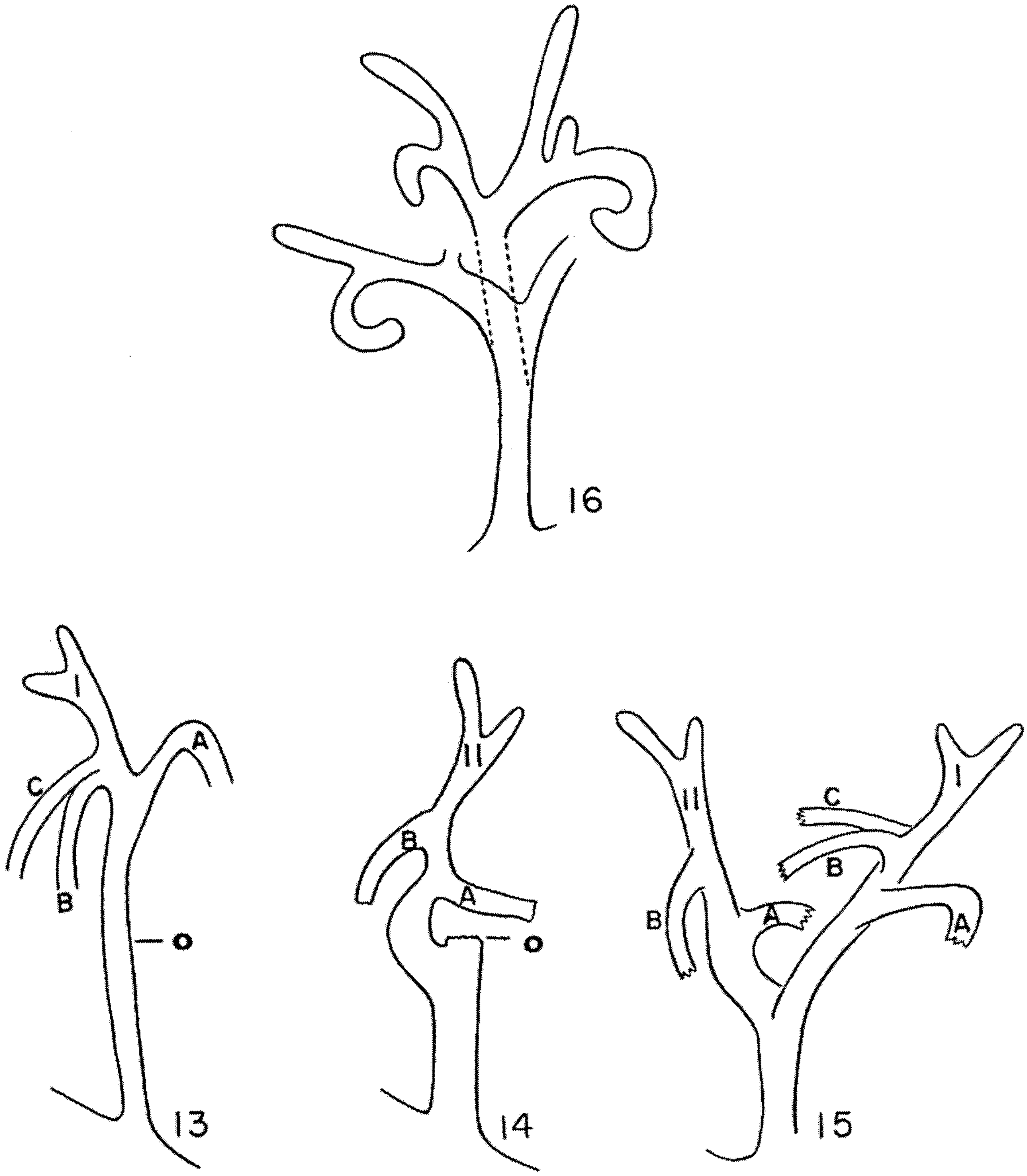
DIAGNOSIS

Calamophyton **bicephalum** Leclercq and Andrews, sp. nov.

