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A new reconstruction of the iridopteridalean *Ibyka amphikoma* Skog et Banks from the Middle Devonian of Gilboa, New York State

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Ibyka from Gilboa

Plant fossil, Iridopteridales, Horsetails.

Abstract

- Premise of the Research

Clarifying the basic anatomy and morphology of Devonian fossils is essential for understanding the origin and radiation of land plants in deep time. Iridopteridales is a major Devonian plant group for which there is no presently established whole plant concept.

- Methodology

The type material of the iridopteridalean *Ibyka amphikoma* Skog et Banks was reprepared and redescribed to clarify the details of branching patterns, and enable comparison with the previously described anatomy.

- Pivotal Results

At least three orders of branching are known. Insertions of laterals is dominantly whorled, sometimes imperfectly, with distinct internodes. Within a whorl, branches may substitute for dichotomous appendages, with the latter more numerous. A new reconstruction is presented. Based on the partially preserved anatomy, and on the basis of comparison with anatomically preserved Iridopteridales, we infer that traces to the branches and appendages are emitted one from each arm of a multi-ribbed actinostele. This pattern contrasts with the only other iridopteridalen preserved both anatomically and morphologically, *Compsocradus laevigatus* Berry et Stein, in which traces are emitted from alternate ribs in each whorl, with angular offset between adjacent whorls.

- Conclusions

This basic understanding of the essentially whorled organisation in Iridopteridales, as well as the overall morphology and anatomy, will benefit attempts to infer the broader phylogeny of early land plants, including the origins of horsetails and ferns.

Introduction

Amongst the most reproduced reconstructions of Middle Devonian plants is that of *Ibyka amphikoma* Skog et Banks (1973), including a model until recently featured in the palaeontological displays at the Smithsonian Institution, Washington D.C., USA. Skog and Banks' reconstruction shows an upright main axis with branches and dichotomous laterals arranged on it in a lax helical arrangement. Several coalified compressions showing morphological features of three orders of branching were described. In addition, anatomically preserved sections of two paratype specimens, probably second order axes, were illustrated. A deeply ribbed protostele with peripherally arranged protoxylem was demonstrated. This specimen revealed in one area a pattern of trace departure suggesting to the authors a helical insertion of laterals, including branches and appendages. Skog and Banks erected a new order, Ibykales, to accomodate this plant.

Stein (1982a) included *Ibyka* in the order Iridopteridales, derived from the Iridopteridineae of Arnold, a group previously known only from anatomically preserved material. He asserted that the strongly ribbed primary xylem with trace departure from peripheral mesarch protoxylem strands were the only unique features suitable for distinguishing this group among higher taxa of Devonian plants. However, in contrast to what was described from *Ibyka*, other members of Iridopteridales emit traces to branches and appendages in a whorled rather than helical pattern.

Discussions of the significance of *Ibyka* have always involved a second group, Cladoxylopsida Pichi Sermolli (1959). These plants were first recognised on the basis of the highly dissected steles of the Early Carboniferous genus *Cladoxylon* (Unger 1856). Later discoveries have proved the existence of similarly ribbed and dissected primary xylem in Devonian genera such as *Calamophyton* and *Pseudosporochnus* (Kräusel and Weyland 1932, Leclercq and Schweitzer 1965, Leclercq and Banks 1962, Leclercq and Lele 1968). The latter are also known from compressions and currently placed within Pseudosporochnales (Berry and Fairon-Demaret 2002, Giesen and Berry 2013). Other genera, such as *Eospermatopteris*/*Wattieza* (Stockmans 1968, Berry 2000, Stein et al. 2007) and *Lorophyton* (Fairon-Demaret and Li 1993) are presently included in Pseudosporochnales based on compression evidence, and the whole-plant concept of the order is increasingly well understood (Fairon-Demaret and Berry 2000, Stein et al. 2007, Giesen and Berry 2013).

There have been a number of interpretations of the evolutionary significance of *Ibyka*, many relating to the early origin of horsetails. However preliminary review of the evidence (Stein et al. 1984) concluded that there was no reason to prefer *Ibyka* to cladoxylopsids (such as *Hyenia* or *Calamophyton*) as a potential horsetail ancestors based on the then-current evidence. These authors specifically questioned some aspects of the interpreted morphology of *Ibyka*, especially concerning the pattern of insertion of branches and appendages. This concern was also revisited by Soria and Meyer Berthaud (2003) based on the occurrence of whorled architecture in *Pietzschia polyupsilon*, an anatomically preserved non-pseudosporochnalean cladoxylopsid from the Lower Carboniferous (Mississippian) of USA. As whorled architecture seems crucial to the understanding of *Ibyka*, we decided to reinvestigate the type material in the light of present knowledge of Middle Devonian plants.

Materials and Methods

The type collection of *Ibyka amphikoma* Skog et Banks was borrowed from Cornell University Palaeobotanical Collection (CUPC). It consists of prepared sections of pyritized axes plus compression fossils preserved in an indurated grey/green medium sandstone matrix. The pyritized sections of axis in the type and other specimens were observed as prepared by Skog and Banks (1973). Although the matrix is both coarse and hard, application of the dégagement technique (Leclercq 1960, Fairon-Demaret et al. 1999) was employed to uncover bases of lateral appendages. Also in significant areas thick layers of coaly material were locally removed from the surface of the axis compressions to reveal the position of the bases of lateral branches and appendages departing into the matrix from the lower stem surface. These were photographed under low angle incident light to bring out the pattern of depressions on impression surfaces indicating the insertion of lateral branches and appendages.

According to Skog and Banks (1973), the material was derived from a single large block from the east bank of Schoharie Creek, directly below the spillway of the Gilboa dam, near Gilboa, Schoharie County, New York State (VanAller Hernick 2003; Stein et al. 2021). It likely came from material unearthed during construction of the dam, and is therefore believed to derive from the Cooperstown Formation correlative with the Manorkill Formation (late Middle Devonian/Givetian, likely mid to upper Givetian) based on lithostratigraphic correlation and limited palynostratigraphical control (see Stein et al. 2021). Two further unillustrated specimens (NYSM 5202) were mentioned as residing in the New York State Museum, Albany. Six slabs bearing collection number 5202 have been studied by us, and the material seems identical with the concept of *Ibyka* reported in this paper. The New York State Museum catalogue entry for this collection reads ‘Ithaca beds. Fossil Plants. Gilboa, N.Y., ¼ mile downstream from bridge. W. Goldring and J. Bylancik, Colls., 1920.’ Given that the present Gilboa dam was built at the site of the former bridge, the locality is likely to be at the southern end of the Riverside Quarry site (Skog and Banks 1973, Stein et al. 2021).

The type material from Schoharie Creek is retained in Cornell University Palaeobotanical Collection, nos. CUPB 179 (holotype) and 180-189 (paratypes). The Riverside Quarry material mentioned above, and not described further in this paper, is retained in the New York State Museum, NYSM 5202.

Description

This description is supplementary to that by Skog and Banks (1973), emphasising the new interpretations of branching patterns. Branches bear higher order branches or dichotomous sterile or fertile appendages. Following Skog and Banks (1973) orders of branching are designated 1 (the largest), 2, 3 and 4 (the smallest), and n+1 implies the next higher order of branching.

First order axes

The longest axis studied (180 - figs 1, 2, 3a) is 450 mm in maximum length. It varies along its length between 13-17 mm in preserved diameter, with no evidence of distal tapering. A second specimen (179 - figs 3b, 4f) varies between 9 and 11 mm diameter. For most of their length both first order axes were covered with crudely permineralised (pyritised) remnants of the vascular system or a thick layer of coaly material. Some of the latter were removed in order to reveal the pattern of insertion of lateral branches and appendages preserved on the impressions. Counterparts of the largest specimen were coated with bioplastic by previous investigators making more complete study of the axes now impossible.

Two types of organs are observed attached to the first order axes, these being second order axes and dichotomous appendages (see below).

Specimen 180 (figs 1, 2, 3a, 4c) yields the most information about the branching patterns. Numerous appendages and some second order axes are visible on the matrix beside, and attached to, the first order axis. Removal of coaly material from the stem compression revealed the impression of the surface of the far side of this axis and demonstrated the exact position of attachment of buried laterals.

Attached appendages are indicated by upturned U-shaped or more crescentic depressions often infilled with coaly material (fig. 1a). Where not visible beside the first order axis, the attachment of axes of the second order is presumed to be marked by the larger, less well-defined depressions on the larger impressions, but this cannot be determined with certainty without much further damage to the specimen.

A whorled or semi-whorled arrangement of lateral organs, including both branches and appendages, involves distinct nodes and internodes as deduced from the revealed stem surface. Thirteen nodes are identified on the lower 260 mm of the best-preserved portion of the axis (fig. 2a). The average spacing of these nodes is 20.8 mm, although this varies between 18.6 and 24.7 mm. At node *3*, where the most complete information is presented, the attachment of six appendages is preserved (figs 1a, 2a-b, 4c). Appendage *a* is visible on the left-hand side slightly above the plane of the compressed fossil and *f* is preserved lying flat beside the axis on the right-hand side. Attachments *c-e* are visible on the lower surface of the stem itself (fig 2b). The base of appendage *b* was uncovered going down into the matrix on the left-hand side (fig. 2b). Projected continuation of this pattern around the unavailable counterpart of the stem suggests that this main axis carried nine or ten lateral organs in this and probably other whorls. Higher on this axis (e.g. nodes *8*, *9* – fig. 3a) three attachment sites are visible on the stem surface as well as two appendages laterally, suggesting at least eight lateral organs in one complete whorl and therefore some diminution of the number of laterals distally.

