

1 **A new phylogeny of the cladoxylopsid plexus – contribution of an early cladoxylopsid from the**
2 **Lower Devonian (Emsian) of Quebec**

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14 Running head: NEW EARLY DEVONIAN CLADOXYLOPSID AND PHYLOGENY

15 **Abstract**

16

17 **PREMISE OF THE STUDY:** Cladoxylopsids formed earth's earliest forests and gave rise to the
18 ancestors of sphenopsids and ferns. Lower Devonian (Emsian) strata of the Battery Point Formation
19 (Quebec, Canada) contain new anatomically preserved cladoxylopsids, one of which is described
20 here. To assess the phylogenetic position of this fossil and address questions of cladoxylopsid
21 phylogeny, we conducted a comprehensive phylogenetic study.

22

23 **METHODS:** Permineralized axes were studied in serial sections using the cellulose acetate peel
24 technique. We evaluated phylogenetic relationships among cladoxylopsids using a dataset of 36 new
25 morphological characters and 31 species, in parsimony-constrained analyses.

26

27 **KEY RESULTS:** We describe *Adelocladoxis praecox* gen. et sp. nov., a cladoxylopsid with small
28 actinostelic axes bearing dichotomously-branched, helically-arranged ultimate appendages and
29 fusiform sporangia. *Adelocladoxis* provides the oldest evidence of cladoxylopsid anatomy, including
30 ultimate appendages and sporangia. In agreement with non-phylogenetic classification schemes, our
31 phylogenetic analysis resolves a basal grade of iridopterids and a clade of cladoxylopsids s.s., which
32 includes a pseudosporochnalean cladoxylopsid clade, a cladoxylalean cladoxylopsid clade, and
33 *Adelocladoxis*.

34

35 **CONCLUSIONS:** Our phylogenetic analysis illuminates aspects of tempo and mode of evolution in
36 the cladoxylopsid plexus. Originating prior to the Emsian, cladoxylopsids reached global distribution
37 by the Frasnian. Iridopterids and cladoxylopsids s.s. radiated in the Emsian-Eifelian. The sequence of
38 character change recovered by our phylogeny supports a transition from actinostelic protosteles to
39 dissected steles, associated with an increase in xylem rib number and medullation generating a
40 central parenchymatous area.

41

42 **KEY WORDS:** Cladoxylopsida; Devonian; fossil; *Adelocladoxis*; Iridopteridales; paleobotany;
43 phylogeny; Pseudosporochnales; stele evolution

44 The Devonian was a key interval in the evolution of plants (Hilton et al., 2003; Meyer-Berthaud et al.,
45 2010). Although vascular plants rose before the end of the Silurian (Libertin et al., 2018; Servais et
46 al., 2019), it is the Devonian period that holds for plant evolution an importance that matches that of
47 the Cambrian explosion for the evolution of animals. The impact that Devonian plant diversification
48 had on the subsequent structure of ecosystems (Meyer-Berthaud et al., 2010) is unparalleled, at
49 least in a broad taxonomic perspective. The Devonian witnessed tremendous morphological and
50 anatomical innovations in plants, such as leaves (Hao and Beck, 1993; Hao and Xue, 2013) and
51 rooting systems (Morris et al., 2015), along with associated mycorrhizal symbioses (Remy et al.,
52 1994; Selosse and Strullu-Derrien, 2015), secondary growth (Gerrienne et al., 2011; Hoffman and
53 Tomescu, 2013), and seeds (Gerrienne et al., 2004). The end of the Devonian is associated with
54 extinction events in the marine realm, induced in part by changes in water chemistry due to the
55 impact of the first forests formed by the oldest known arborescent plants – archaeopterids and
56 cladoxylopsids, as well as lycopsids –, which started affecting earth systems (soils, weathering) as
57 early as the Middle Devonian (Algeo et al., 2001; Meyer-Berthaud et al., 2010; Berry and Marshall
58 2015; Stein et al., 2020).

59 The cladoxylopid plexus includes early euphyllophyte species known from the Lower
60 Devonian into the Mississippian (Stein and Hueber, 1989; Soria and Meyer-Berthaud, 2005; Meyer-
61 Berthaud et al., 2007; Xue et al., 2010, 2016). The taxonomy of plants traditionally assigned to this
62 group has been revised multiple times and is still in flux. The latest treatments of the cladoxylopid
63 plexus (Xue et al., 2016; Wang et al., 2018) recognize three groups, as proposed earlier by Wang and
64 Berry (2006) and Meyer-Berthaud et al. (2007). One of these groups is the Iridopteridales
65 (iridopterids), which were treated as a lineage within the traditional all-encompassing
66 Cladoxylopsida (cladoxylopsids *s.l.* hereafter) by most authors, until Meyer-Berthaud et al. (2007)
67 excluded them from the class. The other two groups from Meyer-Berthaud et al.'s Cladoxylopsida
68 (cladoxylopsids *s.s.* hereafter): the Pseudosporochnales and the non-pseudosporochnalean
69 cladoxylopsids. (Note: when used without a specifier, “cladoxylopid” refers to the cladoxylopsids
70 *s.l.*, hereafter.)

71 Biogeographically, cladoxylopsids were present mainly in Euramerica (Xue et al., 2010), with
72 fossils recorded in the USA and Canada (Stein and Hueber, 1989), France (Rowe and Galtier, 1989),
73 Germany (Fairon-Demaret and Berry, 2000), Norway (Berry, 2005), Belgium (Fairon-Demaret and Li,
74 1993), and Scotland (Long, 1968). Cladoxylopid material has also been reported in Gondwana –
75 Venezuela (Berry and Stein, 2000), Morocco (Soria et al., 2001; Soria and Meyer-Berthaud, 2005),
76 Australia (Meyer-Berthaud et al., 2007; Champreux et al., 2020) –, as well as in China (Wang and
77 Berry, 2006; Wang, 2008; Xue et al., 2016). The group is characterized by steles with ribbed or

78 dissected primary xylem (Read and Campbell, 1939; Chambers and Regan, 1986; Stein and Hueber,
79 1989; Cordi and Stein, 2005), mesarch and permanent (sensu Beck and Stein, 1993) protoxylem
80 strands (Scheckler, 1974; but see *Polyxylon*, Chambers and Regan, 1986; Meyer-Berthaud et al.,
81 2007), and filiform, dissected ultimate appendages. The cladoxylopsids are highly relevant to
82 questions of basal euphyllophyte phylogeny because of (1) their age, which implies early divergence
83 among euphyllophytes; (2) their anatomy and morphology that are transitional between those of
84 simple Early Devonian plants and the more derived plants of the Middle and Late Devonian (Berry
85 and Stein, 2000); and (3) their membership in the “permanent protoxylem” group of Beck and Stein
86 (1993) and Stein (1993), characterized by multiple mesarch protoxylem strands that have
87 independent trajectories along axes. This group, synonymized with Infradivision Moniliformopses by
88 Kenrick and Crane (1997), is one of two major groups to which complex Devonian euphyllophytes
89 have been assigned – the other main group is the radiatopsids [the “radiate protoxylem” group of
90 Beck and Stein (1993) or Infradivision Radiatopses of Kenrick and Crane (1997)].

91 The focus of this study is a new Emsian (Early Devonian, 400-395 Ma) anatomically
92 preserved plant from the Battery Point Formation of Gaspé Bay (Québec, Canada). The plant,
93 characterized by a mesarch actinostele with permanent protoxylem strands at the xylem lobe tips
94 and filiform dichotomous ultimate appendages, is among the oldest known representatives of the
95 cladoxylopsid plexus, and the earliest of them to be characterized anatomically. This new plant
96 provides the first evidence on the anatomy of cladoxylopsid ultimate appendages and sporangia. To
97 exploring the systematic position of the new Gaspé plant we performed phylogenetic analyses
98 centered on cladoxylopsids, which clarify relationships within the group. In turn, the relationships
99 recovered inform classification schemes, suggest sequences of character evolution, especially on the
100 evolution of stelar architecture, and illuminate the tempo of diversification within the cladoxylopsid
101 plexus.

102

103 **MATERIALS AND METHODS**

104 The new species is based on three axis fragments and multiple ultimate appendages, some attached
105 to the axes and others dispersed in the rock matrix. The specimens exhibit variable preservation
106 (both between and within specimens) that ranges from fairly well preserved anatomy to crushed,
107 shriveled or otherwise distorted specimens. Although the material described here comes from a
108 single rock specimen, fragments belonging to this new species are found throughout several other
109 rock samples from the same locality.

110 The Battery Point Formation consists of terrigenous deposits associated with braided river
111 systems and their coastal sectors (Cant and Walker, 1976; Griffing et al., 2000). These Early Devonian

112 (Emsian; McGregor, 1977) deposits host plants preserved as carbonaceous compressions and
113 permineralizations. The plant fossils of the Battery Point Formation have been studied ever since the
114 first report by Dawson (1859) and represent the most diverse Early Devonian flora known in North
115 America, including 12 species described to date based on anatomically-preserved specimens:
116 *Crenatacaulis verruculosus* Banks and Davis (1969); *Psilophyton dawsonii* Banks et al. (1975);
117 *Psilophyton forbesii* Gensel (1979); *Drepanophycus spinaeformis* Hartman (1981); Gensel's (1984)
118 unnamed plant; *Franhueberia gerriennei* Hoffman and Tomescu (2013); *Eddianna gaspiana* Pfeiler
119 and Tomescu (2018); *Leptocentroxyloa tetrarcha*, *Stenoloboxyla ambigua*, *Jowingeria triloba*, and
120 *Tainioxyloa quebecana* Bickner and Tomescu (2019); and *Gmujij tetraylopteroides* Pfeiler and
121 Tomescu (2020).

122 The fossil specimens are preserved by calcium carbonate permineralization of the
123 terrigenous matrix and plant material, in blocks (cobbles) collected in 1965 by the late Francis M.
124 Hueber (Smithsonian Institution—NMNH) in 1965 from exposures of the Battery Point Formation in
125 the vicinity of Douglstown, on the southern shore of Gaspé Bay (Québec, Canada). The age of the
126 plants, based on palynostratigraphy, is mid- to late Emsian, c. 402-394 Ma (Pfeiler and Tomescu,
127 2018). The fossils were studied in serial anatomical sections obtained using the cellulose acetate
128 peel technique (Joy et al., 1956). Slides for bright-field microscopy were mounted with Eukitt (O.
129 Kindler, Freiburg, Germany) mounting medium. Fossils were imaged using a Nikon Coolpix 8800VR
130 digital camera mounted on a Nikon E400 compound microscope (Nikon Corporation, Tokyo, Japan),
131 and an Olympus DP73 digital camera mounted on an Olympus SZX16 microscope (Olympus
132 Corporation, Tokyo, Japan). Material for scanning electron microscopy was obtained from cellulose
133 acetate peels using the method detailed in Matsunaga et al. (2013). SEM images were generated
134 using a FEI Quanta 250 (Field Electron and Ion Company, Hillsboro, Oregon, USA). Images were
135 processed using Adobe Photoshop (Adobe, San Jose, California, USA). Measurements were obtained
136 directly on material mounted on slides, in transmitted light microscopy using an eyepiece
137 micrometer, or on high-resolution micrographs using ImageJ software (US National Institutes of
138 Health; <https://imagej.nih.gov/ij/>); where necessary, sizes of plant parts were reconstructed
139 trigonometrically from series of sections, based on relative Z-axis and plane positions (those sizes are
140 marked “*t” in the description). All cobble slabs, acetate peels, and slides are stored in the U.S.
141 National Museum of Natural History – Smithsonian Institution (USNM no. 557820-2).

142 The phylogenetic analyses are based on an initial matrix of 31 taxa and 36 discrete
143 characters constructed in Mesquite 3.61 (Maddison and Maddison, 2009) (Appendices S1-S5; see
144 Supplemental Data associated with this article). The taxa were selected to sample as much of the
145 known cladoxylopsid diversity as possible (see Discussion). Taxon selection was limited by the

146 proportion of characters that could be scored for each taxon, considering that our characters
147 codified aspects of both the morphology and anatomy of the plants. Thus, taxa that have been
148 characterized only based on anatomy or only on morphology, and wherein even the anatomy or
149 morphology (respectively) are incompletely documented, were not included. In the case of
150 *Arachnoxylon kopfii*, because of significant differences between specimens documented in the
151 literature, we scored two separate terminals: one referred to as *Arachnoxylon kopfii* Read, based on
152 the Windom Shale specimen and Read's (1938) specimens (all of which are reported in Stein, 1981);
153 and the other referred to as *Arachnoxylon kopfii* Stein, reported by Stein et al. (1983). Hypotheses of
154 organographic homology underlying the more delicate aspects of character construction are
155 outlined below, in the discussion section. Characters were scored based on the published literature
156 (Appendices S1-S5); where needed, textual descriptions were supplemented with (or replaced by)
157 direct observations of the published illustration. The new Gaspé plant was scored based on direct
158 observations of specimens. Our decisions in scoring the more contentious characters in specific taxa
159 are explained in Appendix S5.

160 We performed three analyses to (1) address the position of the new Gaspé plant among
161 cladoxylopsids, and (2) assess the level of support that our dataset lends to previous classifications
162 within the group. A first analysis (Analysis 1) included all 31 taxa and 36 characters. In a second
163 analysis (Analysis 2; 26 taxa, 36 characters) we excluded the four taxa with the highest amounts of
164 missing data (*Compsocradus givetianum*, *Ibyka vogtii*, *Rhymokalon trichium*, and *Xenocladia*
165 *medullosina*), as well as *Arachnoxylon kopfii* (Stein et al., 1983), whose sole addition to the reduced
166 dataset of Analysis 2 decreased resolution almost to the same level as that of Analysis 1 (probably
167 because of the high level of homoplasy induced by the combination of characters of this taxon). In a
168 third analysis (Analysis 3; 19 taxa, 36 characters), to further reduce the amount of missing data in
169 character scoring, we excluded *Anapaulia moodyi*, *Lorophyton goense*, and *Wattieza casatii*, which
170 are only known morphologically; for the genera *Cladoxylon* and *Pietzschia*, both represented by
171 several species in Analyses 1 and 2, we only kept the most completely characterized species,
172 excluding *Cladoxylon taeniatum*, *C. mirabile*, *Pietzschia levis*, and *P. polyupsilon*.

