Journal of the Geological Society

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Notes

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HOWARD J. FALCON-LANG[1] & RANDALL F. MILLER[2]

[1]*Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK (e-mail: howard.falcon-lang@bris.ac.uk)*
[2]*Natural Science Department, New Brunswick Museum, 277 Douglas Avenue, Saint John, N.B., E2K 1E5, Canada*

Abstract: The Pennsylvanian Lancaster Formation ('Fern Ledges') of Saint John, New Brunswick, Canada contains a world-famous fossil biota. Largely unstudied since the works of Hartt, Dawson, Matthew, and Stopes in the mid-nineteenth to early twentieth century, we present new data concerning biostratigraphy, taxonomy, palaeoenvironments, and palaeoecology. Megafloral assemblages suggest a mid- to late Langsettian age for the succession, making it approximately coeval with the classic Joggins Formation of nearby Nova Scotia. Facies analysis suggests deposition on a tectonically influenced coastal plain whose braided channels drained into a shallow brackish gulf. Most of the historical fossil collections are derived from flooding surfaces formed by abrupt subsidence events along the coastline. Three communities are recognized. Phoronids, crustaceans, and xiphosurans lived in brackish coastal waters. A lowland community of gastropods, insects, arachnids, and myriapods inhabited coastal forests. Coastal vegetation was dominated by shrubby cordaitaleans and pteridosperms whereas ferns, sphenopsids, and lycopsids were rare. An upland or dryland community, discernible from allochthonous assemblages, comprised forests of giant cordaitaleans, archaic pteridosperms, and plants of uncertain affinity.

The Pennsylvanian Lancaster Formation of New Brunswick (which includes the famous 'Fern Ledges' locality) has an important place in the annals of palaeontology (Falcon-Lang & Miller 2007). Initial discovery of fossil plants (Gesner 1840) was followed, in 1860–1863, by the documentation of a rich biota by C. F. Hartt and G. F. Matthew (Dawson 1861, 1862, 1868), and other members of the Natural History Society of New Brunswick. Of special interest was the occurrence of insects, one specimen preserving a putative stridulating organ (Scudder 1868*a*, *b*). This fact allowed Darwin (1871) and others to imagine primeval forests alive with chirping (Miller & Buhay 1988).

The age of the Lancaster Formation was, at first, controversial, being assigned to the Devonian Period (Dawson 1861, 1862, 1871), and subsequently to the Silurian Period (Matthew 1910*a*, *b*). However, repeated protests that plant remains were clearly of Pennsylvanian age (Hagen 1881; Ami 1900*a*, *b*; White 1902, 1911) eventually led the Geological Survey of Canada to approach Marie Stopes to resolve the debate. Her classic monograph (Stopes 1914) confirmed the Pennsylvanian age of the succession once and for all (Falcon-Lang & Miller 2007).

Subsequently, the fossil biota received almost no scientific study, although the systematic position of a few taxa has been revised (e.g. Bell 1944; Copeland 1957; Hantzschel 1975; Robbins 1994; Miller 1995*a*, *b*; Wagner 2001, 2005*a*, *b*). The aim of this paper is to improve knowledge of the geological setting, taxonomy, biostratigraphy, palaeoenvironment and palaeoecology of the site.

## Stratigraphic nomenclature

The Pennsylvanian rocks of Saint John were first mapped as Little River Group, and subdivided into the Dadoxylon Sandstone and Cordaites Shale members (Dawson 1868). Later attempts to map these members regionally (Ells 1907) proved unsuccessful and their usage was abandoned. The Little River Group was renamed the Lancaster Formation by Ami (1900*a*, *b*), and Alcock (1938) extended the concept to include beds near Saint Martins and Musquash Harbour, southern New Brunswick. However, the Saint Martins sections were subsequently placed in the Tynemouth Creek Formation (Hayes & Howell 1937; Plint & van der Poll 1982) whereas the Musquash Harbour sections were recognized as belonging to a younger, as yet, unnamed unit (van der Poll 1995). In this paper, the term Lancaster Formation is restricted to Pennsylvanian rocks near Saint John. This *c.* 400 m thick unit conformably overlies the Mississippian(?) Balls Lake Formation in its central area (Currie & Nance 1983), and unconformably oversteps Neoproterozoic rocks towards the SE and NW (McLeod *et al.* 1994*a*, *b*).

Geological setting

Understanding tectonic context is essential for interpreting the palaeoenvironment of the Lancaster Formation. Basement rocks in this part of eastern Canada include the Avalon and Meguma terranes, which accreted during the mid-Devonian Acadian Orogeny (Gibling 1995). The terrane boundary is defined by the Fundy–Cobequid Fault, which was reactivated during Late Devonian times as a result of the far-field effects of Gondwanan convergence. The palaeotropical Maritimes Basin developed along this fault axis in response to dextral strike-slip, and comprised several sub-basins (Calder 1998).

The Lancaster Formation accumulated within the small (55 km by 220 km) Cumberland sub-basin, which straddles northern Nova Scotia and SE New Brunswick, bounded along its SE margin by the Fundy–Cobequid Fault (Fig. 1a–c). Alluvial fan deposits dominate basin-fill adjacent to this fault-line. Closer to the basin centre, alluvial plain, coastal plain, and brackish bay facies are common (Davies *et al.* 2005). These latter sediments mostly formed in a paralic setting with fluvial systems draining northeastwards (Gibling *et al.* 1992) into a mid-European sea
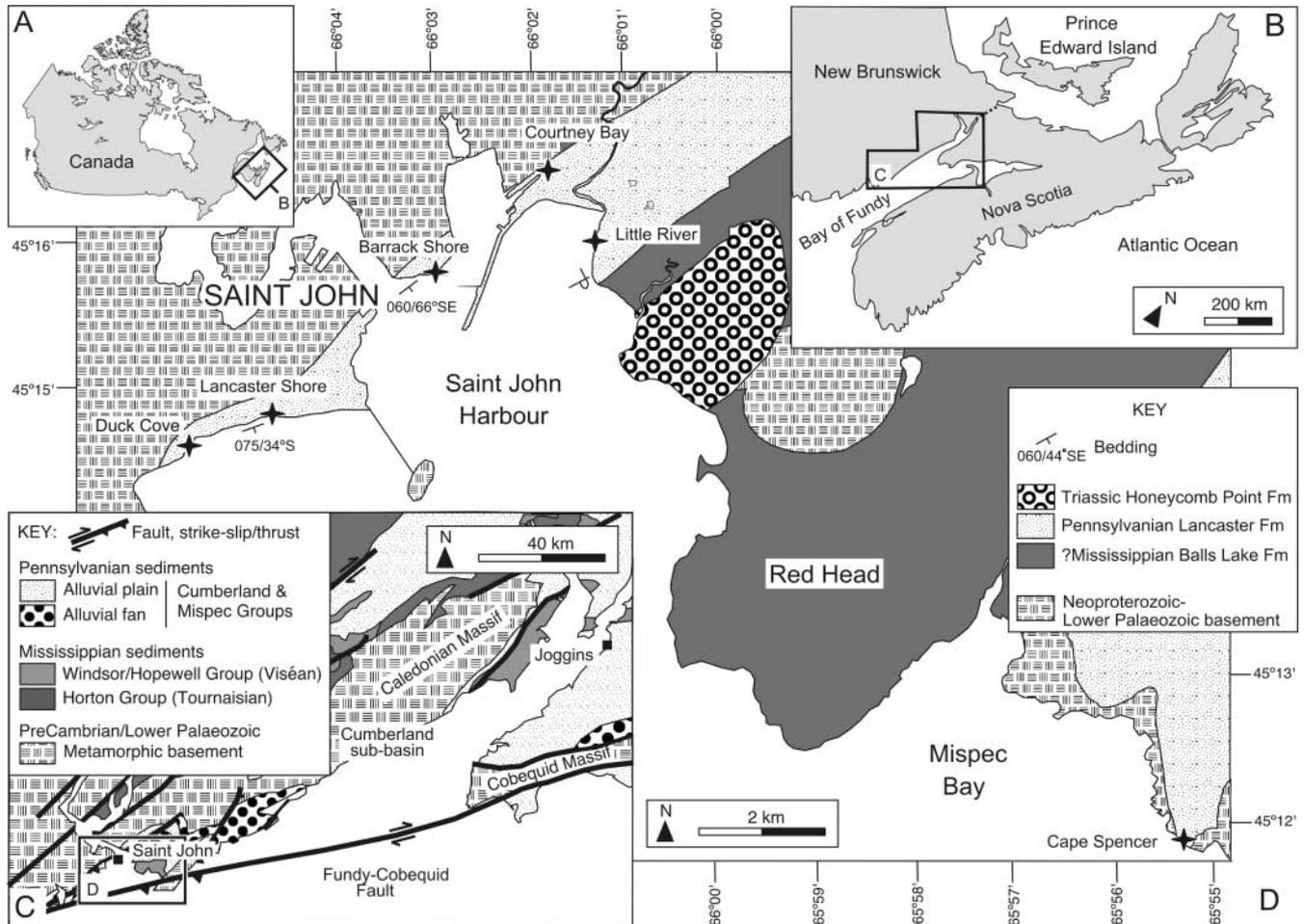
Fig. 1. Geological setting. Location details in eastern Canada (**a**) and southern New Brunswick (**b**). (**c**) Geology of Cumberland sub-basin (after Falcon-Lang 2006b). (**d**) Geological map of the Saint John region showing the main localities studied (modified after McLeod *et al*. 1994a, b).

