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A RECONSIDERATION OF *HYENIA ELEGANS* KRÄUSEL ET WEYLAND AND *HYENIA 'COMPLEXA'* LECLERCQ: TWO MIDDLE DEVONIAN CLADOXYLOPSIDS FROM WESTERN EUROPE

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Two taxa of Middle Devonian Cladoxylopsida from localities in Belgium and Germany are redescribed. A counterpart of one of the missing type specimens of *Hyenia elegans* Kräusel et Weyland from Kirberg, Germany, demonstrates that rather than having simple forked fertile appendages (as apparent from the type description), more complex fertile units were present; these consisted of two daughter segments (resulting from a proximal dichotomy), each of which bore three pairs of elongate sporangia on short recurved stalks proximal to a terminal bifurcation. Specimens from Oë, Belgium, informally referred to as *Hyenia 'complexa'* by Leclercq, were shown to have a similar fertile organ that lacked the tuft of filiform extensions previously believed to be present. The parallel axes of this plant are now interpreted to be derived from a digitate branch rather than from a horizontal rhizome. Both taxa, *H. elegans* and *H. 'complexa'*, therefore demonstrate fertile appendage morphology and other characters that are typical of the Middle Devonian cladoxylopid *Calamophyton primaevum* Kräusel et Weyland, which has priority.

Keywords: Devonian, plant fossils, Cladoxylopsida, *Hyenia*, *Calamophyton*.

Introduction

Devonian Cladoxylopsida occupy an important place in many current theories of early land plant evolution (e.g., Skog and Banks 1973; Stein et al. 1984; Doyle 1998). The class Cladoxylopsida was originally founded on Lower Carboniferous permineralizations, for which morphological details are lacking. They have a dissected primary vascular system characterized by a number of interconnected columns or plates of primary xylem. The most completely known Devonian Cladoxylopsida, including *Pseudosporochnus* Potonié et Bernard (1904) and *Calamophyton* Kräusel et Weyland (in Weyland 1925), share these anatomical characteristics. In both cases, the original descriptions were essentially made from compression fossils, and discovery of cladoxylopid anatomy in these genera was reported relatively recently. Devonian cladoxylopid genera share some characteristics that are observable in compression fossils, including digitate branching, dichotomously divided lateral appendages, and a characteristic speckled surface pattern on compressions, which now allow the recognition of members from compression material only (e.g., *Lorophyton*; Fairon-Demaret and Li 1993).

The history of the Middle Devonian genera *Hyenia* Nathorst (1914) and *Calamophyton* has been one of confusion and uncertainty with regard to their identities, habits, and morphologies; it has also been one of debate with regard to their possible ancestral relationship to ferns and horsetails. We have been involved in a project, the goal of which is to reconsider

the morphology of the Devonian Cladoxylopsida in order to move toward a modern assessment of the place of these plants in the vascular plant phylogeny. In this study we resolve the issue of the identity of *Hyenia elegans* (based on previously unstudied material from the type locality), and we give a new interpretation of *Hyenia 'complexa'* Leclercq (1961).

Historical Account and Previous Interpretations

Nathorst (1914) described a number of plants from western Norway, including the new genus and species *Hyenia sphenophylloides*. He derived the name from the nearby Hyenfjords. This plant consisted of “leafy” axes with thickened bases attached to a fragmentary larger branch. The “leaves” were described as being branched once or twice and as being arranged in verticils, with four to possibly six leaves per whorl. Nathorst perceived a likeness to *Sphenophyllum*, hence the specific name.

Kräusel and Weyland (in Weyland 1925) described narrow axes that were collected at Elberfeld in Germany and that bore bifurcating laterals, which they attributed to *H. sphenophylloides* Nathorst. They also gave a short description of a new taxon from the same locality, *Calamophyton primaevum*, with the intention of providing a fuller treatment in a later publication. Their illustration shows a digitately dividing branch with transverse ridges plus a smaller transversely elongated superficial ornament bearing dichotomously divided lateral appendages.

Kräusel and Weyland (1926) described a number of taxa from Germany, three of which are of relevance to this study. These included a new species of *Hyenia*, *H. elegans*, based on a reconsideration of the German specimens formerly ascribed

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to *H. sphenophylloides*. Their taxon consisted of stems that were up to 4 mm wide, which bore narrow “leaves” that were up to 25 mm long and up to four times bifurcate. Fertile leaves divided once, and each segment bore two or three elliptical sporangia (fig. 1a). Kräusel and Weyland provided a simple diagnosis for *Hyenia*, emphasizing the supposed verticillate arrangement of the leaves. They noted that the stems converged basally and thought that this convergence was toward an upright stem rather than a rhizome.

Their promised elaboration on *C. primaevum* was based mainly upon material from the same locality, am Kirberg in the Honseler Schichten, near Elberfeld. The plant was very similar to *H. elegans* except that the larger axes were more profusely bifurcate (including digitate branches), with irregular nodes and a pattern of pores on the surface. Sporangia were borne singly on the recurved terminations of the apparently once-bifurcate sporangiophores (fig. 1d). Some details of tracheids were recorded, and the vascular system was thought to leave a longitudinal ribbing on preserved stem compressions. Leaves were one to many times bifurcate and were borne in verticils at the nodes. A single specimen of a new species, *Cladoxylon scoparium* (also from the same locality), was interpreted to have fan-shaped sporangiophores and the beginnings of webbed leaves. Detail of the gross anatomy, which showed many plates of xylem, allowed *C. scoparium* to be regarded as an early member of the *Cladoxylon* group, based on the type *Cladoxylon mirabile* Unger (1856).

Kräusel and Weyland (1926) erected the class Protoarticulatae to accommodate the orders and families Hyeniales and Hyeniaceae and Calamophytales and Calamophytaceae. Thus, their conclusion was to regard these plants as precursors of horsetails, as Nathorst had concluded for *H. sphenophylloides*. However, Scott (1926), in commenting on the paper of Kräusel and Weyland, doubted that *Hyenia* and *Calamophyton* were sufficiently distinct to merit separate families.

Kräusel and Weyland (1929) further examined *H. elegans* and emended their diagnosis to recognize that the larger axes were branched dichotomously several times and that multiple distal branches were oriented in parallel alignment. More details were supplied of a folded V-shaped xylem plate. New diagnoses were also prepared for *Calamophyton* and for *C. primaevum*.

Høeg (1931) illustrated new specimens of *H. sphenophylloides* from western Norway. He noted that the leaves may have been oriented in verticils but that there was neither a very regular arrangement nor any sign of segmentation on the axes. The regularity of the leaf insertions increased distally. He supported a “not improbable” (Høeg 1931, p. 15) relationship between *Pseudosporochmus*, *Hyenia*, and *Calamophyton*.

Kräusel and Weyland (1932) described a specimen of *H. elegans* from Gräfrath (Germany), which they interpreted as a number of leafy axes arising from a thick rhizome, each with a clublike base. This specimen was very small. Kräusel and Weyland also described a specimen from Böhlerhof bei Elberfeld (Germany), also with a putative horizontal rhizome and vertical aerial axes. They provided a semireconstruction of the specimen, clearly displaying their interpretation, with no branching visible in the vertical axes. They also offered an interpretation of the nonillustrated material of Nathorst, sug-

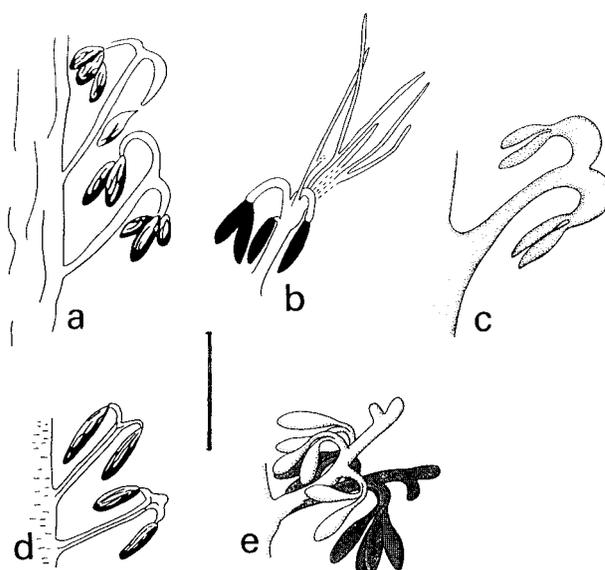


Fig. 1 Line drawings of the fertile appendage of *Hyenia* (a–c) and *Calamophyton* (d, e) according to the following: a, Kräusel and Weyland (1926, fig. 22, p. 135); b, Leclercq (1940, fig. 4, p. 9); c, Schweitzer (1972, fig. 13f, p. 165); d, Kräusel and Weyland (1926, fig. 27, p. 139); e, Leclercq and Andrews (1960, fig. 8, p. 11). Scale bar = 5 mm.

gesting that the narrow axes of *H. sphenophylloides* arose from an 8-cm-thick rhizome.

Leclercq (1940) published details of *H. elegans* from Oé, Belgium. In one specimen (ULg EH1/1459; see our fig. 2a), she believed that the many subparallel axes originated from a rhizome (mostly missing), for which she saw some evidence on the slab. She also found some ribbed (?polystelic) axes, which she interpreted as possible rhizomes. In addition, Leclercq reported that the sporangia were borne in groups of one to three on variously branched recurved sporangiophores that had long filiform distal extensions (in Leclercq 1940, fig. 4, reproduced here in fig. 1b). She published a reconstruction of the EH1 specimen with the aerial axes originating from a horizontal rhizome (see also Leclercq 1939). Leclercq (1940) also described some specimens of *Calamophyton*, including a new species, *C. renieri*, from Mousset, and she gave a new diagnosis for *Calamophyton* (Leclercq 1940, p. 37).

Høeg (1942) placed some new material from Spitzbergen in *Hyenia* (subg. *Hyeniopsis*) *vogtii*, new subgenus and species. This plant bore divided leaves in whorls on spinous narrow axes. The first-order axes also bore second-order axes irregularly in place of leaves at the whorls. It was the branching pattern that persuaded Høeg to erect a new subgenus. Høeg (1945) later described a further specimen of *H. sphenophylloides*, which he believed would confirm his opinion that the plant grew from a rhizome. He also described a few fragmentary specimens with bifurcate appendages and lateral branches (which lacked spines) and named them *Hyenia* (*Hyeniopsis*) *ramosa*.

During the Second World War, Kräusel and Weyland’s illustrated specimens of *Hyenia*, *Calamophyton*, and *Cladox-*

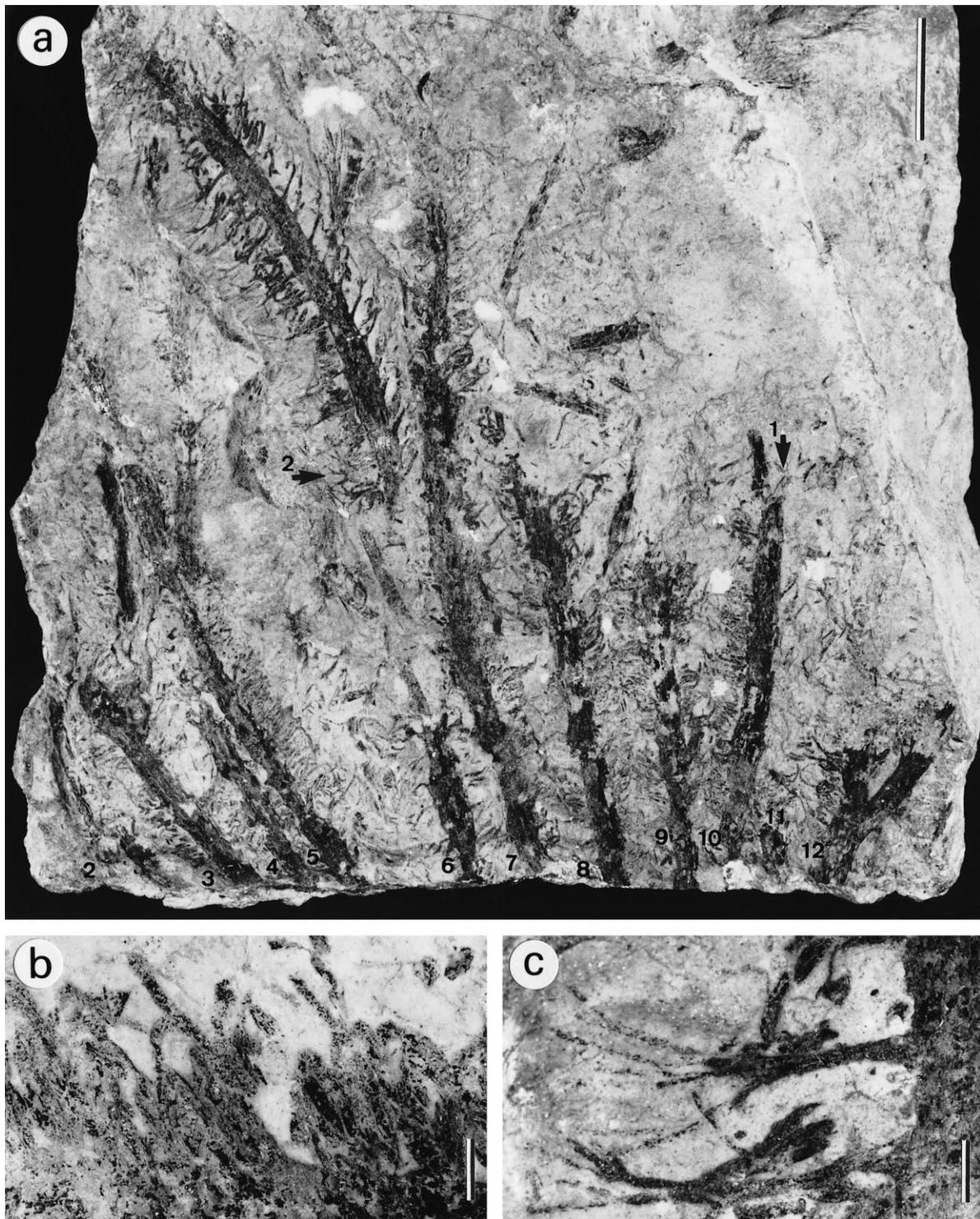


Fig. 2 *Hyenia elegans*'*complexa*' of Leclercq (1940, 1961), specimen from Oë, Belgium, illustrated by Leclercq (1940, pl. 1, fig. 3, and pl. 2, fig. 7), ULg EH1/1459. *a*, General view of the specimen with 12 axis fragments; arrowheads indicate the fertile appendages that have been degaged along axes 6 (figs. 11, 13) and 10 (fig. 11*d*). *b*, Detail of *a*, showing the entangled appendages along the right-hand margin of axis 5. *c*, Detail of *a*, with two fertile appendages situated along the concave margin of axis 6, showing apparent distal filiform extensions. Scale bars: *a* = 20 mm; *b*, *c* = 2 mm.

ylon, although removed from the Senckenberg Museum for safekeeping, were nevertheless destroyed. Thus, the type material of their three species was believed to have been lost.

