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

3

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14 *Ibyka* from Gilboa

15

16 **Plant fossil, Iridopteridales, Horsetails.**

17

18 Abstract

19

20 • Premise of the Research

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

25 • Methodology

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

29 • Pivotal Results

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

40 • Conclusions

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

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53 Introduction

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

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

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



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

101

## 102 **Materials and Methods**

103

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

117           According to Skog and Banks (1973), the material was derived from a single  
118 large block from the east bank of Schoharie Creek, directly below the spillway of the  
119 Gilboa dam, near Gilboa, Schoharie County, New York State (VanAller Hernick 2003;  
120 Stein et al. 2021). It likely came from material unearthed during construction of the  
121 dam, and is therefore believed to derive from the Cooperstown Formation correlative  
122 with the Manorkill Formation (late Middle Devonian/Givetian, likely mid to upper  
123 Givetian) based on lithostratigraphic correlation and limited palynostratigraphical  
124 control (see Stein et al. 2021). Two further unillustrated specimens (NYSM 5202)  
125 were mentioned as residing in the New York State Museum, Albany. Six slabs

126 bearing collection number 5202 have been studied by us, and the material seems  
127 identical with the concept of *lbyka* reported in this paper. The New York State  
128 Museum catalogue entry for this collection reads 'Ithaca beds. Fossil Plants. Gilboa,  
129 N.Y., ¼ mile downstream from bridge. W. Goldring and J. Bylancik, Colls., 1920.'  
130 Given that the present Gilboa dam was built at the site of the former bridge, the  
131 locality is likely to be at the southern end of the Riverside Quarry site (Skog and  
132 Banks 1973, Stein et al. 2021).

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

137

138

### 139 **Description**

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

145

#### 146 **First order axes**

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

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

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

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

168 A whorled or semi-whorled arrangement of lateral organs, including both  
169 branches and appendages, involves distinct nodes and internodes as deduced from  
170 the revealed stem surface. Thirteen nodes are identified on the lower 260 mm of the  
171 best-preserved portion of the axis (fig. 2a). The average spacing of these nodes is  
172 20.8 mm, although this varies between 18.6 and 24.7 mm. At node 3, where the most  
173 complete information is presented, the attachment of six appendages is preserved  
174 (figs 1a, 2a-b, 4c). Appendage *a* is visible on the left-hand side slightly above the  
175 plane of the compressed fossil and *f* is preserved lying flat beside the axis on the  
176 right-hand side. Attachments *c-e* are visible on the lower surface of the stem itself (fig  
177 2b). The base of appendage *b* was uncovered going down into the matrix on the left-  
178 hand side (fig. 2b). Projected continuation of this pattern around the unavailable  
179 counterpart of the stem suggests that this main axis carried nine or ten lateral organs  
180 in this and probably other whorls. Higher on this axis (e.g. nodes 8, 9 – fig. 3a) three  
181 attachment sites are visible on the stem surface as well as two appendages laterally,  
182 suggesting at least eight lateral organs in one complete whorl and therefore some  
183 diminution of the number of laterals distally.

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

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

195 In the second illustrated first order axis (Specimen 179; figs. 3b, 4f - arrows)  
196 the attachments of appendages on the right-hand side of nodes 3 and 4 are both  
197 displaced acropetally compared with the remaining attachments at each node. A third  
198 first order axis (Specimen 180 – 1994.12; Fig. 4a) of 10 mm diameter has three  
199 organs (presumed appendages) attached arranged diagonally across the stem plus

200 two with attachment beside the stem. This suggests local approximation to helical  
201 insertion, but this pattern does not continue over the complete whorl.

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

206

#### 207 Second order axes

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

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

224

#### 225 Third and fourth order axes

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

232 It is probable that fourth order branches are also present. Axis 186, which is 3  
233 mm in diameter, and therefore in the size-range expected for third order branches,  
234 seemingly bears a smaller axis a little over 1 mm in diameter in place of an  
235 appendage at one or more whorls (fig. 4b - arrow). Because of lack of attachment, it

236 is impossible to demonstrate if an interpretation of branch versus appendage based  
237 on size alone is altogether accurate.

238

### 239 Appendages

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

250 Appendages are not very well preserved on second order branches. One  
251 found beside the second order branch on specimen 180 has three dichotomies (fig.  
252 4e - arrows), the first probably perpendicular to the surface of the slab. The total  
253 preserved length of this appendage is at least 18 mm. The best example previously  
254 illustrated by Skog and Banks (1973, fig. 11) suggests that there are up to five  
255 dichotomies over a length of about 20 mm, the segments terminating in recurved tips.  
256 On possible third order axes the appendages are up to about 18 mm in total length  
257 (fig. 4b). Transfer preparations by Skog and Banks (1973, fig. 3) demonstrated that  
258 appendages are covered by very small spines at least to the second dichotomy. In  
259 terminal portions of putative fourth order axes (fig. 4b - arrow) the lateral branching  
260 systems are less than 5 mm in total length.

261

### 262 Fertile appendages

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

266

### 267 Comparisons

268

269 Our new interpretation of *Ibyka amphikoma* differs from that of Skog and  
270 Banks (1973) primarily in the demonstration that branching is predominantly whorled  
271 with distinct nodes and internodes. The whorls are most strict in the lower orders of  
272 branching and tend towards more irregular insertion, possibly approximating a helical

273 pattern within individual nodes in the higher orders. A true ontogenetic helix is not  
274 observed in any region of the plant. The  $n+1$  order of branching is located on the  $n$ th  
275 order in place of a dichotomous appendage within the whorl. Skog and Banks'  
276 interpretation was for a very lax helical pattern of branch and appendage insertion  
277 tending towards whorled in the higher orders of branching.

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

282

### 283 Comparison to other Iridopteridales

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

301 Outside North America, Berry and Edwards (1996) described a new plant,  
302 *Anapaulia moodyi*, from the Middle or lowermost Upper Devonian of western  
303 Venezuela, based on compression fossils only. This plant had four orders of axes,  
304 arranged in a predominantly whorled pattern, and was covered in small spines. Both  
305 dichotomous appendages and second order axes were found at nodes on first order  
306 axes. There are some minor differences between the Venezuelan plant and the  
307 interpretation of *Ibyka amphikoma* presented here. Firstly, in *Anapaulia*, the bases of  
308 the second order branches and appendages sometimes join in a ring around the first  
309 order axis to form a deep groove on the impression surface, rather than being

310 spaced out, crescentic and non-contiguous as in *Ibyka*. Secondly the distances  
311 between nodes on first order axes are much greater in *Anapaulia*, being from 25-75  
312 mm (these closest spaced whorls being only reported recently by Berry and Fairon-  
313 Demaret 2001, their Fig. 7.1C). Thirdly only third order axes are found attached to  
314 second order axes, no dichotomous appendages being present at this level of  
315 branching. Lastly sporangia are numerous and relatively well preserved in *Anapaulia*  
316 and are borne in pairs on strongly recurved terminal segments of fertile appendages.  
317 Thus we presently retain *Anapaulia* as a separate genus.

