

Discussion on ecology of earliest reptiles inferred from basal Pennsylvanian trackways

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David Keighley, John Calder, Adrian Park, Ronald Pickerill & John Waldron write: In a recent article, Falcon-Lang *et al.* (2007, p. 1113) claim ‘trackways representing the earliest evidence for the origin of reptiles (amniotes) are reported from the basal Pennsylvanian Grande Anse Formation, New Brunswick’. We note inaccuracies in the paper and bring attention to various lines of evidence, any one of which casts serious doubt on their claim.

Age of the Grande Anse Formation. Falcon-Lang *et al.* (2007, p. 1113) report a location at Shepody Bay, ‘on the eastern side of the Maringouin Peninsula, New Brunswick’ (actually located on the western side, Fig. 1) that preserves interface sedimentary structures that they interpret as amniote trackways. The authors infer an earliest Langsettian (earliest Westphalian), or possibly latest Namurian, age for the Grande Anse ‘Formation’ at this locality (the unit is not formally defined). This interpreted age of the strata was based on two lines of evidence: (1) a palynological age determination from an unpublished report; (2) its reported stratigraphic position equivalent to the Little River Formation of Nova Scotia, conformably overlying the Boss Point Formation.

(1) The report cited by Falcon-Lang *et al.* (2007) actually states that the spores indicate an age ‘no older than the early middle Langsettian’ (Dolby 1999, p. 43). Therefore, the Grande Anse Formation would not be of identical biostratigraphic age to that reported for the Little River Formation, which is of probable late Namurian to basal Westphalian (basal Langsettian) age (Calder *et al.* 2005). Regardless, Upper Palaeozoic strata in eastern Canada (Fig. 2) lack many of the stratigraphically diagnostic marine index fossils and European miospores recorded in the literature (Calder 1998; Utting *et al.* 2005) and so it is not currently possible to unequivocally constrain the age of the Grande Anse strata. In addition, recent recognition of rapid Mississippian stratigraphic inversions in SE New Brunswick (e.g. Park & St. Peter 2005) has supported interpretations that at least some spore assemblages in the region are entirely reworked (e.g. Dolby 2004).

(2) It should also have been mentioned that there is considerable uncertainty as to the lithostratigraphic relationships of the Grande Anse Formation. The thin interval of undated red sandstone and mudstone in the core of the tightly folded Hard Ledges syncline (Fig. 1; no biostratigraphy available from this location) is on Boss Point Formation rocks, and so can be considered part of the Cumberland Group (Fig. 2), and equivalent to the Little River Formation of Nova Scotia. If this red-bed unit is then to be correlated with the red-beds of the Grande Anse Formation, the syncline must be in faulted contact with the Grande Anse Formation section to the north at Shepody Bay and similar outcrop to the east (e.g. Falcon-Lang *et al.* 2007, fig. 1). However, strata in these other outcrops typically have gradually varying dips of less than 25°, concordant with overlying, younger, Salisbury Formation (Pictou Group in New Brunswick) strata, with which they collectively define a gently ENE-plunging syncline (Fig. 1). On this basis, the trackway-bearing section of

the Grande Anse Formation has also been included in the Pictou Group and the boundary with rocks of the Hard Ledges syncline considered an unconformity, as previously shown by Gussow (1953, fig. 5). The disputed boundary is not currently exposed, although it is constrained by our field observations to within 2 m on the macrotidal foreshore of Shepody Bay, where structural and sedimentological relationships are most easily reconciled with the presence of an angular unconformity. With this interpretation, the red-bed unit in the core of the Hard Ledges syncline remains as Little River Formation but is not correlated with the Grande Anse Formation, which post-dates the folding of the Hard Ledges syncline and the rocks exposed within it (Fig. 1).

