Diverse tetrapod trackways in the Lower Pennsylvanian Tynemouth Creek Formation, near St. Martins, southern New Brunswick, Canada

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A B S T R A C T
Newly discovered tetrapod trackways are reported from eight sites in the Lower Pennsylvanian Tynemouth Creek Formation of southern New Brunswick, Canada. By far the most abundant and well-preserved tracks comprise pentadactyl footprints of medium size (32–53 mm long) with slender digits and a narrow splay (mostly <55°). Digit lengths typically approximate a phalangeal formula of 23453 (manus) and 23454 (pes), but this may vary due to extramorphology. These tracks are referred to Pseudobradyopus and they are attributed to early amniotes. A second type of track (rare) comprises very small (5–8 mm long) tetradactyl manus, and incompletely preserved pedes. Referred to Barochichnus, these are attributed to temnospondyl amphibians. A third type (also rare) comprises small pentadactyl pedes (20–25 mm long) showing stubby, widely splayed (152°) digits with a terminal bulge. Manus are probably pentadactyl (preservation incomplete) with a narrower digit splay. These footprints, classified as Baropoza, are attributed to anthracosaurs. Facies analysis at the most prolific site (179 footprints documented) suggests that the tetrapods lived amongst small alethopterid trees colonizing the abandoned floor of a seasonally active fixed-channel river and a similar dryland context is probable for the seven other sites. The dominance of amniotes in these dryland alluvial facies contrasts markedly with coeval wetland facies in the nearby Joggins Formation, where skeletal and trackway assemblages are amphibian-dominated. This may imply that amniotes were better adapted to seasonally dry settings and sheds new light on the community ecology of tetrapods during a key evolutionary phase.

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1. Introduction

Trackways represent a major under-utilized resource for unraveling the ecology and early evolution of tetrapod communities. They are much more common than skeletal remains, and when studied in the context of sedimentary facies, can provide important information about gait, behaviour, community ecology, habitat and evolution (Sundberg et al., 1989; Tucker and Smith, 2004; van Allen et al., 2005; Falcon-Lang et al., 2007; Kubo and Benton, 2008; Kubo and Ozaki, 2009; Mazin et al., 2009; Falcon-Lang, 2010; Niedzwiedzki et al., 2010). Perhaps one reason why trackways have been overlooked in earlier syntheses is the difficulty of identifying the trackmaker with sufficient taxonomic precision (Voigt et al., 2007). To overcome this problem, Carrano and Wilson (2001) proposed a cladistic approach whereby trackmakers are identified primarily by skeletal structures preserved in the tracks and synapomorphies of the body-fossil clade. This has two advantages: (1) identification is based on diagnoses not descriptions, and (2) it is possible to positively identify candidate trackmakers, even if merely to the level of order or family, while excluding others.

The mid–Carboniferous is one time when trackways have much to contribute to our knowledge of tetrapod evolution (Benton, 2005). During this important interval tetrapod communities diversified and amniotes emerged (Milner, 1987), paving the way for complex, fully terrestrial ecosystems that occupied many sectors of ecospace both beside the rivers and lakes, and in drier and higher locations (Clack, 2002). Our knowledge of these events is primarily based on discoveries of abundant skeletal remains in the Lower Pennsylvanian Joggins Formation of Nova Scotia, Canada (Falcon-Lang, 2006a; Falcon-Lang et al., 2006). However, far less well known are the abundant tetrapod trackways that occur in the Joggins Formation and other Early Pennsylvanian deposits surrounding the Bay of Fundy in Nova Scotia and New Brunswick (Sarjeant and Mossman, 1978; Cotton et al., 1995; Falcon-Lang et al., 2007). The aims of this paper are (1) to describe new Early Pennsylvanian trackway sites near St. Martin’s, New Brunswick and (2) to synthesize the literature on Late Mississippian to Early Pennsylvanian trackways from eastern Canada (Fig. 1).
Findings shed new light on the community ecology of tetrapods at a key evolutionary phase.

2. Geological setting

The new trackway assemblages were discovered in August 2008 and July 2009 during an investigation of the Lower Pennsylvanian Tynemouth Creek Formation of southern New Brunswick. This unit is ~700-m thick and crops out in high sea-cliffs over a 15 km stretch of coastline between Emerson Creek (Latitude 45°16′N; Longitude 65°47′W) and Roger’s Head (Latitude 45°18′N; Longitude 65°35′W), southwest of St. Martins, southern New Brunswick (Fig. 2). Plint and van de Poll (1982) interpreted this succession as the deposit of a northwestward-prograding alluvial fan based on the occurrence of laterally extensive conglomerate sheets, coarsening-upward patterns over several hundred metres of stratal thickness, and rather uniform palaeoflow. Although small alluvial fans may have contributed to the formation, the great thickness and abundance of sandstone and mudstone suggests deposition on a fluvial megafan laid down where large, mixed-load drainage systems entered the basin from adjoining uplands (cf. Singh et al., 1993). The megafan was probably shed off an oblique-slip thrust front developed between the Meguma and Avalon terranes during the accretion of Pangaea (Plint and van de Poll, 1984; Nance, 1986, 1987). It accumulated at the western end of the Cumberland Basin, about 120 km southwest of the depocentre of the Joggins Formation (Falcon-Lang et al., 2006).