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

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

338 *Hyenia* (*Hyeniopsis*) *vogtii* Høeg (1942), from the Middle Devonian of  
339 Spitsbergen was based on axes from 5-7 mm in diameter. Two orders of branching  
340 were illustrated. Dichotomously branching 'leaves' (i.e. appendages) were arranged  
341 on both orders in a manner which was described as 'more or less verticillate, causing  
342 a corresponding articulation in the axes' (p. 83 of Høeg 1942), the distance between  
343 successive verticils being 'about two or three times the diameter of the axis'. The  
344 second order axes were described significantly as being 'invariably developed in the  
345 place of leaves, and not in the leaf axils'. The axes were longitudinally grooved,  
346 suggesting the impression of a ribbed vascular system, and carbonaceous traces into



347 lateral branching systems was preserved in the compressions. Spines or ‘thorns’,  
348 rarely up to 2 mm in length, were found on the margins of axes, and were  
349 represented on the surface of impressions by ‘small dots or scars’. Høeg recognised  
350 that the plant was different from the material from Norway and Germany described  
351 under the names *Hyenia sphenophylloides* (Nathorst 1915; Høeg 1931, 1935), the  
352 type species of *Hyenia*, and *H. elegans* (Kräusel and Weyland 1926) because of the  
353 differences in branching patterns and the presence of spines. However, the presence  
354 of dichotomous appendages seems enough to have persuaded him to place the  
355 material in *Hyenia*, albeit in the subgenus *Hyeniopsis*. No fertile material was  
356 present. Schweitzer (1999) transferred the species to the cladoxylopsid  
357 *Pseudosporochnus*. Re-examination of Høeg’s specimens, and confirmation of a  
358 whorled branching pattern, lead to the plant being transferred to *Ibyka vogtii* (Høeg)  
359 Berry by Berry (2005). New collections of this plant from the type locality have  
360 recently been made which should further clarify relationship with *I. amphikoma*  
361 (CMB).

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

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

378

379 Comparison to Cladoxylopsida

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

384 Demaret and Berry 2000 – including much material formerly assigned to *Hyenia*,  
385 Giesen and Berry 2013), *Pseudosporochnus* (Potonié and Bernard 1904, Berry and  
386 Fairon-Demaret 1997, 2002), *Eospermatopteris/Wattieza* (Berry 2000, Stein et al.  
387 2007) and *Lorophyton* (Fairon-Demaret and Li 1993). The principal morphological  
388 similarity of these genera with *Ibyka* is that they share lateral appendages that are  
389 based upon dichotomous units - this seems to have been taken as almost diagnostic  
390 for the genus *Hyenia* in the first half of the 20th Century. In pseudosporochnalean  
391 cladoxylopsids sporangia are generally arranged terminally and in pairs. In  
392 *Pseudosporochnus* the fertile lateral branching systems share the same basic  
393 morphology as the sterile ones, whereas those of *Calamophyton* have a modified  
394 sporangiophore (e.g. Leclercq and Andrews 1960).

395       Early reports of the arrangements of the appendages of *Hyenia*  
396 *sphenophylloides* (Nathorst 1915), *Hyenia elegans* (Kräusel and Weyland 1926,  
397 1929) and *Calamophyton primaevum* (Kräusel and Weyland 1932) emphasised a  
398 verticillate arrangement of appendage insertion. This has not been substantiated by  
399 recent work on these taxa (e.g. Leclercq and Andrews 1960; Schweitzer 1972, 1973;  
400 Fairon-Demaret and Berry 2000), excepting *H. sphenophylloides* as mentioned  
401 above. In the only Pseudosporochnales where the insertion pattern has been studied  
402 in detail (*Pseudosporochnus hueberii* - Stein and Hueber 1989; *P. nodosus* - Berry  
403 and Fairon-Demaret 1997; *Wattieza* Berry 2000) insertion has been shown to be  
404 neither helical or verticillate, instead having no regular geometric pattern.

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

415

#### 416 **A new reconstruction of *Ibyka amphikoma***

417

418       Our new reconstruction of *Ibyka* is shown in Figure 6a and can be compared  
419 with the reconstruction of Skog and Banks (1973, fig. 1; fig. 6b). Most obviously it can  
420 be seen that we recognise a basically whorled insertion of laterals which suggests a

421 more dense, profusely-branched arrangement contrasting starkly with the more lax,  
422 distantly spaced appendages and branches of the original. Our diagram was  
423 prepared from an overlay of a photograph of the largest specimen (180), and  
424 superposing branches and appendages onto the attachment points on the stem  
425 compression. It shows only a partial reconstruction of the plant as now possible to  
426 interpret it.

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

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

437         We include the recurved tips of appendages as illustrated by Skog and Banks  
438 1973 (their fig. 5) and in this paper (fig. 4b).

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

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

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

445

## 446 **Discussion**

447

### 448 *Relationship between anatomy and morphology*

449

450         Anatomical preparations taken from the type material of *Ibyka* include axes of  
451 about 4 mm diameter (Skog and Banks 1973, their figures 16, 17, 24) and have 5 or  
452 6 ribs with peripheral mesarch protoxylem strands. These are therefore interpreted  
453 by us to show the anatomy of second or probably third order axes. These  
454 preparations demonstrate a nodal arrangement of terete 'minor' traces presumably to  
455 appendages. These are inserted in a pattern possibly suggesting oblique plane of  
456 section or a shallow helix rather than a strict whorl. The latter observation is very

457 much in agreement with observations made of higher order branches on the  
458 compression fossils.

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

470 In *A. kopfii*, the 'major' trace is proximally a bipolar primary xylem strand  
471 elongated tangentially with two protoxylem strands. From each a terete 'subsidiary'  
472 trace is given, departing in a tangential direction. Once the xylem trace becomes  
473 elaborated distally into a four-ribbed primary xylem strand, Stein (1981, plate 6, fig.  
474 32, 24) a further pair of terete 'subsidiary' traces is produced from the abaxial ribs.  
475 Subsequent sections of the axis do not preserve the rest of the 'major' trace. Rather  
476 than interpret traces as comprising distinct pairs, it is also possible to interpret these  
477 traces as part of a basal whorl, as the oblique section cut through the 'major' trace  
478 would in the lowest sections reveal only the presence of traces on the abaxial ribs.  
479 We have not observed pairs of tangential lateral branching systems equivalent to the  
480 proximal pair of traces in *Ibyka*, but clearly observe the presence of whorls of  
481 appendages on second order branches.