(Calder 1998), the inferred source of the brackish transgressions (Falcon-Lang 2005).

The Lancaster Formation was deposited near the western end of the Cumberland sub-basin, where a restraining bend of the Fundy−Cobequid Fault inhibited dextral offset (Yeo & Gao 1986). In this compressional setting (Fig. 1c), the formation became locally overturned within a fold and thrust belt (Rast *et al*. 1984). Chlorite spots (Nance 1987) and black palynomorphs (spore alternation index of 10; Dolby 1989) imply upper greenschist-facies metamorphism (van der Poll 1995) consistent with fossil plant preservation as highly altered graphitic streaks lacking cuticles (Stopes 1914).

Study material

More than 8000 fossil specimens were collected from the Lancaster Formation by the Natural History Society of New Brunswick (Miller & Buhay 1988). These are almost entirely plants (>99%), with fewer than 70 specimens of fauna known. The historical collections derived from coastal outcrops at Duck Cove [UTM 19T 728325 5014150], Lancaster Shore, also known as 'Fern Ledges' [UTM 19T 728963 5014433], Barrack Shore [UTM 19T 731157 5016428], and Little River [UTM 19T 733202 5017677; Map Sheets NTS 21 G/01E, NTS 21 H/05]. We studied sedimentary facies and fossil taphonomy at each of these sites, in addition to outcrops at Courtney Bay and Cape Spencer (Fig. 1d).

During his work on the most prolific fossil site at Lancaster Shore,

Hartt (in Dawson 1868) produced a bed-by-bed record of fossil assemblages, recognizing eight principal fossil beds (LS1−8). As well as recording alpha diversity, Hartt noted the relative abundance of each taxon using a semi-quantitative scheme (simplified in Table 1 as rare, occasional, common, and abundant). We identified five of Hartt's fossil beds (LS1, 2, 3, 4? and 8) at Lancaster Shore. As a consequence, most fossil collections (reviewed below) can be assigned to our facies scheme.

Megafloral remains

Stopes (1914) was the last worker to fully revise fossil plant systematics, although a few taxa have subsequently been restudied (Bell 1944; Wagner 2001, 2005a, b). A primary revision of the plant assemblage is beyond the scope of this paper (this work is being undertaken by R. H. Wagner). Here we merely collate an updated taxonomic list, and give relative abundance data for each taxon at Lancaster Shore (Table 1). Taxa were fully illustrated by Stopes (1914).

Dominance−diversity characteristics

Cordaitaleans overwhelmingly dominate the assemblage, and *Cordaites* leaves are especially abundant. The true diversity of *Cordaites* is difficult to assess because of their conservative morphology, but at least two species are present: *C. principalis*

Table 1. *Taxonomic list of fossil plants from the Lancaster Formation updated from Stopes (1914), and giving the relative abundance of each taxon at Lancaster Shore (after Hartt, in Dawson 1868)*

Plant taxon (revised from Stopes 1914)	Hartt's beds (in Dawson 1868)								Abundance
	1	2	3	4	5	6	7	8	
Class Lycopsida									
cf. *Lepidodendron* sp.		R					R	R	Rare
cf. *Sigillaria* sp.		R							Rare
Stigmaria ficoides Brongniart									Rare
Class Sphenopsida									
Annularia sp.		A	C				A		Common
Annularia stellata (Schlotheim) Wood	A	R	C						Common
Asterophyllites equisetiformis Brongniart	A	R			C		C	O	Common
Asterophyllites grandis (Sternberg) Göppert		O							Occasional
Calamites sp.	A	O	O		O	A		O	Common
Calamites suckowii Brongniart	A	O					R	C	Common
Paracalamostachys sp.		R							Rare
Pinnularia sp.									Rare
Sphenophyllum ?cuneifolium (Sternberg) Zeiller									Rare
Class Filicopsida									
Lobatopteris miltoni (Artis) Wagner							R		Rare
Oligocarpia brongniartii Stur									Rare
Renaultia (Sphenopteris) rotundifolia Andrä (Zeiller)		C	R		C		C		Common
Senftenbergia plumosa (Artis) Stur							R		Rare
Sphenopteris valida Dawson									Rare
Class ?Progymnospermopsida									
Pseudadiantites rhomboideus Ettingshausen (Wagner)		A	O				O	O	Occasional
Class Cycadopsida									
Alethopteris discrepans Dawson		R	C		C	A	A	A	Abundant
Alethopteris lancifolia Wagner		A							Occasional
Cyclopteris sp.									Rare
Diplothmema furcatum (Brongniart) Stur		A					R	R	Occasional
Laveineopteris loshii (Brongniart) Cleal *et al.*		A	C		A	A	O	O	Abundant
Lyginopteris hoeninghausii (Brongniart) Gropp		C	R						Rare
Megalopteris dawsonii Hartt				R					Rare
Neuralethopteris schlehanii Stur (Cremer)									Rare
Paripteris gigantea (Sternberg) Gothan									Rare
Pteridospermostrobus bifurcates Stopes									Rare
Rhacopteris busseana Stur		R							Rare
Whittleseya dawsoniana White		R							Rare
Whittleseya brevifolia White									Rare
Class Coniferopsida									
Artisia transversa Artis (Presl)				(Facies 1 and 2)					Occasional
Cordaites borassifolius Sternberg (Unger)		A	A	A	A	A	A	A	Abundant
Cordaites principalis (Germar) Geinitz		A	A	A	A	A	A	A	Abundant
Cordaianthus devonicus Dawson		R							Rare
*Cardiacarpus*4 sp.	R	A	O	R		A	C	O	Common
Dadoxylon ouangondianum Dawson				(Facies 1 and 2)					Common
Dicranophyllum glabrum Dawson		O	O	R	C				Occasional
Poacordaites sp.									Rare

Semi-quantitative descriptors are used: R, rare; O, occasional; c, common; a, abundant.

and *C. borassifolius*. A third type of cordaitalean leaf, *Poacordaites*, is rare. Other cordaitalean remains include *Dadoxylon ouangondianum* tree-trunks (Dawson 1868; Matthew 1910*a*) with *Artisia*-type piths, *Cardiacarpus* (four species) ovules and *Cordaianthus* fertile axes.

Of the remaining gymnosperms, medullosan pteridosperms are also abundant and include abundant *Alethopteris* (two species) and *Laveineopteris loshii*, together with rare *Megalopteris dawsonii*, *Neuralethopteris schlehanii*, *Paripteris gigantea*, and various fertile organs. Archaic pteridosperms include *Rhacopteris*. The coniferopsid, *Dicranophyllum* is occasionally present.

