



# Morphology, anatomy, and upland ecology of large cordaitalean trees from the Middle Pennsylvanian of Newfoundland

Howard J. Falcon-Lang<sup>a,\*</sup>, Arden R. Bashforth<sup>b,1</sup>

<sup>a</sup>Department of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK

<sup>b</sup>Department of Earth Sciences, Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1B 3X5

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## Abstract

We describe the morphology and anatomy of large cordaitalean trees, preserved in Pennsylvanian (Bolsovian) alluvial deposits in southwest Newfoundland. Remains include more than one hundred calcite-permineralized stumps, trunks, and branches, including the largest cordaitalean trunk ever discovered, as well as common adpressed leaves. Reproductive organs are not preserved. We propose a sterile reconstruction of this tree based on directly attached organs and anatomical similarities between isolated, but facies-associated, organs. At  $\leq 48.5$  m high, mature cordaitaleans were the tallest trees in the Pennsylvanian tropical zone, and consisted of a straight, unbranched trunk topped by a dark, shading canopy, similar in gross morphology to extant araucarian conifers. A comprehensive review of the taphonomic occurrences of these large cordaitalean remains suggests that they grew in alluvial fan and extrabasinal terrains across Euramerica, and represent the earliest widespread upland forests.

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## 1. Introduction

The Cordaitales is an extinct gymnosperm order, closely related to the conifers, characterized by strap-shaped, coriaceous leaves, pycnoxylic wood, axillary branching, and platyspermic seeds (Rothwell, 1988).

The group formed a significant component of the tropical vegetation of Euramerica and Cathaysia between latest Mississippian and Permian times (DiMichele and Phillips, 1994; Wang et al., 2003; Falcon-Lang, 2005a). Studies of stem anatomy (Trivett and Rothwell, 1988; Trivett, 1992) and especially leaf cuticular morphology (Šimůnek, 2000; Zodrow et al., 2000) suggest that tropical Cordaitales were a highly diverse group (Trivett and Rothwell, 1991).

Four Pennsylvanian mire-dwelling cordaitaleans, preserved in Euramerican coal balls, have been reconstructed as whole plants. *Pennsylvanioxydon birame*

\* Corresponding author.

E-mail address: [howard.falcon-lang@bris.ac.uk](mailto:howard.falcon-lang@bris.ac.uk)  
(H.J. Falcon-Lang).

<sup>1</sup> Present address: Department of Earth Sciences, Dalhousie University, Halifax, Nova Scotia, Canada B3H 3J5.

(Baxter) *Costanza* was a c. 5 m high tree with stilt roots (Cridland, 1964; Costanza, 1985), one variety occupying putatively brackish substrates with another favouring freshwater settings (DiMichele and Phillips, 1994). A second species, *P. nauertianum* (Andrews) *Costanza* was a scrambling shrub that occupied freshwater mires (Rothwell and Warner, 1984; Costanza, 1985; Rothwell, 1993). Two further plants, *Mesoxylon priapi* Trivett and Rothwell and *Cordaixylon iowaensis* (Wilson and Johnson) Trivett, were also shrubs or small trees, and occupied similar habitats (Trivett and Rothwell, 1985; Trivett, 1992). A fifth cordaitalean, *Shanxioxylon sinense* Tian and Wang reconstructed from Lower Permian coal balls from the Cathaysian realm, was a small mire-dwelling tree (Wang et al., 2003).

In contrast, abundant remains of much larger cordaitalean trees (permineralized trunks  $\leq 22.15$  m long and  $\leq 1.46$  m in diameter) have been found in fluvial channel facies since the early nineteenth century (Winch, 1817; Lindley and Hutton, 1831; Witham, 1831; Black, 1837; Dawes, 1845; Dawson, 1846). These fluvial assemblages clearly represent an archi-

tecturally distinct cordaitalean species, or group of species, with different ecological preferences to the smaller mire taxa. Early taphonomic studies indicated an upland (extrabasinal) habitat for these plants (Dawson, 1853), which were later reconstructed as 20–30 m high trees with a straight, unbranched trunk (Grand'Eury, 1877). These conclusions have been supported by more recent research (Falcon-Lang and Scott, 2000).

One of the most important, yet poorly studied, fossil assemblages containing large cordaitalean trunks is located in southwest Newfoundland (Fig. 1), and was first discovered in the late nineteenth century (Murray and Howley, 1881; Dawson, 1891). We have previously given a brief overview of this site (Falcon-Lang and Bashforth, 2004), and in this current paper, give further details about the geological context, morphology, and anatomy of the cordaitalean assemblage, resulting in a sterile whole plant reconstruction. We also review the taphonomic occurrence of large cordaitalean trunks across Euramerica, and demonstrate more clearly than before, that these trees forested the upland environments of the Pennsylvanian tropical zone.

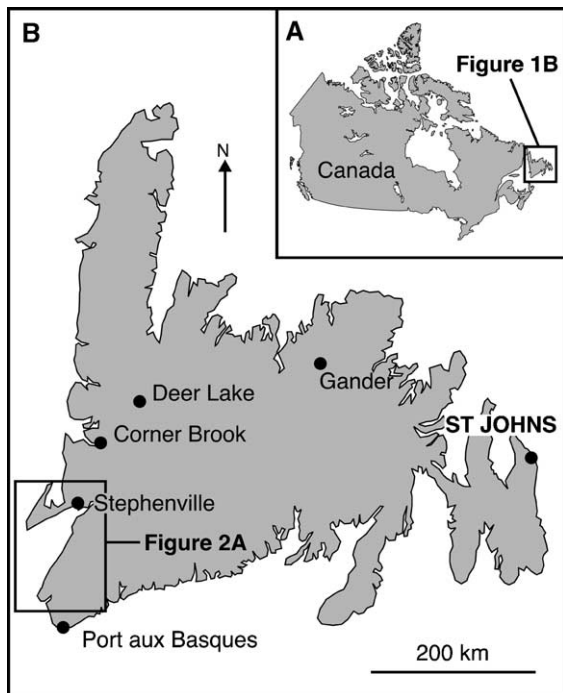


Fig. 1. Location details of study area; (A) Canada, (B) Newfoundland.

## 2. Geological setting

The fossils occur in the uppermost stratigraphic unit of the c. 4000-m-thick Barachois Group of southwest Newfoundland (Knight, 1983), which was deposited in the Bay St. George Basin (Fig. 2A; Hyde, 1995). The Barachois Group awaits complete stratigraphic description. The Searston Formation has been erected for a lower unit comprising alluvial fan and alluvial plain deposits, but to date upper lithostratigraphic intervals are referred to as the 'undivided Barachois Group' (Knight, 1983). This undivided succession crops out in two outliers (10 km and 25 km in diameter; Fig. 2A), which probably represent erosional remnants of coarse-grained alluvial strata deposited prior to the final inversion of the Bay St. George Basin (Hall et al., 1992).

Cordaitalean remains occur in the younger and smaller of these outliers, located near Stephenville, on the northwest margin of the Bay St. George Basin (Fig. 2B). This succession, informally termed the 'Blanche Brook formation,' is of Middle Pennsylvanian