Leclercq and Andrews (1960) recognized a new species of *Calamophyton*, *C. bicephalum*, from the Middle Devonian of Goé, Belgium. They demonstrated the complex structure of the sporangiophore, revealed by painstaking dégageage. This organ bifurcates proximally, and each of the daughter axes bears three pairs of recurved sporangia laterally before terminating in a distal bifurcation (fig. 1e). Sterile appendages were found to be dichotomously branched up to four times and to be three-dimensional (nonplanated). Similar fertile organs were subsequently reported for *C. bicephalum* from New York State (Bonamo and Banks 1966) and for *C. primaevum* from near the type locality in Germany (Leclercq 1969). In this latter report, Leclercq provided an emended diagnosis for the genus *Calamophyton*.

Leclercq (1961) provided new observations on her *H. elegans* from Oé, suggesting that the sporangiophores were arranged in pairs. Because of the observed differences with the then known characters of *Hyenia*, including the long filiform extensions of the sporangiophores, she suggested a new specific name, *H. 'complexa'*, which was never published in valid form.

In 1964, *Calamophyton* and *Hyenia* were included in the Sphenopsida volume of the *Traité de Paléobotanique* (Boureau 1964). However, Leclercq and Schweitzer (1965) were able to demonstrate cladoxylalean anatomy in *Calamophyton* from Goé, Belgium, and Lindlar, Germany. Therefore, *Calamophyton*, but not *Hyenia*, was later included in the Cladoxylopsida chapter of the *Traité* volume devoted to Filicopsida (Leclercq 1970).

Schweitzer (1972, 1973) devoted sizable monographs to both *H. elegans* and *C. primaevum* from Lindlar, Germany. *Hyenia elegans* was reconstructed as having digitately branched aerial axes arising from a prostrate rhizome. Sporangia were borne in pairs on the recurved tips of simple dichotomous appendages (fig. 1c). In *Calamophyton*, however, the digitate leafy axes arose from the sides of an upright trunk. Sporangioophores were similar to those described by Leclercq and Andrews for *C. bicephalum*.

Skog and Banks (1973) considered that Hyeniales (*Hyenia* and *Calamophyton*) might be intermediate between their lilykales (=Iridopteridales, in part) and both Sphenophyllales and Calamitales, thus reinforcing the concept that *Hyenia* and *Calamophyton* were potential ancestral horsetails. Stein et al. (1984) tested the then-available data regarding Devonian Cladoxylopsida and Iridopteridales and concluded that current evidence was unable to favor either group as the origin of Sphenopsida.

Mustafa (1978) provided an emended diagnosis for *C. primaevum* based on his material from the Brandenburg Beds in Sauerland (Germany), which included well-preserved permineralizations, and on information from a number of other localities, including the morphological description of Schweitzer.

Schweitzer and Giesen (1980) located a fragment of the counterpart of Kräusel and Weyland's type specimen of *Cladoxylon scoparium* and demonstrated that it had many of the characters of *Calamophyton primaevum*. They believed that the webbed leaves and sporangiophores of *C. scoparium*, as

described by Kräusel and Weyland, were caused by overlap and fortuitous preservation.

The current consensus on the distinction between the genera *Calamophyton* and *Hyenia* is therefore that *Hyenia* grows from a rhizome and has simple bifurcating fertile appendages (except for the case of *Hyenia 'complexa'*) and that *Calamophyton* grows with a more treelike habit and has complex fertile appendages.

There is no general agreement on how to classify these plants. In the textbook of Stewart and Rothwell (1993), *Hyenia* and *Calamophyton* are to be found in the chapter entitled "The Origin of the Sphenopsida," whereas in Taylor and Taylor (1993), they are treated in the chapter entitled "Ferns."

Material and Methods

Provenance and Stratigraphy

German specimen. A single specimen of *Hyenia elegans* (GIK1690, Institute of Geology, University of Köln, Germany), collected by Weyland from the Middle Devonian Honseler Schichten of Kirberg, is restudied in this article (fig. 3a). The specimen is fertile. It was drawn to our attention because it was recorded in a notebook of Suzanne Leclercq (from 1959) as the counterpart of type material of *H. elegans*, the illustrated specimens themselves having been lost in World War II. The specimen is a counterpart to that presented in two photographic illustrations in the original description of Kräusel and Weyland (1926, pl. 9, figs. 8, 9). Reversed prints of the counterpart are reproduced here for comparison with the original illustrations (see our figs. 3b, 4). Of the specimens illustrated by Kräusel and Weyland (1926) and named *H. elegans* (i.e., the type collection), we believe that the Köln specimen is the only sample (albeit a counterpart) presently available for study.

Most of the vegetative and all of the fertile specimens of *H. elegans* described by Kräusel and Weyland (1926, 1929), including the Köln specimen, were collected in a small quarry named am Kirberg, which lies along the road from Elberfeld to Sonnborn on the right bank of the River Wupper. This quarry was made famous by the plant remains that it yielded. It is the type locality for *H. elegans*, *Calamophyton primaevum*, *Cladoxylon scoparium*, *Duisbergia mirabilis*, *Asteroxylon elberfeldense*, and *Aneurophyton germanicum*, and it has also yielded specimens of *Leclercqia complexa* Banks et al. (Fairon-Demaret 1980). The sandstone and alternating shale layers in the am Kirberg quarry belong to the Upper Honseler Schichten, which, according to the German Devonian correlation chart (Weddige 1996, 1998), are Givetian (late Middle Devonian), with the Honseler Schichten positioned in the middle part.

Kräusel and Weyland mentioned only three additions to the am Kirberg occurrence of *H. elegans*. Two vegetative specimens from the old Piedboeuf collection from the Brandenburg Schichten (Upper Eifelian, early Middle Devonian) in Oben zum Hölz, near Gräfrath (Germany) were located, one each in Berlin and Stockholm. The third vegetative specimen was illustrated by Kräusel and Weyland 1932, and this specimen was from Böhlhof, another locality in the Elberfeld area where the Funklochschichten are exposed. These strata en-

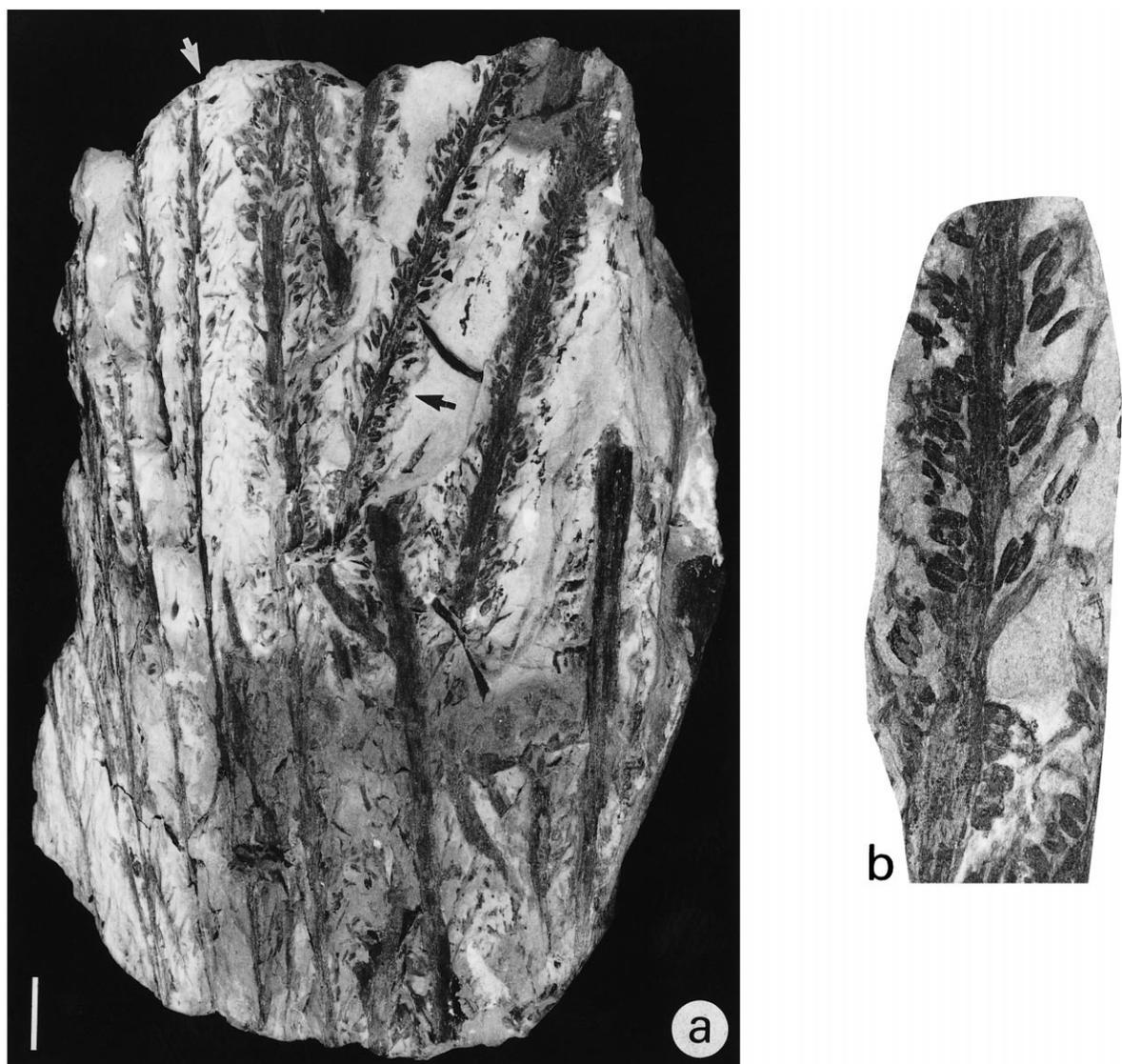


Fig. 3 Counterpart of specimen of *Hyenia elegans* from Kirberg, Germany; illustrated by Kräusel and Weyland (1926, pl. 9, figs. 8, 9), GIK1690. *a*, Complete specimen; white arrow points to fertile appendage illustrated in fig. 8. *b*, Enlargement of fertile axis in area marked by black arrow in *a*, printed in reverse (cf. Kräusel and Weyland 1926, pl. 9, fig. 9). Scale bars = 10 mm.

compass the Eifelian-Givetian boundary (Weddige 1998) and are of the same age as the Belgian specimens from Oé.

Belgian specimens. *Hyenia* has been described and illustrated from only one locality in Belgium. Three specimens were collected and illustrated by Leclercq (1940) and are restudied here. They come from Oé in the Vesdre (=Verviers) Synclinorium from a small quarry called La Carrière, which had already been abandoned by 1939. La Carrière is located ca. 2 km southeast of Eupen (province of Liège) on the left bank of the river Vesdre. The green fossiliferous sandstone in La Carrière belongs to the Pepinster Formation in the Gileppe Unit on the south flank of the Oé fault (Hance et al. 1996). Biostratigraphical data obtained from the green sandstone facies of the Pepinster Formation have been shown to be equivalent

within the whole Gileppe Unit. These green fossiliferous sediments are dated from the A.D. pre-Lem biozone and are Late Eifelian to earliest Givetian (mid-Middle Devonian) in age (Hance et al. 1996). From Oé, in addition to *H. elegans* (= *H. 'complexa'* of Leclercq 1961), fragmentary remains of *Rellimia* (= *Protopteridium* in Leclercq 1940), *Calamophyton* (Leclercq 1940), and *Leclercqia* (Fairon-Demaret 1981) have been reported.

The specimens restudied here from Oé include a large slab bearing a number of subparallel axes, ULg EH1/1459 (fig. 2*a*), and its counterpart ULg EH1'/1459 (hereafter referred to as EH1 and EH1') and ULg EH55/1467 part and counterpart (hereafter referred to as EH55, Paleobotany Department, University of Liège, Belgium).



Fig. 4 Counterpart of *Hyenia elegans* illustrated by Kräusel and Weyland (1926, pl. 9, figs. 8, 9), GIK1690. Enlargement of distal part of some axes, printed in reverse (cf. Kräusel and Weyland 1926, pl. 9, fig. 8). Scale bar = 10 mm.