Our sedimentological observations closely accord with the earlier palaeoenvironmental work of Plint and van de Poll (1982). Thick conglomerate sheets and lenses record prominent episodes of energetic fluvial transport, but the bulk of the formation comprises fluvial sandstone and mudstone. Narrow channel-sandstone bodies a few metres thick show steeply incised margins, and poorly channelized sandstone sheets are common. Because palaeoflow data are few, it is possible that some sandstone sheets represent fl ow-parallel cuts through narrow channel bodies. The channels are mainly filled with vertically stacked layers of massive and trough cross-bedded sandstone and mudstone, and only a few channel bodies contain barform accretion sets. Bedforms indicative of high-flow-stage conditions are rare. These fixed-channel bodies (cf. Gibling, 2006) imply episodic deposition in shallow channel systems cut into relatively indurated floodplain deposits. In terms of their architectural style, the channel bodies range from isolated to amalgamated in different intervals.

Interbedded with these channel bodies are mudstone-rich successions, which are predominantly red and poorly stratified, with concave-up joints and some carbonate nodules. They represent cumulative palaeosols with vertisol-like features, indicative of seasonally dry conditions (Tandon and Gibling, 1994; Driese and Ober, 2005). Within the mudstone-rich successions are siltstone packages a few metres thick, many of which have upright calamitean trunks and irregular bed surfaces (Briggs et al., 1984; Falcon-Lang, 2006b). The uneven bedding variously reflects floodplain degradation and sediment mounding and scour around standing trees, and the packages are interpreted as levee and crevasse-splay complexes derived from overbank flooding. Plint and van de Poll (1982) interpreted these strata as interchannel and distal fan deposits.
Large arthropod trackways (Diplichnites) are prominent in these facies at numerous localities, one well-documented example winding through a grove of upright calamitean trees (Briggs et al., 1984).

Also present in overbank strata are a few successions containing evidence for persistent bodies of standing water. Some of these comprise interstratified calcareous siltstone and mudstone units with rain prints, which may represent shallow evaporative lakes (Plint, 1985). Other similar deposits coarsen upward and are capped by channelized sandstone bodies, suggesting drainage diversion into more substantial standing-water bodies. Associated plant fossils are relatively common in the form of standing trees (including some at incised-channel margins), rooted zones, transported logs at channel bases, and fine plant fragments in thin carbonate intervals. Organic deposits accumulated in local wetlands and abandoned channels. Rare bioclastic limestone units containing Spirorbis, ostra-codes and gastropods (Plint and van de Poll, 1982), and mudstone successions with xiphosuran walking traces (Falcon-Lang, unpublished data), may represent cryptic expressions of brackish marine transgressions (Schultze, 2009), as seen at many discrete intervals in the Lower Pennsylvanian fill of the Maritimes Basin (Falcon-Lang and Miller, 2007).

In summary, the Tynemouth Creek Formation was deposited in a dryland alluvial setting with many narrow channel systems where flow was periodic and probably ephemeral but not markedly energetic. Channels filled vertically and lateral migration was limited. Precipitation was seasonal, the climate was probably sub-humid to semi-arid, and the plains were locally well vegetated with good evidence for riparian plants. Terrestrial invertebrates were common. A similar spectrum of alluvial channel forms and facies characterizes modern megafan successions (Wells and Dorr, 1987; Singh et al., 1993) and those of the ancient record (Nichols, 1987; Hirst, 1991), and degradational floodplain surfaces are prominent on and below alluvial plains in seasonal climates (Gibling et al., 2005). In terms of its climatic setting and fluvial style, the Channel Country of inland Australia (Gibling et al., 1998) shows some similarities, although the deposits are overall much finer grained than those of the Tynemouth Creek Formation.

3. Stratigraphy and biostratigraphy

To date the most complete stratigraphic analysis of the Tynemouth Creek Formation has been undertaken by Plint and van de Poll (1982). They logged four contiguous sections (Fig. 3) at metre-scale, but they were unable to correlate them precisely because of widespread faulting and folding (beds locally overturned). Their Section 1, which conformably overlies the Boss Point Formation near Giffin Pond, represents the lowermost part of the formation (Plint and van de Poll, 1984). Their Sections 2 and 3, east and west of Tynemouth Creek, respectively, and their Section 4, from Gardner Creek to McCoy Head, are all characterized by upward coarsening over hundreds of metres of vertical succession. Based on this common 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, 2006b). Given that the Tynemouth Creek Formation overlies the Boss Point Formation, based on lithostratigraphic considerations, it must be correlated (at least in part) with one or more of the Little River, Joggins and Springhill Mines formations in the eastern part of the Cumberland Basin because these units also overlie the Boss Point Formation (Calder et al., 2005).