Plants consist of a main stem, the basal portion of which is unknown, which divides in a digitate fashion into two to several branches; these branches in turn divide in more or less equal dichotomies. Transverse striations are occasionally present on the main stem and lower portions of the primary branches. The shoot system, above the main axis, appears to be predominantly fertile or sterile. The sterile appendages (leaves) are somewhat more robust on the main stem than above, with a single vascular bundle, and dichotomize one to four times in a three-dimensional pattern and attain a length of about one cm. Fertile appendages are aggregated to form a specialized branch but not in definite cones; 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 twelve 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 diameter, with possibly a line of dehiscence on the ventral side.
Holotype: No. 5011/609. Paratypes: No. 5012/337, No. 5009/588. All preserved in the Laboratoire de Paléontologie Végétale, Université de Liège.
Horizon: lower Givetian, Middle Devonian.
Locality: Carrières Brandt (north quarry), Goé, Belgium.

DISCUSSION

With the exception of the general organization of the branch system the new species of *Calamophyton* described here presents characters, particularly in the nature of the ultimate fertile and sterile appendages, that are quite new. In these features our plant differs sharply from *Calamophyton* as portrayed in all recent text-books. It was quite surprising to find these appendages so complex and it might be supposed that we are actually dealing with plants that should not be identified with this genus. Yet it may be noted that our specimens showed, on the initial split of the rock, rudimentary leaf-like organs (sterile appendages) which are small and once or twice divided apparently in one plane as previously



Text figs. 13–16. 13. A fertile appendage from specimen No. 5012/337 as it appeared originally. 14. Same appendage with segment I removed and underlying segment (II) revealed. Appendage I was formerly attached at break indicated by line ---o. 15. Partial restoration of same appendage. 16. Another appendage from specimen No. 5012/337. Detailed explanation in text.

described for *C. primaevum.* The same holds true for the sporangiophore; for example, these structures give the impression before degagement (figs. 22, 23) of being once forked and in only one plane. This aspect is apparently very similar to the sporangiophore of *C. renieri* (Leclercq, 1940) with the difference that the small axis of the sporangiophore of *C. bicephalum* is prolonged as an erect appendage. Thus, in order to determine whether *C. primaevum* K. and W. actually had three dimensional leaves a specimen of this species (figs. 17, 18) formerly described by Aderca (1932) was selected for re-investigation.

Figure 15 shows two leaves that were selected as they appeared initially; both dichotomize and of the two resultant branches the left one in both undergoes another forking and, in the case of the lower leaf the left fork is again apically notched. Beginning at their apical extremeties the two leaves were degaged away down to the point indicated by the lines o----o, at which point a branch was found dipping down into the rock matrix. When completely exposed these underlying branches appeared as shown in figure 16 distal to the line o----o. The latter were thus directly beneath the branches shown in figure 15 and in both leaves the second dichotomy was at right angles to the first; these leaves are shown restored in text figure 5. Thus, in view of the identical morphology found in *C. bicephalum* we consider the three dimensional branching to have generic value.

The prominent characters of *C. bicephalum* are the three dimensional sterile and fertile appendages. The former was a fairly rigid, terete structure with somewhat varied form; wedge-shaped ones, notched at their apex, were found along the lower portions of the primary branches. Higher up the branching of the leaf became more pronounced until the "mature" stage, characterized by four orders of branching, was attained. Attention may be called to the fact that such mature leaves were found on the lower portion of the primary branches of *fertile* twigs.

It may next be of interest to consider the possible homology of the sterile and fertile appendages. In 1936, Eames noted that "from the evidence provided by *Hyenia* and *Calamophyton* it is apparent that 'leaves' and the fertile tips in this group are homologous". Our study indicated that this is undoubtedly true if one compares a "mature" leaf with a sporangiophore. The latter divides into two main branches, referred to previously as superior and inferior segments, which may correspond to the initial dichotomy of the sterile appendage. Beyond this point the fertile appendage is more complex in that each segment produces three side branches each of which bears a pair of sporangia while the segment proper is elongate and usually terminates in a forked apex. Whether or not the sterile appendages may be termed "leaves" is perhaps a matter of opinion but there would seem to be no doubt that they functioned as such.