In figure 5, the most important localities in Germany and in Belgium yielding *Hyenia* and/or *Calamophyton* are arranged according to their current stratigraphic position. *Hyenia* and *Calamophyton* occur together in the same localities from the Middle Eifelian up to the Middle Givetian.

Techniques

The main method of study of the compression material has been that of *dégagement* (Fairon-Demaret et al. 1999), whereby sediment is removed from the fossil through a method that involves sharpened triangular needles, which are struck with a small hammer under the binocular microscope. Photographs were taken (using polarized light) and camera lucida drawings made to record the successive stages of uncovering of the complex organs in order that three-dimensional reconstructions could be prepared. Attempts to transfer material from Oé in order to obtain spores from the sporangia failed; small pieces taken from the three old specimens completely disintegrated.

Descriptions

A Counterpart of a Type Specimen of Hyenia elegans Kräusel et Weyland

Approximately 12 axes are visible on one side of slab GIK1690 (fig. 3a) from Kirberg, Germany. The fossils are vis-

ible as brown and black coalified compressions (adpressions) against the gray-green fine-grained matrix that is weathered to a shade of brown in places. When fully exposed, axes are 3–4 mm wide; others are narrower, possibly because of lateral compression in the matrix. The longest exposed axis is 10.7 cm in length. None of the visible axes are branched. They lie more or less parallel on the rock.

Beside most of the axes, many lateral appendages and sporangia are visible (fig. 3a). An example of an unprepared fertile appendage (figs. 6a, 7a) is distally bifurcate. The left-hand segment is poorly preserved. The right-hand segment appears to branch basally, the left-hand branch being very short, but the right-hand branch terminates in one or perhaps two sporangia. A more complete example (figs. 6b, 7b) demonstrates a similar branching pattern. In this case, however, the left-hand segment is associated with two sporangia. An extension of the left-hand segment terminates in a bifurcate apex and is subtended by a recurved arm, which bears a pair of sporangia. Both of these fertile appendages are visible in the enlargement of the stem provided by Kräusel and Weyland (1926, pl. 9, fig. 9). We give a reversed enlargement of this area of the stem in figure 3b.

A fertile appendage was selected for *dégagement* in a relatively well-preserved area of the rock, an area that was mostly covered by matrix. Only four sporangia and the base and tip of the fertile lateral appendage are visible (figs. 8a, 9a).

The first stage of *dégagement* demonstrated that the largest sporangia (*a1*, *a2*) are attached to segment I of the lateral appendage by a long narrow stalk (figs. 8a, 9a), the stalk being recurved in such a manner that the sporangia are pointing back toward the main axis. Further *dégagement* demonstrates that the fertile appendage consists of two segments (I, II) resulting from a proximal bifurcation (figs. 8d, 9) and that each of the segments terminates in a distal bifurcation. Two more pairs of sporangia (*A1*, *A2*; *B1*, *B2*) are demonstrated to be attached to the second segment (II) of the branching system in a similar manner to that described above. The attachment of each recurved stalk bearing pairs of sporangia is distal to the first (proximal) point of bifurcation of the fertile organ.

A reconstruction of the fertile appendage uncovered in this example is given in figure 9f. The overall length of the organ is 11 mm, and it bifurcates 5 mm from the base. The segments lie subparallel and fork again 1 mm from the tip. Each of the segments bears paired sporangia on laterally attached recurved stalks that are up to 2 mm in length.

A second fertile organ was also uncovered (fig. 6c, 6d; fig. 7c–7e). Here, three pairs of sporangia are found to be laterally attached on recurved stalks to the one-half (segment I) of the fertile appendage that was uncovered.

Sporangia measure from 1.8 to 3.1 mm in length ($\bar{X} = 2.4$) and from 0.6 to 0.9 mm in maximum width ($\bar{X} = 0.73$). They are rounded at each end and lack an obvious dehiscence.

In conclusion, the fertile appendages of a counterpart to one of the type collection of *Hyenia elegans* are more complex than the simple bifurcate axes bearing sporangia on recurved tips, as originally illustrated by Kräusel and Weyland (1926; our fig. 1a). Up to three pairs of sporangia are borne laterally on short recurved stalks on each of two terminally forked segments distal to the first bifurcation of the organ. This complex morphology is comparable with that demonstrated for

	Lindlar (Mühlenberg Schichten)	Gräfrath Ambrock (Brandenburg Schichten)	Böhlerhof Kortzert (Funkloch Schichten)	Goé North (Nappe de Goé)	Oé + Gileppe (Unité de la Gileppe)	Mousset (Pepinster Formation)	Kirberg (Honseler Schichten)
Givetian							 <i>C. primaevum</i> ^{1,2} <i>H. elegans</i> ^{1,3} <i>Cl. scoparium</i> ¹
	Lower					 <i>C. renieri</i> ¹⁰ <i>C. primaevum</i> ¹⁰	
Upper AD-pre Lem			 <i>C. primaevum</i> ^{1,2,7} <i>H. elegans</i> ³	 <i>C. primaevum</i> ^{8,9}	 <i>C. primaevum</i> ^{8,10} <i>H. complexa</i> ¹⁰		
Eifelian	Upper	 <i>C. primaevum</i> ^{1,2,6} <i>H. elegans</i> ^{2,3}					
	Middle	 <i>C. primaevum</i> ^{4,9} <i>H. elegans</i> ⁵					
	Lower						

Fig. 5 Main Middle Devonian localities yielding *Calamophyton* and/or *Hyenia* in Germany and in Belgium according to their current biostratigraphical positions. 1, Kraüsel and Weyland 1926; 2, Kraüsel and Weyland 1929; 3, Kraüsel and Weyland 1932; 4, Schweitzer 1973; 5, Schweitzer 1972; 6, Mustafa 1978; 7, Leclercq 1969; 8, Leclercq and Andrews 1960; 9, Leclercq and Schweitzer 1965; 10, Leclercq 1940.

Calamophyton primaevum (Leclercq 1969) and *Calamophyton bicephalum* (Leclercq and Andrews 1960; Bonamo and Banks 1966).

Hyenia elegans and *Hyenia* 'complexa'
Leclercq 1961

The well-known reconstruction of *Hyenia* by Leclercq (1939, 1940) is based on the best, most complete specimen from Oé, EH1 (Leclercq 1940, pl. 1, fig. 3, illustrated again here as our fig. 2a) and on counterpart EH1'. It shows a dozen fertile axis fragments aligned more or less parallel to each other but disposed in different levels in the sediment. The plant remains (adpressions) are dark brown to black in color on the yellow green fine-grained to coarse matrix that locally appears to be very sandy. The axes located near the left-hand edge on the part (axes 2, 3, 4, and 5; axis 1 of Leclercq, located at the very edge of the slab, is not visible on the figure) are slightly curved. Neither the apices of the axes nor their bases are preserved because a joint (natural break in matrix perpendicular to bedding) truncates them at the same level. The longest preserved fragment measures 19.5 cm in length. One short axis fragment (axis 12 in fig. 2a) is bifurcate.

This specimen has previously been interpreted to have been preserved *in situ* (Leclercq 1940) and to show a confirmation of the rhizomatous habit of *Hyenia*. The whole rhizome was not present, but Leclercq deduced its occurrence from the ori-

entation and disposition of the axes and also from the observation at the very edge of the block of a short fragment of axis that is oriented perpendicularly to the others and that is thought to correspond to a cross section through the mostly missing rhizome (see pl. 1, fig. 3, in Leclercq 1940). Moreover, axes 2, 3, 4, and 5, with their gentle curving, were regarded as belonging to the apical part of the rhizomatous plant. However, as already emphasized by Leclercq (1961), specimen EH1 is not well preserved: it shows signs of transport. Many of the appendages present alongside the axes have been locally distorted. Moreover, on the surface of the block and within the sediment, diversely oriented tiny fragments of other plants are present. We do not believe specimen EH1 to be autochthonous (preserved *in situ*). When reconsidering both part and counterpart, evidence of a creeping rhizome that connected all the stem fragments could not be found. Rather, the axes seem to converge toward a common main stem that has not been preserved. Such a hypothetical ramification system appears reasonable when the axes are visually projected downward, outside the preserved block (fig. 10); they seem to converge toward a single cluster of origins. Moreover, they appear to be arranged into two groups, thus possibly branching in a way comparable to that seen in the models presented by Schweitzer (1973) for *Calamophyton*.

Leclercq (1961) restudied the fertile appendages preserved on this specimen (EH1). They were described as being emitted

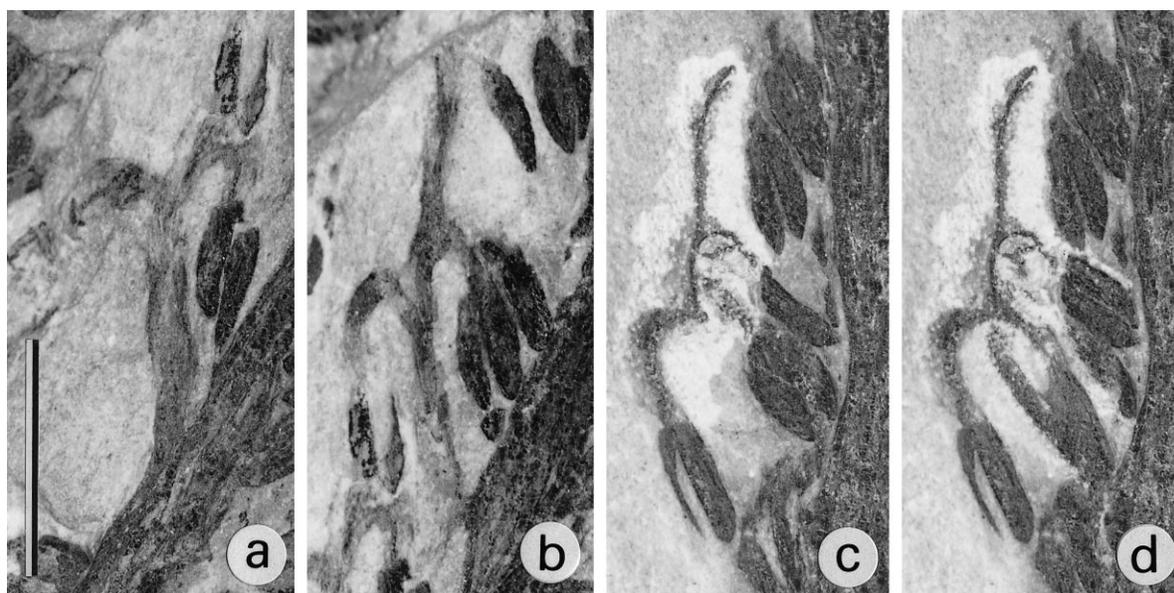


Fig. 6 Counterpart of *Hyenia elegans* illustrated by Kraüsel and Weyland (1926, pl. 9, figs. 8, 9), GIK1690. *a, b*, Untouched fertile appendages (see fig. 7*a, 7b*). *c, d*, Two stages in the dégageage of fertile appendage (see fig. 7*c–7e*). Scale bar = 5 mm.

by pairs, each member of a pair giving off three lateral recurved stalks ending in a pair of sporangia; filiform distal extensions were attached where the lateral stalks bent over, as seen in our figure 1*b*.

On specimen EH1, the fertile lateral systems are three-dimensionally disposed around the stems, but no regular organization can be observed: they appear either widely spaced along the margins of the axis (as, for example, along the right margin of axis 6, figs. 2*a, 11b*) or are tightly adpressed against each other (fig. 2*b*, e.g., and along the left-hand margin of axis 6, figs. 2*a, 11b*). The distal filiform extensions, appearing as tufts on top of several fertile appendages (figs. 2*c, 11a–11c*), are obvious in one area only, along the concave margin of axis 6 (fig. 11*a, 11b*), where the appendages are crowded and inserted at an angle of 90° or wider (fig. 11*a, 11b*). The appendages spaced along the opposed convex side of the axis are attached at a more acute angle, one approaching 45° (fig. 11*a, 11b*), a difference that can be accounted for by the curvature of the axis. Closer examination shows that some of these appendages are actually attached to the front of (fig. 11*a, 11b*, at small arrows) or behind (fig. 11*a, 11b*, at large arrow) the compressed axis in question rather than at its sides. They have been flattened and distorted, pressed down in the plane of the axis compression. Therefore, incomplete views and overlap of parts of several fertile organs (that falsely appear as one) make their interpretation complex. In some cases, two successive appendages, one attached along the margin of the compressed axis and the other arising in front of it or from its back, are so close that they appear to form a pair.

Within a tuft of filiform extensions (figs. 2*c, 11c*), the ultimate bifurcation does not occur at the same level, a fact already noted by Leclercq (1940, text, fig. 4, reproduced here as our fig. 1*b*), who clearly showed that in such a tuft, only two of

the filiform extensions divide symmetrically at exactly the same level (fig. 11*c*, arrows). From our observations, the grouped appearance of these terminal bifurcate extensions, as to form tufts, is the result of the entanglement of usually two (exceptionally three) variously oriented but closely inserted appendages that overlap. These filiform extensions in a tuft are disposed in slightly different levels in the sediment (figs. 2*c, 11c*), and no connection exists between the proximal part of one of the appendages and the others.

When it is possible to uncover (where they are neither too decolorized by the repeated application of liquids by previous investigators nor too entangled), the distal parts of these fertile appendages always consist of only two once-bifurcate extensions (figs. 11*d, 12f*). Their length varies between 1 and 2 mm (17 measured; $\bar{X} = 1.7$ mm). On axis 10, a fertile lateral unit still embedded in the sediment was dégagee (fig. 2*a*, arrowhead 1). It is clearly borne singly (fig. 11*d*). A first bifurcation occurs proximally, before the midlength of the appendage. The resulting segments diverge at an acute angle. The right-hand segment dichotomizes once more distally; it bears two recurved lateral stalks, each ending in one incompletely preserved, pendulous sporangium (fig. 11*d*). This fertile unit is not complete.