Nodes appear to be strict whorls (i.e., all laterals inserted at the same level on the stem) in some cases and in others the node is slightly spread out along the axis (e.g. nodes *3*, *8* – figs 1b, 3a). In this paper we refer to close proximity of branching points on the axis as a node, and the length of stem between such nodes as internodes. It appears from the evidence that where second order axes occur, they replace appendages in the whorls. When a second order axis is attached rather than an appendage, it appears slightly higher on the axis (e.g. fig. 1c 2a, – node *9*).

Between nodes *1* and *13*, including only the organs attached laterally in the plane of the rock surface, there are five second order axes (fig. 1c – arrows) and 19 appendages visible. This indicates approximately one in five lateral organs are likely to be second order axes, which suggests one or two per whorl.

In the second illustrated first order axis (Specimen 179; figs. 3b, 4f - arrows) the attachments of appendages on the right-hand side of nodes *3* and *4* are both displaced acropetally compared with the remaining attachments at each node. A third first order axis (Specimen 180 – 1994.12; Fig. 4a) of 10 mm diameter has three organs (presumed appendages) attached arranged diagonally across the stem plus two with attachment beside the stem. This suggests local approximation to helical insertion, but this pattern does not continue over the complete whorl.

Minute depressions, often filled with a plug of coal, are found scattered over the surface of the first order axes (fig. 1b). These are interpreted as the bases of fine hairs or spines as were seen on other orders of branching when prepared using the transfer method (Skog and Banks 1973, fig. 3).

Second order axes

Second order branches are 4-7 mm in diameter and are inserted on first order branches at a high angle with a slightly widened decurrent base (fig. 1c). The longest second order branch found in attachment is 220 mm in length and is 4.5 mm wide (figs 1c - upper left, 4e, 5b). The bases of numerous appendages, and some third order axes, are represented by upside down U-shaped depressions on the impression surface. These laterals are not attached in strict whorls, rather they are inserted in close proximity as nodes approximating to helical in places, but with noticeable internodes between most nodes. The position of the insertion points suggests six or seven per node. The lack of a counterpart makes this pattern difficult to establish precisely. A third order axis is also attached distally (fig. 1c – large arrow).

A second axis of 6 mm diameter, believed to be of the second order based on size (figs 4d – arrows, 5a), shows the attachments of appendages in almost strict whorls in the central region, but potentially more irregularly (approximating locally to helically) arranged proximally and distally but with still distinct nodes and internodes. Each node is separated by up to 30 mm, with seven or eight appendages per whorl.

Third and fourth order axes

Third order axes are sometimes attached in the place of appendages at the nodes on second order axes (fig. 1c - arrow, fig. 2a). They are from 3-4 mm in diameter when found attached to second order axes. It is impossible to establish the arrangement of laterals directly on the third order axis, but the presence of small bumps and depressions on the surface of the impressions/compressions suggests whorls of 4-5 appendages.

It is probable that fourth order branches are also present. Axis 186, which is 3 mm in diameter, and therefore in the size-range expected for third order branches, seemingly bears a smaller axis a little over 1 mm in diameter in place of an appendage at one or more whorls (fig. 4b - arrow). Because of lack of attachment, it is impossible to demonstrate if an interpretation of branch versus appendage based on size alone is altogether accurate.

Appendages

Where attached to first order axes these organs are very poorly preserved. However, some detail can be established. On specimen 179 a visible bifurcation is observed some 20 mm from the base of the appendage in the plane of the slab surface (figs 3b – node *5*, 4f - small arrow). In this case the total length of the appendage is 28 mm before preservation fails, but other appendages are usually only preserved over shorter lengths than this. On specimen 180, to the right-hand side of node 10 (fig. 2a), faint indication of a bifurcation can be made out some 12 mm from the base of the appendage. The bifurcation is perpendicular to the surface of the slab, meaning that it is only exposed in this case because of fortuitous fracturing of the stem surface, but not discernible in our photographs.

Appendages are not very well preserved on second order branches. One found beside the second order branch on specimen 180 has three dichotomies (fig. 4e - arrows), the first probably perpendicular to the surface of the slab. The total preserved length of this appendage is at least 18 mm. The best example previously illustrated by Skog and Banks (1973, fig. 11) suggests that there are up to five dichotomies over a length of about 20 mm, the segments terminating in recurved tips. On possible third order axes the appendages are up to about 18 mm in total length (fig. 4b). Transfer preparations by Skog and Banks (1973, fig. 3) demonstrated that appendages are covered by very small spines at least to the second dichotomy. In terminal portions of putative fourth order axes (fig. 4b - arrow) the lateral branching systems are less than 5 mm in total length.

Fertile appendages

We were unable to find any fertile material. Specimens illustrated by Skog and Banks (1973, fig. 4) were prepared away, so we are unable to confirm their report.

Comparisons

Our new interpretation of *Ibyka amphikoma* differs from that of Skog and Banks (1973) primarily in the demonstration that branching is predominantly whorled with distinct nodes and internodes. The whorls are most strict in the lower orders of branching and tend towards more irregular insertion, possibly approximating a helical pattern within individual nodes in the higher orders. A true ontogenetic helix is not observed in any region of the plant. The n+1 order of branching is located on the nth order in place of a dichotomous appendage within the whorl. Skog and Banks' interpretation was for a very lax helical pattern of branch and appendage insertion tending towards whorled in the higher orders of branching.

Other main features of the plant include the presence of dichotomous appendages on three or four orders of branching and the presence of hairs or small spines found on most parts of the plant. We were neither able to confirm nor elaborate on the reported presence of sporangia.

Comparison to other Iridopteridales

Stein (1982a) erected a new order, Iridopteridales, to contain some of the genera previously assigned to Iridopteridineae by Arnold (1940). Stein considered the only characters unique to the plants he included to be anatomical. These included a protostele with a number of centrally united but sometimes bifurcated ribs, mesarch protoxylem located solely at the periphery of each rib, and 'large' and 'small' vascular traces to laterals arranged in whorls. Anatomically preserved taxa from North America now placed in the order include *Iridopteris eriensis* (Arnold 1940), *Arachnoxylon kopfii* (Arnold 1935, Read 1938, Stein 1981), *Arachnoxylon minor* (Stein, Wight and Beck, 1983) and *Asteropteris noveboracensis* (Dawson 1881, Bertrand 1913). *Ibyka amphikoma* was included on the basis of its anatomical characteristics only since Stein considered the known morphological characters of this plant to be shared by a number of higher taxa. More recently re-described *Rotoxylon (Cladoxylon) dawsonii* (Read) Cordi et Stein (2005) has also been assigned to the Iridopteridales sharing features of bifurcated xylem ribs, protoxylem and whorled trace departure. However, the number of xylem ribs is far larger and primary xylem overall appears to be dissected toward the center of the stem along lines typically observed in members of the Cladoxylopsida.

Outside North America, Berry and Edwards (1996) described a new plant, *Anapaulia moodyi*, from the Middle or lowermost Upper Devonian of western Venezuela, based on compression fossils only. This plant had four orders of axes, arranged in a predominantly whorled pattern, and was covered in small spines. Both dichotomous appendages and second order axes were found at nodes on first order axes. There are some minor differences between the Venezuelan plant and the interpretation of *Ibyka amphikoma* presented here. Firstly, in *Anapaulia*, the bases of the second order branches and appendages sometimes join in a ring around the first order axis to form a deep groove on the impression surface, rather than being spaced out, crescentic and non-contiguous as in *Ibyka*. Secondly the distances between nodes on first order axes are much greater in *Anapaulia*, being from 25-75 mm (these closest spaced whorls being only reported recently by Berry and Fairon-Demaret 2001, their Fig. 7.1C). Thirdly only third order axes are found attached to second order axes, no dichotomous appendages being present at this level of branching. Lastly sporangia are numerous and relatively well preserved in *Anapaulia* and are borne in pairs on strongly recurved terminal segments of fertile appendages. Thus we presently retain *Anapaulia* as a separate genus.

Berry and Edwards (1996) argued that the morphology of *Anapaulia* was that one would expect for an iridopteridalean plant given the known characteristics of the anatomy of *Arachnoxylon* and the then known morphology and anatomy of *Ibyka*. This seems to have been borne out by the present study, suggesting that the Iridopteridales may be recognized by compression evidence alone in at least the mid to early late Devonian.