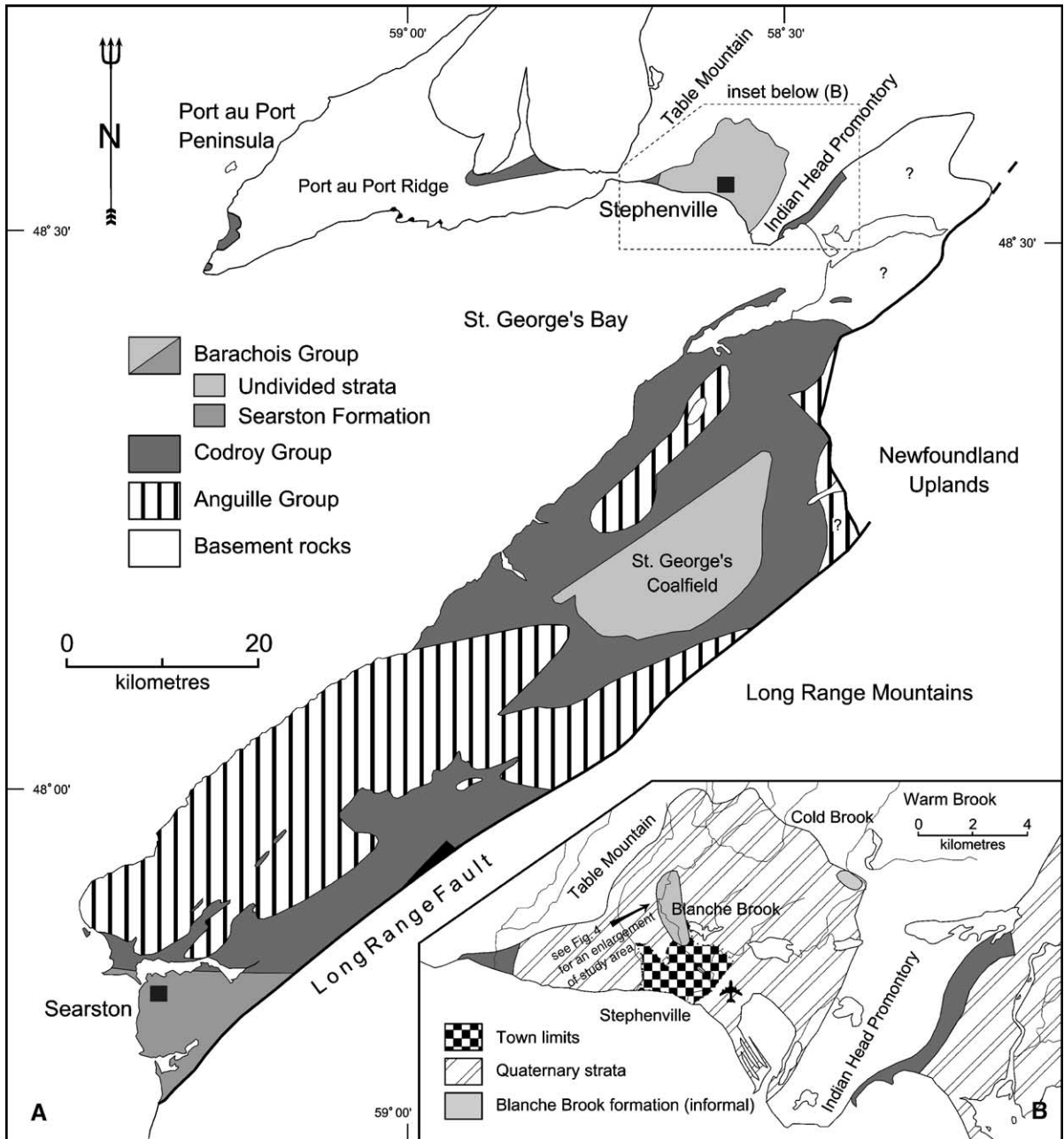


Fig. 2. Geological setting: (A) geological map of the Upper Palaeozoic Bay St. George Basin of SW Newfoundland (after Knight, 1983; Hyde, 1995), (B) detailed geology map of the Stephenville outlier that contains the cordaitalean material studied in this paper.

nian (late Bolsovian) age based on megafloral and palynofloral assemblages (Fig. 3; Hyde et al., 1991; Bashforth, in press). The only major exposure is along a 20–50 m wide gravel streambed (Blanche Brook),

beginning within Stephenville (UTM 83757875, Map Sheet 12B/10) and ending at a location 4.7 km (measured along the sinuous stream bed) north of the town (UTM 831819). A second, minor outcrop is located

Chronozones		Lithostratigraphy Bay St. George Basin (Knight 1983)	Lithostratigraphy Maritimes Basin (Gibling 1995)
Early Permian		SW	NE
Pennsylvanian	Stephanian		Pictou Group
	Westphalian	Westphal. D	Cumberland Gp. (=Morien Gp. in Sydney Basin)
		Bolsovian	
		Duckmantian	
		Langsettian	
Namurian	Searston Formation?	Mabou Group	
Mississippian	Viséan	Codroy Group	Windsor Group
	Tournaisian	Anguille Group	Horton Group
	Devonian (part)		

Fig. 3. Stratigraphy of Upper Palaeozoic basins in Eastern Canada. Highlighted units comprise the Barachois Group of Newfoundland (Gibling, 1995).

along Warm Brook, close to the unconformity with the Cambrian Kippens Formation, between UTM 8988155 and 896818 (Map Sheet 12B/9). Although the general location of this outcrop was previous mapped (Riley, 1962; Knight, 1983; Williams, 1985), its exact position is now more accurately constrained (Fig. 2B).

### 3. Sedimentary facies and plant assemblages

At both localities, beds dip shallowly, outcrop is discontinuous and only a few, 1–6 m high, vertical

outcrops occur; most of the outcrop is along the stream floor, sub-parallel to the bedding surfaces. Although the nature of this outcrop facilitates the widespread exposure of the cordaitalean remains, it makes accurate measurement of section thickness and sedimentary facies analysis difficult.

#### 3.1. Warm Brook section

The c. 45-m-thick Warm Brook succession is positioned <200 m downstream from the present basin margins. It consists of metre-scale lenses of brown, polymictic, clast-supported, pebble to cobble conglomerate with sub- to well-rounded igneous and metamorphic clasts. Conglomeratic lenses fine upwards and may contain weak stratification defined by centimetre-thick layers of green/grey, medium- to very coarse-grained, pebbly sandstone. A single calcite-permineralized cordaitalean trunk occurs within one conglomerate unit.

#### 3.2. Blanche Brook section

The c. 115-m-thick succession along Blanche Brook is positioned >3 km downstream from the present basin margins. It contains up to 4-m-thick units of pebbly, medium- to very coarse-grained, lithic sandstone (Fig. 4). These coarse units have sub-horizontal erosive bases over tens of metres, contain trough cross-beds and plane bedding, and fine upwards into medium-grained sandstones. Trough cross-beds indicate a widely variable palaeoflow with a southwest mode ( $n=196$ ). At one site, a c. 2-m-thick package of low-angle strata was observed, orientated sub-perpendicular to the local palaeoflow (as indicated by trough cross-beds). At a second site, ridge and swale topography was observed on top of another sandstone body.

Metre-sized, calcite-permineralized cordaitalean trunks, branches, and stumps are abundant in approximately eleven channel bodies in the succession. They occur throughout the sandstone bodies, but are particularly abundant near the bases. Most (77.1%) of the trunks are sub-horizontal (<10°) relative to stratigraphic dip; however, some trunks rest at higher angles (typically 20–30°, but locally up to 86°), including one stump that was deposited upright. The orientation of the long-axis of the trunks is widely

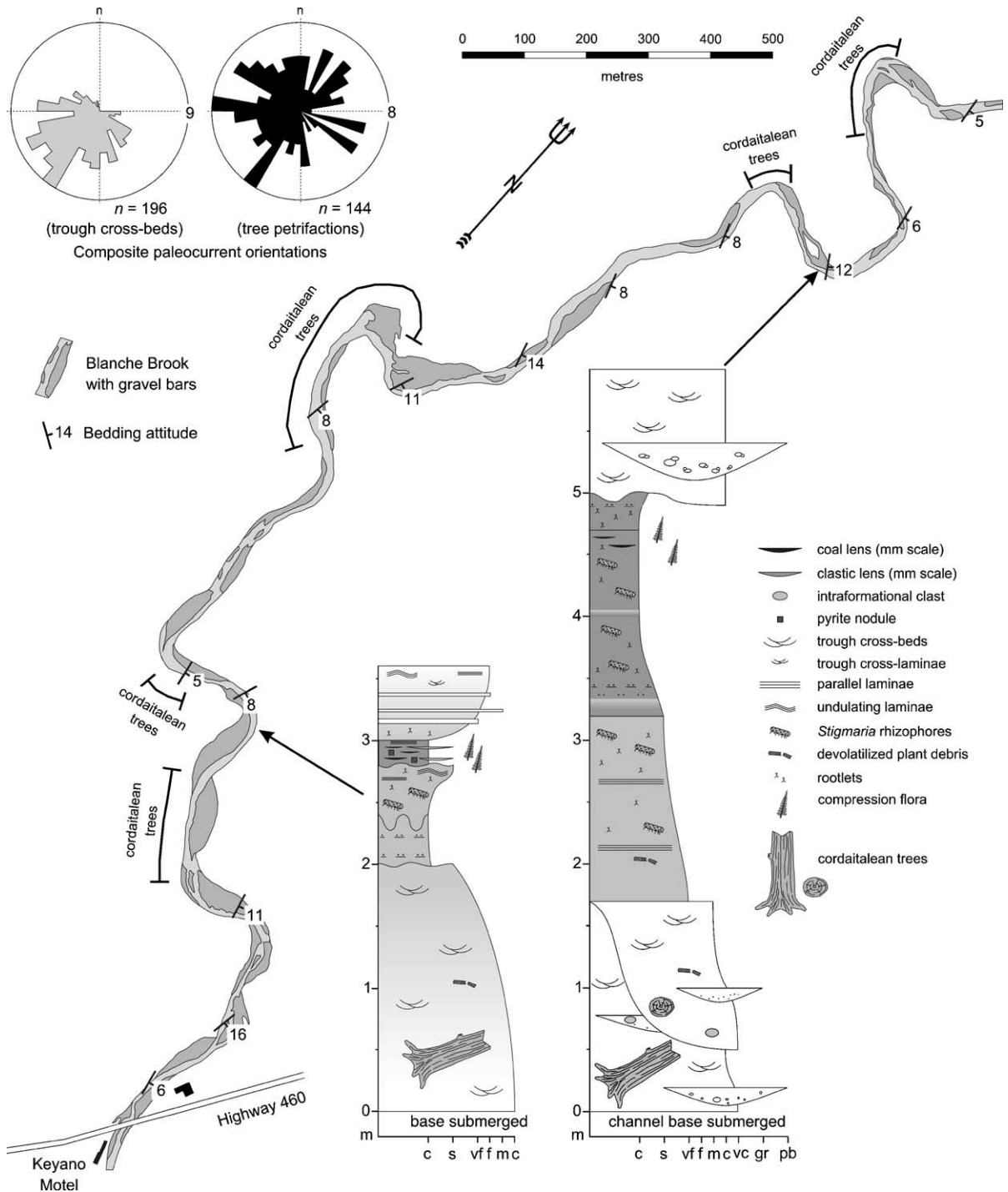


Fig. 4. Map of the Blanche Brook stream section showing sedimentary logs for two representative outcrops, and the main cordaitalean localities. Rose diagrams show palaeocurrent data for trough cross-beds in the alluvial channels, and orientation data for the cordaitalean trunks.

variable, although many trees preferentially dip upstream or perpendicular to the regional southwesterly palaeoflow (Fig. 4). At a few sites, cordaitalean trunks occur in very high densities (e.g., 13 metre-sized trunks in  $3 \times 4$  m area), lack any localized preferred orientation, and contain many specimens disposed at high angles. At another site, trunks are oriented sub-parallel to ridge and swale topography. Facies-associated plants include *Artisia*, *Cordaites*, *Cordaicladus*, *Calamites* and *Sigillaria*.

