

Ecology of earliest reptiles inferred from basal Pennsylvanian trackways

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Abstract: Trackways representing the earliest evidence for the origin of reptiles (amniotes) are reported from the basal Pennsylvanian Grande Anse Formation, New Brunswick, Canada. Amniote characters include pentadactyl manus and pes, slender digits whose relative lengths approximate a phalangeal formula of 23453 (manus) and 23454 (pes), narrow digit splay (40–63°), putative transverse scale impressions on digit pads, and straight tail drag. The trackways occur in the deposits of a seasonally active dryland river channel. Sedimentological context suggests, for the first time, that early amniotes existed in water-stressed environments, where the cleidoic egg would have presumably conferred reproductive advantage.

The origin of reptiles (amniotes), and specifically the acquisition of the cleidoic egg, was a key event in the history of life; it allowed tetrapods to escape the need to lay eggs in water and thereby colonize continental drylands (Benton 2005). The earliest skeletal remains of amniotes occur in the Lower Pennsylvanian (mid-Langsettian; *c.* 314 Ma) Joggins Formation of Nova Scotia, eastern Canada (Falcon-Lang *et al.* 2006). However, these assemblages include representatives of both synapsid and saurapsid lineages of amniote evolution (Milner 1996), implying an earlier amniote ancestry (Benton & Donoghue 2007). The extent of this inferred prehistory is poorly constrained because no localities with terrestrial tetrapod skeletal fossils are known for the preceding 20 Ma interval, and older assemblages at East Kirkton and Cheese Bay, Scotland (Late Viséan; *c.* 330–335 Ma) contain only stem-amniotes (Smithson *et al.* 1994; Paton *et al.* 1999; Ruta & Clack 2006). Abundant tetrapod trackways in eastern Canada (Sarjeant & Mossman 1978) provide an alternative source of evidence for assessing early reptile evolution (Chesnut *et al.* 1994). Here we report the discovery by one of us (H.J.F.L.) of distinctly reptilian trackways in the Lower Pennsylvanian Grande Anse Formation of New Brunswick (St. Peter & Johnson 1997). These fossils underlie the Joggins assemblage by *c.* 1 km (Calder *et al.* 2005), and thus represent the earliest evidence of amniotes.

Geological context

Our site is located *c.* 1 km south of Grande Anse, at Shepody Bay, on the eastern side of the Maringouin Peninsula, New Brunswick (Fig. 1a; 45°47'48"N, 64°30'29"W). Beds comprise the lower part of the *c.* 600 m thick Grande Anse Formation (Cumberland Group). Although faulted against Boss Point Formation at Shepody Bay, Black Point and Minudie (Map Sheets NTS 21 H/15 and H/16), the Grande Anse Formation also occurs within the centre of the Hardledges Syncline, where it conformably overlies the Boss Point Formation (St. Peter & Johnson 1997). Palynological assemblages indicate an earliest Langsettian (earliest Westphalian), or possibly latest Namurian, age for the Grande Anse Formation in its type section at Shepody Bay (Dolby 1999). These data allow lateral correlation with the lithologically similar Little River Formation in Nova Scotia, which also conformably overlies the Boss Point Formation and is of identical biostratigraphic age (Fig. 1b; Calder *et al.* 2005). As

the Little River Formation conformably underlies the Joggins Formation (Map Sheet 90-12), and reptile skeletal remains occur 627 m above the base of the Joggins Formation (Falcon-Lang *et al.* 2006), as much as 1 km of strata separate that fossil interval from our trackways.

Sedimentary facies and palaeoenvironment

The trackway-bearing succession comprises two facies associations (Fig. 2). A fine-grained association, totalling ≤ 5 m in thickness, contains: (1) red indurated mudstone showing vertical (drab halo) root traces penetrating *c.* 1 m deep; (2) lenticular fine-grained red sandstone cut by ripple cross-laminated sandstone ribbons, ≤ 1.3 m thick and ≤ 1.9 m wide; (3) channel bodies, ≤ 1.3 m thick and ≤ 4.7 m wide, filled by red mudstone and fine-grained sandstone, showing lateral accretion. A coarse-grained association comprises a ≤ 1.6 m thick and ≥ 21 m wide, erosive-based channel body (margins not observed) that fines from lenses of polymictic pebbly sandstone (extraformational clasts ≤ 31 mm diameter) at the base to medium-grained sandstone near the top. Bedforms include trough cross-beds (080° mean palaeoflow, $n = 19$) and ripple cross-lamination. Red mudstone lenses, ≤ 30 –55 mm thick, occur in some intervals, and overlying sandstone beds contain red mud clasts and preserve toolmarks, rain prints, and tetrapod trackways on their base.

