Small cordaitalean trees in a marine-influenced coastal habitat in the Pennsylvanian Joggins Formation, Nova Scotia

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Abstract: The Cordaitales, an extinct order of plants closely related to the conifers, occupied a wide range of environments during Pennsylvanian times including wetlands, drylands, and uplands. However, claims that some species of cordaitalean grew on marine-influenced coastal margins, and therefore represented the earliest known mangrove communities, have been met with scepticism. Based on new data from the Joggins Formation of Nova Scotia, the ‘cordaitalean mangrove hypothesis’ is reassessed. Small fossil trees in growth position are described from micro-tidal deposits, a sedimentary association inferred to have formed on the margins of a brackish epicontinental sea. The autochthonous trees, which are morphologically different from lycopsid and calamitean trees commonly observed with the Joggins Formation, are probably cordaitalean. This affinity is indicated, in part, by facies-associated paraautochthonous remains, which comprise Cordaites leaves, Cordaictladium branches, Cardiocarpus seeds, Cordaitanthus reproductive organs, and Dadoxylon wood, a distinctively cordaitalean assemblage. Scour-and-mound structures in beds surrounding the upright trunks show that cordaitalean trees were, at times, submerged in shallow, flowing water. However, Limnopus tetrapod trackways at other horizons demonstrate periodic emergence, indicating that water depths fluctuated in these coastal forests. Analysis of rooting patterns shows that trees persisted through flooding events, despite partial burial by sheets of very fine sandstone and siltstone, survival being facilitated through the development of an adventitious rooting system. However, two key adaptations to growth in marine-influenced soils commonly seen in modern mangrove trees (low shoot:root ratios and small leaves) are not present in the cordaitalean trees. Furthermore, although the trees probably grew in close proximity to the brackish seacoast, direct evidence for marine influence in the fossil forest interval itself is lacking. Consequently, although the cordaitaleans were probably adapted to periodically submerged conditions, and additionally may have tolerated occasional brackish incursions, it is inappropriate to describe them as mangroves in the strict sense.

Keywords: Carboniferous, Joggins Formation, brackish-water environment, mangrove swamps, cordaitaleans.

The Cordaitales, an extinct gymnosperm order related to the conifers, formed a diverse and widespread component of Pennsylvanian vegetation (Rothwell 1988). Although common in temperate regions of Angara and Gondwana (DiMichele et al. 2001), it is in the Euramerican tropics that the anatomy, architecture, diversity and ecology of these plants is best understood (Trivett & Rothwell 1991; DiMichele & Phillips 1994). Some tropical cordaitaleans grew in lowland peat mires, either dominating such ecosystems (Raymond 1988), or more typically, co-occurring with calamitans, tree-ferns, and lycopsids (DiMichele & Phillips 1994). Others occupied poorly to well-drained mineral soils, forming fire-prone communities on drier sites (Falcon-Lang 2003a–c; Falcon-Lang et al. 2004b). A few giant forms additionally grew in uplands (Falcon-Lang & Scott 2000; Falcon-Lang & Bashforth 2004).

However, the assertion that some species of tropical cordaitalean may have grown in marine-influenced coastal mires has proved somewhat controversial (Raymond & Phillips 1983). One variant of Pennsylvanioxylon birame has been reconstructed as a 5 m high mangrove tree with stilt roots, an interpretation based on the occurrence of roots with aerenchyma, lenticels, pith, and clusters of lateral, adventitious roots (Cridland 1964; Costanza 1985). A mangrove habit is further supported by very low shoot:root ratios (0.15) in coal balls, a feature typical of mangrove peats, and pyrite rims surrounding roots (Raymond 1987, 1988; DiMichele & Phillips 1994; Hogarth 1999). If confirmed, these plants would represent the earliest known mangrove communities (Raymond & Phillips 1983).

However, in recent years, the concept of cordaitalean mangroves has become unpopular with palaeobotanists. Critical to this change in viewpoint has been the recognition that observed root morphological features are more broadly consistent with growth in aquatic habitats rather than specifically saltwater settings (Raymond & Phillips 1983; Costanza 1985). In addition, it has been pointed out that putatively marine-influenced coals share a close petrographic similarity with unequivocally freshwater deposits (Raymond et al. 2001). In this paper, Early Pennsylvanian cordaitalean trees in growth position are documented from micro-tidal coastal deposits within the Joggins Formation of Nova Scotia, Canada (Fig. 1a and b). These data allow the ‘cordaitalean mangrove hypothesis’ to be further tested and permit the ecology of these enigmatic trees to be reconstructed in more detail.

Geological setting
The Early Pennsylvanian (mid-Langsettian; 313–314 Ma) Joggins Formation was deposited in the Cumberland sub-basin (Fig. 1b and c), a rapidly subsiding arm of the strike-slip Maritimes Basin (Calder 1994; Gradstein et al. 2004), which initiated in Late Devonian times following the oblique convergence of Gondwana with Laurasia (Gibling 1995; Pascucci et al. 2000). The recent recognition of brackish to fully marine facies at many intervals throughout the Maritimes basin-fill (Wightman et al. 1994; Archer et al. 1995; Gibling 1995; Tibert & Scott 1999) has shown that, at times of maximum flooding, the basin was
connected eastward to the Tethys Ocean by a narrow strait (Ziegler 1988; Gibling et al. 1992; Calder 1998).

Cryptic marine transgressions occur at many intervals in the Joggins Formation (Archer et al. 1995; Calder 1998) between Lower Cove and the old Joggins Wharf on the Bay of Fundy, Nova Scotia (45°42′N, 64°26′W). Sequence stratigraphic analysis of this spectacular cliff-section has identified repeated sedimentary rhythms, which are typically 29–96 m thick, although rarely up to 210 m thick (Fig. 2; Davies & Gibling 2003). Each rhythm begins with a coal seam, normally overlain by a brackish open water facies association (OW), marking a rapid base-level rise event. These deposits are succeeded first by a poorly drained floodplain facies association (PDF), which records bay-filling by wetland deltas and second, in some examples, by a well-drained floodplain association (WDF), deposited following floodplain aggradation above base level (Davies & Gibling 2003). The predominance of flooding surfaces and the absence of unequivocal palaeovalley incisions or associated mature palaeosols suggest that sedimentary rhythms primarily resulted from tectonism, and were modified by glacioeustasy (Davies & Gibling 2003; Falcon-Lang 2003b).