The present study is an initial one dealing with the fossil plants from the Goé locality. The difficulty of working with Devonian plants is emphasized by this investigation but in no less degree it is demonstrated that reliable information may be obtained from such ancient land plants when they are well preserved.

It seems pertinent to add a few comments concerning previous work with both *Hyenia* and *Calamophyton* since they are undoubtedly closely related. Of the several species of these two genera that have been described to date none is known in its entirety.

The problem of making significant comparisons with previously described species is rendered difficult by the fact that during the recent war the material described by Kräusel and Weyland (1926, 1929, 1932) was destroyed although two fragments of the fertile branch system of *C. primaevum*, from Dr. Kräusel's collections, are preserved in the Department of Geology of the University of Cologne. The two fragments on which *C. renieri* (Leclercq, 1940) is based are preserved at the University of Liège. 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 two other species to try to determine the real value of the three specific epithets. It is, however, questionable whether the remaining specimens of the earlier described species are sufficiently well preserved to allow effective comparison, consequently our only course seemed to be to assign a new specific name to the Goé specimens.

In the light of what is now known it seems safe to assert that the only dependable difference between *Hyenia* and *Calamophyton* lies in the general habit of the two. Even this is complicated by the fact that we do not know anything about the basal part of the shoot system of *Calamophyton*. Our specimens do, however, suggest a habit that may be worth a few words of speculation. It seems likely that *C. bicephalum* consisted of upright shoots that were predominantly fertile (fig. 21) or sterile (fig. 7, lower right). If this was the case it seems unlikely that the fertile shoots would have had sufficient photosynthetic tissue to have maintained themeselves independently. In explanation it may be supposed that both were borne either on a common erect small "trunk" that would have given the plant a shrub-like appearance, or they were borne on a common rhizome with a relationship comparable to that found in the modern *Equisetum arvense*. It is expected that further studies of the Goé fossils will contribute toward solving this and other problems relating to both *Calamophyton* and *Hyenia*.

SUMMARY

The material on which this study is based came from the lower Givetian (Middle Devonian) of Belgium.

A new species, *Calamophyton bicephalum* Leclercq and Andrews, is created in view of the complexity of the fertile appendages which contrast with homologous structures in the previously described species *C. primaevum* Kräusel and Weyland and *C. renieri* Leclercq.

The investigation has dealt chiefly in elucidating the structure of the sterile and fertile appendages.

The sterile appendages (leaves) are shown to be three dimensional organs that forked once (young leaves) to four times (mature leaves) and were probably rather rigid and terete in cross section. The three dimensional structure of these appendages is considered to have generic value.

The fertile appendage branched into upper and lower segments; each was erect and supported three curved side stalks attached at slightly different levels; each of these stalks terminated in a pair of pendulous sporangia. Thus the entire appendage bore twelve sporangia when all developed. The sporangia were cylindrical and pointed at the distal end, with possibly a line of dehiscence in the ventral side.

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Je suis particulièrement reconnaissante à Monsieur José Lewalle, Assistant, et à Monsieur Maurice Discry, Préparateur-technicien, de l'aide continue qu'ils ont apportée à l'exécution des nombreux documents photographiques nécessités par cette étude. (Professeur S. Leclercq)

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Explanation of Plate

PLATE I

Calamophyton bicephalum Leclercq and Andrews
Figures 1–6: specimen No. 5012/337

Fig. 1. A large specimen shown natural size. Figs. 2–5. Sterile appendages taken from points *a–d*, respectively, on specimen shown in fig. 1; all magnified × 5. Fig. 6. A partially preserved fertile appendage; see also text fig. 16 and description in text (p. 14); magnified ×5.