173 Tree searches used parsimony as the optimality criterion and were performed using TNT 1.5
174 (Goloboff and Catalano, 2016) in Windows. Analyses were run using a traditional search with 10000
175 replications, using tree bisection-reconnection. Group support was calculated with absolute
176 jackknifing frequencies and bootstrapping of the strict consensus tree, each with 1000 replicates.
177 The time-scaled tree constructed from Analysis 2 was produced using R software (R Core Team,
178 2017) with the functions *timePaleoPhy* and *geoscalePhylo* from the packages *paleotree* and *strap*
179 (Bapst, 2012; Bell and Lloyd, 2015).

180

181 **RESULTS**

182

183 **Systematics**

184

185 **Class**—Cladoxylopsida Pichi-Sermolli 1959

186

187 **Genus**—*Adelocladoxis* Durieux, Lopez et Tomescu, gen. nov.

188

189 **Generic diagnosis**—Small axes with simple dichotomously branched ultimate appendages. Primary
190 xylem actinostelic with large central metaxylem area and relatively short lobes. Mesarch protoxylem
191 strands shallow, single at tips of primary xylem ribs. Metaxylem tracheids with oval-horizontal and
192 circular bordered pits. Traces to ultimate appendages, tangentially elongated and possessing two
193 mesarch protoxylem strands, diverge radially from single xylem ribs of the stele. Ultimate
194 appendages helically arranged, possessing above the first dichotomy terete xylem with one centrarch
195 protoxylem strand. Sporangium axially elongated, with wall more than one cell thick and longitudinal
196 dehiscence.

197

198 **Etymology**—The genus name *Adelocladoxis* combines the Ancient Greek ἀδελος, meaning invisible,
199 with the connotations of concealed, improbable, and -cladoxis, in reference to the unexpected
200 placement of this plant among cladoxylopsids in a phylogenetic context, despite apparent iridopterid
201 similarities.

202

203 **Type species**—*Adelocladoxis praecox* Durieux, Lopez et Tomescu, sp. nov.

204

205 **Specific diagnosis**—Axes c. 1-1.5 mm thick. Primary xylem an actinostele with five or six lobes that
206 protrude 200-400 μm from the central area. Metaxylem tracheids up to 24-34 μm in diameter,
207 bordered pits up to 9.5 μm wide, usually 5-6 μm . Phloem layer thin around xylem, with thin-walled
208 fusiform cells 3.8-5.0 μm wide. Cortex parenchymatous, 150-200 μm wide. Epidermis of axes,
209 ultimate appendages, and sporangia with axially elongated cells 25-50 μm in width, with rectangular
210 outline. Epidermal cells with robust primary walls and secondary metabolite content fossilized inside
211 as solid rods of dark, compact material. Xylem traces to ultimate appendages hourglass-shaped,
212 tangentially elongated to 200 μm . Ultimate appendages 650-700 μm wide at base, isotomously
213 branched at least twice and at least 7 mm in overall length, some with recurved tips. Ultimate

214 appendage segments up to 500 μm thick, with terete xylem up to 230 μm thick. Sporangia erect,
215 attached at tips of ultimate appendage segments, fusiform, at least 2 mm long and 0.4-0.5 mm thick.
216 Sporangium wall comprising epidermis and parenchymatous inner layer(s), with inner periclinal walls
217 of innermost sporangium wall cells forming a degradation-resistant membrane. Sporangium wall
218 thinner in area of the single longitudinal dehiscence slit, where sporangial epidermis and
219 degradation-resistant membrane fuse. In situ spores c. 60 μm diameter.

220

221 **Etymology**—*praecox* (Latin for early, precocious) refers to the fact that this species is the oldest
222 anatomically-described cladoxylopid *s.l.* known to date.

223

224 **Holotype**—Axis with attached appendages in slabs D and E of cobble USNM 557820-2 (Figs. 1, 2, 4,
225 5A, 5B, 5F, 5G, 6, 7F, 7G, 7H; Supplemental figs. 1, 2, 3, 4, 9, 10, 11, 12, 13, 14, 18, 19, 24, 25).

226

227 **Paratypes**—Two incompletely preserved axes with appendages in slabs D and E of cobble USNM
228 557820-2 (Figs. 3, 5C, 5E, 7A, 7B, 7C, 7D, 7E; Supplemental figs. 5, 6, 7, 8, 20, 21, 22, 23; all
229 supplemental figures are part of Appendix S6 - see Supplemental Data with this article), separate
230 ultimate appendage in slab E of cobble USNM 557820-2 (Supplemental figs. 15, 16, 17), and separate
231 ultimate appendage in USNM 557820-4 A1top (Fig. 5D).

232

233 **Locality**—South shore of Gaspé Bay (Quebec, Canada), in the vicinity of Douglstown.

234

235 **Stratigraphic position and age**—Battery Point Formation, Lower Devonian; mid- to late Emsian
236 (McGregor, 1977; Hoffman and Tomescu, 2013), c. 402-394 Ma.

237

238 **Description**

239 Although they exhibit widely variable quality of preservation (Figs. 1A, 5F; Supplemental figs. 1-8)
240 the three axes of *Adelocladoxis praecox* are easily recognized as conspecific based on xylem
241 architecture, tracheid pitting, and characteristic epidermal histology. While the best-preserved
242 specimen (Figs. 1, 2; Supplemental figs. 1, 3, 4) provides most of the histological information on axis
243 anatomy and the most complete data on the divergence of traces to ultimate appendages, the more
244 incompletely preserved axes (Supplemental figs. 5-8) have yielded evidence for anatomical
245 connection of ultimate appendages (Fig. 3) and variability in xylem architecture. Multiple ultimate
246 appendages exhibiting a broad range of preservation quality but also of anatomical variability,
247 whether attached to the axes (Figs. 2-4, 5A, B, F, G, 6, 7; Supplemental figs. 10, 13, 14, 24, 25) or

248 observed as disconnected specimens (Figs. 5C-E; Supplemental figs. 15-17), complete the picture of
249 the morphology and anatomy of this plant. Because of this variable quality of preservation within
250 and between specimens, the description provided here is a summation of complementary
251 information provided by individual specimens.

252

253 **Main axis**—The axes are small, about 1 mm in diameter, possibly up to 2 mm; their taphonomic
254 distortion in many cases makes it difficult to perform exact measurements of their size. The largest
255 of these axes was exposed in serial sections over c. 14 mm of length. The better preserved
256 specimens reveal the concentric layering of the primary tissues (Fig 1A, Supplemental fig. 1). At the
257 center, the actinostele consists of a lobed xylem strand with five or six lobes that protrude 200-400
258 μm outwards from the central area. A thin layer of phloem is partially preserved around the xylem.
259 Around the stele, the cortex is 150-200 μm wide and a dark outer layer of cells forms the epidermis.

260 The epidermis has variable preservation, but where it is not taphonomically distorted it
261 reveals relatively large cells (25-50 μm thick) with rectangular outline often elongated radially (in
262 cross section) (Figs. 1B, 2; Supplemental figs. 9, 10). The epidermal cells have relatively robust walls
263 and most of them contain fossilized secondary metabolites that form consistently solid rods of dark,
264 compact material that are just slightly smaller than the cell lumen (Figs. 1B, 2; Supplemental figs. 9,
265 10). The cortex, well preserved in only one of the axes (Figs. 1A, 1B, 2; Supplemental figs. 1, 3, 4),
266 consists of parenchyma cells up to 20 μm in size, with relatively robust cell walls. The phloem layer,
267 probably originally continuous around the xylem, is incompletely preserved (Supplemental fig. 1) and
268 seems to have been only a few cells thick. Phloem cells, fusiform, have very thin walls and are
269 narrow, 3.8-5.0 μm wide (Figs. 1C, D, F).

270 The primary xylem has five or six lobes (Figs. 1A, 1B, 2; Supplemental figs. 1, 3-8) whose
271 length (as observed in cross sections) varies along the axes. One axis shows a transition from five
272 conspicuous lobes to only four lobes, among which one appears dissected at the tip (Supplemental
273 fig. 2). The xylem lobes have mesarch protoxylem strands towards the tips (Fig. 1A; Supplemental fig.
274 1). The protoxylem is shallow (*sensu* Stein, 1993), i.e., (1) the transition in tracheid size from larger
275 tracheids (metaxylem) to the narrow protoxylem tracheids is sharp and involves only a few
276 metaxylem tracheids around the protoxylem strand; and (2) there are few (if any) observable
277 protoxylem tracheids. In the central area of metaxylem, collapsed tracheids sometimes give the
278 impression of protoxylem strands at random locations within the xylem (Fig. 1A; Supplemental figs.
279 1, 3, 4). Close examination of these occurrences demonstrated limited longitudinal extent and
280 random distribution, both of which are inconsistent with procambial architecture, thus confirming
281 their accidental nature and rejecting interpretation as protoxylem strands. In contrast, the

282 protoxylem strands in the xylem lobes, although relatively inconspicuous, can be followed
283 longitudinally through serial sections. Overall, the presence of continuous protoxylem strands in the
284 xylem lobes and their absence from the center of the xylem corresponds to the architecture
285 described as ‘permanent protoxylem’ by Beck and Stein (1993). Metaxylem tracheids are up to 24-34
286 μm in diameter. The pitting pattern of metaxylem tracheids consists exclusively of relatively large
287 circular to oval-horizontal bordered pits (Figs. 1C, E, F; Supplemental figs. 11, 12) that can be up to
288 $9.5 \mu\text{m}$ wide, but usually $5\text{-}6 \mu\text{m}$.

289

290 **Lateral appendages**—Vascular traces to the ultimate appendages arise as xylem bundles that
291 diverge radially from the xylem ribs of the actinostele (Fig. 2; Supplemental figs. 10, 13). Each
292 ultimate appendage is supplied by a single trace diverging from a single rib. Incomplete preservation
293 (i.e., compressive distortion of the region where the base of an appendage is connected to the axis;
294 Fig. 2A) did not allow observation of the protoxylem architecture in the region of trace emission.
295 Nevertheless, immediately distal to its divergence from the stele, as it is traversing the cortex of the
296 axis, the ultimate appendage trace is tangentially elongated to $180\text{-}200 \mu\text{m}$ and has an elliptical or
297 hourglass shape, with two mesarch protoxylem strands (Figs. 1B, 2B, C; Supplemental figs. 9, 10, 13).
298 At the base, the ultimate appendages are c. $600\text{-}750 \mu\text{m}$ wide and exhibit histology directly
299 comparable to that of the axes (Fig. 2D; Supplemental figs. 10, 13).

300 Ultimate appendages diverge from axes individually at different levels (Figs. 3, 4;
301 Supplemental fig. 14), consistent with alternate taxis. Because in the two cases we observed
302 successive ultimate appendages diverge from main axes from neighboring xylem ribs (Figs. 4;
303 Supplemental fig. 14), we interpret the appendage taxis as helical (albeit not following a Fibonacci
304 pattern).

305 The anatomy of appendages exhibits a broad spectrum of preservation states. Some of the
306 appendages (Figs. 4, 5C, 7F-H; Supplemental figs. 15-17, 24, 25) show almost complete histology,
307 while others exhibit partial preservation of cortical anatomy, with only cells immediately adjacent to
308 the epidermis and to the stele preserved (Figs. 5B, E, F; Supplemental figs. 15-17). Still others, have
309 portions where anatomical preservation is so incomplete that they can only be used to demonstrate
310 physical connection (Fig. 3). A survey of all the appendages reveals that the different qualities of
311 preservation form a continuous series of inter-grading anatomies (Figs. 5, 6).

312 Whether their physical connection to the axes can be traced directly or they are found
313 detached from axes, in the rock matrix, these appendages are up to $500 \mu\text{m}$ thick, with terete xylem
314 up to $230 \mu\text{m}$ thick, and they all share a set of features, which is important for ascertaining the
315 conspecificity of the dispersed specimens. First, they occur in abundance in the same rock slabs as

316 the main axes and around the main axes; in fact, very few other plant types are present in the rock
317 slabs that contain *Adelocladoxis*. Second, they all share the same tracheid pitting pattern (Figs. 5A, G,
318 6) and the same type of epidermal cells containing compact dark rods (Figs. 5, 6), which they also
319 share with the main axes. Third, they all have centrarch xylem strands (Fig. 5), which we interpret as
320 resulting from dichotomous branching of the basal hourglass-shaped trace with two protoxylem
321 strands.

322 Several specimens that we observed in detail through serial sections (Figs. 3, 4;
323 Supplemental figs. 14-17) allow us to characterize the morphology of ultimate appendages. One
324 appendage (Supplemental fig. 14) observed starting at its divergence from the main axis
325 demonstrates two successive dichotomies. The first occurs ca. 4 mm (*t) from the base of the
326 appendage. One of the resulting segments dichotomizes again ca. 1.4 mm (*t) from the first
327 branching point, and the resulting ultimate segments are c. 2 mm long (*t). Incomplete preservation
328 does not allow for ascertaining whether the other segment produced by the first dichotomy is also
329 branched and whether the appendage as a whole exhibited symmetrical branching. Nevertheless,
330 based on the comparable sizes of the segments produced, the dichotomies appear isotomous.
331 Additionally, the tips of the ultimate segments are recurved (Supplemental fig. 14).