The upper portions of fining-upward successions comprise dominantly grey, rooted mudstone/siltstone units up to 2.5 m thick. At two stratigraphic levels, these fine-grained deposits contain thin coal seams, 3 cm and 12 cm thick (Hyde et al., 1991), which are laterally discontinuous over a few tens of metres, contain common clastic splits, and have very high ash (19–34%) and sulphur (6.3%–10.5%) contents. These beds contain a rich compression flora (46 morphospecies) comprising lycopsids, sphenopsids, ferns, pteridosperms, and cordaitaleans (Bashforth, in press). Locally mudstone beds may be red or mottled red/grey and unfossiliferous.

### 3.3. Palaeoenvironmental interpretation

The succession is interpreted as an alluvial plain deposit that accumulated in an intramontane basin distant from marine influence, presumably on the elevated margin of the Laurentia–Greenland craton (Ziegler, 1988). Clast-supported conglomerate units at Warm Brook are interpreted as high-energy sheet-flood deposits, proximal to the basin margins. In the Blanche Brook section, coarse-grained sandstone units are interpreted as alluvial channel deposits, fine-grained units representing floodbasin facies. Channels were locally sinuous as indicated by low-angle strata dipping perpendicular to palaeoflow and ridge and swale structures. These features represent lateral accretion surfaces formed by point bar migration and scroll bar deposits superimposed on the point bar by fluctuating discharge conditions (Nanson, 1980). Channel sinuosity is also indicated by the sub-horizontal nature of the channel bases over tens of metres (implying lateral cut-bank erosion), and the considerable spread of palaeoflow data (cf. Nami, 1976). The coarse sediment grade at Blanche Brook and especially at Warm Brook indicates high-energy conditions, with

sediment being shed from an elevated regions beyond the confines of the c. 10 km wide basin.

Cordaitalean remains are allochthonous, including one upright stump, interpreted as being deposited in its most hydrodynamically stable orientation (cf. Fritz, 1980). The common occurrence of stumps bearing roots (28.3% of all specimens) indicates that trees may have entered the alluvial channels by lateral cut-bank erosion (Ash and Creber, 2000), which gradually freed roots from the floodbasin soils. Most woody debris became waterlogged, sank, and was buried by migrant megaripples near the channel thalwegs, while a few other buoyant specimens became stranded on the upper point bar surfaces during times of fluctuating discharge (Nanson, 1981). The absence of preferred trunk orientation to palaeoflow is typical for fluvial channel systems (Gastaldo, 2004). Very dense, randomly oriented trunk accumulations may represent log-jams that formed as coarse woody debris periodically blocked the channels (Keller and Swanson, 1979).

Fine-grained units between channel sandstone beds are interpreted as the deposits of narrow, densely vegetated, inter-channel floodbasins, within which localized lycopsid peat mires periodically established. The high ash content and dominance of sigillarian palynomorphs within the coals (Hyde et al., 1991) indicate flood-disturbed mire conditions (Smith, 1962; DiMichele and Phillips, 1994). At other times, floodbasin soils were well-drained as indicated by red, oxidized units.

## 4. Material and methods

The fossil assemblage hosted in the fluvial channel facies was analyzed to produce a whole plant reconstruction of the large cordaitalean trees. Although this material is allochthonous in several channel deposits formed over a period of time, morphological and anatomical data (see below) indicate that probably only one cordaitalean species is present. Trunks of widely varying sizes, but uniform cellular anatomy, are interpreted as representing trees of different ages. However, given that woods lack annual growth rings, this assumption cannot be confirmed.

In total, the morphology of 127 calcite-permineralized fossils was quantitatively studied. Complete

description was hindered by localized burial in modern fluvial gravel, and occasional submergence in up to 10–70 cm of fast-flowing water. A photographic record of key fossils is provided where possible, but the morphology of a few permanently submerged specimens is illustrated with line drawings (based on underwater photographs and field sketches). Due to their large size, only small hand samples were collected, but their context in the overall fossil was recorded. These are archived in the Geology Museum of the University of Bristol Earth Science Department, UK (BRSUG 27196-27197).

The cellular anatomy of ten well-preserved tree specimens was studied using petrographic thin sections prepared along standard radial longitudinal (RLS), tangential longitudinal (TLS), and transverse (TS) sections, and imaged using a Nikon Opti-Phot microscope with a Nikon E5000 digital camera system. To investigate intra-tree variability (Falcon-Lang, 2005b), the anatomy of juvenile and mature trunk woods, and root woods was studied separately. In modern tree trunks, the juvenile–mature transition is identified using mechanical and anatomical indicators not applicable to fossil studies (Lee and Wang, 1996), but is typically located between the twentieth and fortieth annual growth increment, depending of species. As our cordaitalean woods do not contain annual growth rings, woods from the inner 5 cm of the trunk were defined as juvenile, and those from >40 cm from the trunk centre were defined as mature. Root woods were collected directly from attached roots. Thin sections are stored in the Provincial Museum of Newfoundland (NFM F-433 to F-452).

Three specimens of charred wood were also studied, their mode of preservation being recognized by their black colour, high reflectance, sooty streak, cubic morphology, and exquisitely preserved anatomy. These were washed in dilute HCl for 1 day, and 40% HF for 7 days, to remove mineral matter, and allowed to dry, before being gold coated, and studied using a Hitachi S-3200 Scanning Electron Microscope housed at the NRC Institute of Marine Biology in Halifax, Nova Scotia. Due to their fragile nature, they have not been archived in a formal repository.

Finally, a few compressed cordaitalean leaves, and compressed/sandstone-cast cordaitalean branches were also studied. Leaf cuticles were macerated for 2–8 h in a solution of 70% HNO<sub>3</sub> and 2–5 g KCl,

treated with 4.5% ammonium hydroxide, and viewed with transmitted light microscope. Specimens are stored at the Geological Survey of Canada, Ottawa (GSC 125271) and the University College of Cape Breton, Palaeobotanical Collection (CBM B34c1(3), CBM.997-294-1014).

## 5. Morphology of calcite-permineralized fossils

The morphology of the calcite-permineralized cordaitalean specimens was studied to elucidate tree architecture (Falcon-Lang and Bashforth, 2004). Due to their large size, most specimens consist of multiple attached organs, and two groups could be identified. Specimens representing the lower parts of the tree consist of stumps that locally exhibit an attached rooting system and/or a basal trunk up to 7 m in length ( $n=36$ ). Specimens representing the upper parts of the tree consist of straight trunk fragments, up to 7.55 m in length, that locally exhibit lateral branches, but lack an attached stump ( $n=91$ ).

Enclosing strata have been shallowly buried (vitrinite reflectance: 0.45–0.63%; Hacquebard and Donaldson, 1970; Hyde et al., 1991), and all calcite-permineralized specimens have undergone some compression. The degree of compression was ascertained by calculating the ratio between trunk diameter along orientations normal and parallel to the inferred compression direction (Fig. 5). Values ranged from 0 to 86% (mean: 49.5%;  $n=110$ ), but thin section analysis showed that compression was mostly accommodated by tracheid crushing/squashing in the compression-parallel plane. Consequently, field measurements of trunk diameter in the normal direction are probably closely similar to the original, pre-compression trunk diameter, a conclusion supported by experimental studies (Rex and Chaloner, 1983).

### 5.1. Stumps

Stump specimens are identified by their pronounced basal flare, and in 77.7% of the 36 examples, by attached rooting systems (Fig. 6A–F). Stumps range between 22 and 192 cm in diameter (mean: 79.16 cm;  $n=36$ ) at the point of maximum flare (measured immediately above the locus of root departure), and between 16 and 117 cm (mean: 46.56 cm;

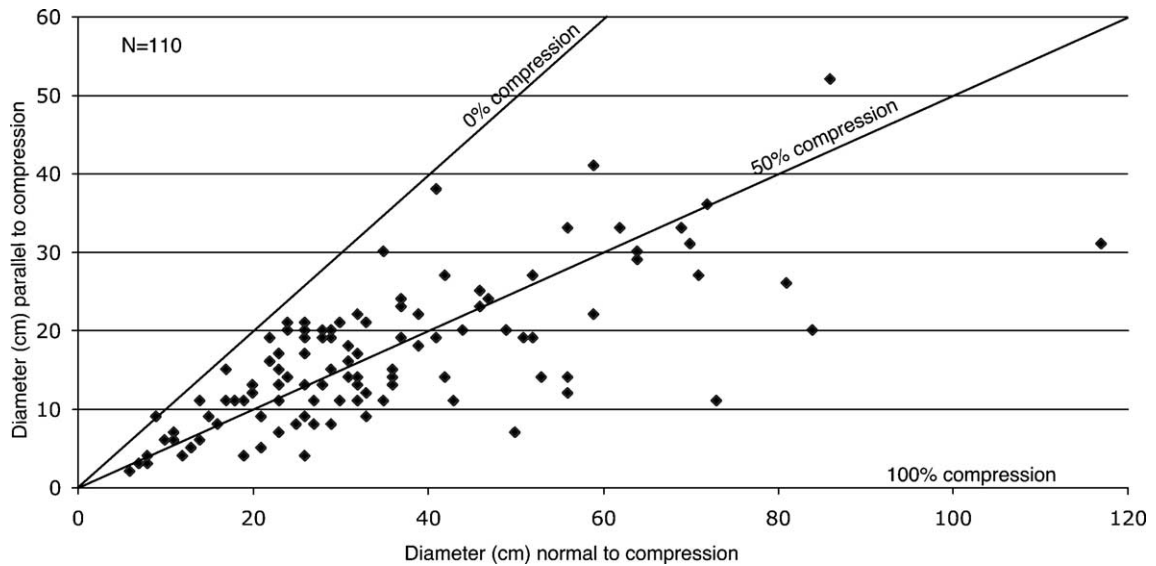


Fig. 5. Scatter graph illustrating the degree of cordaitalean trunk compression.

