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1 **Environmental influences on the stable carbon isotopic composition of**
2 **Devonian and Early Carboniferous land plants**

3
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26

27 **Abstract**

28 Systematic analysis of the stable carbon isotopic composition of fossil land plants ($\delta^{13}\text{C}_p$)
29 has the potential to offer new insights regarding paleoclimate variation and plant-environment
30 interactions in early terrestrial ecosystems. $\delta^{13}\text{C}_p$ was measured for 190 fossil plant specimens
31 belonging to 10 genera of Early to Late Devonian age (*Archaeopteris*, *Drepanophycus*, *Haskinsia*,
32 *Leclercqia*, *Pertica*, *Psilophyton*, *Rhacophyton*, *Sawdonia*, *Tetraxylopteris*, and *Wattieza*) and 2
33 genera of Early Carboniferous age (*Genselia* and *Rhodeopteridium*) collected from sites located
34 mainly in the Appalachian Basin (22-30 °S paleolatitude). For the full carbon-isotopic dataset (n
35 = 309), $\delta^{13}\text{C}_p$ ranges from -20.3 ‰ to -30.5 ‰ with a mean of -25.5 ‰, similar to values for
36 modern C_3 land plants. In addition to a secular trend, $\delta^{13}\text{C}_p$ exhibits both intra- and intergeneric
37 variation. Intrageneric variation is expressed as a small (mean 0.45 ‰) ^{13}C -enrichment of leaves
38 and spines relative to stems that may reflect differential compound-specific compositions.
39 Intergeneric variation is expressed as a much larger (to ~5 ‰) spread in the mean $\delta^{13}\text{C}_p$ values
40 of coeval plant genera that was probably controlled by taxon-specific habitat preferences and
41 local environmental humidity. Among Early Devonian taxa, *Sawdonia* yielded the most ^{13}C -
42 depleted values (-27.1 ± 1.7 ‰), reflecting lower water-use efficiency that was probably related
43 to growth in wetter habitats, and *Leclercqia*, *Haskinsia*, and *Psilophyton* yielded the most ^{13}C -

44 enriched values (-23.0 ± 1.6 ‰, -22.3 ± 1.3 ‰, and -24.8 ± 1.6 ‰, respectively), reflecting higher
45 water-use efficiency probably related to growth in drier habitats.

46

47 *Keywords:* water-use efficiency; early plants; canopy effect; *Archaeopteris*; *Drepanophycus*;
48 *Sawdonia*

49

50 **1. Introduction**

51 The Devonian was a period of revolutionary changes in terrestrial floras, landscapes, and
52 continental climates ([Algeo et al., 1995, 2001](#); [Gibling and Davies, 2012](#); [Gibling et al., 2014](#)).

53 Although bryophytes (non-vascular plants) had appeared during the mid-Ordovician and

54 tracheophytes (vascular plants) by the late Silurian ([Wellman et al., 2003](#); [Steemans et al.,](#)

55 [2009](#)), the continents remained sparsely vegetated until the Devonian. That period witnessed

56 major morphological adaptations and diversifications among vascular land plants as well as

57 order-of-magnitude increases in the complexity and geographic extent of terrestrial ecosystems

58 ([Gensel and Edwards, 2001](#); [Taylor et al., 2009](#)). Early Devonian land plants were mostly small

59 (heights of no more than a few tens of centimeters), shallowly rooted where known, and

60 limited to moist lowland habitats ([Xue et al., 2016](#)). By the end-Devonian, vascular land plants

61 had evolved leaves, complex root systems, secondary supporting tissues (leading to tree

62 stature), and desiccation-resistant reproductive propagules (seeds) that facilitated their spread

63 into drier upland habitats ([Mosbrugger, 1990](#); [Driese et al., 1997](#); [Gerrienne et al., 2004](#); [Meyer-](#)

64 [Berthaud et al., 2010](#); [Hao and Xue, 2013a](#); [Silvestro et al., 2015](#)). [Note: “upland” is a general

65 term signifying land lying above the level of local stream flow and flooding.] These changes

66 resulted in an increase in organic carbon burial, a rise of O₂ and a drawdown of CO₂ in the
67 atmosphere, and global climatic cooling, setting the stage for the Late Paleozoic Ice Age that
68 began in the Early Carboniferous (Algeo et al., 1995, 2001; Berner, 1997; Le Hir et al., 2011).

69 The stable carbon isotopic composition of plants ($\delta^{13}\text{C}_p$) differs from that of their carbon
70 source (atmospheric CO₂) owing to photosynthetic fractionation (Farquhar et al., 1982, 1989).
71 Modern C₃ plants fix carbon via the Calvin-Benson cycle with an average fractionation of ca.
72 -20 ‰, yielding organic material with a $\delta^{13}\text{C}$ value of -26 ± 5 ‰ (Raven et al., 2004). Devonian
73 vascular land plants are thought to have been exclusively C₃ plants (Taylor et al., 2009), and
74 their carbon isotopic compositions are therefore likely to have been controlled by the same
75 climatic and environmental factors as for modern C₃ plants (e.g., temperature, humidity, and
76 atmospheric $p\text{CO}_2$ and $\delta^{13}\text{C}_{\text{CO}_2}$). To date, the carbon isotopic compositions of specific Devonian
77 terrestrial plant fossils (as opposed to bulk sedimentary organic carbon) have been investigated
78 in only a few studies of fungi (Boyce et al., 2007), lichens (Fletcher et al., 2004), liverworts
79 (Graham et al., 2010), and vascular plants (Beerling et al., 2002; Feng et al., 2014).

80 The present study is the first systematic investigation of carbon isotopic variation among
81 a large group of Devonian and Early Carboniferous vascular land plants and represents by far
82 the largest such analytical dataset to date. We made 309 measurements of $\delta^{13}\text{C}_p$ (p = plant) on
83 190 unique specimens of fossil plants belonging to 12 widespread genera of Early Devonian to
84 Early Carboniferous age (Table S1). Our goals in this study were to (1) characterize $\delta^{13}\text{C}_p$
85 variation for each fossil plant taxon, (2) investigate time-independent $\delta^{13}\text{C}_p$ variation within and
86 among taxa that might reflect large-scale geographic (e.g., paleolatitudinal) or local
87 environmental influences, and (3) use these patterns of variation to draw inferences concerning

88 the ecology of individual early land plant taxa. Here, we show that there are significant
89 differences in $\delta^{13}\text{C}_p$ between the 12 genera of this study that are probably of primary (*in vivo*)
90 origin, and that were most likely related to local humidity and habitat preferences among early
91 vascular land plants.

92

93 **2. Fossil plant taxonomy and paleoecology**

94 *2.1. Fossil plant taxa*

95 The fossil plants analyzed in this study belong to 12 different genera of tracheophytes,
96 representing early members of the lycophyte and euphyllophyte lineages (Fig. 1A). All of the
97 fossil plants in this study have been the subject of at least partial morphological reconstructions
98 (Fig. 1B). Although many fossil specimens were identified to the species level, we conducted
99 our evaluation of $\delta^{13}\text{C}_p$ variation at the genus level owing to (1) lack of species assignments for
100 about half of the individual specimens, (2) uncertainty in some species-level assignments, and
101 (3) the impracticability of analyzing carbon-isotopic patterns in a dataset with excessive splitting
102 into species. Among the 12 genera analyzed, 10 have overlapping ranges extending through
103 part or all of the Devonian (*Archaeopteris*, *Drepanophycus*, *Haskinsia*, *Leclercqia*, *Pertica*,
104 *Psilophyton*, *Rhacophyton*, *Sawdonia*, *Tetraxylopteris*, and *Wattieza*) and two are entirely of
105 Early Carboniferous age (*Genselia* and *Rhodeopteridium*; Fig. 2). A brief summary of the key
106 anatomical features and paleoecologic/geographic characteristics of each genus follows:

107 *Sawdonia* (Dawson) Hueber is one of the early zosterophylloids, belonging to the
108 Lycophyta. This plant is pseudomonopodially branched with circinate tips; reniform sporangia
109 are borne along the sides of some stems and anatomy consists of an exarch haplostele (Hueber,

110 1971; Rayner, 1983; Gensel et al., 1975; Taylor et al., 2009; Gensel and Berry, 2016). It was
111 widespread during the Early Devonian (Gensel, 1992; Kenrick and Crane, 1997; Gensel and
112 Berry, 2016) but is also found in the Late Devonian (Hueber and Grierson, 1961). Our dataset
113 includes both *S. ornata* and *S. acanthotheca*, although most specimens were not distinguished
114 at the species level.

115 *Drepanophycus* Göppert belongs to the Drepanophycaceae, sister to other lineages of
116 Lycopsidea (Kenrick and Crane, 1997). Stems range from several millimeters to centimeters in
117 diameter and from several centimeters to a meter in length. Leaves are unbranched falcate
118 microphylls up to several millimeters long with a single prominent middle vascular thread, and
119 they were arranged spirally or randomly on the stem. Reniform sporangia occur on short stalks
120 between the leaves (Li and Edwards, 1995; Li et al., 2000). However, this genus exhibits
121 considerable variation in leaf morphology and may be in need of revision. This taxon had a
122 creeping to erect and sometimes dichotomizing rhizomatous growth habit. It existed through
123 most of the Devonian Period and is found in eastern Canada, northeastern USA, China, Russia,
124 and Europe (Stubblefield and Banks, 1978; Gensel and Berry, 2001; Xu et al., 2013). About half
125 of the specimens used in the present study belong to *D. spinaeformis*, and the remainder were
126 not distinguished at the species level.

127 *Leclercqia* Banks, Bonamo and Grierson is a member of the Protolopodendraceae
128 (Lycophyta) (Gensel and Kasper, 2005; Gensel and Albright, 2006). It is a slender, herbaceous
129 plant, with distinctive leaves that typically exhibit five divisions and that bear sporangia on their
130 upper surface. At least some species exhibit hook-shaped leaves that may have allowed a vine-
131 like climbing habit (Xu et al., 2011). *Leclercqia* is distinguished in being a homosporous plant

132 with a ligule; ligules otherwise are found only in heterosporous taxa (Grierson and Bonamo,
133 1979; Bonamo et al., 1988; Taylor et al., 2009; Benca et al., 2014). It existed from the late Early
134 to the Middle Devonian and has a particularly wide distribution, being found in North America,
135 Europe, Africa, Australia, and China (Banks et al., 1972; Bonamo et al., 1988; Meyer-Berthaud et
136 al., 2003; Taylor et al., 2009; Xu et al., 2011; Prestianni et al., 2012; Benca et al., 2014). It was
137 present mainly in warm, dry climates (Berry, 1994; Meyer-Berthaud et al., 2003), although
138 some studies have claimed a wider environmental range (Xu and Wang, 2008). Our dataset
139 includes both *L. complexa* and *L. andrewsii*, although half of the specimens were not
140 distinguished at the species level.

141 *Haskinsia* Grierson and Banks is a herbaceous lycopsid (Bonamo et al., 1988; Xu et al.,
142 2008; Yang et al., 2008; Taylor et al., 2009). It was once regarded as a species of *Drepanophycus*
143 but was later placed with the Protolepidodendrales because of the presence of petiolate
144 deltoid-shaped sporophylls (Grierson and Banks, 1983; Berry and Edwards, 1996; Xu and Berry,
145 2008). This taxon was widespread during the Middle to early Late Devonian age, being known
146 from North America, South America, Russia, and China; it had wide environmental tolerances,
147 thriving in both warm tropical and cool temperate conditions (Xu et al., 2008). The relatively
148 small number of specimens in our dataset includes *H. hastata*, *H. sagittata*, and specimens not
149 identified at the species level.

150 *Psilophyton* (Dawson) Hueber is one of the best-known members of the trimerophyte
151 grade of basal euphyllophytes (Andrews et al., 1968; Banks et al., 1975; Doran et al., 1978;
152 Trant and Gensel, 1985; Stein, 1993; Gerrienne 1995, 1997). The plant consists of a main axis
153 and multiply divided lateral branches, some of which terminate in pairs of fusiform sporangia.

154 Stem anatomy, where known, is a centrarch haplostele. Intrageneric variation in sporangial
155 length and in the presence and type of emergences is significant (Doran, 1980; Gerrienne, 1995;
156 Taylor et al., 2009). *Psilophyton* was widespread in the Early to earliest Middle Devonian and
157 has been found in the northeastern United States (Maine and New York), Canada (Quebec and
158 New Brunswick), Belgium, the Czech Republic, and Yunnan, China (Taylor et al., 2009; Gensel,
159 2017). The most common species in our dataset is *P. princeps*, although specimens of *P.*
160 *crenulatum*, *P. dawsonii*, and *P. forbesii* are also present, as well as some specimens not
161 identified at the species level.

162 *Pertica* Kasper and Andrews is also a basal euphyllophyte (Kasper and Andrews, 1972;
163 Granoff et al., 1976). It exhibits a dominant main stem with regularly arranged lateral branches,
164 organized either in a tight spiral or a four ranked/decussate pattern. Lateral branch morphology
165 varies from equally dichotomous to a more pseudomonopodial pattern. These plants bore
166 numerous fusiform sporangia in dense clusters on ultimate branchlets (Kasper and Andrews,
167 1972; Granoff et al., 1976; Taylor et al., 2009). *Pertica* existed from the Early to the Middle
168 Devonian, with occurrences known from northern Maine, New Brunswick, and Quebec. Our
169 dataset consists mainly of the species *P. varia* along with some specimens not identified at the
170 species level.

171 *Wattieza* refers to compression fossils belonging to the order Pseudosporochnales
172 within the class Cladoxylopsida (Leclercq and Banks, 1962; Gensel et al., 2001; Berry and Fairon-
173 Demaret, 2002). Pseudosporochnaleans are all similar in their adult forms, consisting of small
174 to large trees with a main trunk bearing a dense crown of frond-like branches. Instead of
175 leaves, the branches bear densely ramified ultimate appendages with either terminally erect

176 (*Pseudosporochnus*) or reflexed (*Wattieza*) sporangia. The specimens analyzed for this study,
177 which came from the West Cave Mountain and Steenberg/South Mountain quarries in New
178 York, possessed key characteristics of Pseudosporochnaleans including distinctive clusters of
179 sclerotic cells (Leclercq and Banks, 1962; Gensel et al., 2001; Berry and Fairon-Demaret, 2002)
180 but lacked sporangia. However, a recent study of new South Mountain specimens identified
181 them as *Wattieza* and linked them to the fossil tree trunks known as *Eospermatopteris* (Stein et
182 al., 2007). Pseudosporochnaleans existed from the Middle to early Late Devonian in Europe,
183 Venezuela, North America, and possibly China (Gensel and Andrews, 1984; Taylor et al., 2009).