More information was obtained by development of another fertile appendage along axis 6 (indicated by arrowhead 2 on fig. 2*a*). This appendage was chosen because it showed the forked endings of the two segments (I and II; figs. 13, 14), despite the fact that a stalk with a pair of sporangia attached to the adjoining fertile unit has displaced segment II (figs. 13*a, 14a*). The proximal part of the fertile appendage under consideration is obscured where it is attached to the axis. Many more or less complete elongate sporangia are visible. These sporangia lie in slightly different levels in the sediment, a fact that is not easily appreciated from the illustrations but which

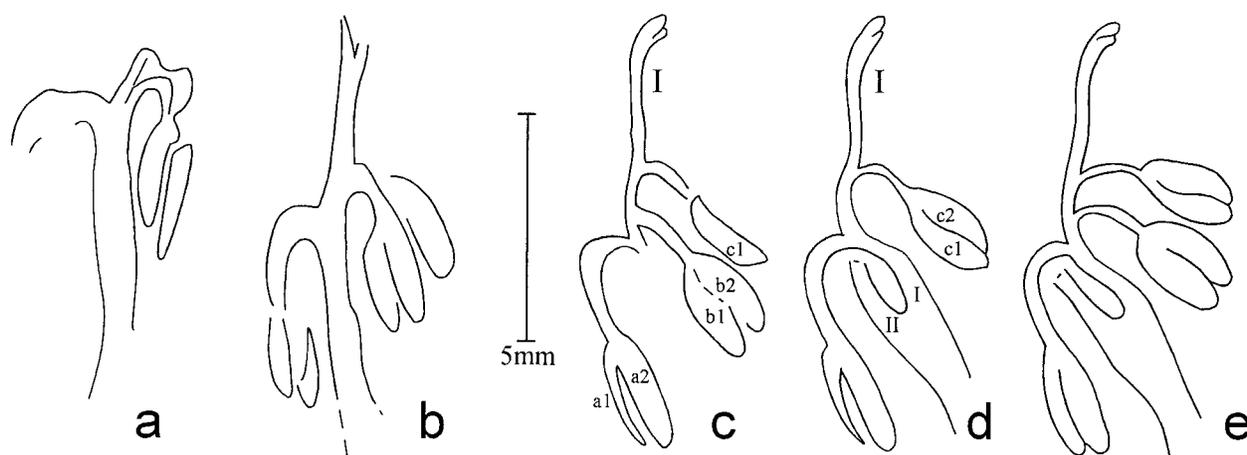


Fig. 7 Counterpart of *Hyenia elegans* illustrated by Kraüsel and Weyland (1926, pl. 9, figs. 8, 9), GIK1690. *a, b*, Untouched fertile appendages (see fig. 6*a, b*). *c, d*, Two stages in the dégagement of fertile appendages (see fig. 6*c, d*). *e*, Partial reconstruction of one-half of fertile appendage.

was of great help in understanding the organization of the whole three-dimensional organ. Two recurved stalks are seen attached to segment I (figs. 13*a, 14a*). The more distal stalk apparently bore one sporangium that was so thick and that showed such an unusual outline that a closer examination revealed partial superposition of three sporangia (fig. 14*a*). Two of these sporangia (*a1* and *a2*, fig. 14*a*) belong to a pair that is actually attached to the more distal stalk, but the third one belongs to the pair of sporangia that is attached to the more proximal stalk (*b1*, fig. 14*a*). Another more or less complete elongate sporangium (*C1*) and the carbonaceous distal end of still another one (*C2*) are also visible. A pair of superposed sporangia (left-end margin of figs. 13*a, 14a*) that is still attached to a fragment of stalk is observed detached to the left of sporangium *a1*. On the counterpart (figs. 13*c, 14c*), the stalk of the sporangial pair *A1* and *A2* can be seen. Demonstration of the stalk's attachment to the small preserved part of segment II, of which only the proximal end remains, was impossible. Segment II is lying at the uppermost level, and only its distal part and a few fragments (figs. 13*c, 14c*) were preserved when the rock was fractured. By removing the pair of overlying sporangia from the adjacent fertile unit along segment II, occurrence of another stalk (unfortunately without preserved sporangia) was demonstrated (figs. 13*d, 14c*, arrow). Sporangium *C2* was uncovered; with sporangium *C1* it forms a pair that is attached to a fragment of segment II (figs. 13*c, d; 14c*). On the complementary specimen (the part), the proximal undivided part of the fertile appendage was partly overlain by sporangium *C1*, which was removed. In the process, a supplementary pair of sporangia was also revealed. This final pair was shown to be attached to a long stalk belonging to the adjacent appendage (fig. 14*b*).

The reconstruction of the fertile appendage (incorporating all our observations) (fig. 14*d*) shows that a proximal bifurcation gave rise to two superposed segments. One of these (background) bore at least two lateral stalks, which ended in pairs of recurved elongate sporangia; on the second segment (foreground), attachment of one sporangiferous stalk was dem-

onstrated, and attachment of another two pairs of sporangia is inferred. The distal end of each segment is bifurcate. One of the two segments of the adjacent fertile appendage (fig. 14*a, 14b*) also possessed three lateral stalks with pairs of pendulous sporangia.

The same organization of the fertile appendage was observed again on specimen EH55 (fig. 12*a*), which was illustrated in part by Leclercq (1940, pl. 3, fig. 18). This fertile axis fragment, measuring 6.0 cm in length, is not well preserved, but the fracture of the rock split the stem obliquely, exposing a promising fertile appendage, which was attached to its back side (fig. 12*a*, arrow). Part and counterpart have been uncovered.

On the part, the exposed fertile appendage (fig. 12*b*) appears to be bushy, with three elements arising from what looks like a common base. Attachment to the main axis is not clear. An elongate sporangia (*c2*) and the proximal part of a second one (*c1*) are visible, apparently connected by stalks to segment I (fig. 15*a*). The proximal carbonaceous part of a third sporangium (*b1*) is also visible. A fourth elongate, incomplete sporangium (*A1*), is observed—possibly connected to segment II—in addition to a fifth incomplete sporangium (*a1* on fig. 15*a*), which is slightly detached from segment I. Dégagement demonstrated that the two sporangia, *c1* and *c2*, are in fact members of a pair at the end of a common stalk that is attached to segment I (figs. 12*c, 15b*). The carbonaceous distal end of sporangium *b1* was demonstrated to be attached to a more distal stalk on segment I (figs. 12*c, 15b*). Segment I thus possesses three recurved stalks ending in sporangia. On segment II, the connection between sporangium *A1* and its stalk was verified.

On the counterpart (fig. 12*d, 12e*; fig. 15*c, 15d*), sporangium *A1* is easily recognized. Its full length was uncovered. It is cigar shaped, measuring 2.8 mm long and 0.5 mm wide; a longitudinal slit indicates a possible dehiscence line (fig. 12*e*). Below the attachment point of its stalk a bump (fig. 12*d, 12e*; fig. 15*c, 15d*) along the right-hand margin of segment II indicates the occurrence of a second stalk. After dégagement it was shown to end in two sporangia, *B1* and *B2*, which lie one

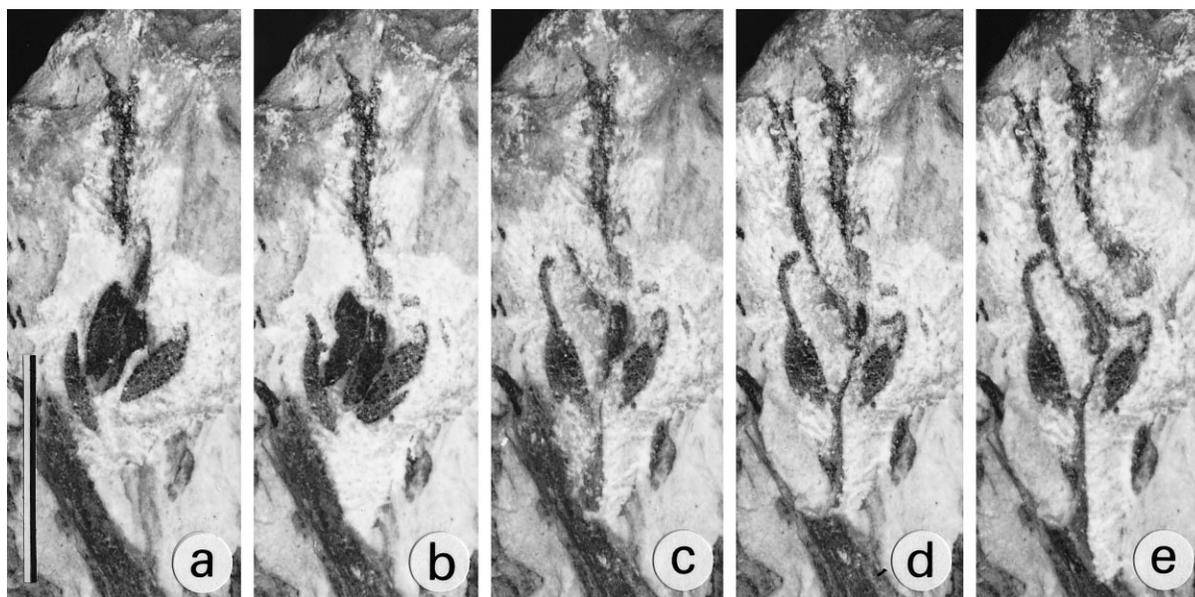


Fig. 8 Counterpart of *Hyenia elegans* illustrated by Kraüsel and Weyland (1926, pl. 9, figs. 8, 9), GIK1690. *a–e*, Successive stages in the dégageage of single fertile appendage (see fig. 9) indicated by white arrow in fig. 3*a*. Scale bar = 5 mm.

above the other (figs. 12*e*, 15*d*). The connection between the fertile appendage and the axis was also uncovered, and in the process, a fragment of sporangium *b1* was observed (figs. 12*c*, 15*b*). On segment II, only two stalks and their sporangia (out of the three expected to be present, as on segment I) could be demonstrated. A reconstruction of this fertile appendage is given in figure 15*e*.

In conclusion, no evidence can be substantiated for the occurrence of a rhizome for specimen EH1 from Oé, as reconstructed by Leclercq (1940). The fertile appendages of *H. 'elegans'* and *H. complexa* from Oé have a different morphology from that illustrated by Leclercq (1940, 1961; our fig. 1*b*). They show a proximal bifurcation; the two resulting segments bear three recurved lateral stalks, which are three-dimensionally arranged. Each recurved stalk ends in a pair of elongate sporangia. The distal end of each segment is bifurcate. Appendages are not inserted in pairs. The fertile appendages therefore have a similar morphology to that of *C. primaevum* (Leclercq 1969) and *C. bicephalum* (Leclercq and Andrews 1960; Bonamo and Banks 1966).

Discussion

The Status of the Genus Hyenia Nathorst

The genus *Hyenia* Nathorst is based on material of the type species *Hyenia sphenophylloides* from western Norway. As illustrated by Nathorst, this material includes axes with pronounced longitudinal ribbing. No digitate branching is observed, although in two specimens (pl. 1, fig. 1, and pl. 2, fig. 1, from Nathorst 1914), the axes seem to radiate from a branching point or common point of attachment that is not preserved. Other axes emerge from the sides of a large axis (pl. 1, figs. 3, 4, from Nathorst 1914). In these examples, the

bases of the daughter axes are better preserved, thus showing their whole width (indicating that the ribbed examples are the remains of the xylem in badly preserved axes rather than the whole axis). These bases are enlarged and slightly decurrent on one side. Only one side of the larger axis is preserved, as the rock has fractured down the center of the major axis. Inserted upon the smaller axes at an acute angle are forked appendages (usually 10–15 mm long; maximum, 20 mm). These were believed to bifurcate once or perhaps twice. Nathorst claimed that these appendages were inserted in whorls in the lower parts of the axes with four to six appendages per whorl. Successive whorls were believed to be superposed. In the distal parts of the axis the verticillate pattern was stated to be less obvious, and no actual nodal line could be observed. Høeg (1931) reported new specimens in which verticils may have been present, but he was uncertain. Høeg (1935) later noticed, on new specimens from western Norway, that the lateral appendages branched two or three times. However, in these plants, the appendages were observed to be opposite toward the top, yet they gave the impression of being helically arranged lower down. In 1945 Høeg reported, on a specimen collected by Halle from the type locality, another main axis with lateral branches with swollen cushions at their bases. At present, fertile material is unknown, as are details of the branching patterns of lateral (second-order) axes.

