**Mid-Carboniferous diversification of continental ecosystems inferred from trace fossil
suites in the Tynemouth Creek Formation of New Brunswick, Canada**

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Abstract. We report Skolithos, Scoyenia and Mermia Ichnofacies from sub-humid tropical
fluvial megafan deposits in the Lower Pennsylvanian Tynemouth Creek Formation of New
Brunswick, Canada, and discuss their evolutionary and palaeoecological implications, especially
regarding the colonization of continental freshwater/terrestrial environments. The Skolithos
Ichnofacies comprises annelid/arthropod spreite in the upper storey of a fluvial channel. The

Scoyenia Ichnofacies comprises tetrapod tracks, arthropleurid trackways, and shallow annelid/arthropod burrows in active/abandoned fluvial channels and rapidly aggrading levees/splays in proximal interfluvial areas. The Mermia Ichnofacies comprises abundant xiphosuran trackways, along with diverse traces of other arthropods, annelids, mollusks, and fish, in shallow freshwater lakes, ponds, and coastal bays in slowly aggrading distal interfluvial areas. Transitional Mermia/Scoyenia Ichnofacies comprise tetrapod, mollusk and annelid/arthropod traces in coastal bay deposits on the distal edge of the megafan. These trace fossil suites (1) provide the clearest documentation yet of the mid-Carboniferous diversification event, when tropical continental environments became more densely populated; (2) suggest that euryhaline visitors (xiphosurans, microconchids, and other taxa) from open marine settings played a key role in this episode of freshwater colonization; and (3) provide empirical support for the “Déjà vu Effect”, the evolutionary concept that new or empty ecospace, recurrent in spatially and temporally variable environments, is colonized by simple ichnocoenoses.

Keywords: Pennsylvanian, fluvial megafan, ichnology, euryhaline, freshwater, colonization

1. Introduction

Trace fossil assemblages are an important, but under-utilized, source of information for tracking the early colonization of continental (terrestrial and freshwater) environments (Hasiotis, 2007; MacEachern et al., 2007; Buatois and Mángano, 2011a). Compilations of ichnological data (Buatois and Mángano, 2004, 2007) show that animals began to make temporary, amphibious excursions onto land in the Cambrian/Ordovician (MacNaughton et al., 2002). Nonetheless, trace fossils remain rare in continental facies until close to the Silurian-Devonian boundary (Buatois et

al., 1998a), when the initial diversification of tracheophytes (vascular plants) presumably provided a richer source of detrital organic material (Edwards and Wellman, 2001) for terrestrial deposit-feeding organisms than had previously existed (Miller and Labandeira, 2002). A further step-change in the frequency, complexity and diversity of terrestrial ichnocoenoses occurred in the mid-Carboniferous (Buatois and Mángano, 2004, 2007, 2011b; Davies and Gibling, 2013), suggesting that continental environments became more densely populated at that time (Buatois and Mángano, 2007). These early continental ichnocoenoses are referred to as the *Mermia*, *Scoyenia* (Buatois and Mángano, 1993, 1995), or less commonly, *Skolithos* Ichnofacies (Keighley and Pickerill, 2003), and the key characteristics of each association are summarized in Table 1.

Much remains to be learned about the “mid-Carboniferous diversification event”, which witnessed the first appearance of many ichnotaxa in continental settings, the rise of new ichnotaxa, and a significant change in the style of continental ichnocoenoses (Buatois and Mángano, 2004, 2007, 2011b; Davies and Gibling, 2013, fig. 21). Devonian and early Carboniferous (Mississippian) continental ichnocoenoses generally are rare, depauperate, restricted to marginal lacustrine facies, and lack clear ichnofacies differentiation, suggesting limited utilization of ecospace and rather generalized modes of adaptation (Smith, 1909; Pollard et al., 1982; Pollard and Walker, 1984; Walker, 1985; Pickerill, 1992; Keighley and Pickerill, 2003; Smith et al., 2012). In contrast, by the late Carboniferous (Pennsylvanian) – Permian, continental ichnocoenoses had become more abundant, widespread, and sharply differentiated into *Scoyenia*, *Mermia* and *Skolithos* Ichnofacies, with ichnocoenoses recording specific patterns of behaviour and adaptive traits in subtly different environments (Buatois et al., 1997, 1998abc, 2005, 2010; Park and Gierlowski-Kordesch, 2007; Pazos et al., 2007).

In this paper, we describe trace fossil suites (assigned to the *Mermia*, *Scoyenia* and *Skolithos* Ichnofacies) from sub-humid fluvial megafan deposits in the Lower Pennsylvanian Tynemouth Creek Formation of New Brunswick, Canada, which shed further light on the mid-Carboniferous diversification of continental ecosystems. To date, this critical time interval has been the focus of few detailed case studies (e.g., Keighley and Pickerill, 1997, 1998, 2003; Davies and Gibling, 2013). Specifically, we document trace fossil suites that comprise simple surface to shallow grazing/feeding trails and arthropleurid/tetrapod trackways, associated with possible microbial textures, which provide empirical support for what has been termed the “Dejà vu Effect”, the concept that the initial invasion of largely empty ecospace results in recurrent patterns of simple traces (Buatois and Mángano, 2011*b*). This study thus contributes to ongoing debates concerning ichnological evidence for the mid-Carboniferous colonization of continental environments by animals (Davies and Gibling, 2013) and, in turn, landscape evolution (Gibling and Davies, 2012; Gibling et al., 2014).

2. Geological context

The trace fossil suites occur in a 16 km long sea-cliff section between Emerson Creek (Latitude 45°16'N; Longitude 65°47'W) and Rogers Head (Latitude 45°18'N; Longitude 65°35'W), southeast of St. Martins, southern New Brunswick, Canada (Fig. 1).

2.1. Stratigraphy and correlation of sections

Rocks exposed along this section of coastline are assigned to the ~ 700-m thick Tynemouth Creek Formation (Hayes and Howell, 1937; Plint and van de Poll, 1982; Falcon-Lang, 2006), a unit of the Cumberland Basin, which is part of the late Palaeozoic Maritimes

Basin complex of Atlantic Canada (Gibling et al., 2008). The Lower Pennsylvanian (Bashkirian; Langsettian) Tynemouth Creek Formation conformably overlies the Boss Point Formation near Giffin Pond (Fig. 1C), and may be correlated (at least in part) with one or more of the Little River (Calder et al., 2005), Joggins (Davies et al., 2005) and Springhill Mines (Rygel et al., 2014) formations in the eastern part of the Cumberland Basin, and with the Lancaster Formation in the far western part of the basin (Falcon-Lang and Miller, 2007) based on biostratigraphy (Falcon-Lang et al., 2006, 2010; Utting et al., 2011; Bashforth et al., 2014) and marine-based lithostratigraphy (Falcon-Lang et al., 2016) (Fig. 2).

The most complete stratigraphic analysis of the Tynemouth Creek Formation was undertaken by Plint and van de Poll (1982). They logged four contiguous sections (Fig. 3) at metre-scale, but were unable to correlate them precisely because of widespread faulting and folding. Their Section 1, east of Giffin Pond (Fig. 1C), represents the lowermost part of the formation where it conformably overlies the Boss Point Formation (Plint and van de Poll, 1984; Rygel et al., 2015). Their Sections 2 and 3, east and west of Tynemouth Creek, respectively, and their Section 4, from Gardner Creek to McCoy Head (Fig. 1C), are all characterized by upward coarsening over hundreds of metres of vertical succession, with conglomeratic units in the uppermost parts. Based on this sedimentological motif and structural considerations, Sections 2–4 are likely correlative equivalents, with the youngest strata seen in the upper part of Section 4 at McCoy Head (Fig. 3; Falcon-Lang, 2006). Additional sections, which were not logged by Plint and van de Poll (1982), occur at Emerson Creek and Reeds Beach (Fig. 1C). Structural considerations and a predominance of fine-grained strata suggest that these sections correlate with the lower part of the formation (Fig. 3; Bashforth et al., 2014).

2.2. *Syntectonic fluvial megafan interpretation*

Plint and van de Poll (1982) interpreted the Tynemouth Creek Formation as the deposits of a large, northward-prograding alluvial fan, highlighting the presence of laterally extensive conglomerate sheets, coarsening-upward patterns over several hundred metres of stratal thickness, and rather uniform northward palaeoflow. While concurring with the observations of Plint and van de Poll (1982), Bashforth et al. (2014) suggested that the predominance of channelized sandstone and pedogenically altered mudstone in the coarsening-upward successions was best explained in terms of a fluvial megafan, with a proximal gravel-bed fluvial system that passed basinward into a distributive system of narrow, fixed, mixed-load channels (cf. Nichols, 1987; Wells and Dorr, 1987; Hirst, 1991). This re-evaluation is consistent with the growing recognition of a spectrum of proximal distributive fluvial systems that range from small, steep, coarse-grained “alluvial fans” to large, lower gradient megafans (Stanistreet and McCarthy, 1993; Hartley et al., 2010; Weissmann et al., 2011, 2013).