332 The anatomy of this appendage is only partially preserved in its basal portion, where it is
333 attached to the main axis (Figs. 5F, G). The epidermis, discontinuous, consists of the rectangular cells
334 with compact dark bodies characteristic of *Adelocladoxis*. Here, the central xylem strand, seen in
335 longitudinal section, has conspicuous circular pits (Figs. 5G). The overall quality of preservation in
336 this region of the appendage is comparable to that seen in cross sections of more distal regions (e.g.,
337 Fig. 5B). These cross sections show the terete centrarch primary xylem surrounded by a layer of
338 radially-elongated cells with darker content (Figs. 5B, 6E) that appear parenchymatous. As
339 demonstrated by such cross sections, as well as by longitudinal radial (Figs. 5A, 6A, C) and tangential
340 sections (Fig. 6B, D, E), these cells are evenly distributed, with spaces separating them, suggestive of
341 an aerenchymatous layer. In sections through better preserved regions of this appendage, tracheids
342 are up to 140 μm long. Here, a layer of fusiform cells with thin walls, probably representing phloem,
343 is sandwiched between the outermost xylem tracheids and the cortical parenchyma with dark
344 content (Figs. 5A, 6A). The xylem strand has roughly constant thickness throughout the appendage.
345 Close to the tips of this appendage (Figs. 6B, C), preservation of the cortex is more complete and the
346 xylem consists primarily of tracheids that are wider and have horizontally elongated, slit-shaped pits
347 that form a scalariform pattern. This tracheid thickening pattern seems to be present only at the tips
348 of the appendage, because just proximally to the portion with scalariform pitting, the tracheid
349 thickenings show a transition to bordered pits (Figs. 6D, E).

350 An ultimate appendage attached to the same main axis as the appendage described above,
351 but at a different level, is also incompletely preserved (Supplemental fig. 14). Nevertheless, this
352 appendage dichotomizes close to its base, thus illustrating variability in the branching pattern of
353 ultimate appendages.

354 Some of the appendages observed in the rock matrix around the *Adelocladaxis* axes have
355 morphology and anatomy different to some extent from the appendages that diverge from the axes
356 (described above). These appendages have undulating outlines in cross section, indicative of
357 longitudinal ridges and grooves (e.g., Fig. 5C). Their histology matches exactly that of the axes, as
358 well as the histology of the appendage bases that diverge from the axes (Fig. 2; Supplemental figs.
359 10, 13). The central xylem strand is thinner and has narrower tracheids than the appendages
360 described above. Around the xylem strand is a more-or-less continuous layer of cortical cells that are
361 mostly parenchymatous, and some of which have dark content (Fig. 5C), similar to those of the
362 epidermis. Supplemental figs. 15-17 shows the dichotomy of one of these appendages, with the
363 different segments cut in various planes of section that expose the anatomy in both transverse and
364 oblique-longitudinal views.

365 One appendage holds a sporangium (Figs. 3, 7A-E; Supplemental figs. 20-23). Although parts
366 of this appendage have very incomplete, fragmentary preservation, its morphology can be
367 reconstructed with two dichotomies, the first c. 1.75 mm (*t) from the base of the appendage, and
368 the second immediately distal to the first. The sporangium is erect, attached at the tip of one of the
369 segments produced by the second dichotomy (Figs. 3, 7B). The sporangium is fusiform in shape, c. 2
370 mm (*t) long and 0.4-0.5 mm wide (Figs. 7A-C). The outermost layer of the sporangium (sporangial
371 epidermis) consists of cells with thin walls and containing rods of dark material (Figs. 7A, D, E;
372 Supplemental figs. 20-23), identical to the epidermal cells of all other organs of *Adelocladaxis*. To the
373 inside of this epidermal layer, the sporangium contains a membranous sac that is distanced from the
374 epidermis in most sections (Figs. 7A, D, E; Supplemental figs. 20, 21) and is fused to the sporangial
375 epidermis along the line of dehiscence (Figs. 7A, C). The dehiscence line is longitudinal. A few spores
376 are preserved inside the sporangium (Figs. 7A, D, E; Supplemental figs. 21-23). The spores are c. 60
377 μm in diameter, but their incomplete preservation precludes characterization of spore morphology
378 or wall structure.

379 Another appendage (Fig. 4) is darker in color and its tissues appear shriveled and more
380 condensed, rendering its anatomy less well defined. Nevertheless, the appendage shows circular
381 tracheid pitting and typical epidermal cells containing dark bodies (Fig. 7F). This appendage
382 dichotomizes c. 3 mm (*t) from its base and one of the resulting segments ends in an inflated
383 elliptical structure (Figs. 7G, H; Supplemental figs. 24, 25). The inflated end of the appendage, well

384 preserved, is 1.4 mm (*t) long and 0.5 mm thick. It has a thin central xylem strand surrounded by
385 larger parenchymatous cells, all enclosed by the typical *Adelocladoxis* epidermis (Figs. 7G, H;
386 Supplemental figs. 24, 25). The very tip of this appendage is not preserved, but given its shape and
387 size, the inflated terminal part could represent a developing sporangium.

388

389 **Phylogeny**

390

391 **Tree topology**—Analysis 1, including the full character and taxon sampling, resulted in 713 maximum
392 parsimony (MP) trees (length 114; CI = 0.447; RI = 0.654), whose consensus resolved the ingroup as a
393 polytomy. This polytomy includes two resolved clades: one consisting of *Lorophyton*, *Calamophyton*,
394 *Pseudosporochnus*, and *Wattieza* (referred to as pseudosporochnalean cladoxylopsids, below) and
395 the other consisting of *Xenocladia*, *Polyxylon*, and the three species of *Pietzschia* (included in the
396 cladoxylalean cladoxylopsid clade, below) (Supplemental fig. 26).

397 Analysis 2, based on a reduced matrix of 26 taxa (see Material and Methods), resulted in 40
398 MP trees (length 105; CI = 0.486; RI = 0.662), bringing added resolution in the phylogeny. The strict
399 consensus tree (Fig. 8A) resolves a clade including *Anapaulia* and *Ibyka amphikoma* as sister to a
400 large clade containing the rest of the ingroup. This large clade consists of two clades sister to each
401 other. The first of these two clades has a basal polytomy including *Arachnoxylon kopfii* Read,
402 *Asteropteris*, *Arachnoxylon minor*, and a clade in which *Arachnoxylon minor* is sister to *Iridopteris* +
403 *Compsocradus laevigatus*. The second clade has a basal polytomy including *Denglongia*, *Serripteris*,
404 *Adelocladoxis*, and two clades. The first of these two clades consists of *Lorophyton* and
405 *Calamophyton* in a polytomy basal to *Wattieza* + *Pseudosporochnus*. The second clade has a basal
406 polytomy including *Polypetalophyton*, the three *Cladoxylon* species, *Metacladophyton*, *Rotoxylon*,
407 *Panxia*, and a clade wherein *Polyxylon* is sister to the *Pietzschia* clade. The majority rule tree of
408 Analysis 2 (Fig. 9-11) reveals potential patterns of relationship within some of the polytomies of the
409 strict consensus tree. *Denglongia* and *Serripteris* form a grade basal to two clades. In one of these
410 two clades, *Adelocladoxis* is sister to the *Lorophyton-Calamophyton-Pseudosporochnus-Wattieza*
411 clade, but only in 55% of the most parsimonious trees. The basal polytomy of the second clade (as
412 resolved in the strict consensus tree of Analysis 2) includes *Polypetalophyton*, *Cladoxylon taeniatum*,
413 and a clade supported in 72% of the MP trees. Within this clade, a group including *Cladoxylon*
414 *radiatum* and *Cladoxylon mirabile* is sister to a group wherein *Metacladophyton* + *Rotoxylon* is sister
415 to *Panxia* + the *Polyxylon-Pietzschia* clade.

416 Analysis 3, based on the most reduced taxon sampling (19 taxa; see Material and Methods),
417 resulted in four MP trees (length 94; CI = 0.543; RI = 0.587). The strict consensus of the two trees

418 (Fig. 8B) adds more resolution in the phylogeny, while supporting the overall topology of the
419 majority rule tree of Analysis 2. In this strict consensus tree, *Adelocladoxis* is resolved as part of a
420 polytomy with *Calamophyton* + *Pseudosporochnus* and with the clade including *Polypetalophyton*-
421 *Cladoxylon*-*Metacladophyton*-*Rotoxylon*-*Panxia*-*Polyxylon*-*Pietzschia*.

422

423 **Synapomorphies**—The *Ibyka amphikoma* + *Anapaulia* clade (Fig. 8A) shares epidermal extensions
424 (Character 1 = 1) as a synapomorphy, but is otherwise characterized by a combination of
425 plesiomorphic character states. The large clade sister to *Anapaulia*-*Ibyka*, which includes the
426 remainder of the ingroup, is supported by major traces possessing bilateral symmetry at the base
427 (C30 = 1) and two (or more, in later-diverging taxa) protoxylem strands (C29 = 1). The *Asteropteris*-
428 *Arachnoxylon minor*-*A. kopfii* Read-*Iridopteris*-*Compsocradus* clade shares ultimate appendages with
429 whorled taxis (C2 = 2) as a synapomorphy, but is otherwise characterized by a combination of
430 plesiomorphic character states. Synapomorphies identified for the clade formed by the remainder of
431 the outgroup taxa are branches attached at different nodes than ultimate appendages (C27 = 0) and
432 erect ultimate appendage tips (C5 = 0), the latter having a significant amount of missing data. The
433 *Lorophyton*-*Calamophyton*-*Wattieza*-*Pseudosporochnus* clade is supported by the presence of
434 sclereid groups in the ground tissues (C10 = 1) and low angle branching in the distal branches (C26 =
435 1). The *Panxia*-*Polyxylon*-*Pietzschia* clade is supported by planation in the branching system (C7 = 1).
436 The node subtending the *Polyxylon*-*Pietzschia* clade is supported by the presence of: sclereid groups
437 in the ground tissues (C10 = 1), a cylinder of parenchyma at the center of the stele (C12 = 1), and
438 protoxylem lacunae (C23 = 0).

439

440 **DISCUSSION**

441

442 **The ultimate appendages of *Adelocladoxis praecox***

443 This is the first detailed account of the anatomy of ultimate appendages in a cladoxylopsid. The
444 ultimate appendages of *Adelocladoxis* span a continuum of anatomies that include as end-terms
445 specimens with grooved profiles and good preservation of all tissues (e.g., Figs. 5C, D), and
446 specimens with more rounded profiles and incomplete cortex preservation (e.g., Figs. 5A, B). Several
447 appendages that fit along the continuum of anatomies and of preservation quality defined by these
448 two end-terms can be traced back to their connection to main axes, which demonstrates their
449 conspecificity. Furthermore, whether attached to axes or dispersed in the rock matrix (within
450 millimeters to centimeters of main axes), all the appendages recognized by these anatomies share,
451 among themselves and with the main axes, (1) the same type of tracheids with horizontal-elliptical

452 to circular bordered pits, and (2) the same type of epidermal cells (i.e., containing solid dark rods of
453 fossilized secondary metabolites) (Fig. 5). It is unclear to what extent the differences in preservation
454 and anatomy (more or less grooved profiles, thinner or thicker xylem strands; e.g., Fig. 5) are due to
455 taphonomy, development, or anatomical differentiation along the appendages. For example,
456 specimens with thicker xylem strands (Figs. 5D, E) that are traced in several instances to their
457 divergence from axes may be more characteristic of the basal portions of the ultimate appendages
458 of *Adelocladoxis*, while those with thinner xylem strands (Fig. 5B, C) may represent more distal parts.
459 The presence in these latter specimens of what looks like an aerenchymatous cortex would be
460 consistent with the primarily photosynthetic function of the ultimate appendages, as photosynthetic
461 tissue typically exhibits high volumes of intercellular space. It is also possible that the different
462 anatomies represent different developmental stages. For example, the specimens with incompletely
463 preserved cortex could represent immature, developing appendages that had more delicate cells,
464 which did not preserve well.

465 Overall sizes of ultimate appendages have not been reported consistently by previous
466 authors describing cladoxylopsid species. Sizes of cladoxylopsid ultimate appendages range between
467 c. 5 mm (in *Anapaulia*; Berry and Edwards, 1996) and 30 mm (in *Lorophyton*; Fairon-Demaret and Li,
468 1993). The ultimate appendages of *Adelocladoxis*, measuring up to 7-8 mm (based on available
469 specimens reconstructed in serial sections) are, like the axes of the plant, some of the smallest
470 known among cladoxylopsids. They are comparable in size to the ultimate appendages of *Anapaulia*
471 *moody*, whose third- and fourth-order axes are < 1 mm in diameter. They also reach into the lower
472 end of the size range of *Ibyka amphikoma* ultimate appendages (Skog and Banks, 1973), the third-
473 order axes of which are at least twice the diameter of *Adelocladoxis* axes. Like *Adelocladoxis*, both
474 *Anapaulia* and *Ibyka* have ultimate appendages that are isotomously dissected and recurved at the
475 tips.

476

477 **The sporangia of *Adelocladoxis praecox***

478 The structure of basal euphyllophyte sporangia is best documented in the trimerophyte *Psilophyton*
479 *dawsonii* (Banks et al., 1975; Noetinger et al., 2018). The sporangium wall of *Psilophyton* consists of
480 an epidermal layer of large cells with substantially thickened walls, and a subjacent layer of
481 parenchyma cells. Both of these layers taper off in the vicinity of the dehiscence line. Importantly,
482 the inner periclinal walls of the innermost cells in the parenchymatous layer, which are adjacent to
483 the spore mass, are more resistant to degradation than the rest of the parenchymatous layer.
484 Noetinger et al. (2018) hypothesized that this reflects reinforcement of the inner periclinal walls by
485 impregnation with sporopollenin during building of the spore walls adjacent to them. When the

486 parenchymatous layer of the sporangial wall is degraded taphonomically, the process leaves an
487 empty space between the sporangial epidermis and a membranous sac formed formed around the
488 spore content by the resistant periclinal walls. When the spores are dispersed, the membranous sac
489 is left inside the sporangium.