Thus, the genus *Hyenia*, as typified by *H. sphenophylloides* from its type locality, gives no firm evidence of the branching patterns of this plant, nor does it give solid evidence of the fertile appendages or anatomy. Furthermore, those characters that can be listed (presence of lateral branches and bifurcate appendages, possibly ribbed vascular system) are insufficient to distinguish the plant from other Middle Devonian plants attributable to such diverse groups as Cladoxylopsida, Pro-

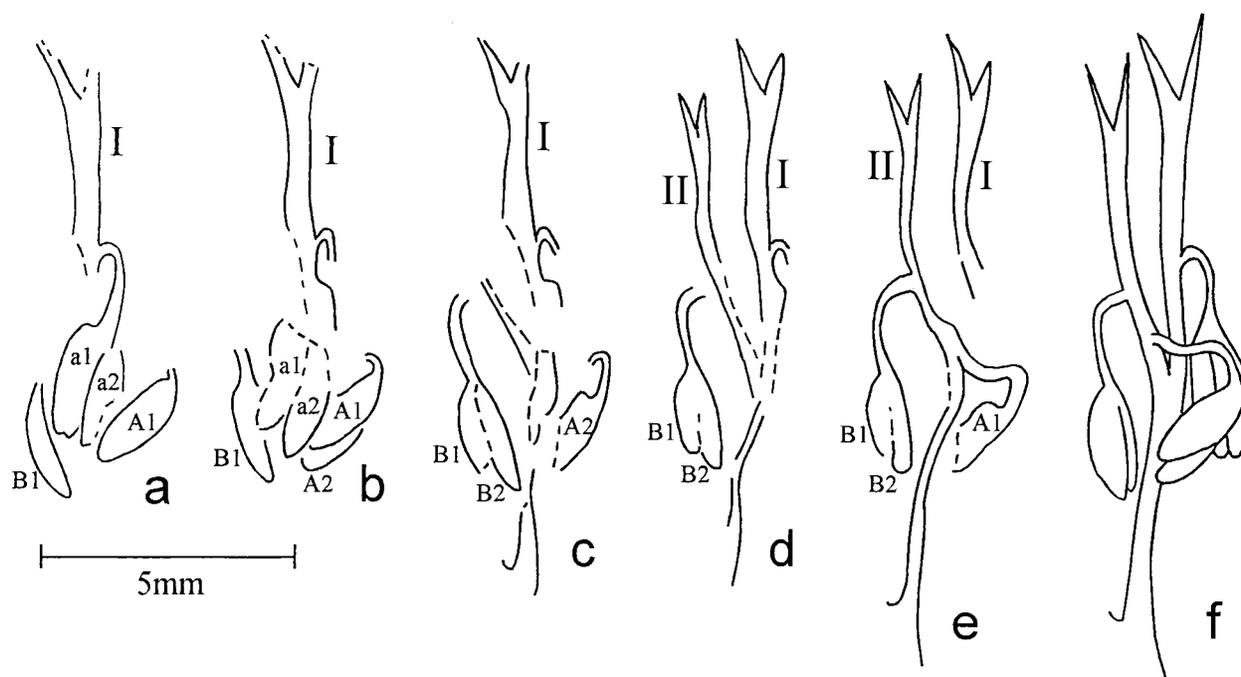


Fig. 9 Counterpart of *Hyenia elegans* illustrated by Kräusel and Weyland (1926, pl. 9, figs. 8, 9), GIK1690. a–e, Successive stages in the dégageage of single fertile appendage (see fig. 8). f, Composite reconstruction of fertile appendage.

gymnospermopsida, Iridopteridales, or Trimerophytopsida. The presence of vertically superposed whorls of lateral appendages is more typical of iridopteridalean than cladoxylipsoid plants (Stein 1982; Berry and Edwards 1996), although this character is not accepted in all accounts of *H. sphenophylloides*. Other plants attributed to *Hyenia* (under the name *H. vogtii*) by Høeg (1942) can be more strongly argued to be iridopteridalean on the basis of whorled appendages and branch insertion. The actual high-level taxonomic assignment of *H. sphenophylloides* is therefore presently in doubt.

The generic name *Hyenia* Nathorst is not presently suitable for plants in which branching patterns, fertile units, anatomy, and higher rank botanical classification are relatively well constrained. However, if *H. sphenophylloides* was at some later date shown to have complex fertile appendages similar to those we currently regard as typical of *Calamophyton*, then *Hyenia* would have priority over *Calamophyton*.

The Identity of *Hyenia elegans* and *Calamophyton primaevum* of Kräusel and Weyland 1926

Hyenia elegans was first described by Kräusel and Weyland (1926, pp. 133–136). They gave a generic diagnosis recognizing digitate branching, leaves arranged in whorls (but without marked nodes), and sporangia on lateral organs arranged in spikes. For the specific diagnosis, the leaves were thought to be mostly once-divided, but several divisions were possible, and the fertile organs were composed of elongate sporangia that were borne recurved on bifurcate lateral appendages, with two or three to each tip (fig. 1a).

Calamophyton primaevum Kräusel and Weyland was first briefly described in Weyland (1925) and was only later de-

scribed in detail (Kräusel and Weyland 1926, pp. 137–142). The genus *Calamophyton* was defined to have regular nodes, with an ornamentation of small elongate scars on the internodes, axes with a woody triangular vascular bundle surrounded by pith, whorled leaves, and sporangia that were borne on forked lateral organs organized into fertile regions. Thus, the occurrence of nodes (i.e., marked nodal lines traversing the stem) was considered an important feature for distinguishing *Calamophyton* from *Hyenia*. The species *C. primaevum* was further diagnosed as having abundantly bifurcated axes with *Knorria*-like protuberances and a cortex with numerous transversely elongated pores (i.e., the typical cladoxylipsoid speckled pattern of sclerenchyma nests). The nodes were sometimes displaced. The vascular bundle produced longitudinal ribbing on stem compressions and was made up of a triangular xylem consisting of tracheids with scalariform and round pits that were rarely bordered. Secondary growth was thought to be present. The leaves were said to be straight and bifurcated one to many times, with elongate-ovoid sporangia on bifurcate lateral appendages arranged in spikes. The illustration of Kräusel and Weyland (1926, fig. 27; see fig. 1d) indicates single sporangia.

The differences between *H. elegans* and *C. primaevum* were therefore very small. These small differences can now be attributed to the vagaries of preservation and to lack of adequate preparation. Both descriptions might match unprepared material of either *Hyenia* or *Calamophyton*.

In 1929, Kräusel and Weyland further modified their specific diagnosis of *H. elegans* to note that the axes were many times bifurcate, and the final branches were oriented in parallel. They later modified their generic diagnosis (Kräusel and Weyland

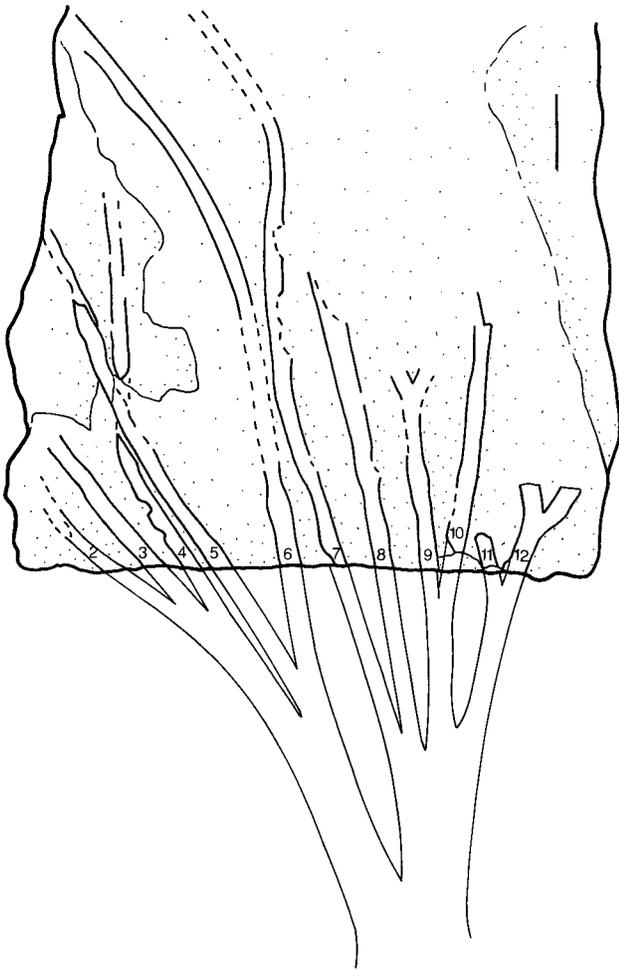


Fig. 10 *Hyenia* 'complexa' of Leclercq, specimen ULg EH1/1459. Hypothetical reconstruction of the branching system of the axes (see fig. 2a); the axes appear organized into two groups; the ramification is digitate.

1932) with the implication that the axes of *Hyenia* grew from a horizontal rhizome, although this determination was not based on evidence from the type locality of *H. elegans*.

We are not surprised, therefore, that preparation of a counterpart to type material of *H. elegans* (above) revealed a more complex fertile appendage than was originally described, the new morphology being identical to that which has, over the years, come to be recognized as typical of *Calamophyton* (e.g., *Calamophyton bicephalum*; fig. 1e). The fertile appendage is very unlike the once-bifurcate sporangiophore originally suggested for *H. elegans* by Kräusel and Weyland (1926, 1929), based on type collections and maintained by Schweitzer (1972; based on material from Lindlar [fig. 1c] that has not been examined in this study). All apparent differences between *Hyenia* and *Calamophyton* in the Kirberg material can be attributed to preservational accident (e.g., the "nodal lines" observed on *C. primaevum*) and to the differing states of preservation and exposure of lateral appendages that were revealed because of fracturing of the rock surface, as well as to observational error.

In conclusion, Kräusel and Weyland's 1926 and subsequent accounts of *H. elegans* and *C. primaevum* (for Kirberg) are believed to refer to one and the same species.

The Identity of Cladoxylon scoparium Kräusel et Weyland 1926

Kräusel and Weyland (1926) described a single hand specimen (considered here as the type specimen) under the name *Cladoxylon scoparium* sp. nov. from the same locality as *H. elegans* and *C. primaevum*, which were described in the same paper. Several axes, up to 22 cm long, were arranged in superposed layers. Because they all appeared to converge toward a common base, Kräusel and Weyland deduced that all these axes were part of the same plant, reconstructing it with digitate branching. With drawings, they illustrated two kinds of appendages. Sterile appendages ("leaves") were forked several times but were shown as widened and more flattened than those of *Hyenia* or *Calamophyton*. They further figured a small specimen collected earlier by Piedboeuf at Oben zum Holz; the vegetative appendages along the short axis fragments were thought to show the same morphology as those of the specimen from Kirberg, but on the photographic illustration (Kräusel and Weyland 1926, pl. 13, fig. 2), they are not clearly discernible. The fertile appendages, present only on the type specimen from Kirberg, were fan shaped and deeply dissected and were thought to have sporangia placed distally in depressions at the tips of the lobes. These organs were not well represented by their photographic illustration (Kräusel and Weyland 1926, pl. 12, fig. 5; pl. 13, figs. 1, 2). Parts of the axes were locally permineralized, and the authors were able to demonstrate the occurrence of a dissected vascular system with radially oriented xylem plates, which they considered similar enough to the Lower Carboniferous *Cladoxylon mirabile* to include the specimen in the genus *Cladoxylon* Unger. The type specimen of *C. scoparium* from Kirberg and the second specimen from Oben zum Holz were destroyed during World War II, and because no other specimens of *C. scoparium* were ever identified from any other localities, the results of Kräusel and Weyland's study went unchallenged for 54 yr, and their reconstruction continues to be reproduced in many botany and paleobotany textbooks. Schweitzer and Giesen (1980), however, were able to locate a small part of the counterpart of the type specimen of *C. scoparium*. Although there are some small differences between the part and counterpart (see figs. 12, 15, in Schweitzer and Giesen 1980), these can be explained as the result of chips of sediment that shifted away from the originally exposed surface at the top and bottom of the counterpart, and there seems to be every reason to agree with Schweitzer and Giesen's identification of the specimen. By preparing some of the appendages (visible at the lower-right-hand corner of their fig. 14c, p. 17, as well as on the original specimen) along the margin of the axes, Schweitzer and Giesen demonstrated them to be fertile and actually similar to those of *Calamophyton*. Although incomplete, the principal structural elements (bifurcate axis, paired sporangia borne laterally after the fork on recurved stalks) of the *Calamophyton* appendages, as described originally by Leclercq and Andrews (1960), were present. Schweitzer and Giesen (1980) further demonstrated that the flattened sterile "leaves" and fanlike fertile appendages sug-