Facies are interpreted as alluvial-plain deposits with palaeo-current data indicating easterly flow, consistent with regional drainage patterns off the adjacent Caledonia Highlands (Rygel & Gibling 2006). The coarse-grained association formed in a broad, through-going river channel whose sedimentary fill vertically aggraded through accumulation of sandy bedforms. At times, current velocities were sufficiently high to transport pebbles, but mudstone lenses moulding rain prints and trackways imply periodic cessation of flow (ponding) and exposure of the channel floor. Preservation of rain prints and trackways implies that mud had dried out and hardened prior to resumption of channel flow. However, tool marks on the base of overlying sandstone beds, and mud clasts, indicate that on resumption flow was locally erosive. Fine-grained intervals represent deposition between primary channels, where flooding was minimal and soils well drained, as indicated by deep vertical root traces. Mud-dominated channels with lateral accretion, and sandstone lenses cut by

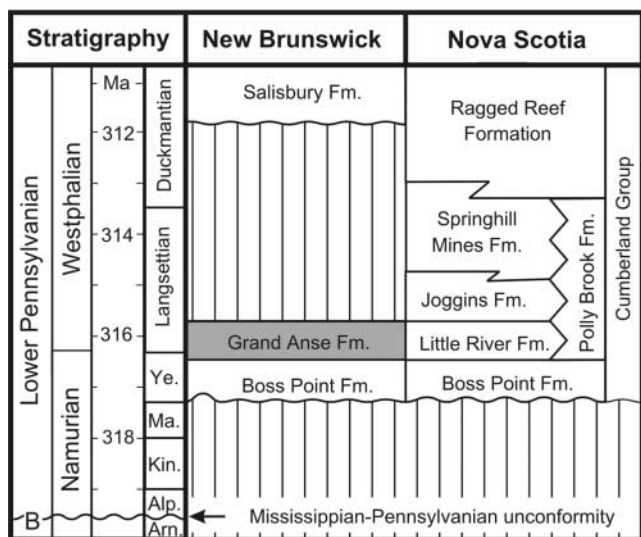
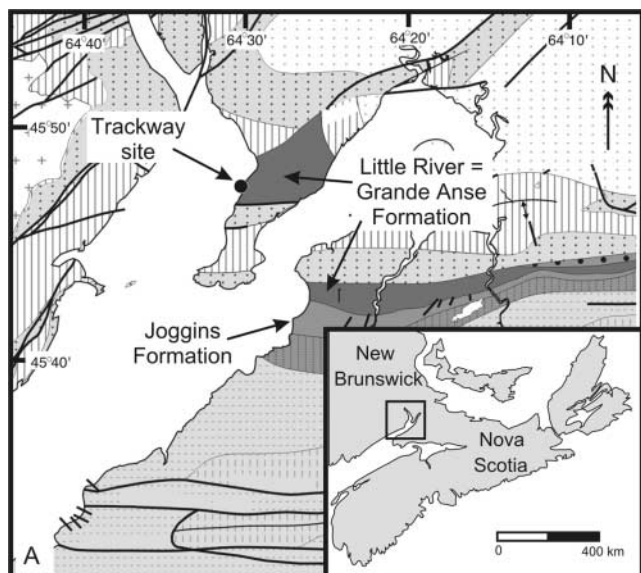


Fig. 1. Geological setting. (a) Location of trackway site at Shepody Bay, eastern side of the Maringouin Peninsula, New Brunswick (45°47'48"N, 64°30'29"W), within the Grande Anse Formation (after Davies *et al.* 2005); (b) Lower Pennsylvanian stratigraphy of the Cumberland Basin of Atlantic Canada (modified from Calder *et al.* 2005), showing the age of the Grande Anse Formation and its relationship to the Joggins Formation (Falcon-Lang *et al.* 2006).

ribbons may represent sinuous offshoots and crevasse splays from primary channels that internally drained into depressions. Seasonally active river systems in Australia may provide a possible modern analogue (Gibling *et al.* 1998).