Floral biozonation confirms this lithostratigraphic correlation in general terms. Palynological assemblages collected from the middle of Sections 2 and 3 of the Tynemouth Creek Formation suggest a late Yeadonian–Langsettian age (Dolby, 1997; Utting et al., 2005), whereas studies of megafossil remains imply a slightly younger Langsettian–Duckmantian age (Utting and Wagner, 2005; Wagner, 2008). Medullosalean pteridosperms in megafossil assemblages collected during the course of this current study also suggest a Langsettian–Duckmantian age for the Tynemouth Creek Formation. One key taxon, Neuroleptopteris schelehani (Fig. 4A), although rare in the succession, is especially abundant in the middle of Section 2. This species went extinct at the Langsettian–Duckmantian boundary (Wagner, 1984; Cleal and Thomas, 1994; Goubet et al., 2000), indicating that lower parts of the succession are Langsettian in age (Fig. 3). Another important biostratigraphic indicator is Paripitres linguaefolia (Fig. 4B), which is very abundant in one bed in the middle of Section 4. This species first appears in lowest Duckmantian strata in western Europe (Wagner, 1984; Laveine, 1987; Cleal and Thomas, 1994), suggesting that upper parts of the Tynemouth Creek Formation are Duckmantian in age. Alethopteris urophylla (Fig. 4C, E), which occurs sporadically in the lower part of the formation, ranges from the middle Namurian (Kinderscoutian) to early Bolsovian but is mostly confined to the Langsettian and Duckmantian (Wagner and Álvarez-Vázquez, 2008). Finally, the most common pteridosperm is Neuropteris obliqua (Fig. 4D), a long-ranging taxon that extends from the latest Namurian (Basukrian) to the top of the Bolsovian, but is most abundant in lower Langsettian to middle Duckmantian strata in western Europe (Laveine, 1987; Cleal and Thomas, 1994; Cleal, 2007). These palynofloral and megafossil data compare closely with those from the Little River, Joggins and Springhill Mines formations in Nova Scotia, which indicate a late Yeadonian–Duckmantian age for those units (Calder et al., 2005), with tetrapod skeletal remains in the upper part of the Joggins Formation being of probable late Langsettian age (Falcon-Lang et al., 2006).
4. Trackway localities

Trackway assemblages were found at eight separate sites along the coastal outcrop belt of the Tynemouth Creek Formation, and their coordinates were fixed with a GPS (NAD83) or using a 1:50,000 map (21/H5; Loch Lomond). From west to east, these are located at (1) McCoy Head, 45°15.552′N; 65°43.866′W, (2) Wallace Beach, 45°15.874′N; 65°43.954′W, (3) west of Gardner Creek, 45°16.533′N; 65°43.383′W, (4) east of Gardner Creek, 45°16.39′N; 65°42.48′W, (5) west of Tynemouth Creek, 45°17.21′N; 65°40.01′W, (6) on the headland comprising the east side of Tynemouth Creek, 45°17.422′N; 65°39.110′W, (7) west of Giffin Pond, 45°18.490′N; 65°35.709′W, and (8) a second site west of Giffin Pond, 45°18.305′N; 65°35.997′W (Fig. 2).

Almost all the trackways occur on blocks of sandstone that have toppled out of the cliffs and are scattered across the beach. However, in most cases, the bed of origin (and hence the height in Plint and van de Poll's, 1982 sections) could be established by comparing the thickness and lithology of the fallen block with the in situ succession, and by locating in situ examples of footprints (this proved impossible for a few water-worn transported blocks). This indicates that all eight sites are confined to the lower to middle part of the Tynemouth Creek Formation and are thus probably of late Langsettian to early Duckmantian age based on co-occurring megafloral assemblages (Fig. 3). All the blocks comprise beds of fine- to medium-grained sandstone, typically 0.11–0.54 m thick, and trackways are preserved in convex hyporelief on the base of the bedding surface, where they are impressed in thin (typically < 5 mm thick) laminae of red mudstone.

As the blocks were mostly too large to collect from the remote localities (long axes up to 0.86 m), photographs of each surface were obtained, color-printed, and tracks directly drawn onto the prints while still in the field. It proved essential to draw the tracks in the field because their apparent morphology varied depending on the angle and intensity of sunlight. Tracks were viewed under variable light conditions to ensure accurate description. Where possible some of the smaller blocks, or representative fragments broken off the larger blocks, were collected to create a reference collection and check findings. Latex casts of some surfaces were also obtained. In total, eleven specimens, and associated latex casts, were collected and deposited in the New Brunswick Museum, Saint John, under accession numbers NBMG 14589–14596, 14624, and 15061–15062.

5. Tynemouth Creek headland site

The most prolific trackway site was positioned near the southwest corner of the headland on the eastern side of Tynemouth Creek.
Here, eleven blocks of sandstone bearing ~179 footprints including five or six partial trackways were observed at the bottom of the cliff. As trackways were also observed on the base of a lithologically-similar sandstone bed exposed a third of the way up the cliff, the horizon of origin was fixed with certainty (98 m level in Section 2 of Plint and van de Poll, 1982). The trackways were studied in the context of a ~15 m thick succession exposed on the southwest face of the headland (Fig. 5B–F), which immediately overlies the famous “Earthquake Bed” described by Plint (1985). This surface comprises a prominent palaeosol offset by syn-sedimentary faulting and dramatically demonstrates that active tectonism accompanied sedimentation. The earthquake bed is the topmost surface of a conglomeratic channel body 7 m thick, deeply incised into well-bedded sandstones that were laid down in standing-water bodies (Fig. 5C; see Plint, 1985). The presence of Neuralethopteris schlehanii (Fig. 4A) and palynological assemblages (CS96-407 and CS96-408; Dolby, 1997) constrain the age of these strata to the Langsettian.