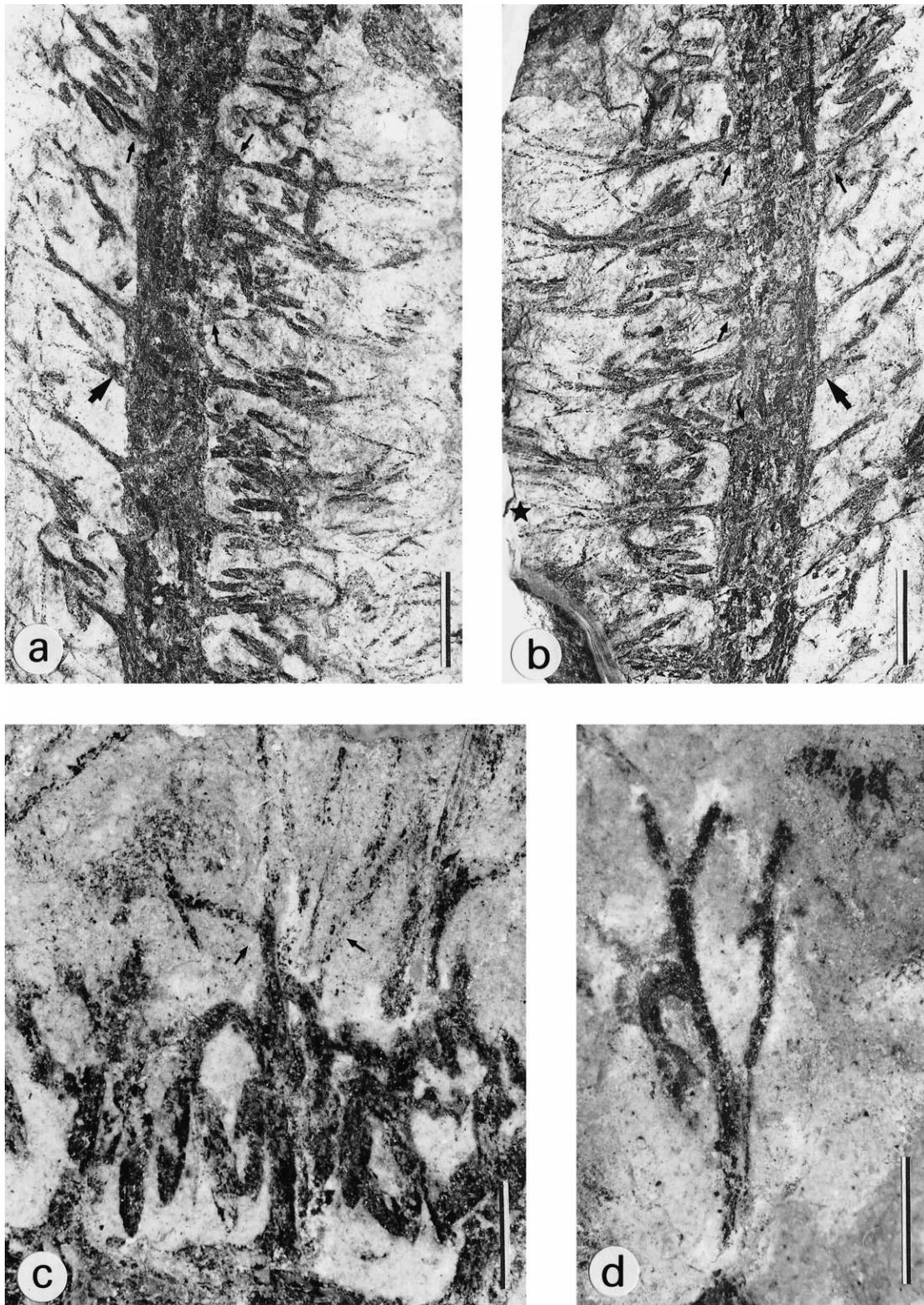


Fig. 11 *Hyenia 'complexa'* of Leclercq (1940, 1961), specimen ULg EH1/1459 and counterpart ULg EH1/1459. *a, b*, Details of upper region of axis 6, part and counterpart. Note the variability of the angle of insertion and the local entanglement of the appendages; several of these appear disposed in pairs (arrows). Bouquets of distal filiform extensions are obvious along one margin of the axis only. A star indicates the lateral fertile unit detailed in *c*. *c*, Detail of one fertile appendage (specimen ULg EH1/1459) drawn by Leclercq (1940, text-fig. 4), showing the grouped distal filiform extensions that are disposed in slightly different levels in the sediment. *d*, Incomplete fertile appendage distally uncovered on axis 10 (specimen ULg EH1/1459). Scale bars: *a, b* = 30 mm; *c, d* = 2 mm.

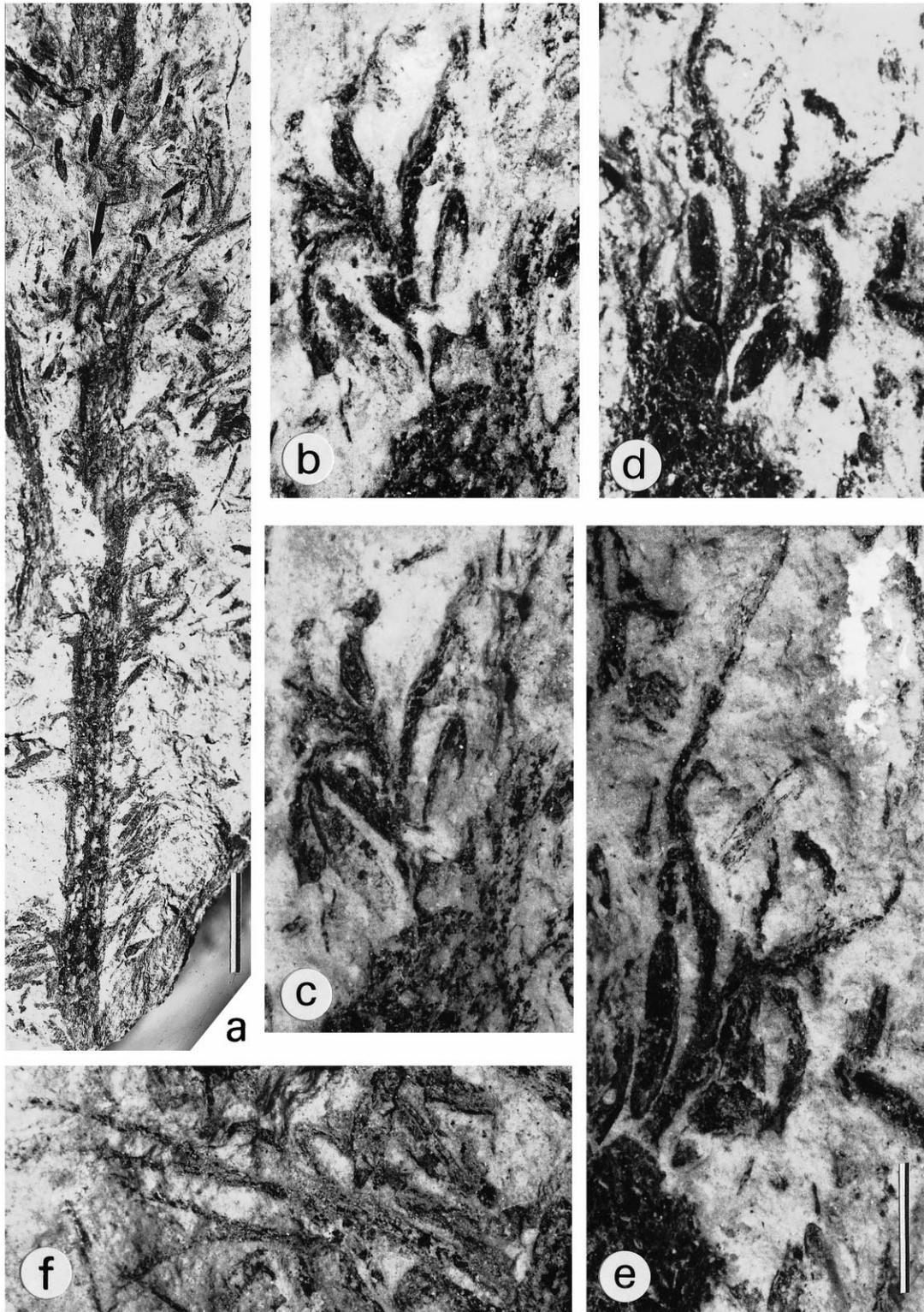


Fig. 12 *a-e*, Specimen of *Hyenia elegans* illustrated by Leclercq (1940, pl. 3, fig. 18), ULg EH55/1467. *a*, General view of the fertile axis (part). An arrow points to the fertile appendage attached to the backside of the axis and is partially exposed by the splitting of the block. *b, c*, Successive stages of dégage of the fertile appendage on the part. *d, e*, On the counterpart. *f*, Detail of specimen of *Hyenia elegans*' *complexa*' ULg EH1/1459 (illustrated by Leclercq 1940, pl. 1, fig. 3), showing forked distal segments of fertile appendages on top of axis 6. Scale bars: *a* = 10 mm; *b-f* = 2 mm.

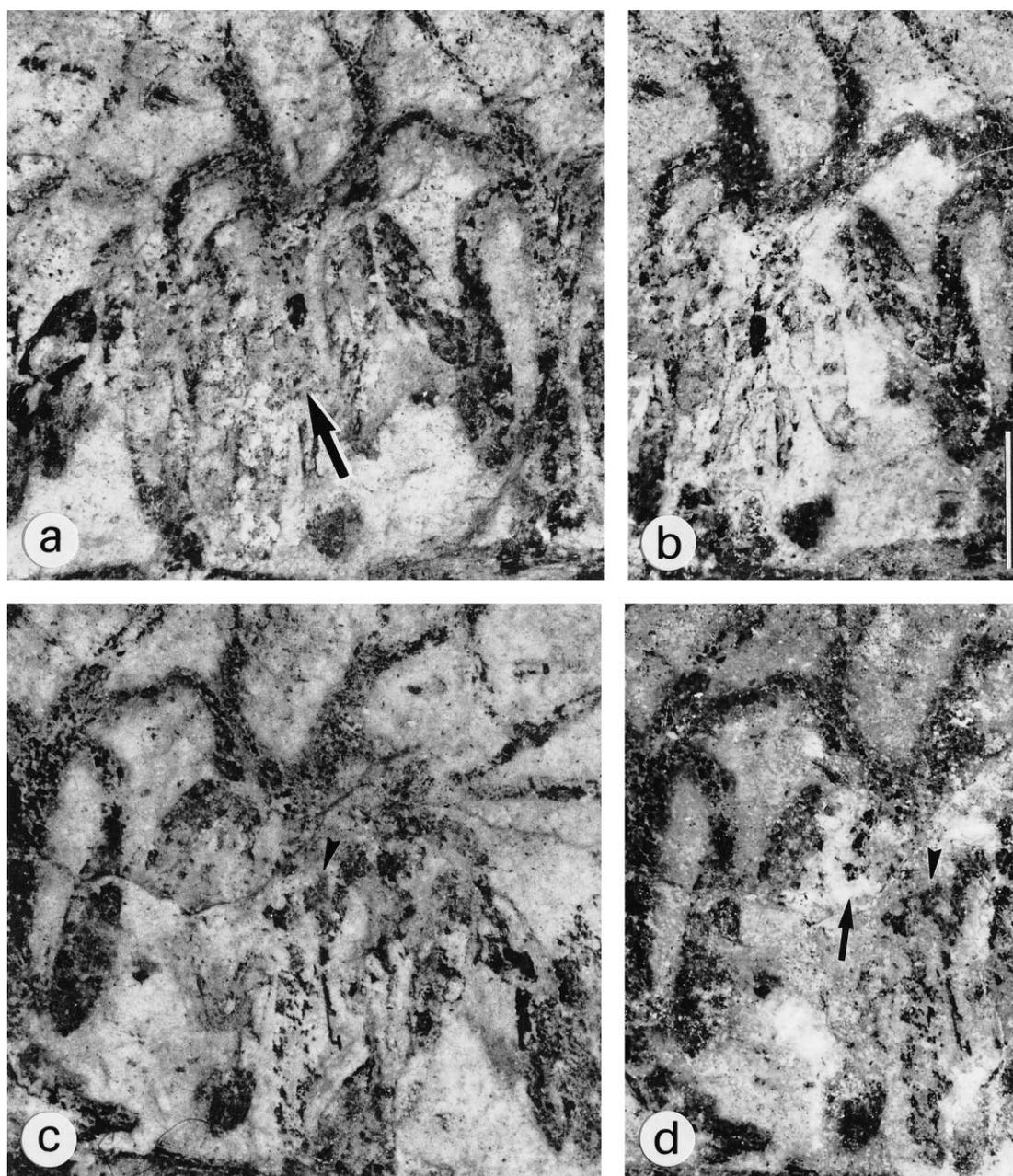


Fig. 13 *Hyenia 'complexa'* of Leclercq, specimen ULg EH1/1/1459. Details of successive stages of dégagement (*a, b*) on the part and (*c, d*) on the counterpart of one fertile appendage along axis 6 (arrowhead 2 on fig. 2*a*); a pair of sporangia attached to the adjoining fertile appendage has displaced segment II (compare with fig. 14). *a*, The arrowhead points to an isolated fragment of segment II; it is located at an upper level, above an elongate shining sporangium (C1 on fig. 14). *b*, The attachment of the appendage to the main axis is demonstrated; a second pair of sporangia attached to the adjoining appendage is shown. *c*, On the counterpart, attachment (arrowhead) of the pair of sporangia (C1 and C2 on fig. 14) to segment II is shown. *d*, Occurrence of a second stalk (arrow) on segment II is demonstrated; as on *c*, the arrowhead points to the attachment of sporangia C1 and C2. Scale bar = 2 mm.

gested for *C. scoparium* by Kräusel and Weyland (1926) were in fact the result of superposition and compression of the normal, several times-bifurcated sterile appendages of *Calamophyton*. When considering together the external appearance of the axes, the morphology of the vegetative and fertile ap-

pendages and their mode of preservation, and the characteristics (as far as they were known) of the vascular system, Schweitzer and Giesen considered *C. scoparium* to be a later synonym of *C. primaevum* Kräusel et Weyland (in Weyland 1925). The hypothesis that *C. scoparium* and *C. primaevum*