184 *Rhacophyton* Crépin belongs to the order of Rhacophytales *sensu* Taylor et al. (2009;
185 n.b., assigned to Rhacophytaceae or Protopteridales by others). According to Andrews and
186 Phillips (1968), this plant grew to ~1-m-tall bushes, and its foliage consisted of a main axis
187 bearing pairs of lateral branches that fork twice basally. Two of the lateral branches were
188 multiply divided and terminated in elongate sporangia, and the other two extended further and
189 bore higher-order branches. In some cases, the fertile branches were produced as second-
190 order units on first-order laterals. The stem anatomy of the lateral branches consisted of
191 clepsydroid primary xylem surrounded in some instances by a limited amount of secondary
192 xylem. *Rhacophyton* existed during the Late Devonian and has been found in North America,
193 Europe, possibly Bear Island (New Brunswick), and western Siberia (Andrews and Phillips, 1968;
194 Cornet et al., 1977; Dittrich et al., 1983; Cressler, 1999, 2006; Taylor et al., 2009). Our dataset
195 includes a few specimens identified as *R. ceratangium* although the majority were not
196 identified at the species level.

197 *Rhodeopteridium* (Presl) Zimmermann (formerly *Rhodea* Presl) is a genus based mainly
198 on foliage compression/impression fossils that is thought to represent an early seed plant
199 ([Jennings, 1976](#)). Pinnately compound leaves terminate in barely laminate ends ([Read, 1955](#)).
200 Similar fossil leaves with well-preserved petioles are known from early seed ferns of Late
201 Mississippian (Chesterian) age in Illinois ([Jennings, 1976](#)). Most specimens are of Early
202 Carboniferous (Tournaisian-Namurian A) age, but it may extend into the basal late
203 Carboniferous. None of the small number of *Rhodeopteridium* specimens in our dataset was
204 identified at the species level.

205 *Tetraxylopteris* Beck is an aneurophytalean progymnosperm ([Beck, 1957](#); [Bonamo and](#)
206 [Banks, 1967](#); [Scheckler and Banks, 1971](#); [Hammond and Berry, 2005](#)). It is characterized by a
207 main stem with extensive secondary xylem and bearing several orders of laterals in a decussate
208 pattern, each with a four-armed vascular strand. In fertile regions, second-order laterals
209 dichotomize twice, and each division bears pinnately arranged clusters of sporangia.
210 *Tetraxylopteris* existed during the Givetian and early Frasnian. To date, it is known from only
211 two areas: the Catskill Delta in New York, and the Campo Chico Formation in northwestern
212 Venezuela. A few of our specimens are assigned to *T. schmidtii* but most were not identified at
213 the species level.

214 *Archaeopteris* (Dawson) Stur belongs to the Archaeopteridalean progymnosperms. It
215 was a tall tree similar to some modern conifers, but it had pseudomonopodial branching in the
216 lateral branch system ([Beck, 1962](#)) and laminate leaves with helices or decussate patterns of
217 leaf attachment ([Scheckler, 1978](#)). Some ultimate clusters of leaves appear cone-like, bearing
218 sporangia on their adaxial surfaces, but all species are thought to have been free-sporing and

219 heterosporous. *Archaeopteris* is usually preserved as impression and compression fossils, and
220 its fossilized trunks, named *Callixylon* when found separately, exhibit extensive secondary
221 xylem. It ranged from the latest Middle to Late Devonian, with a number of different species
222 being known from localities in North America, Russia, Europe, Morocco, China, Australia, and
223 Colombia (Beck and Wight, 1988; Cressler, 1999, 2006; Meyer-Berthaud et al., 1999; Berry et
224 al., 2000). By the middle of the late Frasnian, monospecific archaeopterid forests had become
225 the dominant vegetation type in lowland areas and coastal settings over a vast geographic area
226 (Algeo et al., 2001). About one third of the 51 specimens in our dataset are assigned to various
227 species, including *A. fissilis*, *A. halliana*, *A. jacksonii*, *A. macilenta*, and *A. rogersii*, although most
228 specimens were not identified at the species level.

229 *Genselia* Knaus may have been a seed fern (Knaus, 1995; Taylor et al., 2009). This genus
230 has bipinnate compound leaves, non-bifurcate rachises, and in some, bifurcations at the tip of
231 stems, terminating in elongated sporangia (Knaus, 1994, 1995; Skog and Gensel, 1980; Taylor et
232 al., 2009). It is found in the Lower Carboniferous Pocono and Price Formations of Pennsylvania,
233 Maryland, West Virginia and Virginia, in the Appalachian Basin of North America. None of the
234 *Genselia* specimens in our dataset was identified at the species level.

235

236 2.2. Paleoclimate and paleoenvironments

237 The locales from which fossil plants in this study were collected have a quasi-global
238 distribution (Fig. 3A), although a large majority of the analyses ($n = 289$ of 309, or 93 % of the
239 total dataset) are of specimens from the Appalachian Basin or other areas in eastern North
240 America, at locales ranging from southwestern Virginia in the south to the Gaspé Peninsula of

241 Québec in the north (Fig. 3B). Laurentia (Paleozoic North America) drifted northward during
242 the Devonian Period (416-359 Ma), causing the Appalachian Basin to shift from ~40–35 °S in the
243 Early Devonian to ~30–25 °S in the Late Devonian (van der Voo, 1988, 1993). Thus, many of the
244 present study locales moved from the humid temperate zone into the dry subtropical zone
245 during this interval. However, this shift occurred at tectonic timescales (i.e., over a ~50-Myr
246 interval) and was monotonic in direction (i.e., did not reverse), so any regional climate changes
247 induced by plate motion during this interval are likely to have been slow and steady. More
248 rapid climate changes (i.e., at timescales of a few million years or less) are likely to have had
249 non-plate-tectonic causes. Most of the remaining fossil plant specimens ($n = 20$, 7 % of total)
250 are from a few sites in northwestern China (Xu et al., 2015; Zheng et al., 2016) and Venezuela
251 (Berry, 1994; Berry and Edwards, 1996).

252 The depositional environments in which the 12 fossil plant taxa of the present study
253 grew ranged from coastal deltas to upper floodplains, with the former being the most common
254 environment. Coastal deltas are represented, for example, by most of the fossil-plant-bearing
255 strata of the Emsian Battery Point Formation in Gaspé Bay, Quebec, and the more western
256 portions of the Emsian-lower Eifelian Campbellton Formation in New Brunswick (Griffing et al.,
257 2000; Hotton et al., 2001; Kennedy et al., 2012, 2013). Especially at Gaspé Bay, paleocurrent
258 data document mainly seaward transport of sediment by rivers, and multistory sandstone
259 bodies are interpreted as deposits of high-sinuosity river channels (Griffing et al., 2000). Closer
260 to the coastline, bidirectional cross-bedding records tidal influence (Bridge, 2000; Griffing et al.,
261 2000) and some trace fossils (e.g., *Diplocraterion*) may represent brackish conditions within
262 estuaries (Lawrence, 1986). Deltaic processes are evidenced by a complex stratigraphic

263 architecture of levees and crevasse splays, freshwater lakes and marshes, lacustrine deltas,
264 brackish marshes and interdistributary bays, and sandy and muddy tidal flats (Griffing et al.,
265 2000).

266 Coastal wetlands apparently developed frequently during the late Givetian to early
267 Frasnian, especially at times of relatively high sea level, which resulted in marine incursions into
268 generally terrestrial environments (Baird and Brett, 2008). Multiple wetland subenvironments
269 are represented by stacked dark meter-thick sandstones at Riverside Quarry, Gilboa (Stein et
270 al., 2012), dark siltstones and shales at Blenheim, Gilboa (Banks et al., 1972), and lighter gray to
271 yellowish-brown sandstones at Manorkill Falls, Gilboa (Driese et al., 1997). Similar
272 environments developed in the Late Devonian, as in the Famennian Hampshire Formation at
273 Elkins, West Virginia (Scheckler, 1986a). In these settings, trees and understory plants appear
274 to have had limited root penetration. During the Late Devonian, wetland floral diversity was
275 relatively limited: *Archaeopteris* and *Rhacophyton* were endemic, although other taxa
276 (especially arborescent lycophytes) occupied peri-swamp habitats and were washed in during
277 floods and storms (Scheckler, 1986a). By the Tournaisian, coastal swamp habitats were
278 increasingly dominated by lycophytes (Scheckler, 1986b; Rygel et al., 2006; Gensel and Pigg,
279 2010).

280 Upper floodplain settings are represented by fine-grained, multistory sandstone bodies
281 and red mudstones in fining-upward successions lacking any evidence of marine influence.
282 These deposits represent wide, meandering upland river channels and overbank (floodplain)
283 deposits that were subject to frequent wet-dry cycles, e.g., through seasonal flooding (Cressler,
284 1999, 2006; Cressler et al., 2010). Examples of this type of environment are found in the

285 Famennian Duncannon Member of the Catskill Formation at Red Hill, Pennsylvania.
286 Taphonomic observations indicate that both fossil plants and animals lived close to their sites of
287 deposition. Fossil plant remains are often found in reduced lenses of greenish-gray mudstone,
288 probably representing floodplain pond deposits related to major channel avulsion events
289 (Cressler, 1999, 2006; Cressler et al., 2010).

290

291 **3. Methods**

292 The study specimens consist of well-preserved compression fossils of whole plants or
293 parts of plants (i.e., stems, branches, and/or leaves) that are intact or nearly so (Fig. 4). All
294 specimens were inspected using a binocular microscope to verify the state of fossil
295 preservation, and a subset was examined using scanning electron microscopy. We initially bulk
296 macerated each plant fossil in acid baths, yielding bulk organic material that was
297 undifferentiated by plant anatomical parts. These specimens were digested successively in
298 hydrochloric acid (HCl) and hydrofluoric acid (HF), with three rinses in distilled water between
299 dissolution steps. We subsequently sampled the plant fossils by peeling pieces of organic
300 material from the surface of each compression fossil, permitting us to analyze specific
301 anatomical parts of each plant (e.g., stems, leaves, spines, and sporangia). These specimens
302 were treated individually with HCl and HF, as needed, to remove rock matrix adhering to the
303 organic material. Organic fragments were picked out of the residue, rinsed in distilled water,
304 dried, and inspected under a binocular microscope to verify the removal of all impurities.

305 Carbon isotopic analyses were performed using EA-IRMS systems at the Stable Isotope
306 Research Facility (SIRF) of the Department of Earth and Atmospheric Sciences of Indiana

307 University, Bloomington (IU) and the Department of Earth and Environmental Sciences of the
308 University of Texas at Arlington (UTA). Analytical protocols were similar in the two laboratories:
309 powdered samples were weighed into silver capsules that were acidified repeatedly with 6%
310 sulfurous acid (H_2SO_3) in order to remove carbonate phases. Samples were analyzed using a
311 Costech 4010 elemental analyzer interfaced with a Thermo Finnigan ConFlo III device to a
312 Thermo Finnigan Delta Plus XP isotope ratio mass spectrometer (IRMS). All isotopic results are
313 reported in per mille (‰) variation relative to VPDB. At UTA, the average standard deviation
314 was 0.04 ‰ for both the USGS-24 standard ($\delta^{13}\text{C} = -16.049$ ‰) and unknowns. At IU, the
315 average standard deviation was 0.06 ‰ for Acetanilides #1, #2, and #3, and Corn starch #1
316 (Schimmelmann et al., 2016) and unknowns. Interlaboratory calibration was undertaken by
317 analyzing a common set of 12 samples at both IU and UTA. The co-analyzed samples yielded a
318 correlation (r^2) of 0.997 with an offset of 0.21 ‰ between the two labs, which was corrected
319 for in the integrated C-isotope dataset by averaging the difference (i.e., by reducing UTA values
320 by 0.10 ‰ and increasing IU values by 0.10 ‰).

321

322 **4. Results**

323 *4.1. General results*

324 In this study, we generated a total of 309 analyses of plant $\delta^{13}\text{C}$ from 190 unique plant
325 specimens (Table S1). The number of analyses per taxon varied considerably: the four most
326 analyzed taxa were *Archaeopteris* (80 analyses of 51 unique specimens), *Drepanophycus*
327 (40/21), *Rhacophyton* (33/18), and *Tetraxylopteris* (31/21) (Table 1). About half of the
328 specimens were analyzed twice, mostly to generate paired $\delta^{13}\text{C}$ values for different anatomical

329 parts (e.g., stems and leaves) but sometimes to check on the reproducibility of results for the
330 same anatomical part of a single specimen. A handful of specimens were analyzed three or
331 more times. The full dataset of 309 analyses yielded a mean $\delta^{13}\text{C}_p$ of -25.5‰ with a standard
332 deviation of 1.8‰ and a range from -20.3‰ to -30.5‰ . Individual taxa yielded mean $\delta^{13}\text{C}_p$
333 ranging from $-22.3\pm 1.3\text{‰}$ for *Haskinsia* to $-27.3\pm 1.7\text{‰}$ for *Sawdonia* (Table 1).

334 The full $\delta^{13}\text{C}_p$ dataset exhibits a distinct secular pattern (as reflected in a LOWESS curve)
335 that is dominated by a long-term shift toward higher $\delta^{13}\text{C}_p$ values through most of the Devonian
336 and Early Carboniferous (note: this secular pattern is not shown and will not be considered here
337 because it is the focus of a companion paper that is in preparation). To determine the non-
338 secular component of total $\delta^{13}\text{C}_p$ variation, we calculated the difference between each $\delta^{13}\text{C}_p$
339 value and the age-equivalent mean for the full $\delta^{13}\text{C}_p$ dataset as given by the LOWESS curve, i.e.,
340 $\Delta^{13}\text{C}_p$ (Fig. 5). Thus, a fossil specimen with a $\Delta^{13}\text{C}_p$ of 0‰ has a carbon-isotopic composition
341 identical to the LOWESS mean for the $\delta^{13}\text{C}_p$ dataset at a given time, and positive and negative
342 $\Delta^{13}\text{C}_p$ values represent ^{13}C enrichment and depletion of the specimen, respectively, relative to
343 the age-equivalent LOWESS mean value. In this manner, the overall tendency of each fossil
344 plant taxon toward ^{13}C enrichment or depletion can be evaluated independently of long-term
345 secular variation in the $\delta^{13}\text{C}_p$ dataset (Fig. 6). The non-secular variance in our $\delta^{13}\text{C}_p$ dataset has
346 two components: (1) variance among different plant taxa ('intergeneric variation'), and (2)
347 variance within individual taxa ('intrageneric variation'). The proportion of total variance in the
348 $\Delta^{13}\text{C}_p$ dataset represented by intrageneric variance (i.e., $\sigma^2_{\text{intra}} / \sigma^2_{\text{total}}$) was calculated as:

349
$$\left(\sum_{i=1}^{12} [\Sigma(X-\mu_i)^2 / N_i] \right) / [\Sigma(X-\mu_t)^2 / N_t] \quad (1)$$

350 where X is the $\Delta^{13}\text{C}_p$ for a given fossil specimen, μ_i is the mean $\Delta^{13}\text{C}_p$ for a given plant genus i ,
351 and μ_t is the mean $\Delta^{13}\text{C}_p$ for all fossil specimens. The numerator of the equation sums the
352 variances of the 12 fossil plant genera ($\sum_{i=1}^{12}$) calculated separately (i.e., $[\sum(X-\mu_i)^2 / N_i]$), and it
353 is divided by the total variance for all fossil specimens (i.e., $[\sum(X-\mu_t)^2 / N_t]$) to yield the fraction
354 of total variance attributable to intrageneric variance (70%); the remainder (30 %) represents
355 intergeneric variance. Below, we analyze intrageneric and intergeneric patterns of variation as
356 a function of possible taxonomic, anatomical, geographic, and environmental controls (Tables
357 2-3). Note that this analysis is conducted on the basis of $\Delta^{13}\text{C}_p$ values (Table S1), i.e., the
358 deviations from the long-term secular $\delta^{13}\text{C}_p$ trend (Fig. 6), and is thus independent of the
359 secular component of variance in the $\delta^{13}\text{C}_p$ dataset.