Compsocradus laevigatus Berry et Stein (2000) was described from further compressions and permineralizations from a slightly older Givetian horizon in Venezuela. The new plant shared anatomy essentially equivalent to *Arachnoxylon* or *Ibyka*, but differed in that only every other rib of the primary xylem column produced a trace at each node, with alternate angular insertion of the laterals in adjacent whorls. *Compsocradus* also lacked spines. A further species of *Compsocradus*, *C. givetianus* (Wang) Fu et al. (2011) was recognised on the morphological characters alone, including the alternating insertion of whorls on the smooth axes, based on material from Xinjiang, China. Very recently it has been suggested that the type species of *Hyenia*, *H. sphenophylloides* Nathorst 1915, based on compressions from the Middle Devonian of Norway, may also show a similar alternation of whorls and lacks spines (Berry, Stein and Wyatt, 2021), and the genus *Hyenia* (*sensu stricto*) may therefore belong to Iridopteridales, potentially close to *Compsocradus*, and not to Cladoxylopsida as sometimes attributed.

Hyenia (*Hyeniopsis*) *vogtii* Høeg (1942), from the Middle Devonian of Spitsbergen was based on axes from 5-7 mm in diameter. Two orders of branching were illustrated. Dichotomously branching 'leaves' (i.e. appendages) were arranged on both orders in a manner which was described as 'more or less verticillate, causing a corresponding articulation in the axes' (p. 83 of Høeg 1942), the distance between successive verticils being 'about two or three times the diameter of the axis'. The second order axes were described significantly as being 'invariably developed in the place of leaves, and not in the leaf axils'. The axes were longitudinally grooved, suggesting the impression of a ribbed vascular system, and carbonaceous traces into lateral branching systems was preserved in the compressions. Spines or ‘thorns’, rarely up to 2 mm in length, were found on the margins of axes, and were represented on the surface of impressions by ‘small dots or scars’. Høeg recognised that the plant was different from the material from Norway and Germany described under the names *Hyenia sphenophylloides* (Nathorst 1915; Høeg 1931, 1935), the type species of *Hyenia*, and *H. elegans* (Kräusel and Weyland 1926) because of the differences in branching patterns and the presence of spines. However, the presence of dichotomous appendages seems enough to have persuaded him to place the material in *Hyenia*, albeit in the subgenus *Hyeniopsis*. No fertile material was present. Schweitzer (1999) transferred the species to the cladoxylopsid *Pseudosporochnus*. Re-examination of Høeg’s specimens, and confirmation of a whorled branching pattern, lead to the plant being transferred to *Ibyka vogtii* (Høeg) Berry by Berry (2005). New collections of this plant from the type locality have recently been made which should further clarify relationship with *I. amphikoma* (CMB).

Hyenia banksii Arnold (1941), from the Middle Devonian Bellvale Flags of Orange County, New York State, was based on a single specimen consisting of a 5 mm diameter main stem bearing two smaller lateral branches inserted at the same level. To both orders were attatched two- or three-times forked dichotomous appendages, arranged in whorls approximately 8 mm apart. This material is more fragmentary than *Ibyka vogtii*, yet the branching pattern again suggests a closer affinity to Iridopteridales than to Cladoxylales. Description of this material is currently insufficient to make a meaningful comparison to *Ibyka*.

Other anatomically preserved specimens outside North America at least tentatively assigned to the Iridopteridales include *Serripteris* (Rowe & Galtier 1989) from the Lower Carboniferous (Mississippian - Mid Tournasian) Montagne Noir of France and *Keraphyton* (Champreux et al. 2020) late Fammenian in age from New South Wales, Australia. Both taxa, known from anatomical data alone, potentially extend the age and geographic range for the group. However, the anatomy of each differs substantially from better known representatives, so their membership within the Iridopteridales remains uncertain.

Comparison to Cladoxylopsida

Devonian genera belonging to Cladoxylopsida have a confusing taxonomic history that need not be repeated here. The currently recognised genera of the Middle and Upper Devonian Pseudosporochnales for which morphological information is available are *Calamophyton* (Kräusel and Weyland 1926, Fairon-

Demaret and Berry 2000 – including much material formerly assigned to *Hyenia,* Giesen and Berry 2013), *Pseudosporochnus* (Potonié and Bernard 1904, Berry and Fairon-Demaret 1997, 2002), *Eospermatopteris*/*Wattieza* (Berry 2000, Stein et al. 2007) and *Lorophyton* (Fairon-Demaret and Li 1993). The principal morphological similarity of these genera with *Ibyka* is that they share lateral appendages that are based upon dichotomous units - this seems to have been taken as almost diagnostic for the genus *Hyenia* in the first half of the 20th Century. In pseudosporochnalean cladoxylopsids sporangia are generally arranged terminally and in pairs. In *Pseudosporochnus* the fertile lateral branching systems share the same basic morphology as the sterile ones, whereas those of *Calamophyton* have a modified sporangiophore (e.g. Leclercq and Andrews 1960).

Early reports of the arrangements of the appendages of *Hyenia sphenophylloides* (Nathorst 1915), *Hyenia elegans* (Kräusel and Weyland 1926, 1929) and *Calamophyton primaevum* (Kräusel and Weyland 1932) emphasised a verticillate arrangement of appendage insertion. This has not been substantiated by recent work on these taxa (e.g. Leclercq and Andrews 1960; Schweitzer 1972, 1973; Fairon-Demaret and Berry 2000), excepting *H. sphenophylloides* as mentioned above. In the only Pseudosporochnales where the insertion pattern has been studied in detail (*Pseudosporochnus hueberii* - Stein and Hueber 1989; *P. nodosus* - Berry and Fairon-Demaret 1997; *Wattieza* Berry 2000) insertion has been shown to be neither helical or verticillate, instead having no regular geometric pattern.

With the exception of *Lorophyton* (which may be a juvenile individual), Pseudosporochnales have distinctive branches that show a close series of dichotomies often described as a digitate or palmate overall pattern. Most also have a marked or sometimes less obvious pattern of small nests of sclereids in the outer cortex which leads to a speckled pattern on the surfaces of compressions. All of this contrasts with the organised, regular nodal insertion of both appendages and branches found in *Ibyka* and the presence of hairs or spines on the compression surfaces. Pseudosporochnales also have a large trunk to which branches are attached. Although this remains possible for the Iridopteridales, no attachment to portions of a larger plant body has yet been demonstrated.

A new reconstruction of *Ibyka amphikoma*

Our new reconstruction of *Ibyka* is shown in Figure 6a and can be compared with the reconstruction of Skog and Banks (1973, fig. 1; fig. 6b). Most obviously it can be seen that we recognise a basically whorled insertion of laterals which suggests a more dense, profusely-branched arrangement contrasting starkly with the more lax, distantly spaced appendages and branches of the original. Our diagram was prepared from an overlay of a photograph of the largest specimen (180), and superposing branches and appendages onto the attachment points on the stem compression. It shows only a partial reconstruction of the plant as now possible to interpret it.

We have assumed that the appendages attached to the first order branches are dichotomous three times. Dichotomies of these structures are rarely observed and there is direct evidence for dichotomies only 12 and 20 mm from the base. This is perhaps the least satisfactory aspect of this reconstruction, as comparison with appendages on other orders of branching suggest that they could divide as many as five or six times. Drawing them with three dichotomies (terminating in recurved tips) is a compromise between the observed and the expected, but allows the rest of the branching pattern to be observed clearly.

A single fourth order branch is drawn - evidence of this order is not conclusively proven.

We include the recurved tips of appendages as illustrated by Skog and Banks 1973 (their fig. 5) and in this paper (fig. 4b).

Spines are drawn in a manner which is diagrammatic only - the spines appear finer and more closely spaced on the fossils than shown in the current reconstruction.

The first order axis is drawn as a pseudomonopodial stem. This is suggested by the symmetry of the second order branches on the largest slab, but this interpretation is not the only one possible.

We have no evidence of the rooting or basal structures of these plants.

Discussion

Relationship between anatomy and morphology

Anatomical preparations taken from the type material of *Ibyka* include axes of about 4 mm diameter (Skog and Banks 1973, their figures 16, 17, 24) and have 5 or 6 ribs with peripheral mesarch protoxylem strands. These are therefore interpreted by us to show the anatomy of second or probably third order axes. These preparations demonstrate a nodal arrangement of terete ‘minor’ traces presumably to appendages. These are inserted in a pattern possibly suggesting oblique plane of section or a shallow helix rather than a strict whorl. The latter observation is very much in agreement with observations made of higher order branches on the compression fossils.

No larger permineralised axes of *Ibyka* are known. However, because of the similarity of the known anatomy to the larger axes (up to 14 mm diameter) of *Arachnoxylon kopfii* (Stein 1981) some deductions can be made on the basis of this material. In *Arachnoxylon kopfii* there are six or seven xylem ribs which give out a trace each in each whorl, originating from the protoxylem strand. There are two types: terete 'minor' traces and larger 'major' traces which become ribbed a few milimeters distal to departure from the main vascular system. In the case of the 'Windom Shale' specimen of *A. kopfii* two 'major' traces are borne in the single node present, with six traces total. The obvious interpretation is that 'major' traces are the vascular systems of attached branches, whereas more numerous dichotomous appendages are supplied by the 'minor' traces.