The Joggins section has recently been logged for the first time since 1843 (Logan 1845; Rygel & Shipley 2005), resulting in regional stratigraphic revision. The revised Joggins Formation comprises 14 sedimentary rhythms in total (Rygel et al. 2004a). This paper mainly focuses on the second rhythm, positioned 35–68 m above the base of the Joggins Formation (Fig. 2), and consisting of a 9 m thick OW unit overlain by a 24 m thick PDF–WDF succession (Rygel et al. 2004a). Gibling discovered several cordaitalean trees in growth position within this succession in 2001 (Davies & Gibling 2003, fig. 11). The sedimentary facies, ichnology, palaeobotany, and taphonomy of this tree-bearing interval are described in the present paper. These data are used to infer cordaitalean architecture and ecology and to evaluate the extent to which these trees may be termed mangroves (Cridland 1964; Raymond & Phillips 1983).

**Sedimentary facies and fossil assemblages**

The studied succession is exposed in vertical cliffs, up to 14 m high, and in wave-cut platform exposures, partially buried by
tidal gravel, 25–40 m WSW of the cliff-line. These beds, positioned between 35 and 68 m above the base of the Joggins Formation, and cropping out c. 550 m SSW of the Lower Cove access point (Figs 3 and 4), comprise the lower part of the second rhythm. In addition to section logging, channel architecture was studied using photomontages (Fig. 5).

**OW Facies Association**

This 9 m thick association, positioned between 35 and 44 m in the section, comprises two main sedimentary facies. Facies 1 consists of 1–12 cm thick beds of light to medium grey limestone, locally lensoid or nodular, that intergrade with medium to dark grey, well-laminated mudstone beds, 8–211 cm thick. Limestone beds are fossiliferous, locally dominated by either bivalves or ostracodes, and exhibit a micritic matrix (wackestone to packstone). The bivalves, *Naiadites* and *Curvirimula*, typically are disarticulated, fragmented, crushed, and randomly oriented. Fish skeletal material including palaeoniscid scales are common on some bedding surfaces.

Mudstone beds that intergrade with the limestone units also preserve bivalves, ostracodes, and fish scales at some intervals, but in lower concentrations. Additional features include rare burrows, small, scattered siderite nodules (2–3 cm diameter), and locally abundant plant compressions. Plant fossils are limited to three discrete intervals at 37.7 m, 40.8 m, and 42.9 m in the section. Remains are fragmentary and include rare decorticated lycopsid trunks, rare *Asterophyllites*, rare *Cordaites* leaves, very rare *Cordaitianthus* fertile organs, common pinnules and pinnae of *Alethopteris* and *Pseudaiantites*, common *Trigonocarpus* seeds, and rare large, branching woody stems (up to 7 cm diameter) of indeterminate affinity.

Facies 2, positioned between 39.5 m and 42.4 m in the section, consists of 3–20 cm thick fine-grained sandstone sheets interbedded with laminated, red–grey mottled mudstone and siltstone units, up to 30 cm thick. The sheet-sandstone beds have sharp, erosive bases, exhibiting grooves and flutes. Some sandstone units infill cracks up to 7 cm deep in underlying mudstone beds. Upper surfaces are undulatory and locally exhibit symmetrical ripples with north–south crest orientations. Internally, sandstone beds contain ripple cross-lamination, locally climbing, and hummocky cross-stratification. Trace fossils on bedding surfaces include *Coelichnus*, *Koupichnium*, *L. Limulocubichnus*, and vertical, locally paired burrows attributed with reservation to *Arenicolitites* (Fig. 6). The only identifiable plant remains include charred *Dadoxylon* wood fragments, up to 5 mm in diameter.

**PDF Facies Association**

This 7 m thick association, positioned between 44 and 51 m in the section (Fig. 4), comprises three main facies. Facies 3 consists of 5–29 cm thick sheets of medium grey siltstone to very fine-grained sandstone interbedded with 11–162 cm thick units of medium grey mudstone, positioned between 44 and 47.4 m. The siltstone–sandstone sheets are lensoid over tens of metres, have gradational bases, and locally gradational tops, and exhibit horizontal lamination, ripple cross-lamination and widespread rootlets. Ripple cross-lamination commonly exhibits mud drapes, especially in the toesets, and locally shows a bimodal NE–SW palaeocurrent direction (n = 18). Locally, lenses are cut by small channel bodies of fine-grained, heterolithic sandstone, up to 29 cm thick and up to 7 m wide. Associated mudstone beds are typically well laminated but contain widespread rootlets of indeterminate type. Red–grey mottling with millimetre-scale pedogenic carbonate spots occurs in some intervals, whereas in others siderite nodules (<1 cm diameter) are present.

Upright trees rooted in siltstone–sandstone lenses or mudstone beds, the focus of this study, occur within a 1.7 m thick package between 45.8 and 47.4 m in the section (Figs 4 and 5). Plant compressions associated with the mudstone beds, but also locally within siltstone–sandstone lenses, include highly abundant *Cordaites* leaves, common *Cardiocarpus* seeds, rare *Cordaitidius* branches, rare *Cordaitianthus* fertile organs, very rare *Alethopteris* pinnae, and very rare *Asterophyllites*. Charred *Dadoxylon* wood fragments, up to 1 cm in diameter, also rarely occur. At one interval (43.8 m), a prone coalified tree trunk, morphologically similar to the upright trees, is preserved in a mudstone bed. Ichnotaxa associated with the siltstone–sandstone lenses include rare tetrapod trackways and a few, small vertical burrows exhibiting radial feeding patterns.

Facies 4, positioned approximately between 47 and 49.5 m (Fig. 4), comprises numerous fine-grained sandstone channel bodies. In the lower part of this succession (Facies 4a), channel bodies are c. 0.9–1.5 m thick and up to 6–14 m wide. Channel-fill units are distinctively heterolithic and are locally characterized by low-angle dipping strata that extend from the base to the top of bodies (IHS). Only one IHS unit, exposed at the cliff-base, could be examined in detail. This unit contained small-scale trough cross-beds and ripple cross-lamination with bimodal palaeoflow vectors oriented subperpendicular to the dip of the IHS surfaces. Cross-laminae commonly exhibit mud drapes on the toesets and foresets, which are rarely paired. *Cordaites* leaves are locally abundant near the channel bases, together with *Cardiocarpus* seeds and *Cordaitidius* branches.