360 We considered the possibility of a geographic gradient in $\Delta^{13}\text{C}_p$, e.g., along a
361 paleolatitudinal transect. Modern plants show a distinct latitudinal gradient in $\delta^{13}\text{C}_p$ that is a
362 function of temperature and precipitation influences (Diefendorf et al., 2010) and/or light levels
363 (Kohn, 2010). However, the high proportion (>90 %) of specimens from the Appalachian Basin
364 in this study (Figs. 2-3) leads to a clustering of data within a relatively narrow range of
365 paleolatitudes, resulting in our inability to identify any significant paleolatitudinal trends. A
366 more robust test of geographic influences on Devonian fossil plant $\delta^{13}\text{C}$ will require a larger
367 dataset covering a wider range of paleolatitudes.

368

369 4.2. Intrageneric variation in plant $\delta^{13}\text{C}$

370 For a subset of specimens ($n = 32$), we analyzed carbon from both the stem and the leaf
371 or spine (not interpreted as a leaf homologue) of the fossil plant, allowing us to evaluate

372 variation in $\delta^{13}\text{C}_p$ as a function of plant anatomy. The assessment of anatomical variation was
373 made for 6 plant genera (Table 3). Among these genera, four showed higher $\delta^{13}\text{C}_p$ for
374 leaves/spines than for stems, although the difference was statistically significant (based on a
375 Student's t-test) only for *Sawdonia*, which yielded the largest $\Delta^{13}\text{C}_{(\text{spine-stem})}$ value of any genus
376 (1.6 ‰). The relatively small number of analyses per genus was a factor limiting the statistical
377 significance of these results for individual plant taxa. All 6 genera together ($n = 32$) yielded a
378 mean leaf/spine-vs-stem difference of 0.45 ‰, which is statistically significant ($p(\alpha) = 0.01$;
379 Table 3). These results suggest that fossil plant leaves and spines are systematically slightly
380 enriched in ^{13}C relative to stems of the same fossil plant specimen (as seen in 29 out of 32 of
381 the paired analyses).

382

383 4.3. Intergeneric variation in plant $\delta^{13}\text{C}$

384 The 12 fossil plant genera of this study exhibit systematic differences in $\Delta^{13}\text{C}_p$ (Fig. 7).
385 Three taxa yielded mean $\Delta^{13}\text{C}_p$ values that are significantly higher than the age-equivalent
386 LOWESS mean: *Haskinsia* (+2.4±1.5 ‰; $n = 4$), *Leclercqia* (+1.8±1.0 ‰; $n = 24$), and *Psilophyton*
387 (+0.9±1.5 ‰; $n = 25$), and one taxon yielded a significantly lower mean value: *Sawdonia*
388 (-1.2±1.8 ‰; $n = 28$) (note: for all, $p(\alpha) \leq 0.01$; Student's t-test; Table 2). The remaining eight
389 taxa have mean $\Delta^{13}\text{C}_p$ values within ± 0.5 ‰ of the average for the dataset as a whole, among
390 which only *Archaeopteris* yielded a significantly different mean (-0.4±1.2 ‰; $p(\alpha) = 0.002$),
391 mainly as a result of the exceptionally large number of analyses of this taxon ($n = 80$; Table 2).
392 However, the result for *Archaeopteris* must be viewed cautiously because there are relatively
393 few coeval Late Devonian taxa in our dataset from which to construct the LOWESS mean trend.

394 Thus, we consider only *Haskinsia*, *Leclercqia*, *Psilophyton*, and *Sawdonia* to deviate significantly
395 in $\Delta^{13}\text{C}_p$ from age-equivalent LOWESS mean values.

396 The critical time interval of our dataset for evaluating interspecific $\Delta^{13}\text{C}_p$ variation is the
397 late Early through late Middle Devonian (~405-385 Ma), during which 6 of the 12 plant taxa
398 analyzed in this study have largely overlapping stratigraphic ranges. The overlap in stratigraphic
399 ranges facilitates intergeneric comparisons, and, not coincidentally, all four of the taxa showing
400 large deviations from mean LOWESS $\delta^{13}\text{C}_p$ values are present in this interval, with three taxa
401 showing ^{13}C -enriched values (*Haskinsia*, *Leclercqia*, and *Psilophyton*) and one showing ^{13}C -
402 depleted values (*Sawdonia*) (see above). Importantly, the offsets in $\delta^{13}\text{C}_p$ between these taxa
403 are relatively constant despite an overall increase in mean LOWESS $\delta^{13}\text{C}_p$ of ~3 ‰ from the late
404 Early Devonian to the late Middle Devonian (Algeo et al., in preparation). We attribute these
405 taxon-specific differences in ^{13}C enrichment to local environmental controls (see Section 5.3).
406 In contrast, the 6 plant genera analyzed from the early Late Devonian to Early Carboniferous
407 (~385-345 Ma) have only partially overlapping stratigraphic ranges, with no more than 2 taxa
408 present in any given time window. The more limited dataset for this time interval renders
409 uncertain evaluation of deviations in $\Delta^{13}\text{C}_p$ from the mean LOWESS trend (thus our caution with
410 regard to interpreting *Archaeopteris* $\Delta^{13}\text{C}_p$ values).

411

412 5. Discussion

413 5.1. Robustness of plant $\delta^{13}\text{C}$ proxy

414 The fossil plant specimens used in this project were preserved as compressions of
415 stems, branches, leaves and spines (Fig. 4A-B). During the carbonization process, most water

416 and volatile organic compounds in the plant tissue were lost, and the remaining material was
417 preserved as a black organic film that consists largely of carbon (Guo et al., 2010). Even though
418 compressed as flat layers, many fossils show well-preserved cell-scale anatomical features such
419 as tracheids (Fig. 4C) and cuticle (Fig. 4D). These observations confirm that pre-burial bacterial
420 decay of these relatively resistant tissues was limited in the specimens that were selected for
421 carbon-isotopic analysis in this study.

422 Vascular land plants exhibit internal carbon isotopic variation, commonly with a >5 ‰
423 range in $\delta^{13}\text{C}$ among their constituent compounds (O'Leary, 1988; Pate and Arthur, 1998).
424 Although most types of compounds decay rapidly in the burial environment, the surviving
425 compounds generally retain their characteristic carbon isotopic compositions (Benner et al.,
426 1987). Cellulose and lignin are among the most resistant compound types and commonly
427 dominate the terrestrial organic fraction preserved in sedimentary rocks (Arens et al., 2000),
428 especially in compression fossils of the type analyzed in this study. Cellulose is up to ~3 ‰
429 heavier and lignin up to ~4 ‰ lighter than bulk plant $\delta^{13}\text{C}$ (Benner et al., 1987; O'Leary, 1988;
430 Marino and McElroy, 1991; Badeck et al., 2005). Biomarker analysis of plant compression fossils
431 typically yields a range of alkanes, alkenes, benzenes, pristenes, and polysaccharides derived in
432 large part from decay of these primary compounds (e.g., Gupta et al., 2007), so a part of the
433 variance in the $\Delta\delta^{13}\text{C}_p$ of an individual taxon in our dataset may reflect specimen-specific
434 variation in the proportions of cellulose versus lignin and their derivatives (Arens et al., 2000).

435 Burial diagenesis can potentially modify the $\delta^{13}\text{C}$ composition of organic material
436 through thermal cracking and release of methane at high temperatures (i.e., >160 °C, or beyond
437 the 'oil window'; Faure and Mensing, 2005). The released methane is depleted in ^{13}C by 10-

438 30 ‰, resulting in a small increase in the $\delta^{13}\text{C}$ of the remaining kerogen (generally <1 ‰). The
439 thermal maturity of Devonian sediments in the central Appalachian Basin exhibits a strong
440 lateral gradient: maturity is high on the eastern basin margin ($R_o >2.0$; $T >160$ °C) but low to
441 moderate on the western basin margin ($R_o <1.0$; $T <100$ °C) (Obermajer et al., 1997; Milici and
442 Swezey, 2006; Rowan, 2006; Repetski et al., 2008). In our study areas in eastern New York and
443 central West Virginia, the maximum burial depths of Upper Devonian strata were from ~4 to 10
444 km, with peak burial temperatures estimated to have been between ~150 and 170 °C (Friedman
445 and Sanders, 1982; Dorobek, 1989; Repetski et al., 2008). Thermal maturity is also variable in
446 New Brunswick and the Gaspé Peninsula of Québec in eastern Canada. There, some Devonian
447 strata have been buried just a few kilometers (Heroux et al., 1979), whereas other units have
448 experienced maximum burial depths up to 12 km (Utting and Hamblin, 1991), yielding peak
449 burial temperature estimates ranging from ~50 to 280 °C (Bertrand and Malo, 2001; Chi et al.,
450 2001). We tested the possibility of burial thermal effects on our dataset by plotting $\delta^{13}\text{C}_p$
451 against inferred maximum burial depths, but this yielded almost no correlation ($r = +0.03$; $n =$
452 309 ; $p(\alpha) >0.5$). We are cognizant that the carbon isotopic compositions of our plant fossils
453 may have been influenced by bacterial and thermal decay. However, the $\delta^{13}\text{C}_p$ values of a
454 single taxon at a specific outcrop tend to be relatively consistent in our dataset (mostly showing
455 <1 ‰ variation), indicating a general lack of random diagenetic effects on the plant fossils
456 during burial.

457

458 *5.2. Sources of anatomical variation in plant $\delta^{13}\text{C}$*

459 Among modern plants, different plant parts exhibit systematic differences in carbon
460 isotopic compositions. Based on a compilation of >400 plant taxa, leaves are on average
461 0.96 ‰ and 1.91 ‰ more depleted in ¹³C than roots and woody stems, respectively (Badeck et
462 al., 2005). This pattern is strong but not universal as ~10 % of the taxa examined in that study
463 yielded leaf δ¹³C greater than stem δ¹³C. This pattern appears to be independent of climatic
464 conditions, as plants from semi-arid habitats also exhibit leaf δ¹³C lower than stem δ¹³C (by an
465 average of 1.51±0.42 ‰) (Nilson and Sharifi, 1997). The origin of these differences is not
466 known with certainty: two leading ideas relate it to carbon-isotopic fractionation in generating
467 different types of organic compounds (see Section 5.1), or preferential release of ¹³C-enriched
468 respiratory CO₂ from leaves (Badeck et al., 2005).

469 In our dataset, leaves and spines are somewhat ¹³C-enriched relative to stems (by
470 0.45 ‰ on average; Table 3; see Section 4.2). If the δ¹³C values of leaves and spines were
471 originally lower than that of stems by ~1-2 ‰ in Devonian plants, then burial decay must have
472 caused a relative shift of +1.5 to +2.5 ‰ in leaf/spine δ¹³C relative to stem δ¹³C. Such a shift
473 might have occurred owing to a greater loss of lipids and/or increase in cellulose-derived
474 compounds in the carbonized residue of leaves and spines relative to stems during the
475 fossilization process. Further investigation will be needed to validate the existence and
476 significance of internal δ¹³C variation in Devonian and Carboniferous fossil plants.

477

478 5.3. Sources of intergeneric variance in plant δ¹³C

479 5.3.1. Water-use efficiency

480 One mechanism that can lead to systematic differences in $\delta^{13}\text{C}$ values between plant
481 taxa is differences in water-use efficiency (WUE): plants that grow in wet habitats do not need
482 to limit water loss and, hence, tend to open their stomata more widely in order to maximize
483 CO_2 uptake at the cost of low water-use efficiency. This process leads to maximum internal-leaf
484 $p\text{CO}_2$ and maximum carbon isotope discrimination (i.e., lower $\delta^{13}\text{C}_p$) (Farquhar et al., 1989). In
485 contrast, plants that grow in drier habitats are forced to limit water loss through their stomata
486 (i.e., higher water-use efficiency), leading to less CO_2 uptake, lower internal-leaf $p\text{CO}_2$, and
487 reduced carbon-isotope discrimination (i.e., higher $\delta^{13}\text{C}_p$) as a result of a larger fraction of
488 internal-leaf CO_2 being utilized in photosynthesis (Farquhar et al., 1989).

489 The carbon isotopic composition of modern C_3 land plants exhibits a strong negative
490 relationship to mean annual precipitation (MAP) (Miller et al., 2001; Liu et al., 2005; Roden et
491 al., 2005; Diefendorf et al., 2010; Kohn, 2010). An increase in MAP from 0 to 1000 mm yr^{-1}
492 correlates with a $\sim 4\text{-}5 \text{ ‰}$ depletion in $\delta^{13}\text{C}_p$, although this relationship is non-linear because
493 $\delta^{13}\text{C}_p$ becomes less sensitive to changes in precipitation at high MAP (Diefendorf et al., 2010).
494 This relationship exists because land plants are more commonly water-limited than carbon-
495 limited and have a strong incentive to engage in greater water-use efficiency where water is
496 scarce (Bacon, 2004; Macfarlane et al., 2004). Plants tend to reduce stomatal conductance in
497 arid regions in order to conserve water, which causes a larger proportion of the CO_2 that
498 diffuses into the leaf to be used in photosynthesis, resulting in reduced fractionation (relative to
499 the atmospheric carbon source) and heavier $\delta^{13}\text{C}_p$ values (Farquhar et al., 1989; Brugnoli and
500 Lauteri, 1991; Poss et al., 2000). The opposite pattern is found in humid regions, causing $\delta^{13}\text{C}_p$

501 values to become lighter. This relationship accounts for ~55 % of $\delta^{13}\text{C}$ variance among modern
502 C_3 plants (Diefendorf et al., 2010).