Structural and sedimentological considerations suggest that the Tynemouth Creek Formation megafan built northwards from an active thrust-front developed along the Fundy-Cobequid Fault at the southern edge of the Cumberland Basin (Plint and van de Poll, 1984; Nance, 1986, 1987). Evidence for syntectonic sedimentation is abundant, but is most spectacularly represented by the so-called “Earthquake Bed” at the headland east of Tynemouth Creek, where a series of buried fault scarps that evidently broke the palaeosurface are preserved (Plint, 1985). Outcrop extent and palaeocurrent arrays imply that the megafan was > 20 km in diameter (Plint and van de Poll, 1982; Rast et al., 1984; Plint, 1985). The predominance of Vertisol-like paleosols, sedimentary evidence for episodic deposition in all environments, and the prevalence of cordaitalean-dominated plant fossil assemblages point to deposition under a

seasonal sub-humid tropical climate (Falcon-Lang et al., 2012; Bashforth et al., 2014; Ielpi et al., 2014). Based on the interpreted dimensions, syntectonic context, and climatic setting of the megafan, the Kosi Fan of India (Singh et al., 1993) may be an appropriate modern analogue for the Tynemouth Creek Formation.

3. Trace fossil suites

Twenty-seven trace fossil suites (Table 2), containing 23 distinct ichnotaxa (Table 3), were identified in the Tynemouth Creek Formation during near-annual field visits over the course of a decade (beginning in 2004). Co-ordinates of the trace fossil suites (TFS) were determined by GPS (NAD83). Their stratigraphic position and sedimentological context was established with reference to Plint and van de Poll (1982) and Bashforth et al. (2014) (Fig. 3). Where possible, one or more examples of each trace fossil type was collected, or a latex mould was obtained where collection was not possible. Specimens are accessioned in the New Brunswick Museum, Saint John, Canada (NBMG 6004, 6398, 9103, 9201, 14589–14596, 14602–14609, 14624, 15059, 15061–15062, 16046–16047, 16274).

In the Tynemouth Creek Formation, Bashforth et al. (2014) recognized ten sedimentary facies distributed among two principal facies associations. The fluvial channel association (FA1) includes three, mostly coarse-grained facies: gravel-bed channel deposits (GBC facies), sand-bed channel deposits (SBC facies), and abandoned channel deposits (ABC facies). The interfluvial association (FA2) can be segregated into facies from three main environmental settings: (1) interfluvial channel deposits (IFC facies), levee/crevasse splay deposits (CVS facies), and distal interfluvial deposits (DIF facies), which accumulated in rapidly aggrading areas proximal to the main fluvial channels; (2) paleosols (PAL facies), perennial lake deposits (LAC facies), and

stagnant pond deposits (PND facies), which accumulated in slowly aggrading or degrading areas distal to the main fluvial channels; and (3) brackish-marine bay deposits (BBY facies), which accumulated on the most distal part of the megafan. This facies model, summarized in Table 2, is used to place our ichnological study into sedimentary context (Fig. 4).

3.1. Active fluvial channel (GBC, SBC facies) traces ($n = 3$)

Trace fossils associated with the deposits of active fluvial channels are rare (Table 2). Two trace fossil suites (TFS) occur in the gravel-bed channel (GBC) facies on the headland east of Tynemouth Creek (Fig. 1C), at ~ 90 m in Section 2 of Plint and van de Poll (1982) (Fig. 3; see log in Wilson, 1999, fig. 6.11). The upper surface of a well-exposed conglomeratic channel body, 7 m thick, is crosscut by a prominent fissure (Fig. 5A, C, E), interpreted to be a ground-surface rupture generated by earthquake waves (Plint, 1985). The uppermost 0.4 m of the channel body is a medium-grained sandstone that has a bleached top and contains hollow molds of stigmarian rhizomorphs (lycopsid ‘roots’). This bleached paleosol surface (PAL facies) resembles a siliceous soil that developed due to prolonged exposure under seasonal climatic conditions (Gibling and Rust, 1990). The bleached paleosol preserves dense monotypic paired burrows with thin connecting tubes. These are only observed in bedding plane view but are identified as *Diplocraterion* with spreite (Fig. 6A; TFS 1). *Diplocraterion* burrows are less common or absent adjacent to stigmarian rhizomorphs, suggesting that burrowing pre-dated rooting and soil formation. The upper bedding surface of the channel body, which is sharply overlain by grey and post-depositionally reddened shales of the PND facies, also displays a 0.25 m wide *Diplichnites cuithensis* arthropleurid trackway (Plint, 1985) preserved in concave epirelief (TFS 2).

Trace fossils in the sand-bed channel (SBC) facies (Table 2) comprise one occurrence (TFS 3) located 300 m southwest of Gardner Creek (Fig. 1C), at ~ 60 m in Section 4 of Plint and van de Poll (1982) (Fig. 3). The traces occur in a coarse-grained sandstone channel body, 7 m thick, that exhibits trough cross-bedding in its lower part (SBC facies) and is sharply overlain by red siltstone (ABC facies) that partly infills a shallow hollow in the top of the body. *Taenidium* burrows (Fig. 6B) are present in massive, fine- to medium-grained sandstone in the uppermost 0.5 m of the channel body.

3.2. Abandoned channel (ABC facies) traces ($n = 4$)

Trace fossils are moderately common in the abandoned channel (ABC) facies (Table 2). The most important occurrence (Falcon-Lang et al., 2010) is at the headland east of Tynemouth Creek (Fig. 1C), at 98 m in Section 1 of Plint and van de Poll (1982) (Fig. 3). Here, a large channel body, which contains three distinct beds, sits within and eventually overtops a hollow that developed on a degraded paleosol surface (PAL facies) (Fig. 5A – D). The lower bed (Unit 5a) is a medium-grained, trough cross-bedded sandstone body, up to 5 m thick. The middle bed (Unit 5b), which infills a broad shallow hollow in the channel body, is a thinly bedded package of sandstone and siltstone that oversteps the channel margin and shows abundant *Planolites beverleyensis* burrows and common roots on some surfaces (Fig. 6C) (TFS 4). The upper bed (Unit 5c) is a sharp-based, trough cross-bedded, fine-grained sandstone, 1.5 m thick, the base of which shows nearly two hundred tetrapod footprints preserved in convex hyporelief, including trackways assignable to *Baropezia* (Fig. 6D), *Pseudobradypus* (Fig. 6E), and *Batrachichnus* (TFS 5; Fig. 6F; Falcon-Lang et al., 2010). Two additional examples of trace fossil suites in the ABC facies occur in an unlogged portion of the Giffin Pond section, as described in Falcon-Lang

et al. (2010). They comprise indeterminate, poorly preserved tetrapod footprints that co-occur with *Planolites* (TFS 6) and an arthropleurid trackway of *Diplichnites cuithensis* (TFS 7).

3.3. Proximal interfluvial (IFC, CVS, DIF facies) traces ($n = 13$)

Trace fossils are relatively common in the interfluvial channel, crevasse splay and distal interfluvial (IFC, CVS, DIF) facies, which represent rapidly aggrading interfluvial settings close to fluvial channel systems (Table 2) and involve two associations. The first association, which comprises arthropleurid trackways (*Diplichnites cuithensis*) preserved in concave epirelief, is exemplified by a site located 200 m southwest of Gardner Creek (Fig. 1C), at ~ 10 m in Section 4 of Plint and van de Poll (1982), first reported by Briggs et al. (1984) (Fig. 3). Here, a succession of thinly bedded sandstone sheets and red siltstone (CVS facies) contains abundant, closely spaced stem-casts of *Calamites* in growth position. At the top of one rooted siltstone surface is a 0.4 m wide trackway of *Diplichnites cuithensis*, which has a sinuous pathway over 5 m long that appears to wind through the *Calamites* stand (TFS 8). Wilson (1999) documented two additional examples of this *Diplichnites cuithensis* association (Fig. 6H): (1) in the CVS facies, 300 m east of the Tynemouth Creek headland, below the ‘Earthquake Bed’, at 75 m in Section 2 of Plint and van de Poll (1982) (TFS 9; Figs. 5C); and (2) in the IFC facies, 1 km southeast of Reeds Beach, in an unlogged section (TFS 10). We have observed three other examples, all associated with the CVS facies: (1) 500 m east of Gardner Creek, in an unlogged section (TFS 11–12; Falcon-Lang, 2006); and (2) 500 m west of Giffin Pond, in an unlogged section (TFS 13).