The upper part of this succession (Facies 4b) comprises a sequence of small channels that cut down into the IHS units. These differ from the underlying units of Facies 4a in that channel-fills, up to 1.7 m thick, are dominantly composed of...
Fig. 4. Sedimentary succession between 35 and 51 m in the measured Joggins Formation of Davies & Gibling (2003). Left log based on foreshore outcrops positioned 25–40 m west of the cliff-section (right log).
fine-grained sandstone with a relatively low mudstone–siltstone content. Inclined stratification, dipping towards the channel margin, is locally present. Channel-fills grade laterally into subhorizontal, thinly bedded units of light grey mudstone and fine-grained sandstone that contain ripple cross-lamination and Calamites stems in growth position, rooted at several horizons. In addition, a single sandstone-cast lycopsid stump with vertical ribbing suggestive of Sigillaria was observed where these units crop out on the foreshore.

Facies 5, positioned between 49.5 and 51 m in the section (Fig. 4), comprises lenses of siltstone, up to 7 cm thick; poorly laminated to blocky, light grey to grey–red mottled, rooted, mudstone units, up to 78 cm thick; and two intervals of dull, banded coal, 10 cm and 2 cm in thickness, locally underlain by Stigmaria root systems.

Palaeoenvironmental interpretation

The succession is interpreted as representing the infilling of an extensive, open water body (OW Facies Association) by progradation of a poorly drained floodplain system (PDF Facies Association). Critical to assessing whether the upright trees, preserved close to the OW–PDF boundary, were mangrove communities is the demonstration that the OW Facies Association was deposited in a marine-influenced water body. Assessment of the OW salinity is achieved through analysis of sedimentary and faunal characteristics preserved in the OW unit at 35–44 m, and with reference to other similar OW units throughout the Joggins Formation (Fig. 2; Davies & Gibling 2003).

**Facies 1 and 2: deposits of a brackish epicontinental sea**

The succession between 35 and 44 m clearly represents an extensive, open water body as indicated by the complete absence of roots (ubiquitous elsewhere in the succession), the rarity of allochthonous plant fossils (common elsewhere), and the common presence of aquatic fauna (palaeniscid fish, bivalves, ostracodes). Coarsening-upward rhythms culminating in wave-rippled sandstone sheets, and capped by limestone beds, suggest that bays were filled by shoreline progradation, punctuated by renewed flooding.

Limestone and associated mudstone beds (Facies 1) were formed at times of maximum flooding when clastic sediment supply was suppressed, and the position of the shoreline at its most distant. Given the low gradient of the basin floor, maximum water depths of up to only a few tens of metres may have been sufficient to cause the requisite extensive transgression. Rare plant assemblage in this distal facies may contain an amplified upland signal following widespread lowland drowning, as pre-
viously argued by Falcon-Lang (2003b). This interpretation is consistent with assemblage composition, which contains common Pseudadiantites, a putative progymnospermous pseudopinnate frond considered to be an extra-basinal element according to independent analyses (Wagner 2001).

Sandstone sheets with basal flute casts, hummocky cross-stratification, and climbing ripple-lamination (Facies 2) probably formed in slightly shallower waters, being deposited by unsteady, waning combined flows (Davies & Gibling 2003). Although symmetrical ripples, putative desiccation cracks, and pedogenic mottling imply that shallow-to-emergent conditions prevailed at certain times, their restriction to the sandstone bed tops indicates that sandstone deposition typically occurred below normal wave base. Flows may have been storm-triggered or represent hypopycnal underflows sourced from deltaic distributary channels, indicating the proximity of the coastline (Davies & Gibling 2003).

Faunal data indicate that the open water bodies were almost certainly marine influenced, probably representing the distal expression of Euramerican marine bands (Duff & Walton 1973). Although no unequivocal fully marine fauna occurs in the OW Facies Association, many of the aquatic taxa (protists, crustaceans, bivalves, arthropods, annelids, fish) seen in the Joggins Formation are facies-associated with marine fossils in coeval basins in Europe and North America (Table 1) and were, therefore, tolerant of marine-influenced conditions (Calder 1998).

For example, in the British Coal Measures, Naiadites and Curvirimula (the bivalve genera present in the Joggins Formation), may occur immediately above and below marine bands, being locally facies-associated with Lingula (although never with other marine fossils). They disappear basinwide precisely coincident with the last marine band in Bolsovian times (Davies & Trueman 1927; Trueman & Weir 1946–1968; Eagar 1947). Similar patterns can be discerned for the other faunal elements within the Joggins Formation. These data, combined with the complete absence of stenohaline fauna such as goniatites, provide strong support for marine-influenced, but not stenohaline conditions (i.e. brackish conditions).

The brackish water bodies preserved within the Joggins Formation clearly covered a wide area as indicated by the lateral continuity of some OW Facies Association units (limestone beds), which may be traced for tens of kilometres across the Cumberland sub-basin (J. H. Calder, pers. comm.). However, limestone beds with very similar facies characteristics to those seen within the Joggins Formation also occur within Westphalian coal-bearing strata across the whole Maritimes Basin (Gibling & Kalkreuth 1991). Although these limestone beds cannot be correlated between sub-basins, their distribution from SW Newfoundland to western Nova Scotia (Gibling 1995) implies that, at times of maximum flooding, a continuous brackish water body may have occupied most of the Maritimes Basin, with the possible exception of a few, emergent fault blocks.

Palaeogeographical reconstructions show that during Westphalian times the Maritimes Basin was enclosed to the north, west, and south by uplifted zones (Ziegler 1988), and, as indicated by regional palaeocurrent datasets (Gibling et al. 1992), drained in a northeasterly direction towards Western Europe (Calder 1998). Based on global palaeogeographical reconstructions, the Maritimes brackish water body probably connected to the Tethys Ocean by a tortuous route (Fig. 7), and therefore represented the most inland gulf of a large epicontinental sea some 2300 km in length (Calder 1998).