503 A fundamental divide exists between species with high hydraulic conductivity and low
504 embolism resistance and those with low hydraulic conductivity and high embolism resistance
505 (Wilson, 2016). Mapping of hydraulic ecospace shows that the high-conductivity/low-safety-
506 margin domain was occupied by many early vascular land plants, including trimerophytes,
507 lycophytes, cladoxyloids, and sphenopsids, all of which developed tracheids with scalariform
508 pits that maximized hydraulic conductivity (Wilson and Knoll, 2010; Wilson and Fischer, 2011;
509 Wilson, 2013, 2016). For some plants, this strategy was associated with perennially wet
510 habitats in which the danger of desiccation was limited, e.g., as for arborescent lycophytes and
511 other plants that inhabited tropical lowland swamps during the Carboniferous Period. For
512 other plants, this hydraulic mechanism was associated with an ecological strategy based on
513 rapid growth and generational overturn (known as 'live fast, die young'), which possibly
514 included all of the zosterophyllophytes and basal euphyllophytes of the present study. For
515 example, *Psilophyton dawsonii* may have grown rapidly, as suggested by xylem with large pits
516 similar to that of some modern small ferns whose aerial vegetative structures rarely persist for
517 more than a year (Wilson, 2016). An additional factor in the high conductivity of early vascular
518 plants was high atmospheric CO_2 levels, which permitted smaller and less numerous stomata
519 (thus minimizing some types of cavitation hazards) and generally higher water-use efficiency
520 (Sperry, 2003).

521 It has been suggested that early land plants were mostly generalists, occupying a wide
522 range of habitats (Spicer, 1989; Meyer-Berthaud et al., 2003). However, the systematic

523 variation in $\Delta^{13}\text{C}_p$ among Devonian plant taxa observed in this study (Fig. 7), if due to
524 environmental controls, implies that some early vascular land plants may have been more
525 specific in their habitat preferences than previously thought. Wetter habitats may have been
526 favored by most zosterophyllophytes, which typically had small, shallow root systems (Gensel
527 et al., 2001; Xue, 2012). *Sawdonia* exhibits the relatively most ^{13}C -depleted compositions
528 among the 12 study taxa (Fig. 7). It occupied a wide range of environments but was most
529 common along the margins of interdistributary basins in lower delta plain settings (Griffing et
530 al., 2000; Hotton et al., 2001; Kennedy et al., 2012). Sedimentologic investigations have not
531 established for certain whether these basins were inundated mainly with brackish (Hotton et
532 al., 2001) or fresh waters (Kennedy et al., 2012). The low $\Delta^{13}\text{C}_p$ compositions of *Sawdonia*
533 documented in the present study are more consistent with fresh waters, because C_3 plants
534 growing in coastal salt marshes or in areas of elevated groundwater salinity tend to become
535 ^{13}C -enriched rather than ^{13}C -depleted (Brugnoli and Lauteri, 1991; Malamud-Roam and Ingram,
536 2001).

537 Drier habitats may have been occupied by some of the plant taxa examined in this
538 study. In particular, *Leclercqia*, *Haskinsia*, and, to a lesser degree, *Psilophyton* exhibit ^{13}C -
539 enriched compositions consistent with higher water-use efficiency (Fig. 7). This inference is
540 supported by the anatomical features of these plants. The morphologies of *Leclercqia* and
541 *Haskinsia* are similar to modern *Lycopodium* s.l., which often grows in seasonally dry habitats
542 (Fernandez et al., 2008). In these taxa, densely crowded and overlapping leaves can create a
543 boundary layer effect that is effective at minimizing water loss during gas exchange, and which
544 is therefore favored in dry habitats. In addition, the leaves of *Leclercqia* and *Haskinsia* partially

545 enclosed the sporangia, protecting them from drying out (Meyer-Berthaud et al., 2003; Gensel
546 and Kasper, 2005; Gensel and Albright, 2006). Certain features in *Psilophyton* may have
547 adapted it to sunny, seasonally dry habitats, e.g., forked cylindrical lateral branchlets and a
548 prominent outer cortex of axial fibers that provided mechanical support (possibly against
549 wilting) and UV protection (via the high lignin content of fibrous cell walls) (Trant and Gensel,
550 1985; Gerrienne, 1995, 1997). These ^{13}C -enriched taxa may have grown where soils were
551 better drained, e.g., on river levees or in upper floodplain settings that were further inland and
552 somewhat drier than coastal environments, as proposed for *Psilophyton* (Hotton et al., 2001).

553 In areas of limited precipitation, increases in soil salinity can exert a strong influence on
554 $\delta^{13}\text{C}_\text{p}$. Experimental and in-situ studies of modern C_3 plants have shown that $\delta^{13}\text{C}_\text{p}$ increases by
555 2-5 ‰ with rising soil salinity (Brugnoli and Lauteri, 1991; Poss et al., 2000; Winter and Holtum,
556 2005). A similar effect is observed in coastal salt marshes, where the $\delta^{13}\text{C}_\text{p}$ of C_3 marsh plants
557 increases by several per mille with rising watermass salinity (Malamud-Roam and Ingram, 2001;
558 Cloern et al., 2002). This effect is linked to the need to conserve water in more saline
559 environments, leading to reduced stomatal conductance and photosynthetic fractionation and,
560 thus, higher $\delta^{13}\text{C}_\text{p}$ values (Farquhar et al., 1989; Brugnoli and Lauteri, 1991; Poss et al., 2000).
561 However, there is no evidence that any early vascular land plant grew in saline soils or brackish-
562 water environments (Kennedy et al., 2012), and our results are consistent with this inference.
563 The apparent water-use efficiencies of our fossil plant taxa suggested by their $\Delta^{13}\text{C}_\text{p}$ values (Fig.
564 7) correspond well with predictions of habitat preference based on paleoecological analyses
565 (see Section 5.4). Further carbon isotopic study of early vascular land plants may prove
566 invaluable in helping to define their habitat preferences.

567

568 5.3.2. Forest understory $\delta^{13}\text{C}$ gradient

569 A second environmental factor that can lead to systematic differences in $\delta^{13}\text{C}$ values
570 between plant taxa is vertical $\delta^{13}\text{C}_{\text{CO}_2}$ variation in the forest understory atmosphere. Forests are
571 characterized by a higher rate of soil respiration than most other vegetation biomes (Raich and
572 Tufekciogul, 2000), as well as by more limited air mass exchange than in open landscapes owing
573 to the sheltering effects of a closed canopy (Feigenwinter et al., 2004). This combination of
574 factors results in elevated $p\text{CO}_2$ in the forest understory atmosphere along with a significant
575 vertical $\delta^{13}\text{C}_{\text{CO}_2}$ gradient (Jackson et al., 1993). At 0.5 m above the forest floor, up to ~20 % of
576 CO_2 is soil-derived (Da Silveira et al., 1989), exposing low-growing plants to strongly ^{13}C -
577 depleted (-28 to -25 ‰) soil-respired CO_2 (Farquhar et al., 1989; Jackson et al., 1993). As a
578 consequence, CO_2 in the forest understory atmosphere may be up to ~3-5 ‰ depleted relative
579 to CO_2 in the open atmosphere, and this isotopic signature can be transferred to understory
580 plants (Schleser and Jayasekera, 1985; Flanagan et al., 1996). In modern forests, >50 % of $\delta^{13}\text{C}$
581 variance in understory plants is linked to local variations in $\delta^{13}\text{C}_{\text{CO}_2}$ (Da Silveira et al., 1989).

582 'Canopy effects' are unlikely to have played any role in the intergeneric differences in
583 $\Delta^{13}\text{C}_p$ of the present study. The largest differences in $\Delta^{13}\text{C}_p$ values are seen among Early and
584 early Middle Devonian plants that existed prior to the first forests (Fig. 6). These early plants
585 grew in patchy floral communities consisting largely of clonal vegetation whose shoots would
586 have lacked any capacity to limit air mass exchange (Gensel and Edwards, 2001; Edwards and
587 Richardson, 2004), and whose limited productivity did not generate high excess soil $p\text{CO}_2$ (Mora
588 et al., 1996; Elick et al., 1998). The appearance of the first forests during the late Givetian to

589 early Frasnian (Decombeix et al., 2011; Stein et al., 2012; Berry and Marshall, 2015), an event
590 known as 'afforestation' (Scheckler, 2001), resulted in denser floral communities with closed
591 canopies formed by large leafy trees that, for the first time, would have generated understory
592 niches with varying environmental characteristics. In our dataset, the only co-existing Late
593 Devonian taxa that have the potential to exhibit $\Delta^{13}\text{C}_p$ differences due to a 'canopy effect' are
594 *Archaeopteris*, a canopy tree, and *Rhacophyton*, a much smaller woody bush (Fig. 1). However,
595 *Rhacophyton* yields $\Delta^{13}\text{C}_p$ values that are on average ~1.5 ‰ heavier than those of
596 *Archaeopteris* (Fig. 6), which is the opposite of the pattern expected for canopy-versus-
597 understory plants. We infer that the higher $\Delta^{13}\text{C}_p$ values of *Rhacophyton* are more likely due to
598 its preference for dry habitats, leading to enhanced water-use efficiency (see Section 5.3.1).

599

600 5.4. Relationship of $\delta^{13}\text{C}$ to habitat preferences of early vascular plants

601 Although it has been proposed that early land plants were mostly generalists (Spicer,
602 1989; Meyer-Berthaud et al., 2003), the carbon-isotopic evidence of the present study suggests
603 that Devonian and Early Carboniferous plant taxa varied considerably in their habitat
604 preferences. Systematic interspecific differences in $\Delta^{13}\text{C}_p$ among the 12 taxa examined (Fig. 7)
605 were probably controlled mainly by water-use efficiency, related to humidity levels at their sites
606 of growth (see Section 5.3.1). To illustrate inferred differences in habitat, we have generated
607 reconstructions of Early, Middle, and Late Devonian terrestrial ecosystems (Fig. 8A-C). These
608 reconstructions focus on the distributions of the 12 plant genera of the present study, with the
609 spatial distribution of each taxon shown to conform to its relative water-use efficiency as
610 inferred from taxon-specific differences in $\Delta^{13}\text{C}_p$.

611 Our reconstructions of Devonian land-plant habitats were informed by the findings of
612 earlier studies of terrestrial ecosystems. One consideration in habitat reconstruction is the in-
613 situ versus transported character of land plant fossils. Most plant fossils have been transported
614 prior to final deposition and burial (e.g., [Pratt and van Heerde, 2017](#)), although fossils that
615 consist of intact stems and leaves and are well-preserved suggest limited transport distances
616 ([Hotton et al., 2001](#); [Allen and Gastaldo, 2006](#); [Kennedy et al., 2012](#); [Gastaldo, 2016](#)). Nearly all
617 of the fossil plant specimens of the present study are well-preserved and relatively intact, often
618 consisting of complete stems, twigs or leaves, and more rarely of dense intertangled mats of
619 vegetation. Thus, it is unlikely that they were transported long distances prior to burial (cf.
620 [Berry and Edwards, 1996](#); [Gastaldo, 2016](#); [Pratt and van Heerde, 2017](#)). Such fossils are
621 considered to be 'parautochthonous', i.e., transported to only a limited degree and thus useful
622 for environmental interpretations of their growth habitat ([Hotton et al., 2001](#); [Allen and](#)
623 [Gastaldo, 2006](#); [Kennedy et al., 2012](#)).

624 During the Early to Middle Devonian, land plants were concentrated in coastal delta and
625 lower floodplain habitats ([Hotton et al., 2001](#)). From the Middle Devonian, land plants began to
626 penetrate more deeply into continental interiors and increasingly occupied upper floodplain
627 settings ([Algeo et al., 1995](#); [Berry et al., 2000](#); [Berry and Fairon-Demaret, 2001](#); [Cressler et al.,](#)
628 [2010](#); [Retallack and Huang, 2011](#)). However, the upland regions of continental interiors
629 remained mostly devoid of vegetation until the advent of seed plants in the latest Devonian to
630 Early Carboniferous ([Algeo and Scheckler, 1998](#); [Decombeix et al., 2011](#)). Early to Middle
631 Devonian plants appear to exhibit a wider range of $\Delta\delta^{13}\text{C}_p$ variation than Late Devonian to Early
632 Carboniferous plants. This pattern may reflect greater environmental variation in Early-Middle

633 Devonian terrestrial habitats. During this early stage of landscape colonization, higher land
634 plants had probably densely colonized some areas (e.g., delta plains) and sparsely colonized
635 others (e.g., upland floodplains), while leaving broad continental interiors largely unvegetated.
636 As a consequence of this mosaic floral distribution, land areas may have exhibited substantial
637 spatial variation in environmental characteristics (e.g., humidity, soil development, albedo, etc.)
638 (cf. [Edwards and Richardson, 2004](#)).

639 Early Devonian terrestrial ecosystems ([Fig. 8A](#)) have been analyzed in studies of the
640 Emsian-age Battery Point Formation on the Gaspé Peninsula of Québec and the Campbellton
641 Formation in New Brunswick. Facies A of the Cap-aux-Os Member of the Battery Point
642 Formation contains unimodal paleocurrent indicators in coastal delta-plain facies that have
643 been interpreted as crevasse splay or storm washover deposits ([Hotton et al., 2001](#)). The most
644 common taxon in this setting is *Sawdonia*, which is inferred to have lived close to the shoreline
645 on the margins of interdistributary basins that were subject to frequent flooding. [Hotton et al.](#)
646 [\(2001\)](#) inferred that flooding events introduced brackish or marine waters, but [Kennedy et al.](#)
647 [\(2012\)](#) inferred that similar occurrences of *Sawdonia* in the Campbellton Formation existed in
648 fully freshwater habitats. Facies B of the Cap-aux-Os Member represents prograding fluvial
649 channel deposits, hence mainly freshwater conditions, although some of the sandstones
650 contain asymmetric bimodal cross-bedding indicative of tidal influence ([Hotton et al., 2001](#)).
651 This facies contains abundant *Pertica* and *Drepanophycus* (as well as other taxa not analyzed in
652 this study) that are thought to have grown along lower floodplain channel margins, whereas
653 *Psilophyton* was inferred to have occupied an equivalent habitat somewhat further upstream.
654 Similar assemblages containing *Pertica*, *Drepanophycus*, *Psilophyton*, and *Leclercqia* have been

655 reported from coastal delta plain and freshwater fluvial deposits of the Campbellton Formation
656 in New Brunswick (Kennedy et al., 2012) and the Trout Valley Formation of Maine (Allen and
657 Gastaldo, 2006).

658 Early Devonian vascular plants were dominantly ground-hugging rhizomatous
659 lycophytes (*Sawdonia*, *Drepanophycus*, *Leclercqia*, *Haskinsia*) and shrubby trimerophytes
660 (*Psilophyton*, *Pertica*), mostly with heights of <1 m (Fig. 1B; Algeo and Scheckler, 1998). Many
661 Early Devonian plants grew in dense monospecific stands, facilitated by predominantly
662 rhizomatous growth strategies, allowing local resource domination (Fig. 8A; DiMichele and
663 Hook, 1992; Xue, 2012). However, mixtures of plant fossil debris in many formations imply that
664 such patchiness was relatively local, and that there was considerable taxonomic heterogeneity
665 in Early Devonian landscapes at a slightly larger spatial scale (Allen and Gastaldo, 2006; Cressler
666 et al., 2010; Gastaldo, 2016). This pattern may reflect habitat specialization ('floral
667 partitioning') on the basis of environmental variability in soil moisture, nutrient levels, or
668 environmental characteristics such as frequency of flooding or other disturbances (Allen and
669 Gastaldo, 2006; Greb et al., 2006).