5.1. Sedimentary facies

The studied succession comprises four principal depositional units (Fig. 5B). Unit 1, which directly overlies the “Earthquake Bed”, consists of two sheet-like bodies of red fine-grained sandstone, each 2–3 m thick. These bodies show undulatory bedding with thin mudstone laminae, and locally contain upright trees, especially calamiteans (Fig. 5D), and rooting organs of lycopsids (Stigmaria). Each body is capped by a thin rooted mudstone. Above these beds is a poorly exposed succession of weakly stratified red mudstone, 2.5 m thick, which locally contains very thin beds of carbonate-rich laminae. Unit 1 is interpreted as a stacked set of vegetated levee and splay deposits. The undulating bedding reflects sedimentation around upright trees, generating vegetation-induced sedimentary structures (Rygel et al., 2004), and the presence of lycopsids suggests a poorly drained setting. The capping red mudstone represents a stable floodplain, with good drainage and modest palaeosol development. Carbonate-rich laminae may imply the ephemeral occurrence of shallow evaporative lakes.

Unit 2 comprises a large channelized body of medium- to coarse-grained sandstone cut down into the underlying red mudstone, and contains three subunits (Unit 2a–c). The main channel body (Unit 2a) is up to 5 m thick but thins towards the western end of the outcrop where its margin is exposed (Fig. 5B). The eastern margin is not seen, but the body thins towards the edge of the outcrop, about 140 m eastwards. Trough cross beds are present locally in the channel-fill but the dominant sedimentary motif is metre-thick sheets of massive sandstone. In the upper part of the channel-fill, the sandstone is more thinly bedded (Unit 2b) and oversteps the western channel margin, where sandstone and siltstone sheets a few centimetres to decimetres thick are interbedded with red mudstone that is locally calcareous. The basal strata contain back-filled horizontal burrows (Fig. 5E), and a few pteridosperm pinnules and roots are present in the upper part. These beds are overlain abruptly by a 1.5 m unit (Unit 2c) of medium-
grained sandstone containing trough cross beds (Fig. 5F). The tetrapod trackways are preserved at the base of this sandstone. Traced westward from the thickest sandy deposits of Unit 2a, the thinly bedded strata and the overlying “trackway bed” dip gently and occupy a shallow depression that extends over the adjoining floodplain deposits of Unit 1 (Fig. 5B).

The channel body of Unit 2 is interpreted as a fixed channel cut into relatively consolidated and locally cemented floodplain muds. The fill of stacked sandstone sheets (Unit 2a) indicates that the channel aggraded vertically, and the parent channel at the time of abandonment and relocation lay against floodplain muds at the western margin. Following abandonment, water ponded in the abandoned channel where accumulation of mud was periodically interrupted by thin flood sheets of sand and silt (Unit 2b). The standing water provided a suitable habitat for burrowing organisms, probably arthropods, and carbonate-rich laminae suggest development of short-lived evaporative ponds. As the channel filled, vegetation inhabited by tetrapods colonized the area. Subsequently, a thick sandstone (Unit 2c) with dune deposits was emplaced across the vegetated surface, representing a major flood that probably filled the abandoned channel to the level of the topmost channel fill further east. This cast the tetrapod trackways on its basal surface.

Units 3 and 4 were not accessible in the cliff, but were studied from photographs. The base of Unit 3 is defined by a major incision surface that can be traced across the outcrop belt and comprises a number of narrow channels that cut down several metres into Unit 2. These channels are infilled with mudstone, siltstone, and thinly bedded sandstone in their lower part, and coarsen upward into a series of thick, laterally extensive sandstone units, 2–3 m thick, with some more extensive red mudstones. A coarser sandstone body caps these beds; it has an erosional base that steps down towards the west, with a maximum erosional topography of 4 m. These deposits represent a set of fixed channels and floodplain remnants. A 5 m thick polymictic pebble conglomerate (Unit 4) caps the top of the headland, marking a return to highly energetic flow.

Further research is needed to understand the relationship between the conglomeratic and sandstone–mudstone units. The thick conglomeratic channel bodies may represent major feeder channels on the megafan, bringing coarse detritus to more distal parts of the alluvial megafan where finer sediment was laid down in smaller fixed channels and floodplains (cf. Allen et al., 1983). Alternatively, the apparently abrupt intercalation of the two sets of strata may imply major events on the megafan or in the adjoining uplands, linked to tectonism, climate, or both.