An excellent present-day analogue for this extensive, epicontinental sea may be the micro-tidal Baltic Sea (Andersson et al. 1992, 1994). In this shallow water body (mean depth 55 m), salinity decreases from near marine (35.29‰ salinity) close to Denmark to near freshwater (2.46‰ salinity) 1600 km further inland in the Gulf of Bothnia. Widespread brackish conditions (dominantly 5–15‰ salinity) are maintained because mixing with the Atlantic Ocean is restricted through the narrow, shallow Skaggerak straits, and the enclosed sea is freshened by riverine input (Andersson et al. 1992). Application of this model to the Maritimes Basin implies that this Westphalian epicontinental sea was connected to the Tethys Ocean by similarly narrow straits.
Cochlichnus, Kouphichnium, Pygocephalus, and Megalichthys. Gyracanthus and Naiadites. Bellinurus (Chelicerates) This Pennsylvanian taxon is associated with brackish bays (Baird 1997; Calder 1998). Extant (Foraminifera) (Gibling Transgression direction inferred from the inverse of fluvial palaeocurrents embayment within the Maritimes Basin (modified from Ziegler 1988). Maximum flooding (after Calder 1998). (connection of Maritimes Basin to the Tethys Ocean during marine Fig. 7. Joggins palaeogeographical setting. (a) Global palaeogeographical reconstruction (after Scotese & McKerrow 1990) showing putative connection of Maritimes Basin to the Tethys Ocean during marine maximum flooding (after Calder 1998). (b) Reconstruction of central Euramerica at maximum sea level, showing an extensive brackish embayment within the Maritimes Basin (modified from Ziegler 1988). Transgression direction inferred from the inverse of fluvial palaeocurrents (Gibling et al. 1992).

Strong evidence for the existence of a restricted neck to the Maritimes Basin is provided by the occurrence of very thick evaporite successions within the Viséan component of the Maritimes basin-fill (Gibling 1995), whose formation would have required, amongst several necessary factors, limited mixing with the Tethys Ocean.

In addition, the Baltic Sea analogue helps counter one major past objection to the prevalence of brackish-water conditions during the deposition of OW units. $^{87}\text{Sr}/^{86}\text{Sr}$ ratios recorded in aragonitic bivalve shells (0.7094), and palaoniscid (0.7097) and xenanth (0.7103) fish remains from the Joggins Formation (Brand 1994; Falcon-Lang, cited by Calder 1998) fall well outside the range for Langsettian marine faunas (<0.7086; Veizer et al. 1999), a fact that led Brand (1994) to interpret the OW units as deep freshwater lakes. However, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios for the present-day Baltic Sea range from 0.7092 at the near-marine end (35.29‰ salinity) of the system to 0.7097 at the near-freshwater end (2.46‰ salinity), values comparable with the Joggins Formation data (Andersson et al. 1992). The elevated Baltic ratios resulted from fluvial drainage of a granitic cratonic hinterland. As rivers entering the epicontinental sea preserved in the Joggins Formation probably contained similarly enriched $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (Brand 1994), isotopic measurements of fossil skeletal material are entirely consistent with brackish-water conditions. That said, recent models have suggested that $^{87}\text{Sr}/^{86}\text{Sr}$ ratios may be poor indicators of palaeosalinity in marginal-marine systems where riverine input dominates (Flecker et al. 2002).

**Facies 3 and 4a: deposits of a micro-tidal coastline**

These heterolithic deposits probably formed in a seacoast setting as suggested by their gradational contact with the underlying units interpreted as brackish sea deposits (Facies 1 and 2), without any sedimentary breaks. Small channels containing Inclined Heterolithic Stratification (IHS), locally present in Facies 4a, are interpreted as the deposits of small, sinuous channels that migrated by cut-bank erosion and corresponding point-bar growth under fluctuating flow velocities. Although IHS channel-fills have been interpreted as the deposits of seasonally active dryland river systems elsewhere in the Joggins Formation (Falcon-Lang et al. 2004b), the additional occurrence of bimodal flow indicators and local mud drapes, rarely paired, within one channel body at the present site may suggest deposition under weak tidal influence (Thomas et al. 1987). Putative evidence for weak tidal influence within the Joggins Formation is consistent with the partially enclosed epicontinental

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**Table 1. Inferred salinity range of the aquatic fauna in the OW Facies Association based on comparison with other Euramerican sites**

<table>
<thead>
<tr>
<th>Selected aquatic taxa</th>
<th>Facies association</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Trochammina, Ammobaculites</em> and <em>Ammonium</em> (Foraminifera)</td>
<td>These ecologically conservative taxa of agglutinated Foraminifera are characteristic of brackish-water settings (Wightman et al. 1994; Archer et al. 1995)</td>
</tr>
<tr>
<td>Ostracodes (taxonomy currently being revised)</td>
<td>Some Joggins Formation taxa are facies-associated with marine ostracodes at many Westphalian sites in the USA including representatives of the Paraparichthaca, Kloedenellacea, and Bairdiacea (N. E. Tibert &amp; C. P. Dewey, pers. comm.)</td>
</tr>
<tr>
<td><em>Bellinurus</em> (Chelicerates)</td>
<td>This Pennsylvanian taxon is associated with brackish bays (Baird 1997; Calder 1998). Extant horseshoe crabs prefer marginal marine settings with high sedimentation rates such as lagoons or mangroves, but may temporarily exist in freshwater environments (Anderson &amp; Shuster 2003; Towle &amp; Henry 2003)</td>
</tr>
<tr>
<td><em>Naiadites</em> and <em>Curvirimula</em> (bivalves)</td>
<td>These taxa occur above and below marine bands in the British Westphalian (Davies &amp; Trueeman 1927; Trueman &amp; Weir 1946–1968; Eagar 1947), being generally interpreted as brackish-water associations (Anderson et al. 1997)</td>
</tr>
<tr>
<td><em>Gyracanthus, Ageleodus, Xenacanthus, Ctenophtichus, Megalichthys, Sagenodis</em> (fish)</td>
<td>These taxa had very broad environmental tolerances and are generally considered euryhaline (Schneider 1996; Schultz &amp; Chorn 1997)</td>
</tr>
<tr>
<td><em>Pygocephalus</em> and <em>Spirorbis</em> (Crustacea)</td>
<td>These taxa were components of brackish to freshwater crustacean communities (Schram 1981)</td>
</tr>
<tr>
<td><em>Kouphichnium, Arenicolites, Plagutichnus, Haplotichnus, Cochlichnus, Treptichnus</em> and <em>Gordia</em> (trace fossils)</td>
<td>This arthropod–annelid trace fossil assemblage is commonly associated with tidally influenced settings in the mid-continental region of the USA (Feldman et al. 1993; Archer et al. 1994, 1995)</td>
</tr>
</tbody>
</table>
context inferred for the brackish sea deposits. Such settings are characterized by micro-tidal regimes. For example, the Baltic Sea has a tidal amplitude of <10 cm over most of its area. Identification of cryptic tidal signatures in the deposits of such settings is fraught with difficulties, and there has been little discussion as to what constitutes a diagnostic number of tidal indicators (Brettle et al. 2002). Consequently, in the absence of clear lamina-cyclicity (Kvale et al. 1989), the origin of channels with IHS-fills, bimodal paleoflow vectors, and mud drapes, the only examples of their kind in the Joggins Formation (Davies & Gibling 2003), remains cryptic. To date, tidal influence has been inferred for only two other units in the Pennsylvanian basin-fill of eastern Canada (Stellarton and Malagash formations), an interpretation based on the presence of heterolithic strata containing >50% paired mud drapes (Naylor et al. 1998; Costain 2000).