In *A. kopfii*, the 'major' trace is proximally a bipolar primary xylem strand elongated tangentially with two protoxylem strands. From each a terete 'subsidiary' trace is given, departing in a tangential direction. Once the xylem trace becomes elaborated distally into a four-ribbed primary xylem strand, Stein (1981, plate 6, fig. 32, 24) a further pair of terete 'subsidiary' traces is produced from the abaxial ribs. Subsequent sections of the axis do not preserve the rest of the 'major' trace. Rather than interpret traces as comprising distinct pairs, it is also possible to interpret these traces as part of a basal whorl, as the oblique section cut through the 'major' trace would in the lowest sections reveal only the presence of traces on the abaxial ribs. We have not observed pairs of tangential lateral branching systems equivalent to the proximal pair of traces in *Ibyka*, but clearly observe the presence of whorls of appendages on second order branches.

Stein (1981, p. 99) described that in *A. kopfii* 'the order of trace departure….. may be described best as "imperfectly" whorled.' In transverse section, traces appear to be in slightly different stages of departure. However, no simple helical pattern may be employed to describe these differences. Furthermore, it is clear that the differences in level of departure for the various appendage traces are quite small when compared to the entire length of the specimen, two thirds of which contains no traces at all'. This is also our opinion of the morphology of *Ibyka*, where the arrangement of the lateral branching units and lower order branches is nodal, but not strictly whorled, yet has distinct internodes.

Based on our knowledge of the morphology of *Ibyka*, *Anapaulia*, *Ibyka vogtii* and '*Hyenia*' *banksii*, and the anatomy of *Ibyka* and *Arachnoxylon* we can now suggest a model for the basic architecture of iridopteridalean plants most closely related to *Ibyka*.

Branches bear spines, and have ribbed steles composed of primary xylem with protoxylem strands a permanent feature located near the peripheral tips of each rib. Dichotomous lateral appendages are borne upon branches in a nodal-internodal fashion (approximating to whorls), each appendage supplied by a terete trace derived from the protoxylem of the branch primary xylem. The distance between nodes, with some variation in insertion of appendages, generally decreases within higher branch orders. The appendages are isotomously divided a number of times in three dimensions (successive dichotomies are probably more or less perpendicular) and terminate in either recurved tips or pairs of elliptical sporangia. Within nodes, one or more of the appendages may be replaced by a branch of the next order, also supplied by a ribbed primary xylem strand. Higher order branches are likely smaller versions of lower order ones, having fewer xylem ribs and fewer lateral appendages per whorl. There may be up to at least four orders of branching formed in this way, with an overall iterative architecture.

Higher level taxononomy and relationships

Arnold (1940) erected a new suborder Iridopteridineae within the Coenopteridales, to accommodate his new genus *Iridopteris* plus *Arachnoxylon kopfii* (Arnold) Read (1938) and *Reimannia aldenense* Arnold (1935) based on permineralized specimens only. Skog and Banks (1973) erected a new order, Ibykales, to contain the new genus *Ibyka* as well as *Arachnoxylon* of Read and possibly *Protohyenia* Ananiev (1957). Although Skog and Banks combined both morphological information as well as anatomical details in their diagnosis of Ibykales, Stein (1982a, p. 414) concluded that ‘the only feature suggested by Skog and Banks that make the group recognizable (i.e., diagnostic characters that are unique to the group and clearly derived beyond some ancestral condition for Middle Devonian plants as a whole) are those of primary vascular architecture: highly ribbed mesarch primary xylem with protoxylem strands only near the tips of the ribs’. He accordingly elevated Arnold’s Iridopteridineae promoting it to ordinal status as the Iridopteridales. Based on this interpretation, he excluded *Reimannia* (see Stein 1982b) and *Protohyenia*. However, *Ibyka* clearly belongs within the Iridopteridales.

Recently a cladistic analysis of known Iridopteridales, Cladoxylopsida and seemingly closely related plants, including examples from China, has been undertaken by Durieux et al. (2021). Their analysis did not recognise Iridopteridales as a single clade (Durieux et al. (2021 figure 9)). Instead, based predominantly on morphology, *Ibyka* and *Anapaulia* formed one clade and anatomically preserved *Arachnoxylon*, *Iridopteris*, and *Asteropteris* formed another along with *Compsocradus*. The clade containing *Arachnoxylon* was placed as a sister group to an extended cladoxylopsid complex, and the *Ibyka*/*Anapaulia* clade as a sister group to the *Arachnoxylon* clade plus cladoxylopsids. *Rotoxylon*, with dissected primary xylem in their analysis, appears within cladoxylopsids, despite all other features being essentially iridopteridalean. Iridopteridalean features that can be noted include peripheral “permanent” protoxylem strands only, whorled trace departure, size relationship of tracheids within individual xylem ribs, and mode of trace departure reminiscent of both *Arachnoxylon* and *Iridopteris*. The only features that suggest cladoxylopsid relationship are vascular size and apparent dissection of the xylem column.

For any cladistic analysis of plants in these groups, the problem remains that only members of the Pseudosporochnales and the genus *Pietzschia* are currently recognized as something resembling whole plants, whereas all other taxa analysed represent highly fragmentary remains. Thus, despite a comprehensive survey of published material, any constructed dataset remains highly heterogeneous, permitting a wide range of possible whole-plant interpretations for the fragments. Under these circumstances, use of parsimony or maximum likelihood cladistic procedures operate without much constraint based on known features, and as a result must be viewed as yielding results with low confidence.

As examples of the issues, Durieux et al. (2021) resolve a monophyletic iridopteridalean clade based on fragmentary anatomical taxa (including *Arachnoxylon* species) plus *Compsocradus laevigatus*, but morphologically preserved *Ibyka* and *Anapaulia* fall outside of it. Here we compare their data and analysis for *Arachnoxylon kopfii* Read (sensu Stein 1981) and *Ibyka amphikoma* (Durieux et al. 2021; their fig. 9; appendix S2 and S4).

Of 13 largely morphological characters (1-9, 33-36) 9 include missing data in one or the other species and 2 further characters are scored identically. We examine here the two remaining characters which are scored differently. Character 1 (presence or absence of spines) is recorded as present in *Ibyka* and absent in *Arachnoxylon*. However, lack of preserved spines in *Arachnoxylon* is not a supported observation given the lack of preservation of the outer parts of the cortex and epidermis (Stein, 1981). Character 2 (taxis of ultimate appendages) is recorded as helical for *Ibyka*, but whorled in *Arachnoxylon*. Here taxis is defined as based on the highest order preserved. We know from the present study that in *Ibyka* taxis changes from essentially whorled in the first order axis to nodal approximating to helical in the third and fourth order branches, so the level of branching selected affects the character state recorded. In *Arachnoxylon* taxis is only established for anatomically preserved axes which are equivalent in size to the first order axes of *Ibyka*, and is unknown for higher orders of axes. So this character is not equivalent between the two genera. We therefore conclude that of the 13 characters examined, none can meaningfully be scored as different between *Arachnoxylon* and *Ibyka*.

Of 23 largely anatomical characters (10-32) 2 include missing data and a further 17 are identically scored. We examine here the remaining 4 characters currently scored differently. Character 16 (dissection of xylem ribs) is scored as 'bifurcate' in *Ibyka* and 'some trifurcate' in *Arachnoxylon*. This distinction is not obvious from the relevant publications although multiple bifurcations in ribs are known in some instances. The apparent trifurcation indicated (Stein 1981, figure 39), which appears to us more like close dichotomies, may be related to the size of the stem. One interpretation is that the stele is constructed from 3 centrally united major ribs. If this is the case then large axes will require additional dissection of the stele to supply the higher number of lateral appendages and branches than smaller axes with less. Thus we might expect trifurcation of ribs to be related to the size difference (and relative order of branching) between permineralized *Ibyka* and *Arachnoxylon*. Character 17 (geometry of xylem ribs) is scored as broader at tip in *Ibyka* and parallel sided in *Arachnoxylon*. We cannot observe this difference as stated by the authors, particularly relating to the broad tips of *Ibyka*. Neither of these characters is adequately distinctive to be conclusive between different orders of branching. Character 29 (number of protoxylem strands at base of branch/major appendage) is scored as single strand in *Ibyka* and more than 2 strands in *Arachnoxyon.* However, this feature is very likely linked to "major" versus "minor" trace types probably produced in each. (Note, however, evidence for larger branches supplied by "major" traces in *Ibyka* is not observed, but can reasonably be inferred from available compression and anatomical evidence.) Character 30 (symmetry of branch/major trace in basal-most portion) is scored as radial in *Ibyka* and bilateral in *Arachnoxylon*. Both of these characters, like characters 2 and 16 mentioned above, probably relate to the fact that only smaller branches in *Ibyka* were anatomically preserved, whereas larger axes of *Arachnoxylon kopfii* were included in the final cladograms. Smaller axes of *Arachnoxylon minor* are essentially identical to those of *Ibyka* to the extent known.

Durieux et al.'s 2021 analysis separates *Arachnoxylon kofii* Read and *Ibyka* into separate clades. However our analysis of the 6 characters scored differently (out of 36) between the two taxa shows that we cannot be confident that any of them can be reliably confirmed to be different. Rather we might be tempted to suggest that *Arachnoxylon* must be a good candidate to be the preserved anatomy of a large second order or distal first order axis of *Ibyka* or very closely related plant. Most observable differences perhaps relate to size and position. The major difference between *Arachnoxylon* and the proximal known first order axis of *Ibyka* is that we might expect a small number of additional ribs to match the number of appendages and branches found in a whorl on *Ibyka*.

