

Devonian landscape heterogeneity recorded by a giant fungus

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ABSTRACT

The enigmatic Paleozoic fossil *Prototaxites* Dawson 1859 consists of tree-like trunks as long as 8 m constructed of interwoven tubes <50 mm in diameter. *Prototaxites* specimens from five localities differ from contemporaneous vascular plants by exhibiting a carbon isotopic range, within and between localities, of as much as 13‰ $\delta^{13}\text{C}$. Pyrolysis–gas chromatography–mass spectrometry highlights compositional differences between *Prototaxites* and co-occurring plant fossils and supports interpretation of isotopic distinctions as biological rather than diagenetic in origin. Such a large isotopic range is difficult to reconcile with an autotrophic metabolism, suggesting instead that, consistent with anatomy-based interpretation as a fungus, *Prototaxites* was a heterotroph that lived on isotopically heterogeneous substrates. Light isotopic values of *Prototaxites* approximate those of vascular plants from the same localities; in contrast, heavy extremes seen in the Lower Devonian appear to reflect consumption of primary producers with carbon-concentrating mechanisms, such as cryptobiotic soil crusts, or possibly bryophytes. *Prototaxites* biogeochemistry thus suggests that a biologically heterogeneous mosaic of primary producers characterized land surfaces well into the vascular plant era.

Keywords: *Prototaxites*, terrestrial ecosystems, isotope geochemistry, Paleozoic, paleobotany, paleoecology.

INTRODUCTION

From its origin in the Late Silurian more than 420 m.y. ago until the evolution of large trees ~50 m.y. later, *Prototaxites* was the largest organism known to have lived on land (Fig. 1A; GSA Data Repository Fig. DR1¹). It produced unbranched trunks as long as 8 m and 1 m in diameter, constructed only of a relatively homogenous tissue of interwoven tubes of three size classes, 5–50 μm in diameter (Fig. 1B). Although originally described as a conifer (Dawson, 1859), its distinctive anatomy is utterly unlike any living or fossil land plant. Subsequent interpretations as a lichen, a red, green, or brown alga, or a fungus (Carruthers, 1872; Church, 1919; Jonker, 1979; Hueber, 2001) are also problematic. For example, interpretation of *Prototaxites* as a giant fungal fruiting body (Hueber, 2001) accounts for its hyphae-like anatomy, but remains controversial (e.g., Selosse, 2002) because its sheer size and lack of clear reproductive structures are more difficult to reconcile. The identity of *Prototaxites* may never be proven by anatomy

alone (save for the consensus it was not a vascular plant); its bizarre form is the very source of its enduring interest. Carbon isotopic and organic analyses of *Prototaxites* fossils provide a morphology-independent assessment of its evolutionary relationships and indirect evidence for the nature of its surrounding ecosystem.

The organic composition of fossils can be influenced as much by locality of preservation as by original biology (Abbott et al., 1998), but comparison of multiple specimens within individual localities controls for factors that might influence preserved C isotopic or organic chemistry, including diagenesis and variations in climate, background inorganic $^{12}\text{C}/^{13}\text{C}$, or atmospheric CO_2 concentration (Boyce et al., 2002, 2003). To this end, organic and isotopic comparisons were made between *Prototaxites* and associated vascular plants (two vascular plant-derived coals, silicified *Callixylon*, and carbonate-permineralized *Psilophyton*) within one Upper Devonian and two Lower Devonian localities (ca. 375 Ma and 405–400 Ma, respectively). *Prototaxites* isotopes also were analyzed from two Lower Devonian localities for which no other fossils were associated. Carbon isotopes reflect in part the organism's metabolism. Organic analyses further constrain the risk that isotopic composition was unduly affected by differential taphonomic history within a locality. All *Prototaxites* samples are

¹GSA Data Repository item 2007096, Figure DR1 (photos of *Prototaxites* trunk), Table DR1 (samples and carbon isotopic composition), and Methods, is available online at www.geosociety.org/pubs/ft2007.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