$n=25$ ; Fig. 7A) when measured at the height at which the sides of the trunk became parallel (equivalent to, and referred to hereafter as, the diameter at breast height [DBH]). Basal stump flare increases linearly with DBH ( $R^2=0.57$ ;  $n=36$ ) so that small stumps are less flared than large stumps. The proportional increase in basal stump flare relative to DBH appears to be approximately constant despite great variability.

Wood in small stump specimens ( $DBH \leq 40$  cm) is characterized by tracheids that are dominantly oriented parallel to sides of the trunk. In contrast, in the largest specimens, a “ropy structure” is commonly developed, defined by zones of tracheids that are contorted along their length. In addition, transversely oriented wrinkles (compression bands) occur in basal stump regions of very large specimens, especially at the point where major roots depart from the stump. Both these features are seen in mature stumps of modern and ancient trees (Ash and Creber, 2000) and are formed by stump expansion across the angular discordance at the trunk–root transition.

The smallest stumps ( $DBH \leq 25$  cm) exhibit a broad *Artisia* pith cavity, which tapers from 41–50 mm in diameter at the stump base to 21–22 mm in diameter, 25 cm higher up the tree trunk. The pith cavity of these specimens shows very widely spaced septa; the basal septa may be up to 21–35 mm apart, with septa spacing decreasing to 4–5 mm at higher

levels. In contrast, larger stumps ( $DBH \geq 25$  cm) lack a septate pith cavity entirely, instead possessing a subconical, sandstone-cast basal cavity that may be up to 19 cm in diameter and extend up to 38 cm in height (Fig. 6A).

### 5.2. Rooting systems

Root specimens are identified by their attachment to stumps, in 94.4% of 36 examples, and by a radiating pattern of roots (Fig. 6A–F). Root system morphology is complex and variable, its characteristics closely related to DBH. The angle at which the primary roots depart from the stump relative to the horizontal plane was ascertained for those roots oriented perpendicular to the compression direction (the departure angle of all other roots has been altered during specimen compression).

The smallest stumps ( $DBH \leq 25$  cm) are characterized by a mass of fine, densely arranged, vertically oriented roots (<1–2 cm diameter) that extend for up to 30 cm (Fig. 6F). Medium-sized stumps ( $DBH$  25–40 cm) contain better developed root systems characterized by slender primary roots (range: 3–17 cm diameter; mean: 11.36 cm,  $n=31$ ) that exhibit high departure angles (range: 22–90°; mean: 59.70°;  $n=31$ ) and up to three orders of bifurcation (bifurcation angle ranges from 39 to 70°). Secondary roots are

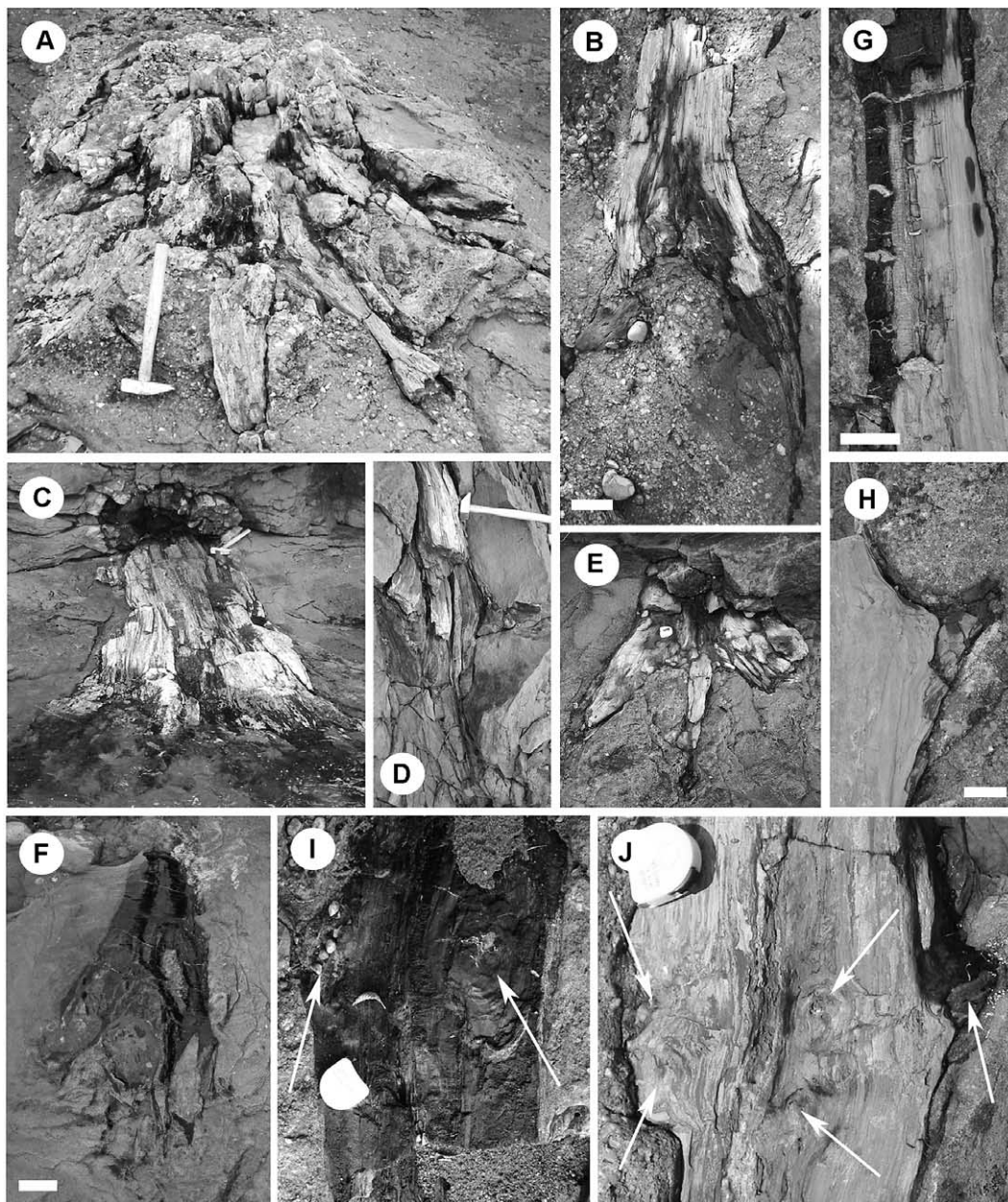


Fig. 6. Stumps, rooting systems, and branches, hammer: 35 cm, tape: 10 cm. (A) Large, upright stump with wide, sand-filled basal cavity. (B) Medium-sized tree with vertically oriented roots, scale: 5 cm. (C) Large lower trunk specimen showing submerged roots and pronounced basal flare. (D) Stump specimen with vertical tap root that extends for 1 m. (E) Medium-sized tree with vertically oriented roots. (F) Small stumps with mass of fine roots, scale: 5 cm. (G) Small trunk with *Artisia* pith, scale: 5 cm. (H) Small trunk with lateral branch angled upwards based on trunk taper direction, scale: 5 cm. (I–J) Small trunks with whorled branches, arrows indicate branch scars.

2–5 cm in diameter, while tertiary roots are 0.5–1 cm diameter, and may terminate in numerous fine roots (range: 1–3 mm diameter). Many medium-sized

stumps also exhibit a taproot, up to 15 cm in diameter, which extends vertically from the stump base to a depth of up to 1 m (Fig. 6D).