490 *Adelocladoxis* provides the first glimpse of the anatomy of cladoxylopsid sporangia. These
491 sporangia conform to the general organization of basal euphyllophyte sporangia, as seen in
492 *Psilophyton*. Like in the latter, the sporangial epidermis is continuous with that of the rest of the
493 plant, histologically, i.e., it shows the same type of cells with relatively robust primary walls and
494 containing dense dark rods of fossilized secondary metabolites. The sporangia of *Adelocladoxis* also
495 feature an inner membranous sac that is detached from the epidermis. We interpret this as
496 representing the sporopollenin-impregnated inner periclinal walls of cells that formed a
497 parenchymatous internal layer of the sporangium that was lost to taphonomy. Like in most other
498 early euphyllophytes, *Adelocladoxis* sporangia dehisce along a single longitudinal line. Along this line,
499 the sporangium wall is thinner and the membranous sac is connected to the sporangial epidermis,
500 like in *Psilophyton*.

501

502 **Reconstructing *Adelocladoxis praecox***

503 *Adelocladoxis praecox* is represented by small axes c. 1-2 mm thick vascularized by actinosteles. The
504 mesarch protoxylem strands at the tips of the actinostele ribs qualify as shallow (*sensu* Stein, 1993),
505 which may indicate that growth of the axes was based mainly on cell proliferation and to a lesser
506 extent on cell elongation; an alternative explanation of the shallow protoxylem is that tracheid
507 differentiation in the protoxylem areas was delayed to a later ontogenetic stage. The axes bear
508 helically-arranged ultimate appendages that extend 7 mm or more. The ultimate appendages
509 dichotomize isotomously two or more times into fine terete segments and can have recurved tips.
510 Sporangia, fusiform and dehiscing along single longitudinal lines, are attached at the tips of some of
511 the appendages.

512 Several features of *Adelocladoxis* remain to be documented in future studies, as additional
513 specimens are discovered. For instance, we do not have information on the branching of
514 *Adelocladoxis* axes, nor do we know whether these small axes were part of larger plants with more
515 robust axes subtending them. The only other cladoxylopsids known in the Battery Point Formation
516 were reported by Stein and Hueber (1989) and Chu and Tomescu (2015). It is not clear whether the
517 fossils in these two reports represent the same plant type, as neither has provided descriptive
518 details. The cladoxylopsid reported by Chu and Tomescu (2015), which will be described in an
519 upcoming paper, is the only other plant in the permineralized assemblages of the Battery Point

520 Formation to possess oval and circular bordered pits. However, this plant is much larger than
521 *Adelocladoxis* and its xylem forms a dissected stele much more complex than that of *Adelocladoxis*.
522 Conversely, *Adelocladoxis* is also unlike the branches of this larger plant in its xylem anatomy.

523 It is also unclear whether the axes and ultimate appendages of *Adelocladoxis* typically had
524 longitudinal grooves and ridges, as seen in some of the specimens, or whether these features are a
525 reflection of taphonomy. Another major unknown about *Adelocladoxis* concerns whether the
526 sporangia are paired, like those of *Psilophyton* and other trimerophytes, and those of the majority of
527 iridopterids and pseudosporochneans. The single sporangium we found and the incomplete
528 preservation of the appendage that bears it do not provide an unequivocal answer. Similarly,
529 incomplete preservation precludes detailed description of the spores of *Adelocladoxis*. More
530 generally, information on cladoxylopsid sporangia, especially their anatomy, as well as their spores,
531 is scarce.

532

533 **Taxonomic affinities of *Adelocladoxis***

534 ***Comparative taxonomy and phylogenetic systematics***—Taxonomy has relied traditionally (i.e., for
535 most of the last two millennia) on a comparative approach. In more recent times, this approach has
536 been rooted in the Natural System developed by scientists about two centuries ago (Mishler, 2000).
537 Whether quantitative (and, arguably, more objective), as in the case of phenetics, or centered on
538 arguments from authority, as in the case of evolutionary systematics, the comparative approach is
539 aimed at identifying similarity as a basis for taxonomic placements. Only about a half-century ago did
540 we start to emphasize phylogeny and the patterns of character distribution arising from shared
541 ancestry, as the fundamental organizing principle for biological classification (Mishler, 2009). While
542 phylogenetic classification has become the norm in “neontological” systematics, paleobotany has
543 continued to employ the comparative approach, in the overwhelming majority of studies, for
544 taxonomic placements. Inroads into the realm of phylogenetic systematics have become more
545 frequent in paleobotany only recently. This apparent methodological conservatism is justifiable to
546 some extent. First, it is important to recognize that overall similarity still plays an important part in
547 any taxonomically-oriented endeavor, even if it is just to broadly circumscribe the affinities of an
548 organism as a preliminary working hypothesis. Second, fossils may exhibit autapomorphic
549 characters, combinations of many such characters, or combinations of plesiomorphic characters of
550 multiple well-circumscribed younger groups. Any of these situations makes it difficult to (1)
551 recognize close relatives of new fossils; (2) compare them to other taxa; or (3) select outgroups for
552 phylogenetic analyses (a problem that also plagues phylogenies of extant taxa that include long
553 branches). The severity of such difficulties only increase the deeper one probes in geologic time,

554 where the likelihood of encountering ancestors, stem lineages of younger, well-circumscribed
555 groups, or extinct sister-groups of well-circumscribed clades, increases. Third, and often dramatically
556 conflating problems of autapomorphy, the majority of fossils preserve only subsets of the defining
557 characters of the natural species they represent. This results in significant percentages of missing
558 data in phylogenetic matrices. In turn, this often produces phylogenies with low levels of resolution
559 and of clade support. In extreme cases – of small numbers of preserved diagnostic characters, low
560 phylogenetic resolution, or high proportions of autapomorphic characters –, the comparative
561 approach is the only applicable. Often, in such cases, even the comparative approach can only be
562 used to reach taxonomic decisions by an eliminatory process (e.g., Steenbock and Tomescu, 2013) or
563 by weighting the very few characters available for the fossil in question for their frequencies of
564 occurrence in the groups to which the fossil is compared (e.g., Mamontov and Ignatov, 2019).

565 In conclusion, comparative taxonomy, as well as phylogenetic systematics, each have
566 weaknesses, especially when working with fossils. Here, we use both a comparative approach and a
567 phylogenetic approach to explore the taxonomic affinities of *Adelocladoxis*. The former allows us to
568 recognize *Adelocladoxis* as a member of the cladoxylopsid *s.l.* plexus and to reject placement among
569 previously described genera and species of this group. The phylogenetic approach places
570 *Adelocladoxis* in a clade that excludes iridopterids and suggests affinities with the cladoxylopsids *s.s.*

571

572 **Assignment to the cladoxylopsid plexus**—*Adelocladoxis* possesses a set of characters that allow its
573 placement within well-defined groups at several taxonomic ranks, in a comparative approach. These
574 characters include actinostelic primary xylem with the xylem lobes thin as compared to the broader
575 central area of the stele; mesarch primary xylem maturation and permanent protoxylem strands
576 only at the tips of the xylem lobes; tracheids with oval-horizontal to circular bordered pitting; and
577 dichotomous ultimate appendages, each supplied by a trace that diverges from a single lobe of the
578 stele. The mesarch protoxylem places *Adelocladoxis* squarely among the euphyllophytes. The
579 protoxylem strands with straight, independent trajectories and only present at the lobe tips
580 (“permanent protoxylem”; Beck and Stein, 1993) are typical of the Moniliformopses (Kenrick and
581 Crane, 1997; Berry and Stein, 2000; Gerrienne et al., 2016).

582 Devonian moniliformopsids with mesarch protoxylem include the cladoxylopsids *s.l.*,
583 archaeocalamitalean sphenopsids, stauropterids, and rhacophytaleans (Gerrienne et al., 2016).
584 These groups possess distinctive stele types. The cladoxylopsid plexus includes plants with a variety
585 of stelar configurations, ranging from actinosteles similar to that seen in *Adelocladoxis* to ribbed
586 steles with different degrees of dissection and different patterns of distribution of central
587 parenchyma. The Archaeocalamitales have steles with a central pith surrounded by radial xylem ribs

588 with protoxylem canals (Galtier, 1970). The Devonian stauropterid *Gillespiea* possesses a terete
589 protostele (Erwin and Rothwell, 1989). The stele of *Rhacophyton* axes, incompletely documented, is
590 most likely an actinostele with central parenchyma (Leclercq 1951; Dittrich et al., 1983). Like
591 *Adelocladoxis*, *Rhacophyton* produces tangentially elongated traces to laterals that possess two
592 protoxylem strands. However, the laterals of *Rhacophyton* are much bigger than the ultimate
593 appendages of *Adelocladoxis*, they possess protoxylem loops, and they develop significant amounts
594 of secondary xylem. Thus, among Devonian moniliformopsids, *Adelocladoxis* matches most closely
595 the stelar configuration of plants in the cladoxylopid plexus, especially iridopteridalean
596 cladoxylopsids and some other taxa of less certain affinity within the group (*Denglongia*) – see
597 comparisons below. These considerations based on comparative taxonomy led us to include
598 *Adelocladoxis* in a phylogenetic analysis of the cladoxylopid plexus, in order to refine its taxonomic
599 placement.

600

601 **Comparisons**—Few cladoxylopsids cross into the Early Devonian (Ananiev and Zakharova, 1986;
602 Stein and Hueber, 1989; Gerrienne, 1992; Chu and Tomescu, 2015). The two that have been
603 documented in some detail – *Foozia* (Gerrienne, 1992) and *Protohyenia* (Ananiev and Zakharova,
604 1986) – are not characterized anatomically, consequently their placement in the group is somewhat
605 tentative. Of these two, *Adelocladoxis* is comparable to *Foozia* in terms of size and morphological
606 simplicity, and shares with the latter the same type of tracheids with oval-scalariform to circular
607 bordered pits. However, *Adelocladoxis* differs from *Foozia* in its ultimate appendages, which are
608 more dissected. Furthermore, it is as yet unclear whether the sporangia of *Adelocladoxis* were
609 paired, like those of *Foozia* and of most cladoxylopsids. More importantly, whereas *Foozia* is known
610 from compressions, thus its anatomy is poorly documented, *Adelocladoxis* is based on
611 permineralizations that allow access to a wealth of anatomical information, which supports
612 cladoxylopid affinities. As a result, the two taxa cannot be compared directly and are diagnostically
613 disjunct. Together, these considerations imply that *Adelocladoxis* is the oldest representative of the
614 cladoxylopid plexus known anatomically, to date.

615 Anatomically, *Adelocladoxis* compares well with some iridopterid taxa – *Ibyka amphikoma*,
616 *Iridopteris*, *Arachnoxylon kopfii* Stein, *Rotoxylon* –, as well as with members of the cladoxylopid
617 plexus that have somewhat uncertain taxonomic placement: *Serripteris* and *Denglongia*. Except for
618 *Arachnoxylon kopfii* Stein, these taxa do not possess xylem with a large central area (as compared to
619 the size of the ribs), like that seen in *Adelocladoxis*. In *Arachnoxylon kopfii* Stein, the center of the
620 stele consists of parenchyma, also different from *Adelocladoxis*. Additionally, except for *Denglongia*,
621 all these taxa are different from *Adelocladoxis* in possessing prominent protoxylem lacunae.

622 *Denglongia* and *Iridopteris* typically have two protoxylem strands at the tips of xylem lobes, unlike
623 *Adelocladaxis*. *Rotoxylon* exhibits stele dissection, another feature distinguishing it from
624 *Adelocladaxis*. Unlike *Adelocladaxis*, *Ibyka* possesses spiny epidermal extensions. Additionally,
625 compared to all these taxa that have axes >3 mm (e.g., *Serripteris*, *Denglongia*), the axes of
626 *Adelocladaxis* are smaller (1-2 mm). In summary, while *Adelocladaxis* is similar to some actinostelic
627 taxa – mostly iridopterids –, it also combines characters that distinguish it from each of those taxa,
628 justifying erection of a new genus.

629

630 **Phylogenetic placement**—In our analyses, *Adelocladaxis* is placed in a clade that excludes traditional
631 iridopterids (Fig. 8A) as well as iridopterid-like taxa, such as *Denglongia* and *Serripteris* (Fig. 8B). This
632 placement is at odds with the anatomy of *Adelocladaxis*, which is more consistent with iridopterid
633 affinities. However, *Adelocladaxis* is not the only taxon in this situation. *Denglongia* and *Serripteris*,
634 which also exhibit iridopterid-like anatomy, are placed in the same clade that excludes traditional
635 iridopterids and includes cladoxylopsids s.s. (the latter, characterized by dissected steles) (Fig. 8).
636 While this clade lacks resolution at the base, it is nevertheless well supported by our dataset, being
637 recovered in all the MP trees of Analyses 2 and 3. The synapomorphies that unite members of this
638 clade are the erect tips of ultimate appendages and the mode of branching, wherein ultimate
639 appendages and branch axes do not occur at the same nodes (in *Adelocladaxis* and *Rotoxylon* this
640 character could not be scored due to missing data).

641 A possible explanation for the apparent discrepancy between the implications of
642 comparative morphology and those of the phylogenetic analysis is that *Denglongia*, *Serripteris*, and
643 *Adelocladaxis* represent a transitional group that shares characters of both typical iridopterids and
644 typical cladoxylopsids s.s. – as suggested by their placement in a paraphyletic configuration between
645 these two groups (Fig. 8B). Another possible explanation is that *Adelocladaxis* represents a branch of
646 a larger plant with cladoxylopsid s.s. affinities. Such a plant has been identified in the Battery Point
647 Formation (Chu and Tomescu, 2015) and is currently being described. However, connections
648 between axes of this plant and *Adelocladaxis* axes have not been identified, and the laterals of this
649 plant do not have the anatomy of *Adelocladaxis* axes. In this context it is important to note that (1)
650 the Battery Point Formation hosts allochthonous assemblages consisting of fragmented, dispersed
651 plant fossils; and (2) systematic exploration of the diversity of permineralized plants preserved in
652 this formation is still in its early stages. Based on these considerations, it is too early to dismiss the
653 hypothesis of a larger plant bearing *Adelocladaxis* branches, which could be discovered in the future.