In contrast, the dominant features of Facies 3 (laminated mudstone beds and lenses of siltstone to very fine-grained sandstone), which locally occur in association with the putatively tidal-influenced channel-fills, probably represent coastal deposits. The absence of symmetrical ripple marks indicates that the site of deposition was protected from wave action. Relatively low-energy conditions are indicated by the dominance of laminated mudstone beds, and lenses of cross-laminated siltstone to very fine-grained sandstone indicate periodic unidirectional flows, perhaps representing overbank or levee deposits of adjacent micro-tidal channels. The common occurrence of roots, including upright trees, and small tetrapod trackways on some surfaces, suggests periods of subaerial emergence.

Facies 4b and 5: freshwater coastal plain

Sandstone-filled channel bodies containing inclined stratification (Facies 4b), which cut down into the micro-tidal coastal complex (Facies 3 and 4a), are interpreted as the deposits of small, sinuous distributary channels (Davies & Gibling 2003). The absence of heterolithic stratification and the occurrence of calamiteans and rare sigillarian lycopsids in growth position, interpreted as freshwater plants (DiMichele & Phillips 1994), may indicate a coastal-plain setting further inland than Facies 4a, where brackish-water influence was more restricted or completely absent. Calamitean groves dominated point-bars, persisting in these disturbed settings by virtue of their prolific ability to resprout from underground rhizomes (Gastaldo 1992).

Overlying grey mudstone beds containing Stigmaria and associated with thin coal layers (Facies 5) are interpreted as freshwater interdistributary environments where clastic sediment influx was periodically excluded and rheotrophic mires, dominated by lycopsids, were able to establish.

Fossil forests

Fossil trees in growth position are preserved in coastal deposits (Facies 3), located between 45.8 and 47.4 m in the section (Fig. 4). They were studied in detail to determine the identity of the trees and elucidate aspects of their ecology. During the study interval (summers of 2001, 2002, 2003, and 2004), a total of six trees were observed. Trees first observed during 2001 had almost been destroyed by wave action by 2004.

Tree taphonomy and architecture

The fossil trees have a distinctly different taphonomy and architecture compared with upright lycopsid and calamitean trees, which are more commonly seen in the Joggins Formation (Falcon-Lang et al. 2004a). One important difference is that the trees are not easily detected (Fig. 8a and c). Whereas lycopsid and calamitean trees consist of a coalified, sandstone-cast cylinder infilled by top-down sediment injection, a process that results in a typically clear contrast in sediment grade and colour between the inside and outside of the trunk, the trees described here occur as a coalified structure showing no such contrast. Their poor visibility is emphasized by their mode of discovery. Investigations throughout the Joggins Formation had identified a class of Vegetation-Induced Sedimentary Structures (VISS) formed by current flow around standing trees (Rygel et al. 2004b). When these structures were observed in the second sedimentary rhythm, a targeted search was then made for the presence of upright trees, resulting in the discoveries reported here.

The six fossil trees have preserved trunk heights ranging from 16 to 81 cm (measured from the top of the palaeosol) and basal trunk diameters of 3–18 cm. The trunks of the largest trees show a significant taper, the diameter decreasing by 25% over the lower 35–50 cm. Trunks are composed of a subcircular siltstone-filled pith cavity that increases in diameter from 3 cm at a height of 50 cm to 3.5 cm at the trunk base (Fig. 8d). Despite careful excavation and examination of the pith, no transverse septa were observed. The outer coalified cylinder is woody, very thick (>1.5–2 cm radius), and apparently solid, apart from the pith and a few irregular mudstone- or siltstone-filled cavities that almost certainly represent decay-related features rather than architectural elements. Viewed in cross-section, trunks possess three prominent ridges (buttresses) that increase in radius downward from 2 cm to 5 cm, ultimately flaring out into the rooting system (Fig. 9). Despite SEM analysis of a coalified trunk specimen, no diagnostic wood anatomical characters could be seen, apart from a generic fibrous structure.

The rooting system is preserved in detail for only one of the trees. This example comprises a subvertical (82°) tap root that tapers from c. 10 cm in diameter at the base of the stump to 1–2 cm at a depth of 51 cm below the top of the palaeosol (Fig. 8a and c). A number of smaller (<3.1 cm in diameter) subhorizontally oriented roots also occur, departing from either the tap root or the stump (Fig. 8e). Many of these smaller roots have upward trajectories in the palaeosol profile, and extend laterally for >101 cm from the upright trunk, exhibiting up to four orders of branching. Many of these roots penetrate a 8–14 cm thick siltstone to fine-grained sandstone lens that was demonstrably deposited after the tree established. The relative timing of tree growth and sediment emplacement is indicated both by the position of the stump base beneath the sediment lens and by the presence of VISS within the lens itself, implying flow around the trunk (see below for details). Other smaller trees have less extensive and complex rooting systems (Fig. 8b), but it is unclear whether this difference is ontogenetic or results from incomplete preservation.