5.2. Description of tracking surface

The trackways, which form the focus of this paper, are preserved in convex hyporelief (1–9 mm) on the base of Unit 2c. Evidently, footprints were impressed into the topmost red mudstone surface of the underlying Unit 2b, and were preserved when the sand sheet of Unit 2c was rapidly emplaced on top, covering the tracks. Thus the trace fossils comprise true tracks (sensu Milan and Bromley, 2006), rather than under-tracks or eroded tracks. This is confirmed by preservation of various subtle features on the tracking surface including casts of abundant rain prints, very localized mud cracks and tool marks in addition to the widespread footprints and tail drag marks. All these features demonstrate that the surface bearing the tracks was sub-aerially exposed and, therefore, also the surface on which the animals were walking.

Tetrapod footprints generally occur with very high density on this bedding surface, with one slab showing at least 56 footprints or partial footprints over a surface area of <0.5 m². Consequently, later footprints have commonly overprinted earlier traces, and in most cases it is difficult to distinguish discrete trackways (hence isolated footprints are the most commonly observed phenomenon). Further, more, in some slabs, footprints show multiple, opposing directions of travel, while in others most of the footprints have the same orientation. The former observation suggests that the tetrapods either occurred in very high density, or repeatedly trampled over the same restricted area. The tracking surface was evidently of variable firmness; some footprints with prominent digit-drags and repositioned digits imply locomotion on a slippery surface, while other undistorted, low-relief footprints imply a firm substrate.

Scattered across the tracking surface, with no preferred orientation, are the impressed and/or coalified remains of at least eight woody tree-trunks, up to 0.11 m diameter and <1.7 m long (Fig. 6). These trunks are slightly curved along their length and show evidence of downward-recurred lateral branching characteristic of medullosan pteridosperms. In a few examples, the trunks flare at one end and terminate in an area with concave hyporelief (implying the existence of a mound in the underlying bed). This suggests that at least some of the trees remain rooted in growth position, despite being preserved parallel to bedding. A few rare impressions of Alethopteris urophylla pinnae and pinnules occur in association with these trunks and this species is very common through the general succession in which the trackways occur. Thus the trunks and the pinnule impressions may be the remains of alethopterid pteridosperms, which colonized the abandoned channel in which the tetrapods lived.

5.3. Description of trackways

Three morphotypes of footprint were observed at the Tynemouth Creek headland site (Fig. 7), but one type is by far the most abundant and well preserved, comprising at least 160 of the 179 footprints documented. These abundant footprints, referred to Pseudobradypus, include four partial trackways. The other two morphotypes, Batracichnus (n = 13) and Baropeza (n = 6) are comparatively rare. The following description of the three morphotypes is based on field descriptions complemented by examination of collections in the lab (NBMG 14590, 14591, 14593, 15061 and 15062). Where two morphotypes comprised a trackway, the larger footprint defining the greatest track width was assumed to represent the pes, while the smaller footprint was assumed to represent the manus.

5.3.1. Pseudobradypus longidigitatus (Sternberg, 1933)

The first morphotype, Pseudobradypus, comprises plantigrade footprints, 32–53 mm long and 27–41 mm wide. Where well preserved, both manus and pes are demonstrably pentadactyl.Digits are slender with a length/width ratio of ≤0.1 (manus) and ≤0.4 (peses) and may terminate with an acuminate tip. Digit splay is mostly in the range of 40–55° though a few outliers have splays of <80°. The pes is usually slightly larger with an elongate rounded heel mark and somewhat distinct from the smaller manus, which shows a prominent concavity in the heel region. A feature seen in one pes is the occurrence of transverse ribbing near the tip of the third digit (Figs. 7D and 8). Locally tail drag marks, which are straight or slightly curved, occur along the mid-line of some partial trackways of Pseudobradypus-type. In terms of size and shape of the foot, and digital ratios, these footprints are closest to Pseudobradypus longidigitatus (Sternberg, 1933) described from the nearby River Phillip site in Nova Scotia (Sternberg, 1933).

The most complete Pseudobradypus trackway comprises at least nine pentadactyl footprints including representatives of all four feet (Trackway A in Fig. 9). Although more footprints are preserved on the left side of the trackway, the seven prints on this side are distorted by toe-drags and slide marks, such that the two prints on the right side give a more faithful indication of foot morphology. The best-preserved manus (Rm1) is 41 mm long by 37 mm wide (Fig. 7C). It comprises narrowly splayed (42°) digits whose relative lengths approximate a phalangeal formula of 2:4:5:3:3. The heel mark is rather wider than it is long and contains a prominent concave...
A second Pseudobradypus trackway comprising up to seven footprints, also occurs on the same block and displays footprints of a similar morphology and size (Trackway B in Fig. 9). A well-preserved left manus is 39 mm long and 36 mm wide with slender, narrowly splayed (52°) digits approximating a phalangeal formula of 23454 (possibly 23453) and convex heel mark. A right pes is 44 mm long and 38 mm wide. Two further partial trackways of Pseudobradypus-type occur on other blocks (not illustrated), both showing a straight tail drag along the mid-line. In addition, a large number of isolated footprints are present, which cannot be grouped into well-defined tracks (e.g., Fig. 7D, E), but are of similar size and morphology to Pseudobradypus. In some examples of these isolated footprints (probably the manus), the third digit is the longest (rather than the fourth), but this may be extramorphology (Fig. 7D).