654

655 **Phylogeny and taxonomy of cladoxylopsids**

656 ***Cladoxylopsid organographic homologies***—Sporophyte organization in early tracheophytes evolved
657 from simple branching axes that lacked organographic differentiation to sporophyte bodies of
658 modular construction based on the repetition of differentiated, specialized organs (stems, leaves,
659 roots) (Stewart and Rothwell, 1993). It is now clear that several tracheophyte lineages followed this
660 evolutionary path independently (Friedman et al., 2004; Tomescu, 2009; Corvez et al., 2012) –
661 although the number of instances this happened is still debated –, and that in some of these
662 instances the evolutionary transition included stages of increasing complexity, paralleled by
663 progressive morphological and functional differentiation of the branching systems (Stewart, 1964;
664 Kenrick and Crane, 1997; Beerling and Fleming, 2007). The main chapters of this evolutionary
665 process span the Early and Middle Devonian. Plants of the cladoxylopsid plexus, encompassing this
666 Devonian interval, are key to understanding these evolutionary patterns, as they represent
667 transitional stages that record snapshots in the evolutionary process. However, for these same
668 reasons, the organization of these plants also challenges concepts of homology.

669 Morphological character construction (*sensu* Wiens, 2001) for phylogenetic studies requires
670 unequivocal, clearly defined hypotheses of homology. The cladoxylopsid plexus is especially
671 challenging in this context. All cladoxylopsids *s.l.* possess complex branching systems, many of them
672 exhibiting multiple orders of branching that may or may not form hierarchically organized
673 architectures (Berry, 2000; Berry and Stein, 2000; Meyer-Berthaud et al. 2007). Different lineages of
674 the cladoxylopsid plexus are thought to have given rise to sphenopsids and (possibly multiple)
675 pteridophyte-grade lineages (Skog and Banks, 1973; Stein et al. 1984; Stewart and Rothwell, 1993;
676 Kenrick and Crane, 1997; Rothwell, 1999; Berry and Stein, 2000), all of which possess leaves, which
677 are thought to have evolved from branching systems all across the euphyllophyte clade (Kenrick and
678 Crane, 1997; Friedman et al., 2004; Beerling and Fleming, 2007; Harrison and Morris, 2017).
679 However, whereas leaves are easily recognized as differentiated organs based on morphological
680 criteria (Tomescu, 2009), their organographic precursors span a broad spectrum of degrees of
681 differentiation of the ancestral branching systems. This renders the building of hypotheses of
682 organographic homology delicate, and the hypotheses themselves blurry. The difficulty is
683 exacerbated by the fact that all these transitional stages are only known from the fossil record, with
684 preservational limitations that preclude, in many cases, access to all potential diagnostic characters.
685 Nevertheless, tackling cladoxylopsid phylogeny requires the parsing of branching architecture into
686 characters based on hypotheses of homology. Essentially, this amounts to recognizing morphological
687 boundaries within hierarchies of “sticks-upon-sticks-upon-sticks”. While this is a daunting task, such
688 boundaries can be identified in many cases if features such as growth determinacy, anatomy, and
689 position in the branching hierarchy are considered. Below, we discuss our approach to the two main

690 aspects of morphological boundary identification that underlie several of our characters but have
691 been especially challenging to resolve, given our dataset.

692 One of the most vexing problems encountered in constructing morphological characters for
693 cladoxyllopsids and most other Early and Middle Devonian euphyllophytes devoid of leaves, is that of
694 recognizing ultimate appendages and distinguishing them from lower, subtending orders of
695 branching. Ultimate appendages are coded for in our characters C2-6, C8-9, C27, and C33-36.
696 Whether vegetative or fertile, they are usually recognized by their determinate growth and the fact
697 that they are reiterated, with consistent morphology, throughout the plant body. We also
698 recognized them as possessing the simplest anatomy, where preserved – i.e., they are represented
699 by the “minor traces” in taxa where appendages with different anatomies diverge from the same
700 subtending axis, with the corollary that “major traces” are homologized with lower order branch
701 axes. Together, these criteria allow for recognition of homologous structures, even though
702 characters related to them, such as taxis and planation can be difficult to score in cases where only
703 short stretches of anatomy or only morphology are preserved.

704 Branching architecture poses delicate questions of homology also in the lower orders of
705 branching, in terms of distinguishing main axes from subordinate branches. In some cases, this can
706 be resolved easily, when the latter are differentiated from the former by their anatomy. Such is the
707 case of “major traces” that diverge from subtending axes whose anatomy is different from theirs.
708 Such is the case of branches characterized by (anatomical) bilateral symmetry (C31) or by adaxial-
709 abaxial polarity (C32) that are attached to subtending axes that possess radial symmetry. In other
710 cases, planated (C7) or digitate branching (C26), when it can be ascertained, have been considered
711 to imply branch homology. However, in many cases (1) no anatomical differentiation exists
712 (branches only have smaller versions of the same anatomy anatomy as the subtending axes); (2)
713 anatomy is unknown (in taxa that preserve only morphology); or (3) the fragmentary state of fossils
714 does not allow construction of insightful whole-plant concepts. One or several of these issues marr
715 many taxa of the cladoxyllopsid plexus. Furthermore, distinguishing between main axes and branches
716 affects the scoring of related characters downstream, whether these encode anatomy (e.g., C11-17)
717 or branching architecture (e.g., C25). In such cases, we have scored main axis and branch characters
718 based on the biggest axes known for a taxon and their branches. We recognize that this (and other
719 similar decisions) introduces arbitrariness that may confound hypotheses of homology. However, in
720 some cases this is the only workable approach to this delicate problem if we are to start addressing
721 the phylogeny of cladoxyllopsids with extensive taxon sampling. Further exploration of this issue in
722 experiments with alternative character coding and scoring, although not the scope of this paper, is
723 certainly an avenue to be addressed in future studies. New fossil discoveries will also add missing

724 information as well as clarity to this issue. Together with the inclusion of continuous characters,
725 these are bound to improve phylogenetic resolution of the cladoxylopsids plexus.

726 At the same time, a number of characters not associated with specific organographic
727 categories, such as those encoding epidermal extensions (C1), tissue histology (C10), primary and
728 secondary xylem anatomy (C18-24), or characters encoding branch emission features (C28-C31), are
729 not challenging in terms of homology, unless they change during development, a fact that we
730 considered improbable, although we recognize that it would be difficult to ascertain in fossils.

731 In closing this section, it is important to recognize that the categories encoded in
732 morphological characters often represent the result of complex developmental processes that are
733 driven by intricate networks of regulatory interactions, often involving multiple interconnected
734 regulatory modules. Thus, hypotheses of homology about morphological features imply homology of
735 whole networks of modules regulating developmental processes. While such “wholesale”
736 homologizing is not optimal, it can be avoided only if and when these regulatory interactions and
737 their morphological fingerprints are understood, thus leading to construction of morphological
738 characters that reflect more accurately biological processes and their evolution. Short of that, at any
739 stage in the continuing evolution of our understanding of fossil organisms, we can only try our best
740 to reflect the state of knowledge at that moment in the way we construct morphological characters
741 for phylogenetic analyses.

742

743 ***Traditional classification***—The phylogenetic relationships recovered by our analyses allow for re-
744 evaluation of the taxonomy of cladoxylopsids. This group has been recognized for more than 100
745 years (Potonié and Bernard, 1904; Pichi-Sermolli, 1959) and it occupies a key position in discussions
746 of the origins of both ferns and sphenopsids (Skog and Banks, 1973; Stein et al., 1984; Stewart and
747 Rothwell, 1993; Stein, 1982; Kenrick and Crane, 1997; Xue et al., 2010). The steady addition of taxa
748 to the group and their taxonomic treatments have led to several classification schemes that are
749 partially overlapping, yet not entirely congruent (e.g., Berry and Stein, 2000; Cordi and Stein, 2005;
750 Meyer-Berthaud et al., 2007; Xue et al., 2010; Wang et al., 2018). Despite this situation, to date, only
751 one study has addressed phylogenetic relationships in this group (Xue et al., 2010). This is due,
752 among other reasons, (1) to difficulties in characterizing the organization of these plants in terms of
753 morphological characters (due, in turn, to blurry homology in the hierarchy of branching
754 architecture), as well as (2) to high disparity in the level of detail (anatomical and morphological) to
755 which each species has been characterized. The phylogenetic analysis of Xue et al. (2010) brought
756 some light onto the relationships of cladoxylopsids with other putatively related groups – early

757 sphenopsids, zygopterids. However, the relatively sparse taxon sampling of the group in that analysis
758 did not produce satisfactory resolution of the difficult cladoxylopsid plexus.

759 Phylogeny can, and should, inform taxonomy, so our analysis took advantage of the
760 opportunity provided by the discovery of a new species with cladoxylopsid affinities to explore in
761 more detail relationships among cladoxylopsids, in a phylogenetic context. Our taxon sampling and
762 character construction are directly aligned with these goals. The set of morphological characters we
763 generated is inspired by characters used in previous phylogenetic studies and discussions centered
764 on the cladoxylopsids or otherwise (Cordi and Stein, 2005; Xue et al., 2010; Toledo et al., 2018), as
765 well as by major reviews of the taxonomy of this group (Berry and Stein, 2000; Cordi and Stein, 2005;
766 Meyer-Berthaud et al., 2007). Our results reveal patterns of relationships relevant to these
767 taxonomic discussions.

768 The latest treatments of the cladoxylopsids (Xue et al., 2016; Wang et al., 2018) divide these
769 plants into three groups, as proposed initially by Wang and Berry (2006) and Meyer-Berthaud et al.
770 (2007). The three groups are the Iridopteridales [treated as a lineage within the Cladoxylopsida by
771 most authors, until Meyer-Berthaud et al. (2007) excluded them from the class] and two groups
772 within Meyer-Berthaud et al.'s Cladoxylopsida s.s.: the Pseudosporochnales and the non-
773 pseudosporochnalean cladoxylopsids. Whereas the Pseudosporochnales are considered
774 monophyletic by Xue et al. (2010, 2016), non-pseudosporochnaleans are an informal group including
775 plants that cannot be included among either Pseudosporochnales or Iridopteridales (Meyer-
776 Berthaud et al., 2007; Wang et al., 2015). Although the Iridopteridales have been excluded from the
777 formally circumscribed Cladoxylopsida (Meyer-Berthaud et al., 2007), their close relations to the
778 latter are widely accepted.

779 The Iridopteridales include a number of species (Berry and Stein, 2000; Meyer-Berthaud et
780 al., 2007; Xue et al., 2016; Appendix S1), some of which are only known morphologically from
781 adpression fossils – *Anapaulia moodyi* (Berry and Edwards, 1996), *Compsocradus givetianus* (Wang,
782 2008; Fu et al., 2011), *Ibyka vogtii* Høeg (Høeg, 1942; Berry, 2005) –, while others are known
783 primarily by their anatomy – *Arachnoxylon minor* (Stein et al., 1983), *Arachnoxylon kopfii* (Arnold,
784 1935; Stein, 1981; Stein et al., 1983), *Asteropteris noveboracensis* (Dawson, 1881; Bertrand, 1913;
785 Seaby, 1972), *Iridopteris eriensis* (Stein, 1982), *Rotoxylon dawsonii* (Read, 1935; Cordi and Stein,
786 2005) –, and yet others are more completely characterized in terms of both anatomy and
787 morphology – *Compsocradus laevigatus* (Berry and Stein, 2000), *Ibyka amphikoma* (Skog and Banks,
788 1973; Berry, 2005). Additionally, *Serripteris feistii* (Rowe and Galtier, 1989), *Metacladophyton*
789 *tetraxylum* (Wang and Geng, 1997), *Metacladophyton ziguinum* (Wang and Lin, 2007), and

790 *Denglongia hubeiensis* (Xue and Hao, 2008; Xue et al., 2010) have been discussed as putative
791 iridopterids.

792 According to Meyer-Berthaud et al. (2007), the Pseudosporochnales comprise the genera
793 *Calamophyton* (Leclercq and Andrews, 1960; Leclercq and Schweitzer, 1965), *Pseudosporochnus*
794 (Leclercq and Banks, 1962; Leclercq and Lele, 1968), *Lorophyton* (Fairon-Demaret and Li, 1993), and
795 *Wattieza* (Stockmans, 1968; Berry, 2000; Stein et al., 2007); and the non-pseudosporochnalean
796 cladoxylopsids include *Panxia* (Wang and Berry, 2006; Xue et al., 2016), *Rhipidophyton* (Berry and
797 Wang, 2006), *Polypetalophyton* (Hilton et al., 2003), *Pietzschia* (Read and Campbell, 1939; Soria et
798 al., 2001; Soria and Meyer-Berthaud, 2003, 2005), *Cladoxylon* (Bertrand, 1935; Mustafa, 1978), and
799 *Polyxylon* (Read and Campbell, 1939; Chambers and Regan, 1986; Meyer-Berthaud et al., 2007). In
800 the intervening period since the review by Meyer-Berthaud et al. (2007), *Xinicaulis* was described by
801 Xu et al. (2017) with cladoxylopsid affinities.

802

803 **Levels of support**—Our strict consensus trees show low nodal support values (Fig. 8). This is typical
804 of phylogenies based on sets of characters that have significant proportions of missing data or data
805 sets with relatively low character to taxon ratios, which may recover low levels of nodal support,
806 even when resolution is high. In such cases, the relative instability of taxa with missing entries can
807 lower commonly employed measures of clade support (Flores et al., 2021) and, in extreme cases,
808 low support values can mask well-supported relationships (Wilkinson, 2003). Nevertheless, the tree
809 topologies we recovered are congruent between the three levels of inference we addressed. Thus,
810 the well-resolved strict consensus trees obtained upon inclusion of fewer taxa (Analyses 2 and 3) are
811 broadly congruent with the majority rule consensus trees generated under the broader taxon
812 sampling regimes (e.g., Fig. 8B and 9). Such congruence indicates the presence of strong
813 phylogenetic signal in the morphological data, despite the shortcomings of fossils (missing data and
814 taxon instability). Together, these considerations lend us confidence that the topologies (and their
815 implications) discussed here reflect real, natural relationships and evolutionary trends.