Tetrapod trackways

Trackways were studied on sandstone blocks derived from the coarse-grained facies association. The two richest and best-preserved blocks were discovered by one of us (H.J.F.L.) in August 2006, and are stored in the New Brunswick Museum, Saint John, Canada. NBMG 14143 is 0.72 m by 0.65 m wide, and NBMG 14144 is 0.88 m by 0.63 m wide. Blocks taper from

115 mm to 20 mm thick, and comprise a single set of trough cross-bedding.

Trackways are preserved in convex hyporelief on the underside of the bedding plane in both specimens. Locally, red mudstone adheres to the base of NBMG 14144, demonstrating that trackways were impressed into one of the mud layers in the cliff section (the tracking surface). This observation, together with the occurrence of putative scale impressions (see below), suggests that traces represent true tracks rather than undertracks (Manning 2004; Milan & Bromley 2006). Multiple crosscutting trackways occur, and tracks are evenly spaced (non-random distribution) implying surface saturation (presumably earlier tracks have been erased by successive overprinting when the sediment was still moist). There are six full trackways on NBMG 14143, two on NBMG 14144, and numerous partial trackways and isolated footprints ($n = 114$ footprints in total).

Seven full trackways, and most isolated footprints (97% of all traces), belong to a single morphotype assigned here to early amniotes; one trackway is of a temnospondyl amphibian (not discussed herein). Quantitative characteristics for the two most complete amniote trackways are summarized (Table 1), and illustrated (Fig. 3), but except where stated measurements are for all seven amniote trackways. The amniote trackways are linear in plan view (one is curvilinear) with preserved lengths of ≤ 858 mm. Manus and pes are positioned directly behind one another with even spacing, and are oriented parallel to the track midline (Fig. 3a). External trackway width is in the range of 170–231 mm (manus) and 186–340 mm (pes). A tail drag (6–9 mm wide), or body drag (≤ 33 mm wide), is prominent along the midline. Mean pace angulation typically ranges from 49 to 66° (Table 1), although it may be as high as $\leq 121^\circ$ in some tracks.

To help distinguish genuine skeletal features from extramorphology (Fig. 3b), multiple footprints of the same manus or pes (Fig. 3c and d) were compared. Results show that the manus and pes are exclusively pentadactyl, plantigrade, and have a clear convex heel mark. Mean manus length ranges between 31 and 54 mm, whereas mean width ranges between 28 and 53 mm. Pedes are slightly larger, with a mean length and width in the range of 46–99 mm and 41–77 mm, respectively. Digits locally show toe drag, but where clearly impressed (most footprints in Table 1) they are slender, with maximum length/width ratios of 8.4 (manus) and 11.6 (pes). Manus and pes digit length increases from I to IV, with digit V being of similar length to digit II (manus) or digit II or III (pes). Well-preserved digits terminate with acuminate claw marks and show putative transverse scale impressions some *c.* 400 μ m across on the digit pads (Fig. 3e). These scale impressions are not structural features because they occur only within the digit outline, and are unlikely to be taphonomic artefacts produced by sediment loading because their axis is perpendicular to the digit axis (Manning 2004). Nevertheless, we admit a degree of uncertainty in the interpretation of this phenomenon.

Our trackways resemble the ichnogenus *Pseudobradypus* Matthew 1903, which comprises pentadactyl manus and pes with well-defined convex heels, and slender digits that increase in length from I to IV and show acuminate claw marks (Haubold 1971, pp. 27–28). *Pseudobradypus* is present in the Lower Pennsylvanian units of Nova Scotia at Joggins, River Phillip, and Parrsboro (Haubold 1971; Mossman & Grantham 1999; Calder *et al.* 2006), but these occurrences are younger than our material (mid-Langsetian–Duckmantian) and the earliest amniote skeletal remains (Falcon-Lang *et al.* 2006). Additional younger occurrences occur in the USA (Carmen 1927), and Germany (Schmidt