Vegetation-Induced Sedimentary Structures

Associated with four upright trunks are what Rygel et al. (2004b) have termed Vegetation-Induced Sedimentary Structures (VISS). These hydrodynamic structures occur in the siltstone to very fine-grained sandstone lenses and sheets that entomb the upright trees. A range of structures occur (Fig. 8a and b). The most common feature is the thickening of sandstone lenses (by up to 300%) on one side of the tree relative to the other. Where ripple cross-lamination is preserved, thickening is always on the downstream side of the tree, and extends in this...
direction for up to several metres. Internal laminations are typically concordant with the mound surface and commonly are upturned where preserved in proximity to the upright trunk (Rygel et al. 2004b).

More complex forms of the same class of VISS comprise erosive scours up to 15 cm deep and 50 cm long on the upstream side of the tree and sediment mounds on the downstream side. The scour profile is typically asymmetric, being steepest on the side adjacent to the tree. In one example, both mounds and scours also occur on the downstream side of the tree, presumably resulting from complex interaction with additional trees not currently exposed in the cliff-section (Rygel et al. 2004b).

Other VISS comprise centroclinal cross-stratification located around the upright tree (Underwood & Lambert 1974); these typically occur on top of the sandstone bed, and are infilled by overlying mudstone layers. Both latter classes of VISS, which comprise erosive features, are associated with trough cross-beds whereas the dominantly accretionary mounds described above are associated with ripple cross-lamination.

**Associated plant assemblages**

Quadrat analysis was undertaken of compressed plant remains preserved on bedding surfaces (Scott 1977; Falcon-Lang 2003a) associated with the upright trees. Because of the difficulty in extracting material from a vertical cliff-section, only 20 cm × 20 cm quadrats were used. Given this relatively small sample area, data should be interpreted with caution. The fossil compo-
nents are described in Table 2. Plants were rare or absent, except in a 2 m thick unit whose base corresponds to the lowest in situ tree horizon in Facies 3, and whose top marks the upper surface of Facies 4a. In this fossiliferous interval, plants were observed on 18 bedding surfaces. Large, unfragmented leaves of *Cordaites principalis* were found to make up 96% (by area cover) of the compressed plant biomass (Fig. 10a and b), the remaining proportion being equally distributed between *Cardiocarpus dawsonii* (2%; Fig. 10c) and *Cordacladus* (2%; Fig. 10d). *Dadoxylon*, preserved as charcoal (Fig. 11), together with *Cordaianthus*, *Alethopteris*, and *Asterophyllites* compressions were represented by either one or two specimens and therefore were a negligible component in the analysis.

Because of their great dominance and the relatively small sample area, meaningful taphonomic patterns could be discerned for only the *Cordaites* remains (Fig. 12). Highest concentrations of *Cordaites* leaves occurred in mudstone beds corresponding approximately to the base of in situ trees (interpreted as the entisolic soil surface), where percentage cover values ranged from 15 to 79% (mean 55.3%; n = 8). Leaves were oriented randomly in these beds and mostly preserved as flat compressions. Lower concentrations of *Cordaites* leaves occurred in the siltstone lenses (3–21% cover; mean 14.8%; n = 5), whereas concentrations in IHS channel-fill units of Facies 4a were more variable (11–63%; mean 27.6%; n = 5). In both of these latter facies-assemblages, *Cordaites* leaves showed localized preferred orientation, and a considerable three-dimensionality seen in the pronounced curvature of the leaf bases.

**Trackways**

Quadrupedal trackways occurred on top of some siltstone lenses associated with the upright trees, especially at 46.45 m (Fig. 13). These comprise tetradactyl manus impressions, 4–6 mm in length, with short, broad digits, and pentadactyl pes impressions, 5–6 mm in length, with long, narrow digits. Trackways are 15–16 mm wide when measured for manus impressions and 18–20 mm wide for pes impressions. Stride length is 17–18 mm with the stride:footlength ratio ranging from 2.8 to 4.5.

In their recent pioneering statistical analysis of tetrapod ichnology, Tucker & Smith (2004) proposed that trackways of this type be classified as *Limnopus* (subgenus *Batrachichnus*), a trace fossil indicative of stem-lissamphibian temnospondyls (Benton 1997; Ruta & Coates 2004). Given the 17–18 mm stride of these trackways, they are assigned to the *Limnopus* ichnospecies *Batrachichnus*.
length, the track maker can have had a total body length of only up to 5 cm. To date, the only preserved skeleton approximating to this size is a juvenile specimen of *Dendrerpeton* illustrated by Milner (1996).

**Similar fossil forests in the Joggins Formation**

Fossil forests closely comparable with those described above also occur at two other intervals in the Joggins Formation. The best documented example was described by Dawson (1855, p. 172), and his illustration is reproduced in Figure 14. Dawson’s fossil tree, which has long since been destroyed by erosion, was probably rooted at 808 m in the Joggins Formation (middle of Rhythm 12). The tree was buried in a heterolithic sandstone and mudstone unit, and underlain by the Joggins Main coal seam and a dark grey, laminated shale containing *Naiadites* and *Spirorbis* (Fig. 14). Applying the nomenclature of Davies & Gibling (2003), the tree was positioned at the boundary between an open water (OW) and poorly drained floodplain (PDF) facies association, a context closely similar to that of the trees described in detail above and interpreted as a brackish coastal setting.

Dawson (1855) referred to his tree as ‘coniferous’ and described it as consisting of a solid coalified trunk. Based on his illustration (Fig. 14), the trunk was 16 cm in diameter (above the zone of basal flare), with a preserved height of 4.6 m. The rooting system was well preserved, shallowly penetrative, and complex, exhibiting at least three orders of branching. Anatomical observations of the coalified wood indicated a pycnoxylic structure, which Dawson (1855) referred to as ‘coniferous’. Although he did not explicitly name the genus of wood observed, it is very probable that the wood was of *Dadoxylon*-type (the only coniferopsid wood he ever described from the Joggins Formation). Dawson (1865) noted that *Cordaites* leaves were abundant in the beds immediately beneath the tree, and that in many cases they were encrusted by *Spirorbis* crustaceans.

More poorly preserved and enigmatic trees (*n = 3*) are currently preserved within one additional interval of the Joggins Formation positioned at 883 m (middle of Rhythm 14). The trees occur close to the OW–PDF boundary (brackish coastal depos-
and one pteridosperm (*Alethopteris*) found in the coastal deposits, two sphenopsids (*Dadoxylon*). In fact, only three non-cordaitalean specimens were containing upright calamiteans.