### 5.3.2. Batrachichnus ichsp.

The second morphotype, Batrachichnus ichsp., is represented by a single partial trackway comprising seven footprints (Fig. 10), and six additional isolated footprints scattered over several other blocks (Fig. 7G). Although Tucker and Smith (2004) synonymised Batrachichnus with Limnopus, based on similar morphology and a continuum of sizes between the two forms, Batrachichnus is retained here as a useful term to describe very small footprints representing this morphotype. These footprints are very subtle features (~1 mm relief). Where preserved in their entirety, footprints interpreted as manus are demonstrably tetradactyl and only 5–8 mm long and 4–7 mm wide. Digit splay is in the range of 67–78° and the third digit is usually the longest (length/width ratio ≤ 3.4). Other footprints may represent pentadactyl pes, but are too incompletely preserved to identify with confidence. The only partial trackway observed is probably <20 mm wide, but pace angulation could not be determined.

### 5.3.3. Baropezia ichsp.

The third morphotype, Baropezia ichsp., is represented by a few plantigrade to digitigrade footprints, including one poorly preserved trackway, collected as NBMG 14589 (Fig. 10). The best example of a pes has been partially overprinted by another footprint on one side, making description difficult (Fig. 7F). It is 26 mm wide and >20 mm long and comprises five, widely splayed digits (152°). Digits are short...
and fat (length/width ratio $\leq 2.6$) and terminate with a prominent bulge about twice the width of the digit. Two, or three, variably preserved manus occur nearby, presumably part of the same trackway, and are of similar size with digits that show less splay ($80^\circ$–$90^\circ$) and are more slender (length/width ratio $\sim 3.5$) terminating in a bulge. It is uncertain whether the manus are tetradactyl or pentadactyl due to incomplete preservation, but at least one specimen apparently shows a partly preserved fifth digit (Fig. 10). Feet are

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Fig. 9. Photograph and interpretative sketch of sandstone block 1 from the Tynemouth Creek headland site (Site 6; 45°17.422′N 65°39.110′W) showing two trackways, and various isolated footprints, of *Pseudobradypus* type. A single small footprint of *Batrachichnus* is overprinted on Lm1 (lower left).

Fig. 10. Photograph and interpretative sketch of sandstone block 9 from the Tynemouth Creek headland site (Site 6; 45°17.422′N 65°39.110′W) showing various isolated footprints, of *Pseudobradypus* type. A partial trackway of *Batrachichnus* (right middle) and *Baropezia* (top right) is shown. The gray area was collected, and accessioned under NBGM14589.
7. Identity of trackmakers

In order to identify the tetrapods that made the trackways, qualitative and quantitative characteristics of the footprints were compared with apomorphies of the body fossil clades (Carrano and Wilson, 2001) for basal amphibians and amniotes (Table 1). The most abundant morphotype, *Pseudobradypus*, has generally been attributed to early amniotes in previous studies (Haubold, 1971) and some tracks have been attributed to the basal amniote group, the pelycosaurs.

Table 1

<table>
<thead>
<tr>
<th>Apomorphies of manus and pes of basal amphibians and amniotes.</th>
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<tr>
<td><strong>Tetrapoda</strong></td>
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<tr>
<td>1. Dactylly: manus and pes incorporating a series of articulating load-bearing digits (Gaffney, 1979; Panchen and Smithson, 1988, p. 2; Ruta et al., 2003, p. 330).</td>
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<tr>
<td>2. Wrist joint in forelimb, hinged; ankle joint rotary (Rackoff, 1980; Panchen and Smithson, 1988, p. 3).</td>
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<tr>
<td>3. Five-digit manus and five-digit pes (primitive character for amniotes, and presumably for tetrapods; Panchen and Smithson, 1988, p. 8).</td>
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<td><strong>Amphibia (+ Temnospondyli + Lissamphibia + Lepospondyli)</strong></td>
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<tr>
<td>1. Four-digit manus (primitive character for the clade; Panchen and Smithson, 1988, p. 8; Ruta et al., 2003, p. 330).</td>
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<td><strong>Terrestrial Formations</strong></td>
</tr>
<tr>
<td>1. No more than three digits in the manus (Ruta et al., 2003, p. 330).</td>
</tr>
<tr>
<td>2. Pes phalangeal formula reduced from primitive 23455 to 23343 (Panchen and Smithson, 1988, p. 16; but also seen diadectomorphs and seymouriomorphs).</td>
</tr>
<tr>
<td>3. Short 5th metatarsal relative to the 4th metatarsal (Müller and Reisz, 2006, p. 505).</td>
</tr>
<tr>
<td><strong>Diapsida</strong></td>
</tr>
<tr>
<td>1. Manus long and slender, rather than short and broad (Gauthier et al., 1988, p. 137).</td>
</tr>
<tr>
<td>2. Short 4th metatarsal relative to tibia (Müller and Reisz, 2006, p. 505).</td>
</tr>
<tr>
<td>3. Short 5th metatarsal relative to the 4th metatarsal (Müller and Reisz, 2006, p. 505).</td>
</tr>
<tr>
<td><strong>Reptilia</strong></td>
</tr>
<tr>
<td>1. Five-digit manus and pedes (primitive character for reptiles; Panchen and Smithson, 1988, p. 330).</td>
</tr>
<tr>
<td>2. Pes phalangeal formula reduced to 23443 or 23343 (Müller and Reisz, 2006, p. 304).</td>
</tr>
</tbody>
</table>