We therefore suspect that the polyphyly of iridopteridaleans in Durieux et al.'s 2021 analysis, including the separation of largely anatomically vs largely morphologically preserved taxa, and potentially the loss of *Rotoxylon* from the group, may be a result of the methodology adopted, including missing data and fragmentary material relating to non-equivalent parts of the plants.

Whole-plant Concept for the Iridopteridales

In constructing a whole-plant concept for the Iridopteridales possibly suitable for cladistics analysis, two taxa - *Ibyka amphikoma* and *Compsocradus laevigatus* - clearly stand out. In both, there is evidence of advanced anatomy beyond that of *Psilophyton* unique to the group, combined with overlapping evidence of at least portions of these plants provided by compressions. These two taxa, in part mirrored by other less complete specimens, suggest diversity potentially deserving recognition as sub-groups. On the one hand, *Ibyka amphikoma* most clearly corresponds to *Arachnoxylon kopfii* and *A. minor* on the basis of anatomy, with all three showing 'imperfect' whorls of lateral elements consisting of major traces to branches or minor traces to appendages. Notably in these, whorls of lateral elements are for the most part superimposed in orthostichous ranks. A similar pattern can be inferred from compressions of *Ibyka vogtii* and *Anapaulia*. Differences between compression taxa occur in the widths of axes, distances between successive nodes, number of lateral appendages or branches per node, and the proportions of appendages to branches in the nodes of any particular order of branching. These plants all bear spines on surfaces of larger axes.

By contrast, *Compsocradus*, while lacking spines, otherwise also shows anatomical evidence comparable to *Arachnoxylon*, although interestingly with angular offset of vascular traces and appendages in successive whorls. Similar 'alternate whorls' are observed in anatomically preserved *Iridopteris* and *Rotoxylon*. In *Compsocradus* every other primary xylem rib contributes to a whorl of lateral elements, whereas in *Iridopteris*, each rib contributes traces asymmetrically to supply 'alternate' whorls. Additionally, *Iridopteris* seemingly exhibits bilateral symmetry of the vascular system (Stein 1982a), although it must be emphasized that the presence of only five primary xylem ribs in both known specimens may inadvertently confer this appearance. *Rotoxylon* represents an apparently larger axis 15 mm in diameter perhaps suggesting that at least some iridopteridalean whole plants were much larger and more complex than previously supposed. This taxon has 18 radially directed primary xylem ribs and permanent protoxylem strands. Small vascular traces possibly corresponding to appendages, are seemingly produced radially as in *Arachnoxylon*, whereas others are offset to subsequent whorls very much as in *Iridopteris*.

Although lateral organs produced in whorls is currently important in recognizing the Iridopteridales, the diversity of stelar configurations directly points to the necessity of incorporating known developmental processes into study of these fossil plants. It is known in modern plants, for instance, that initiation of lateral appendages largely determines the developmentally subsequent pattern of provascular and xylem differentiation via hormonal influence (Sachs 1991, Stein 1993, Chomicki et al. 2017). In the Iridopteridales, we suggest that similar developmental processes likely produced a rough correspondence of primary xylem ribs to the number of lateral elements produced at each whorl. However, the fossils clearly show that this correspondence was far from exact, and other hormonal or physical factors, including size of the main shoot apex, probably also played a role. Specifically, these additional factors may also have influenced the number of xylem ribs, determined xylem rib radial length, established the pattern of radial rib bifurcation, as well as in the case of *Rotoxylon*, dissection of the entire xylem system. As a result, in comparing *Compsocradus* with *Iridopteris* for instance, although sharing 'alternate' vascular trace departure, this pattern may have become modified into strikingly different outcomes by subtly divergent developmental systems governing xylem maturation as a whole, possibly related to axis size.

In sum, the diversity of morphology and especially anatomy assigned to the Iridopteridales rather than serving as clear cut differences suitable for phylogenetic study, strongly points to what we have yet to learn about this group as whole plants. Critical issues remain to be resolved, not the least among them is their overall plant stature and habit. Previous work on *Hyenia* has commonly inferred a rhizomatous habit potentially applicable to the group as a whole (e.g. Høeg 1945), but convincing evidence for this view has yet to be confirmed. Moreover, *Asteropteris* and *Rotoxylon* points to the possibility that some of these plants were significantly larger and more complex than currently supposed. *Asteropteris* showing production of mostly major traces, suggests more basal portions of Iridopteridaleans may have involved mostly branch production. *Rotoxylon* with a dissected xylem column may point to the Cladoxylopsida, possibly even pseudosporochnaleans, as a model for their eventual reconstruction.

The discussion above focusses on the key taxa essentially described from North and South America we understand to have clear iridopteridalean characteristics, be it anatomically preserved taxa (*Iridopteris*, *Arachnoxylon*, *Asteropteris*, *Rotoxylon*), morphologically preserved (*Anapaulia*), or both (*Ibyka*, *Compsocradus*). These are the genera identified in the Durieux et al. (2021) as 'iridopterids', plus *Rotoxylon*. All of these taxa are found in rocks dating from approximately late Eifelian to early Frasnian (c. 390-380 Ma).

Two further genera have been linked to the Iridopteridales. *Keraphyton* Champreux et al. 2020, is from the late Famennian (c. 360 Ma) of Australia. This fragmentary anatomically preserved plant has a very different xylem configuration from other iridopteridaleans, with prominent non-equal dichotomies of the outer parts of the xylem ribs. Modes of branching and organotaxis are not established. *Serripteris* Rowe et Galtier 1989 also shares some basic anatomical characters with iridopteridaleans, yet has helical branching, and is closer to 350 Ma in age. While offering some intriguing possibilities for the possible later evolution of the iridopteridalean body plan, at this juncture, these taxa cannot contribute much to the understanding of the Iridopteridales as a group of plants, restricted in time and perhaps in space, as addressed in this paper.

Ibyka, Iridopteridales and the origins of Horsetails

Stein, Wight and Beck (1984) examined the then current evidence concerning the plants that were likely to be related to early horsetails, and concluded that there was no evidence to favour Ibyka/Iridopteridales over Cladoxylopsida or other likely potential ancestral groups.

Kenrick and Crane (1997) take a different and potentially inconsistent approach to their treatment of *Ibyka*. In their cladistic analysis they treat the branching pattern as ‘helical’. Within their table 7.2, p. 231 of ‘synapomorphy-based definitions of monophyletic higher taxa’ they consider that the synapomorphies of Equisetopsida are 1) whorled appendages; 2) sporangiophore morphology; 3) stelar morphology; 4) regular alternation of appendages at successive nodes; 5) microphyllous leaves’. They state that ‘characters supporting a close relationship between the early fossil *Ibyka* and sphenopsids include 1) whorled branching (Stein, Wight and Beck 1984) and 2) protoxylem disintegration to form lacunae’. Although the synapomorphies are not explicitly stated in each case and so cannot be verified, *Ibyka* certainly does not demonstrate synapomorphy 4, having superposed whorls rather than alternation of appendages at nodes. Nevertheless, in another table (7.5, p. 252) *Ibyka* is listed as the first appearance of the clade Equisetopsida.

In assessing phylogeny using cladistics methods, it has been common practice to look for differences between known groups considered to be monophyletic and then to search for these features among earlier fossil forms. It must be emphasized, however, that this is a retrospective view that assumes that one or another of observed features in later groups actually occurred earlier in time, thus allowing the researcher to polarize characters if desired. A prime example of this is the regular occurrence of ‘whorled’ versus ‘helical’ organotaxis in cladistic studies as a means for establishing relationships of Mid Devonian plant fossils, including Iridopteridales and Pseudosporochnales, with later ferns or sphenopsids. However, what appears to be emerging from direct study of the fossil plants is an unexpected degree of developmental indeterminance (or ‘imperfection’) in organotaxis and xylem configuration that might easily be viewed as encompassing multiple outcomes, only some of which are recognized as character differences in later groups. As a result, the retrospective approach fails to capture the reality of the situation. This is both a warning for current cladistics practice, as well as an opportunity to view these ancient plants for what they actually were. A degree of developmental indeterminance in many aspects of both anatomy and overall morphology might in fact represent the primitive state from which recognizable differences in later taxa ultimately evolved. This may have occurred not by cladistic state change from one later morphology to another as is commonly envisioned, but instead by regularization of potential outcomes of a common developmental system by the innovation of additional constraint (Stein 1998, Stein and Boyer 2006).

Systematic Palaeobotany

Order - Iridopteridales Stein 1982a

Genus - *Ibyka* Skog et Banks 1973 emend.

At least three orders of branching known. Branches of n+1 order and appendages arranged in whorls, or approximating whorls, with distinct internodes, on nth order, successive whorls being superposed in orthostichous ranks. Appendages are dichotomously divided several times, with successive dichotomies in different planes, distal tips recurved. Terminal sporangia borne in pairs on otherwise unmodified dichotomous appendages. Axes of all orders and proximal parts of appendages bearing small spines or hairs. All growth primary. Primary xylem a protostele with with centrally united ribs that sometimes bifurcate radially, maturation mesarch in permanent strands at the periphery of each xylem rib, primary phloem surrounding the primary xylem; traces to lateral appendages terete.