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

491 Based on our knowledge of the morphology of *Ibyka*, *Anapaulia*, *Ibyka vogtii*  
492 and '*Hyenia*' *banksii*, and the anatomy of *Ibyka* and *Arachnoxylon* we can now

493 suggest a model for the basic architecture of iridopteridalean plants most closely  
494 related to *Ibyka*.

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

509

510

#### 511 *Higher level taxonomy and relationships*

512

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

528         Recently a cladistic analysis of known Iridopteridales, Cladoxylopsida and  
529 seemingly closely related plants, including examples from China, has been

530 undertaken by Durieux et al. (2021). Their analysis did not recognise Iridopteridales  
531 as a single clade (Durieux et al. (2021 figure 9)). Instead, based predominantly on  
532 morphology, *Ibyka* and *Anapaulia* formed one clade and anatomically preserved  
533 *Arachnoxylon*, *Iridopteris*, and *Asteropteris* formed another along with  
534 *Compsocradus*. The clade containing *Arachnoxylon* was placed as a sister group to  
535 an extended cladoxylopsid complex, and the *Ibyka/Anapaulia* clade as a sister group  
536 to the *Arachnoxylon* clade plus cladoxylopsids. *Rotoxylon*, with dissected primary  
537 xylem in their analysis, appears within cladoxylopsids, despite all other features  
538 being essentially iridopteridalean. Iridopteridalean features that can be noted include  
539 peripheral “permanent” protoxylem strands only, whorled trace departure, size  
540 relationship of tracheids within individual xylem ribs, and mode of trace departure  
541 reminiscent of both *Arachnoxylon* and *Iridopteris*. The only features that suggest  
542 cladoxylopsid relationship are vascular size and apparent dissection of the xylem  
543 column.

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

553 As examples of the issues, Durieux et al. (2021) resolve a monophyletic  
554 iridopteridalean clade based on fragmentary anatomical taxa (including *Arachnoxylon*  
555 species) plus *Compsocradus laevigatus*, but morphologically preserved *Ibyka* and  
556 *Anapaulia* fall outside of it. Here we compare their data and analysis for  
557 *Arachnoxylon kopfii* Read (sensu Stein 1981) and *Ibyka amphikoma* (Durieux et al.  
558 2021; their fig. 9; appendix S2 and S4).

559 Of 13 largely morphological characters (1-9, 33-36) 9 include missing data in  
560 one or the other species and 2 further characters are scored identically. We examine  
561 here the two remaining characters which are scored differently. Character 1  
562 (presence or absence of spines) is recorded as present in *Ibyka* and absent in  
563 *Arachnoxylon*. However, lack of preserved spines in *Arachnoxylon* is not a supported  
564 observation given the lack of preservation of the outer parts of the cortex and  
565 epidermis (Stein, 1981). Character 2 (taxis of ultimate appendages) is recorded as  
566 helical for *Ibyka*, but whorled in *Arachnoxylon*. Here taxis is defined as based on the

567 highest order preserved. We know from the present study that in *Ibyka* taxis changes  
568 from essentially whorled in the first order axis to nodal approximating to helical in the  
569 third and fourth order branches, so the level of branching selected affects the  
570 character state recorded. In *Arachnoxyton* taxis is only established for anatomically  
571 preserved axes which are equivalent in size to the first order axes of *Ibyka*, and is  
572 unknown for higher orders of axes. So this character is not equivalent between the  
573 two genera. We therefore conclude that of the 13 characters examined, none can  
574 meaningfully be scored as different between *Arachnoxyton* and *Ibyka*.

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



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

613 We therefore suspect that the polyphyly of iridopteridaleans in Durieux et al.'s  
614 2021 analysis, including the separation of largely anatomically vs largely  
615 morphologically preserved taxa, and potentially the loss of *Rotoxyton* from the group,  
616 may be a result of the methodology adopted, including missing data and fragmentary  
617 material relating to non-equivalent parts of the plants.

618

619 Whole-plant Concept for the Iridopteridales

620

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

637 By contrast, *Compsocradus*, while lacking spines, otherwise also shows  
638 anatomical evidence comparable to *Arachnoxyton*, although interestingly with angular  
639 offset of vascular traces and appendages in successive whorls. Similar 'alternate

640 whorls' are observed in anatomically preserved *Iridopteris* and *Rotoxylon*. In  
641 *Compsocradus* every other primary xylem rib contributes to a whorl of lateral  
642 elements, whereas in *Iridopteris*, each rib contributes traces asymmetrically to supply  
643 'alternate' whorls. Additionally, *Iridopteris* seemingly exhibits bilateral symmetry of the  
644 vascular system (Stein 1982a), although it must be emphasized that the presence of  
645 only five primary xylem ribs in both known specimens may inadvertently confer this  
646 appearance. *Rotoxylon* represents an apparently larger axis 15 mm in diameter  
647 perhaps suggesting that at least some iridopteridalean whole plants were much  
648 larger and more complex than previously supposed. This taxon has 18 radially  
649 directed primary xylem ribs and permanent protoxylem strands. Small vascular  
650 traces possibly corresponding to appendages, are seemingly produced radially as in  
651 *Arachnoxylon*, whereas others are offset to subsequent whorls very much as in  
652 *Iridopteris*.

653         Although lateral organs produced in whorls is currently important in  
654 recognizing the Iridopteridales, the diversity of stelar configurations directly points to  
655 the necessity of incorporating known developmental processes into study of these  
656 fossil plants. It is known in modern plants, for instance, that initiation of lateral  
657 appendages largely determines the developmentally subsequent pattern of  
658 provascular and xylem differentiation via hormonal influence (Sachs 1991, Stein  
659 1993, Chomicki et al. 2017). In the Iridopteridales, we suggest that similar  
660 developmental processes likely produced a rough correspondence of primary xylem  
661 ribs to the number of lateral elements produced at each whorl. However, the fossils  
662 clearly show that this correspondence was far from exact, and other hormonal or  
663 physical factors, including size of the main shoot apex, probably also played a role.  
664 Specifically, these additional factors may also have influenced the number of xylem  
665 ribs, determined xylem rib radial length, established the pattern of radial rib  
666 bifurcation, as well as in the case of *Rotoxylon*, dissection of the entire xylem system.  
667 As a result, in comparing *Compsocradus* with *Iridopteris* for instance, although  
668 sharing 'alternate' vascular trace departure, this pattern may have become modified  
669 into strikingly different outcomes by subtly divergent developmental systems  
670 governing xylem maturation as a whole, possibly related to axis size.