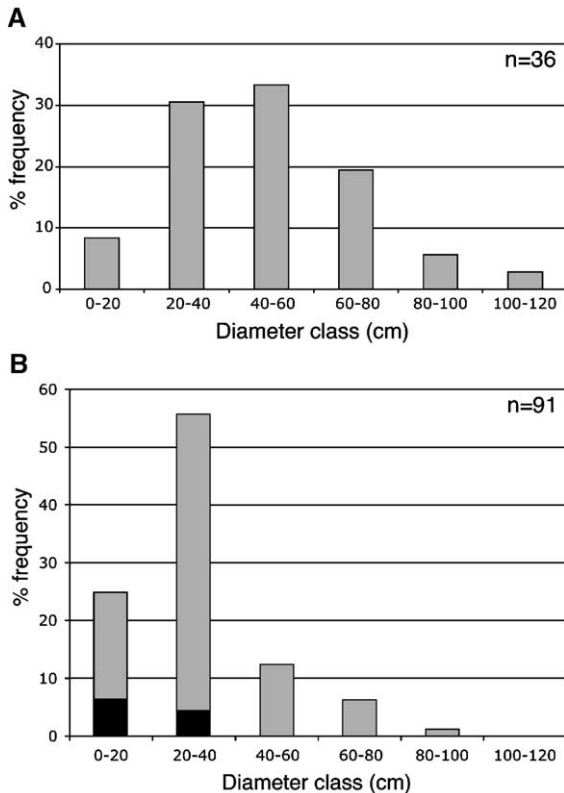


Fig. 7. Axis diameter data; (A) stump diameter above the basal flared zone (DBH). (B) Diameter of trunk sections that lack stumps. Specimens bearing branches are indicated in black.

In contrast, the largest stumps ( $\text{DBH} \geq 40$  cm) have very large primary roots (range: 10–43 cm diameter; mean: 19.77 cm,  $n=43$ ), with a dominantly sub-horizontal orientation (range:  $15\text{--}61^\circ$ , mean:  $33.92^\circ$ ). Up to six primary roots may depart from around the stump's circumference, being spaced between  $45$  and  $75^\circ$  apart in plan view. Primary roots possess septate pith cavities up to 24 mm in diameter. Up to three orders of bifurcation occur, secondary roots being 4–9 cm in diameter, and tertiary roots being 2–4 cm in diameter; terminal fine roots are not preserved in mature stump specimens (Fig. 6A, C, E). The maximum preserved diameter of mature rooting systems ranges up to about twice the diameter of the stump buttress; however, the broken ends of the large tertiary roots indicate original root plate diameter was considerably, but indeterminately, greater (Fig. 6A).

### 5.3. Straight trunk fragments

Trunk specimens are identified by their large unbranched length (typically several metres) and parallel sides (Fig. 6G). Some specimens (up to 7 m long) are attached to stumps and represent the lower part of the cordaitalean trees ( $n=11$ ). Most, however, lack stump features such as basal flaring and root systems, and represent upper parts of the trees. Specimens in this latter group have diameters that range from 6 to 84 cm (mean: 30.61;  $n=91$ ; Fig. 7B), rather smaller than the stump DBH range (Fig. 7A).

Several trunk specimens exhibit septate pith cavities (range: 19–43 mm diameter;  $n=5$ ) with septa spaced 0.7–2.1 mm apart, the most slender trunks having the widest pith cavities with the greatest septa spacing (Fig. 6G). In other specimens, the pith cavity was noted to be exceptional wide (5–13 cm diameter), sandstone-cast, and lacking septa entirely. These latter features likely represent piths that have become widened by rotting.

### 5.4. Branches

Branches, identified by their lateral attachment to straight trunk specimens, occur sparsely (Fig. 6H–J). Neither juvenile nor mature trunk specimens with attached stumps exhibited lateral branches, even in examples where up to 7.55 m of the lower trunk was preserved. Lateral branches were only found attached to relatively small diameter trunks (range: 7–36 cm diameter; mean: 23.55 cm;  $n=9$ ).

Branches are 2.5–10 cm in diameter (mean: 4.85 cm;  $n=13$ ), circular to oval in cross-section, are commonly coarsely recrystallised and therefore lack visible *Artisia* pith features. They are arranged in opposite pairs or in irregular whorls with up to 4–7 branches at a particular level (Fig. 6I–J), and project from the vertical trunk at an angle of  $31\text{--}50^\circ$ . It is difficult to determine which way is up on most trunks, but in one example, it is likely that branches angle up from the trunk (Fig. 6H), based on the observed direction of trunk taper.

A woody girdle overarches and partially encloses the broken basal ends of some branches. In other examples, oval bulges in the trunk wood may mark the position of branches that have been completely

overgrown in this manner. It proved impossible to break open trunks to demonstrate whether they indeed contained embedded branches (cf. Williams et al., 2003).

## 6. Anatomy of calcite-permineralized fossils

Analyzed in thin section, the cordaitalean specimens exhibit two phases of mineralization. A first phase of anhedral to euhedral pyrite commonly occurs as a discontinuous layer around the inner surface of the trunk and branch pith. Pyrite also is distributed throughout the wood as isolated euhedral to subhedral crystals, or in nodules that replace cellular details. A second, more widespread, calcite mineralization phase is locally nucleated on the surface of the pyrite crystals. It consists of very fine calcite crystals that infill individual cells, cryptocrystalline calcite which mineralizes the cell walls, and coarsely crystalline calcite spar that fills late stage fractures or has resulted from local recrystallisation. This mineralization history implies that plant decay initially generated anoxic and acidic conditions, but that subsequent porewaters were oxic and alkali (Scott and Collinson, 2003).

### 6.1. Primary anatomy

Although *Artisia* pith characteristics were observed in several specimens, primary anatomy was only preserved at the cellular level in one specimen (Fig. 8A–F). This upper trunk specimen comprises a 27 mm diameter septate pith (Fig. 8A–B) surrounded by a 76 mm diameter trunk. The outer pith region is composed of large, rectangular parenchyma (60–80  $\mu\text{m}$  diameter) arranged in vertically oriented rows (Fig. 8B). Primary maturation is endarch (Fig. 8C) with the inner 6–8 tracheids (16–20  $\mu\text{m}$  in diameter) of the xylem showing an outward progression from spiral to scalariform to reticulate thickening (Fig. 8E–F), ultimately succeeded by bordered pitting. Rays, continuous with the pith, are 1–3-seriate in the primary tissue (Fig. 8C). Leaf traces, a key character in cordaitalean taxonomy (Trivett and Rothwell, 1988), are not preserved in this specimen, consistent with its position in the trunk.

### 6.2. Secondary xylem anatomy

More detailed anatomical information could be extracted from the secondary xylem (wood) which generally shows better and more extensive preservation. However, although root, stump, and trunk specimens all locally showed good anatomy, no anatomical details could be discerned in branch specimens. All of the well-preserved specimens ( $n=10$  trees) are anatomically similar, and assignable to *Dadoxylon materiarium* Dawson. This taxon is characterized by tracheids with alternate, multiseriate bordered pitting (Fig. 8G) and araucarioid cross-field pitting. Although initially attributed to walchian conifers (Dawson, 1891), its probable cordaitalean affinity has subsequently been indicated by *Artisia* pith features (Falcon-Lang, 2003), a characteristic seen in conifers only rarely (Rothwell and Mapes, 2001).

Wood anatomical features were found to show some variation with ontogenetic age and the position within each tree. Juvenile and mature trunk woods were very similar, both being characterized by 16–44  $\mu\text{m}$  diameter tracheids exhibiting 1–3-seriate, circular or hexagonal, contiguous, alternate bordered pits (6–10  $\mu\text{m}$ ) on the radial tracheid walls, and blank tangential walls (Fig. 8H, J). Cross-field regions contained 1–8 circular, araucarioid cross-field pits (4–6  $\mu\text{m}$ ). Rays were typically uniseriate, with short biseriate portions (Fig. 8I). In general juvenile wood rays were composed of shorter (44–108  $\mu\text{m}$ ) and fatter (16–28  $\mu\text{m}$ ) parenchyma cells compared to mature wood (120–164  $\mu\text{m}$ ; 16–20  $\mu\text{m}$  respectively). Furthermore, juvenile wood rays had significantly reduced lengths (up to 4.1 mm), heights (1–16 cells), and tangential spacing (1–6 tracheids) compared to mature woods (up to 17.2 mm; 1–29 cells; 1–12 tracheids, respectively).

Root wood showed the same anatomical features as trunk wood with one key difference, this being that tracheids were of much greater diameter (28–68  $\mu\text{m}$ ) and therefore exhibited more numerous rows of bordered pitting (up to 2–5-seriate) on the radial walls (Fig. 8K–M). All woods lacked true growth rings, but a very few specimens showed very faint growth interruptions.

Charred sub-cubic blocks of wood, up to 14 mm diameter, containing a pyrite mineralization phase, could not be assigned to a particular cordaitalean organ but exhibited the same general anatomy of *Dadoxylon materiarium* as seen elsewhere (Fig.