816

817 **Phylogenetic relationships**—Our phylogenetic analyses recover a general pattern of relationships
818 among cladoxylopsids that remains stable under different taxon sampling regimes, increasing in
819 support and resolution as taxa with high proportions of missing data are excluded. While these
820 relationships are in agreement with many aspects of previous classifications, our results also support
821 some departures from previous classification schemes. The traditional distinction between
822 Iridopteridales and Cladoxylopsida s.s. is apparent in the results of our analyses (Fig. 11), with the
823 former recovered as a paraphyletic group basal to the latter. Within the iridopterids, two clades are

824 resolved (Fig. 8). One of these clades includes *Anapaulia* and *Ibyka amphikoma*. The other clade,
825 referred to here as core iridopterids because it has synapomorphies traditionally thought as defining
826 the Iridopteridales, is composed of *Asteropteris*, two *Arachnoxyton* species (*A. minor* and *A. kopfii*
827 Read), *Iridopteris*, and *Compsocradus laevigatus* (Fig. 8). *Denglongia* and *Serripteris* form a grade of
828 “transitional cladoxylopsids” between the two earlier-diverging iridopterid clades and the clade that
829 includes the cladoxylopsids s.s. (Fig. 8).

830 Within this cladoxylopsid clade, we distinguish a well resolved clade, the
831 pseudosporochnalean cladoxylopsids of Meyer-Berthaud et al. (2007; also recovered in the analyses
832 of Xue et al., 2010), that includes *Lorophyton*, *Calamophyton*, *Wattieza*, and *Pseudosporochnus* (Fig.
833 8, 9); *Adelocladoxia* holds an unresolved position that is, nevertheless, closely related to this clade
834 and the rest of the cladoxylopsids s.s. (see “Taxonomic affinities of *Adelocladoxia*” above). The
835 remaining members of the cladoxylopsid clade, formerly thought of as an informal “non-
836 pseudosporochnalean” group (Meyer-Berthaud et al. 2007), are recovered in our analyses as a well-
837 supported clade, termed here cladoxylalean cladoxylopsids. This clade, named in reference to
838 *Cladoxylon*, the first described cladoxylopsid (Unger, 1856), also includes *Polypetalophyton*,
839 *Metacladophyton*, *Rotoxylon*, *Panxia*, *Polyxylon*, and *Pietzschia* (Fig. 8, 9).

840 In terms of genus-level systematics, our phylogeny suggests that the genera *Arachnoxyton*
841 and *Cladoxylon* are not monophyletic. *Xenocladia* is placed within the pseudosporochnalean
842 cladoxylopsids (Analysis 1; Supplemental fig. 26), consistent with the traditional taxonomic
843 placement of this genus. *Rotoxylon dawsonii*, placed among the iridopterids by Cordi and Stein
844 (2005), is recovered as a member of the cladoxylalean cladoxylopsids, sister to *Metacladoxylon*
845 *ziguinum*, which is more consistent with the initial placement of this species in the genus *Cladoxylon*
846 (*C. dawsonii* Read 1935).

847 Overall, these results have much in common with the classification scheme of Meyer-
848 Berthaud et al. (2007) and suggest that their loosely-defined non-pseudosporochnalean
849 cladoxylopsids form a monophyletic group (our cladoxylalean cladoxylopsids). In summary, our study
850 provides phylogenetic support for the following relationships among cladoxylopsids s.l.: the
851 Iridopteridales form a paraphyletic group that includes the (*Anapaulia* + *Ibyka amphikoma*) clade
852 and a clade of core iridopterids. A grade of later-diverging transitional cladoxylopsids subtends a
853 monophyletic Cladoxylopsida s.s., split into two clades: the pseudosporochnalean cladoxylopsids and
854 the cladoxylalean cladoxylopsids.

855

856 **Implications of a new phylogeny**

857 **Patterns of character change**—The distribution of character states across our phylogeny indicates
858 that the plesiomorphic combination of characters of cladoxylopsids *s.l.*, shared by two earliest-
859 diverging lineages in the clade, the *Anapaulia-Ibyka* group and the core iridopterids clade, includes
860 whorled taxis of branches (C25 = 2) (Fig. 10), which are attached at the same nodes as ultimate
861 appendages (C27 = 1), and recurvation of the ultimate appendages (C5 = 1). Two of these characters
862 have reversals to these ancestral states within the cladoxylalean cladoxylopsids: C25 = 2 and C5 = 1.
863 The *Anapaulia-Ibyka* clade shares with the core iridopterids and the two transitional cladoxylopsids,
864 *Denglongia* and *Serripteris*, an actinostele with xylem ribs broader at the tips (C11 = 1 or 2; C17 = 2)
865 and lacking parenchyma (C12 = 0), as well as branch traces supplied by only one xylem rib and
866 possessing two or a single protoxylem strand (C28 = 0; C29 = 0 or 1). Within this paraphyletic group,
867 *Arachnoxylon kopfii* Read is an exception (C17 = 0 and C29 = 2). These characters change in the
868 cladoxylopsids *s.s.*, which evolve a dissected stele (C11 = 3) that contains central parenchyma [that is
869 irregularly distributed (C12 = 2) in the early-diverging members of the clade] and possesses parallel-
870 sided xylem ribs (C17 = 0). Branch emission also evolves in this clade to traces diverging from more
871 than one xylem rib (C28 = 1) and possessing more than two protoxylem strands (C29 = 2).
872 Subsequently, in the *Polyxylon-Pietzschia* clade the stele evolves from irregularly distributed central
873 parenchyma to parenchyma forming a central cylinder (C12 = 1).

874 A few other characters exhibit trends in their phylogenetic distribution that we can
875 speculate on, although they do not carry unequivocal phylogenetic signal. Metaxylem tracheid
876 pitting, typically consisting of oval to circular pits (C18 = 2) in the plesiomorphic condition (exclusive
877 of *Asteropteris*, characterized by circular pits; C18 = 3), changes to circular pits in the the
878 cladoxylalean cladoxylopsids (exclusive of *Cladoxylon*, whose species have scalariform pitting; C18 =
879 1). Patterning of metaxylem tracheid size within the xylem ribs, wherein tracheids at the rib center
880 are larger and tracheid diameter decreases toward the sides of the ribs (C20 = 1), characterizes the
881 *Panxia-Polyxylon-Pietzschia* clade and *Rotoxylon*. Aside from this group of later-diverging taxa, a lack
882 of conspicuous radial patterning of tracheid size within the ribs (C20 = 0) may be the plesiomorphic
883 condition among cladoxylopsids *s.l.*; nevertheless, *Compsocradus laevigatus*, *Iridopteris*, and
884 *Denglongia* are earlier-diverging taxa that also exhibit the same patterning seen in the *Panxia-*
885 *Polyxylon-Pietzschia* clade.

886

887 **Stele evolution in cladoxylopsids *s.l.***—The distribution of characters in our phylogeny supports a
888 sequence of character changes that is relevant to hypotheses on the evolution of stelar architecture
889 (Fig. 11). In general, stelar architecture trends from actinosteles (C11 = 1 or 2) – with few xylem ribs
890 (4-12) in the earliest diverging taxa (iridopterids) – to highly dissected steles (C11 = 3) with numerous

891 (24-90) xylem ribs (or vascular segments) in the most derived members of the cladoxylopsids s.s..
892 Among the latter, the pseudosporochnaleans and the *Pietzschia-Polyxylon* clade evolved in parallel
893 to possess steles with the highest numbers of xylem ribs. Also among the cladoxylopsids s.s., the
894 pattern of stele dissection exhibits a transition from irregularly dissected steles [i.e., with some of
895 the xylem ribs anastomosing along their vertical trajectories and appearing connected at the center
896 in cross sections (C13 = 0)] in the earlier diverging cladoxylalean cladoxylopsids, to derived steles
897 that are organized into a ring of rib-like xylem segments (C13 = 1) that surrounds a well-defined
898 central region of parenchyma (C12 = 1) containing scattered vascular bundles (C14 = 1), in the
899 *Pietzschia-Polyxylon* clade. Intermediate within this pattern, earlier-diverging cladoxylalean
900 cladoxylopsids (*Cladoxylon taeniatum*, *Rotoxylon*, *Polypetalophton*) have steles with 12-24 xylem ribs
901 that also possess some vascular bundles in a less regularly shaped central parenchymatous region
902 (C12 = 2). This stelar architecture is also present in *Pseudosporochnus*, thus, it evolved in parallel in
903 the pseudosporochnalean cladoxylopsids.

904 In summary, the evolutionary sequence that emerges from our system of phylogenetic
905 relationships encompasses a transition from terete protosteles to actinostelic protosteles, followed
906 by dissection of the latter, in parallel with an increase in number of xylem ribs and, eventually,
907 medullation that results in a large central parenchymatous area containing free xylem bundles
908 (medullary bundles) (Fig. 11). Another stele character, dissected xylem ribs (C16 = 1 or 2), seems to
909 be the plesiomorphic condition in the cladoxylopsids s.l., whether this anatomy represents a stable
910 stelar configuration or is related to trace emission. Within the cladoxylopsids s.s., this character
911 changes to xylem ribs that are not dissected and subsequently reverts to dissected ribs in (most of)
912 the cladoxylalean cladoxylopsids.

913 Interestingly, the arborescent habit is associated with (1) steles possessing high numbers of
914 xylem ribs (segments) and a large central parenchymatous area (*Pietzschia* model of growth; Meyer-
915 Berthaud et al., 2010), as well as with (2) secondary growth (*Calamophyton* model of growth; Giesen
916 and Berry, 2013), in the largest cladoxylopsids s.s.; these count among them pseudosporochnaleans
917 (*Watiezza-Eospermatopteris*, *Pseudosporochnus*, *Calamophyton-Duisbergia*, and possibly
918 *Lorophyton*; Berry and Fairon-Demaret, 2002; Stein et al., 2007; Giesen and Berry, 2013) and
919 cladoxylaleans (*Pietzschia*; Meyer-Berthaud et al., 2010). These features linked to the arborescent
920 habit are most clearly associated in the largest cladoxylopsid trunks – *Xinicaulis lignescens* (not
921 included in our analysis; Xu et al., 2017) and, potentially, *Eospermatopteris-Watiezza*. The co-
922 occurrence of these traits in two groups that have independently evolved an arborescent habit
923 suggests that this combination of characters may be strongly coupled at the regulatory level.

924 Another interesting association of characters is the increase in size and complexity of steles
925 that are paralleled by the advent of laterals supplied by multiple xylem ribs of the stele. Whereas the
926 simpler actinosteles seen in iridopterids supply laterals from single xylem ribs (C28 = 0), the
927 dissected steles of cladoxylopsids *s.s.* are associated with laterals supplied by multiple xylem ribs
928 (C28 = 1). Among these dissected steles, those featuring the highest numbers of xylem ribs and large
929 central parenchymatous areas – the *Pietzschia-Polyxylon* clade –, are also associated with lateral
930 branching systems that possess planated architecture (C7 = 1) (Fig. 10). However, planated
931 branching systems also evolved independently outside of this clade, in *Pseudosporochnus*. Like in the
932 case of arborescence, this pattern of association between stele size and complexity, on one hand,
933 and the vascular supply and morphology of laterals, on the other hand, may be underpinned by both
934 developmental and functional connections that explain the independent evolution of this set of
935 characters in two groups.

936 Functionally, the larger steles with higher numbers of xylem ribs, allowed for the
937 development of larger axes. In turn, this led to the evolution of larger central parenchymatous areas
938 and of more robust laterals. The central parenchymatous area defrayed some of the physiological
939 costs that would have incurred in the production of progressively larger and functionally oversized
940 actinosteles. The more robust laterals required a more substantial vascular supply, derived from
941 multiple ribs of the stele. Developmentally, the sequence of character change recovered in our
942 phylogeny – advent of medullation in association with an increase in (1) axis and stele size, and (2) in
943 the complexity of laterals –, is consistent with hypotheses that explain stelar evolution as a result of
944 size- and lateral appendage-driven radial redistribution of vascular identity specifiers (Stein, 1993;
945 Tomescu, 2021).

946

947 ***Distinguishing taxonomic groups among cladoxylopsids***—The characters that distinguish the
948 different groups of cladoxylopsids *s.l.* have been discussed by Berry and Stein (2000), Cordi and Stein
949 (2005), Meyer-Berthaud et al. (2007), and Xue et al. (2010). These discussions indicate that
950 pseudosporochnalean cladoxylopsids are united by several characters: a dissected stele composed of
951 several radial primary xylem ribs (or vascular segments) with mesarch protoxylem; more than one
952 rib contributing to branch tracees; a dense and irregular branching system; and hierarchized
953 architecture with a single type of laterals per node. Non-pseudosporochnalean cladoxylopsids
954 include plants that exhibit the typical dissected stele or branching patterns of the Cladopsyllopsida,
955 but cannot be included among either Pseudosporochnales or Iridopteridales (Meyer-Berthaud et al.,
956 2007) based on other evidence. Tholohe same discussions point to the Iridopteridales as being
957 characterized by deeply ribbed actinosteles with four to 12 xylem ribs and permanent mesarch

958 protoxylem strands at the rib tips; whorled laterals; iterative architecture with branches replacing
959 ultimate appendages at nodes and, thus, two types of vascular traces at nodes; traces to laterals
960 diverging from just one xylem rib; and metaxylem with larger tracheid the midplane of xylem ribs
961 (Stein, 1982; Berry and Edwards, 1996; Berry and Stein, 2000; Meyer-Berthaud et al., 2007).

962 The pattern of character variation recovered in our phylogenetic analyses (Fig. 10-11)
963 supports some of the characters previously proposed to distinguish the different groups of
964 cladoxylaleans. For the Iridopteridales (i.e., the *Anapaulia-Ibyka* clade and the core iridopterids),
965 these characters include actinosteles, vascular traces to laterals supplied by single xylem ribs, and
966 whorled branch taxis, with ultimate appendages attached at the same node as branches. However,
967 ultimate appendages are not whorled in higher order branches, as previously proposed, in *Anapaulia*
968 and *Ibyka*. Another character discussed in the literature as useful for differentiating the
969 Iridopteridales, from the cladoxylaleans s.s., is epidermal extensions, such as spines reported for
970 some iridopterids by Berry and Stein (2000). We recover epidermal extensions as a synapomorphy
971 only for the *Anapaulia-Ibyka* clade (they also occur among the cladoxylalean cladoxylaleans in
972 Metacladophyton). For the cladoxylaleans s.s., our results are consistent with dissected steles,
973 branch traces supplied by more than one xylem rib, and a single type of lateral at nodes, as
974 distinguishing characters. Additionally, we recovered low-angle branching (digitate branching) as a
975 diagnostic character for the pseudosporochnelean cladoxylaleans.