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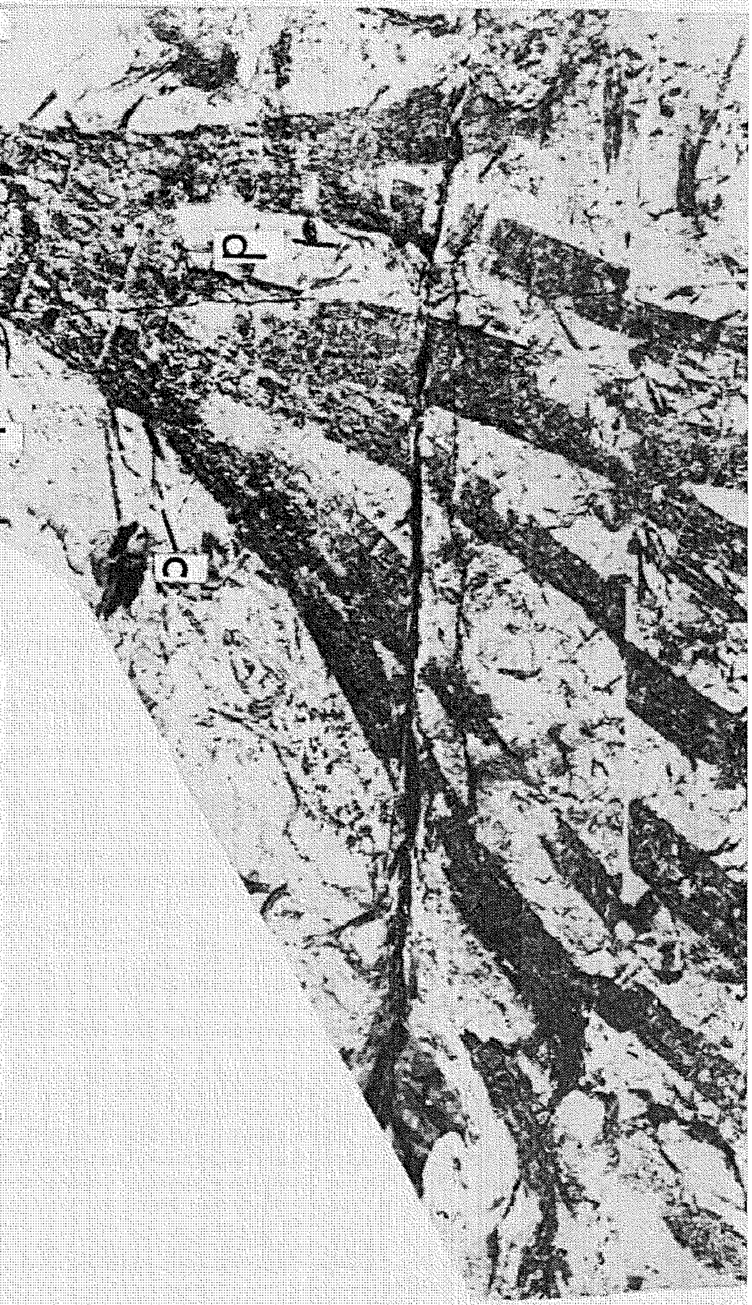

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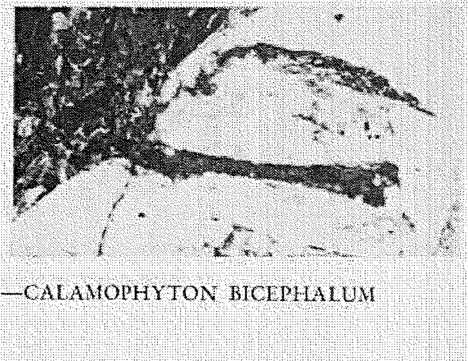