Of the pteridophytes, sphenopsids are the most common plants, represented by *Calamites* axes (two species) and foliage of *Annularia* (two species) and *Asterophyllites* (two species) types. *Sphenophyllum* is very rare. Ferns are also rare although they comprise a diversity of arborescent and herbaceous forms including *Lobatopteris*, *Oligocarpia*, *Renaultia*, *Senftenbergia*, and *Sphenopteris*. Remains of arborescent lycopsids and putative progymnosperms (*Pseudadiantites*) are extremely rare.

Biostratigraphic implications

Comparison of our updated megafloral list (Table 1) with range charts for European taxa allows for biostratigraphic inferences. In key reference sections in central England (Cleal 2006) and Wales (Cleal 2007), several taxa in our assemblage either have a first appearance datum in the early or late part of the Langsettian substage of the Westphalian or a last appearance datum in the late Langsettian (Fig. 2); however, a few of these taxa originate earlier in central Europe. Ranges suggest a mid- to late Langsettian age (*Laveineopteris loshii* subzone of Cleal 1991), although taxonomic revision (R. H. Wagner, pers. comm.) may
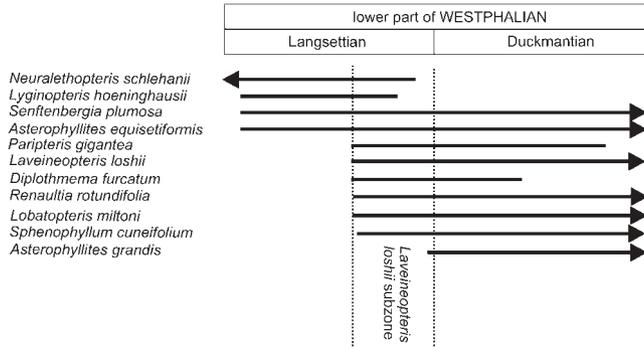
Fig. 2. Composite biostratigraphic ranges of 11 significant plant taxa in the Lancaster Formation compared with their occurrence in reference sections in England (Cleal 2006) and Wales (Cleal 2007). Ranges indicate a mid- to late Langsettian age.

alter these findings. The Lancaster Formation is therefore coeval, in part, with the mid-Langsettian Joggins Formation at the eastern end of the Cumberland sub-basin in Nova Scotia (Falcon-Lang 2006a; Falcon-Lang *et al.* 2006).

Fauna remains

In contrast to the abundant plants, fewer than 70 specimens of fauna are known. Many specimens, once thought lost, have now been rediscovered, and we provide a list of museum numbers (Table 2). Fossils are generally poorly preserved, and many are considered dubious taxa (Hantzschel 1975). As the fauna has

never been properly monographed, we provide a photographic record of the best specimens (Fig. 3).

Aquatic fauna

The aquatic fauna includes phoronids, crustaceans and xiphosurans (Table 2). One of the most common taxa is *Spirorbis erianus* (Matthew 1895*a*), a probable synonym of *Spirorbis carbonarius* (Fig. 3a), encrusted on *Cordaites* leaves. Recent work has shown they are 'spirorbiform microconchids' related to phoronid worms (Taylor & Vinn 2006).

Crustaceans are represented by *Amphipeltis paradoxus* (Salter 1863) (Fig. 3b), described from a single specimen with a second found later (Matthew 1895*b*), and *Leaia silurica* (Matthew 1910*b*) (Fig. 3c), a branchiopod (Copeland 1957). A third taxon, *Asmussia* (Copeland 1957), has been excluded as locality data confirm that specimens are of Mississippian age.

Xiphosurans were recognized based on *Belinuropsis wigudensis* (Matthew 1910*b*). Re-examination of type material shows that this genus was erected from two specimens that cannot be reunited as illustrated by Matthew (Miller 1995*b*). One is indeterminate and the other is arthropod cuticle (Fig. 3d; S. J. Braddy, pers. comm.) of possible, but uncertain, affinity to eurypterids (W. Shear, pers. comm.). Despite the dubious nature of *Belinuropsis*, trackways of *Kouphichnium* showing 'pusher prints' (Fig. 3e) provide independent support for the existence of xiphosurans in the Lancaster Formation and are known from equivalent facies elsewhere in the Cumberland sub-basin (Archer *et al.* 1995; Falcon-Lang 2005).

Although eurypterids were reported we consider these occurrences as questionable. Their record is based, in part, on

Table 2. *Taxonomic list of fauna from the Lancaster Formation updated from various sources*

Faunal remains	Specimen number	Bed number
Phylum Mollusca		
Class Gastropoda		
Order Pulmonata (land snails)		
Dendropupa grandaeva (Dawson)	RM 2384	LS2
Dendropupa primaeva (Matthew)	NBMG 3332	LS2
Phylum Phoronida		
'Spirorbiform microconchids'	NBMG 3333–3335	L
Phylum Arthropoda		
Subphylum Hexapoda		
Class Insecta		
Subclass Pterygota		
Infraclass Paleoptera		
Order Paleodictyopterida		
Archaeoscolex corneus Matthew	NBMG 3008	LS2
Dyscritus vetustus Scudder	NBMG 3009	LS8
Pseudohomothetus fossilis (Scudder)	NBMG 3014	LS8
Order Protodonata		
Aedaeophasma acadica Matthew	NBMG 3007	LS
Platephemera antiqua Scudder	NBMG 3016	LS7
Infraclass Neoptera		
Superorder Endopterygota		
Order (?)Miomoptera		
Geroneura wilsoni Matthew	NBMG 3011, GSC 8135	LS2
Xenoneura antiquorum Scudder	NBMG 3018, MCZ 8268	LS2
Order Incertae sedis		
Gerephemera simplex Scudder	NBMG 3010, MCZ 8627	LS2
Lithentomum harttii Scudder	NBMG 3015, MCZ 3853	LS8
Pseudohomothetus erutus (Matthew)	NBMG 3013, GSC 8135	LS8
Subclass Incertae sedis		
Archaeophasma grandis Matthew	NBMG 12154	LS
Geracus tubifer Matthew	NBMG 3012	LS2
Podurites saltator Matthew	NBMG 3017	LS2

(*continued*)

Table 2. (*continued*)

Faunal remains	Specimen number	Bed number
Subphylum Crustacea		
Class Branchiopoda		
Order Phyllopoda		
Leaia silurica Matthew	NBMG 4573a	below LS2
Class Malacostraca		
Amphipeltis paradoxus Salter	NHM In.60441, NBMG 3001	LS2
Subphylum Myriapoda		
Class (?)Diplopoda (millipedes)		
Euphoberia atava Matthew	NBMG 3022	LS8
(?)*Euphoberia* sp.	NBMG 3309–3313	LS2
Order Arthropleurida (?)		
(?)*Eurypterus pulicaris* Salter	NHM uncat., NBMG 3315	LS2
Class Chilopoda (centipedes)		
Chilopus dubius Matthew	NBMG 3019	LS2
(?)*Xylobius* sp.	NBMG 1762	LS
Class Incertae sedis		
Beaconites isp.	Not collected	LS, DC
Diplichnites gouldi Trewin & McNamara	NBMG 3024–3034	BS
(?)*Eileticus antiquus* Matthew	NBMG 3020	LS2
(?)*Palaeocampa obscura* Matthew	NBMG 3023	LS2
Subphylum Chelicerata		
Class Arachnida		
Order Incertae sedis		
Eurymartus latus Matthew	NBMG 3003	LS2
(?)*Eurymartus spinulosus* Matthew	NBMG 3004	LS2
Eurymartus sp.	NBMG 3005	LS8
(?)*Eurymartus*	NBMG 3314	LS2
Order Trigonotarbida(?)		
Eurypterella ornata Matthew	NBMG 3002	LS2
Class Merostomata		
Order Xiphosura (horseshoe crabs)		
Kouphichnium isp.	NBMG 13915	LS, DC
Subphylum Incertae sedis		
Belinuropsis wigudensis Matthew	NBMG 3307–3308	DC
Phylum Annelida		
Class Incertae sedis		
Planolites montanus Richter	Not collected	DC
Phylum Chordata		
Superclass Tetrapoda (dubious tetrapod tracks)		
(?)*Hylopus variabilis* Matthew	NBMG 3041–3043	LS
(?)*Nanopus vetustus* Matthew	NBMG 3045	LS

L, Lancaster Formation, locality unknown; LS, Lancaster Shore; LS number, Hartt's fossil bed number at Lancaster Shore; DC, Duck Cove; BS, Barrack Shore; RM, Redpath Museum, Montreal; NBMG, New Brunswick Museum, Saint John; GSC, Geological Survey of Canada, Ottawa; MCZ, Museum of Comparative Zoology, Harvard; NHM, Natural History Museum, London (some material is uncatalogued).