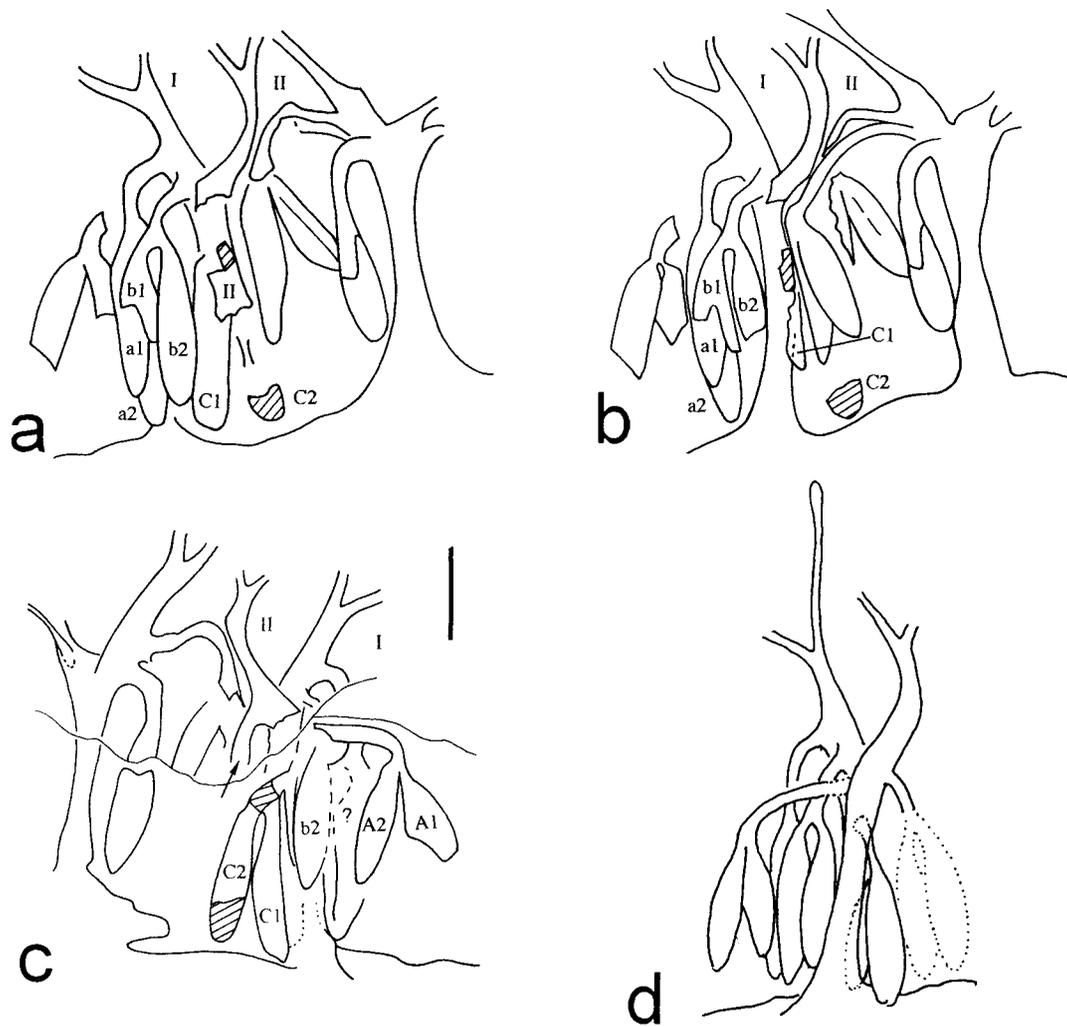


Fig. 14 *Hyenia 'complexa'* of Leclercq, specimen ULg EH1/1/1459. Drawings corresponding to the successive stages of dégagement shown in fig. 13. *a, b*, On the part; cf. fig. 13*a, 13b*. *c*, On the counterpart; cf. fig. 13*d*. *d*, Proposed reconstruction of the fertile appendage combining the data obtained from dégagement of the part and counterpart. Scale bar = 2 mm.

from Kirberg represent the same plant has not been universally accepted (e.g., Gensel and Andrews 1984; Stein and Hueber 1989), but having considered the evidence to the best of our knowledge, we believe this hypothesis to be true.

In conclusion, the plants referred to by Kräusel and Weyland (1926) as *C. primaevum*, *H. elegans*, and *C. scoparium* from Kirberg are one and the same species.

The Identity of Hyenia complexa of Leclercq 1961

Hyenia 'complexa', the new species briefly described by Leclercq (1961; based on specimens she first illustrated in 1939 and 1940 as *H. elegans*), was never published in a valid manner. This new specific name was tentatively proposed in an abstract in order to recognize the peculiarities of the fertile appendages on the Oê specimen, which appeared to be very different from the German *Hyenia*, as described by Kräusel and Weyland.

In *Hyenia 'complexa'*, the fertile appendages (sporangio-

phores) were reported to arise in pairs. Actually, such apparent pairs are the result of close insertion of appendages along the margin of the axis compression, laterally or slightly in front of or behind it. The sporangiophores were described (Leclercq 1940, 1961) as being apparently trisected, with two pendulous sporangia at the end of each segment or stalk. Each recurved fertile stalk was thought to bear distal filiform appendages that were inserted at the level of the curvature (fig. 1*b*). We have shown that the fertile units are in fact organized as in *Calamophyton*, with a first proximal bifurcation occurring before the midlength; each of the two daughter segments supports three short recurved lateral stalks that end in a pair of elongate sporangia and terminates in a single terminal fork, thereby resulting in two slender segments (fig. 14).

Vegetative appendages are not observed along the fertile axes of the Belgian specimens. On specimen EH1, Leclercq (1940) described only a short isolated fragment of vegetative axis that is not oriented in the same direction as the other fertile axes.

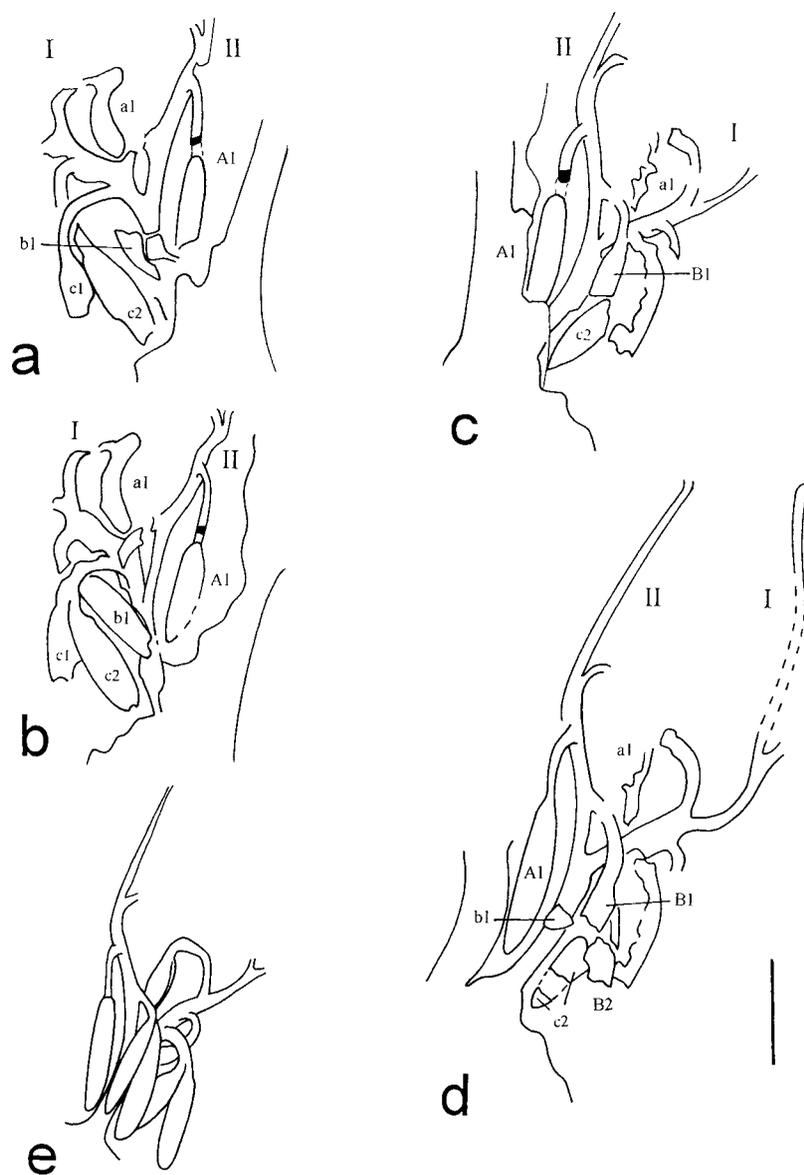


Fig. 15 Drawing corresponding to the stages of dégagement illustrated in fig. 12b–12e. *a, b*, On the part. *c, d*, On the counterpart. *e*, Proposed reconstruction of the fertile appendage illustrated in fig. 12b–12e and fig. 15a–d. Scale bar = 2 mm (*a–d*).

On this detached fragment, transverse lines (sometimes regarded as being typical of *Calamophyton*) are obvious on the axis compression (Leclercq 1940, pl. 1, fig. 3, along axis 7). The vegetative appendages are difficult to observe in detail; apparently two of them—showing up to three levels of bifurcation—are entangled (cf. Leclercq 1940, fig. 6, p. 15). On specimen EH26, a narrow axis determined to be *Hyenia* sp. by Leclercq, the vegetative appendages also display three successive bifurcations (observable on pl. 1, fig. 4, from Leclercq 1940), branching three dimensionally in a manner similar to the vegetative appendages of *Calamophyton*. Their supposed whorled insertion appears, as already stated by Leclercq, to be “confused.” Their length of 10–13 mm is similar to the dimension of the vegetative appendages of *Calamophyton* (up to 15 mm long for the vegetative appendage of *C. bicephalum*

from New York in Bonamo and Banks 1966; up to 16 mm long for those of *C. primaevum* from Lindlar in Schweitzer 1973).

Leclercq, who inferred the presence of a rhizome on specimen EH1 from Oé in 1940, did not reconsider its occurrence in 1961. As a rhizomatous axis was then considered typical of *Hyenia*, this specimen was attributed to that genus, despite some similarities between this fertile appendages and those of *C. bicephalum* Leclercq et Andrews (1960) from Goé. We were unable to demonstrate the occurrence of a prostrate rhizome at the base of the branches preserved on the Oé specimen. The matrix is full of other variously oriented plant fragments, and connection between the fragment of plant axis inferred to be a portion of rhizome by Leclercq (1940) and the subparallel fertile axes could not be demonstrated. Our alternative hy-

pothesis (fig. 10) is that these subparallel axes correspond to the distal part of a ramifying branch system, as is well known for *Calamophyton*.

In conclusion, the lateral appendages, vegetative and fertile, of the plant from Oé, referred to as *H. 'complexa,'* and *Hyenia* sp. share the same morphological characteristics as those attributed to *Calamophyton*. Occurrence of a rhizome, on which strong emphasis was formerly placed, could not be demonstrated. In reality, no real difference can be demonstrated between the Belgian specimens of '*Hyenia*' and *Calamophyton*; they belong to the same genus.

Anatomy

The anatomy of *Calamophyton* was first described by Kräusel and Weyland under the name *C. primaevum* (1926, fig. 28) and *C. scoparium* (1926, figs. 39–44). This revealed a stele made up of a number of radiating plates, some of which were joined together to form U, W, or more complex configurations. Tracheids were pitted. Kräusel and Weyland later (1929, their fig. 16) illustrated the ends of the xylem arms, showing protoxylem strands near the extremities of the plates.

Leclercq and Schweitzer (1965) demonstrated the dissected stele of *Calamophyton* from both Belgium and Germany and therefore removed *Calamophyton* from Sphenopsida. Mustafa (1978) examined transverse sections of the permineralized anatomy of *C. primaevum* from the Brandenburg beds of Germany. Nests of sclereids in the cortex were found to be responsible for the patterns on the stem surface. Mustafa described the steles as having 36 or more ribs joined together inwardly and interpreted them to form three or more groups surrounding a pith. Vascular traces to the lateral units were emitted singly. This observation contrasts sharply with the multiple vascular traces per lateral unit produced from adjacent peripheral protoxylem strands in all other members of the Cladoxylopsida in which trace departure is known. In *Pseudosporochnus*, one, two, or three trace groups supply a single lateral branching system/appendage (Stein and Hueber 1989), which is, however, more profusely branched than that seen in *Calamophyton*, which often consists of a central axis with a number of suboppositely arranged bifurcating ultimate branching units (Berry and Fairon-Demaret 1997).

Habit

As a matter of dogma, the main difference between *Hyenia* and *Calamophyton*—at the generic level—was considered to be the habit of the plants, this being a creeping rhizome with erect aerial axes in the case of *Hyenia* and an upright trunk bearing lateral digitate branches in the case of *Calamophyton*.

Hyenia was first illustrated with a main axis in a recumbent position by Nathorst (1914) in his illustrations of *H. sphenophylloides* (pl. 1, figs. 3, 4). Kräusel and Weyland (1932) studied Nathorst's material in Bergen and Stockholm and were convinced that a rhizome was present. However, they produced no substantial evidence to carry their argument. Høeg's (1945) reconstruction also showed unbranched axes arising from a rhizome.

Kräusel and Weyland (1932) described two specimens of *H. elegans* from Germany and claimed to demonstrate some sort of growth of aerial axes from a rhizome. However, in our

opinion, the first specimen, from Gräfrath (fig. 1), can be reinterpreted as normal "*Calamophyton*-style" digitate branching rather than as branches arising from a rhizome. The second specimen, from Böhlerhof (figs. 2, 3), shows a broad axis from which nearly perpendicular "aerial shoots" arise. In this example (as in those of Nathorst and Høeg), only one-half of the width of the basal "hizome" is preserved, and so the true arrangement of laterals is not known. This specimen is now lost. Basally, and usually asymmetrically, all supposed "aerial axes" showed evidence of thickening. In contrast to the above authors, we consider this and other similar specimens to be one-half of a vertical trunk with attached lateral branches (each with proximally thickened supporting bases).

Leclercq (1940) reconstructed her *H. elegans*, later *H. 'complexa,'* from Belgium, with axes arising from a horizontal rhizome. In the main specimen, as shown earlier, there is no real evidence of the existence of a rhizome. We presume the subparallel axes of this specimen have arisen from a *Calamophyton*-style digitate branch, the branching point of which is not preserved (fig. 10).