671         In sum, the diversity of morphology and especially anatomy assigned to the  
672 Iridopteridales rather than serving as clear cut differences suitable for phylogenetic  
673 study, strongly points to what we have yet to learn about this group as whole plants.  
674 Critical issues remain to be resolved, not the least among them is their overall plant

675 stature and habit. Previous work on *Hyenia* has commonly inferred a rhizomatous  
676 habit potentially applicable to the group as a whole (e.g. Høeg 1945), but convincing  
677 evidence for this view has yet to be confirmed. Moreover, *Asteropteris* and *Rotoxylon*  
678 points to the possibility that some of these plants were significantly larger and more  
679 complex than currently supposed. *Asteropteris* showing production of mostly major  
680 traces, suggests more basal portions of Iridopteridaleans may have involved mostly  
681 branch production. *Rotoxylon* with a dissected xylem column may point to the  
682 Cladoxylopsida, possibly even pseudosporochnaleans, as a model for their eventual  
683 reconstruction.

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

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

702

703 *Ibyka*, Iridopteridales and the origins of Horsetails

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

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

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

743

744 Systematic Palaeobotany

745

746 Order - Iridopteridales Stein 1982a

747

748 Genus - *Ibyka* Skog et Banks 1973 emend.

749

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

760

761 *Ibyka amphikoma* Skog et Banks 1973 emend.

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

764

765 Conclusions

766

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

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

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

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

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

802

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812 **References**

813

814 Ananiev AR 1957 New plant fossils from the Lower Devonian of Torgachino in the  
815 south-eastern part of Western Siberia. Bot Zh 42:691-702.

816

817 Arnold CA 1935 Some new forms and new occurrences of fossil plants from the  
818 Middle and Upper Devonian of New York State. Bull Buffalo Soc Nat Sci 17:1-12

819

820 Arnold CA 1940 Structure and relationships of some Middle Devonian plants from  
821 western New York. Am J Bot 27:57-63.

822

823 Arnold CA 1941 Observations on fossil plants from the Devonian of eastern North  
824 America. V. *Hyenias banksii* sp. nov. Contrib Mus Paleontol Univ Mich 6:53-57.

825

826 Berry CM 2000 A reconsideration of *Wattieza* Stockmans (here attributed to  
827 Cladoxylopsida) based on a new species from the Devonian of Venezuela. Rev  
828 Palaeobot Palynol 112:125-146.

829

830 Berry CM, 2005 '*Hyenias*' *vogtii* Høeg from the Middle Devonian of Spitsbergen – Its  
831 morphology and systematic position. Rev Palaeobot Palynol 135:109-116.

832

833 Berry CM, D Edwards 1996 *Anapaulia moodyi* gen. et sp. nov., a probable  
834 iridopteridalean compression fossil from the Devonian of Venezuela. Rev Palaeobot  
835 Palynol 93:127-145.

836

837 Berry CM, M Fairon-Demaret 1997 A reinvestigation of the Cladoxylopsid  
838 *Pseudosporochnus nodosus* Leclercq et Banks from the Middle Devonian of Goé,  
839 Belgium. Int J Plant Sci 158:350-372.

840

841 Berry CM, M Fairon-Demaret 2001 The Middle Devonian Flora Revisited. 120-139. In  
842 Gensel PG, D Edwards (eds) Plants Invade the Land. Columbia University Press, New  
843 York

844

845 Berry CM, M Fairon-Demaret 2002 The architecture of *Pseudosporochnus nodosus*  
846 Leclercq et Banks: A Middle Devonian cladoxylopsid from Belgium. Int J Plant Sci  
847 163(5): 699-713.

848



849 Berry CM, W Stein 2000 A New Iridopteridalean from the Devonian of Venezuela. Int  
850 J Plant Sci 161:807-827.  
851

852 Berry CM, W Stein, Wyatt A 2021 Untangling *Ibyka*: Morphology of Devonian  
853 Iridopteridales from Laurussia and western Gondwana. Abstracts, Botany 2021.  
854 <http://www.botanyconference.org/engine/search/index.php?func=detail&aid=751>  
855

856 Bertrand P 1913 Étude du stipe de l'*Asteropteris noveboracensis*. Compte rendu 12e  
857 Congrès géologie du Canada: 909-924.  
858

859 Champreux A, B Meyer-Berthaud, AL Decombeix 2020 *Keraphyton* gen. nov., a new  
860 Late Devonian fern-like plant from Australia. *PeerJ*, 8, e9321.  
861 <https://doi.org/10.7717/peerj.9321>  
862

863 Chomicki G, M Coiro, SS Renner 2017 Evolution and ecology of plant architecture:  
864 integrating insights from the fossil record, extant morphology, developmental  
865 genetics and phylogenies. *Ann Bot* 120: 855-891.  
866

867 Cordi J, WE Stein 2005 The Anatomy of *Rotoxylon dawsonii* comb. nov. (*Cladoxylon*  
868 *dawsonii*) from the Upper Devonian of New York State. *Int J Plant Sci* 166:1029-  
869 1045.  
870

871 Dawson JW 1881 Notes on new Erian (Devonian) plants. *Q J Geol Soc Lond*  
872 37 :299-308.  
873

874 Durieux T, MA Lopez, AW Bronson, AMF Tomescu 2021 A new phylogeny of the  
875 cladoxylopsid plexus: contribution of an early cladoxylopsid from the Lower Devonian  
876 (Emsian) of Quebec. *Am J Bot* 108: 2066– 2095.  
877

878 Fairon-Demaret M, CM Berry 2000 A reconsideration of *Hyenia elegans* Kräusel et  
879 Weyland and *Hyenia 'complexa'* Leclercq: two Middle Devonian Cladoxylopsids from  
880 Western Europe. *Int J Plant Sci* 161:473-494.  
881

882 Fairon-Demaret M, J Hilton, CM Berry 1999 Morphology - surface preparation of  
883 fossils. Pages 33-35 in T Jones, N Rowe, eds. *Fossil Plants and Spores; modern*  
884 *techniques*. Special Publication of the Geological Society of London.

885

886 Fairon-Demaret M, Li C-S 1993 *Lorophyton goense* gen. et sp. nov. from the Lower  
887 Givetian of Belgium and a discussion of the Middle Devonian Cladoxylopsida. Rev  
888 Palaeobot Palynol 77:1–22.

889

890 Fu Q, Y Wang, CM Berry, H-H Xu 2011 Complex branching patterns in a newly  
891 recognized species of *Compsocradus* Berry et Stein (Iridopteridales) from the Middle  
892 Devonian of North Xinjiang, China. Int J Plant Sci 172:707-724.

893

894 Giesen P, CM Berry 2013 Reconstruction and growth of the early tree *Calamophyton*  
895 (Pseudosporochnales, Cladoxylopsida) based on exceptionally complete specimens  
896 from Lindlar, Germany (Mid Devonian): organic connection of *Calamophyton*  
897 branches and *Duisbergia* trunks. Int J Plant Sci 174:665-686

898

899 Høeg OA 1931 Notes on the Devonian flora of western Norway. Kgl Norske Vid  
900 Selsk Skr 6:1-33.

901

902 Høeg, OA 1935 Further contributions to the Middle Devonian flora of western  
903 Norway. Norske Geol Tidsskr 15:1-17.