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LECLERCQ & ANDREWS—CALAMOPHYTON BICEPHALUM

PLATE I


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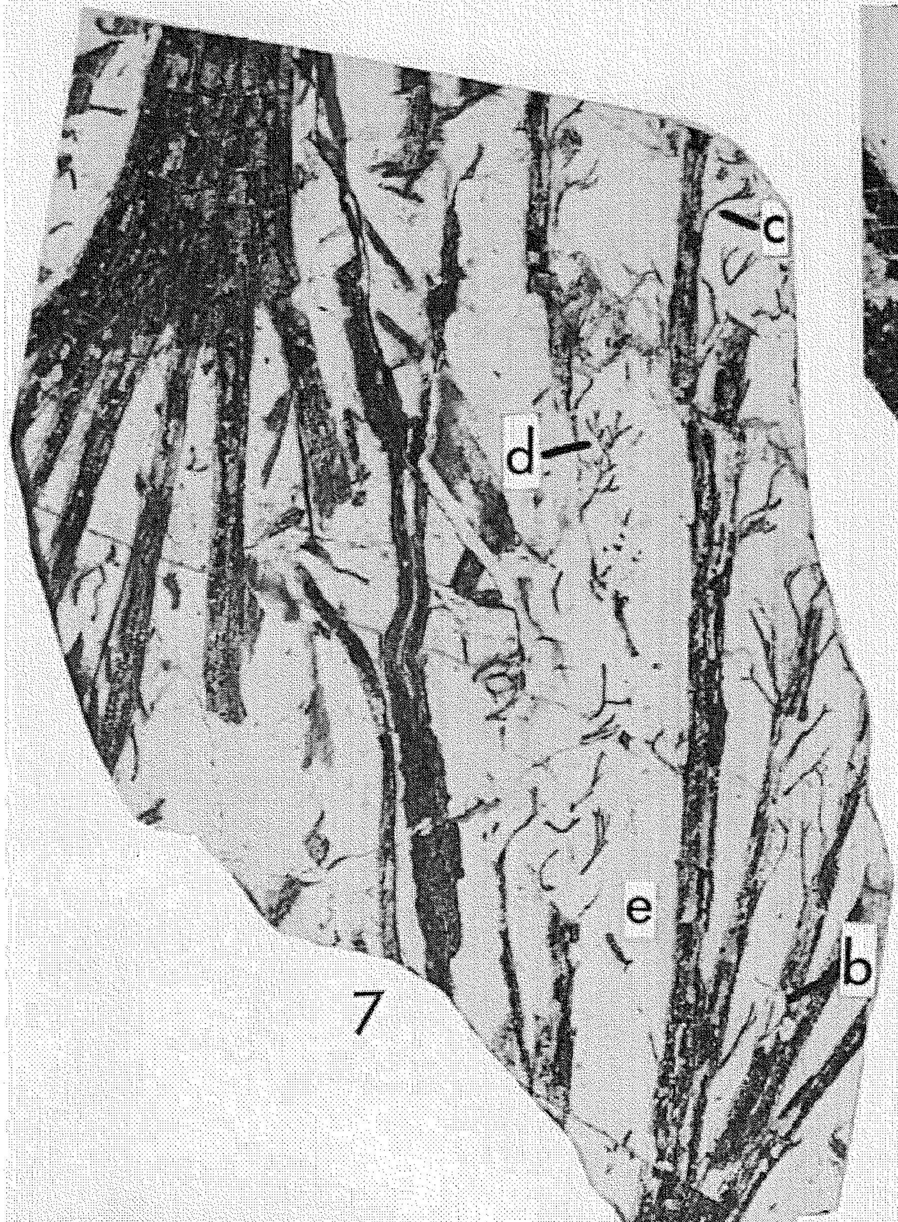
Explanation of Plate

PLATE II

Calamophyton bicephalum Leclercq and Andrews
Figures 7–13: specimen No. 5009/588

Fig. 7. Two specimens shown natural size. Fig. 8. Leaf taken from point *b* in fig. 7; × 5. Fig. 9. Leaf showing four orders of branching; × 5. Fig. 10. Portion of vascular strand from leaf shown in fig. 11; × 62. Fig. 11. Leaf with vascular strand preserved from point *a* in fig. 7; × 3. Fig. 12. Leaf from point *c* in fig. 7; × 5. Fig. 13. Leaf showing four orders of branching from point *d* in fig. 7; × 5.