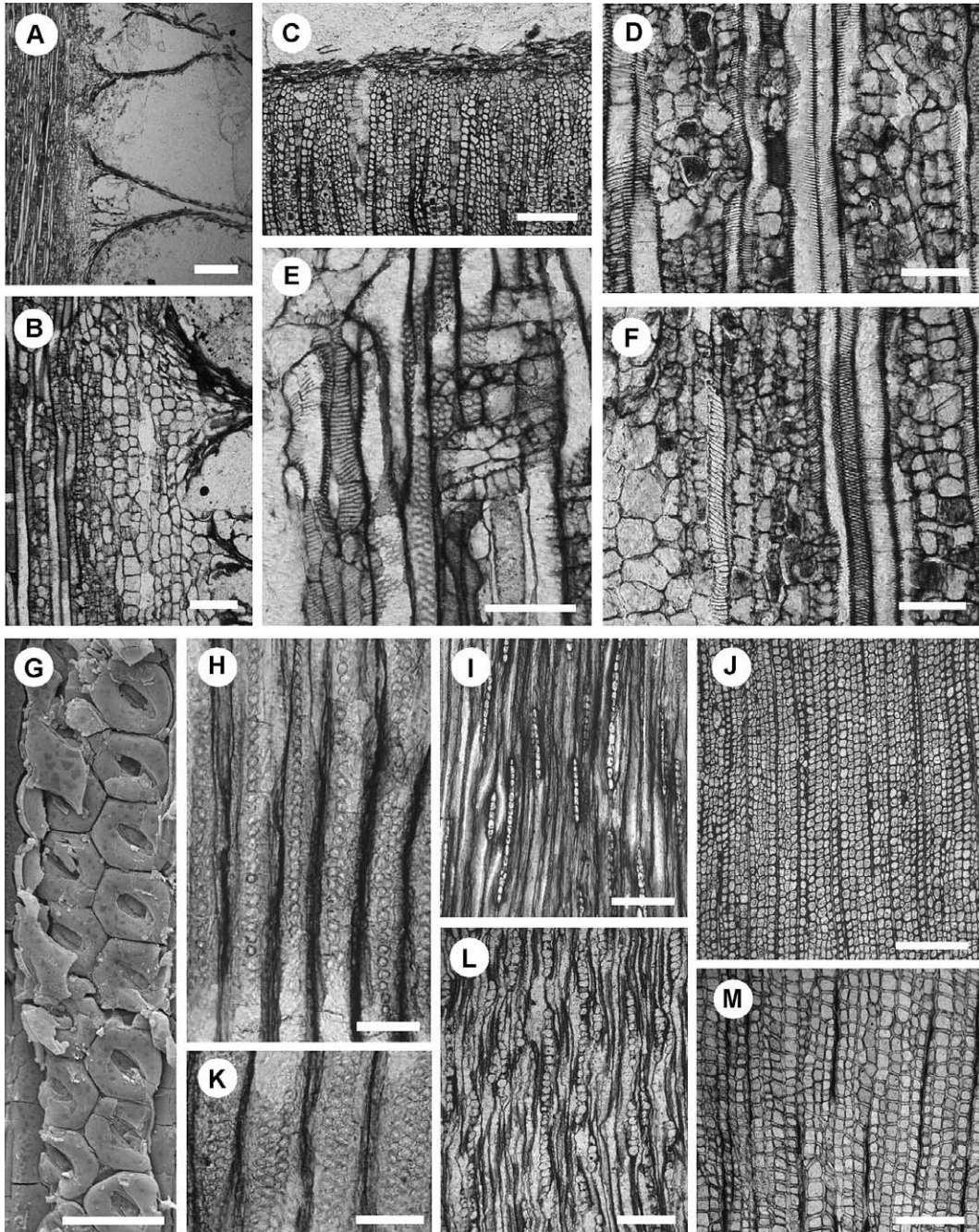


Fig. 8. Cordaitalean stem anatomy. All specimens conform to *Dadoxylon materiarium* Dawson. (A–F) Primary tissue, BRSUG 27196, (G) charred wood, not archived, (H–J) mature trunk wood, NFM F-433, and (K–M) root wood, NFM F-436. (A) Pith septa, RLS, scale: 400  $\mu$ m, (B) parenchyma in inner pith, RLS, scale: 100  $\mu$ m, (C) endarch maturation of xylem, TS, scale: 250  $\mu$ m, (D–F) spiral, scalariform, and reticulate thickened tracheids, and rays, RLS, scale: 50  $\mu$ m, (G) alternate, biseriata, hexagonal bordered pits in charcoal, RLS, scale: 25  $\mu$ m, (H) 1-2-seriate, alternate, bordered tracheid pitting, RLS, scale: 50  $\mu$ m, (I) uniseriate rays, narrow cells, TLS, scale: 150  $\mu$ m, (J) growth rings absent, narrow tracheids, TS, scale: 250  $\mu$ m, (K) 3-4-seriate, alternate, bordered tracheid pitting, RLS, scale: 50  $\mu$ m, (L) uniseriate rays, broad cells, TLS, scale: 150  $\mu$ m, (M) growth rings absent, broad tracheids, TS, scale: 150  $\mu$ m.

8G). The key difference to the calcite-permineralized fossil was the markedly reduced cellular dimensions (by about 20–30%) in this material, linked to the contraction that occurs during the charring process (Scott, 1989).

## 7. Sandstone-cast and compressed fossils

In addition to the permineralized and charred material, a few sandstone-cast and compressed fossils also occur in the fluvial channel assemblage (Fig. 9A–E). Although some of these belong to other plants (*Sigillaria*, *Calamites*), others are cordaitalean, and are likely related to the large woody remains described.

### 7.1. Branches

Branches are locally sandstone-cast, and may contain an *Artisia* pith, up to 29 mm diameter, with horizontal septa spaced 1.0–1.5 mm apart. Such specimens rarely also preserve the position of helically-arranged leaf traces, 3–5 mm wide by 7–9 mm high, cast from the interior surface of the pith, together with a linear impression marking the position of the leaf trace in the protoxylem. In these specimens, leaf trace projections are arranged with an angular spiral of 7–10° and a 5/13 phyllotaxy (Fig. 9B), erroneously given as 1/8 by Falcon-Lang and Bashforth (2004). Other branch specimens are preserved as compressions. These fossils exhibit helically-arranged, oval leaf scars, 8–9 mm wide by 4–5 mm high, on their external surfaces, and are referable to *Cordai cladus* (Fig. 9A). The phyllotaxy of these latter specimens cannot be determined with certainty, but are likely similar to the sandstone-cast specimens.

### 7.2. Leaves

Based on external morphology, Bashforth (in press) identified four types of *Cordaites* leaves within the Blanche Brook formation. However, only one leaf type was found in the alluvial channel deposits associated with the woody cordaitalean remains; the other three were restricted to intercalated coal-bearing floodbasin deposits. The former *Cordaites* leaves are preserved as incomplete compressions, lacking

apices and bases. Leaves are longitudinally split, possibly resulting from mechanical breakage during high-energy transport. The largest observed leaf fragments are 17–45 mm wide and up to 30 cm long, although the fact that leaves are essentially parallel-sided along their preserved length indicates complete leaves must have been longer (Fig. 9C).

The surface of the foliage is smoother than is typical for most *Cordaites* species, and parallel primary veins are spaced 0.35–0.47 mm apart with a vein density of 1.85–2.86/mm (Fig. 9D). Cuticles from these leaves were described by Zodrow et al. (2000), and belong to their cuticular morphotype 3. Epidermal cells generally are longitudinally oblong to somewhat rectangular, although the size and shape of cells are extremely irregular. Stomatal apparatus are circular on adaxial cuticles and lenticular on abaxial cuticles, but more detailed description is difficult due to the presence of opaque carbonaceous matter (Fig. 9E–F). The irregularity of epidermal cells and poor preservation of stomatal apparatus is due, in part, to mechanical and/or biological degradation (Zodrow et al., 2000), entirely consistent with their transport and preservation within coarse-grained sediments where oxidation and decay would have been prevalent.

Despite poor preservation, sufficient morphological and anatomical characters are retained to distinguish these leaves from foliage produced by mire-dwelling cordaitalean forms at Blanche Brooke. Based on taphonomic and anatomical evidence, the *Cordaites* leaf morphospecies recovered from the coarse-grained channel units (cuticular morphotype 3 of Zodrow et al., 2000), although never found attached to woody cordaitalean branches, likely represents the foliage of the large cordaitalean trees. Given the incomplete preservation of our material, and the poor resolution of *Cordaites* taxonomy in general (Šimůnek, 2000), we do not erect a new specific name for these leaves.

## 8. Tree reconstruction

Reconstruction of the large cordaitalean trees is primarily based on direct biological attachment of adjacent organs and secondarily on anatomical similarities between isolated, facies-associated organs. The tree is known in its entirety with the exception