**Fig. 14.** Putative cordaitalean tree in growth position recorded by Dawson (1855, p. 172) from c. 804–813 m above the base of the Joggins Formation. Bed numbering as follows: Beds 1 and 2, Joggins Main Coal and underclay; Bed 3, grey, laminated mudstone casting lycopsid trunks, together with *Naiaidites* and *Spinorbis*; Beds 4–6, grey laminated mudstone and heterolithic sandstone beds containing putative cordaitalean tree in growth position; Beds 7 and 8, heterolithic sandstone beds containing upright calamiteans.

its), are associated with *Cordaites* leaves, and exhibit morphological features entirely consistent with those already described from 45.8–47.4 m and 808 m in the Joggins Formation.

**Tree identity, architecture and palaeoecology**

The identity of the upright trees rooted in the coastal deposits at 45.8–47.4 m in the Joggins Formation, together with the two additional occurrences at 808 m and 883 m, is indicated primarily by associated compression fossils. In the lowermost fossil forest (45.8–47.4 m), megafloral assemblages in mudstone beds corresponding to the base of the trees are interpreted as parautochthonous leaf litter layers, an interpretation supported by the random orientation of leaves. The high abundance (up to 79% cover) and overwhelming dominance (96%) of *Cordaites* leaves in litter layer accumulations strongly implies a cordaitalean affinity for the trees. This interpretation is further strengthened by the composition of the remaining fossil component that comprises cordaitalean branches (*Cordaicladus*), reproductive structures (*Cardiocarpus* and *Cordaianthus*), and wood (*Dadoxylon*) specimens, representing almost every organ of a cordaitalean tree. In fact, only three non-cordaitalean specimens were found in the coastal deposits, two sphenopsids (*Asterophyllites*) and one pteridosperm (*Alethopteris*).

Further indication of cordaitalean affinity is given by the anatomy and architecture of the upright trees. For example, the identity of the tree at 808 m is indicated by its *Dadoxylon* woody trunk, a feature considered to be distinctively cordaitalean in the Joggins Formation (Falcon-Lang 2003c). Although anatomical details are not preserved in the other trees, they exhibit several general architectural features of diagnostic value. The trunks, being characterized by a large pith cavity and a complex adventitious rooting system (see below), are inconsistent with known Pennsylvanian calamitean and lycopsid architecture (Eggert 1962; Phillips & DiMichele 1992), the only taxa previously described as upright trees within the Joggins Formation. Although the tree architecture is superficially comparable with some medullosan pteridosperm whole-plant reconstructions (Stewart & Rothwell 1993), the circular pith, of 3 cm diameter, is more suggestive of cordaitalean affinity (Rothwell 1988). Assuming that the non-septate nature of the pith cavity is an original feature (i.e. not a taphonomic artefact), the tree might be related to *Mesoxylon priapi* (Trivett & Rothwell 1985) or other, as yet unknown, non-septate cordaitalean taxa.

It is difficult to confidently reconstruct the size of these cordaitalean trees. Based on biomechanical trunk diameter–height relationships (Niklas 1994), the trees had maximum buckling heights of the order of 4–16 m (basal diameter range 3–18 cm); however, given observed basal trunk taper, they were probably significantly shorter (perhaps up to 5 m). The best morphological descriptor for these monopodial plants is ‘small tree’ rather than ‘shrub’, the latter term usually being restricted to multi-stemmed plants (Allaby 1992).

Based on the overwhelming dominance of *Cordaites* leaves in Facies 3, and given tree spacing in the 2D cliff-section (*Fig. 5*), these small cordaitalean trees formed a monotypic stand on the edge of the Maritimes brackish sea, colonized by small stem-lissamphibian temnospondyls. However, Pennsylvanian vegetation possessed a very fine-scale heterogeneity (Gastaldo et al. 2004), and given the small area sampled in the quadrat analyses, it is difficult to assess whether the trees were part of widespread cordaitalean coastal forest or merely represented an isolated cluster within a more heterogeneous mosaic. Given that autochthonous cordaitalean trees occur at three intervals in the Joggins Formation, each in a closely similar facies context (brackish coastline), and never co-occurring with other trees, the former interpretation, that these represent cordaitalean-dominated coastal forests, would seem to be the most likely.

Tree growth was frequently disturbed by unidirectional, sediment-laden floodwaters as indicated by VISS developed at multiple intervals around several upright trees (Rygel et al. 2004b), although the presence of tetrapod trackways on some surfaces indicates that the forests were not permanently submerged in water. Some trees evidently persisted through flood events, responding to partial burial by infiltrating newly deposited sediment lenses by adventitious rooting systems. Adventitious and upward-oriented root systems are features characteristic of several extant conifer species that grow in flood-prone conditions (Kozlowski 1984). In such setting the root systems colonize aerated upper soil layers and exploit nutrients in flood-deposited sediments (Stone & Vasey 1968; Yamamoto 1992). Although periodic floods were of sufficiently high velocity to produce trough cross-beds in very fine-grained sand, there is limited evidence of significant flood damage (one specimen shows pronounced tilt). Stump buttressing seen in the cordaitalean trees may have increased their flood-stability, as in some modern tropical forests (Crook et al. 1997).

**Cordaitalean mangroves?**

As outlined in detail in the introduction, cordaitaleans possessed a very broad ecological amplitude. This group, which included scrambling shrubs to giant forest trees, flourished in wetlands,
drylands, and uplands across the Pennsylvanian tropical zone (DiMichele et al. 2001). The plant assemblage described here represents the remains of only one of probably many tens of cordaitalean species, and it should be clear that the following palaeoecological inferences refer only to that particular plant, and not to cordaitaleans in general.