Correlating the lithostratigraphic units across the provincial border into Nova Scotia is not straightforward given the different grouping of formations by the two provincial jurisdictions (Fig. 2). However, at Minudie Point, Nova Scotia (Fig. 1), Calder *et al.* (2005) correlated outcropping red-beds with the Grande Anse Formation to the west, for they are in apparent structural continuity. Those workers, although noting the aforementioned miospore-correlation problem, had suggested a ‘possible’ biostratigraphic correlation with the Little River Formation. This interpretation also requires a faulted contact between the Grande Anse Formation and Cumberland Group successions to the south. Alternatively, the Minudie Point beds have been included as part of an undivided Balfron Formation (Pictou Group) unit, unconformable on Cumberland Group units, by Ryan *et al.* (1990), and equivalent to upper Cumberland Group strata using current Nova Scotia terminology. In this alternative interpretation, the Minudie Point beds, together with younger Pictou Group strata, would have progressively overlapped Mississippian and lower Cumberland Group strata (Boss Point and Little River formations) that were being folded and reworked during a late Langsettian to Duckmantian deformation event associated with evaporite withdrawal (Waldron & Rygel 2005). Accordingly, on both biostratigraphic and lithostratigraphic grounds, it is not possible to assert that the Grande Anse trackways predate the amniote body fossils found nearby at Joggins, Nova Scotia.

Earliest putative evidence of reptiles from trackways. Regardless of the actual age of the Shepody Bay material, the discussion provided by Falcon-Lang *et al.* (2007) is insufficient to prove the contained trackways to be either (1) distinctly amniote or (2) amniote, the oldest recorded evidence of such.

(1) The weight of palaeontological opinion currently considers the earliest unequivocal reptile to be *Hylonomus lyelli*, known from Joggins, Nova Scotia (e.g. Reisz 1997; Clack 2002). Criteria for assessing the amniote condition include almost the entire skeleton, from the skull roof, palate, articulation of the upper vertebrae to ossified carpals and tarsals in the wrists, and number of toes. The pentadactyl condition of the tetrapod manus, although supportive, has never been used alone as a decisive character in determining the amniote condition, nor is it necessarily in synomorphy with the evolution of the cleidoic egg.