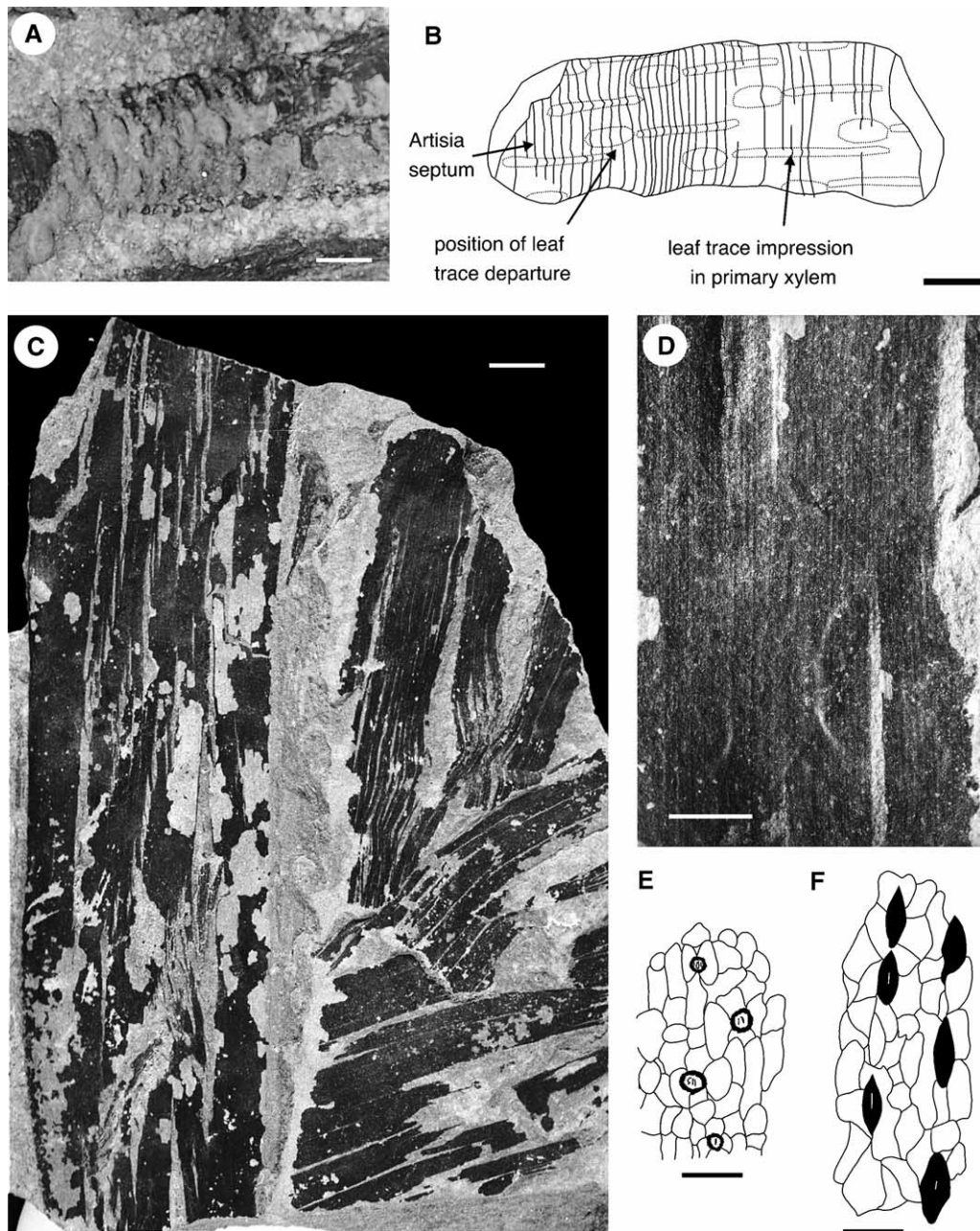


Fig. 9. Leaf morphology. (A) *Cordaiacladus* branch compression showing helically-arranged leaf scars, scale: 1 cm, not collected. (B) Sketch of a water-worn, sandstone-cast *Artisia* pith specimen showing the position of leaf trace departure, scale: 1 cm, BRSUG 27197. (C) *Cordaites* leaves are fragmentary and typically longitudinally split due to mechanical degradation caused by transport within the alluvial channel, scale: 1 cm, GSC125271. (D) Leaf showing characteristic smooth surface with only faint longitudinally-oriented, parallel veins, scale: 2.5 mm, GSC125271. (E) Adaxial cuticle showing oblong to somewhat rectangular epidermal cells, and circular stomatal apparatus surrounded by opaque matter, presumably due to mechanical and/or biodegradation, scale: 50  $\mu$ m, CBM.B34c1(3). (F) Abaxial cuticle showing irregular epidermal pattern, with lenticular stomatal apparatus obscured by opaque matter (Zodrow et al., 2000, Fig. 4), scale: 50  $\mu$ m, CBM.997-294-10/4.

of its fertile organs, which would have had a low preservation potential in the alluvial system.

### 8.1. Architecture and growth

Application of allometric relationships (Niklas, 1994) indicates that cordaitalean stumps likely supported trees ranging from 18.02 to 48.53 m in height (mean: 27.73 m;  $n=36$ ; Fig. 10). These calculations suggest that the cordaitaleans were the tallest trees in the Pennsylvanian tropical zone, the hitherto previous tallest tree being a 35 m high specimen of *Lepidodendron* (Thomas and Watson, 1976).

All the cordaitaleans studied had a straight trunk. Mature trees bore lateral branches on the upper half of the trunk only, as indicated by the exclusive occurrence of branch scars on upper trunk specimens of small diameter (<36 cm). Lower branches may have been progressively abscised as the trees matured as seen in extant araucarian conifers (Enright and Hill, 1995), a hypothesis supported by partially, and possibly fully, overgrown branch scars on some trunk specimens. Lateral branches were sparsely arranged in irregular whorls, spaced c. 2 m apart along the trunk, and given their small diameter (2–10 cm) were likely 3–15 m long (Niklas, 1994).

Data extracted from sandstone-cast pith specimens indicate that closely spaced leaves were borne in densely arranged helices (5/13 phyllotaxy) along the

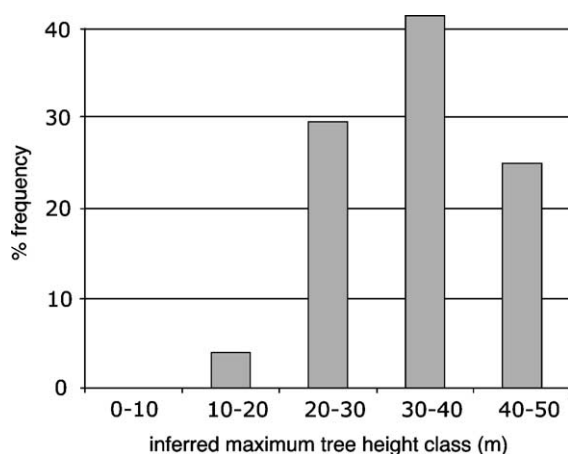


Fig. 10. Histogram showing inferred maximum tree heights calculated from the basal stump diameter data using equation of Niklas (1994).

length of the branches. Leaves of *Cordaites* cuticular morphotype 3 (Zodrow et al., 2000) represent the most likely leaf of this plant as indicated by anatomical similarities and exclusive taphonomic co-occurrence. As the leaves were broad (up to 4.5 cm), of great length (>30 cm), spaced c. 3 cm apart, and distributed on closely spaced branch tiers, cordaitaleans must have possessed a rather dark, shading canopy. The leaf phenology of the large cordaitalean trees is uncertain, but where known in other cordaitaleans, plants were evergreen (Rothwell, 1993).

The large number of preserved stump specimens ( $n=36$ ) of varying size permits insight in the development of the cordaitalean rooting system as trees increased in height. Small juvenile trees were anchored by a vertically orientated mass of small roots that extended up to 30 cm deep, but as trees matured, a large vertical taproot developed, penetrating to up to 1 m depth. Further maturation led to the lateral expansion of the rooting system, the loss of the taproot, the expansion of the basal stump cavity (to 13 cm diameter), and the development of a sub-horizontal root plate.

### 8.2. Whole plant

Our reconstruction compares extremely closely with previous reconstructions (Fig. 11) based on Stephanian assemblages from the Saint Étienne Basin of central France (Grand'Eury, 1877; Scott, 1900; Crookall, 1970). Although Grand'Eury (1877) made detailed field sketches, little of his original material survives, and his collection sites have largely been destroyed. Furthermore, his whole plant reconstructions were based on qualitative, anecdotal descriptions, and appear to have combined plant organs from a variety of taphonomic assemblages. The new material presented here, although closely agreeing with Grand'Eury's (1877) findings, allows the whole plant reconstruction of the large cordaitalean tree to be put on a more rigorous footing, evaluated against quantitative measurements and incorporating data from a single taphonomic context.

## 9. Upland ecology

We have already provided arguments for the upland ecology of the Stephenville cordaitaleans (Falcon-



Fig. 11. Whole plant reconstruction of a large cordaitalean tree (after Grand'Eury, 1877; Crookall, 1970). Note that, for clarity, leaves are shown at twice their actual size. Silhouetted figure is 1.8 m high for scale.

Lang and Bashforth, 2004). In summary, the allochthonous nature of the trees in high-energy channel deposits, located on the margins of the Laurentia–Greenland craton (Palmer et al., 2002), indicates derivation from an extrabasinal, and likely upland, source. Nevertheless, the absence of growth rings clearly may suggest year-round warm temperatures and high rainfall, implying that trees occupied low to medium altitudes (Falcon-Lang, 2004).

### 9.1. Allochthonous cordaitalean trunks

Here we provide, for the first time, a comprehensive review of the occurrence of large cordaitalean remains in Pennsylvanian tropical deposits. Almost all assemblages documented over the past 200 years are allochthonous, hosted in the deposits of large fluvial channels, and located a few tens of kilometres downstream of inferred upland area (Table 1;  $n=29$ ). When these data are plotted on a palaeogeographic map, they clearly show that cordaitalean assemblages are clustered adjacent to upland belts. The largest cluster consists of Lower to Middle Pennsylvanian localities in eastern Canada, where sediments were deposited in a series of narrow strike–slip basins separated by small upland massifs. In this region, upland zones were never more than a few tens of kilometres away in any direction. A second cluster of Upper Pennsylvanian sites is centred on central Europe, where sediments were deposited in small, isolated, intermontane basins within the Variscan mountain belt. In the more open, paralic basins of Britain and eastern USA, records of large cordaitaleans are less common, though when they occur they are always adjacent to upland zones (Fig. 12).