Eurypterella ornata (Matthew 1889). Hantzschel (1975) thought this was a dubious taxon, whereas Tetlie (2004) considered it to be a trigonotarbid. The eurypterid status of a second specimen, *Eurypterus pulicaris* (Salter 1863), has also been questioned (Matthew 1896, 1897), and it has been considered a possible arthropleurid limb (Briggs *et al*. 1979). In our view, there are no unequivocal eurypterids in the assemblage.

Matthew (1910*b*) described *Bipezia bilobata* as a vertebrate trace. Glaessner (1957) considered it to be an invertebrate resting trace synonymous with *Isopodichnus* (= *Oniscoidichnus*). Examination of the type specimens casts doubt that either is a fossil, although NBMG 3038 (Matthew 1910*b*, plate IV, fig. 2) might be an arthropod resting trace.

Terrestrial fauna

The terrestrial fauna comprises gastropods, insects, arachnids, and myriapods (Table 2). Two taxa of terrestrial gastropods, initially described as *Strophites grandaevus* (Dawson 1880) and *Pupa primaeva* (Matthew 1895*a*) (Fig. 3f), were later transferred to *Dendropupa*; they are suspected synonyms of *D. vestusta* (Solem & Yochelson 1979).

Matthew (1895*c*) recognized myriapod specimens including the millipede, *Euphoberia atava* (Fig. 3g) and the centipede, *Chilopus dubius*. The latter is poorly preserved but exhibits 11–12 segments with vague indications of legs. Some tergites appear to be posteriorly notched, possible evidence of scutigeromorph centipede affinities (W. Shear, pers. comm.). Other putative myriapods are poorly preserved; the placement of *Eileticus antiquus* and *Palaeocampa* is uncertain, although the latter has not been re-examined (Hoffman 1969) (W. Shear, pers. comm.). *Eurypterus pulicaris* (Salter 1863), as noted above, may represent an arthropleurid limb (Briggs *et al*. 1979), and *Beaconites* isp., discovered by us, may be an arthropleurid aestivation burrow (Morrissey & Braddy 2004).

Trackways earlier named as *Acripes incertipes*, *A. leavitti* and *A. minor* (Matthew 1910*b*) or *Diplichnites* (Hantzschel 1975; Robbins 1994) are here referred to as probable *Diplichnites gouldi* Type A (Fig. 3h and i; Smith *et al*. 2003). Some specimens demonstrate en echelon sets (≤8–10 long) and
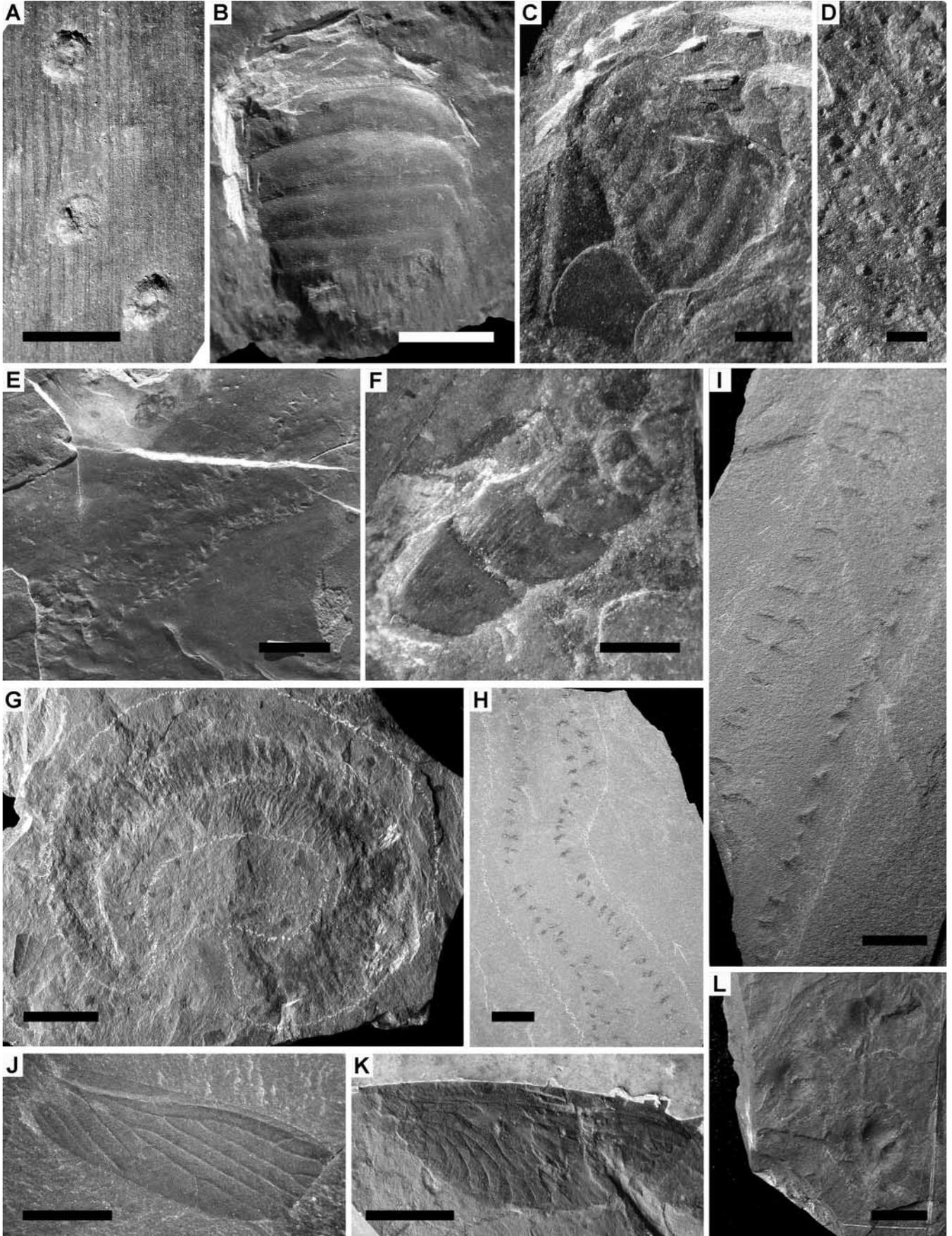
v-shaped appendage marks along part of their length, and represent myriapod walking traces.

Putative arachnids include *Eurymartus spinulosus* (Matthew 1895*b*), which comprises a poorly preserved abdomen, and *E. latus* (Matthew 1895*b*), a more or less complete abdomen, too poorly preserved to name (W. Shear, pers. comm.). Matthew placed *Eurymartus* in the Order Eurymarti, not recognized by later workers. As noted above, *Eurypterella ornata*, originally described as a eurypterid, may be a trigonotarbid arachnid (Tetlie 2004).

Scudder (1868*a*, *b*, 1880, 1885) described insect remains, with later additions by Matthew (1889, 1895*a*, *b*, 1910*b*). Carpenter (1992) described each as a 'little-known genus' and included a taxonomic placement made by Handlirsch (1906) and others. *Geroneura* (Fig. 3j) was placed in the Neoptera, Order uncertain. *Aedaeophasma*, *Gerephemera*, *Lithentomum*, *Pseudohomothetus* (Fig. 3k), and *Xenoneura* were placed in the Pterygota, Order uncertain. *Platephemera* was placed with reservation in the Order Palaeodictyoptera, Family uncertain. *Archaeoscolex corneus* was first considered to be a probable myriapod (Handlirsch 1906), but later reinstated as an insect (Hantzschel 1975). Taxonomic positions in Table 2 are based, in part, on an unpublished re-examination of type material by J. Kukalova-Peck (pers. comm.) and Rowland (1997).