The second association is dominated by tetrapod tracks preserved as convex hyporelief on the base of thin, sheet-like bodies of fine-grained sandstone (CVS facies), locally associated

with small channel sandstone bodies (IFC facies), or in the DIF facies. Falcon-Lang et al. (2010) reported four occurrences (TFS 14–17) that consist of various tetrapod footprints (cf. *Pseudobradypus*, cf. *Baropezia*, cf. *Batrachichnus*) and rare *Planolites* traces from the sections at Giffin Pond, west of Gardner Creek and at McCoy Head. One other site (TFS 18), found in 2011, comprises *Baropezia* tetrapod footprints in the CVS facies directly above the ‘Earthquake Bed’, at 92 m in Section 2 of Plint and van de Poll (1982) (Fig. 5C). Another trackway of *Baropezia* tetrapod footprints, found in 2014, occurs at Reeds Beach in an unlogged section (TFS 19).

Only one trace fossil suite provides evidence that points to the possible co-occurrence of tetrapods and arthropleurids. This site is located 400 m northeast of McCoy Head (Fig. 1C) in strata positioned at 433–435 m in Section 4 of Plint and van de Poll (1982) (Fig. 3). Here, a channel scour that cuts down about 3 m into a succession of red mudstone is filled by a trough cross-bedded, medium-grained sandstone body, which oversteps the channel margin on one side to form a 0.5 m thick ‘wing’ of massive sandstone (CVS facies). Trace fossils (TFS 20) on the base of this sandstone sheet include poorly preserved tetrapod trackways (cf. *Baropezia* or cf. *Megapezia*) that appear to skirt a large cast, preserved in convex hyporelief, resembling the head and anterior tergites of an arthropleurid (Fig. 6G) (Miller et al., 2010). The cast shows a fine granular texture consistent with the millimetre-scale tubercle sculpture of this organism. The bedding surface also exhibits a pustular surface texture that may be microbial in origin, and has parallel groove casts that extend away from the putative arthropleurid cast.

3.4. Distal interfluvial (PND, PAL, LAC facies) traces ($n = 4$)

Trace fossils are relatively common and diverse in the two aquatic lacustrine/pond (LAC, PND) facies, which represent slowly aggrading interfluvial settings distal to fluvial channel

systems. However, these facies are rare in the Tynemouth Creek Formation, and few trace fossil suites have been observed as a consequence (Table 2). In contrast, trace fossils appear to be absent in paleosols (PAL facies), with the exception of roots (Bashforth et al., 2014), despite excellent exposure that permitted examination of many tens of examples of this facies.

The most important trace fossil suite in the lacustrine (LAC) facies (TFS 21) occurs 300 m northeast of McCoy Head (Fig. 1C), at ~ 193 m in Section 4 of Flint and van de Poll (1982) (Fig. 3). Here the trace fossil bed is part of a complex channel body, 2.6 m deep and ~ 17 m in apparent width, that infills a prominent topographic hollow on a degraded paleosol-mantled surface. The channel fill is divided into two units separated by three red- to grey/green-mottled paleosols (Fig. 7A – B). The lower channel-fill unit, confined to the deepest part of the preexisting gully, comprises red fine-grained sandstone, up to 0.8 m thick, with mounded bedforms and woody trees (probably pteridosperms) in growth position. The upper channel-fill unit, up to 1.8 m thick, coarsens upwards from red laminated siltstone containing adpressed plant remains to thinly bedded lenses of coarse siltstone showing symmetrical ripples with interference patterns (Fig. 7C) and a pustular, possibly microbial texture. The symmetrically rippled unit contains abundant *Kouphichnium* xiphosuran trackways, which are unusual in showing bifid, trifid and quadrifid “pusher” tracks, and locomotive patterns that describe ever-decreasing circles (Fig. 8A – C, F). Also present are fish swimming traces (*Undichna britannica*; Fig. 8D), endostratal burrows that twist helically through the sediment and emerge as bilobed trails, which probably were made by conchostracans based on their size and shape (Fig. 8E), *Diplichnites* isp. arthropod trackways (Fig. 8F, I), *Helminthoidichnites tenuis* (not illustrated), and endostratal burrows terminated by *Lockeia siliquaria* and made by ostracods based on the bilobed producer preserved at the end of one burrow (Fig. 8G). An additional enigmatic trace characterized by an

elongate central area from which there are diverging imprints on either side (Fig. 8H) may represent the resting trace of a small crustacean. Another very small enigmatic trace is spirorbiform (Fig. 8J) and probably represents the resting trace of a microconchid, which Plint and van de Poll (1982) also documented from the Tynemouth Creek Formation. Enigmatic ellipsoidal imprints also are present but their producer is unknown (Fig. 8K). Bashforth et al. (2014) documented a similar site (TFS 22), 500 m west of Gardner Creek (Fig. 1C), at ~ 123 m in Section 4 of Plint and van de Poll (1982) (Fig. 3). Here, *Kouphichnium* xiphosuran trackways were found in a succession of thin, planar siltstone and mudstone beds that locally entomb tree-ferns in growth position. The much lower diversity documented in this bed probably reflects poor exposure of bedding surfaces at the locality.

Two trace fossil suites in the stagnant pond (PND) facies occur 300 m east of Reeds Beach (Fig. 1C) in an unlogged section. The trace fossil beds occur in the fill of a small channel body, 1.6 m deep and > 7 m wide (only one channel margin is exposed), that contains rotated slump blocks and infills a hollow mantled by a red or grey/green mottled paleosol (Fig. 7D–E). The paleosol is sharply overlain by a package, up to 0.8 m thick, that includes a thin dark grey carbonaceous shale at the base, above which are medium grey, laminated siltstone beds that coarsen upwards and entomb small woody trees (probably pteridosperms) buried in growth position, and contain adpressed plant remains and skeletal fragments of fish (Fig. 7E). Above these beds is a succession of fine- to medium-grained sandstone with beds that thicken and coarsen upward. A lower sandstone unit shows planar lamination, symmetrical ripples, and *Calamites* stem-casts in growth position surrounded by mounded bedforms. Trace fossils occur on two adjacent siltstone partings that also show rills orientated perpendicular to the channel margin, tool marks, and a pustular, possibly microbial texture (Fig. 7F). The first assemblage

comprises a small form of *Cochlichnus anguineus* (Fig. 9A) and *Didymaulichnus lyelli* (TFS 23). The second comprises *Kouphichnium* xiphosuran trackways and *Lockeia siliquaria* (TFS 24). The upper sandstone unit, 1.2 m thick, which is separated from the lower one by a pedogenically red-mottled layer, contains very shallow channel fills and is capped by a second paleosol.

3.5. Brackish bay shoreline (BBY facies) traces ($n = 3$)

There is only one occurrence of the brackish bay (BBY) facies in the Tynemouth Creek Formation (Falcon-Lang et al., 2016), located 230 m east of Emerson Creek in an unlogged section (Fig. 1C). The studied interval comprises a predominantly grey, coarsening-upward succession, 3.9 m thick, which overlies a red or green/grey-mottled paleosol with Vertisol-like features and is capped by a similar paleosol (Fig. 7G – H). The lower paleosol is overlain and infilled by an echinoderm-rich marine limestone, up to 0.18 m thick. Above this is a medium grey, laminated siltstone, 1.2 m thick, that contains several coarsening-upward cycles, siderite nodules, symmetrical ripples, skeletal fragments of fish, ostracods, plant adpressions, and small woody trees (probably pteridosperms) in growth position (Fig. 7H). The siltstone contains a trace fossil assemblage of *Didymaulichnus lyelli* (Fig. 9B), *Lockeia siliquaria* (Fig. 9B), *Arenicolites* (Fig. 9C), cf. *Selenichnites* (Fig. 9D), and *Helminthoidichnites tenuis* (Fig. 9E) (TFS 25). The upper part of the succession, up to 2.1 m thick, is dominated by planar units of thinly bedded, fine- to medium-grained sandstone that contain symmetrical ripples, shallow scours, and *Calamites* in growth position. Two other trace fossil assemblages occur in these beds: (1) a large *Didymaulichnus lyelli* (Fig. 9H) and a large form of *Cochlichnus anguineus* (Fig. 9I) (TFS 26); and (2) *?Baropezia* paddling/swimming footprints (Fig. 9F) and an enigmatic crozier-like burrow that represents one partial whorl (Fig. 9G) (TFS 27). Mottled red exposure surfaces occur

between some sandstone units, especially at the top of the succession beneath the capping paleosol.