Ibyka amphikoma Skog et Banks 1973 emend.

As Skog and Banks (1973) with the exception of phyllotaxy; up to 10 branches or appendages in each node on largest known axes.

Conclusions

The confusion regarding the morphology of *Ibyka* has been resolved by our new description of the morphology of *Ibyka amphikoma*. The compression fossils reveal that the pattern of insertion of laterals is nodal but not always strictly whorled, which is agreement with the pattern observed in anatomically preserved Iridopteridales, and contrasts with the helical pattern previously interpreted for *Ibyka*.

Ibyka and *Compsocradus* are the only members of Iridopteridales for which both anatomy and morphology have yet been described. Berry and Edwards (1996) inferred from morphology that *Anapaulia moodyi* was probably a compression fossil member of Iridopteridales. This new study of *Ibyka*, showing close comparison of the two plants, acts to confirm the validity of their assessment utilizing cross-preservation inference in the combined study of morphological and anatomically preserved material. Likewise other taxa (e.g. *Ibyka vogtii*, ‘*H.*’ *banksii*) can reasonably be inferred to be members of the Iridopteridales based on compression fossils only.

From this work a morphological and anatomical model of Iridopteridales is proposed. Iridopteridales have a number of orders of branching, each bearing dichotomous appendages in whorls supplied by 'minor' terrete traces. Higher orders of branching are produced in place of appendages in the whorls and are supplied by 'major' traces that develop into smaller versions of the ribbed primary xylem strand of the main axis, with a smaller number of ribs and thus smaller number of lateral organs borne at the nodes. Sporangia are arranged terminally in pairs on lateral branching systems otherwise identical to the vegetative examples.

Two distinct morphologies possibly comprising potential sub-models within the Iridopteridales are suggested. The *Ibyka* type bears one branch or appendage from each rib in the stele at every node in orthostichous ranks, and is spiny. In the *Compsocradus* type laterals are borne from every other rib at the node, and the position of laterals alternates between whorls. Given that this does not cover the full diversity of iridopteridalean anatomy noted above (e.g. *Asteropteris*, *Iridopteris*, *Rotoxylon*) variants on these basic plans are evident, and these possibly suggest other morphotypes within the Iridopteridales.

Iridopteridales now joins the small number of Middle Devonian higher plant taxa for which a synthetic concept is at least partly established (Progymnospermopsida, Pseudosporochnales, Lycopsida). We suggest that this form of synthesis is more likely to bear fruit in searching for the origin of later major groups, such as horsetails and ferns, than piecemeal inclusion of most currently named taxa within cladistics studies.

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Figure captions

Figure 1

Ibyka amphikoma Skog et Banks from Gilboa, New York.

a) Close-up view of node *3*, specimen 180, 1st order, showing attachments of appendages (see fig. 2a). Scale bar = 10 mm.

b) Close-up view of specimen 180, 1st order, nodes *9* and *10*, showing nodal regions with imperfect whorls of attachments of laterals (see fig. 2a). Hair bases marked by fine plugs of coal on stem surface. Scale bar = 10 mm.

c) General view of best preserved part of specimen 180, showing three orders of branching (third order marked by large arrow). Insertion of second order branches on first order at margin of impression marked by narrow arrows (nodes *1*, *7*, *9*, *12*, *13*). For numbering of nodes see fig. 2a. Scale bar = 10 mm.

Figure 2.

Ibyka amphikoma Skog et Banks from Gilboa, New York.

a) Lowest 13 nodes (numbered) of specimen 180, showing position of attachments of visible laterals. Photographic illustration in fig. 1c. Scale bar = 20 mm.

b) Close up of node *3*, showing attachments of six visible laterals in imperfect whorl (compare with fig. 1c, 3a, 4c).

Figure 3.

Ibyka amphikoma Skog et Banks from Gilboa, New York.

Line drawing of insertion of laterals on first order axes.

a) Specimen 180 (see figs 1c, 4c). b) Specimen 179 (see fig. 4f). Appendages which are inserted above rest of whorl (arrows). Scale bar = 20 mm.

Figure 4.

Ibyka amphikoma Skog et Banks from Gilboa, New York.

a) First order axis, demonstrating attachments of appendages at node locally suggesting helical insertion. Scale bar = 10 mm. Specimen 180 (counterpart fragment 1994.12)

b) Probable 3rd and 4th order (arrow) axes. Specimen 186. Note recurved tips of appendages on highest order axis. Scale bar = 10 mm.

c) Close up of 1st order axis, showing arrangement of insertion points of laterals. Note appendage *b* uncovered at node *3* (arrow), for line drawing see fig. 2b. Specimen 180. Scale bar = 10 mm.

d) Second order axis showing well-defined whorls (arrows). Sample number 180 (counterpart fragment 1994.12). For line drawing see fig. 5a. Scale bar = 10 mm.

e) Second order axis with attached 3rd order axis distally, as seen on left margin of main specimen (fig. 1c). Dichotomous appendage visible (dichotomies indicated by arrows). For line drawing showing appendage attachment pattern see fig. 5b. Specimen 180. Scale bar = 10 mm.

f) First order axis. Note attachments of appendages displaced upwards from rest of whorl (large arrows, for line drawing see fig. 3b). Also dichotomy of appendage (small arrow). Specimen 179. Scale bar = 10 mm.

Figure 5.

Ibyka amphikoma Skog et Banks from Gilboa, New York.

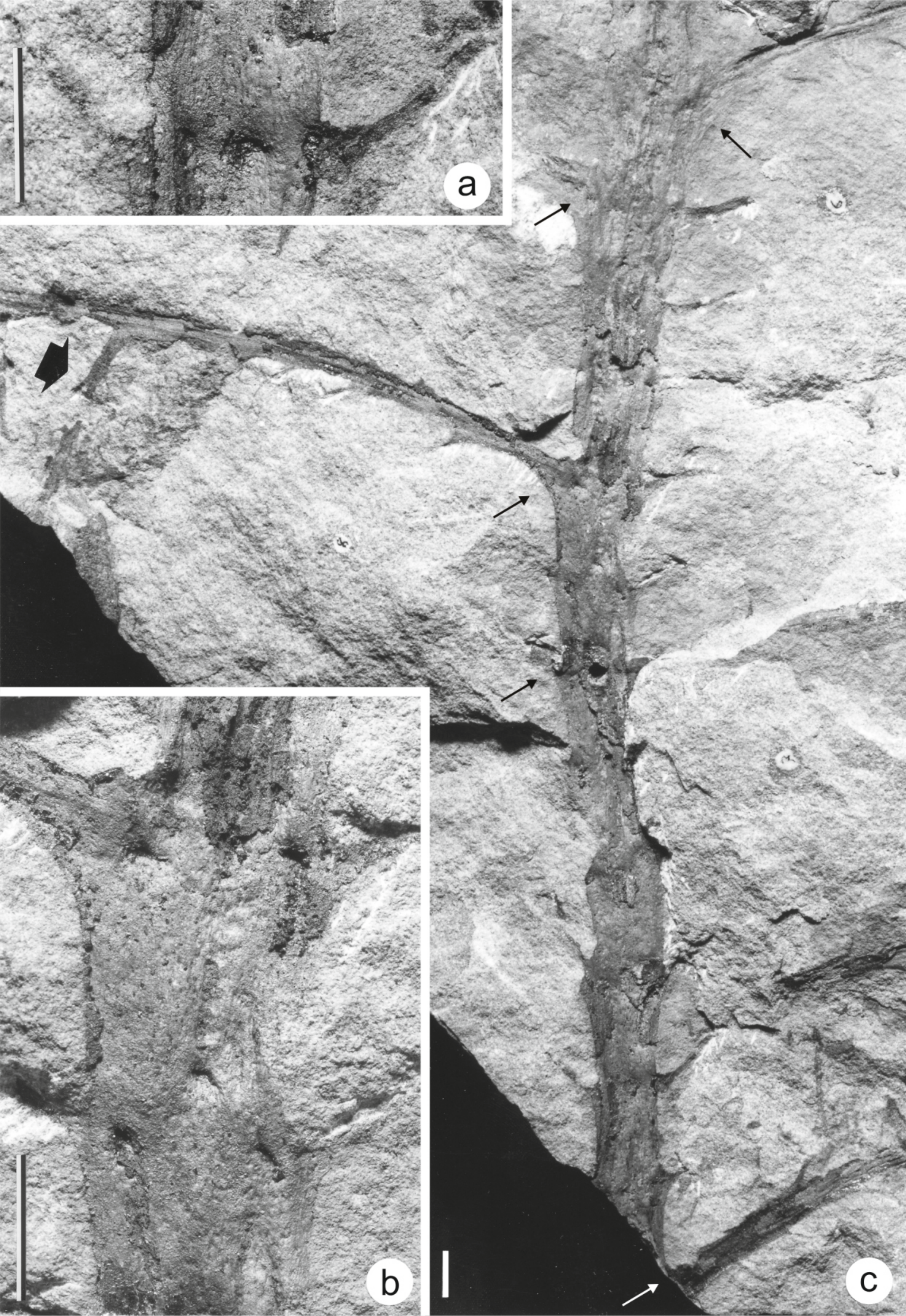
Line drawings of insertion of laterals on second order branches.

a) Sample number 1994.12 (see fig. 4d). b) Specimen 180 (see figs 1c, 4e). Scale bar = 10 mm.