904

905 Høeg, OA 1942 The Downtonian and Devonian flora of Spitzbergen. Norges  
906 Svalbard-og Ishavs-Unders Skr 83:1-228.

907

908 Høeg, OA 1945 Contributions to the Devonian flora of western Norway III. Norsk  
909 Geol Tidsskr 25: 183-192.

910

911 Kenrick P, PR Crane 1997 The origin and early diversification of land plants: a  
912 cladistic study. Smithsonian Institution Press: 441pp.

913

914 Kräusel R, H Weyland 1926 Beiträge zur Kenntnis der Devonflora. II. Abh Senkenb  
915 Natforsch Ges 40:115–155.

916

917 Kräusel R, H Weyland 1929 Beiträge zur Kenntnis der Devonflora. III. Abh Senkenb  
918 Natforsch Ges 41:315–360.

919

920 Kräusel R, H Weyland 1932 Pflanzenreste aus dem Devon. III. Über *Hyenia* Nath.  
921 Senckenbergiana 14:274-280.  
922  
923 Leclercq S 1960 Refendage d'une roche fossilifère et dégagement de ses fossils  
924 sous binoculaire. Seckenb Lethaea 41:483-487.  
925  
926 Leclercq S, HN Andrews 1960 *Calamophyton bicephalum*, a new species from the  
927 Middle Devonian of Belgium. Ann Mo Bot Gard 47:1-23.  
928  
929 Leclercq S, HP Banks 1962 *Pseudosporochnus nodosus* sp. nov., a Middle Devonian  
930 plant with cladoxylalean affinities. Palaeontogr Abt B 110:1-34.  
931  
932 Leclercq S, KM Lele 1968 Further investigation on the vascular system of  
933 *Pseudosporochnus nodosus* Leclercq et Banks. Palaeontogr Abt B 123:97-112.  
934  
935 Leclercq S, HJ Schweitzer 1965 *Calamophyton* is not a sphenopsid. Acad R Belg CI  
936 Sci Bull 51:1395-1403.  
937  
938 Nathorst, AG 1915 Zur Devonflora des westlichen Norwegens. Bergens Mus Arb 9:1-  
939 34.  
940  
941 Pichi-Sermolli R 1959 Pteridophyta. Pages 421-493 in WB Turrill, ed. Vistas in Botany.  
942 Pergamon, London.  
943  
944 Potonié H, C Bernard 1904 Flore dévonienne de l'étage H de Barrande. Pages 1-68  
945 in J Barrande, ed. Système Silurien du centre de la Bohème. Charles Bellmann,  
946 Prague.  
947  
948 Read CB 1938 Some Psilophytales from the Hamilton group in western New York.  
949 Torrey Botanical Club Bulletin, 65:599-606.  
950  
951 Rowe NP, JA Galtier J 1989 A Lower Carboniferous plant assemblage from La Serre  
952 (Montagne Noire, France). Part I. Rev Palaeobot Palynol 61:239-271.  
953  
954 Sachs, T. 1991. Pattern Formation in Plant Tissues. Cambridge Univ. Press 234 pp.  
955  
956 Schweitzer H-J 1972 Die Mitteldevon-Flora von Lindlar (Rheinland). 3. Filicineae-

957 *Hyenia elegans* Kräusel & Weyland. Palaeontogr Abt B 137:154–175.  
958  
959 Schweitzer H-J 1973 Die Mitteldevon-Flora von Lindlar (Rheinland). 4. Filicineae-  
960 *Calamophyton primaevum* Kräusel & Weyland. Palaeontogr Abt B 140:117–150.  
961  
962 Schweitzer H-J 1999 Die Devonflore Spitzbergens. Palaeontographica Abt B 252:1-  
963 122.  
964  
965 Skog JE, HP Banks 1973 *Ibyka amphikoma*, gen. et sp. n., a new protoarticulate  
966 precursor from the late Middle Devonian of New York State. Amer J Bot 60:366-380.  
967  
968 Soria A, B Meyer-Berthaud 2003 Occurrence of whorled organotaxis in the  
969 cladoxylopsid *Pietzschia polyupsilon* Read and Campbell (Lower Carboniferous,  
970 USA). Rev Palaeobot Palynol 124:29-49,  
971  
972 Stein WE 1981 Reinvestigation of *Arachnoxylon kopfii* from the Middle Devonian of  
973 New York State, U.S.A. Palaeontogr Abt B 147:90-117.  
974  
975 Stein WE 1982a *Iridopteris eriensis* from the Middle Devonian with systematics of  
976 apparently related taxa. Bot Gaz 143:401-416.  
977  
978 Stein WE 1982b The Devonian plant *Reimannia*, with a discussion of the Class  
979 Progymnospermopsida. Palaeontology 25: 605-622.  
980  
981 Stein WE 1993 Modeling the evolution of stelar architecture in vascular plants. Int J  
982 Plant Sci 154:229-263.  
983  
984 Stein WE 1998 Developmental logic: establishing a relationship between  
985 developmental process and phylogenetic pattern in primitive vascular plants. Rev  
986 Palaeobot Palynol 102:15-42.  
987  
988 Stein WE, CM Berry, LVA Hernick, F Mannolini 2021 The classic mid-Devonian  
989 *Eospermatopteris* localities, Gilboa NY, USA. Rev Palaeobot Palynol 295: 104520  
990  
991 Stein WE, JS Boyer 2006 Evolution of land plant architecture: beyond the telome  
992 theory. Paleobiology 32:450-482.

993  
994 Stein WE, FM Hueber 1989 The anatomy of *Pseudosporochnus*: *P. hueberi* from the  
995 Devonian of New York. Rev Palaeobot Palynol 60:311-359.  
996  
997 Stein WE, F Mannolini, LV Hernick, E Landing & CM Berry 2007 Giant cladoxylopid  
998 trees resolve the enigma of the Earth's earliest forest stumps at Gilboa. Nature  
999 446:904-907.  
1000  
1001 Stein WE, DC Wight, CB Beck 1983 *Arachnoxylo*n from the Middle Devonian of  
1002 southwestern Virginia Can J Bot 61:1283-1299.  
1003  
1004 Stein WE, DC Wight, CB Beck 1984 Possible alternatives for the origins of  
1005 Sphenopsida. Syst Bot 9:102-118.  
1006  
1007 Stockmans F 1968 Végétaux mésodévonienés récoltés aus confins du Massif du  
1008 Brabant (Belgique). Mém Inst R Sci Nat Belg 159:1-49.  
1009  
1010 Unger F 1856 Beiträge zur Palaeontologie des Thuringer Waldes. Teil 2. Schiefer  
1011 und Sandstein Flora. Kgl Akad Wiss Denkschr 11:139-186,  
1012  
1013 VanAller Hernick L 2003 The Gilboa Fossils New York State Museum Circular 55:  
1014 100pp.  
1015  
1016

1017 **Figure captions**

1018

1019 **Figure 1**

1020 *Ibyka amphikoma* Skog et Banks from Gilboa, New York.