670 By the late Middle Devonian (Givetian; Fig. 8B), the development of secondary
671 supporting tissues resulted in an increase in average plant heights and the development of the
672 earliest forests in coastal wetland regions (DiMichele and Hook, 1992; Greb et al., 2006; Mintz
673 et al., 2010; Stein et al., 2012; Berry and Marshall, 2015). Shrubby stands of aneurophytalean
674 progymnosperms, lycopsids, cladoxylopsids, and zosterophyllophytes were widespread in
675 lowland areas (Fig. 8B; Berry and Fairon-Demaret, 2001; Xue et al., 2018). Early forests
676 consisted of the cladoxylopid tree *Eospermatoperis* with an understory flora that included

677 lycopsids and aneurophytalean progymnosperm shrubs such as *Tetraxylopteris* (Driese et al.,
678 1997; Stein et al., 2007, 2012; Mintz et al., 2010; Xu et al., 2017). The rapid global spread of
679 forests may have been linked to archaeopteridalean progymnosperm trees with laminate
680 leaves and deep root systems. The appearance of early members of this clade in the early
681 Givetian is signaled by the microspore *Geminospora lemurata* and the megaspore
682 *Contagisporites optivus* (Marshall, 1996; Turnau, 2014), and their widespread presence in mid
683 to late Givetian landscapes is attested by specimens of *Svalbardia* or proto-*Archaeopteris*
684 (Berry, 2008).

685 Late Devonian landscapes were dominated by dense monospecific stands of
686 *Archaeopteris*, with *Rhacophyton* and other shrubby plants either occupying open terrain or
687 present as understory elements in forests (Fig. 8C). Archaeopterid progymnosperms formed
688 extensive forests in both lower and upper floodplain environments (Scheckler, 1986a; Beck and
689 Wight, 1988; Meyer-Berthaud et al., 1999), and *Archaeopteris* is thought to have generally
690 favored dry riparian habitats (Cressler, 1999, 2006; Retallack and Huang, 2011). *Rhacophyton*
691 grew as a bushy understory plant in forests subject to frequent ground fires (Cressler, 2001,
692 2006), although it also flourished in peat wetlands (Greb et al., 2006). The earliest known seed
693 plants became established in the mid-Famennian as small bushy colonizers in disturbed
694 habitats, but they did not become important members of terrestrial ecosystems until the
695 Carboniferous (Scheckler, 1986b; Streele et al., 2000; Decombeix et al., 2011).

696

697 5.5. Middle/Late Devonian floral turnover

698 Floral turnovers were a regular feature of early Devonian plant communities owing to
699 the rapid pace of evolutionary innovation at that time (Cascales-Miñana et al., 2010). The
700 rhyniophytes, which, as the earliest tracheophyte clade, were morphologically simple, peaked
701 in dominance during the Late Silurian and earliest Devonian (Lochkovian). By the Early
702 Devonian, the zosterophyllophytes had evolved lateral sporangia, pseudomonopodial
703 branching, and a rhizomatous habit, establishing them as the most morphologically complex,
704 diverse, and abundant clade (Gensel, 1992; Edwards and Richardson, 2004; Cascales-Miñana
705 and Meyer-Berthaud, 2015). They peaked during the mid to late Early Devonian (Pragian-
706 Emsian) but gradually declined as lycophytes and basal euphyllophytes gained in importance
707 during the early Middle Devonian (Eifelian) (Hao and Xue, 2013b; Cascales-Miñana and Meyer-
708 Berthaud, 2015). Among other innovations, basal euphyllophytes developed planate or
709 laminate lateral branched systems resembling proto-leaves (Gerrienne et al., 2014). The
710 turnovers among these clades appear to have been competitive replacements that were not
711 clearly linked to any specific climatic or tectonic event (Cascales-Miñana and Meyer-Berthaud,
712 2015).

713 The Givetian/Frasnian (Middle/Late Devonian) transition appears to mark another major
714 floral turnover (Raymond and Metz, 1995; Silvestro et al., 2015). During this event, primitive
715 spore-bearing plants such as zosterophyllophytes experienced high extinction rates (Cascales-
716 Miñana and Meyer-Berthaud, 2014) and euphyllophytes, including both lignophytes and non-
717 lignophytes, underwent a major diversification (Xue et al., 2018). Among the taxa of the
718 present study, the euphyllophytes *Psilophyton* and *Pertica* declined in the Emsian-Eifelian, and
719 the zosterophyllophytes and lycopsids *Drepanophycus*, *Sawdonia*, *Leclercqia*, and *Haskinsia*

720 declined in the Givetian (Fig. 2). Although some of these taxa (e.g., *Drepanophycus*) persisted
721 through the Famennian, their relative importance in the Late Devonian was greatly reduced.
722 This floral turnover is even more apparent in palynomorph assemblages, which exhibit a sharp
723 decline in diversity and rapid turnover at the Middle/Late Givetian boundary across Russia and
724 eastern Europe and, to a lesser degree, in France, although it has not reported to date from
725 North America (Obukhovskaya, 2000; Turnau, 2014).

726 One important aspect of the Givetian-Frasnian floral turnover was the appearance and
727 diversification of arborescent (tree-sized) lycophytes and lignophytes (Wang et al., 2005; Galtier
728 and Meyer-Berthaud, 2006; Meyer-Berthaud et al., 2010; Decombeix et al., 2011). In this study,
729 the Givetian/Frasnian transition is marked by short-lived arborescent taxa such as *Wattieza* and
730 *Tetraxylopteris*, after which longer-ranging arborescent taxa such as *Archaeopteris* became
731 dominant in the Late Devonian (Fig. 2). The evolutionary development of trees led directly to
732 the first forests, which were of Givetian (late Middle Devonian) to earliest Frasnian (early Late
733 Devonian) age. They were dominated by tree-sized pseudosporochnalean cladoxylopsids such
734 as *Wattieza/Eospermatoperis* with an understory that included aneurophytaleans such as
735 *Tetraxylopteris*, as well as possibly herbaceous and arborescent lycopsids (Driese et al., 1997;
736 Stein et al., 2007, 2012; Mintz et al., 2010). The known distribution of pseudosporochnalean
737 forests is mostly limited to the Euramerican continental block, but they were succeeded by
738 archaeopterid-dominated forests on all continents during the later Frasnian to Famennian
739 (Scheckler, 1986a, 2001). The advent of forests probably generated selective pressures on
740 terrestrial plants either to evolve larger size or to adapt to a shaded understory. The near-
741 simultaneous appearance of woody supporting tissues and tree-sized stature among

742 arborescent lycophytes, sphenopsids, and lignophytes may imply the first strategy
743 (Mosbrugger, 1990; Meyer-Berthaud et al., 2010). Less certain, due to difficulties in sampling,
744 is what might be inferred about plant evolution in the understory. Nevertheless, the spread of
745 forests likely had multifaceted, profound and irreversible consequences for both terrestrial
746 floral communities and global climate conditions.

747

748 **6. Conclusions**

749 Carbon-isotopic variation among 12 genera of Devonian-Early Carboniferous vascular
750 land plants provides insights into their habitat preferences and water-use efficiencies. A total
751 of 309 analyses of 190 unique specimens yielded $\delta^{13}\text{C}_p$ values ranging from -20.3‰ to
752 -30.5‰ with a mean of -25.5‰ , similar to the range and mean of $\delta^{13}\text{C}$ values for modern C_3
753 land plants. *Sawdonia* yielded the most ^{13}C -depleted values (mean $-27.1\pm 1.7\text{‰}$; $n = 28$),
754 reflecting lower water-use efficiency that was probably related to growth in wetter habitats
755 such as lower delta plains. Because salt-marsh vegetation is typically ^{13}C -enriched, the strongly
756 ^{13}C -depleted composition of *Sawdonia* is suggestive of growth in freshwater habitats. In
757 contrast, *Leclercqia*, *Haskinsia*, and *Psilophyton* yielded relatively ^{13}C -enriched values (means
758 $-23.0\pm 1.6\text{‰}$, $-22.3\pm 1.3\text{‰}$, and $-24.8\pm 1.6\text{‰}$, respectively), reflecting higher water-use
759 efficiency related to growth in drier habitats such as upper floodplains. This inference is
760 supported by anatomical adaptations to drier conditions exhibited by these taxa, e.g., related
761 to leaf arrangement and structure. A large majority of our specimens ($>90\%$) are from the
762 Appalachian Basin of eastern North America, precluding effective assessment of large-scale
763 geographic patterns of carbon-isotopic variation in these fossil plant taxa. This study

764 demonstrates that investigations of the carbon-isotopic composition of well-preserved plant
765 fossils have the potential to yield insights regarding habitat preferences and ecosystem
766 structure in paleofloral communities.

767

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775

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777

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1249 **Tables**

1250

1251 Table 1. Summary of carbon isotope analyses by taxon and plant part

1252

1253 Table 2. Mean differences in $\Delta^{13}\text{C}_p$ by taxon

1254

1255 Table 3. Differences in $\delta^{13}\text{C}_p$ between anatomical parts of individual specimens

1256

1257 Table S1. Stable carbon isotope compositions of Devonian-Carboniferous fossil plant specimens

1258

Table 1. Summary of carbon isotope analyses by taxon and plant part

	Number of specimens	Number of carbon isotope analyses					Mean $\delta^{13}\text{C}$				
		Stem	Leaf	Spine	Indet.	Total	Stem	Leaf	Spine	Indet.	Avg.
<i>Archaeopteris</i>	51	36	17		27	80	-25.53	-25.32		-27.16	-26.04
<i>Drepanophycus</i>	21	23		7	10	40	-26.08		-25.52	-25.90	-25.94
<i>Genselia</i>	9	2	1		7	10	-22.66	-23.08		-23.72	-23.44
<i>Haskinsia</i>	4	2			2	4	-22.27			-22.31	-22.29
<i>Leclercqia</i>	13	16		3	5	24	-22.96		-23.91	-22.71	-23.02
<i>Pertica</i>	11	12			8	20	-25.55			-25.26	-25.43
<i>Wattieza</i>	8	6			5	11	-26.21			-26.74	-26.45
<i>Psilophyton</i>	17	13			12	25	-24.46			-25.27	-24.85
<i>Rhacophyton</i>	18	19	4		10	33	-24.51	-25.28		-25.82	-25.00
<i>Rhodeopteridium</i>	3	2	1			3	-23.71	-22.82			-23.41
<i>Sawdonia</i>	14	18		4	6	28	-27.46		-27.08	-25.85	-27.07
<i>Tetraxylopteris</i>	21	19	2		10	31	-25.56	-26.09		-27.01	-26.06
Total / Average	190	168	25	14	102	309	-25.30	-25.18	-25.62	-25.87	-25.50

1259 Notes: Indet. = indeterminate. Avg. = average (of stem + leaf + spine + indet. mean values).

1260

Table 2. Mean differences in $\Delta^{13}\text{C}_p$ by taxon

	Number of analyses	mean (‰)	st. dev. (‰)	s.e. (‰)	Student's t	p(α)
<i>Archaeopteris</i>	80	-0.38	1.18	0.13	3.05	0.002
<i>Drepanophycus</i>	40	-0.26	1.08	0.17	1.32	0.189
<i>Genselia</i>	10	0.37	1.12	0.36	0.69	0.492
<i>Haskinsia</i>	4	2.41	1.48	0.74	3.31	0.001
<i>Leclercqia</i>	24	1.81	1.02	0.21	6.57	0.001
<i>Pertica</i>	20	0.40	0.56	0.12	1.06	0.292
<i>Wattieza</i>	11	-0.51	0.49	0.15	1.28	0.201
<i>Psilophyton</i>	25	0.94	1.55	0.31	3.22	0.001
<i>Rhacophyton</i>	33	0.23	1.32	0.23	0.65	0.517
<i>Rhodeopteridium</i>	3	0.41	0.89	0.51	0.42	0.677
<i>Sawdonia</i>	28	-1.22	1.81	0.34	5.02	0.001
<i>Tetraxylopteris</i>	31	-0.05	1.35	0.24	0.37	0.714

Notes: bold type denotes significant values (= $p(\alpha) < 0.05$); st. dev. = standard deviation;

s.e. = standard error of the mean. Statistical software from [Zaiontz \(2014\)](#).

1261

1262

Table 3. Differences in $\delta^{13}\text{C}_p$ between anatomical parts of individual specimens

	No. of pairs	Stem $\delta^{13}\text{C}$ (‰)	Leaf/spine $\delta^{13}\text{C}$ (‰)	Difference $\Delta^{13}\text{C}$ (‰)	s.e. $\delta^{13}\text{C}$ (‰)	Student's t	$p(\alpha)$
<i>Archaeopteris</i>	13	-0.08	0.33	0.42	0.20	1.54	0.137
<i>Drepanophycus</i>	6	-0.81	-0.12	0.69	0.30	1.15	0.277
<i>Leclercqia</i>	3	1.75	1.96	0.21	0.22	0.45	0.676
<i>Rhacophyton</i>	4	0.51	0.05	-0.46	0.23	1.54	0.173
<i>Sawdonia</i>	4	-2.77	-1.22	1.56	0.21	2.85	0.029
<i>Tetraxylopteris</i>	2	0.10	-0.06	-0.16	0.13	1.25	0.337
Total	32	-0.30	0.15	0.45	0.14	2.64	0.010

1263 Notes: bold type denotes significant values ($=p(\alpha) < 0.05$); s.e. = standard error of the mean.

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1268 **Figure captions**

1269

1270 Figure 1. Devonian plant taxa of the present study: (A) phylogenetic relationships, and (B)
1271 morphological reconstructions. Reconstructions show full shoot system of plant except for
1272 *Tetraxylopteris* (lateral branch); open scale bars equal 10 cm and hachured scale bars equal
1273 1 m. Sources: (A) [Kenrick and Crane \(1997\)](#), [Hilton and Bateman \(2006\)](#), and [Taylor et al.](#)
1274 [\(2009\)](#); (B) *Sawdonia* (<http://www.ucmp.berkeley.edu/IB181/VPL/Lyco/Lyco1.html>),
1275 *Drepanophycus* ([Stewart and Rothwell, 1993](#)), *Leclercqia* ([Bonamo et al., 1988](#)), *Haskinsia*
1276 (<http://dinoera.com/tags/haskinsia>), *Psilophyton*
1277 (<https://openclipart.org/detail/231687/psilophyton-princeps>), *Pertica* ([Kasper and](#)
1278 [Andrews, 1972](#)), *Wattieza* ([Stein et al., 2007](#)) [note: reconstructions of European
1279 *Pseudosporochnus* are slightly different, e.g., [Berry and Fairon-Demaret, 2002](#)],
1280 *Rhacophyton* ([Cornet et al., 1977](#)), *Rhodeopteridium* ([Jennings, 1976](#)), *Tetraxylopteris*
1281 ([Bonamo and Banks, 1967](#)), *Archaeopteris* (www.devoniantimes.org), and *Genselia* ([Knaus,](#)
1282 [1995](#)).