976 A major point of difference between iridopterids and cladoxylaleans s.s. highlighted by
977 Meyer-Berthaud et al. (2007), relates to branching architecture. Those authors contrast the
978 hierarchized architecture of cladoxylaleans, “an ordered sequence of branching, each order of axis
979 being characterized by distinctive geometrical traits” (Meyer-Berthaud et al., 2007, p. 1096), with
980 the iterative architecture of iridopterids (i.e., the same architectural pattern repeated in axes of all
981 orders). *Compsocradus laevigatus* (Berry and Stein, 2000) for the Iridopteridales, and *Calamophyton*
982 (Giesen and Berry, 2013) for the cladoxylaleans s.s., illustrate well this distinction. Additional support
983 comes from the occurrence of branches and ultimate appendages in the same whorls, in the entire
984 iridopterid grade, wherein it suggests interchangeability of these appendages, consistent with
985 iterative architecture. The position of *Denglongia* is also consistent with this architectural
986 separation. *Denglongia* had an unresolved taxonomic position among the cladoxylaleans s.l. (Xue
987 and Hao, 2008) and resembles the iridopterids in its whorled laterals. However, *Denglongia* exhibits
988 hierarchized architecture typical of cladoxylaleans s.s.: its main axes bear exclusively whorls of
989 branches, which, in turn, bear helically arranged ultimate appendages (Xue and Hao, 2008, fig. 14).
990 Consistent with this, we recover *Denglongia* as an early-diverging member of a clade that consists
991 primarily of cladoxylaleans s.s. (Fig. 8).

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Potential of conspecificity among taxa of the cladoxylopid plexus—The cladoxylopid plexus has a significant history of studies that have demonstrated conspecificity of entities previously described as distinct taxa. These include assembly of the *Wattieza-Eospermatopteris* plant (Stein et al., 2007) and the *Calamophyton-Duisbergia* plant (Giesen and Berry, 2013), as well as the demonstration of conspecificity between *Hyenia elegans*, *Calamophyton primaevum*, and *Cladoxylon scoparium* (Fairon-Demaret and Berry, 2000). This taxonomic history begs the question – How likely is it that more of the cladoxylopid taxa are in fact conspecific? More specifically – Is it possible that the different stelar architectures represent different orders of branching of the same species (with smaller, simpler steles representing the higher orders of branching)? Or – Is it possible that the different stelar architectures represent different segments along epidogenetic series of a single axis type?

First, considering the possibility that different stelar architectures (e.g., iridopterid v. cladoxylopid s.s.) represent different orders of branching of the same plant, some observations are consistent with this possibility. (1) The stratigraphic ranges of iridopterids and cladoxylopid s.s. overlap partially. (2) The sizes of the largest iridopterid axes [25 mm for *Asteropteris* (Bertrand, 1913); 15 mm for *Ibyka amphikoma* (Skog and Banks, 1973)] are much smaller than the average cladoxylopid main axes and are only comparable in size to the smallest cladoxylopid branches (20 mm in *Calamophyton primaevum*; Giesen and Berry, 2013) or the smallest cladoxylopid s.s. [*Polypetalophyton*, 9.7 mm (Hilton et al., 2003); *Panxia*, 25 mm (Wang and Berry, 2006); *Cladoxylon mirabile*, 25 mm (Bertrand, 1935); *Rotoxylon*, 15mm (Cordi and Stein, 2005); *Metacladophyton ziguinum*, 12 mm (Wang and Lin, 2007)]. (3) In *Metacladophyton*, the lower order axes possess a more dissected stele than that of the branches attached to them.

However, other observations are inconsistent with hypotheses that taxa with iridopterid v. cladoxylopid steles represent different orders of branching of the same plant. (1) The only anatomically known branches of big cladoxylopid s.s. do not possess actinosteles – instead, they have dissected steles (e.g., *Calamophyton*, *Pseudosporochnus*, *Pietzschia*). (2) *Denglongia*, a taxon known as a whole plant that shows intermediate characters between the Iridopteridales and the cladoxylopid s.s. and is recovered as an early-diverging member of the cladoxylopid s.s. clade, possesses actinosteles in the axes of all orders. (3) Iridopterids and cladoxylopid s.s. do not overlap entirely in terms of morphology: while some iridopterids possess spines, none of the cladoxylopid s.s. do; conversely, while some cladoxylopid s.s. exhibit planated branching, no iridopterids with planated branching are known. (4) The stratigraphic ranges of the two groups overlap only partially – iridopterids disappear before the Famennian-Mississippian range of many cladoxylopid s.s. – and few

1026 cladoxylopsids have been reported from the same rock units as iridopterids. These few instances are
1027 the report of *Wattieza casatii*, *Anapaulia*, and *Compsocradus laevigatus* in the Campo Chico
1028 Formation of Venezuela (Berry and Edwards, 1996; Berry, 2000; Berry and Stein, 2000); of *Rotoxylon*
1029 *dawsonii* and *Arachnoxylon kopfii* in the Genesee Formation of New York State (Stein, 1981; Cordi
1030 and Stein, 2005); and of *Asteropteris* (Sebby, 1972), *Rhymokalon* (Scheckler, 1975) and
1031 *Pseudosporochnus hueberi* (Stein and Hueber, 1989) in the Oneonta formation of New York State.

1032 Along the same lines, the possibility that some non-pseudosporochnaleans (i.e.,
1033 cladoxylalean cladoxylopsids) may represent branches of plants whose main axes have typical
1034 pseudosporochnalean anatomy, is supported by some observations but rejected by others. Thus,
1035 the stratigraphic ranges of the two groups overlap in general, and the sizes of non-
1036 pseudosporochnalean axes [10-160 mm; *Polypetalophyton wufengensis* (Hilton et al., 2003) and
1037 *Pietzschia schulleri* (Soria and Meyer-Berthaud, 2005)] overlap broadly with those of
1038 pseudosporochnalean branches [20-50 mm; *Calamophyton primaevum* (Giesen and Berry, 2013) and
1039 *Wattieza casatii* (Berry, 2000)]. However, no non-pseudosporochnalean cladoxylopsid occurs in the
1040 same rock unit with pseudosporochnalean cladoxylopsids, and the diameter of the biggest
1041 cladoxylalean cladoxylopsid (*Pietzschia levis*) can reach the diameter of pseudosporochnalean
1042 trunks.

1043 A second possibility is that the different stelar architectures represent different segments
1044 along epidogenetic series of a single axis type. In epidogenesis, stelar architecture increases in
1045 complexity distally within a single plant or along a single axis. Examples of such organization are
1046 known in multiple lineages, from the classic example of protostele medullation in *Gleichenia* (Bower,
1047 1908), to lycopsids (Eggert, 1961; Delevoryas, 1964), and archaeopterid progymnosperms (Carluccio
1048 et al., 1966; Scheckler, 1978; Beck, 1979). In cladoxylopsids, an epidogenetic progression would
1049 involve transition from a typical iridopterid actinostele to a plesiomorphic cladoxylopsid s.s.
1050 dissected actinostele (e.g. *Cladoxylon radiatum*), or from the latter to a medullated stele with radial
1051 xylem segments, of the type seen in *Xinicaulis* or *Pietzschia*. While epidogenetic patterns have been
1052 demonstrated in *Pietzschia levis* (Soria and Meyer-Berthaud, 2004) and *Calamophyton primaevum*
1053 (Giesen and Berry, 2013), neither of these plants shows a dramatic transition in stele type along its
1054 axes. Nevertheless, a *Polyxylon* axis documented by Meyer-Berthaud et al. (2007) shows transition
1055 from a dissected stele with xylem ribs connected across the central area, proximally, to more
1056 pronounced dissection, a central parenchymatous area, and medullary xylem bundles, distally.

1057 Whether it is the question of epidogenesis or that of whether different stelar architectures
1058 represent different orders of branching of the same plant, finding unequivocal answers will require
1059 discovery of longer cladoxylopsid axis segments, with anatomy preserved all along and with more

1060 complete branches preserved anatomically. Available data indicate that the likelihood of
1061 conspecificity between the different cladoxylopsid *s.l.* taxa known to date is low and our phylogeny
1062 provides support to previous ideas that iridopterids and cladoxylopsids are distinct taxonomic
1063 groups. Nevertheless, the phylogenetic placement of *Adelocladoxis* is interesting in this context.
1064 Despite its actinostelic anatomy, this plant is recovered in our phylogeny as a member of the
1065 cladoxylopsid *s.s.* clade. It is, therefore, not impossible that *Adelocladoxis* represents a branch of a
1066 larger cladoxylopsid with a dissected stele, which has yet to be discovered.

1067

1068 ***Tempo of cladoxylopsid evolution***—Although compression fossils attributed to cladoxylopsids *s.l.*
1069 have been reported previously from Emsian strata (in Belgium and Siberia; Gerrienne, 1992; Ananiev
1070 and Zakharova, 1986) *Adelocladoxis* is the first cladoxylopsid described anatomically from the Early
1071 Devonian. The only other known Early Devonian permineralized occurrence is only briefly mentioned
1072 by Stein and Hueber (1989) in the same Emsian strata that host *Adelocladoxis* – the Battery Point
1073 Formation. Subsequently, cladoxylopsids reached global distribution by the Frasnian, at which time
1074 they were present in Euramerica, China, and Gondwana. The group persisted for at least 50 million
1075 years and is represented in the lower Mississippian by pseudosporochnaleans and one transitional
1076 iridopterid (*Serripteris*).

1077 The Emsian age of *Adelocladoxis*, together with its derived position among cladoxylopsids
1078 *s.l.*, suggest that several iridopterid and cladoxylopsid *s.s.* lineages had evolved no later than the
1079 early to mid-Emsian (Fig. 9), consistent with an initial early- to mid-Emsian radiation in the
1080 cladoxylopsid plexus. The ages of known iridopterids and cladoxylopsids *s.s.* are consistent with
1081 subsequent Eifelian radiation within some of these lineages, including the core iridopterids, the
1082 pseudosporochnalean cladoxylopsids, and the cladoxylalean cladoxylopsids (Fig. 9). Within the
1083 latter, another radiation followed no later than the Frasnian-Famennian giving rise to the *Polyxylon-*
1084 *Pietzschia* clade. Overall, our results support an initial Emsian radiation, followed by Eifelian
1085 radiations that gave rise to most iridopterid and cladoxylopsid *s.s.* lineages. The interval of highest
1086 cladoxylopsid diversity encompasses the Middle Devonian and first half of the Late Devonian.

1087

1088 **CONCLUSIONS**

1089 *Adelocladoxis praecox* gen. et sp. nov. is a small cladoxylopsid with actinostelic xylem; dichotomous
1090 filiform ultimate appendages arranged helically and supplied by traces derived from single xylem
1091 lobes and bearing two protoxylem strands; fusiform sporangia with longitudinal dehiscence; and
1092 epidermal cells containing dark compact bodies of fossilized secondary metabolites. Preserved as
1093 permineralizations in Emsian strata of the Battery Point Formation, in Quebec (Canada), As the

1094 oldest anatomically preserved representative of the cladoxylopid plexus, *Adelocladoxis* provides
1095 information on the structure of the earliest members of this group. *Adelocladoxis* also yields the first
1096 anatomical information on cladoxylopid ultimate appendages and sporangia. The ultimate
1097 appendages have centrarch terete xylem strands, and the sporangia have walls with organization
1098 similar to that documented in other basal euphyllophytes and characterized in detail in *Psilophyton*
1099 (Banks et al., 1975; Noetinger et al., 2018).

1100 Phylogenetic analyses based on a newly developed set of morphological characters and
1101 addresses the most extensive sampling cladoxylopid taxa to date, provide resolution of
1102 relationships within the cladoxylopid plexus, while also confirming previous non-phylogenetic
1103 classification schemes. The Iridopteridales form a paraphyletic grade basal to a clade of
1104 cladoxylopid s.s.. Within the paraphyletic Iridopteridales, “traditional” iridopterids are recovered
1105 as a clade (referred to as ‘core iridopterids’). The cladoxylopid clade includes two monophyletic
1106 groups: the traditionally recognized pseudosporochnalean cladoxylopid and the cladoxylean
1107 cladoxylopid, previously relegated to the informal non-pseudosporochnaleans cladoxylopid
1108 (Meyer-Berthaud et al., 2007).

1109 Considered in a geochronologic perspective, the phylogenetic relationships recovered
1110 illuminate the tempo and mode of evolution in the cladoxylopid plexus. In terms of evolutionary
1111 tempo, the group, originating prior to the Emsian, had already diversified into several lineages by the
1112 early to mid-Emsian, and reached global distribution by the Frasnian. Iridopterids and cladoxylopid
1113 s.s. radiated further throughout the Eifelian. In terms of mode of evolution, our phylogeny supports
1114 a transition from terete protosteles to actinostelic protosteles, followed by dissection of the latter, in
1115 parallel with increase in number of xylem ribs and, eventually, medullation. The latter is associated
1116 with increase in axis and stele size, and in the complexity of laterals, in parallel, in the two main
1117 clades of cladoxylopid s.s.. These phylogenetically-derived sequences of character evolution
1118 support hypotheses put forth previously by Lemoigne and Lurina (1983), Stewart and Rothwell
1119 (1993) to explain stelar evolution among cladoxylopid, and by Stein (1993) to explain stelar
1120 evolution as a result of size- and lateral appendage-driven radial redistribution of vascular identity
1121 specifiers. Our results also establish a phylogenetic framework for the mechanisms proposed by
1122 Tomescu (2021) to explain the evolution of the cladoxylopid steles in an evo-devo perspective.
1123 Future studies stemming from our results should also address the biogeography of cladoxylopid, as
1124 well as the pattern of relationships between the major lineages of this group and other
1125 euphyllophyte lineages – sphenopsids, rhacophytaleans, stauropterids, stenokolealeans, and
1126 progymnosperms.