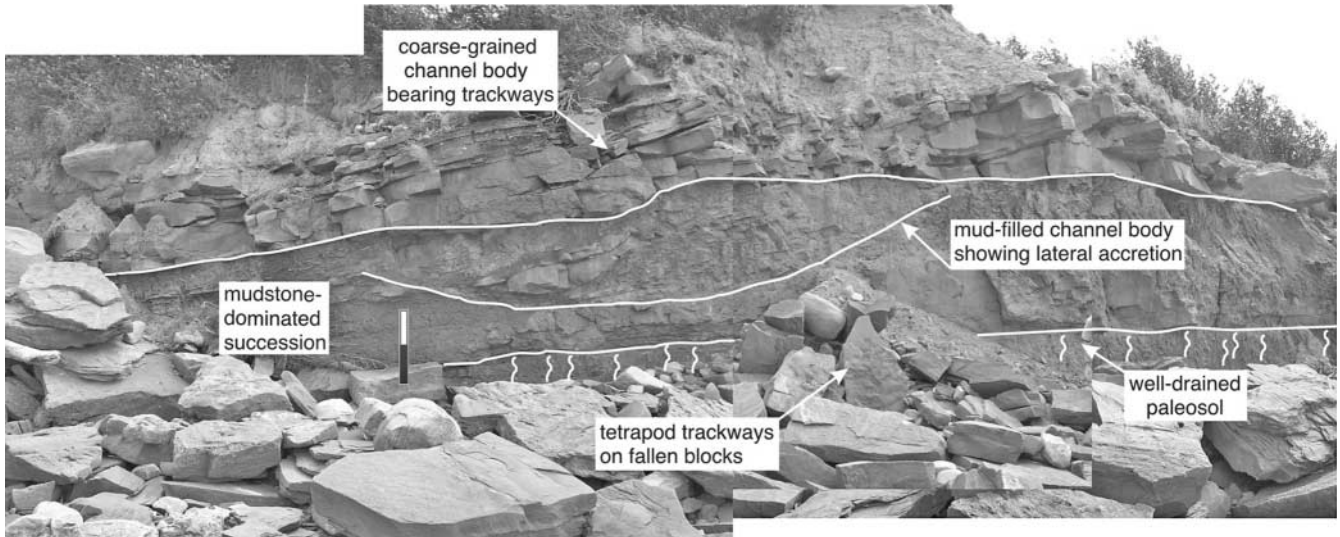


Fig. 2. Interpreted sedimentary facies at the Shepody Bay trackway site on the eastern side of the Maringouin Peninsula, New Brunswick (45°47'48"N, 64°30'29"W). The cliff is up to 5 m high (scale bar represents 1 m).

Table 1. Descriptive statistics for the two best-preserved trackways on NBMG 14143

Characteristic	Track 1		Track 2	
	Manus (<i>n</i> = 9)	Pes (<i>n</i> = 8)	Manus (<i>n</i> = 7)	Pes (<i>n</i> = 6)
External track width (mm)	171 (161–192)	185 (176–211)	185 (163–196)	198 (178–220)
Foot length (mm)	43 (40–48)	55 (49–71)	52 (45–58)	65 (62–69)
Foot width (mm)	40 (33–46)	49 (40–60)	43 (41–46)	54 (50–63)
Digit I length (mm)	9 (7–12)	14 (13–15)	12 (11–13)	21 (20–22)
Digit II length (mm)	16 (14–21)	24 (21–27)	20 (18–21)	32 (28–36)
Digit III length (mm)	22 (19–24)	26 (24–28)	27 (24–29)	38 (33–42)
Digit IV length (mm)	27 (23–29)	29 (28–31)	34 (30–37)	47 (44–50)
Digit V length (mm)	18 (15–22)	26 (25–27)	22 (18–25)	35 (32–38)
Digit length/width	≤8.4	≤11.6	≤7.6	≤11.3
Digit splay angle (°)	45 (28–68)	57 (28–80)	40 (29–50)	63 (42–80)
Pace length (mm)	162 (149–175)	162 (145–175)	166 (122–198)	175 (162–188)
Stride length (mm)	175 (158–195)	175 (162–195)	170 (121–186)	179 (167–206)
Pace angulation (°)	63 (57–66)	66 (55–76)	49 (35–58)	55 (44–68)

Mean values are followed by range values in parenthesis. Pace angulation measurements were fixed from the base of digit IV.