1283

1284 Figure 2. Stratigraphic ages of fossil plant locales and ranges of fossil plant taxa used in this
1285 study. Marine conodont and terrestrial palynomorph zonation are from [Richardson and](#)
1286 [McGregor \(1986\)](#), [Ziegler and Sandberg \(1990\)](#), [Streele et al. \(2000\)](#), and [Playford and Dino](#)
1287 [\(2005\)](#); the timescale is from [Gradstein et al. \(2012\)](#). Locales: Gaspé Peninsula, Quebec, 1
1288 = Haldimand Head, 2 = Aiguillon, Cap-aux-Os, and L'Anse-a-brilliant, and 3 = Seal Rock; New
1289 Brunswick, 1 = south shore Chaleur Bay (localities A, B, F), Dalhousie, Pin Sec Point, and

1290 Peuplier Point, and 2 = Atholville and Restigouche; Hujiersite Fm (Xinjiang, China), 1 =
1291 Gannaren, 2 = Hwy 217, 3 = 251 Hill, and 4 = Hujiersite. Specimens of the Oneonta,
1292 Sonyea, Escuminac, and Pocono formations (*italicized*) are from multiple locales, but all fall
1293 within the narrow age ranges shown for each unit. For plant taxa, solid bars indicate peak
1294 abundance, open bars the full established biorange, and dashed bars uncertain extensions
1295 of the biorange.

1296

1297 Figure 3. Geographic distribution of fossil plant locales, shown on Late Devonian
1298 paleogeographic maps of (A) the world and (B) the Appalachian Basin. (A) Inset rectangle
1299 represents area of map B; abbreviations: A = Alberta, G = Germany, O = Ontario, V =
1300 Venezuela, X = Xinjiang, and Y = Yunnan; base map courtesy of Ron Blakey (Deep-Time
1301 Maps). Note that Laurentia (Paleozoic North America) was rotated $\sim 30^\circ$ clockwise relative
1302 to its present-day orientation ([van der Voo, 1988, 1993](#)). (B) Main fossil plant locales in
1303 Appalachian Basin; site names are positioned either directly above or below site locales
1304 (black dots); county names are given where multiple locales are within a small area. Dark
1305 brown field shows approximate area of basinward progradation of shoreline from the Early
1306 to the Late Devonian. N = present-day north; N_D = Devonian north.

1307

1308 Figure 4. Representative study specimens: (A) *Psilophyton forbesii* stems and leaves, Emsian,
1309 Gaspé Peninsula, Québec; (B) *Archaeopteris* sp. stems and leaves, Frasnian, West Virginia;
1310 (C) tracheids of *Psilophyton charientos*, Emsian, New Brunswick; (D) cuticle of *Sawdonia* sp.,
1311 Emsian, Gaspé Peninsula, Québec. All specimens were inspected using a binocular scope to

1312 verify the state of fossil preservation, and a subset was examined using scanning electron
1313 microscopy.

1314
1315 Figure 5. Model of $\Delta\delta^{13}\text{C}_{\text{p-x}}$ calculations. Relative to the LOWESS curve generated from the full
1316 plant $\delta^{13}\text{C}$ dataset, some fossil plant taxa exhibit systematically higher or lower $\delta^{13}\text{C}$ values.
1317 In this example, Taxon A exhibits higher-than-average $\delta^{13}\text{C}$ (positive $\Delta\delta^{13}\text{C}_{\text{p-x}}$), Taxon B
1318 exhibits average $\delta^{13}\text{C}$ (near-zero $\Delta\delta^{13}\text{C}_{\text{p-x}}$), and Taxon C exhibits lower-than-average $\delta^{13}\text{C}$
1319 (negative $\Delta\delta^{13}\text{C}_{\text{p-x}}$). The complete LOWESS curve for the $\delta^{13}\text{C}_{\text{p}}$ dataset will be published in a
1320 companion study ([Algeo et al., in preparation](#)).

1321
1322 Figure 6. Deviations of $\delta^{13}\text{C}$ of Devonian fossil plant specimens from the LOWESS reference
1323 curve ($\Delta\delta^{13}\text{C}_{\text{p-x}}$) plotted as a function of specimen age. For each genus, the regression of
1324 $\Delta\delta^{13}\text{C}_{\text{p-x}}$ against time is shown as a thin line; these regression lines are shown not to
1325 suggest that the $\Delta\delta^{13}\text{C}_{\text{p-x}}$ of a given taxon changes significantly with time (for most taxa,
1326 there is not enough data to generate a statistically significant time-dependent trend) but,
1327 rather, to show which taxa yield $\Delta\delta^{13}\text{C}_{\text{p-x}}$ values that are systematically higher or lower
1328 than the age-specific mean $\Delta\delta^{13}\text{C}_{\text{p-x}}$ values (0 ‰). Note that some taxa are systematically
1329 ^{13}C -enriched and others are systematically ^{13}C -depleted.

1330
1331 Figure 7. Deviations of $\delta^{13}\text{C}$ of Devonian fossil plants from the LOWESS reference curve ($\Delta\delta^{13}\text{C}_{\text{p-x}}$)
1332 by taxon. Open circles represent individual C-isotope analyses; red diamond, open
1333 rectangle, and horizontal bar represent the mean, standard error of the mean, and

1334 standard deviation range, respectively, for each taxon. The dashed vertical line represents
1335 no offset from the LOWESS trend, and the yellow field represents +/-1 standard deviation
1336 for the dataset as a whole. Note that some taxa are systematically ¹³C-enriched and others
1337 are systematically ¹³C-depleted.

1338

1339 Figure 8. Reconstructions of the ecological distribution of the 10 Devonian vascular land plant
1340 taxa of the present study: (A) Early Devonian (Emsian), (B) Middle Devonian (Givetian), and
1341 (C) Late Devonian (late Frasnian-early Famennian). Note that actual Devonian landscapes
1342 included other vascular and non-vascular plant taxa not shown here; these reconstructions
1343 are intended to show only the relative habitat preferences of the 10 Devonian taxa of the
1344 present study. Note further that the proposed paleo-environmental distributions of these
1345 taxa shown here are consistent with, but not proven by, the available isotopic data, and
1346 that alternative models are possible. Further study of Devonian fossil plant taxa will be
1347 needed to accurately constrain their actual habitat preferences.

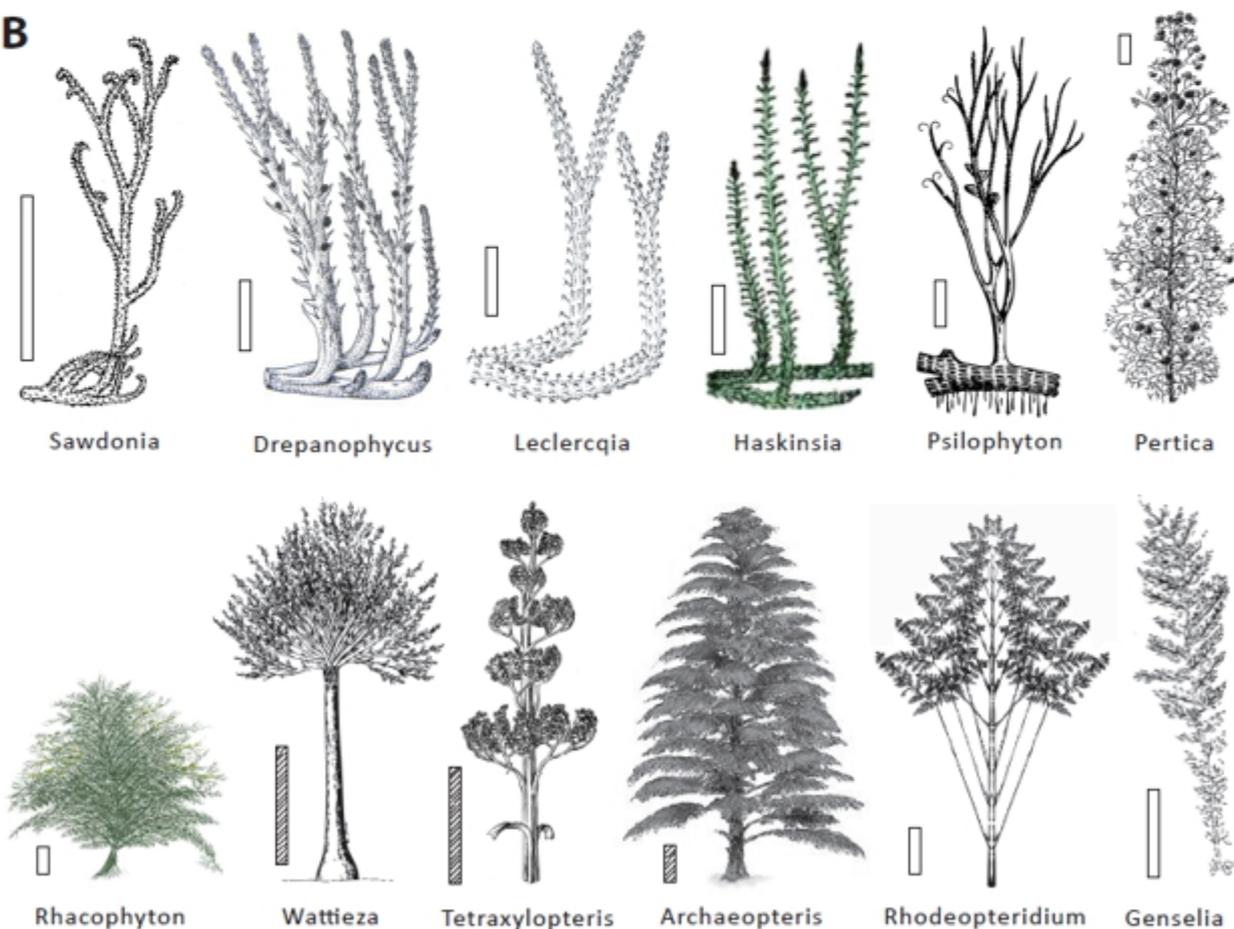
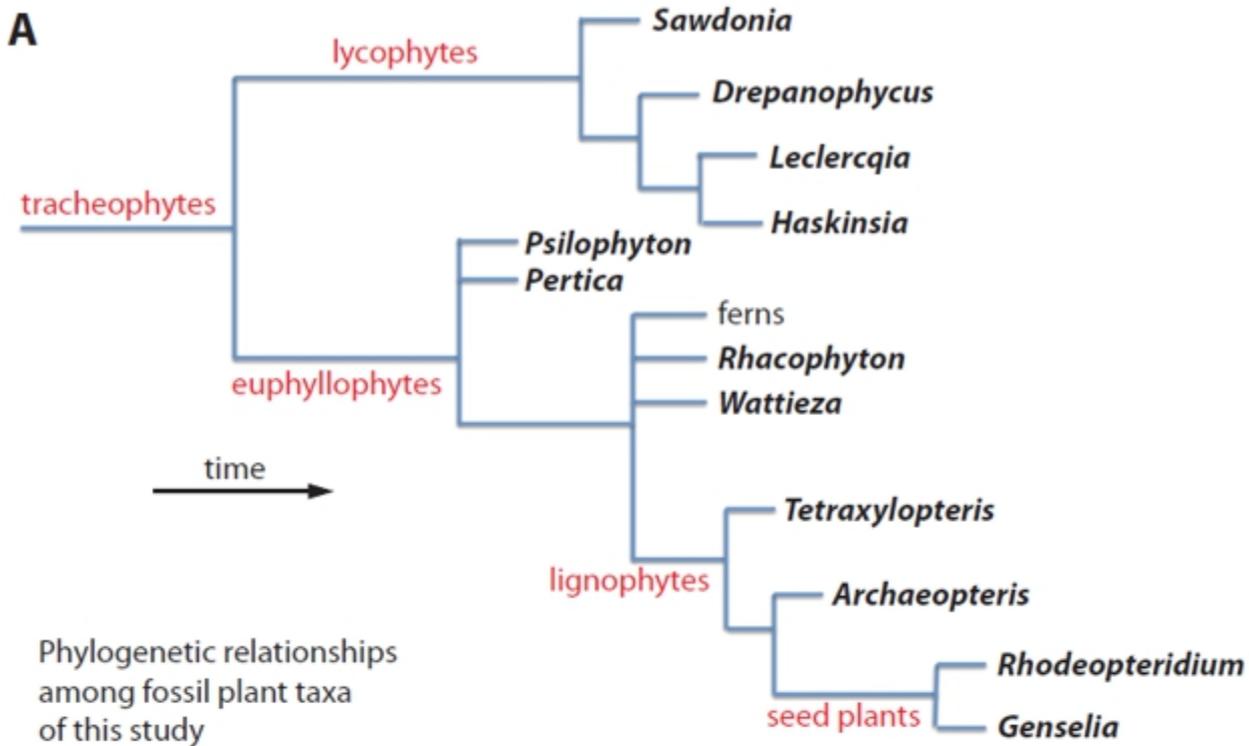
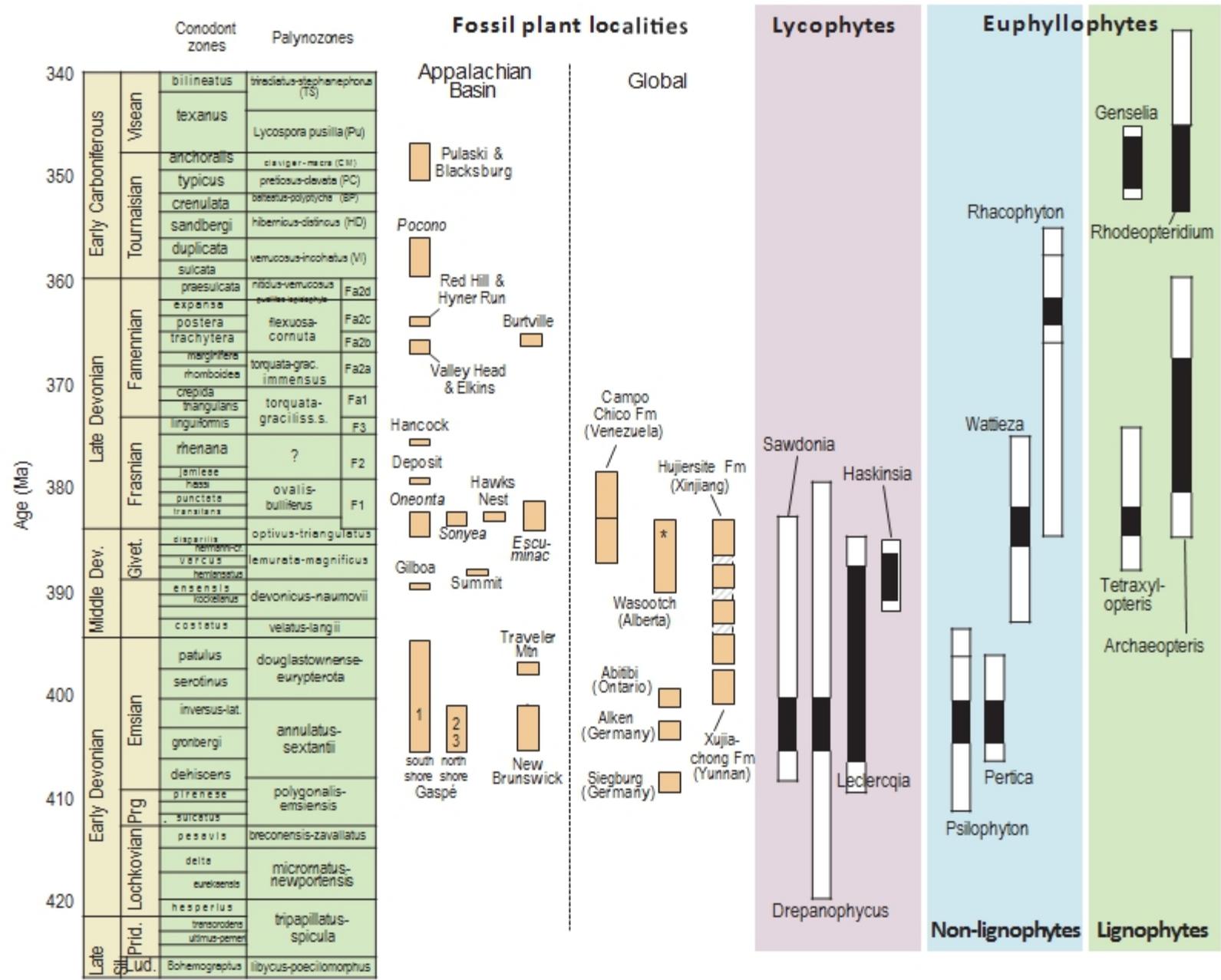