1021 a) Close-up view of node 3, specimen 180, 1st order, showing attachments of  
1022 appendages (see fig. 2a). Scale bar = 10 mm.

1023 b) Close-up view of specimen 180, 1st order, nodes 9 and 10, showing nodal regions  
1024 with imperfect whorls of attachments of laterals (see fig. 2a). Hair bases marked by  
1025 fine plugs of coal on stem surface. Scale bar = 10 mm.

1026 c) General view of best preserved part of specimen 180, showing three orders of  
1027 branching (third order marked by large arrow). Insertion of second order branches on  
1028 first order at margin of impression marked by narrow arrows (nodes 1, 7, 9, 12, 13).  
1029 For numbering of nodes see fig. 2a. Scale bar = 10 mm.

1030

1031 **Figure 2.**

1032 *Ibyka amphikoma* Skog et Banks from Gilboa, New York.

1033 a) Lowest 13 nodes (numbered) of specimen 180, showing position of attachments of  
1034 visible laterals. Photographic illustration in fig. 1c. Scale bar = 20 mm.

1035 b) Close up of node 3, showing attachments of six visible laterals in imperfect whorl  
1036 (compare with fig. 1c, 3a, 4c).

1037

1038 **Figure 3.**

1039 *Ibyka amphikoma* Skog et Banks from Gilboa, New York.

1040 Line drawing of insertion of laterals on first order axes.

1041 a) Specimen 180 (see figs 1c, 4c). b) Specimen 179 (see fig. 4f). Appendages which  
1042 are inserted above rest of whorl (arrows). Scale bar = 20 mm.

1043

1044 **Figure 4.**

1045 *Ibyka amphikoma* Skog et Banks from Gilboa, New York.

1046 a) First order axis, demonstrating attachments of appendages at node locally  
1047 suggesting helical insertion. Scale bar = 10 mm. Specimen 180 (counterpart  
1048 fragment 1994.12)

1049 b) Probable 3rd and 4th order (arrow) axes. Specimen 186. Note recurved tips of  
1050 appendages on highest order axis. Scale bar = 10 mm.

1051 c) Close up of 1st order axis, showing arrangement of insertion points of laterals.

1052 Note appendage *b* uncovered at node 3 (arrow), for line drawing see fig. 2b.

1053 Specimen 180. Scale bar = 10 mm.

1054 d) Second order axis showing well-defined whorls (arrows). Sample number 180  
1055 (counterpart fragment 1994.12). For line drawing see fig. 5a. Scale bar = 10 mm.  
1056 e) Second order axis with attached 3rd order axis distally, as seen on left margin of  
1057 main specimen (fig. 1c). Dichotomous appendage visible (dichotomies indicated by  
1058 arrows). For line drawing showing appendage attachment pattern see fig. 5b.  
1059 Specimen 180. Scale bar = 10 mm.  
1060 f) First order axis. Note attachments of appendages displaced upwards from rest of  
1061 whorl (large arrows, for line drawing see fig. 3b). Also dichotomy of appendage (small  
1062 arrow). Specimen 179. Scale bar = 10 mm.

1063

1064 Figure 5.

1065 *Ibyka amphikoma* Skog et Banks from Gilboa, New York.

1066 Line drawings of insertion of laterals on second order branches.

1067 a) Sample number 1994.12 (see fig. 4d). b) Specimen 180 (see figs 1c, 4e). Scale  
1068 bar = 10 mm.

1069

1070 Figure 6.

1071 a) New partial reconstruction of *Ibyka amphikoma* Skog et Banks based on the  
1072 observations of this study. Width of first order axis at base is approximately 16 mm.

1073 b) Former reconstruction of *Ibyka amphikoma* redrawn from Skog and Banks (1973).