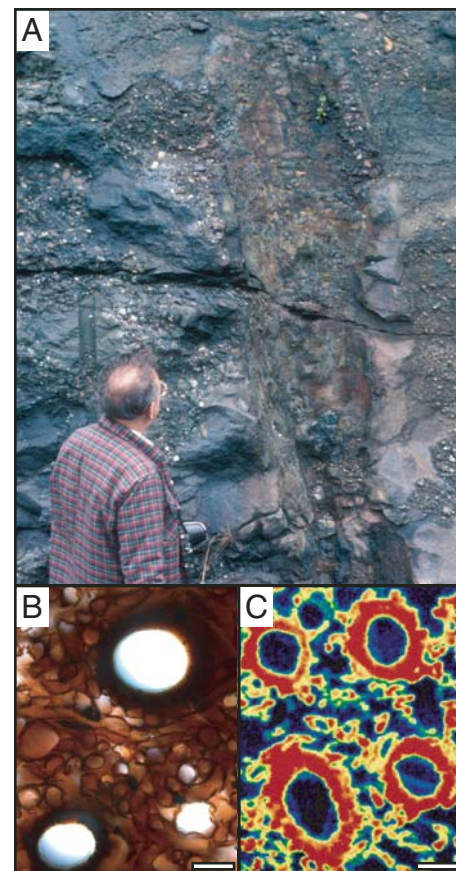


Figure 1. A: Lower Devonian *Prototaxites* fossil in situ, Bordeaux Quarry, Quebec. Approximately 2 m visible of compression fossil. **B:** Optical image of carbon abundance of *Prototaxites* anatomy in cross section. Scale bar = 20 m. **C:** Electron probe map of carbon abundance of *Prototaxites* anatomy in cross section. Scale bar = 20 m. In electron probe map, red indicates high and blue-black indicates low abundance of carbon, qualitatively demonstrating confinement of organic matter to tube walls.

permineralized by silica and preserve anatomy in fine detail, with organic material confined to the tube walls (e.g., Fig. 1C). Samples for isotopic analysis were treated in acid to eliminate any carbonate. Further information concerning samples and methods is in the GSA Data Repository (see footnote 1).

COMPARATIVE GEOCHEMISTRY OF FOSSILS

In the Upper Devonian Kettle Point flora, *Prototaxites* is isotopically similar to the associated woody plant *Callixylon* (and Devonian plants more broadly; Beerling et al., 2002; Boyce et al., 2003), consistent with either a C₃-like photosynthetic organism or a heterotroph that consumed C₃ plants (Fig. 2). In contrast, *Prototaxites* samples from the Lower Devonian (Emsian, ca. 400 Ma) Gaspé south shore flora are either isotopically similar to co-occurring *Psilophyton* and coal or as much as 11‰ heavier. This enormous range is replicated in other Lower Devonian localities: *Prototaxites* isotopes resemble those of C₃ plants at two localities, but are 8‰ heavier than a surrounding coal composed of spiny vascular plant axes at a third locality (Fig. 2).

Molecular structural information derived from pyrolysis–gas chromatography–mass spectrometry of the Gaspé coal (Fig. 3) is consistent with a predominance of lignin-derived geopolymers. The strong prevalence of alkylphenols over dihydroxy aromatics (note trace of eugenol) as well as a complete lack of levoglucosan (a pyrolytic product of cellulose) indicates that the original peat was altered diagenetically to high-rank sub-bituminous to low-rank high volatile bituminous coal. Although Gaspé *Prototaxites* samples also yield predominantly alkylbenzene, alkylphenol, and alkyl-naphthalene moieties, their relative distributions are distinct from the coal and are dominated by alkyl benzenes rather than phenol derivatives. *Prototaxites* and the vascular plant *Callixylon* are similarly distinct at the Upper Devonian locality (Fig. 3). A robust molecular interpretation linking original biochemistry to the specific distribution of molecular species in diagenetically altered material is incomplete even in the well-studied system of vascular plant-derived coal (Hatcher and Clifford, 1997), much less the various potential relatives of *Prototaxites*. However, this consistent predominance of alkyl-phenols versus alkyl-benzenes in organic

matter from the same strata and geologic histories must reflect derivation from biochemically distinct original source organisms.