4. Interpretation of ichnofacies

The 27 trace fossil suites are assigned to three ichnofacies (Table 2): one occurrence of Skolithos Ichnofacies (TFS 1), 19 occurrences of Scoyenia Ichnofacies (TFS 2 – 20), five occurrences of Mermia Ichnofacies (TFS 21 – 25), and two occurrences of a transitional Mermia/Scoyenia Ichnofacies (TFS 26 – 27).

4.1. Skolithos Ichnofacies

TFS 1 is typical of the Skolithos Ichnofacies (Table 1), comprising monotypic dwelling traces of *Diplocraterion* (Buatois et al., 2005). The complex geologic context at the locality where TFS 1 is preserved means that precise interpretation of the environmental setting is not straightforward. The burrows occur near the sandy top of a conglomerate bed (GBC facies), on which is developed a paleosol with stigmarian rhizomorphs, and the whole succession has been displaced along a syn-sedimentary fissure (Fig. 5E). Plint (1985) and Bashforth et al. (2014) interpreted this unit as the deposit of a gravel-bed fluvial drainage that was drowned following earthquake-induced subsidence, and suggested that the burrowed surface formed following submergence in shallow, standing water. However, this palaeoenvironmental interpretation is inconsistent with the Skolithos Ichnofacies, which develops under conditions of rapid aggradation and reworking (Buatois et al., 2005; MacEachern et al., 2007; Buatois and Mángano, 2011a; Table 1).

An alternative hypothesis, more compatible with the available evidence, is that this occurrence of the Skolithos Ichnofacies records organisms that burrowed in the rapidly aggrading sands of the active fluvial tract. This view is supported by the fact that there are no burrows on the fault scarp surface itself, suggesting that the burrows pre-date the earthquake rupture. Furthermore, burrows are absent or less common adjacent to stigmarian rhizomorphs, suggesting the burrowing pre-dated rooting and paleosol formation. As such, association with a siliceous paleosol might be of taphonomic significance if, for example, exposed fluvial sands that contain the burrows underwent rapid induration or cementation during pedogenesis (Gibling and Rust, 1990; Thiry et al., 2006).

What is less certain is whether the burrows represent activity within freshwater tracts of the fluvial channels, or whether they are expressions of marine influence in the distal part of channel systems. The Tynemouth Creek Formation consists overwhelmingly of terrestrial red bed deposits, although a marine bed recently has been identified in the distal megafan (Falcon-Lang et al., 2016). Although *Diplocraterion* is characteristic of marine-influenced shoreface settings, the trace fossil also has been reported from freshwater fluvial channel tracts (Trewin and McNamara, 1994; Kim and Paik, 1997; Buatois and Mángano, 2004; Smith et al., 2012). As such, the possibility of marine influence at this locality is difficult to determine.

4.2. *Scoyenia* Ichnofacies

Trace fossil suites (TFS) 2 – 20 are typical of the *Scoyenia* Ichnofacies (Buatois and Mángano, 2007; Table 1), comprising a predominance of sub-horizontal, meniscate (*Taenidium*) and non-meniscate (*Planolites*) feeding burrows, arthropleurid trackways (*Diplichnites*), tetrapod tracks (*Baropezia*, *Batrachichnus*, cf. *Megapezia*, *Pseudobradypus*), and abundant plant roots.

The most dense and diverse occurrences of tetrapod tracks (temnospondyls, anthracosaurs, amniotes) are associated with abandoned channels (TFS 4 – 6), probably reflecting increased activity around waterholes during dry seasons (Falcon-Lang et al., 2010), as inferred elsewhere for similar Pennsylvanian deposits (Falcon-Lang et al., 2004, 2007). However, they also occur sporadically across proximal interfluvial areas (TFS 14 – 20), where water availability and preservation potential was greater (Bashforth et al., 2014).

Similarly, arthropleurid trackways are associated with active and inactive fluvial channels (TFS 2 and 7) and proximal interfluvial areas (TFS 8 – 13), especially on levee and crevasse splay surfaces that were colonized by dense *Calamites* groves. Arthropleurids were detritivores that fed on pteridophytes (Rolfe et al., 1967), including *Calamites* based on evidence from coprolites (Falcon-Lang et al., 2015), and also may have used dense thickets for shade and concealment from predators. It is noteworthy that tetrapod tracks and arthropleurid trackways are mostly mutually exclusive in their distribution in the Tynemouth Creek Formation, although whether this reflects ecological partitioning or a taphonomic effect is unclear, and we note that tetrapods and arthropleurid traces occur on the same bedding surface at Joggins (Prescott et al., 2014). Cryptic evidence for interaction is provided by TFS 20, which shows anthracosaur tracks of cf. *Baropezia* and/or cf. *Megapezia* apparently circling an unusually large trace that may represent the anterior remains of an arthropleurid (Fig. 6G) (Miller et al., 2010). Mid-Carboniferous tetrapods were mainly piscivores and insectivores (Sahney et al., 2010), but feeding on arthropleurids has also been suspected (Rolfe, 1985).

Burrows (*Taenidium*, *Planolites*) in active and inactive fluvial channels (TFS 3, 4, 6) and levees/crevasse splays (TFS 14 – 17) record the activity of annelids and arthropods that processed detritus-rich sands. These opportunistic deposit-feeders were the only aquatic

organisms able to gain a foothold in proximal interfluvial settings, with rainfall seasonality and associated floods possibly driving a “boom and bust” ecology with brief periods of high productivity, as seen today in seasonally active dryland fluvial systems in central Australia (Jenkins and Boulton, 2003; Balcombe et al., 2007). It is possible that aquatic arthropods or annelids (or their eggs) may have lain dormant in sediment between floods, only to emerge after inundation (Brown and Carpelan, 1971; Boulton and Lloyd, 1992; Jenkins and Boulton, 1998). Alternatively, they may have dispersed from distal interfluvial habitats during the wet season, when shallow bodies of standing water (perennial lakes, stagnant ponds) were connected to fluvial tracts. The frequency of tetrapod tracks associated with *Planolites* burrows may indicate scavenging behaviour as the floodwater subsided.

4.3. *Mermia Ichnofacies*

Trace fossil suites (TFS) 21 – 25 are typical of the *Mermia Ichnofacies* (Buatois and Mángano, 1993, 1995), comprising dominantly horizontal to sub-horizontal grazing (e.g., *Cochlichnus*, *Didymaulichnus*, *Helminthoidichnites*, endostratal burrows) and resting traces (e.g., *Lockeia*, cf. *Selenichnites*, various enigmatic features) produced by mobile detritus and deposit feeders, as well as subordinate locomotion traces (e.g., *Diplichnites* isp., *Kouphichnium* and *Undichna*) of aquatic animals. Trace fossil suites are relatively rich but cosmopolitan, with similar associations occurring in wave-agitated settings across a spectrum of well oxygenated, shallow water environments, including ponded water in abandoned reaches of fluvial channels (waterholes) and in interfluvial hollows (TFS 21 – 24), as well as in shallow freshwater bays adjacent to the coastline (TFS 25; Falcon-Lang et al., 2016).

Some of the most diverse trace fossil suites are found in channel-hosted lakes and ponds (TFS 21, 23 – 24), which were especially dynamic environments that alternated between times of energetic fluvial through-flow (indicated by ripple cross-lamination and tool marks), wave-agitated standing water (symmetric ripples), and low water or exposure (rill structures and paleosol formation), as seen in modern examples of seasonally active dryland fluvial systems in central Australia (Gibling et al., 1998). Also noteworthy is the widespread occurrence on bedding surfaces of traces associated with pustular textures, possibly microbial features. If this attribution is correct, invertebrate grazing generally may have been insufficient to prevent the build-up of microbial films, supporting the conclusion that communities were depauperate (Buatois and Mángano, 2011*b*).

Within the Mermia Ichnofacies, most widespread and abundant are the traces of xiphosurans (*Kouphichnium*, cf. *Selenichnites*), which show pusher print morphology characteristic of juveniles and adults (Caster, 1938), and eccentric patterns of locomotion in ever-decreasing circles (Fig. 8A). Such traumatic behaviour has been documented in modern and fossil xiphosurans (Anderson and Shuster, 2003; Diedrich, 2011), and may be the result of hypersalinity, dysaerobia (Seilacher, 2007), or locomotion in very shallow water (Martin and Rindsberg, 2007); all of these factors could have been significant in small and ecologically stressful waterholes subject to evaporation and exposure (as indicated by paleosol development). Trackways that only preserve the “pusher” tracks (Fig. 8B) may represent undertracks (Goldring and Seilacher, 1971), or could have been produced by animals that were partly swimming (Diedrich, 2011).