**Pareiasauria**

2. Non-terminal phalanges in the manus are extremely short and robust — their length is less than half their width (Lee, 1995, p. 503). |

**Procolophonia**

1. Unguals exceed length of penultimate phalange by at least 50% (de Braga and Rieppel, 1997, p. 300). |
2. Pes phalangeal formula reduced to 23333 or less (Laurin and Reisz, 1995, p. 201). |
3. Pes phalangeal formula reduced to 23343 or less (Laurin and Reisz, 1995, p. 201). |
Yates and Warren, 2000), other than the four-digit manus, seen in cladistic interpretation cannot be attempted because temnospondyls (Haubold, 1971; Sarjeant and Mossman, 1978; Scarboro and Tucker, 1995). Anthracosaurs were basal reptiliomorphs, many secondarily adapted to aquatic life, and they retained the primitive arrangement of digits in hand and foot, most notably a five-digit manus (four digits in Amphibia; Ruta et al., 2003, p. 330) and a digital formula of 23454 in the pes (Panchen and Smithson, 1988, p. 16 and p. 23). The Tynemouth Creek Baropezia resemble anthracosaurs in their short, fat, widely splayed digits and the low length/width ratio of their manus and pes (Table 2). In addition, Ruta and Clark (2006) reported that the anthracosaur, Silvanerpeton has small triangular expanded ends to its unguals, somewhat similar to the terminal bulge seen in the Baropezia material.

8. Palaeoecology

In the Tynemouth Creek Formation, diverse trackways are described, dominated by early amniotes, together with some anthracosaurs and temnospondyls. Facies analysis of the most prolific site at Tynemouth Creek headland (Site 6) suggest that tetrapods lived on the edge of an abandoned river channel on a seasonally dry alluvial plain (Fig. 11). The abandoned channel was colonized by alethopterids and, at times, contained shallow ponded bodies of water (probably during the wet season). Pennsylvaniaan tetrapod trackways and body fossils within the deposits of seasonally active dryland channels have been noted at several sites across eastern Canada (Keighley and Pickrell, 1998; Falcon-Lang et al., 2004, 2007; Van Allen et al., 2005). This repeated association may represent waterhole communities, with animals clustering around point sources of water in an otherwise arid landscape. The very high density of tracks at Site 6 tends to support this hypothesis, suggesting that tetrapods may

Table 2

<table>
<thead>
<tr>
<th>Genus</th>
<th>Key reference</th>
<th>Phalangeal formula</th>
<th>Digit length/width</th>
<th>Digit splay (°)</th>
<th>Foot length/width</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Manus Pes</td>
<td>Manus Pes</td>
<td>Manus Pes</td>
<td>Manus Pes</td>
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<td>Reptiliomorphs</td>
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<td>'Anthracosaurs'</td>
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</tr>
<tr>
<td>2. Archeria</td>
<td>Romer (1957)</td>
<td>23454 23455</td>
<td>7.1 8.1</td>
<td>85 65</td>
<td>1.4 1.5</td>
</tr>
<tr>
<td>Seymouria</td>
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<tr>
<td>4. Seymouria</td>
<td>Berman et al. (2000)</td>
<td>23443 23453</td>
<td>4.4 8.0</td>
<td>110 120</td>
<td>0.9 1.2</td>
</tr>
<tr>
<td>5. Disconius</td>
<td>Klimbara and Bartik (2000)</td>
<td>23453 23453</td>
<td>6.5 5.7</td>
<td>55 65</td>
<td>1.2 1.4</td>
</tr>
<tr>
<td>Diadectomorphs</td>
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<tr>
<td>6. Gobata</td>
<td>Berman et al. (2004)</td>
<td>23453 23454</td>
<td>5.8 4.2</td>
<td>65 65</td>
<td>1.2 1.0</td>
</tr>
<tr>
<td>7. Limnoscelis</td>
<td>Williston (1911)</td>
<td>23453 23454</td>
<td>4.4 4.4</td>
<td>65 40</td>
<td>1.0 1.0</td>
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<td>Outgroup to amniotes</td>
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<tr>
<td>9. Casineria</td>
<td>Paton et al. (1999)</td>
<td>23453 23453</td>
<td>7.8 –</td>
<td>45 –</td>
<td>2.0 –</td>
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<tr>
<td>Amniotes</td>
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<td>Sauropterygia</td>
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<tr>
<td>10. Eocaptorhinus</td>
<td>Heaton and Reisz (1986)</td>
<td>23453 23454</td>
<td>8.4 9.6</td>
<td>90 75</td>
<td>1.5 1.6</td>
</tr>
<tr>
<td>11. Paleothyris</td>
<td>Carroll (1969)</td>
<td>23453 23454</td>
<td>16.1 22.2</td>
<td>65 55</td>
<td>3.0 2.9</td>
</tr>
<tr>
<td>12. Anthracosaurus</td>
<td>Carroll and Baird (1972)</td>
<td>23453 23454</td>
<td>23.0 28.0</td>
<td>40 60</td>
<td>4.0 4.3</td>
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<tr>
<td>13. Petrolacosaurus</td>
<td>Reisz (1981)</td>
<td>23453 23454</td>
<td>13.6 13.6</td>
<td>50 40</td>
<td>3.8 3.4</td>
</tr>
<tr>
<td>Synapsida</td>
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</tr>
<tr>
<td>14. Haplopus</td>
<td>Currie (1977)</td>
<td>23453 23454</td>
<td>12.3 9.6</td>
<td>45 55</td>
<td>2.5 2.3</td>
</tr>
<tr>
<td>Temnospondyls</td>
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<tr>
<td>15. Dendrerpeton</td>
<td>Heaton and Reisz (1986)</td>
<td>23453 23454</td>
<td>8.4 9.6</td>
<td>90 75</td>
<td>1.5 1.6</td>
</tr>
<tr>
<td>Tynemouth Creek Trackways</td>
<td></td>
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</tr>
<tr>
<td>16. Pseudobradypus</td>
<td>This paper</td>
<td>23453 23454</td>
<td>9.8 11.8</td>
<td>40–55 40–55</td>
<td>1.8 2.1</td>
</tr>
<tr>
<td>17. Baropezia</td>
<td>This paper</td>
<td>– 23454</td>
<td>5.6 4.2</td>
<td>80–90 152</td>
<td>1.3 1.2</td>
</tr>
<tr>
<td>18. Batrachichnus</td>
<td>This paper</td>
<td>23333 –</td>
<td>5.4</td>
<td>67–78 –</td>
<td>1.8 –</td>
</tr>
</tbody>
</table>