The putative occurrence of tetrapods is inferred from obscure footprints. Matthew (1910*b*) described (?)*Hylopus variabilus* and (?)*Nanopus vetustus* (Fig. 3l), but both were subsequently considered as doubtful 'footprints' (Abel 1935; Hantzschel 1975). Re-examination of specimens suggests that they may represent poorly preserved undertracks emplaced in soft sediment, but that assignment to *Hylopus* or *Nanopus* is questionable.

Sedimentology and fossil assemblages

We studied the sedimentology and facies distribution of fossils at all coastal exposures of Lancaster Formation (Fig. 1d). As a result of the meticulous work of Hartt (in Dawson 1868) most of the historical fossil collections, together with new collections, could be placed into a facies context. Four fossiliferous facies were recognized, organized into two associations (Fig. 4).

Facies 1

This facies, best seen at Lancaster Shore, comprises multi-storey channel sandstone bodies. The full thickness of bodies is never exposed, but partial thicknesses are ≤22 m and units are traceable laterally for at least several hundred metres. Some storeys contain a basal lens of polymictic pebble conglomerate, ≤1.2 m thick, with igneous, metamorphic, and sedimentary clasts, ≥18 mm in diameter (quartz pebbles predominate). The remaining channel-fill comprises medium-grained (locally coarse- to very coarse-grained), trough cross-bedded sandstone. Troughs are 0.2–0.5 m (locally 0.7 m) high and indicate ENE palaeoflow (mean $068° \pm 33.8°$; $n = 35$). Rarely, ≤2 m thick tabular sandstone bodies are present, which show low-angle planar cross-

stratification. In other channel-fills, thin lenticular mudstone bodies rarely occur. The upper 2–3 m of one multi-storey unit show shallow channelized features, ≤1 m deep and ≤12 m wide, symmetrical ripple marks, and localized palaeosols (described separately as Facies 4).

Plant remains are present within channel-base conglomerate, or more rarely in trough cross-bedded sandstone. Fossils include calcite- or silica-permineralized tree-trunks, up to 35 cm in diameter and >2 m long. Trunks preserve *Dadoxylon* wood anatomy, and in a few specimens show an *Artisia* pith and lateral branching. Charred *Dadoxylon* fragments, compressed *Cordaites* leaves, and rare *Calamites* and cf. *Sigillaria* are also present. Other fossil assemblages occur in mudstone lenses within channel-fills and include compressions of *Rhacopteris*, *Cordaites*, *Cordaicarpus*, *Alethopteris*, *Calamites*, and *Pinnularia*, amongst other indeterminate material (Matthew 1906). *Diplichnites* myriapod trackways occur in fine-grained sandstone showing current lineation at Barrack Shore, and probably derived from Facies 1.

Facies 2

This facies comprises 1.45–7.45 m thick erosive-based channel bodies, 10–28 m wide, and with a basal relief of ≤1 m. Basal channel-fill is composed of medium- to coarse-grained (rarely pebbly) sandstone. This grades up into fine-grained sandstone with 0.2–0.4 m high trough cross-beds, or ripple cross-lamination, which show divergent palaeoflow vectors (NW to SE; $n = 5$), where measurable. Uppermost channel-fills include ≤2.32 m thick units of fine-grained sandstone with symmetrical ripple marks, typically capped by a palaeosol (Facies 4). Fossil assemblages comprise rare *Dadoxylon* trunks, and more common *Calamites*, near the channel-base.

Facies 3

This facies comprises 0.12–2.97 m thick sheets of sediment, which may be lenticular over tens of metres, and show upward coarsening (Fig. 5a). Lowermost mudstone beds are 0.02–0.71 m thick, dark grey (locally red), finely laminated, sharp-based, and may show rhythmic siltstone laminae and lamina-siderite. They grade upwards into fine- to medium-grained sandstone beds, 0.10–2.26 m (typically 0.3–0.7 m) thick, which are horizontally bedded and show symmetrical ripple marks (Fig. 5b). The upper part of some sandstone beds may show low-angle, mutually erosive cross-beds, up to 0.10–0.15 m high, or localized channels, ≤0.20 m deep. Palaeosols (Facies 4) almost always cap coarsening-upward units. Multiple coarsening-upwards units are commonly stacked in successions several metres in thickness, with palaeosols at the top of one unit overlain by sharp-based mudstone beds at the base of the next.

Fossils are most abundant in the sharp-based mudstone beds that directly overlie palaeosols (Fig. 5a). This assemblage comprises almost all of the historical fossil collections from the Lancaster Formation including diverse plant compressions of

Fig. 3. Lancaster Formation fauna. (Abbreviations used in caption: L, Lancaster Formation, locality unknown; LS#, Hartt's fossil bed number at Lancaster Shore; DC, Duck Cove; BS, Barrack Shore; NBMG, New Brunswick Museum, Saint John.) (**a**) 'Spirorbid microconchs' encrusted on a *Cordaites* leaf, NBMG 3333, scale: 5 mm, L. (**b**) *Amphipeltis paradoxus* Salter, NBMG 3001, scale: 5 mm, LS2. (**c**) *Leaia silurica* Matthew, NBMG 4573a, scale: 1 mm, below LS2. (**d**) Indeterminate postulate arthropod cuticle comprising part of *Belinuropsis wigudensis* Matthew, NBMG 3308, scale: 1 mm, DC. (**e**) *Kouphichnium* sp., NBMG 13915, scale: 20 mm, DC. (**f**) *Dendropupa primaeva* Dawson (Solem & Yochelson), NBMG 3332, scale: 1 mm, LS2. (**g**) *Euphoberia atava* Matthew, NBMG 3022, scale: 10 mm, LS8. (**h**) *Diplichnites gouldi* Trewin & McNamara, NBMG 3030, scale: 10 mm, BS. (**i**) *Diplichnites gouldi* Trewin & McNamara, NBMG 3025, scale: 10 mm, BS. (**j**) *Geroneura wilsoni* Matthew, NBMG 3011, scale: 5 mm, LS2. (**k**) *Pseudohomothetus fossilis* (Scudder), NBMG 3014, scale: 10 mm, LS8. (**L**) *Nanopus vetustus*, NBMG 3035, scale: 10 mm, LS.
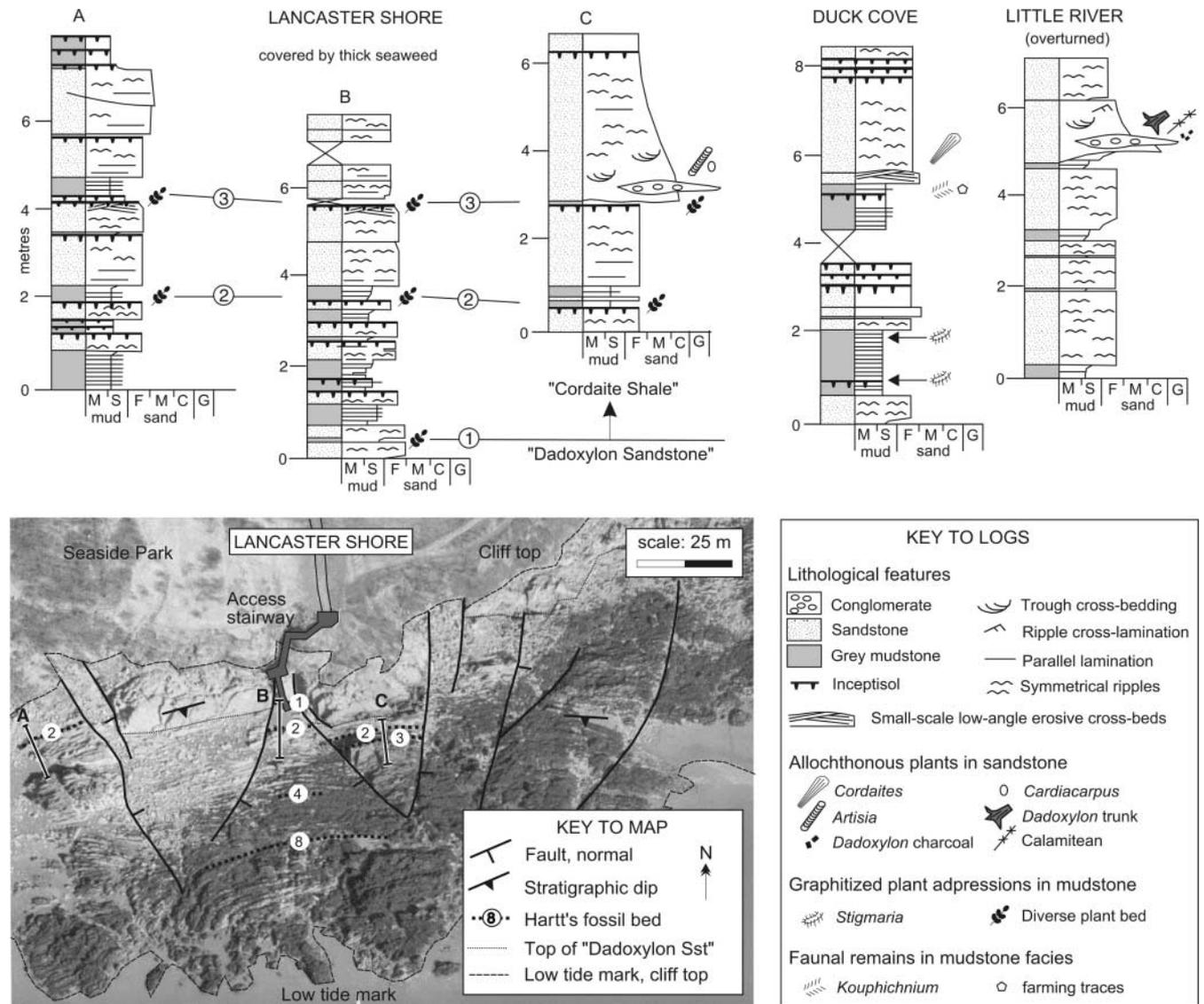
Fig. 4. Sedimentary facies and fossil assemblages for the main coastal sections at Lancaster Shore, Duck Cove, and Little River. Aerial photograph of Lancaster Shore site (reproduced with permission of the City of Saint John) shows position of five of Hartt's fossil beds (in Dawson 1868) relocated in this study.