Extensive taphonomic alteration of organic C isotopic ratios typically involves loss of compounds or constituent functional groups with distinct biosynthetic fractionations (Benner et al., 1987). *Prototaxites* samples spanning a C isotopic range from –15.6‰ to –26.6‰ are all similarly dominated by alkyl benzenes and are clearly differentiated from a local, vascular plant-derived coal, reflecting differences maintained from their original biochemical inheritance. Any extreme and divergent taphonomic modification between specimens—such as methanogenic decay of some, but not all of the individuals—also should have been reflected in the final organic composition, but is not seen. This, along with the uniformly high quality of anatomic preservation, argues that isotopically distinct populations record underlying features of original physiology, not differential taphonomy.

BIOLOGICAL AFFINITY OF PROTOTAXITES

For each *Prototaxites* sample, photosynthetic organisms with similar isotopic discriminations can be identified: lighter values are consistent with terrestrial C₃ photosynthesis and heavier values are consistent with various groups with carbon-concentrating mechanisms. Nonetheless, the overall isotopic range of the *Prototaxites* population is difficult to reconcile with autotrophy. C₄ and crassulacean acid metabolism plants concentrate carbon, but in neither does isotopic variation resemble that of *Prototaxites* (O’Leary, 1988). Macrophytic marine algae can accommodate a larger range of values (Raven et al., 2002), but *Prototaxites* is usually preserved in terrestrial deposits (Griffing et al., 2000; Hotton et al., 2001), and both ecological and geochemical arguments suggest that it was subaerial (Niklas, 1976; Edwards and Richardson, 2000; Hueber, 2001). Moreover, the broad

isotopic spread of algae is related to variations in inorganic carbon source—ranging from HCO₃⁻ pumping to aqueous diffusion of CO₂—unlikely to be encompassed by a single population, particularly of large terrestrial organisms.

Both CO₂ limitation and a shift in background inorganic ¹³C/¹²C could result in more enriched values within an organism, but neither was likely in a Lower Devonian world with an atmospheric CO₂ concentration of 8–10 times modern levels (McElwain and Chaloner, 1995) and C isotopic values of 0‰ to +2‰ for marine carbonates (Veizer et al., 1999), and neither could explain observed isotopic variation within a single assemblage. Rather, the large C isotopic range measured for Lower Devonian *Prototaxites* strongly suggests that this organism was a heterotroph that lived on isotopically distinct substrates: in this context, a fungus. Given its survival of fluvial transport and deposition (Griffing et al., 2000), *Prototaxites*, if fungal, was more akin to a robust, perennial bracket fungus than an ephemeral mushroom.

EARLY DEVONIAN ECOSYSTEMS

The isotopic range of Lower Devonian *Prototaxites* is difficult to reconcile with consumption of a uniform photosynthetic substrate. Lower Devonian terrestrial faunas were vertebrate free and consisted primarily of arthropod detritivores and predators (Shear and Selden, 2001), so trophic enrichment is an unlikely source for variation. Substantial isotopic distinctions between fungi growing on the same substrate could result from digestion of different biochemical components (Hobbie et al., 1999), such as cellulose versus lignin—as in brown and white wood rots. However, most Devonian fungi are small and contained within the host (Taylor et al., 2004) and only white rot is known among the larger fungi capable of extensive translocation (Stubblefield and Taylor, 1988). Furthermore, distinct saprophytic metabolisms are typically employed by different higher-level fungal lineages (Eriksson et al., 1990), not different individuals of the same population. Even if distinct metabolisms were assumed for *Prototaxites* individuals, 4‰–8‰ would be the maximum expected isotopic range for degradation of distinct plant components (Benner et al., 1987), not the 11‰ seen among Gaspé specimens.