Figure 1



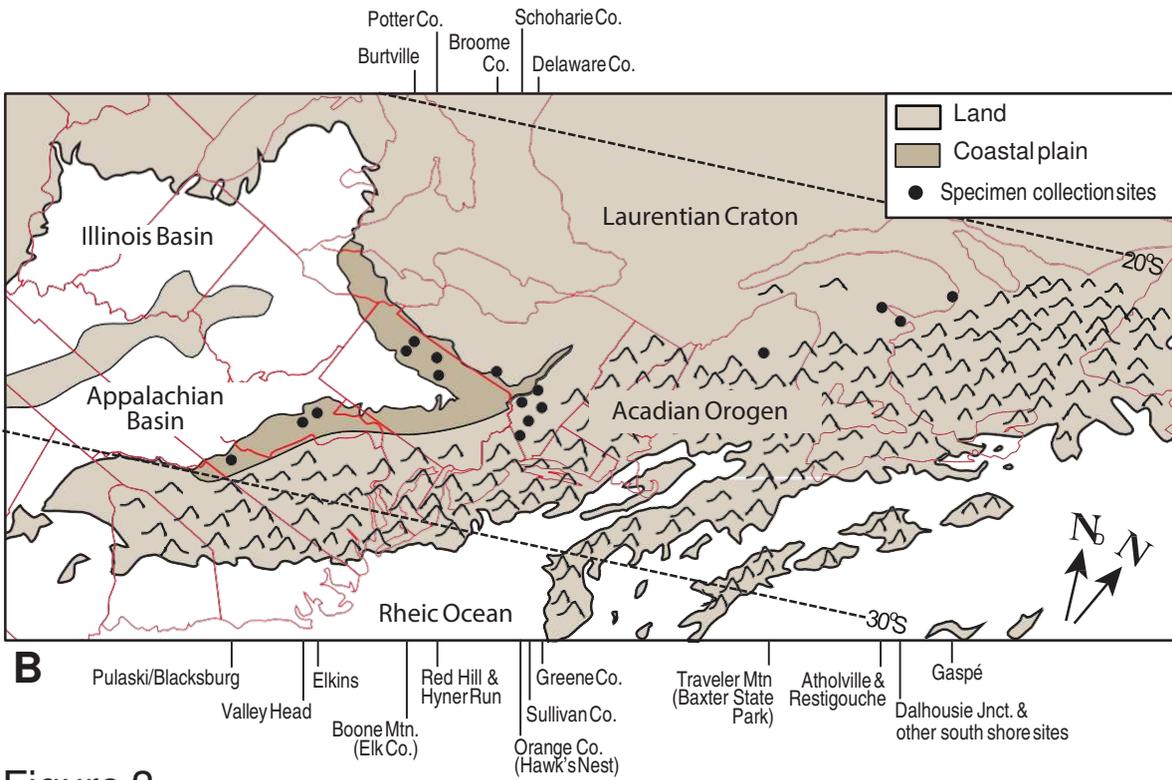
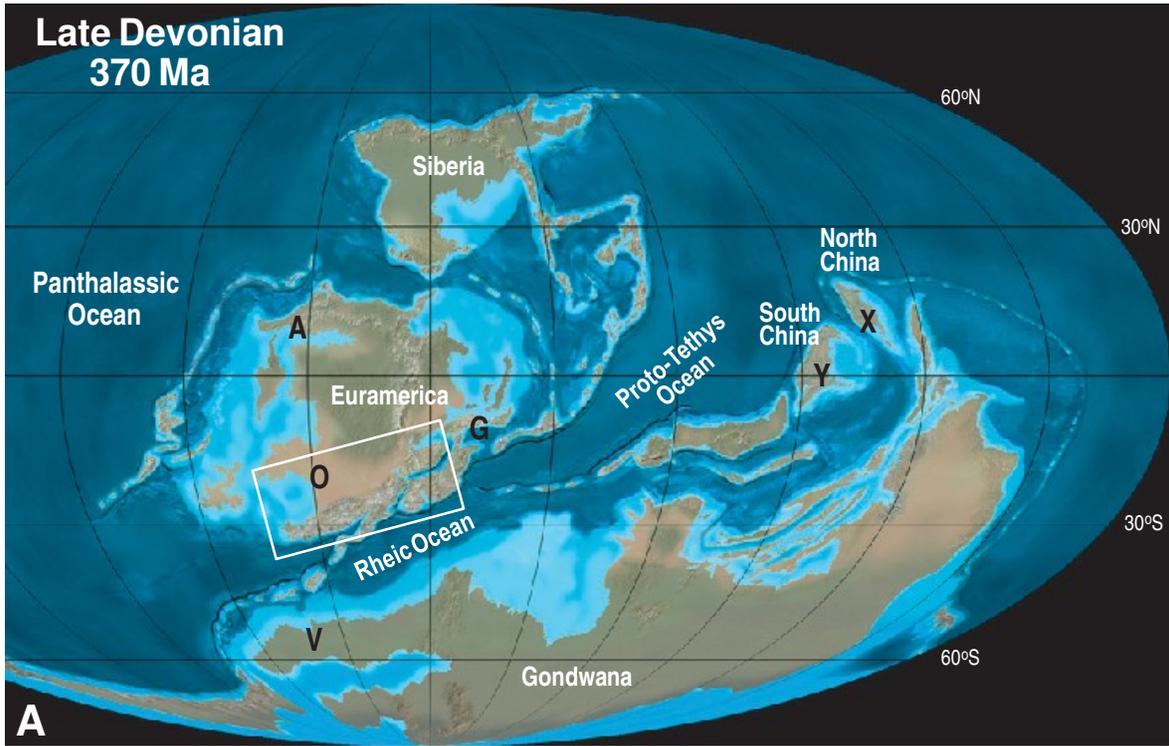


Figure 3

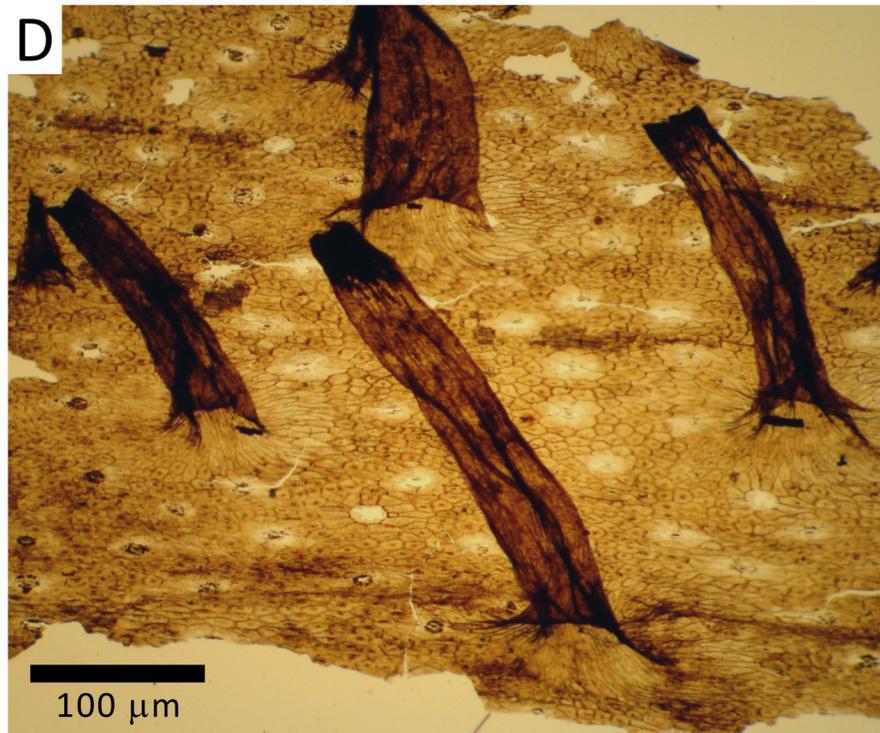
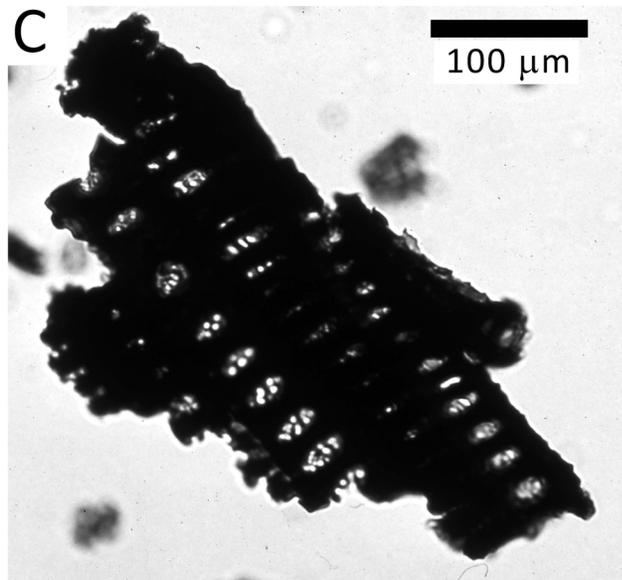