cordaitaleans, sphenopsids, pteridosperms, ferns, and a few lycopsids (Table 1, except where indicated), as well as rare, but diverse, remains of terrestrial and aquatic fauna (Table 2). For the purposes of palaeoenvironmental reconstruction, the presence of *Kouphichnium* xiphosuran trackways and *Planolites montanus* annelid burrows is noteworthy. Most of the fossils come from three mudstone beds at Lancaster Shore (Hartt's fossil beds 2 and 7, 8), and field investigation of bed 2 (the only one currently well-exposed) shows that fossils are limited to the basal 30–35 mm of the sharp-based mudstone, where it overlies a palaeosol.

Facies 4

This facies comprises palaeosols developed within Facies 1–3. Palaeosols show irregularly pitted surfaces with ≤0.13 m of topography (typically ≤0.05 m), abundant, subhorizontal roots, shallowly penetrative to depths of ≤81 mm, and rare upright trees (Fig. 5a and c). Where developed on symmetrically rippled sandstone, irregular patches of dark grey, organic-rich mudstone

have partially replaced the upper 20–50 mm of the bed. Palaeosols may be capped by organic-rich mudstone laminae (O horizon), ≤3 mm thick, locally preserving rain prints. This is distinct from the sharp-based mudstone beds of overlying Facies 3. In thin section, palaeosols show slightly lower feldspar content and higher clay content compared with unaltered sandstone (which comprises subarkose or quartz arenite). Clay plasma fabrics are dull and silasepic, and grain fabrics are granular to intertextic (Brewer 1976).

Fossils are common in the palaeosols, although generally poorly preserved. Rare tree stumps, typically 21–98 mm in diameter (two are *c*. 0.4 m), occur in growth position as obscure sandstone or mudstone casts, or coalified stumps. Where present, localized tree densities may be as high as 16 trees per square metre on a few surfaces, but distribution is extremely patchy. Nineteen stumps are recognizable as *Calamites*. Where present, these form monotypic stands, and are associated with *Asterophyllites* and *Paracalamostachys* compressions (Fig. 5d). Two additional tree stumps with *Stigmaria* rhizophores are lycopsids.
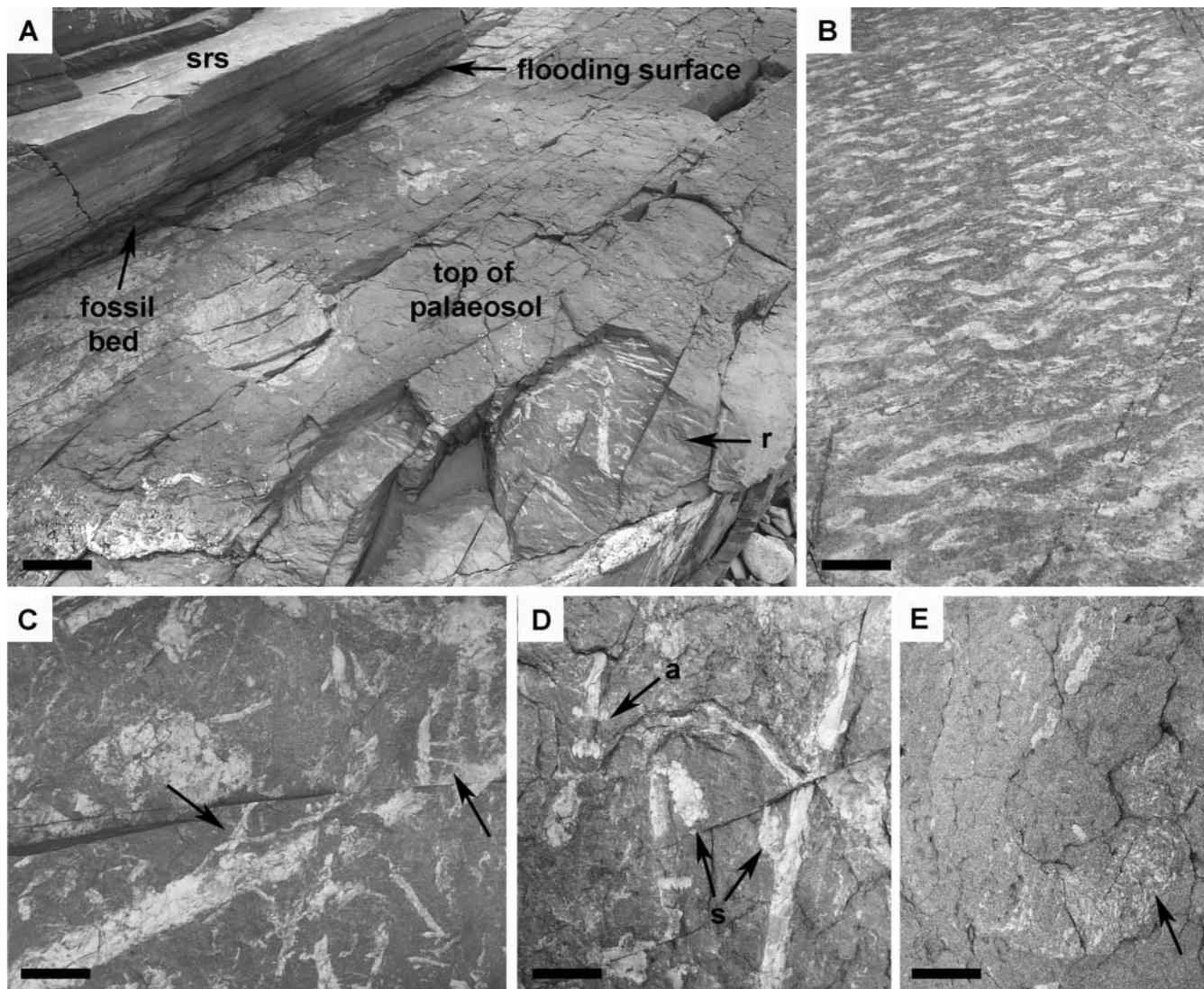
Fig. 5. Sedimentology and features of fossil beds at Lancaster Shore. (**a**) Stacked symmetrically rippled sheets (srs) capped by palaeosol with root layer (r). Fossil beds immediately overlie palaeosols within sharp-based sedimentary sheets interpreted as flooding surfaces, scale: 0.2 m. (**b**) Symmetrical ripples on the top of a sandstone sheet, scale: 60 mm. (**c**) Close-up of root systems shown in (**a**). Arrows highlight departure of secondary and tertiary roots, scale: 35 mm. (**d**) Sphenopsid axes (a) and *Paracalamostachys* strobili (s) within a palaeosol, scale: 35 mm. (**e**) *Beaconites* burrow within a palaeosol, scale: 30 mm. Arrow highlights concave back-fill.