1127

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1143

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1145 AMFT and TD designed the study. MAL and TD prepared the fossil material and collected anatomical
1146 data. TD and AMFT constructed the phylogenetic characters and scored them in taxa selected by TD.
1147 TD and AWB performed tree searches. TD and AMFT produced the illustration and wrote the
1148 manuscript. AWB edited the manuscript.

1149

1150 **DATA AVAILABILITY**

1151 Fossil repository: U.S. National Museum of Natural History – Smithsonian Institution (USNM); See
1152 Materials and Methods for accession numbers. Figures archived in the free public repository
1153 Figshare:
1154 https://figshare.com/collections/Durieux_et_al_American_Journal_of_Botany_2021/5487456

1155

1156 **ONLINE SUPPORTING INFORMATION**

1157 Additional Supporting Information may be found online in the supporting information section at the
1158 end of the article.

1159 Appendix S1. List of taxa included in phylogenetic analyses and literature used to score phylogenetic
1160 characters for each taxon.

1161 Appendix S2. List of characters

1162 Appendix S3. Nexus file of the phylogenetic matrix

1163 Appendix S4. Character scorings table

1164 Appendix S5. Comments on character scoring

1165 Appendix S6. Supplementary figures.

1166

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FIGURE LEGENDS

FIGURE 1 *Adelocladoxis praecox* gen. et sp. nov. main axis anatomy. **(A)** Cross section of main axis showing five-lobed actinostele and concentric layering of primary tissues (see also Supplemental Figs. 1, 3, 4); note xylem trace diverging to supply ultimate appendage (top); protoxylem strands are only visible in four of the primary xylem lobes (black arrowheads), whereas areas with collapsed tracheids (white arrowheads) randomly distributed look misleadingly like additional protoxylem strands; scale bar = 200 μm ; USNM 557820-2 E #51a. **(B)** Cross section of base of ultimate appendage attached to main axis; note hourglass-shaped xylem trace with two protoxylem strands (see also Fig. 2 and Supplemental Figs. 1, 3, 4, 9, 10) and epidermal cells containing dark bodies; scale bar = 200 μm ; USNM 557820-2 E #26a. **(C, D)** Thin phloem layer (arrowheads) adjacent to xylem (right); note very thin walls of narrow phloem cells; scale bar = 30 μm (C) and 40 μm (D); USNM 557820-2 Dbot #50a (C) and E #2a (D). **(E)** Cross section of metaxylem showing tracheids with oval (sometimes biseriate) bordered pits (see also Supplemental Figs. 11, 12); scale bar = 40 μm ; USNM 557820-2 E #70a. **(F)** Cross section of metaxylem showing tracheids with oval bordered pits (SEM; see also Supplemental Figs. 18, 19); note partially preserved phloem cells (arrowheads) adjacent to the xylem; scale bar = 50 μm ; USNM 557820-2 E #68.

FIGURE 2 *Adelocladoxis praecox* gen. et sp. nov. **(A-D)** Divergence of ultimate appendage from main axis in serial sections (proximal in A to distal in D; same as the blue appendage in Supplemental Fig. 14); primary xylem and protoxylem strands - where visible (black dots) - are traced in the lower panel images, which are copies of those in the top panel; note tangentially elongated, hourglass-shaped trace of ultimate appendage with two protoxylem strands (in B and C; the trace is too compressed in A and D); scale bars = 200 μm ; USNM 557820-2 E #82a (A), #45a (B), #7a (C), #2a (D).

FIGURE 3 *Adelocladoxis praecox* gen. et sp. nov. fertile ultimate appendage (same axis as in Supplemental Figs. 6, 7). Serial sections (left panel) and corresponding tracings (right panel) showing an ultimate appendage (green) that bears a sporangium (orange), diverging from an axis (black); top to bottom in the figure is the proximo-distal direction along the main axis; numbers on the left are peel numbers; details of the sporangium are shown in Figs. 7A-E. The appendage has two successive dichotomies distal to the basal segment (b); these produce three segments, two of which are labeled 1 and 2, while the third bears the sporangium at its tip; note highly fragmented preservation of the basal segment and segment 2, and bases of other ultimate appendages diverging from the main axis. Scale bar = 1 mm; USNM 557820-2 Dbot a series.

FIGURE 4 *Adelocladoxis praecox* gen. et sp. nov. ultimate appendage. Serial sections (left panel) and corresponding tracings (right panel) showing an ultimate appendage (green) diverging (at green arrowhead) from an axis (black); top to bottom in the figure is the proximo-distal direction along the main axis; numbers on the left are peel numbers. The appendage has at least one dichotomy distal to the basal segment (b); the two resulting segments are labeled 1 and 2; segment 2 terminates in an inflated tip (asterisk) interpreted as a putative developing sporangium; note the base of another ultimate appendage diverging from the same axis (purple arrowheads). Details of the appendage are shown in Figs. 7F-H. Scale bar = 1 mm; USNM 557820-2 Dbot a series.

FIGURE 5 *Adelocladoxis praecox* gen. et sp. nov. variability in ultimate appendage anatomy. **(A)** Longitudinal section of the recurved apical part of segment 3 in Supplemental Fig. 14; note relatively large metaxylem tracheids, putative phloem cell (arrowhead; see also Fig. 6A), radially-elongated cells with darker content immediately adjacent the central vascular tissues (compare with B and Figs. 6A, C), and epidermal cells containing bodies of compact dark material; scale bar = 200 μm ; USNM 557820-2 E #2a. **(B)** Cross section of ultimate appendage; note terete xylem with shallow centrarch protoxylem, cells with darker content immediately adjacent the central vascular tissues (compare with A and Figs. 6A, C), incompletely preserved cortex, and epidermal cells containing dark bodies; scale bar = 200 μm ; USNM 557820-2 E #2a. **(C)** Cross section of ultimate appendage; note terete centrarch xylem, good preservation of cortex, dark bodies inside epidermal cells, and outline with ridges and grooves; scale bar = 200 μm ; USNM 557820-2 E #2a. **(D)** Cross section of ultimate appendage; note terete centrarch xylem, incomplete preservation of cortex, dark bodies inside epidermal cells, and outline with ridges and grooves; scale bar = 200 μm ; USNM 557820-4 A1top #95b. **(E)** Cross section of ultimate appendage; note terete xylem with shallow centrarch protoxylem, cells with darker content immediately adjacent the central vascular tissues (compare with A, B, and Figs. 6A, C), incompletely preserved cortex, epidermal cells containing dark bodies, and slightly grooved outline; scale bar = 200 μm ; USNM 557820-2 E #2a. **(F)** Longitudinal section of ultimate appendage base diverging from main axis (green appendage in Supplemental Fig. 14); note incompletely preserved cortex and fragmentary preservation of the appendage; scale bar = 400 μm ; USNM 557820-2 E #100a. **(G)** Detail of F; xylem strand supplying base of ultimate appendage, tracheids with circular and oval-transverse bordered pits; scale bar = 200 μm ; USNM 557820-2 E #100a.

FIGURE 6 *Adelocladoxys praecox* gen. et sp. nov. ultimate appendage anatomy. **(A)** Longitudinal section of the recurved apical part of segment 3 in Supplemental Fig. 14; note relatively large metaxylem tracheids, putative phloem cells (arrowheads; see also Fig. 5A), radially-elongated cells with darker content immediately adjacent the central vascular tissues (compare with C and Figs. 5A, B), and epidermal cells containing rods of compact dark material; scale bar = 100 μm ; USNM 557820-2 E #1a. **(B)** Oblique section of ultimate appendage (detail of Supplemental Fig. 14); note incompletely preserved cortex; the fragment at top left is not part of the same plant; scale bar = 400 μm ; USNM 557820-2 E #72a. **(C)** Detail of B; note wider tracheids that show horizontally elongated, slit-shaped pits forming a scalariform pattern, while other tracheids have circular bordered pits; the cells with darker content between the xylem and the epidermis form an aerenchyma-like tissue (compare with E); note rods of compact dark material inside epidermal cells; scale bar = 100 μm ; USNM 557820-2 E #72a. **(D)** Longitudinal section of the green ultimate appendage in Supplemental Fig. 14); note incompletely preserved cortex; scale bar = 400 μm ; USNM 557820-2 E #45a. **(E)** Detail of D; note tracheids with mainly circular and transverse-oval bordered pits, aerenchyma-like tissue of darker cells (compare with C) seen in radial (bottom) and tangential (top right) section, and epidermal cells containing dark bodies; scale bar = 400 μm ; USNM 557820-2 E #45a.

FIGURE 7 *Adelocladoxys praecox* gen. et sp. nov. details of sporangium and putative developing sporangium (see also Supplemental Figs. 20-25). **(A-C)** Oblique sections of sporangium (details of Fig. 3); note dehiscence area (top in all three figures), epidermal cells with thin walls and containing rods of dark material identical to the epidermal cells of all other organs, attachment of sporangium to tip of ultimate appendage segment (B and C), and inner membranous sac lining (or distanced from) the epidermal layer (A); scale bars = 200 μm ; USNM 557820-2 Dbot #41a (a), #66a (B), #74a (C). **(D)** Detail of A; note oblique section through the inner membranous sac (left and bottom), which is distanced from the epidermal layer in some portions, incompletely preserved spore (arrowhead; more spores are shown in Supplemental Figures. 17-19), and rods of compact, dark material in epidermal cells, which are elongated and seem to be helically oriented (especially at bottom left); scale bar = 100 μm ; USNM 557820-2 Dbot #41a. **(E)** Detail of C; note paradermal section of sporangial epidermis with cells containing dark bodies (bottom right), and the best preserved spore (arrowhead), which seems to possess a trilete mark; scale bar = 100 μm ; USNM 557820-2 Dbot #74a. **(F)** Detail of Fig 4, longitudinal section of distal portion of ultimate appendage segment at base of inflated tip; note central xylem with circular and transverse-oval bordered pits forming scalariform pattern, and epidermis with cells containing dark bodies; scale bar = 100 μm ; USNM 557820-2 Dbot #107a. **(G)** Detail of Fig 4, oblique section of inflated ultimate appendage tip;

note thin, central dark area of vascular tissues and cortex with relatively large cells; scale bar = 200 μm ; USNM 557820-2 Dbot #84a. (H) Detail of Fig 4, oblique section of inflated ultimate appendage tip; note thin, central dark area of vascular tissues, cortex with apparent zonation (layer of clear cells around the vascular strand), epidermal cells containing dark bodies, and incompletely preserved distal area (top); scale bar = 200 μm ; USNM 557820-2 Dbot #80a.

FIGURE 8 Strict consensus trees produced by (A) Analysis 2 (26 taxa, 36 characters; 40 most parsimonious trees, length 105; CI = 0.486; RI = 0.662) and (B) Analysis 3 (19 taxa, 36 characters; 4 most parsimonious trees, length 94; CI = 0.543; RI = 0.587); numbers at nodes are bootstrap support values ≥ 3 ; asterisks in A mark taxa not included in Analysis 3 (B).

FIGURE 9 Time-scaled majority-rule consensus tree produced by Analysis 2 (26 taxa, 36 characters; 40 most parsimonious trees, length 105; CI = 0.486; RI = 0.662); taxon ages based on sources listed in Appendix S1; see also Fig. 8 for the strict consensus tree of Analysis 2 and Fig. 9 for node consensus percentages.

FIGURE 10 Majority-rule consensus tree produced by Analysis 2 (same as in Fig. 9, 11) with selected characters mapped; numbers at nodes are node consensus percentages < 100%. Planated branching (C7) refers to segments of the branching system other than ultimate appendages. Tracheid size variation across the width of the xylem ribs (C20) refers to metaxylem; in taxa not marked with a symbol, there is no discernable pattern of size variation; question marks denote taxa in which incomplete preservation precludes scoring the character. Branches and ultimate appendages attached at same node (C27) is associated with whorled branching and is scored based on either compression or permineralized anatomy. Tracheid pitting pattern (C18) refers to metaxylem; taxa were scored for the farthest term of the ontogenetic pit geometry series reached in their tracheids (see character description in Appendix S2). Branch taxis (C25) refers to branches other than ultimate appendages; note polymorphic state in *Pseudosporochnus*. Question marks denote taxa in which incomplete preservation precludes scoring the character.

FIGURE 11 Majority-rule consensus tree produced by Analysis 2 (same as in Fig. 9, 10) with selected characters mapped; numbers at nodes are node consensus percentages < 100%. Xylem ribs not connected at stele center corresponds to C13 and marks only taxa in which there is no connection between the xylem ribs across the center of the stele. Medullary bundles corresponds to C14 and refers to free vascular bundles present aside from the xylem ribs in steles that have a

parenchymatous area at the center. Branch traces supplied by more than one of the ribs of primary xylem corresponds to C28. Parenchyma at stele center corresponds to C12 and is scored in the largest axes known in each taxon; the scoring separates taxa with a central parenchymatous cylinder from those that have parenchyma at the stele center but some of the xylem ribs are connected across that parenchymatous area (irregular). Stele (C11) separates actinostelic taxa from those that have dissected steles, irrespectyve of the type of stele dissection; note polymorphic state in *Compsocradus*. The number of xylem ribs is not a character included in the analysis; here, it is scored in the in the largest axes known in each taxon; the three categories are defined based on consideration of the entire dataset. Xylem ribs corresponds to C17 and refers to the geometry of the ribs as seen in cross sections. Xylem rib bifurcation/trifurcation corresponds to C16; note polymorphic state in *Iridopteris* and *Denglongia*. Solid circles represent characters states scored for the taxa; white circles are characters predicted based on clade membership but whose scoring was precluded by the preservation of the respective fossils. Question marks denote taxa in which incomplete preservation precludes scoring the character.