The third morphotype, Baropezia ich., is interpreted as the trackway of an anthracosaur, based on traditional interpretations (Clack, 1991; Sarjeant and Mossman, 1978; Scarboro and Tucker, 1995). Anthracosaurs were basal reptiliomorphs, many secondarily adapted to aquatic life, and they retained the primitive arrangement of digits in hand and foot, most notably a five-digit manus (four digits in Amphibia; Ruta et al., 2003, p. 330) and a digital formula of 23454 in the pes (Panchen and Smithson, 1988, p. 16 and p. 23). The Tynemouth Creek Baropezia resemble anthracosaurs in their short, fat, widely splayed digits and the low length/width ratio of their manus and pes (Table 2). In addition, Ruta and Clark (2006) reported that the anthracosaur, Silvanerpeton has small triangular expanded ends to its unguals, somewhat similar to the terminal bulge seen in the Baropezia material.
have been restricted to progressively smaller bodies of water as ponds contracted during the dry season.

The dominance by amniotes is of especial ecological interest. Based on skeletal remains, this nascent group comprised only a very small proportion of Early Pennsylvanian communities (Milner, 1987). Their dominance in the Tynemouth Creek Formation therefore may reflect an ecological advantage from possession of the cleidoic egg (Benton, 2005). Although Pennsylvanian amniote body fossil and trackways are known from both wetland and dryland facies, as yet it remains to be shown whether they were generally more common in water-stressed environments. A brief review of Early Pennsylvanian trackways across eastern Canada provides some qualitative support for this hypothesis. Dryland facies containing, or dominated by, putative amniote trackways are known at River Philip (Sternberg, 1933), Mabou (Keighley and Pickerill, 1998), Parrsboro (Mossman and Grantham, 1999), Lower Cove (Calder et al., 2005), and Grande Anse (Falcon-Lang et al., 2007). Conversely, amphibians dominate the region’s richest tetrapod body fossil and trackway assemblages in the Joggins Formation with most of the published material coming from wetland facies (Dawson, 1863, 1868; Matthew, 1903a, 1903b, 1905; Mossman and Grantham, 1996; Davies et al., 2005; Falcon-Lang, 2005; Lucas et al., 2005; Calder et al., 2006; Falcon-Lang et al., 2006). However, this situation is complicated because amphibians are also present in dryland facies (Falcon-Lang et al., 2004), while amniote fossils occur in wetland facies (Falcon-Lang et al., 2006). Thus, detailed quantitative studies of the relative proportions of taxa in different facies are needed to better constrain environmental preferences, and to confirm suggestions that the cleidoic egg conferred ecologic advantage to early amniotes in dryland facies.

9. Conclusions

1. A new and diverse assemblage of tetrapod trackways is reported from eight sites in the Lower Pennsylvanian Tynemouth Creek Formation of southern New Brunswick, Canada.
2. Facies analysis of trackway-bearing sediments indicates that tetrapods colonized dryland alluvial tracts characterized by seasonally flowing rivers, and lived amongst riparian stands of alethopterid trees.
3. Trackways of Pseudobradypus type, inferred to have been made by early amniotes, are most abundant morphotype, but a few putative anthracosaurs (Baropeza) and temnospondyl amphibians (Batrachichnus) were also present.
4. Dominated by amniotes, this dryland assemblage differs from most wetland assemblages, where amphibians are more common. This may imply that early amniotes had an ecological advantage in seasonally dry settings.
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