### 9.2. Large cordaitalean stumps in growth position

Stumps of the large cordaitalean tree have only been recorded in growth position at two sites. This first site is represented by the Upper Pennsylvanian Peronniere Member, Rive de Gier Formation in the Saint Étienne Basin of central France. Grand'Eury (1877) documented autochthonous *Dadoxylon* stumps, locally showing *Artisia* pith casts, very similar to the allochthonous stumps described in this paper. The trees were rooted in alluvial plain facies bracketed by alluvial fan facies, a succession that comprises the

Table 1

Global review of the taphonomic occurrence of large cordaitalean trees in the Pennsylvanian deposits of Euramerica

Locality	Stratigraphic unit	Trunks (N)	Interpreted environment
<i>United States of America</i>			
1. Rock Island, Illinois	Lower Pennsylvanian	several	Palaeovalley cut into bedrock
2. Walker County, Alabama	Lower Pennsylvanian	> 100	Meandering channel
3. Pocahontas, West Virginia	Lower Pennsylvanian	10–20	Fluvial channel
<i>Eastern Canada</i>			
4. New Glasgow, Nova Scotia	Lower Pennsylvanian	4	Fluvial channel
5. Boss Point, Nova Scotia	Lower Pennsylvanian	> 150	Large, braided channel
6. Maringouin, New Brunswick	Lower Pennsylvanian	> 150	Large, braided channel
7. Joggins, Nova Scotia	Lower Pennsylvanian	> 50	Meandering channel
8. Lepreau, New Brunswick	Lower Pennsylvanian	> 150	Fluvial channel
9. Saint John, New Brunswick	Lower Pennsylvanian	> 100	Fluvial channel
10. Giffin Pond, New Brunswick	Lower Pennsylvanian	> 50	Large, braided channel
11. Kempt Head, Nova Scotia	Middle Pennsylvanian	> 150	Large braided channel
12. Grand Lake, New Brunswick	Middle Pennsylvanian	several	Fluvial channel
13. Stephenville, Newfoundland	Middle Pennsylvanian	> 200	Meandering channel
14. Mabou, Nova Scotia	Middle Pennsylvanian	> 50	Large braided channels
15. Clifton, New Brunswick	Middle Pennsylvanian	several	Meandering channel
16. Table Head, Nova Scotia	Middle Pennsylvanian	> 50	Large meandering channel
17. Pictou, Nova Scotia	Middle Pennsylvanian	> 50	Fluvial channel
<i>Central Europe</i>			
18. Czerwionka, Poland	Lower Pennsylvanian	> 50	Meandering channel
19. Intrasudetes, Czech Republic	Lower Pennsylvanian	several	Fluvial channel
20. Saint Etienne, France	Upper Pennsylvanian	several	Fluvial channel
21. Pyrenees, northern Spain	Upper Pennsylvanian	1	Fluvial channel
22. Graissessac, France	Upper Pennsylvanian	several	Fluvial channel
23. Intrasudetes, Czech Republic	Upper Pennsylvanian	> 50	Large braided channel
24. Sudetic Basin, Poland	Upper Pennsylvanian	> 50	Large braided channel
<i>Great Britain</i>			
25. Wipeopen, Ushaw, Durham	Lower Pennsylvanian	3	Large braided channel
26. Priors Close North, Durham	Lower Pennsylvanian	24	Large braided channel
27. Newbiggin, Northumberland	Lower Pennsylvanian	> 10	Large braided channel
28. Darlaston, Staffordshire	Lower Pennsylvanian	1	Fluvial channel
29. Bolton, Lancashire	Lower Pennsylvanian	1	Fluvial channel

Locality 1 (Leary, 1975, 1981), 2 (Gastaldo et al., 1990; Liu and Gastaldo, 1992), 3 (Martin Saffer, personal communication, 2004), 4 (Fred Chandler, personal communication, 1998), 5 (Falcon-Lang and Scott, 2000), 6 (Greg Browne, personal communication, 1998; Guckert and Mossman, 2003), 7 (Falcon-Lang and Scott, 2000), 8–9 (Dawson, 1862; Stopes, 1914), 10 (Plint and van der Poll, 1982), 11 (John Calder, personal communication, 1999), 12 (Knowlton, 1889), 13 (Dawson, 1891; Falcon-Lang and Bashforth, 2004), 14 (Falcon-Lang and Scott, 2000), 15 (Falcon-Lang, 2000), 16 (Penhallow, 1900; Falcon-Lang and Scott, 2000), 17 (Dawson, 1846), 18 (Gradzinski et al., 1982), 19 (Opluštil et al., 1999; Zbynek Šimůnek, personal communication, 2003), 20 (Doubringer et al., 1995), 21 (Carles Martin-Closas, personal communication, 2003), 22 (Galtier et al., 1997), 23 (Zbynek Šimůnek, personal communication, 2003), 24 (Kotasowa and Migier, 1995), 25 (Winch, 1817; Lindley and Hutton, 1831), 26 (Johnson, 1999; Falcon-Lang and Scott, 2000), 27 (Witham, 1831), 28 (Dawes, 1845), and 29 (Black, 1837).

basin margin sediments of a small intermontane basin within the heart of the Variscan mountain belt (Doubringer et al., 1995).

The other locality is the Lower Pennsylvanian Tynemouth Creek Formation of southern New Brunswick, which represents the deposits of a large

alluvial fan, adjacent to the basin margins (Plint and van der Poll, 1982). Here the *Dadoxylon* stumps occur in the upper alluvial fan deposits, associated with sheet-floods and debris flows. Together, these sites represent the only known example of large cordaitaleans in growth position, and their location

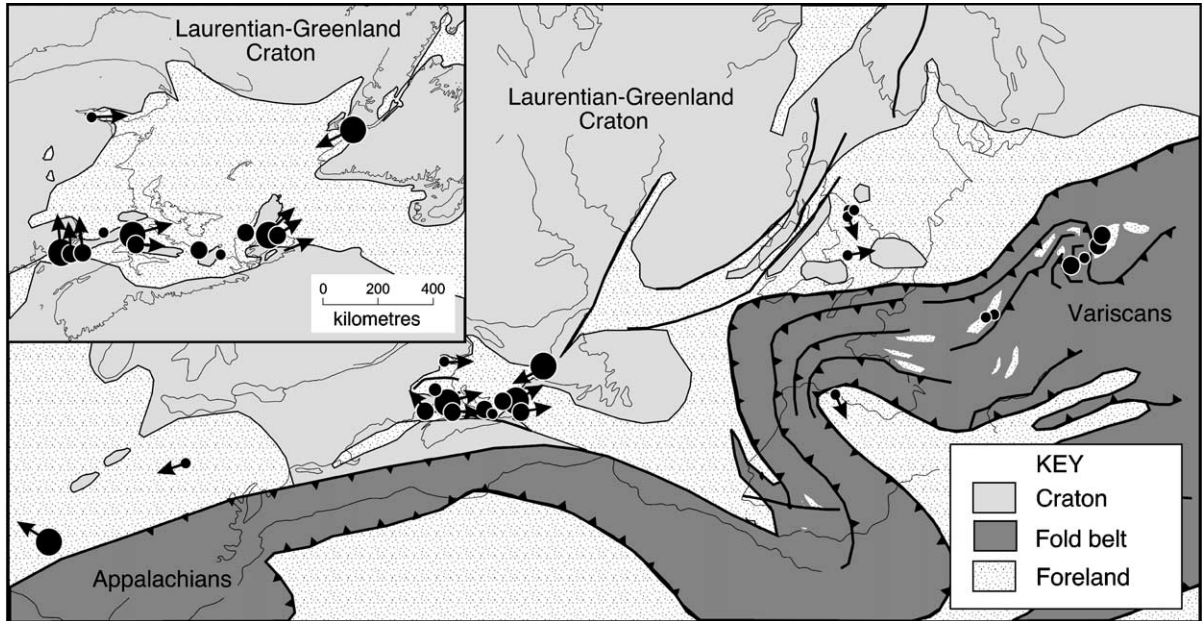


Fig. 12. Pennsylvanian (late Westphalian) palaeogeographic map of tropical Euramerica showing major tectonic elements (after Ziegler, 1988; Vai, 2003; Opluštil, 2004). Localities that bear large cordaitalean trunks in fluvial taphofacies are indicated. Size of spot indicates abundance of remains (small <50 trunks; medium 50–100 trunks; large >100 trunks), whereas arrows indicate transport direction. Data summarized in Table 1. Inset (top, left) shows enlargement of Maritimes Basin, eastern Canada which has the highest density of sites.

immediately adjacent to a major mountain belt strongly supports the hypothesis that large cordaitaleans occupied upland niches.

## 10. Conclusions

- (1) Allochthonous assemblages of cordaitalean stumps, trunks, branches, and leaves are preserved in Pennsylvanian (late Bolsovian) coarse-grained alluvial channel facies in south-west Newfoundland.
- (2) Sterile reconstruction of these trees, based on morphological and anatomical data, indicates that the largest specimens were  $\leq 48.5$  m high. Trunks contained a septate (*Artisia*) pith and were constructed of *Dadoxylon materiarium* wood. Branch scar distribution and branch overgrowths suggest that the crown was restricted to the upper trunk, and that lower branches were progressively shed during maturation. *Cordaites* leaves were borne on lateral *Cordai cladus* branches with a 5/13 phyllotaxy. As trees matured, an initial, vertically oriented

tap root was replaced by a horizontally oriented root plate.

- (3) Taphonomic data from Newfoundland, and other sites across Euramerica, provide strong evidence that these large cordaitalean trees grew in upland terrains, thereby augmenting our knowledge of Pennsylvanian tropical ecosystems.

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