The small cordaitalean trees described from the Joggins Formation grew on a protected coastline dissected by sinuous drainage channels adjacent to a micro-tidal brackish sea (Fig. 15). In the best-studied interval, the lowest cordaitalean tree (45.8 m) is rooted 2.9 m above the highest faunal indicator of brackish-water conditions (42.9 m). Consequently, although trees grew proximal to the seacoast, there is no direct evidence for brackish incursions into these forested regions. However, the occurrence of IHS channel-fills adjacent to the forest interval, which were putatively formed under weak tidal influence, may provide some indirect evidence for marine influence because micro-tidal processes would have presumably resulted in brackish incursions further inland (Leeder 1982). Additional tacit evidence for brackish incursions in the cordaitalean forests is present in the fossil forests at 808 m in the Joggins Formation, where *Cordaites* leaves are encrusted by putatively brackish-water crustaceans (Dawson 1865). However, as the salinity range of *Spirorbis* is poorly known, this interpretation is uncertain (Table 1).

Whether the cordaitalean forests within the Joggins Formation do indeed represent true mangrove communities (i.e. trees adapted to growth in marine-influenced waters) can be further assessed with reference to modern ecosystems. Although the mangrove habit is exclusive to the angiosperms at present, its occurrence in a variety of unrelated lineages suggests that it represents a general adaptation to specific selective pressures (Hogarth 1999), and therefore in favourable circumstances might also evolve in non-angiosperm groups. Mangrove trees exhibit specific physiological adaptations to soil anaerobia and elevated salinity, responses that are expressed through gross morphological features (roots and leaves), and therefore may be preserved in the fossil record.

In permanently waterlogged substrates, microbial respiration quickly results in soil anaerobia in many coastal marine areas. Mangrove trees are adapted to these challenging conditions by producing shallow, horizontally oriented root systems with vertical, subaerial pneumatophores, which may stand up to 30 cm above water level in some species. Both root system and trunk have lenticels (gas exchange pores) and aerenchyma (interconnected air-filled spaces), the former features comprising up to 51% of the volume of some mangrove roots. Together with adventitious rooting in response to partial burial in sediments, these features facilitate adequate oxygen supply to the mangrove tree, requisite for respiration (Hogarth 1999).

Mangrove trees also are adapted to elevated salinity by modification to the rooting system and leaves. Submerged in fully marine waters, trees have to take up water against a large osmotic potential (~2.5 MPa), and consequently have to invest in a very large root mass. The proportion of tree biomass situated below ground increases with rising salinity so that the roots of trees growing in brackish waters (5–20‰) may typically constitute 40% of the tree biomass, whereas in near fully marine conditions (35‰) a value close to 65% may be attained. Stomatal conductance also is limited in mangrove leaves, thereby reducing

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**Fig. 15.** Palaeoenvironmental reconstruction showing putative cordaitalean mangroves occupying a brackish bay margin setting at Joggins. Reconstruction based, in part, on micro-tidal Niger Delta (modified from Leeder 1982, fig. 19.13).
water loss by evapotranspiration. Two consequences of this are that mangrove leaves are typically small (at low stomatal conductance large leaves would overheat) and tree growth rate is slow, as CO₂ uptake is also limited by reduced stomatal conductance (Hogarth 1999).

As these morphological features represent adaptations to general physiological problems, one might expect unrelated groups such as Pennsylvanian cordaitaleans to exhibit similar features if they were utilizing a mangrove strategy. The cordaitalean trees do appear to show adaptation to soil anaerobia as indicated by shallow, horizontally and upward oriented roots, although no pneumatophore-like structures occur. Additionally, some permineralized coal ball species such as *Pennsylvanioxylon birame* show adventitious roots with lenticels and aerenchyma (Cridland 1964; Costanza 1985). However, all these features only demonstrate adaptation to periodically submerged conditions in general, and not to mangrove (saline) conditions specifically.

The ratio between above- and below-ground biomass is very hard to accurately assess for the Joggins cordaitaleans because of incomplete preservation. However, assuming conservative height estimates of 5 m for the largest, best preserved tree (30% of the maximum buckling height), below-ground rooting systems that penetrate to soil depths of up to 51 cm are unlikely to constitute more than 30% of the tree biomass, and perhaps <15%, values lower than those normally seen in mangrove communities (>40%). Although low shoot:root ratios (0.15) have been observed in some Pennsylvanian cordaitalean-dominated coal balls (DiMichele & Phillips 1994), values are highly variable (Raymond 1987, 1988), and probably reflect a variety of taphonomic factors including peat accumulation rates and differential decay. Consequently, root:shoot ratios measured in coal balls cannot be directly related to the ratio of original above- and below-ground biomass.

Another important contrast with mangrove trees is that the cordaitaleans from the Joggins Formation have very large, broad leaves (typically >30 cm long and 4–5 cm wide). It is difficult to see how such large leaves could avoid catastrophic overheating in a tropical climate if the trees were growing in saline soils and stomatal conductance was consequently limited. Nevertheless, without detailed knowledge of cuticular architecture, this argument is somewhat speculative.

Synthesizing this discussion, it is evident that although the cordaitalean trees described from the Joggins Formation grew on a micro-tidal coast adjacent to a brackish sea, and were clearly adapted to periodically submerged conditions, indicators of a mangrove habit are lacking. Specifically, direct evidence for marine influence in the fossil forest layers is absent, and several key physiological adaptations to growth in brackish waters are lacking. Consequently, it is inappropriate to apply the term ‘mangrove’ to these fossil forests in its strict usage.

(4) Nevertheless, these results extend our knowledge of the ecological amplitude of the cordaitaleans, one of the most important Pennsylvanian plant groups, clearly demonstrating that some species grew in a seaward setting.

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Conclusions

(1) Small upright trees discovered in the Lower Pennsylvanian (Langsettian) Joggins Formation of Nova Scotia are identified as cordaitaleans based on associated parautochthonous leaf litter assemblages and trunk anatomy and architecture.

(2) Sedimentary facies analysis indicates that these cordaitalean trees grew on the coastal margins of an open water body interpreted as an extensive brackish epicontinental sea. Trunk buttressing and adventitious root systems imply growth in flood-prone, but not permanently submerged, conditions.

(3) Although the trees grew immediately adjacent to a brackish sea, direct evidence for marine influence in the fossil forest layers is absent, and several key physiological adaptations to growth in brackish waters are lacking. Consequently, it is inappropriate to apply the term ‘mangrove’ to these fossil forests in its strict usage.

(4) Nevertheless, these results extend our knowledge of the ecological amplitude of the cordaitaleans, one of the most important Pennsylvanian plant groups, clearly demonstrating that some species grew in a seaward setting.

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