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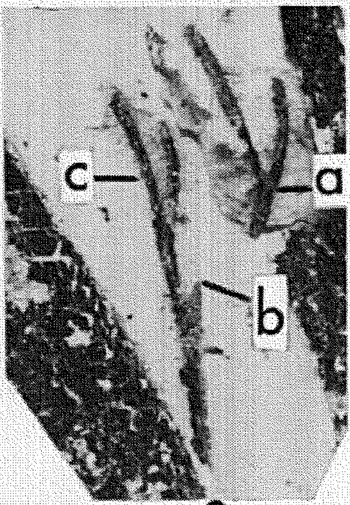

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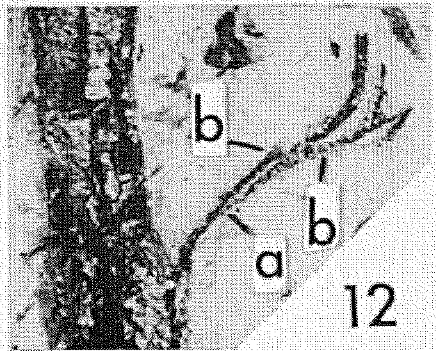

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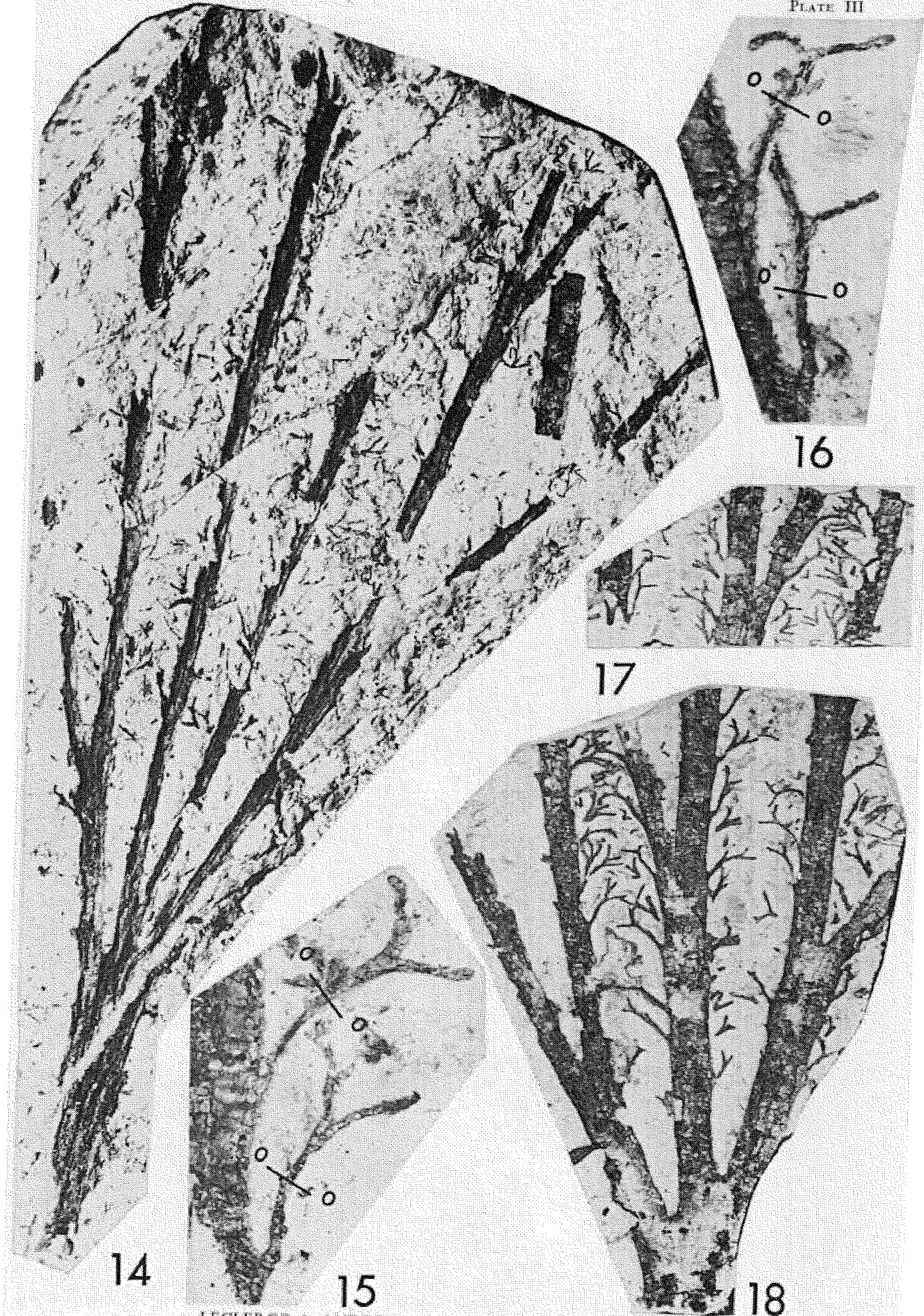
LECLERCQ & ANDREWS—CALAMOPHYTON BICEPHALUM