Figure 6.

a) New partial reconstruction of *Ibyka amphikoma* Skog et Banks based on the observations of this study. Width of first order axis at base is approximately 16 mm.

b) Former reconstruction of *Ibyka amphikoma* redrawn from Skog and Banks (1973).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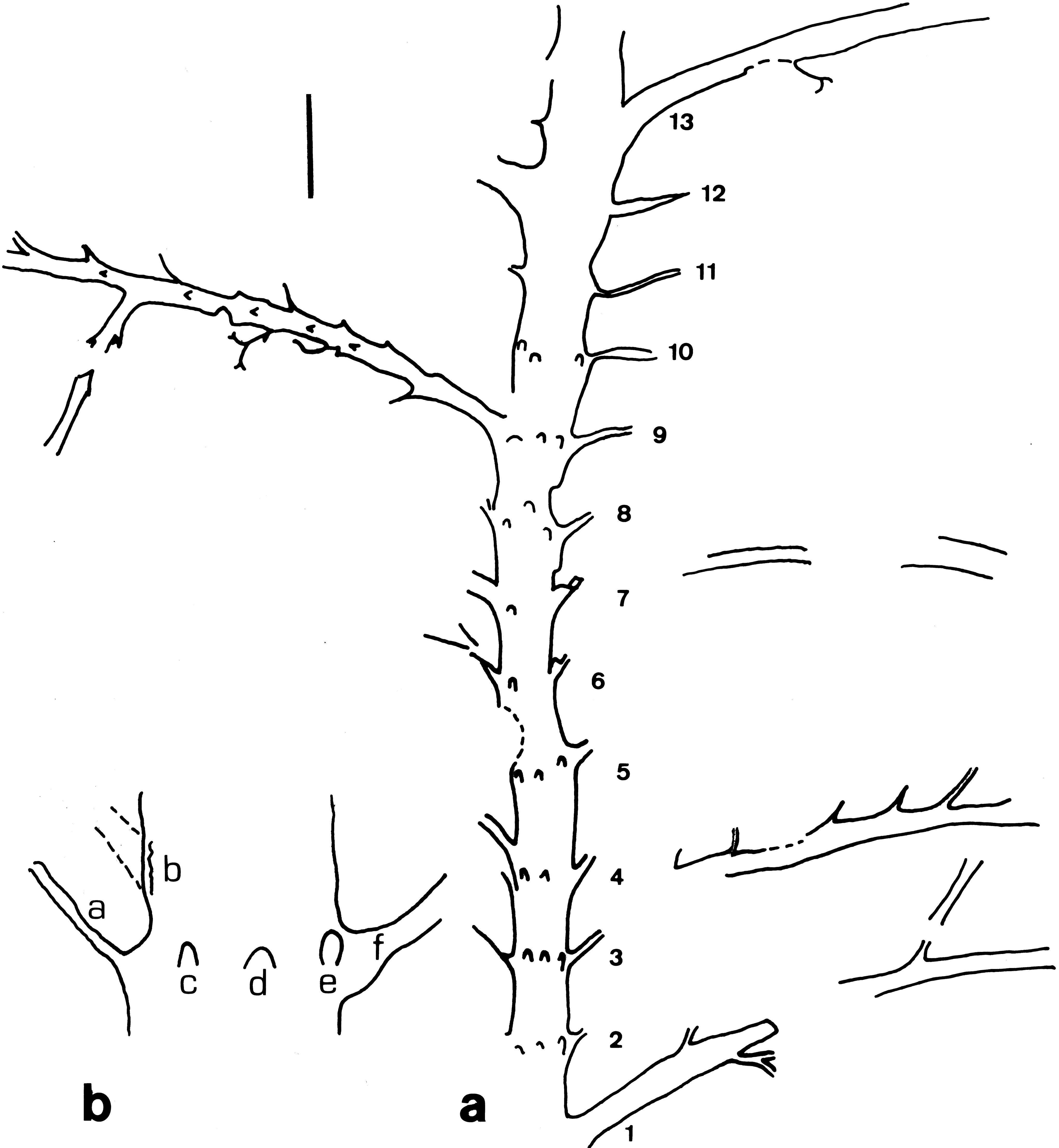