4.4. Transitional *Mermia*/*Scoyenia* Ichnofacies

Trace fossil suites (TFS) 26 – 27 are transitional between the *Mermia* and *Scoyenia* Ichnofacies, and comprise a mixture of horizontal to sub-horizontal grazing traces (*Cochlichnus*, *Didymaulichnus*) of annelids and arthropods, together with swimming/paddling tetrapod tracks (?*Baropezia*) and crozier-like feeding burrows that resemble those produced by unionid bivalves under conditions of periodic emergence (Lawfield and Pickerill, 2006). The trace fossil suites occur in sandy mouth bars that bordered a shallow sea, and record activity in submerged to periodically emergent coastal settings. *Baropezia* has been related to anthracosaurs, which had a serpentine bodyplan (Milner, 1987) compatible with an aquatic feeding ecology.

5. Discussion

There have been few studies of continental (terrestrial and freshwater) ichnocoenoses from the critical mid-Carboniferous interval when life on land was undergoing rapid diversification (Davies and Gibling, 2013). Here we discuss the evolutionary implications of trace fossil suites in the Tynemouth Creek Formation.

5.1. Mid-Carboniferous diversification

Body fossils provide incomplete evidence for the evolution of terrestrial ecosystems because fauna have a low preservation potential in subaerial environments, especially in dry, oxidizing tropical settings (Behrensmeyer et al., 2000). Similarly, freshwater biota is also rarely preserved due to fluctuating lake levels. Consequently, Carboniferous terrestrial/freshwater faunas are rare, scattered in time and space, and subject to major taphonomic biases (Milner, 1987; Falcon-Lang et al., 2006; Sahney et al., 2010). Two mid-Carboniferous body fossil sites that are especially important for unraveling the story of terrestrial ecosystem development are

East Kirkton, Scotland, which is of late Viséan (Brigantian, c. 336 Ma) age (Rolfe et al., 1993) and Joggins, Canada, which is of mid-Bashkirian (Langsettian, c. 314 Ma) age (Falcon-Lang et al., 2006). In the ~ 22 million year interval between these two iconic fossil assemblages, there is evidence for significant “terrestrialization” of various lineages of tetrapods, mollusks, arthropods, annelids, and, most notably, the rise of fully terrestrial amniotes (Carroll, 1964), gastropods (Solem and Yochelson, 1978), and isopods, among others, coincident with the diversification of freshwater biotas (Park and Gierlowski-Kordesch, 2007; Bennett, 2008; Bennett et al., 2012; Carpenter et al., 2014, 2015).

Analysis of Carboniferous ichnocoenoses from terrestrial/freshwater facies in Euramerica identifies both the appearance of new ichnotaxa and first occurrence of many ichnotaxa in continental settings during the mid-Carboniferous (Fig. 10). There also appears to be an increase in the complexity of continental communities at this time, supporting the notion of a mid-Carboniferous diversification event. Terrestrial ichnocoenoses are widespread in the Tynemouth Creek Formation, including diverse trace fossils of tetrapods and arthropleurids. Freshwater ichnocoenoses also are locally rich. Ichnocoenoses of similar Bashkirian (Langsettian) age also are well developed at other sites, although most represent coastal wetland habitats (e.g., Pollard and Hardy, 1991; Buatois and Mángano, 2002; Falcon-Lang et al., 2006). The Tynemouth Creek ichnocoenoses are thus significant in providing a rare record of coeval dryland colonization. In contrast, Middle to Late Mississippian terrestrial/freshwater ichnocoenoses are much more rare, and freshwater examples in particular are somewhat depauperate (e.g., Keighley and Pickerill, 2003). Furthermore, paleosols in the Tynemouth Creek Formation do not seem to have been significantly colonized, although it is commonly difficult to identify trace fossils in such deposits; such an apparent lack is consistent with the inferred Mesozoic origin for the

Coprinisphaera ichnofacies (Genise et al., 2000), although there is evidence for colonization in Permian paleosols (Counts and Hasiotis, 2014).

5.2. Euryhaline colonization

The Tynemouth Creek Formation ichnocoenoses also shed light on the ecological and evolutionary processes that facilitated the colonization of freshwater habitats. A remarkable feature of the Mermia Ichnofacies reported here is the predominance of euryhaline trace-makers. Most common and widespread are trackways and resting traces of xiphosurans (*Kouphichnium*, cf. *Selenichnites*). Xiphosurans have a dominant marine life phase but also make incursions into lower salinity coastal settings to breed (Anderson and Shuster, 2003). In an extreme example, the extant xiphosuran *Carcinoscorpius rotundicauda* has been found up to 90 km upstream on the Hooghly River of Bengal, India, in tidally influenced but freshwater conditions (Chatterji and Parulekar, 1992; Chatterji, 1994). Pennsylvanian xiphosurans appear to have had variable salinity preferences, with *Bellinurus* preferring near-marine conditions and *Euproops* near-freshwater settings (Baird, 1997). Both taxa are known from shallow, brackish bay facies in Lower Pennsylvanian strata in the Maritimes Basin (Dawson, 1868; Jones and Woodward, 1899; Woodward, 1918; Copeland, 1957*ab*, 1958; Falcon-Lang et al., 2006), including a few records from the western end of the Cumberland sub-basin near the sites reported here (Falcon-Lang and Miller, 2007).

Another euryhaline group, the presence of which is indicated by resting traces, is spirorbiform microconchids (Zaton et al., 2012). Although the salinity preferences of this group have been debated (Taylor and Vinn, 2006), critical review of microconchid biology and facies distribution demonstrates a marine-based ecology (Gierlowski-Kordesch and Cassle, 2015), with

a capability to migrate into lower salinity coastal waters (Falcon-Lang et al., 2006; Carpenter et al., 2011). As noted above, *Diplocraterion* burrows (TFS 1) are more characteristic of marine shoreface associations, and could record upstream invasion by marine-based communities. Other taxa represented by traces in the Mermia Ichnofacies also may have represented euryhaline organisms. Many Pennsylvanian fish, ostracods and carideans that comprise the Lower Pennsylvanian fauna of brackish bays in the Maritimes Basin have been inferred to be euryhaline animals based on facies analysis and their pan-tropical distribution (Calder, 1998; Falcon-Lang et al., 2006; Tibert and Dewey, 2006; Carpenter et al., 2015). Traces in Mermia Ichnofacies could represent some of these organisms, but the taxonomic resolution of the traces is insufficient to prove direct association with particular organisms.

In summary, the trace fossil suites reported here support the hypothesis that accelerated colonization of freshwater environments in mid-Carboniferous times (Davies and Gibling, 2013) occurred through upstream penetration of euryhaline invaders (Gray, 1988; Miller and Labandeira, 2002; Park and Gierlowski-Kordesch, 2007; Schultze, 2009; Bennett et al., 2012; Carpenter et al., 2014). Two key ecological advantages for marine taxa to explore freshwater fluvial reaches include access to untapped resources of food and opportunities to spawn away from predation. The apparent dominance of euryhaline visitors in rivers and lakes upstream of the marine coast in the Tynemouth Creek Formation may reflect the sharp mid-Carboniferous rise in the density and productivity of tropical vegetation (Gibling et al., 2010), which would have resulted in greater availability of detrital organic material for predominantly deposit-feeding organisms. In addition, seasonally active rivers that periodically fragmented into isolated waterholes would have created protected niches for spawning (Brown and Carpelan, 1971;

Boulton and Lloyd, 1992; Jenkins and Boulton, 1998), as well as possible higher rates of allopatric speciation in analogy to balance-filled lakes (Gierlowski-Kordesch and Park, 2004).

A review of Carboniferous occurrences of *Mermia* Ichnofacies suggests that freshwater colonization by invading euryhaline taxa may be a general evolutionary pattern. Most occurrences of *Mermia* Ichnofacies are known from freshwater settings adjacent to brackish-marine environments. For example, one of the oldest occurrences is found in Early Mississippian (Tournaisian) rift-related embayments characterized by freshwater to brackish gradients (Pickerill, 1992), perhaps like those seen today in the Baltic Sea (Tibert and Scott, 1999; Rygel et al., 2006). Similarly, the best-documented Pennsylvanian occurrences are in tidal deposits of estuaries and fjords (Buatois et al., 1997, 1998*b*; Pazos et al., 2007; Buatois et al., 2010), positioned upstream of the saline wedge in freshwater settings (Buatois and Mángano, 2007; Buatois et al., 2006, 2010; Netto et al., 2008, 2012), and euryhaline taxa including xiphosurans have been found in the freshwater reaches of fluvio-estuarine systems (Buatois et al., 1998*b*) similar to the Tynemouth Creek Formation.