LECLERCQ & ANDREWS—CALAMOPHYTON BICEPHALUM

EXPLANATION OF PLATE

PLATE III

Calamophyton bicephalum Leclercq and Andrews

Fig. 14. Specimen No. 5007/346. ×1.

Calamophyton primaevum Kräusel and Weyland

Fig. 15. Two leaves from specimen No. 5006, ×5, shown as they appeared originally. Fig. 16. Same leaves as in fig. 15 after degagement; portions distal to lines o----o were revealed after corresponding parts in fig. 15 were degaged away. These two leaves are shown on the right side of the extreme left branch of fig. 17. Fig. 17. Portion of specimen No. 5006, ×1. Fig. 18. Counterpart of specimen No. 5006, ×1.

EXPLANATION OF PLATE

PLATE IV

Calamophyton bicephalum Leclercq and Andrews

Fig. 19. Leaf showing four orders of branching from specimen No. 5009/588, × 5. Fig. 20. Main stem of specimen No. 5011/609, ×1. Fig. 21. Holotype specimen No. 5011/609 shown natural size; figure 20 is counterpart of main stem shown here. Figs. 22–27 show stages in the excavation of a fertile appendage from specimen No. 5011/609; for explanation see text (p. 10); all ×5. Fig. 28. Portion of fertile appendage from specimen No. 5011/609, ×5.

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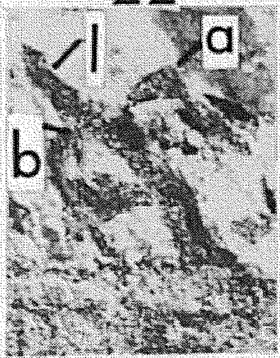

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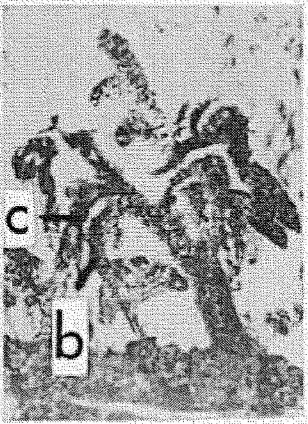