However, identifiable sphenopsid and lycopsid stumps together represent a very small proportion (<2%) of the total number of autochthonous plants observed. Much more abundant and widespread are small stumps, which show a vertical tap root, and a radiating pattern of subhorizontal roots that is traceable for only a few tens of centimetres. Primary lateral roots are ≤21–30 mm in diameter, show up to four orders of branching (angular departure 35–90°), and locally terminate in very fine roots. Their identity is discussed below. Faunal remains are rare in the palaeosols, limited to subhorizontal *Beaconites*-type arthropod burrows, 18–39 mm in diameter, which show concave back-fills of silt-grade sediment (Fig. 5e).

Palaeoenvironmental context

The widespread occurrence of sandstone units containing symmetrical ripple marks (Facies 1–3) suggests that the Lancaster Formation was mostly deposited in, or directly adjacent to, a standing body of water subject to wave activity. The occurrence of xiphosurans, represented by *Kouphichnium* trackways, and the annelid trace maker of *Planolites montanus* suggest a brackish salinity (Calver 1968; Anderson & Shuster 2003; Buatois *et al.* 2005). Pennsylvanian brackish deposits occur widely across eastern Canada (Calder 1998) and represent the sediments of a large epicontinental, microtidal embayment that opened eastwards into the mid-European sea and was perhaps analogous to the present-day Baltic Sea (Falcon-Lang 2005; Wells *et al.* 2005).

Facies interpretation

Facies 1 is interpreted as the deposits of large, eastward-flowing braided fluvial channels. Sandstone body dimensions indicate that channels were hundreds of metres across and many metres deep. Channels filled by the accretion of downstream-migrating subaqueous dunes (trough cross-beds) with minor deposits from laterally accreting bars (large-scale tabular cross-stratification) as

seen in modern sandy braided systems (Cant & Walker 1978). Fine-grained lenses may represent temporary abandonment facies. Metre-thick successions of symmetrically rippled sandstone in some uppermost channel-fills suggest localized wave action. This observation suggests that channels prograded out into the brackish water body described above as deltaic distributaries (Elliot 1986), although direct evidence for either a distributary form or large-scale progradation is lacking.

Facies 2 is interpreted as the deposits of smaller fluvial channels, at most just a few tens of metres wide. The dominance of symmetrically rippled sandstone within the channel-fill suggests strong wave action throughout deposition, and implies that channels fed small delta lobes. Channels are exclusively found within thick successions of symmetrically rippled sandstone sheets and lenses of Facies 3. This latter facies shows upward coarsening and may either represent wave-reworked mouth bar deposits associated with the small channels, or, more likely given their widespread occurrence and extent, the product of linear clastic shorelines (Elliot 1986). Rhythmic bedding in some mudstone beds may record weak tidal influence, and small-scale, mutually erosive, low-angle stratification formed in the shoaling wave zone. Red laminated mudstone at some intervals in Facies 3 may record denudation of oxidized soils upstream, and subsequent redeposition in brackish bays; there is no evidence for *in situ* pedogenesis.

Facies 4 is interpreted as the product of soil formation. Soils developed on emergent substrates, including abandoned channels of various sizes (Facies 1–2) and on mouth bar and shoreface sands after they built up above base level (Facies 3). Shallow penetration of root systems ($\leqslant$81 mm deep) and local preservation of a thin O horizon indicate permanently waterlogged soil conditions. The lack of prominent horizonation, the generally weak alteration of parent material, and the existence of dull plasma fabrics indicate that these were immature soils (inceptisols). Soil immaturity was probably related to repeated flooding by brackish coastal waters.

Facies associations

Two facies associations are recognized at Lancaster Shore where strata are least deformed. Facies Association 1 comprises the lower *c*. 90 m of the succession (mostly covered by glacial till) and is dominated by the deposits of braided fluvial channels (Facies 1; 95% exposed stratal thickness) with minor mouth bar deposits (Facies 3; 5%). This association corresponds to the Dadoxylon Sandstone of Dawson (1868). Facies Association 2 comprises the upper *c*. 45 m of the succession exposed and corresponds to Dawson's Cordaites Shale. It mainly consists of mouth bar and shoreface deposits (Facies 3; 85%), locally cut by small channels (Facies 2; 15%).

Although sediments record interaction between fluvial channels (of various scales) and a standing water body, the absence of a large-scale coarsening-upward succession argues against an overall deltaic model. Facies Association 1 was formed in the wave-influenced mouth of a braided river system. Facies Association 2 was formed by small delta lobes, which coalesced to form a coastal plain, whose shoreline was wave-dominated. The sharp transition from the fluvial-dominated Facies Association 1 and the wave-dominated Facies Association 2 implies abrupt and major base-level rise. In this syntectonic setting (Nance & Warner 1986), large-scale accommodation was probably created by tectonism, although eustatic effects cannot be entirely excluded. During the deposition of Facies Association 2, accommodation and sedimentation generally remained closely balanced, the entire succession accumulating at, or near, base level.

Palaeoecological synthesis

Analysis of fossils in their palaeoenvironmental context, together with historical dominance–diversity data (Hartt, in Dawson 1868), allows insights into the palaeoecology of the Lancaster Formation. Three communities are recognized (Fig. 6).

Brackish bay communities

Aquatic elements of the fauna are presumed to be autochthonous within the shallow brackish waters that flooded the coastal plain following minor subsidence events (Facies 3). This community was dominated by arthropods as reported for similar facies in Western Europe (Calver 1968). The *Planolites* trace-maker was an infaunal deposit-feeding annelid (Buatois *et al*. 2005). Xiphosurans probably fed on benthic invertebrates, and may have made brief amphibious excursions up the sandy beaches to reproduce (Anderson & Shuster 2003). Spirorbiform microconchs (Taylor & Vinn 2006) were filter feeders that encrusted floating plant debris. Conchostracans, which occur in beds isolated from the other taxa, may have inhabited near-freshwater shallow pools along the coastline; they were non-selective filter feeders living off algal and bacterial detritus (Webb 1979).

Coastal forest communities

(Par)autochthonous plant assemblages preserved in inceptisols (Facies 4) developed on top of channel-fill (Facies 2), mouth bars and shoreline deposit (Facies 3) indicate a vegetated coastline on this brackish embayment (Fig. 6). Stump diameter (typically <0.1 m) indicates that most trees were small shrubs, and grew in dense, but generally patchy thickets. Although a few sphenopsids and lycopsids are recognizable in growth position, the majority of stumps are indeterminate. However, compressed megafloral assemblages in overlying mudstone beds (Facies 3) shed light on their identity, and overall coastal forest composition.

The laminated mudstone beds of Facies 3 represent brackish flooding surfaces formed when coastal soils were abruptly drowned by minor subsidence events. Given the small magnitude of subsidence envisaged, the concentration of plant remains in the basal 30–35 mm of Facies 3, and the occasional preservation of intact pteridosperm fronds and *Cordaites* leaf arrays (Stopes 1914), plant fragments are probably locally derived from coastal vegetation. Some remains may be parautochthonous having floated off the palaeosol surface during base-level rise, whereas others may have been washed from flooded coastal forests up to a few kilometres distant. Probably only a small amount of material is distally derived, having been transported via major distributary channels (Facies 1) from inland communities (see below).