5.3. *Déjà vu Effect*

Depauperate examples of the *Mermia*, *Scoyenia* and *Skolithos* Ichnofacies that we report may reflect a macroevolutionary effect related to the early phase of freshwater colonization, and provide support for a phenomenon dubbed the “*Déjà vu Effect*” (Buatois and Mángano, 2011*b*). This concept was proposed to explain the observation of recurrent ichnocoenoses, comprising simple surface to shallow grazing and feeding traces and arthropod trackways associated with probable microbial (elephant-skin) textures, distributed across various environments throughout Earth history. Most notably, such ichnocoenoses are observed in marine settings during the

Ediacaran-Cambrian and non-marine settings during the colonization of land. The significance of elephant skin texture, where confirmed as microbial, is in demonstrating that substrate grazing by invertebrates was insufficient to completely utilize microbial films, and therefore ecospace was not filled to carrying capacity. Hence, rather than being controlled by specific environmental conditions, the occurrence of such ichnocoenoses is purported to reflect a macroevolutionary signal in terms of behavioural strategies employed during initial stages of the exploitation of new or empty ecospace (Buatois and Mángano, 2011*b*).

The recurrence of such ichnocoenoses, which we consider to represent depauperate examples of the *Mermia* Ichnofacies, in the Tynemouth Creek Formation demonstrates a lack of environmental control on their occurrence. This study thus provides additional empirical support for the concept of the “Déjà vu Effect”, which we interpret to reflect the colonization and exploitation of new or empty terrestrial ecospace during the Early Pennsylvanian.

6. Conclusions

- (1) We describe trace fossil suites characteristic of the *Skolithos* ($n = 1$), *Scoyenia* ($n = 19$), *Mermia* ($n = 5$) and transitional *Scoyenia/Mermia* ($n = 2$) Ichnofacies in the Lower Pennsylvanian Tynemouth Creek Formation of New Brunswick, Canada, which record animal communities that occupied varied environments of a sub-humid fluvial megafan.
- (2) The ichnocoenoses provide a snapshot of continental (terrestrial and freshwater) communities during the mid-Carboniferous diversification event, when the complexity and abundance of terrestrial faunas rose dramatically.

- (3) The widespread occurrence of traces suggestive of euryhaline animals (xiphosurans, microconchids, and possibly others) demonstrates that the invasion of freshwater environments was facilitated through upstream penetration by marine invaders.
- (4) Freshwater ichnocoenoses are associated with possible evidence for microbial mats and comprise simple surficial to shallow infaunal feeding and locomotion traces. This association provides empirical support for the “Déjà vu Effect”, the concept that new or empty ecospace, recurrent in spatially and temporally variable environments, is colonized by simple ichnocoenoses.

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Figure captions

Figure 1. Location details and geological context of study sites. A., Southwestern outcrop belt of the Maritimes Basin of Atlantic Canada. B., Cumberland sub-basin of central Nova Scotia and southern New Brunswick on the edge of the Appalachian Orogen. C., Outcrop belt of the Pennsylvanian (Langsettian) Tynemouth Creek Formation of southern New Brunswick (NTS 21 H/05ab). The location of the trace fossil suites (TFS 1 – 27) discussed in the text is indicated by the circled numbers (after Plint and van de Poll, 1982; Barr and White 2004^{ab}; Falcon-Lang, 2006; Bashforth et al., 2014).

Figure 2. Stratigraphic relationships of Lower Pennsylvanian (Langsettian) lithostratigraphic units of the Cumberland sub-basin, Nova Scotia and New Brunswick (after Davies et al., 2005; Falcon-Lang, 2006; Falcon-Lang et al., 2010; Utting et al., 2011; Bashforth et al., 2014), and their approximate relationship to European regional chronostratigraphic boundaries.

Figure 3. Stratigraphic correlation of the main sections studied in the Tynemouth Creek Formation, and the informal division of strata into the distal and proximal deposits of the fluvial megafan (after Plint and van de Poll, 1982; Falcon-Lang, 2006; Bashforth et al., 2014). The approximate stratigraphic position of the trace fossil suites (TFS 1 – 27) discussed in the text is indicated by the circled numbers.

Figure 4. Reconstruction of palaeoenvironments in the fluvial megafan of the Tynemouth Creek Formation (after Bashforth et al., 2014). Key to Facies Association 1 (FA1): (GBC facies) gravel-bed channel; (SBC facies) sand-bed channel; (ABC facies) abandoned channel. Key to Facies Association 2 (FA2): Rapidly aggrading interfluvial areas – (IFC facies) interfluvial channel; (CVS facies) crevasse splays and levees; (DIF facies) distal interfluvial. Degrading or slowly aggrading interfluvial areas – (PAL facies) paleosol; (LAC facies) perennial lakes and

playas; (PND facies) stagnant ponds. Distal megafan – (BBY facies) brackish bays. The inferred distribution of the trace fossil suites (TFS 1 – 27) discussed in the text is indicated by the circled numbers.

Figure 5. Sedimentology of the Tynemouth Creek headland locality (modified from Falcon-Lang et al., 2010), which contains six trace fossil suites (TFS 1 – 2, 4 – 5, 9 and 18). A., Photomosaic to show sedimentary units overlying a fissured surface (“Earthquake Bed” of Plint, 1985). B., Tracing of part of A, with positions of photos D, E and F indicated, and showing position of TFS 4 – 5 and 18. C., Stratigraphic column of the succession showing position of six trace fossil suites; facies codes (GBC, ABC, CVS) as in text. D., Close-up to show position of TFS 4 – 5 within ABC facies in Unit 5 of fluvial channel body. E., Close-up of “Earthquake Bed” showing scarp of co-seismic fissure, and position of TFS 1 – 2 and 18 in GBC and CVS facies, respectively. F., Upright calamitaleans (arrows) in Unit 3 showing position of TFS 18 in CVS facies (scale: hammer is 0.35 m long)

Figure 6. Trace fossils characteristic of fluvial channel systems (GBC, SBC, ABC facies) and proximal interfluves (IFS, CVS, DIF facies). A., *Diplocraterion*, paired burrows with thin connecting tubes interpreted as spreite, in GBC facies at Tynemouth Creek headland (TFS 1). Arrows point to exit tunnels connected by spreite, scale: 40 mm. B., *Taenidium* burrow in SBC facies at Gardner Creek (TFS 3), scale: 25 mm. C., *Planolites* in ABC facies at Tynemouth Creek headland (TFS 4), scale: 20 mm. D., *Baropezia* tetrapod manus print in ABC facies at Tynemouth Creek headland (TFS 5), NBMG 14589, scale: 10 mm. E., *Pseudobradypus* tetrapod manus print in ABC facies at Tynemouth Creek headland (TFS 5), NBMG 14589, scale: 25 mm. F., Diverse tetrapod tracks and tail drags in ABC facies at Tynemouth Creek headland (TFS 5), NBMG 14589, scale: 25 mm. G., Putative arthropleurid

body trace circled by cf. *Baropezia* or cf. *Megapezia* tetrapod tracks (arrows) in CVS facies at McCoy Head (TFS 20), NBMG 14624, scale: 75 mm. H., *Diplichnites* in CVS facies at Tynemouth Creek headland (TFS 9), scale: 150 mm.

Figure 7. Geological context of three sites showing evidence for standing water (LAC, PND, BBY facies), including interpreted field photograph (left column) and corresponding sedimentary log (middle column); the place where the log was measured is indicated by the line on each image. Scale (circled): hammer, 0.35 m long; backpack, 0.45 m high. A – B., Channel fill containing trace fossil suite (TFS) 21 in LAC facies at the Gardener Creek west site, C., Symmetrical interference ripples on trace fossil bed in LAC facies; scale: 150 mm. D – E., Channel fill containing TFS 22 – 23 in PND facies at Reeds Beech. F., Rills and pustular microbial texture on trace fossil bed in PND facies; scale: 40 mm. G – H., Coarsening upward succession containing TFS 25 – 27 in BBY facies at Emerson Creek.