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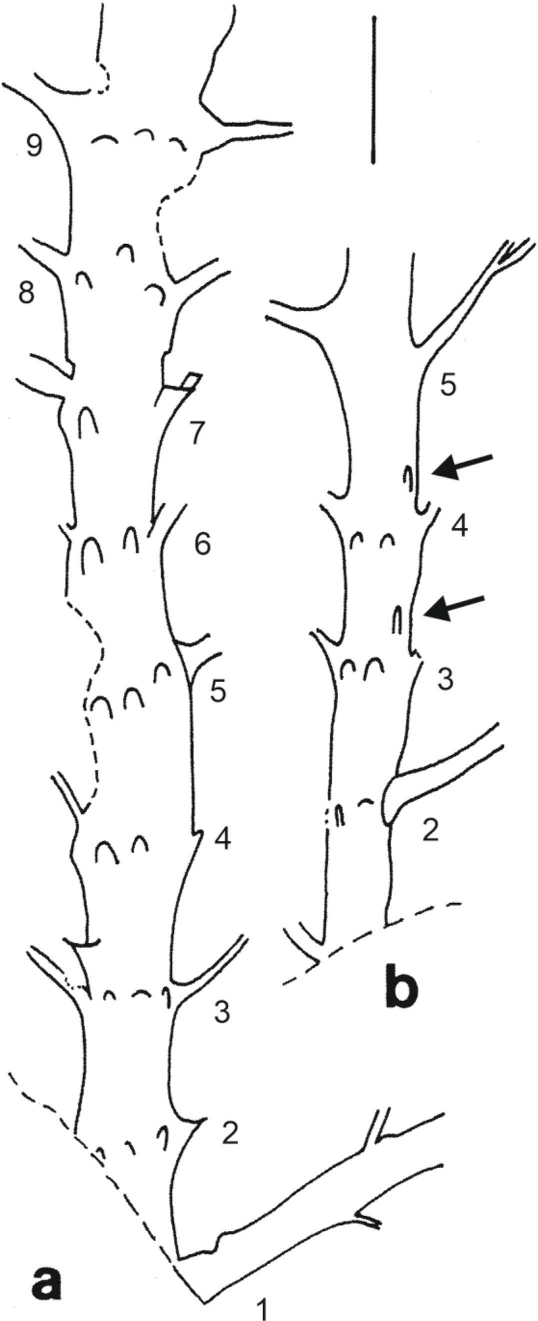
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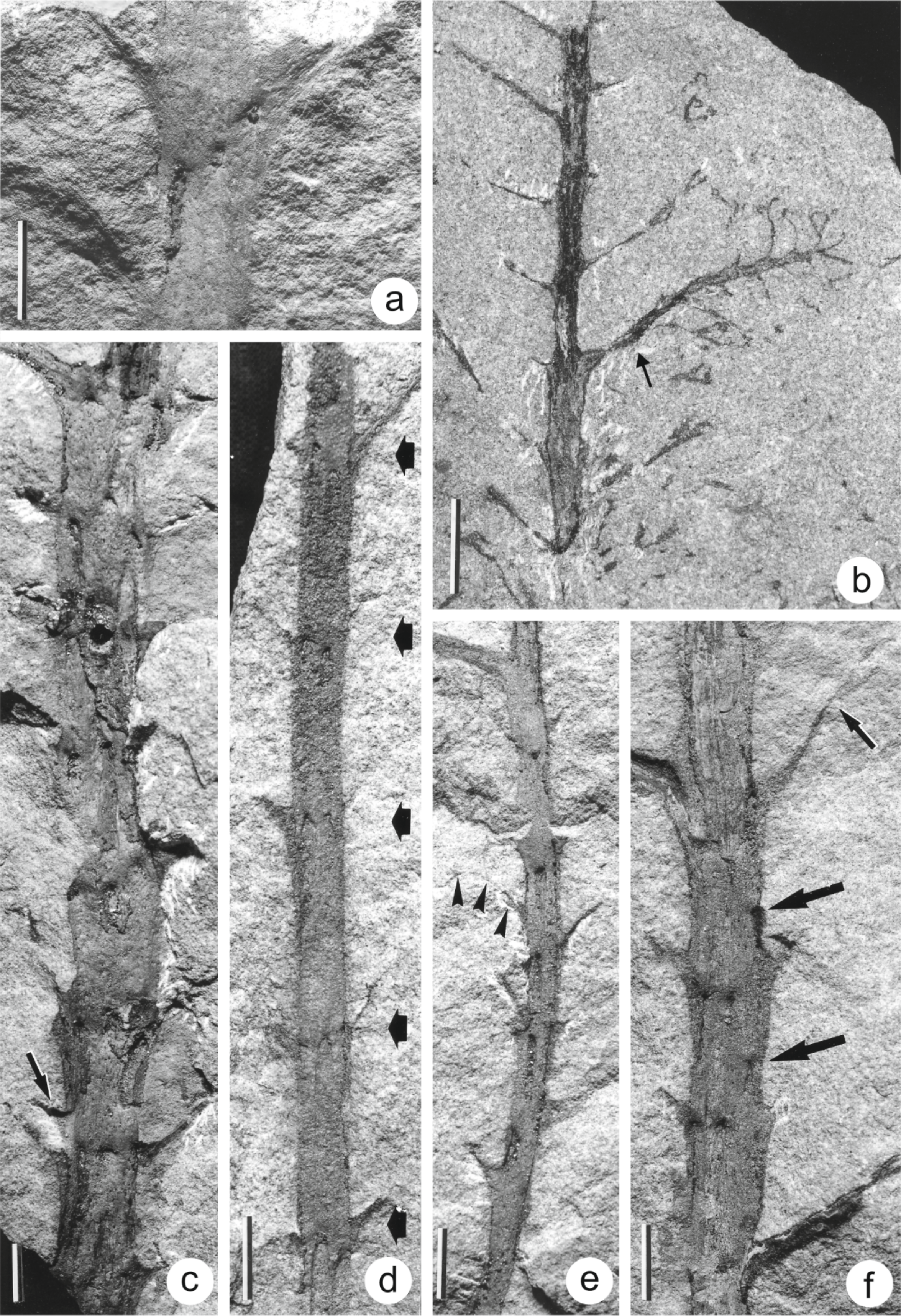
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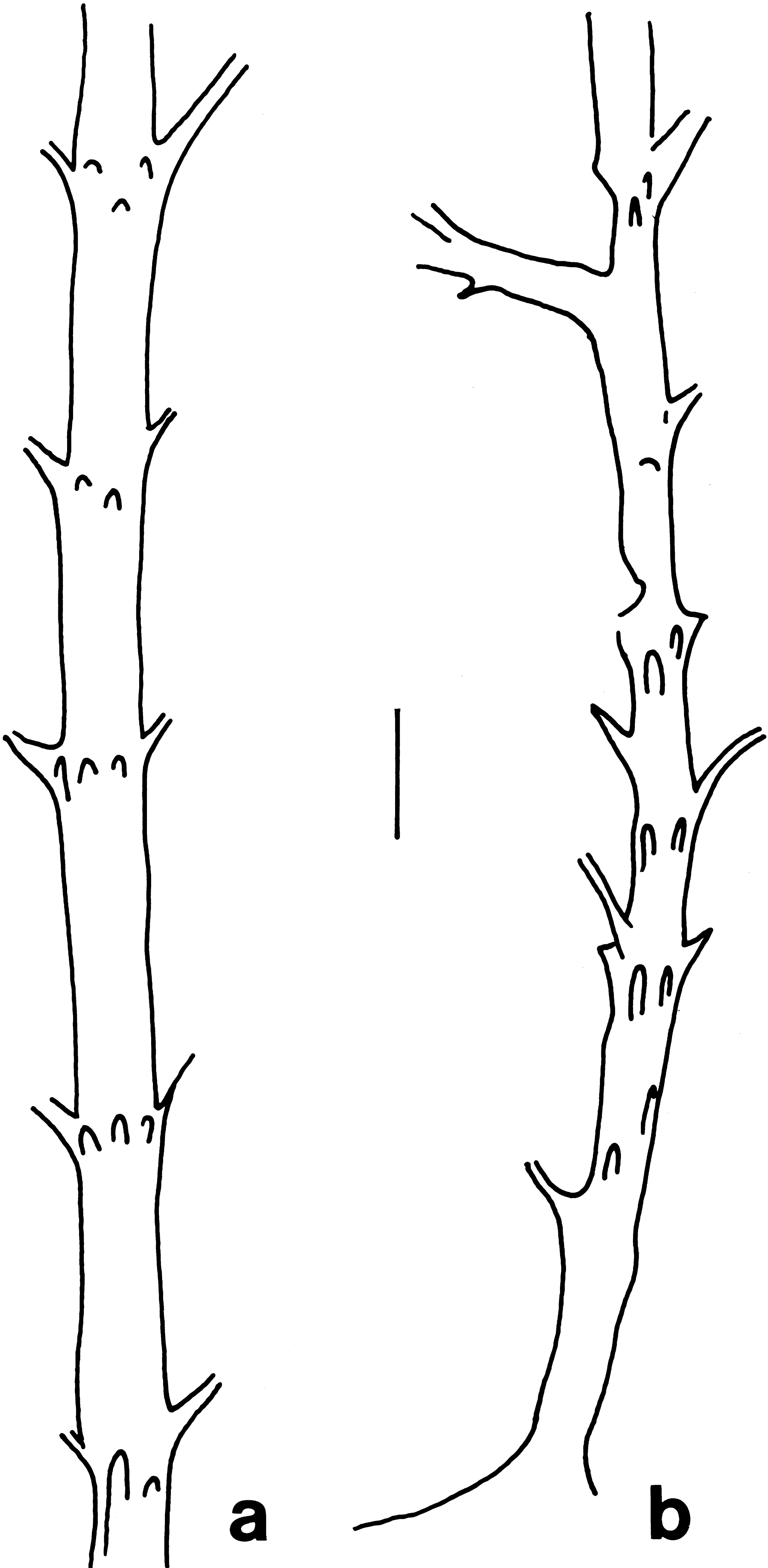
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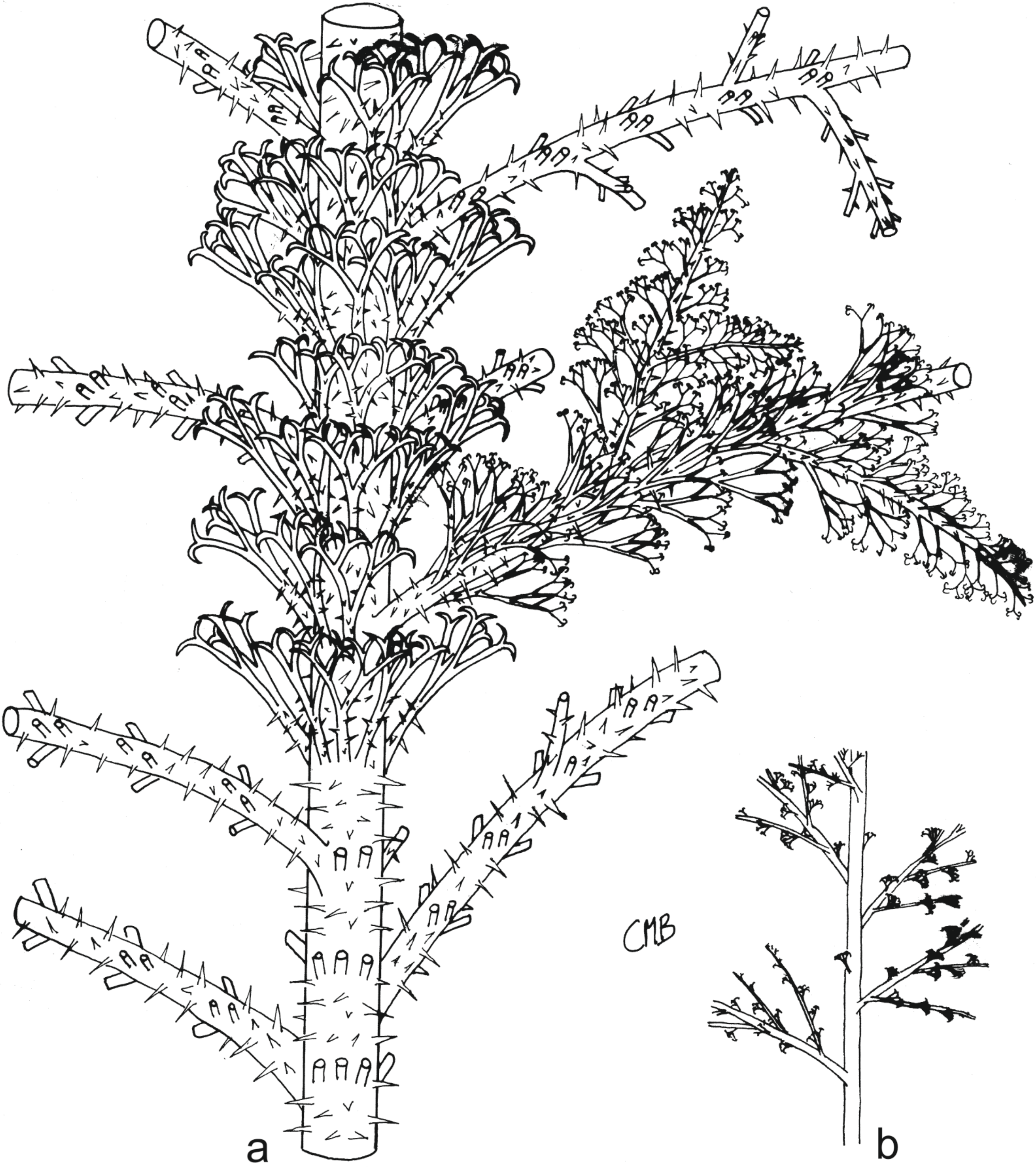
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