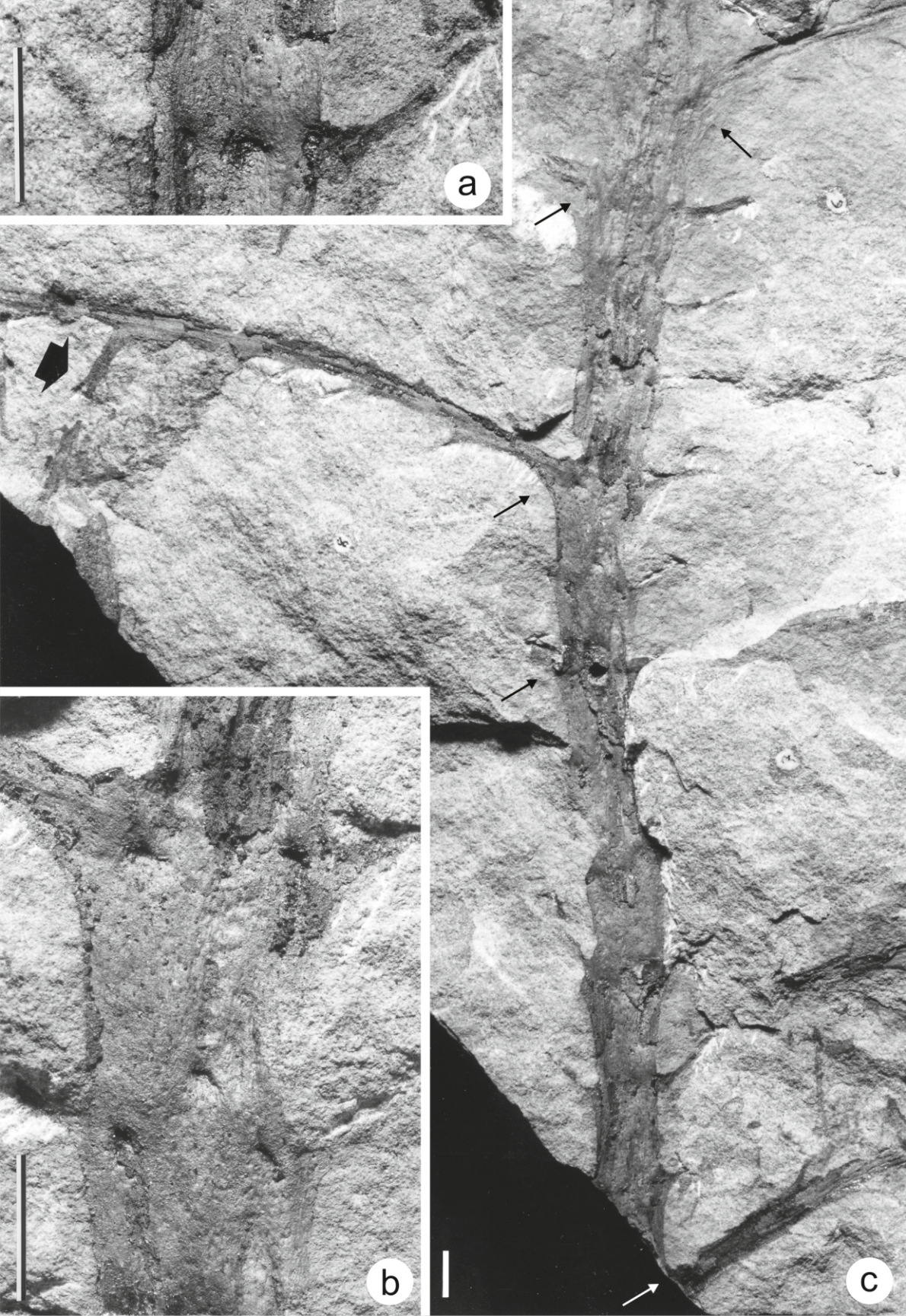
1074

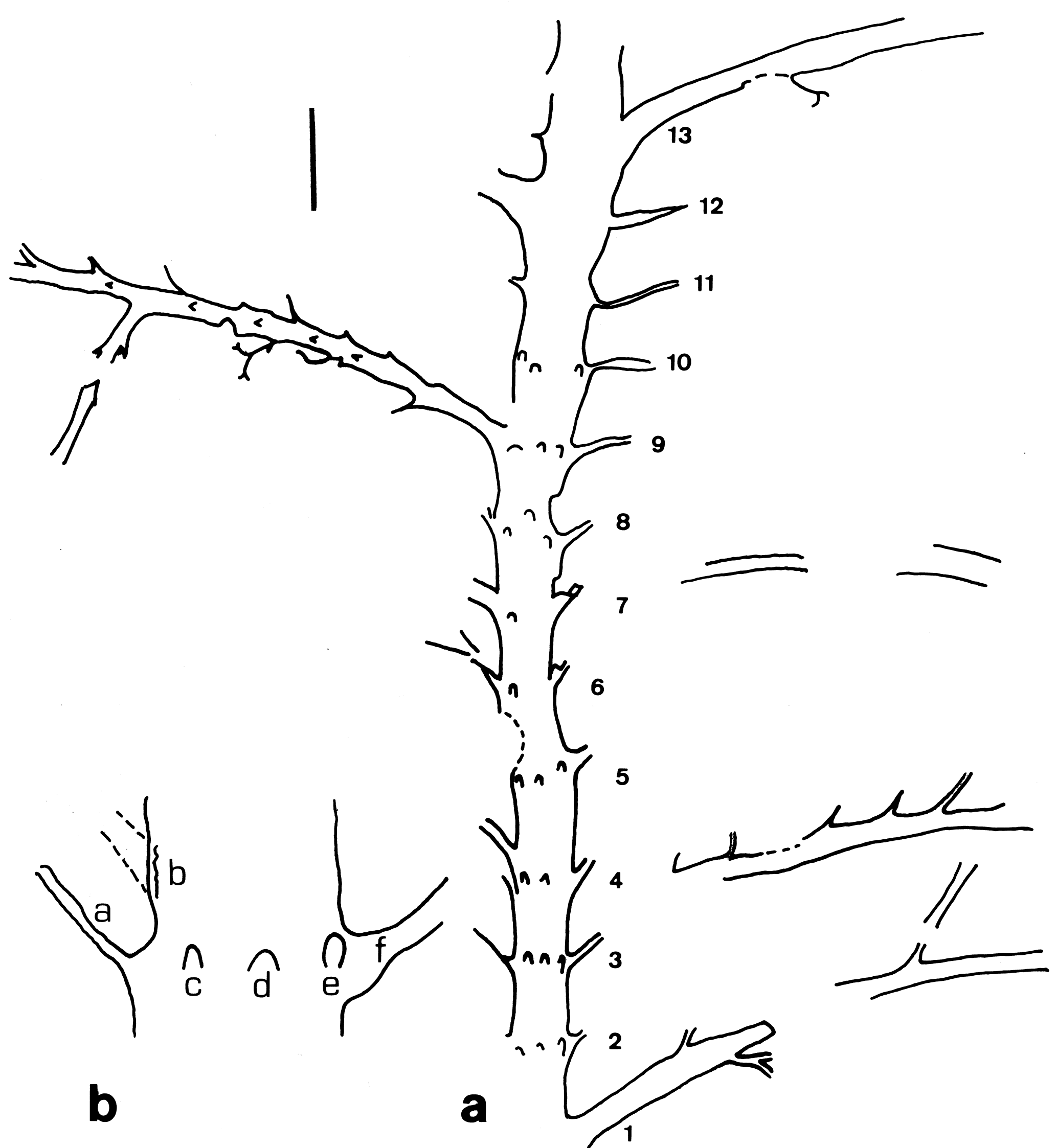
1075

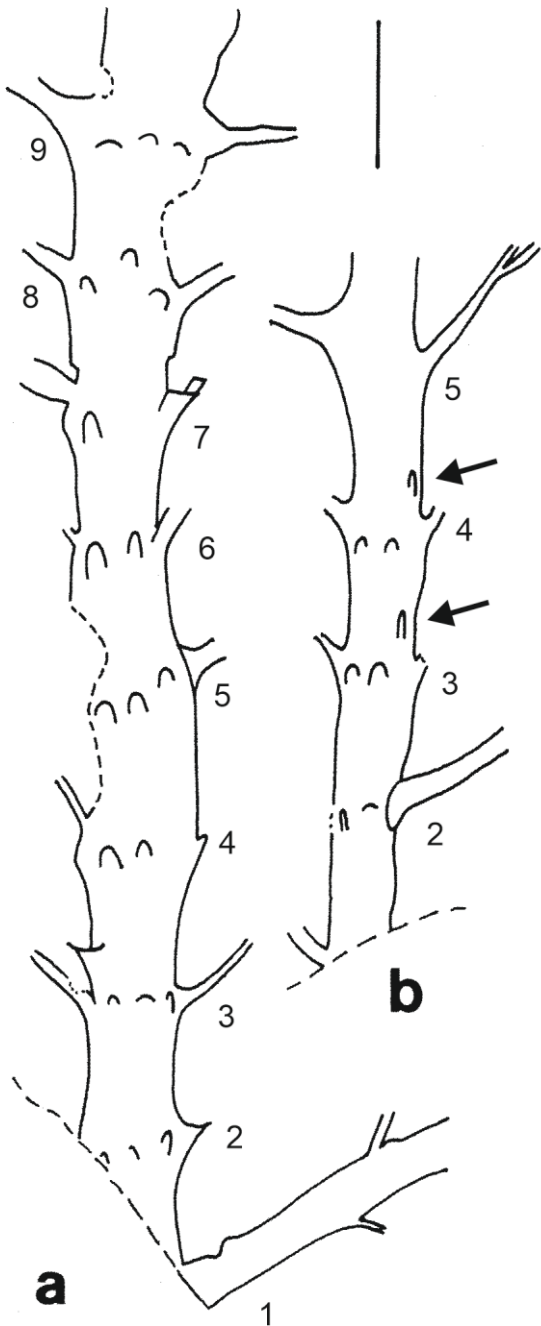
1076

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