1963) in Middle Pennsylvanian strata. Our material is closest to *P. longidigitatus* from River Phillip (Geological Survey of Canada No. 4630).

Distinguishing amphibian and amniote tracks

Most *Pseudobradypus* are probably captorhinomorph tracks (Haubold 1971), although some may belong to another basal amniote group, the pelycosaurs (Milner 1994). Nevertheless, given the significance of our claim that Grande Anse trackways represent the earliest evidence for amniotes (older than definitive skeletal remains), it is essential to assess affinity more rigorously. Carrano & 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. The advantage of this approach is that identification is based on diagnoses not descriptions, and that it is possible to identify candidate trackmakers positively while excluding others.

Adopting this approach, we consider the pentadactyl nature of the manus and pes of our tracks as a key character for

trackmaker assignment. Devonian tetrapods had up to seven or eight digits, and the standard pentadactyl manus and pes became fixed in the phylogeny only at about the Devonian–Carboniferous boundary (Ruta *et al.* 2003). Thereafter, the amphibian lineage tended to reduce manus digits to four whereas, in most cases, the reptiliomorph–amniote lineage retained five. In cladistic analyses of basal tetrapods (Ruta *et al.* 2003), four manus digits is a derived character seen in *Colosteus* (Hook 1983), the temnospondyl–lissamphibian clade, and lepospondyls (except microbrachomorphs, which have three; Ruta *et al.* 2003). Five manus digits are seen in *Greererpeton* and the reptiliomorph branch of the tetrapod tree. *Greererpeton*, an aquatic taxon with an elongate body and reduced limbs, can be ruled out as the trackmaker because it has relatively tiny manus and pes spaced far apart, and broad and stumpy digits (Godfrey 1989). Thus, our trackmaker was a member of the clade Reptiliomorpha, a group that includes ‘anthracosaurs’, seymouriamorphs, and diadectomorphs, as well as amniotes and some close outgroups. The skeletal fossil record of this group begins in the Viséan (Milner 1993).

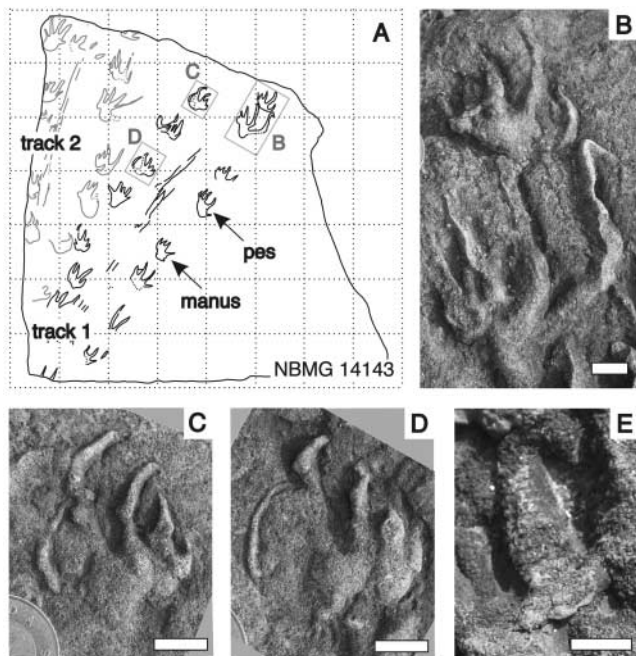


Fig. 3. Trackway assemblage. (a) Drawing of NMG 14143 highlighting the two trackways described in Table 1 (four other trackways are not shown for clarity); grid scale: 10 cm. (b) Right manus (upper) and right pes (lower) in Track 1, showing some of the most extreme extramorphology (toe drag) on the slab; scale: 1 cm. (c, d) Successive prints of the same left manus in Track 1 to compare fidelity of skeletal impression; scale: 1 cm. (e) Transverse ribbing on digit III of right manus shown in (b); scale: 5 mm.