Given the overwhelming dominance of cordaitaleans in the flooding surfaces, we infer that most of the indeterminate stumps in underlying palaeosols belong to these plants. Similar cordaitalean coastal forests have been identified along brackish coastlines in the coeval Joggins Formation (Falcon-Lang 2005). Some coastal cordaitaleans have been reconstructed as small trees with stilt roots for growth in standing water (Cridland 1964), and a similar structure is envisaged here. Medullosans, sphenopsids, and a few tree ferns were interspersed within this cordaitalean framework, but herbaceous ferns were rare, perhaps because of standing water.

A subcommunity within this mosaic is represented by Hartt's fossil bed 1 (Fig. 6). This assemblage is exclusively sphenopsid, and includes some *Calamites* in growth position. Fossil bed 1 is
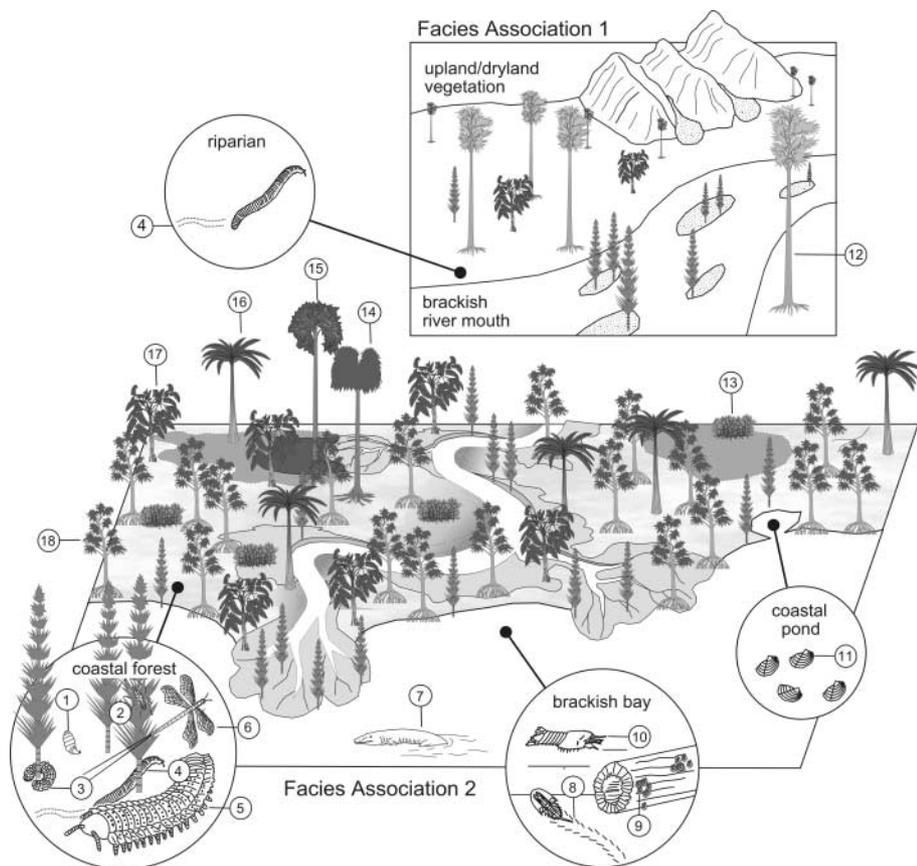
Fig. 6. Ecosystem reconstruction. Top: braided distributary channel system of Facies Association 1. Bottom: coastal plain and brackish bay of Facies Association 2 (modified from Bashforth 2005). Key for fauna: 1, *Dendropupa*; 2, arachnid; 3, centipedes; 4, *Euphoberia* showing *Diplichnites* trackways; 5, *Arthropleura*; 6, Insect; 7, wading tetrapod; 8, *Kouphichnium* xiphosuran trails; 9, 'spirorbid microconchs' encrusting vegetation; 10, *Amphipeltis*; 11, *Leaia.* Key for plants: 12, giant cordaitalean; 13, herbaceous ferns; 14, *Sigillaria*; 15, *Lepidodendron*; 16, tree-ferns; 17, pteridosperms; 18, shrubby cordaitalean.

associated with the major flooding surface that separates Facies Associations 1 and 2. It is probable the remains are of a monotypic stand of *Calamites* that colonized rapidly aggrading substrates at the mouth of a major distributary channel. *Calamites* were well adapted to such a setting by virtue of their ability to resprout from underground rhizomes (Gastaldo 1992).

Terrestrial fauna, including gastropods, insects, arachnids and myriapods, also occur in the flooding surfaces (Facies 3); they are similarly envisaged as being of local derivation, and probably inhabited the coastal forests. The base of the food chain was dominated by detritivores, with most animals living off decaying vegetation in or on the litter layer (DiMichele & Hook 1992). As today, arachnids were probably the main invertebrate predators (Rolfe 1980). Some *Euphoberia* myriapods developed spines and repugnatorial glands to ward off attack from these carnivores (Hoffman 1969). Diverse winged insects were probably detritivores and herbivores living in the forest canopy (DiMichele & Hook 1992). Their abundance and diversity in the Lancaster Formation compared with coeval sites such as the Joggins Formation (Falcon-Lang *et al*. 2006) may be a taphonomic artefact. Perhaps insects became trapped on the surface of the brackish sea, and concentrated in strandline accumulations. Tetrapods probably mostly fed on terrestrial arthropods, and footprints in Facies 3 suggest that some animals paddled out into coastal shallows to feed on aquatic fauna.

Alluvial-plain and upland communities

Evidence for communities living on inland alluvial plains and uplands comes from assemblages in Facies 1 (Fig. 6). The riparian fauna included myriapods, if *Diplichnites* tracks of

uncertain provenance are derived from these beds. Fossil plants in abandonment facies of braided fluvial channels imply that riparian gallery vegetation was dominated by cordaitaleans, rhacopterid pteridosperms, and sphenopsids. Based on the diameter of trunks found within the base of braided channels (<35 cm), these cordaitaleans were very large trees (for a review, see Falcon-Lang & Bashforth 2005), and probably differed from the small shrubby forms inferred to have grown along the coast (Facies 3 and 4). Tree-trunks may be transported great distances in large fluvial channels, and it is possible that some of these remains represent not only riparian vegetation, but also that of uplands further inland. This is supported by the fact that trunks show calcite- and silica-permineralization suggestive of a complex taphonomic history prior to final deposition.

A number of fossil plant taxa found in very low numbers in the coastal deposits (Facies 3) might also represent plants transported down distributary channels from dryland or uplands. These unusual floral elements include the primitive pteridosperms, *Megalopteris* (Leary & Pfefferkorn 1977) and *Rhacopteris* (Galtier *et al*. 1997), the progymnosperm, *Pseudoadidiantites* (Wagner 2001), and the coniferopsid, *Dicranophyllum* (Wagner 2005b). Their dryland or upland interpretation is not based on taphonomic data, but inferred from the typical facies and stratigraphic distribution of these fossils at other sites, where they are characteristic of seasonally dry environments of Mississippian or Late Pennsylvanian age. Their occurrence in lowland deposits in Early Pennsylvanian humid tropical environments implies a dryland or upland source, the only local environment where seasonal conditions might exist. Stopes (1914) was the first to propose this probable intermixture of upland and coastal plants in the Lancaster Formation; this further highlights the quality and

far-reaching implications of her classic monograph (Falcon-Lang & Miller 2007).

Conclusions

(1) The Pennsylvanian fossil assemblage in the Lancaster Formation ('Fern Ledges') is reviewed for the first time since the classic works of Matthew, Hartt, Dawson, and Stopes in the late nineteenth century and early twentieth century.

(2) Megafloral assemblages indicate a mid- to late Langsettian age when ranges are compared with those in European reference sections. The Lancaster Formation is therefore coeval with the famous Joggins Formation of Nova Scotia.

(3) Facies analysis implies deposition on a tectonically influenced coastal plain, whose braided channels drained into a shallow brackish embayment.

(4) Xiphosurans, crustaceans, and phoronids lived in shallow brackish waters. Cordaitalean forests inhabited by gastropods, insects, arachnids, and myriapods existed on coastal sandbars, and were repeatedly drowned by subsidence events. Forests of giant cordaitaleans, archaic pteridosperms, and plants of uncertain affinity existed in upland environments.

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