Depleted *Prototaxites* isotopic values are consistent with consumption of C₃ land plants, but enriched Early Devonian specimens require consumption of autotrophs with a carbon-concentrating mechanism. All CAM and C₄ plants appeared long after the Devonian. Terrestrial lichens have intermediate C isotope discrimination, whether with chlorophyte or cyanobacterial symbionts, and are not consistent with enriched *Prototaxites* values (Jahren et al.,

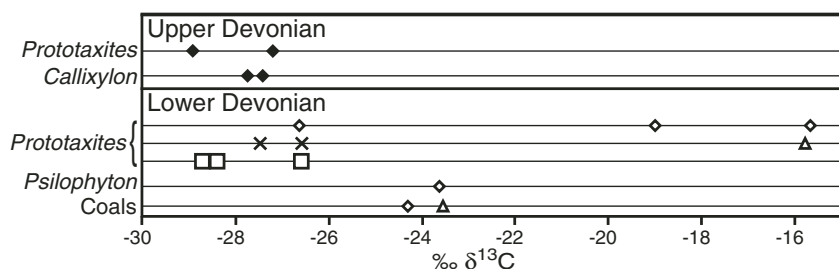


Figure 2. Carbon isotopic values for *Prototaxites* and associated vascular plants *Callixylon* and *Psilophyton* and coal. Upper Devonian fossils are from Kettle Point, Ontario (Frasnian–lower Fammenian). Lower Devonian (primarily Emsian) fossils are from south shore of Gaspé Peninsula, Quebec (diamonds), north shore of Gaspé Peninsula (squares), Baxter State Park, Maine (Xs), and Pin Sec Point, New Brunswick (triangles). Each symbol represents average of two samples from single specimen. Based on acetanilide standards, analytical error associated with each measurement is ±0.2‰. Details in Table DR1 (see footnote 1).