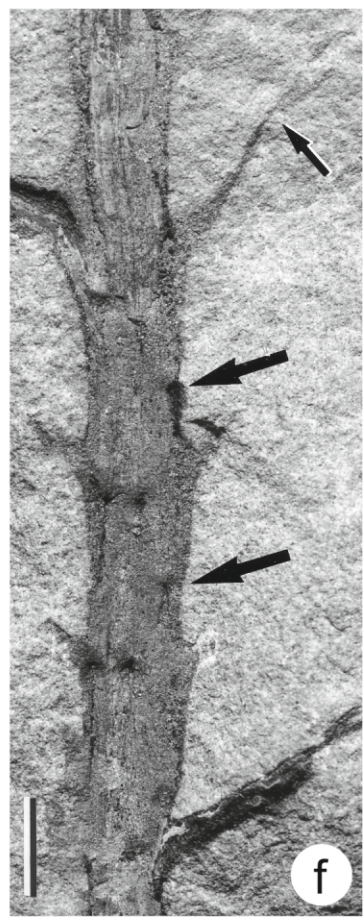
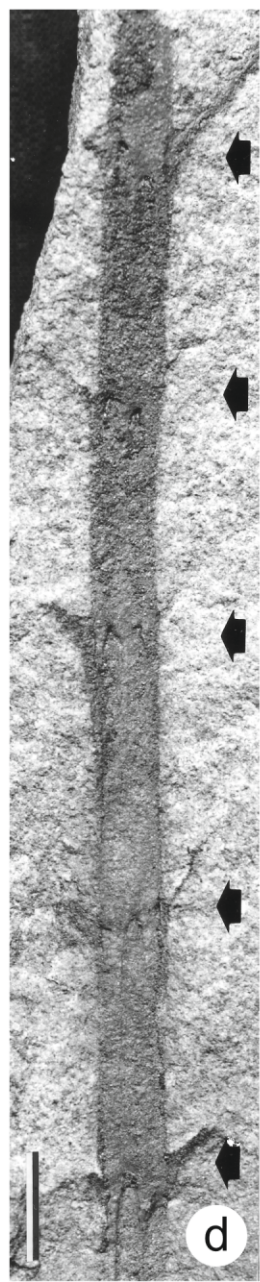


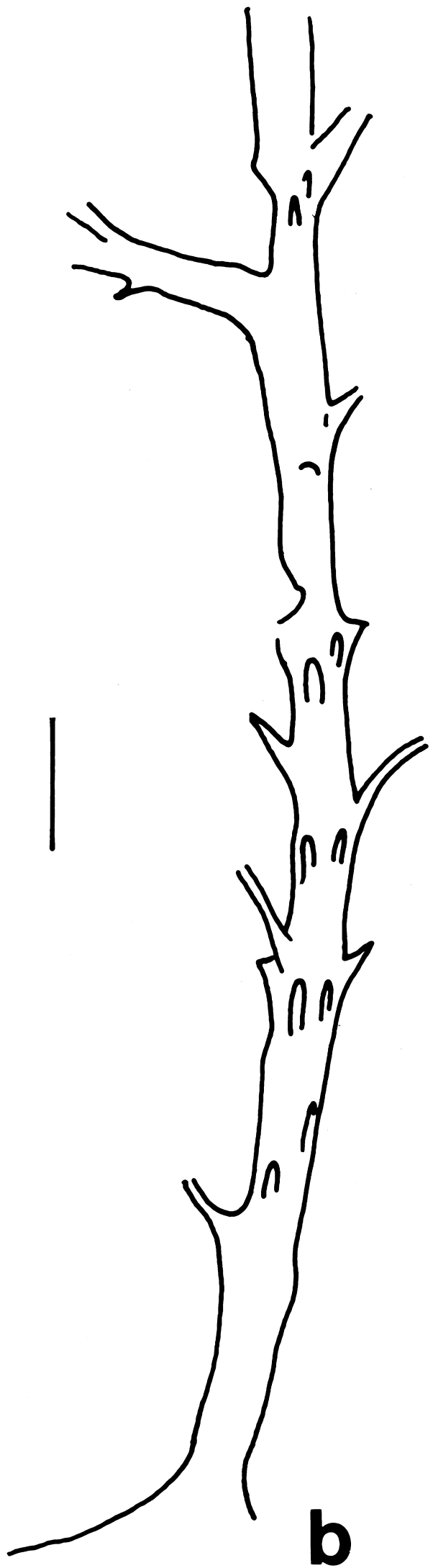
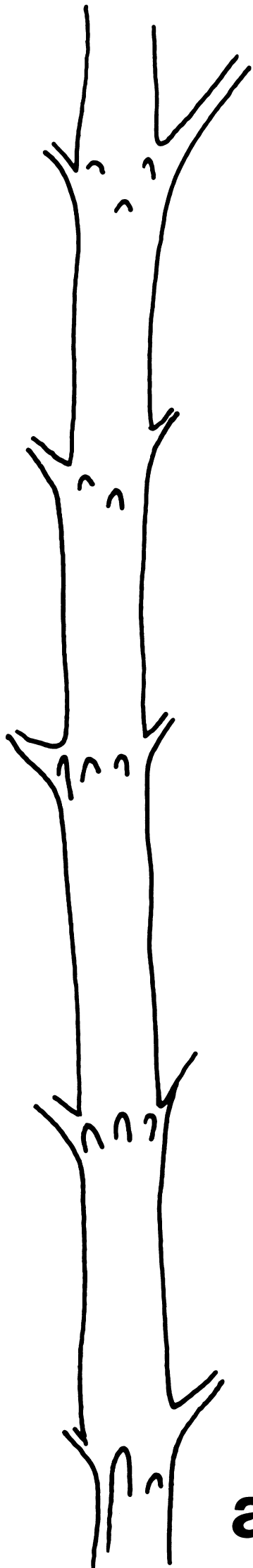












**a**

**b**