Measurements were made of basal reptiliomorphs and amniotes whose manus and pes skeletons are known (Fig. 4) and data show that the two groups may be distinguished (Table 2). Basal reptiliomorph feet have a length/width ratio of 0.9–2.0 (manus) and 1.0–2.0 (pes), and digits are relatively short and stumpy (length/width ratio <8), and radiate fan-like with a splay angle of 45–110° (manus) and 40–120° (pes). Although some amniotes show such broad, short and splayed manus and pes (e.g. *Eocaptorhinus*; Table 1), most other amniotes, including basal

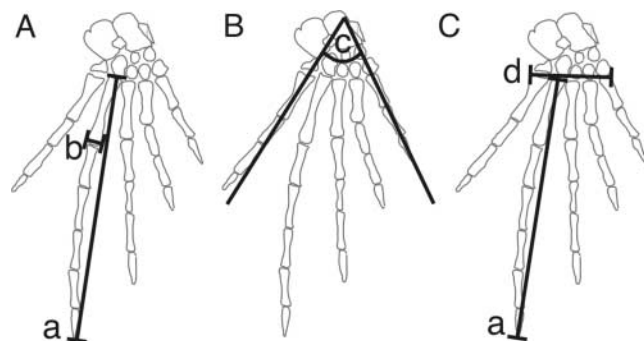


Fig. 4. Diagram showing how measurements of skeletal fossils were made. (a) Digit slenderness = a/b , where a is the length of each digit and b is its widest point. (b) Digit splay = angle c , where the axes are parallel to the basal phalanges of the outer digits. (c) Foot slenderness = a/d , where a is the length of the longest digit and d is the width of foot at the base of the digits.

sauropsids and basal synspsids, all have long slender manus and pes with a splay of 40–65° and length/width ratios of 2.5–4.0 (manus) and 1.6–4.3 (pes). Later, in the Permian, broad, short, splayed manus and pes are seen again among synspsids and sauropsids (e.g. procolophonids, pareiasaurs, and captorhinomorphs). The key point is that slender-toed, long, and narrowly splayed manus and pes from the Carboniferous are indicative of amniotes, either a basal synspsid or a basal sauropsid (captorhinid such as *Paleothyris* or diapsid such as *Petrolacosaurus*). Heaton & Reisz (1986) used the character ‘slender manus and pes’ as a synapomorphy of the clade within Sauropsida that includes Paleothyrididae and Diapsida.

Resemblance of our trackways to those of amniotes (Table 2) is strengthened when trackway measurements (which record flesh over bone) are corrected to allow direct comparison with skeletal data. Studies of salamander feet show that, for comparative purposes, a factor of $\times 1.6$, or greater, must be applied to length/width ratios of manus or pes and digits from trackways (unpublished data). After correction, our tracks show foot and digit slenderness values highly characteristic of basal amniotes. If digit length is a reliable indicator of phalangeal formula (Haubold 1971), our trackmaker probably had formulae of 23453 (manus) and 23454 (pes). Although also seen in non-amniote diadectomorphs, this pattern is most commonly found in basal amniotes. That said, phalangeal formula is an evolutionarily plastic character and its phylogenetic value may be limited.

One notable amniote synapomorphy preserved in our tracks is the transverse scale impressions (although, as noted above, the interpretation of this feature is debatable). Many fossil tetrapods on both amphibian and reptiliomorph lines bore osteoderms (Dias & Richter 2002), but as far as we are aware, horny keratin scales are exclusive to reptiles. In extant forms such as turtles, lizards and crocodylians, scales are organized in transverse rows on the feet for protection, and to improve walking and climbing (Zug *et al.* 1993). Other characters suggestive of amniotes include pace angulation up to 121°, a straight tail drag, and the observation that footprints are oriented forward with the sole print located behind digits III–V (Chestnut *et al.* 1994; Tai Kubo, pers. comm.). These data indicate a partially erect posture with manus and pes positioned under the body during locomotion, as opposed to being spread out in a sprawling gait as seen in most amphibians (Chestnut *et al.* 1994). However, our amniote tracks are rather larger ($\leq 99 \text{ mm} \times 77 \text{ mm}$) than most skeletal remains of known amniotes, although *Haptodus* (75 mm \times 30 mm) and *Petrolacosaurus* (60 mm \times 18 mm) are of similar size.