Leclercq (1940, p. 17) produced another specimen (EH16) from Oé, which she designated "isolated rhizome (cf. Hyeniaceae)," which appeared to show an axis similar to that of *Hyenia* lying to the side of a thicker axis (Leclercq's fig. 8). In this specimen there is no evidence that the smaller axis is *Hyenia* nor is there evidence that her interpretation of the growth position is correct.

The last major study of the habit of *H. elegans* was conducted by Schweitzer (1972) and was based on material from Lindlar in Germany. His reconstruction again involved a horizontal rhizome, but in this case, the aerial axes are digitately branched. However, most of the illustrations of the supposed rhizome (figs. 1, 2a, 3, 5; pl. 30, figs. 1, 2; pl. 33, figs. 1, 2a) again show only one-half of the width of the axis, thereby giving the impression that branching occurred on only one side. Those illustrations that are more complete (pl. 32, fig. 1; pl. 31) show "rhizomes," from which the "aerial" axes appear to emerge on all sides. Schweitzer believed that these aerial axes would all bend around the "rhizome" to point upward, as in some modern ferns. Many of these specimens lack diagnostic features that would allow one to attribute them uniquely to *Hyenia*, and *Calamophyton* is also found at this locality (Schweitzer 1973).

Schweitzer described fertile organs for *Hyenia* that were only 6-mm long and that were once bifurcate, each recurved segment bearing two elliptical sporangia. Detailed observation of the illustrations (pl. 38) shows the poor quality of preservation associated with the coarse-grained sandstone that is typical of this locality. Abrupt constrictions in the width of the axes in these organs, perhaps representing branching points, indicate a more complex morphology than that which has been described. We are accustomed to seeing a similar appearance for fertile material of *Calamophyton*, even in more finely grained matrices, in which the fine extensions (sporangio-phores) of the fertile organs can only be seen because of faithful and exquisite preservation and with considerable amounts of time-consuming technical work. For example, specimen 173 of *C. primaevum* from Köln, as illustrated by Leclercq (1969), is preserved on fracture surfaces in a fine-grained dark matrix (Leclercq's figs. 1–5) and demonstrates that virtually no bifurcate spo-

rangiophores with laterally attached sporangia are visible; rather, the appearance is of many densely arranged, once-bifurcate lateral appendages that bear recurved pairs of elongate sporangia. Leclercq was, however, able to demonstrate their complex morphology by careful dégagement.

Calamophyton lacked a whole-plant reconstruction until the one proposed by Schweitzer (1973); previous attempts illustrated only the branch system (sometimes mistaken as a “whole plant”). Schweitzer’s reconstruction was based on a number of apparent trunks, some of which showed tufts of “roots” at the base and three-dimensionally arranged lateral branches inserted at an acute angle. None of these specimens has been observed to bear appendages typical of *Calamophyton*, either sterile or fertile. None of the trunks bear branches that exhibit digitate ramification, although some of the specimens illustrated as *H. elegans* (Schweitzer 1973) do. Nevertheless, we believe Schweitzer’s reconstruction may be a good model for a whole-plant reconstruction of *Calamophyton*. However, we would modify it to take into account the fact that in all possible “trunk” material of *Calamophyton*, the branches appear to be inserted in a more dense arrangement than is depicted in his drawing. Such a reconstruction would look similar to the very well-preserved remains of a small whole-plant specimen of *Lorophyton* described by Fairon-Demaret and Li (1993). We also believe that such a reconstruction holds true for *Pseudosporochnus* as well (C. M. Berry and M. Fairon-Demaret, unpublished data).

We also can propose a pattern of growth for these Devonian cladoxylopsids. In the juvenile stage, they may have grown as a narrow vertical trunk with a tuft of rootlets at the base and densely arranged acutely inserted branches that were crowded at the crown (as in the juvenile specimen of *Lorophyton*). The lateral branches in the juvenile would likely be undivided, or sometimes forked, yet they would be likely to bear typical appendages upon them. This state of growth might account for the many reports of large axes (or “rhizomes”) bearing smaller undivided lateral axes. An intermediate stage of growth might be that in which the trunk has grown larger and the new branches are bifurcated and divided digitately (as in, e.g., *H. elegans* of Schweitzer 1972, pl. 31). The fully developed plant might eventually reach a height of ca. 2–4 m and bear the sturdy digitate branches we are familiar with under the name of *Calamophyton*.

Other Species of Hyenia Nathorst

Below we briefly survey the identity and possible reinterpretation of the species of *Hyenia* that we have considered in our study. Other mentions of *Hyenia* sp. in the literature have not been illustrated (e.g., Corsin 1933) and/or they refer to fragmentary vegetative specimens (e.g., Stockmans 1968). They do not help one to understand the genus, because they do not show any characters that allow for a distinction between badly preserved *Calamophyton* remains.

***Hyenia sphenophylloides* Nathorst 1914.** As discussed earlier, the type species of *Hyenia* does not demonstrate sufficient characters (beyond those common to many contemporaneous plants belonging to a number of major taxonomic groups) to allow other well-preserved plants to be added to the genus *Hyenia* with any degree of certainty.

***Hyenia rhizoides* Nathorst 1914.** Nathorst himself doubted that these remains belonged with *Hyenia*, and we have uncovered no additional information.

***Hyenia banksii* Arnold 1941.** A single specimen bearing both appendages and a number of lateral branches is known (Arnold 1941). The bifurcate appendages are described as being inserted in whorls, and at least two of the lateral branches are attached at the same level. It is our opinion that this plant is more likely related to Iridopteridales.

***Hyenia (Hyeniopsis) vogtii* Høeg 1942.** This plant with predominantly whorled bifurcate appendages (but which occasionally displays branches inserted at whorls instead of appendages) also bears hairs or enations and is therefore considered to be different from *H. sphenophylloides* and *H. elegans*; Høeg thus erected a new subgenus to accommodate it. It is most likely a member of Iridopteridales (Berry et al. 1997).

***(Hyeniopsis) ramosa* Høeg 1945.** This plant, with similarities to *H. vogtii*, lacked spines and had undivided “leaves.” Its affinities are unclear.

***Hyenia khalfinii* Ananiev et Stepanov 1969.** A single specimen from West Siberia in Ananiev and Stepanov (1969) shows a sporangiophore that appears to be forked only once near the tip, but each segment bears two single sporangia on short recurved stalks. This is immediately reminiscent of unprepared *Calamophyton*. However, the locality is reportedly Early Devonian (Rzhonsnitskaya 1998).

***Hyenia pauxilla* Zalesky 1937/Chirkova-Zaleskaya 1957.** The single specimen collected by Zalesky (1937) is a small fragment (<2 cm long) of a vegetative axis that is 0.5–1 mm wide. It came from a locality dated from the early Upper Devonian on the basis of the few plant remains. From Zalesky’s illustrations, short divided narrow leaves appear to be inserted in verticils on slightly enlarged nodes; the very short internodes are ribbed. This specimen seems different from all ‘*Hyenia*’ illustrated in the literature and is rather reminiscent of *Sphenophyllum subtenerimum* Nathorst, which occurs in mid- to upper-Famennian beds. Chirkova-Zaleskaya mentioned a second specimen collected from a locality with numerous remains of *Archaeopteris fimbriata* Nathorst. In her illustration (Chirkova-Zaleskaya (1957), pl. 29, fig. 143), *H. pauxilla* is indiscernible.

***Hyenia argentina* Frenguelli 1954.** The Argentinian specimens do not show divided vegetative appendages. Fertile appendages are not recorded (Frenguelli 1954). According to Bonamo and Banks (1966, p. 789), “the branching of its axes would put it closer to Høeg’s *Hyeniopsis*.” Obviously, new material is required to demonstrate that this plant belongs to the cladoxylolean complex.

Other specimens (of *Hyenia* sp.). Morel et al. (1993) has reported other specimens of *Hyenia* sp. from the La Punilla Range in Northern Cordillera, Argentina. These fossils, reportedly demonstrating a rhizome with attached “aerial shoots,” are more likely to represent upright monopodial trunks with branches, of which only some are visible. They show no diagnostic characters of *Calamophyton* or other cladoxylopsids.

Taxonomic Considerations: Validity of Names

Generic

Among the various specimens from Kirberg that we consider conspecific but which have previously been attributed to *Hyenia elegans*, *Calamophyton primaevum*, and *Cladoxylon scoparium* by Kräusel and Weyland (1926), we believe that there is strong evidence of digitate branching patterns (Kräusel and Weyland 1926) and fertile appendages (Schweitzer and Giesen 1980; this article). Pending restudy of Nathorst's type material of *Hyenia*, we believe that attribution of the well-studied European material (in which branching patterns and fertile appendages have been comprehensively described) to *Hyenia* is undesirable. The name *Cladoxylon* is also inappropriate, as there is no demonstration of significant similarity to the anatomically preserved Carboniferous type species of *Cladoxylon*, neither anatomically (Bertrand 1935) nor morphologically. Hence, we prefer the generic name *Calamophyton* Kräusel et Weyland (in Weyland 1925) for the material described as *H. elegans*, *C. primaevum*, and *C. scoparium* by Kräusel and Weyland (1926). Demonstration of branching and, most importantly, fertile appendages in Norwegian material of *Hyenia sphenophylloides* would be needed to persuade us that *Hyenia* is the correct name for European and North American material previously assigned to *H. elegans*, *Hyenia 'complexa'*, *C. primaevum*, and *C. bicephalum*. Should restudy of Nathorst's type material show that *H. sphenophylloides* has substantially the same characters as the rest of these taxa, then the correct name for them all would be *Hyenia*. Until then, however, we recommend assignment of these taxa to *Calamophyton*.

Specific

By priority, 'primaevum' is the first validly published name given to the *C. primaevum*/*H. elegans*/*C. scoparium* plant. The earliest described material was collected from the Honseler Schichten near Elberfeld. Although *C. primaevum* is the second of the three named species to appear in the 1926 monograph of Kräusel and Weyland, this name was published as *C. primaevum* Kräusel et Weyland for the first time by Weyland (1925), who produced a short description and drawings of a characteristic vegetative specimen, digitately branched. Accordingly, the correct citation should read *C. primaevum* Kräusel et Weyland in Weyland (1925).

Proposal of a Lectotype

Kräusel and Weyland (1926) did not designate any particular specimens as holotypes for the three new species they described. All the original material has since been thought to be lost. Accordingly, Mustafa (1978), while emending the diagnosis of *C. primaevum*, designated all the 1926 illustrations of *C. primaevum* as syntypes.

Two specimens are now known to exist from the original collection of Kräusel and Weyland (1926) from the type locality. One is the counterpart of one of the illustrated type specimens of *H. elegans*, as described in this work. The second is the counterpart of the type specimen of *C. scoparium*, as

described by Schweitzer and Giesen (1980). Both are fertile. The evidence compiled above demonstrates that they both are to be referred to as *C. primaevum*. One of these two specimens should be selected as the lectotype of *C. primaevum*.

We propose specimen GIK1690 (Institute of Geology of the University of Köln, Germany), collected by Weyland from the Middle Devonian Honseler Schichten of Kirberg, which is restudied in this article, as the lectotype for *C. primaevum*. It is officially registered and can be easily located. It is better preserved than the second specimen restudied by Schweitzer and Giesen (1980), which could be used as an epitype once it is properly located and registered.

Synonymy

Leclercq (1969) noted that her German specimens of *C. primaevum* (from Kortzert near Elberfeld) had fertile appendages that were 5–6 mm in total length, whereas those of *C. bicephalum* from Belgium had fertile appendages that were 8–10 mm in length. She also noted, however, the small diameter of the axes of the German specimens. She thought that size was not a good basis for specific distinction. We agree with her suggestion that these plants are, as can best be determined, conspecific. The fertile appendages of *C. primaevum* from the type locality are of the same dimensions as those described as *C. bicephalum* (from Goé) by Leclercq and Andrews (1960), perhaps the only difference being the seemingly acute tips of the dichotomous fertile units in the German specimens. The dimensions of the fertile appendages of the specimens from Oé are not significantly different. The distal segments resulting from the ultimate bifurcation vary from 1 to 2 mm in length. They usually appear more slender than on *C. bicephalum* from Goé, but they have a similar range of lengths, as do those of *C. primaevum* from Lindlar. Therefore, it would seem appropriate to place all these various German and Belgian specimens in the same species. To these can also be added the specimens of *C. bicephalum* described by Bonamo and Banks (1966).

We concur with the emended generic diagnosis for *Calamophyton* as proposed by Leclercq (1969). However, we intend to present the detailed results of our work on specimens previously determined in a future paper to be *Calamophyton*.

Conclusions

Kräusel and Weyland's observations (1926, 1929) on the type material of their *Hyenia elegans* were incomplete. They failed to recognize the complexity of organization of the fertile organs. They also failed to recognize the same characters in material that they assigned to *Cladoxylon scoparium* and *Calamophyton primaevum* from the same locality at Kirberg. The evidence compiled above shows that their three taxa refer to the same species of plant, *C. primaevum* Kräusel and Weyland. Material from Belgium, referred to as *Hyenia elegans* and later as *Hyenia 'complexa'* by Leclercq (1940, 1961), also belongs to *Calamophyton*. The genus *Hyenia* is presently only represented with certainty by the type species *Hyenia sphenophylloides* Nathorst 1914, which deserves recollection and restudy. Only with the discovery of the fertile organs of *H. sphenophylloides* and with better understanding of its branching patterns will the question of the synonymy of *Hyenia* and *Cal-*

amophyton, and the potential priority of *Hyenia* over *Calamophyton*, be resolved.

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