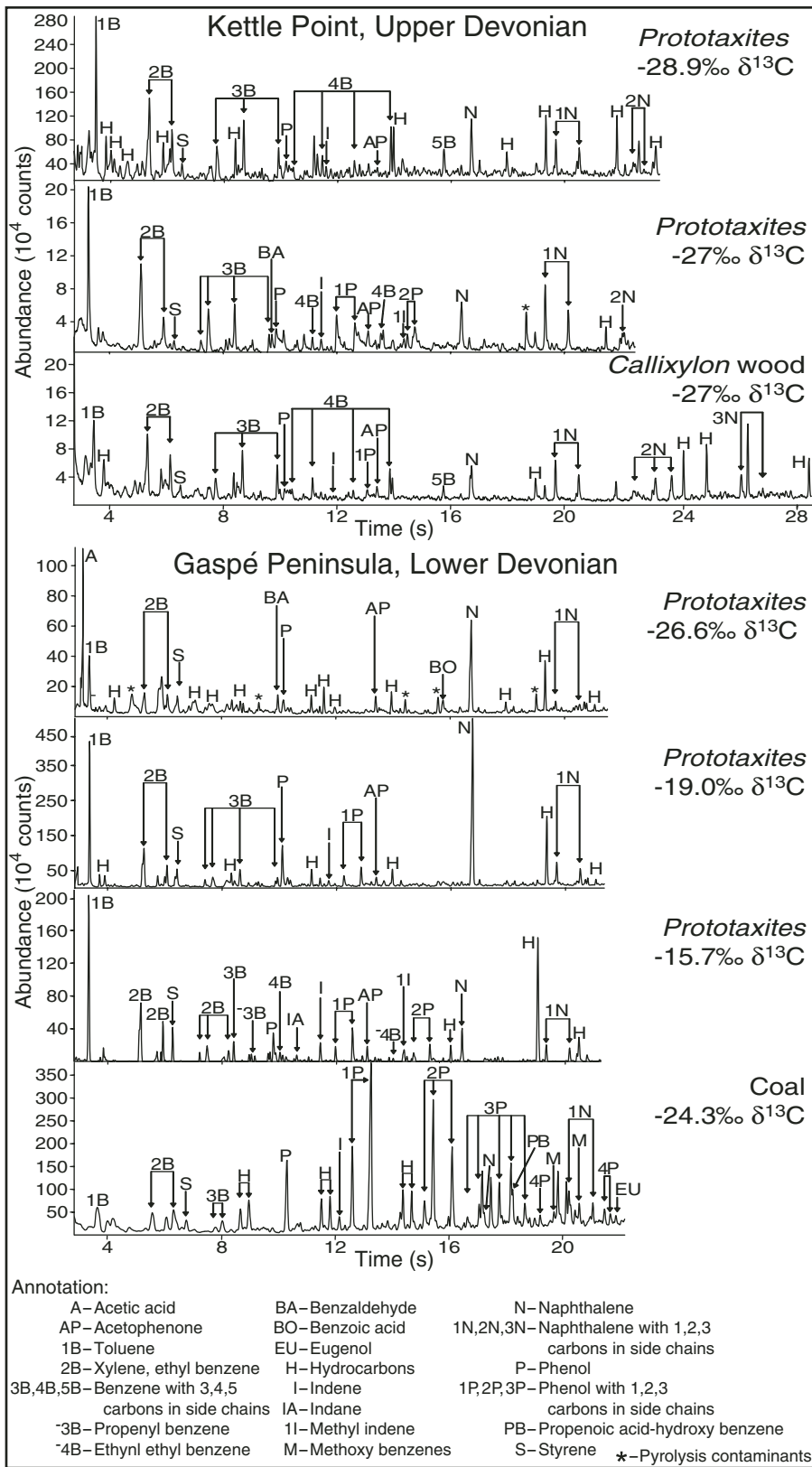


Figure 3. Stacked gas chromatography–mass spectrometry (GC-MS) chromatograms of pyrolysate (plotted as total ion count vs. retention time) of Lower Devonian Gaspé and Upper Devonian Kettle Point samples. Identities of various molecular groups are highlighted and annotated in legend. Labeled contaminants are polydimethyl siloxane products resulting from reaction of HCl released from pyrolyzed minerals with various internal septa of GC-MS; they could not have contributed to isotopic measurements because they are not present in original samples.

2003; Fletcher et al., 2004). Most bryophytes are even more depleted than C_3 tracheophytes (Jahren et al., 2003; Fletcher et al., 2004), but the enriched *Prototaxites* values can be approached by some hornworts when water saturated due to a pyrenoid-based carbon-concentration mechanism (Smith and Griffiths, 1996). Hornworts are unknown before the Cretaceous, but stem-group embryophytes in general extend back at least to the Ordovician (Gray, 1993; Edwards et al., 1995; Wellman et al., 2003).

Enriched *Prototaxites* isotopic values are broadly consistent with consumption of cyanobacteria-dominated microbial soil crusts (Evans and Belnap, 1999). Moreover, mats can be prolific sources of sugars, a preferred substrate for fungal growth that tends to have ^{13}C enriched relative to total biomass (van der Meer et al., 2003). Today, microbial crusts and bryophytes dominate only where vascular plants are excluded (Campbell, 1979; Evans and Belnap, 1999), but they were likely distributed broadly prior to vascular plant evolution (Horodyski and Knauth, 1994; Tomescu and Rothwell, 2006). These alternative sources of primary production are rarely considered for ecosystems that postdate the Silurian appearance of vascular plants, except for some mention of intercalation among vascular plant dominants and debate over how rapidly vascular plants spread from wet lowland environments (Griffing et al., 2000; Edwards and Richardson, 2004). Sedimentology may constrain this transition (Retallack, 1985; Love and Williams, 2000), but the overall narrative is driven by a megafossil record dominated by vascular plants, rather than any positive evidence for displacement of other primary producers. Given prodigious nutrient translocation in fungal mycelia (Boswell et al., 2002), consumption of a substrate consisting of soil crusts intercalated between vascular plants would result in a *Prototaxites* of an averaged intermediate isotopic composition, as would an ephemeral cyanobacterial scum before vascular plants are reestablished after disturbance. Instead, enriched *Prototaxites* values suggest a strict absence of C_3 photosynthesis in persistent, spatially contiguous landscape patches (perhaps quite large given the potential of modern fungi; Smith et al., 1992). One-third of our upper-Lower Devonian *Prototaxites* specimens provide an isotopic record of heterotrophic growth on a nonvascular, non- C_3 substrate, 30–40 m.y. after the Silurian appearance of vascular plants, sampling communities that otherwise would have little chance of fossil preservation. Isotopic analysis of terrestrial arthropods may provide independent evidence for varied sources of Devonian primary production and, together with further sampling of *Prototaxites*, may reveal changing patterns of substrate use through time.

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