Implications

We report trackways from the basal Langsetian Grande Anse Formation, which represent the earliest evidence for reptiles. These predate the earliest known reptile skeletal remains in the Joggins Formation (Falcon-Lang *et al.* 2006), as well as all previously documented reptile tracks (Chestnut *et al.* 1994), which are of mid- to late Langsetian age. Given the *c.* 20 Ma gap between the East Kirkton–Cheese Bay and Joggins assemblage, it is not unexpected that ichnological evidence implies an earlier evolutionary origin for reptiles. Nevertheless, such findings have important implications. One of the most important calibration points for molecular clocks is the bird–mammal split, given as the age of the Joggins assemblage (Reisz & Müller 2004; Benton & Donoghue 2007). Although we merely show that reptiles existed *c.* 1 Ma prior to the Joggins assemblage, the regional trackway record remains poorly studied and it is

Table 2. Measurements of manus and pes of Carboniferous and some Early Permian non-amniote reptiliomorphs and basal amniotes

Genus	Key reference	Phalangeal formula		Digit length/width		Digit splay (°)		Foot length/width	
		Manus	Pes	Manus	Pes	Manus	Pes	Manus	Pes
<i>Non-amniote reptiliomorphs</i>									
Anthracosaurs									
1. <i>Silvanerpeton</i>	Ruta & Clack (2006)	–	23455	–	8.0	–	80	–	2.0
2. <i>Archeria</i>	Romer (1957)	23454	23455	7.1	8.1	85	65	1.4	1.5
3. <i>Proterogyrinus</i>	Holmes (1980)	23454	–	7.7	–	75	–	1.3	–
Seymouriamorphs									
4. <i>Seymouria</i>	Berman <i>et al.</i> (2000)	23443	23453	4.4	8.0	110	120	0.9	1.2
5. <i>Discosauriscus</i>	Klembara & Bartik (2000)	23453	23453	6.5	5.7	55	65	1.2	1.4
Diadectomorphs									
6. <i>Orobates</i>	Berman <i>et al.</i> (2004)	23453	23454	5.8	4.2	65	65	1.2	1.0
7. <i>Limnoscelis</i>	Williston (1911)	23453	23454	4.4	4.4	65	40	1.0	1.0
8. <i>Diadectes</i>	Berman <i>et al.</i> (2004)	–	23453	–	4.3	–	85	–	1.2
Close outgroup to amniotes									
9. <i>Casineria</i>	Paton <i>et al.</i> (1999)	23453	23453	7.8	–	45	–	2.0	–
<i>Amniotes</i>									
Sauropsids									
10. <i>Eocaptorhinus</i>	Heaton & Reisz (1986)	23453	23454	8.4	9.6	90	75	1.5	1.6
11. <i>Paleothyris</i>	Carroll (1969)	23453	23453	16.1	22.2	65	55	3.0	2.9
12. <i>Anthracodromeus</i>	Carroll & Baird (1972)	23453	23454	23.0	28.0	40	60	4.0	4.3
13. <i>Petrolacosaurus</i>	Reisz (1981)	23453	23454	13.6	13.6	50	40	3.8	3.4
Synapsids									
14. <i>Haptodus</i>	Currie (1977)	23453	23454	12.3	9.6	45	55	2.5	2.3
<i>Trackways</i>									
NBMG 14143-1	This paper	23453	23454	13.4	18.6	45	57	1.8	1.8
NBMG 14143-2	This paper	23453	23454	12.2	18.1	40	63	1.9	1.9

Hylonomus not included, as foot reconstruction was based on *Paleothyris*. Statistics for trackway data (Table 1) have been corrected by the following factors: digit length/width ($\times 1.6$); foot length/width ($\times 1.6$).

possible that future studies will push the origin of reptiles well back into the Namurian.

Another important aspect of our studies relates to the ecology of early reptiles. Unlike the Joggins assemblages, where reptiles are associated with wetland rainforests (Falcon-Lang *et al.* 2006), our trackways show reptiles existed on dryland alluvial plains. Trackways are imprinted on the dry bed of a river, and mudstone lenses that preserve them were deposited from ponded water bodies within the channel. Traces may represent tetrapod activity around a waterhole, as seen in similar facies in the Joggins Formation (Falcon-Lang *et al.* 2004). Although climate was seasonally wet, facies data suggest that reptiles existed in water-stressed environments for at least part of the year. In such environments, the cleidoic egg presumably would have conferred reproductive advantage (Benton 2005). This finding broadens our knowledge of early amniote ecology.

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