Figure 4

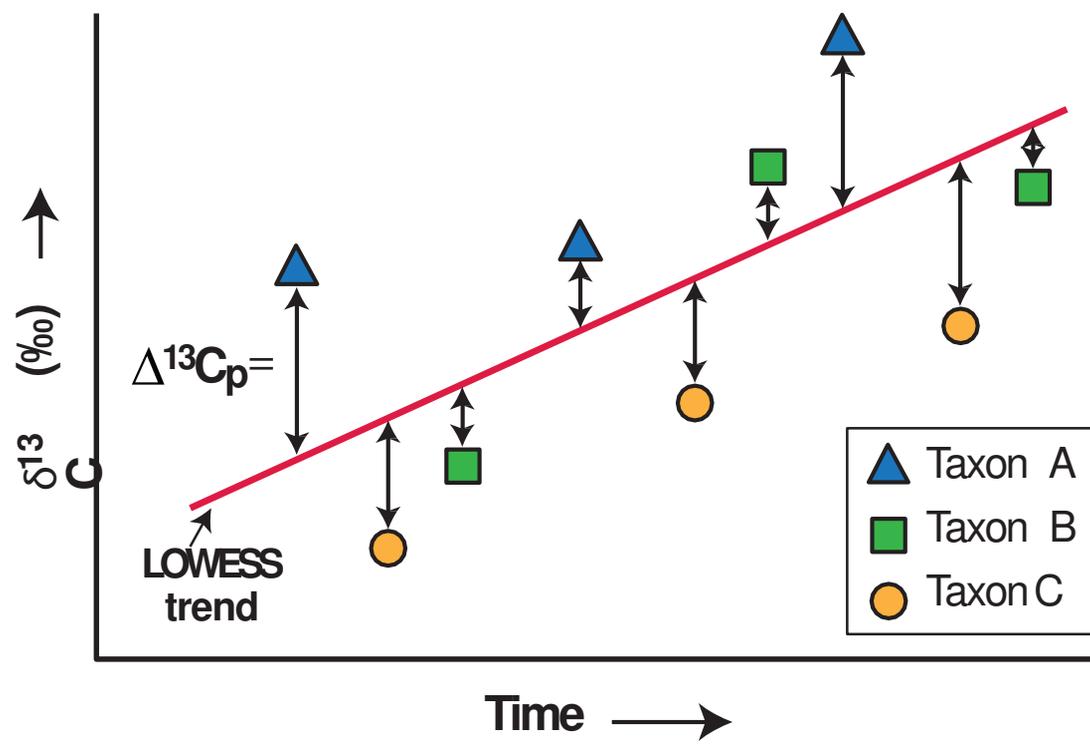


Figure 5

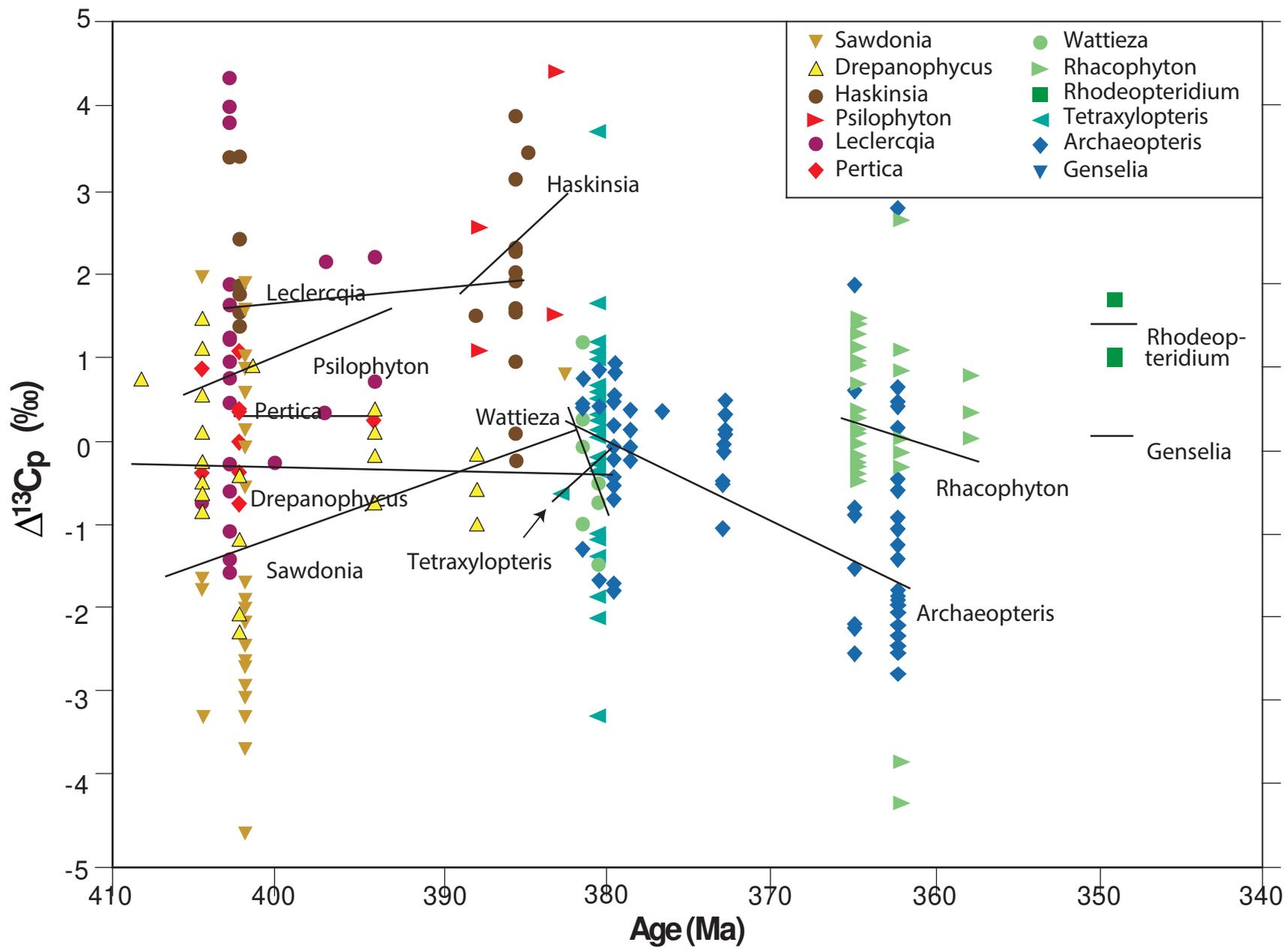


Figure 6

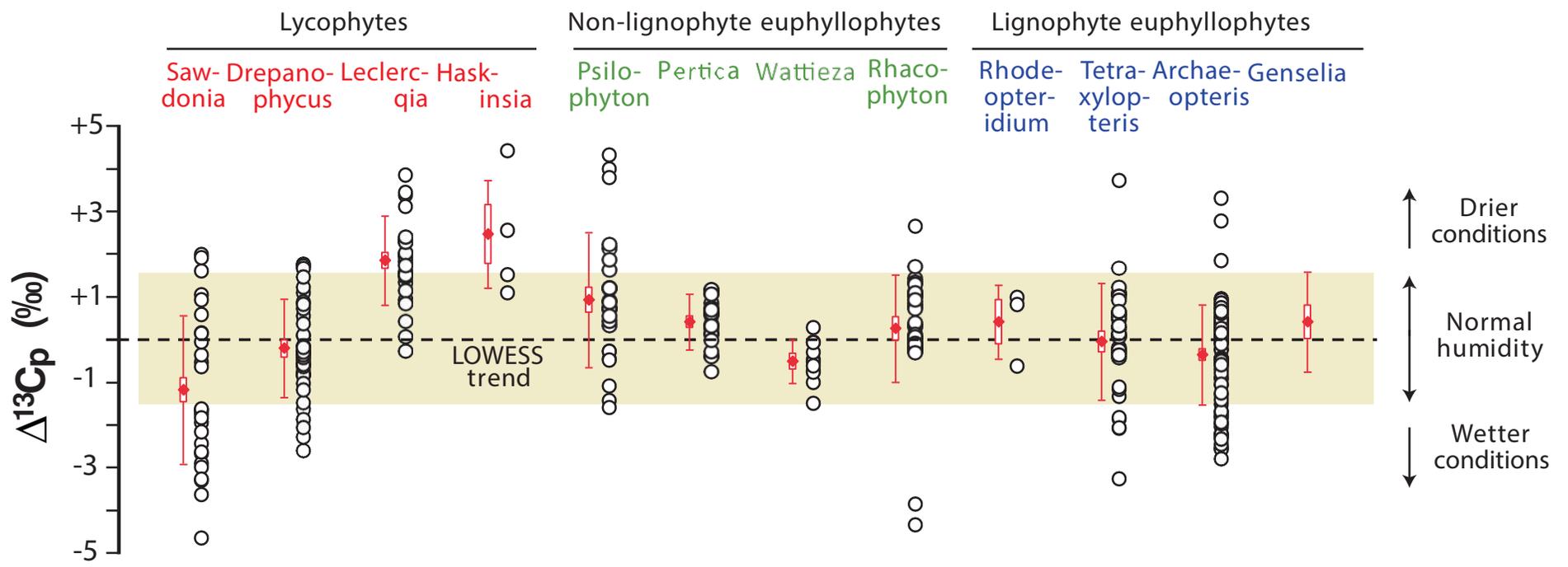
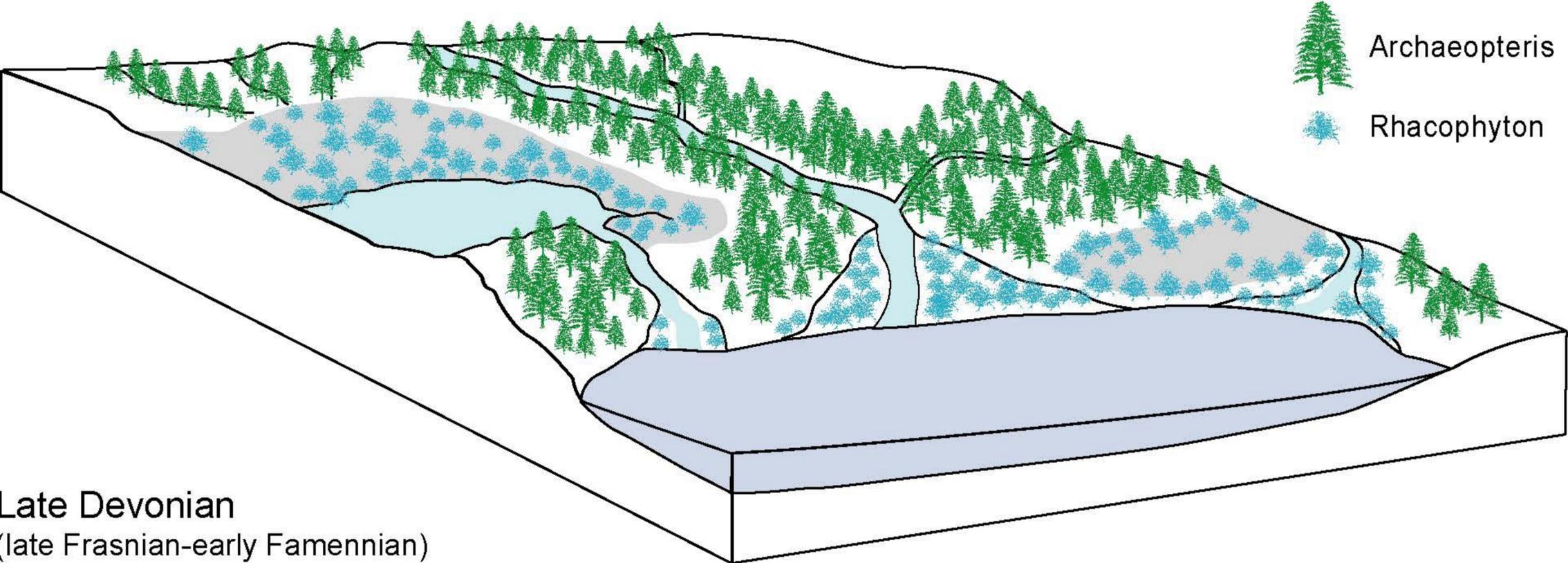
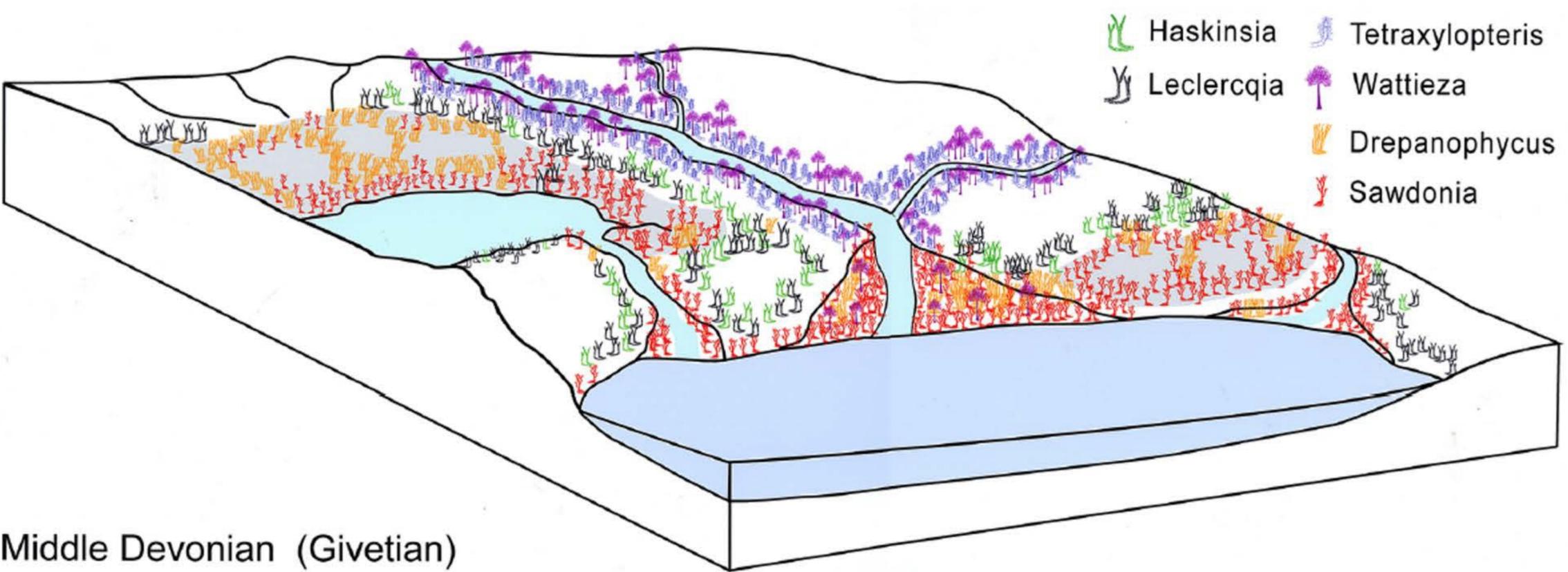


Figure 7



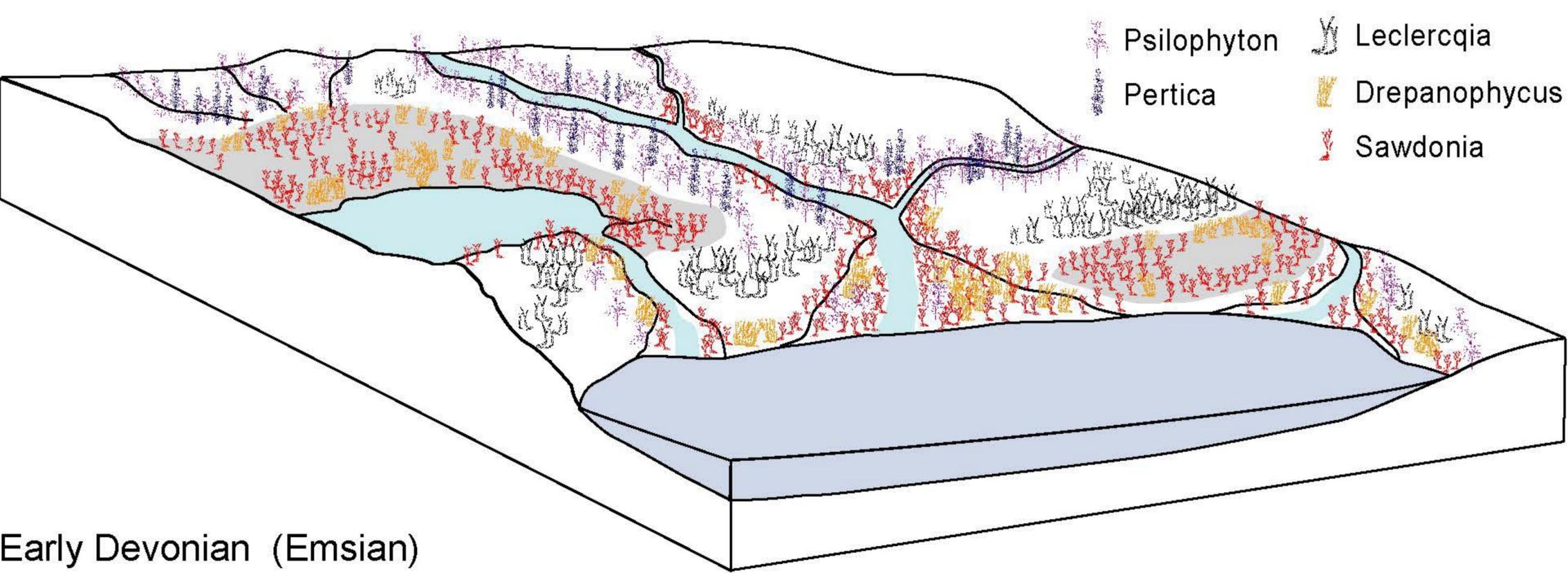
-  Archaeopteris
-  Rhacophyton

Late Devonian
(late Frasnian-early Famennian)



-  Haskinsia
-  Leclercqia
-  Tetraxylopteris
-  Wattieza
-  Drepanophycus
-  Sawdonia

Middle Devonian (Givetian)



-  Psilophyton
-  Pertica
-  Leclercqia
-  Drepanophycus
-  Sawdonia

Early Devonian (Emsian)