Figure 8. Trace fossil suite (TFS) 21 in LAC facies at the Gardener Creek west site (Fig. 7A – C). A., Sketch of area of *Kouphichnium* trackways showing a pattern of ever-decreasing circles; pale grey (1) indicates early-formed trackway; medium grey (2) indicates later-formed trackway; and dark grey (3) indicates last-formed trackway inferred from cross-cutting relationships, scale: 100 mm. B., Close-up of one *Kouphichnium* trackway showing Y-shaped pusher imprints (arrows), scale: 15 mm. C., Diverging trackways showing prints and mid-line, scale 25 mm. D., *Undichna brittanica* fish swimming trace, scale: 20 mm. E., endostratal burrow twisting through sediment (box and sketch highlights twists), scale: 5 mm. F., *Kouphichnium* trail (below) showing quadrifid pushers (highlighted box and sketch) characteristic of juveniles, and *Diplichnites* isp. (above), NBMG 16274, scale: 5 mm. G., endostratal burrows terminated by ostracod-like bilobed *Lockeia* (arrow), scale: 4 mm. H.,

1091 radiating trace that could be a crustacean resting trace, scale: 5 mm. I., *Diplichnites* isp.
1092 arthropod trails, NBMG 16274, scale: 5 mm. J., Spirorbiform resting trace attributed to
1093 microconchids (as highlighted in sketch), scale: 3 mm. K., Enigmatic ellipsoidal imprint,
1094 scale: 5 mm.

1095 Figure 9. A., Trace fossil suite (TFS) 23 in PND facies at Reeds Beach (Fig. 7D – F), B – E.,
1096 Trace fossil suite (TFS) 25 in BBY facies at Emerson Creek (Fig. 7G – H), and F – I., Trace
1097 fossil suite (TFS) 26 – 27 in BBY facies at Emerson Creek. A., Small *Cochlichnus*, scale: 15
1098 mm. B., Small bilobed trails of *Didymaulichnus lyelli* and similar-sized ‘bean’ shaped
1099 *Lockeia*, some of which are bilobed, NBMG 16047, scale: 5 mm. C., Paired vertical burrow of
1100 *Arenicolites*, scale: 5 mm. D., cf. *Selenichnites*, scale: 10 mm. E., Irregular trails of
1101 *Helminthoidichnites tenuis* on surfaces showing microbial wrinkling, NBMG 16046, scale: 5
1102 mm. F., ?*Baropezia* swimming/paddling tracks, scale: 20 mm. G., crosier-like burrow, scale:
1103 5 mm. H., Bilobed trails of *Didymaulichnus lyelli* somewhat larger than in Fig. 9B, scale: 5
1104 mm. I., large form of *Cochlichnus*, scale: 5 mm.

1105 Figure 10. Ranges and frequency of five common Carboniferous ichnotaxa in continental and
1106 freshwater facies in Euramerica (data from Minter et al., 2016), illustrating the mid-
1107 Carboniferous diversification event. Only ichnotaxa that also occur in the Tynemouth Creek
1108 Formation are shown. Gondwanan data are excluded.

1109

1110 **Table captions**

1111 Table 1. General characteristics of the Mermia, Scoyenia, and Skolithos Ichnofacies.

1112 Table 2. Summary of facies associations, facies, trace fossil suites, and ichnofacies (IF) in the
1113 Tynemouth Creek Formation of southern New Brunswick.

1114 Table 3. Ichnotaxa in the Tynemouth Creek Formation, their characteristics, and inferred
1115 trackmaker/behaviour
1116

Figure 1

Figure 2

**DATUM:
FIRST APPEARANCE
OF GRAVELBED
CHANNEL DEPOSITS
(GBC FACIES)**

Figure 4

Figure 5

Figure 6

Figure 7

Lithology	
	Limestone
	Dark gray mudstone
	Medium gray mudstone
	Green-gray mudstone
	Red mudstone
	Sandstone
Sedimentary structures	
	Siderite nodules
	Calcrete nodules
	Green-gray/red mottles
	Ripple cross-lamination
	Horizontal lamination
	Symmetrical ripple marks
	Concave-up joint sets
Megafloal remains	
	Cordaites
	Calamitalean foliage
	Calamitalean axis (upright)
	Woody tree (upright)
	Pteridosperms (and allies)
	Indeterminate rootlets
Faunal remains	
	Ostracods
	Fish
	Brachiopods
	Gastropods
	Echinoderms

Figure 8

Figure 9

Figure 10

Table 1

Ichnofacies	Representative trace fossils	Environmental inferences	References
Mermia	Dominated by horizontal to sub-horizontal grazing (e.g., <i>Mermia</i> , <i>Gordia</i> , <i>Cochlichnus</i> , <i>Helminthoidichnites</i>) and feeding (e.g., <i>Planolites</i> , <i>Treptichnus</i> , and <i>Circulichnus</i>) traces produced by mobile detritus and deposit feeders, as well as subordinate locomotion traces (e.g., <i>Undichna</i> , <i>Maculichna</i>)	Low-energy, well-oxygenated, permanently submerged lacustrine facies	Buatois and Mángano, 1995, 2011a; Buatois et al., 1998a; MacEachern et al., 2007
Scoyenia	Horizontal meniscate (e.g., <i>Scoyenia</i> , <i>Beaconites</i> , <i>Taenidium</i>) or non-meniscate (e.g., <i>Planolites</i>) structures made by mobile deposit feeders, vertical (e.g., <i>Skolithos</i>) or horizontal (e.g., <i>Palaeophycus</i>) dwelling structures; Palaeozoic examples dominated by a mixture of invertebrate (mostly arthropod) and tetrapod tracks, and plant roots	Periodically emergent lacustrine shoreline, alluvial channel, levee and interfluvial facies	Seilacher 1967; Frey and Seilacher, 1980; Buatois and Mángano, 1995; 2004, 2011a; Buatois et al., 1998a; MacEachern et al., 2007
Skolithos	Dominated by vertical simple (e.g., <i>Skolithos</i>), U-shaped (e.g., <i>Arenicolites</i>) burrows; U-shaped spreiten burrows (e.g., <i>Diplocraterion</i>) and three-dimensional boxwork burrows (e.g., <i>Ophiomorpha</i>) of suspension feeders and predators	High-energy, well-oxygenated, permanently submerged marine and non-marine facies	Seilacher, 1964, 1967; MacEachern et al., 2007; Buatois and Mángano, 2011a