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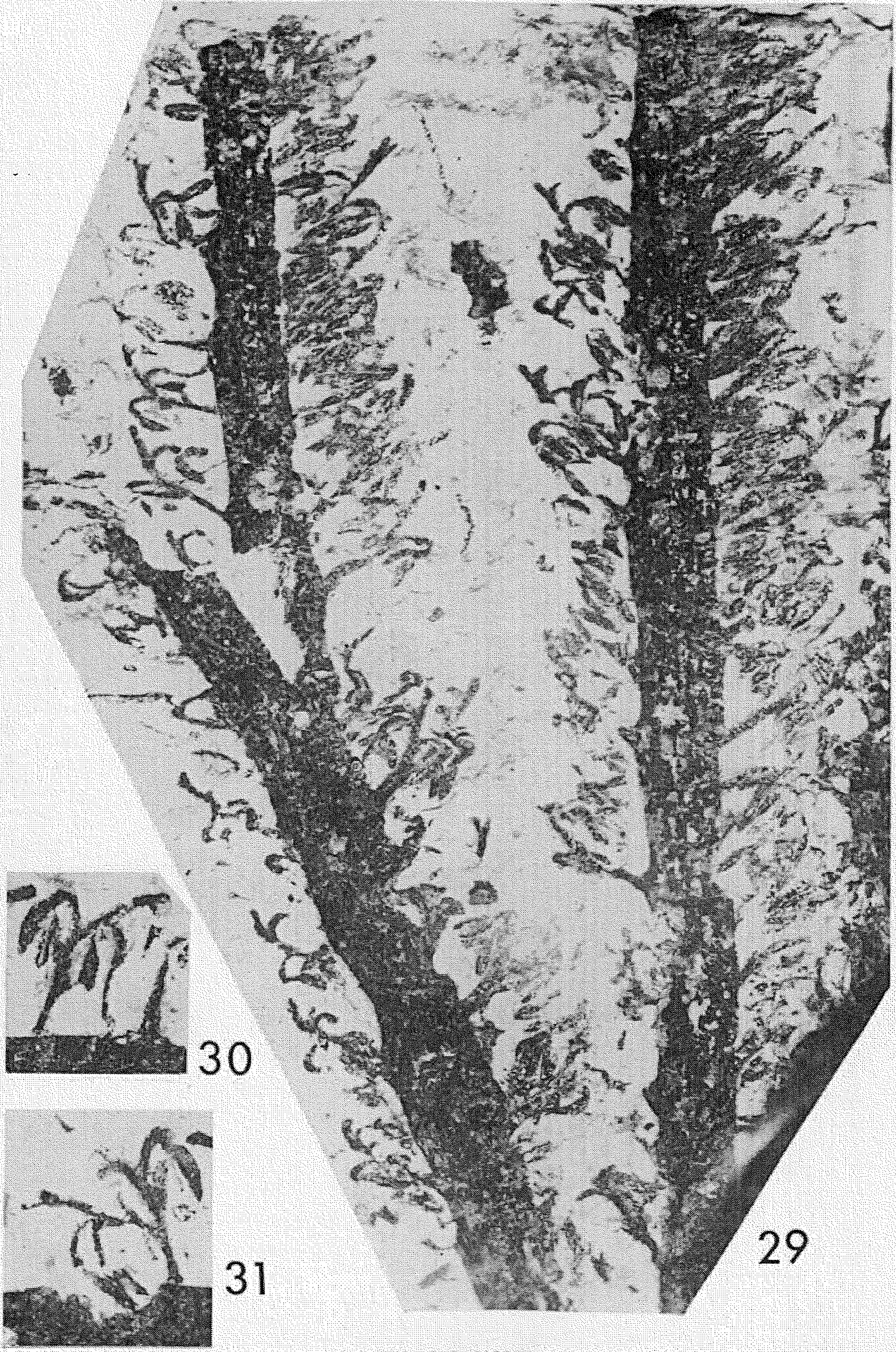
LECLERCQ & ANDREWS—CALAMOPHYTON BICEPHALUM



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LECLERCQ & ANDREWS—CALAMOPHYTON BICEPHALUM

Explanation of Plate

PLATE V

Calamophyton bicephalum Leclercq and Andrews

Fig. 29. Upper portion of holotype specimen No. 5011/609 (as shown in fig. 21) enlarged three times. Figs. 30, 31. Part and counterpart of a fertile appendage from specimen No. 5011/609, ×5; see also text figures 9–12 and description in text (p. 13).