Table 2

Sedimentary	Description	Interpretation	Trace fossil suites	Horizon	Ichnofacies
Facies Association 1 (FA 1): Fluvial channel systems - aggregate thickness ≈ 365 m ($\approx 42\%$) of succession measured by Plint & van de Poll (1982)					
Gravelbed channel (GBC)	Grey, clast-supported, polymictic, massive to tabular cross-stratified conglomerate in sheet-like bodies	Braided channels with deposition by hyperconcentrated flows	Monotypic <i>Diplocraterion</i> burrows in upper part of body (TFS 1), and arthropleurid trackways of <i>Diplichnites cuithensis</i> on top of body (TFS 2); root traces	1	Skolithos (1), Scoyenia (2)
Sandbed channel (SBC)	Red or grey, massive to trough cross-stratified sandstone in lenticular or tabular bodies	Fixed channels filling by vertical aggradation, some becoming braided channels in late stages	<i>Taenidium</i> burrows in upper part of channel bodies (TFS 3); root traces	3	Scoyenia
Abandoned channel (ABC)	Thin, fine-grained intervals above or interdigitating with sandstone and conglomerate bodies	Abandoned parts of fixed or braided channels; waterholes in dry season	<i>Planolites</i> (TFS 4); abundant tetrapod tracks assigned to <i>Baropezia</i> , <i>Batrachichnus</i> , and <i>Pseudobradypus</i> (TFS 5); in addition to poorly preserved tetrapod tracks with <i>Planolites</i> (TFS 6), and arthropleurid trackways of <i>Diplichnites cuithensis</i> (TFS 7); microbial texture and root traces	4, 5, 6, 7	Scoyenia
Facies Association 2 (FA 2): Interfluvial systems - aggregate thickness ≈ 502 m ($\approx 58\%$) of succession measured by Plint & van de Poll (1982)					
Rapidly aggrading interfluvial deposits proximal to FA 1					
Interfluvial channel (IFC)	Red or grey, ripple cross-laminated and/or trough cross-stratified sandstone in lensoid pods	Narrow, shallow channels traversing interfluvies	An arthropleurid trackways of <i>Diplichnites cuithensis</i> (TFS 10) and poorly preserved tetrapod footprints of ? <i>Batrachichnus</i> (TFS 16); root traces	10, 16	Scoyenia
Crevasse splay/levee complex (CVS)	Stacked sheets of light grey, indurated siltstone and sandstone associated with channel bodies	Crevasse splays and proximal levees adjacent to fluvial channels	Common arthropleurid trackways of <i>Diplichnites cuithensis</i> (TFS 8-9, 11-13). Common tetrapod footprints of cf. <i>Baropezia</i> , cf. <i>Batrachichnus</i> , and <i>Pseudobradypus</i> (TFS 17-18). <i>Baropezia</i> (TFS 19). <i>Baropezia</i> , cf. <i>Megapezia</i> and putative arthropleurid resting trace (TFS 20). Some <i>Planolites</i> , microbial texture and root traces.	8, 9, 11, 12, 13, 17, 18, 19, 20	Scoyenia
Distal interfluvial (DIF)	Heterolithic sheets of sandstone, siltstone, and mudstone	Inundation of distal interfluvies by shallow, low-energy, sediment-laden floodwaters	Isolated tetrapod footprints and tracks of cf. <i>Batrachichnus</i> and cf. <i>Baropezia</i> (TFS 14). Horizontal burrows of <i>Planolites</i> (TFS 15); microbial texture and root traces	14, 15	Scoyenia
Degrading or slowly aggrading interfluvial deposits distal to FA 1					
Vertic paleosol (PAI)	Mature examples: red to greenish grey, mottled, well-indurated paleosols with hackly fracture, carbonate nodules, and concave-up joints	Mature examples: Vertisol-like soils developing during prolonged exposure under subhumid, seasonal precipitation	Root traces; no animal traces evident	numerous	Scoyenia
Perennial lake (LAC)	Parallel-bedded siltstone-mudstone couplets in pronounced topographic hollows	Shallow, perennial lakes and ponds filling fixed interfluvial depressions; waterholes in dry season	Dominated by xiphosuran trails of <i>Kouphichnium</i> , with some small <i>Diplichnites</i> , <i>Helminthoidichnites</i> , various <i>Lockeia</i> ostracod and other resting traces, and <i>Undichna</i> fish swimming traces (TFS 21); <i>Kouphichnium</i> (TFS 22); microbial texture and root traces	21, 22	Mermia
Stagnant pond (PND)	Thin, laminated, carbonaceous mudstones above degraded surfaces	Small, stagnant ponds filling shallow interfluvial depressions above paleosols; waterholes in dry season	<i>Cochlichnus</i> , <i>Didymaulichnus</i> (TFS 23) <i>Kouphichnium</i> and <i>Lockeia</i> (TFS 24); microbial texture and root traces	23, 24	Mermia
Distal megafan adjacent to a marine embayment					
Brackish bay (BBY)	Parallel- or ripple cross-laminated siltstone above marine limestone	Shallow bays filling by progradation of small delta or coastal plain	<i>Arenicolites</i> , <i>Didymaulichnus</i> , <i>Helminthoidichnites</i> , <i>Lockeia</i> , and cf. <i>Selenichnites</i> (TFS 25); <i>Cochlichnus</i> and a large <i>Didymaulichnus</i> (TFS 26) and crosier-like burrows and cf. <i>Baropezia</i> (TFS 27); microbial texture and root traces	25, 26, 27	Mermia (25), Scoyenia (26, 27)

Table 3

Ichnotaxon	Description of New Brunswick material	Inferred behavior	Inferred trace-maker (reference)
(1) <i>Arenicolites</i> Salter, 1857	Vertical to slightly oblique U-shaped burrows inferred from paired tubes (Fig. 9C)	Dominichnia	Annelid / arthropod (Häntzschel, 1975; Howard and Frey, 1975)
(2) <i>Batrachichnus salamandroides</i> Geinitz, 1861	Small tetradactyl manus tracks with a digit imprint splay of 67-78° and digit imprint III the longest. Possible pentadactyl pes tracks (not illustrated)	Repichnia	Temnospondyl amphibian (Haubold, 1971; Tucker and Smith, 2004)
(3) <i>Baropezia</i> Matthew, 1903	Plantigrade to digitigrade tracks with short and fat widely splayed digit imprints that terminate with a prominent bulge (Fig. 6D, F, 9F)	Repichnia	Anthracosaur (Haubold, 1971)
(4) <i>Cochlichnus anguineus</i> Hitchcock, 1858	Sinusoidal horizontal trails with a smooth, non-striated, surface. Two types noted (Fig. 9A, I)	Pascichnia	Annelid / nematode / insect larva (Hitchcock, 1858; Moussa, 1970; Metz, 1987)
(5) <i>Didymaulichnus lyelli</i> Rouault, 1850	Bilobate trails with smooth lobes. Separation between lobes less than or equal to their width. Two sizes: small (Fig. 9B) and large (Fig. 9H)	Pascichnia	Ostracod or conchostracan (Pollard and Hardy, 1991)
(6) <i>Diplichnites cuithensis</i> Briggs, Rolfe and Brannan, 1979	Large trackway comprising two parallel rows of closely-spaced tracks oriented perpendicular to the mid-line. No discernible series (Fig. 6H)	Repichnia	Arthropleurid (Briggs et al., 1979, 1984)
(7) <i>Diplocraterion</i> Torell, 1870	Dumbbell-shaped structures on bedding plane surfaces. Represent paired tubes and spreite of vertical U-shaped spreiten burrows (Fig. 6A)	Dominichnia	Polychaete / arthropod (Cornish, 1986)
(8) <i>Diplichnites</i> isp.	Trackway comprising two parallel rows of closely-spaced tracks merging into ridges (Fig. 8F, I)	Repichnia	Arthropod (Brady, 1947)
(9) <i>Helminthoidichnites tenuis</i> Fitch, 1850	Simple, unbranched, horizontal to undulatory trails with angular turns (Fig. 9E)	Pascichnia	Insect larva (Buatois et al., 1998b)
(10) <i>Kouphichnium</i> Nopcsa, 1923	Trackways comprising linear or Y-shaped bifid tracks and trifid or quadrafid tracks. Medial impression may be present (Fig. 8A, B, C, F)	Repichnia	Xiphosuran (Caster, 1938; Diedrich, 2011)
(11) <i>Lockeia siliquaria</i> James, 1879	Small, isolated, circular to ovoid traces. Bilobed in some cases (Fig. 8G, 9B)	Cubichnia	Ostracod or conchostracan (Pollard and Hardy, 1991)
(12) cf. <i>Megapezia</i> Matthew, 1903	Poorly preserved plantigrade to digitigrade tracks with at least three digits that may terminate with a bulge (Fig. 6G)	Repichnia	Amphibian (Miller et al., 2010)

(13) <i>Planolites beverleyensis</i> Billings, 1862	Unlined burrows with massive infill that differs from the host sediment. Unbranched, straight to curved (Fig. 6C)	Fodinichnia	Polychaete / arthropod (Pemberton and Frey, 1982; Buatois and Mángano, 1993)
(14) <i>Pseudobradypus</i> Matthew, 1903	Plantigrade pentadactyl tracks with slender digit imprints that may terminate in an acuminate tip. Digit imprint splay 40-55° (Fig. 6E, F)	Repichnia	Primitive amniote (Haubold, 1971; Falcon-Lang et al., 2007)
(15) cf. <i>Selenichnites</i> Romano and Whyte, 1990	Horseshoe- to lunate-shaped traces (Fig. 9D)	Cubichnia	Xiphosuran (Hardy 1970; Romano and Whyte 1987, 2003; Wang, 1993)
(16) <i>Taenidium</i> Heer, 1877	Unlined burrows with meniscate backfill. Unbranched, straight to curved, and horizontal (Fig. 6B)	Fodinichnia	Arthropod (Morrissey and Braddy, 2004)
(17) <i>Undichna britannica</i> Higgs, 1988	Trail comprising two, overcrossing, sinusoidal waves half out-of-phase with one another (Fig. 8D)	Repichnia	Fish (Anderson, 1976; Higgs, 1988)
(18 – 23) Material described in open nomenclature	Endostratal burrows that twist helically through sediment and transition into bilobed trails (Fig. 8E)	Fodinichnia	Conchostracan (Tasch, 1964)
	Crozier-like burrow consisting of one partial whorl (Fig. 9G)	Pascichnia	Bivalve (Lawfield and Pickerill, 2006)
	Isolated traces with elongate central region and radiating imprints (Fig. 8H)	Cubichnia	Possibly a crustacean
	Very small spirorbiform imprint (Fig. 8J)	Cubichnia	Microconchid (Zaton and Vinn 2011)
	Ellipsoid imprint (Fig. 8K)	Cubichnia	Unknown
	Large trace resembling the anterior part of an arthropleurid (Fig. 6G)	Cubichnia	Arthropleurid (Miller et al., 2010)