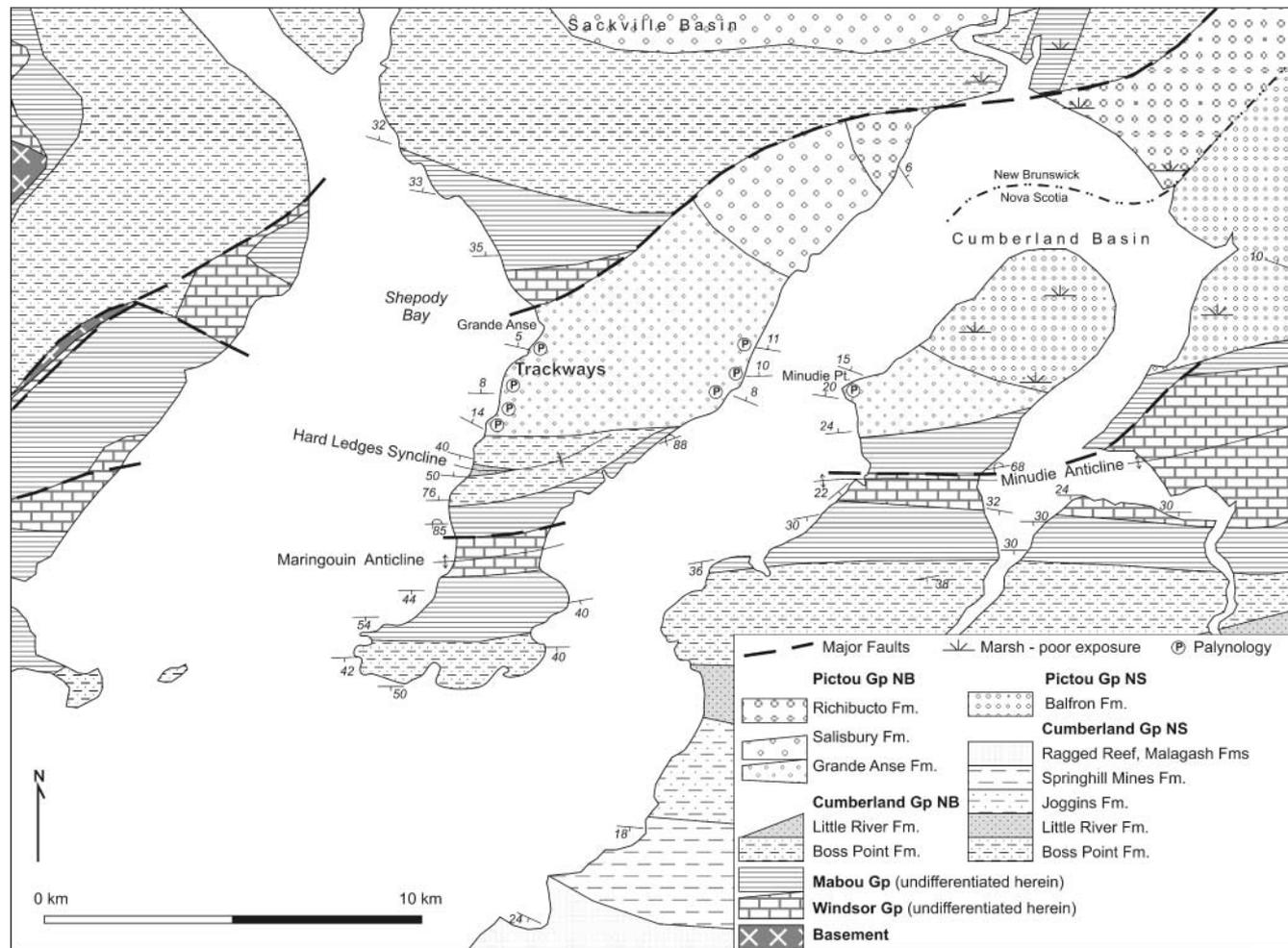


Fig. 1. Map of the Maringouin peninsula and nearby Joggins area, New Brunswick and Nova Scotia, incorporating elements of Gussow (1953), Ryan *et al.* (1990), St. Peter & Johnson (1997) and Calder *et al.* (2005).

A further universal problem when using foot imprints is that of taphonomy, because measuring parameters of a biogenic sedimentary structure to infer such criteria as digit width may be dependent on, for example, substrate consistency and/or foot slippage.

Regardless, the supposed key point of Falcon-Lang *et al.* (2007) is that if manus and pes prints from the Carboniferous are long, slender-toed, and narrowly splayed, they are indicative of an amniote, as opposed to a non-amniote reptiliomorph (NaR). Yet, from their table 2, the measured splay angle in the manus of specimen NBMG 14143-1 is no different from that measured for the NaR *Casineria* and the pes is wider than that of the NaR *Limnoscelis*. The 63° splay angle in the pes of NBMG 14143-2 is much wider than that of *Limnoscelis*, and only 2° narrower than the splay of the NaRs *Archeria*, *Discosauriscus*, and *Orobates*. Additionally, their foot length/width ratios of 1.8–1.9, already enhanced by a factor of $\times 1.6$ (based on unpublished data), are no different from the manus and pes of *Casineria* and the NaR *Silvanerpeton*, and not as long as 4/5 of their tabulated amniotes. As for their debated transverse scale impressions, similar lateral striations have been recorded in footprints from the early to middle Namurian of West Virginia that have been interpreted as anthracosaurian (Sundberg *et al.* 1990).

(2) A fundamental point central to any discussion of earliest evidence is that a rigorous survey has been undertaken to confirm the lack of competing, older evidence from elsewhere in the stratigraphic record. If just one or two of the long, slender-toed, or narrowly splayed factors are even to be considered potentially indicative of an amniote producer (and accurately measurable from footprints), then other reported trackways of likely pre-Langsettian age should have been worthy of discussion. For instance, Milner (1987) and Calder (1998) considered Boss Point equivalent grey-beds of the Port Hood Formation at Cape Linzee, Nova Scotia, to be older than both the fossils at Joggins and the date that Falcon-Lang *et al.* (2007) prefer for the Grande Anse Formation. At the cape, *c.* 250 m above the bed hosting the remains of the problematic tetrapod *Romeriscus nomen dubium* (Baird & Carroll 1967; Laurin & Reisz 1992) are trackways containing pentadactyl imprints (with sole prints behind the outer digits), tail drag marks, and pace angulations similar to the Grande Anse Formation specimens (Keighley & Pickerill 1998). The prints additionally have splay angles estimated as low as 72°, and a length/width ratio estimated at 2.0 (or 3.2 if using the $\times 1.6$ factor). Keighley & Pickerill (1998) also described non-sprawling trackways from 200 m below the base of the Port Hood Formation, in Pomquet Formation (Mabou Group) red-bed

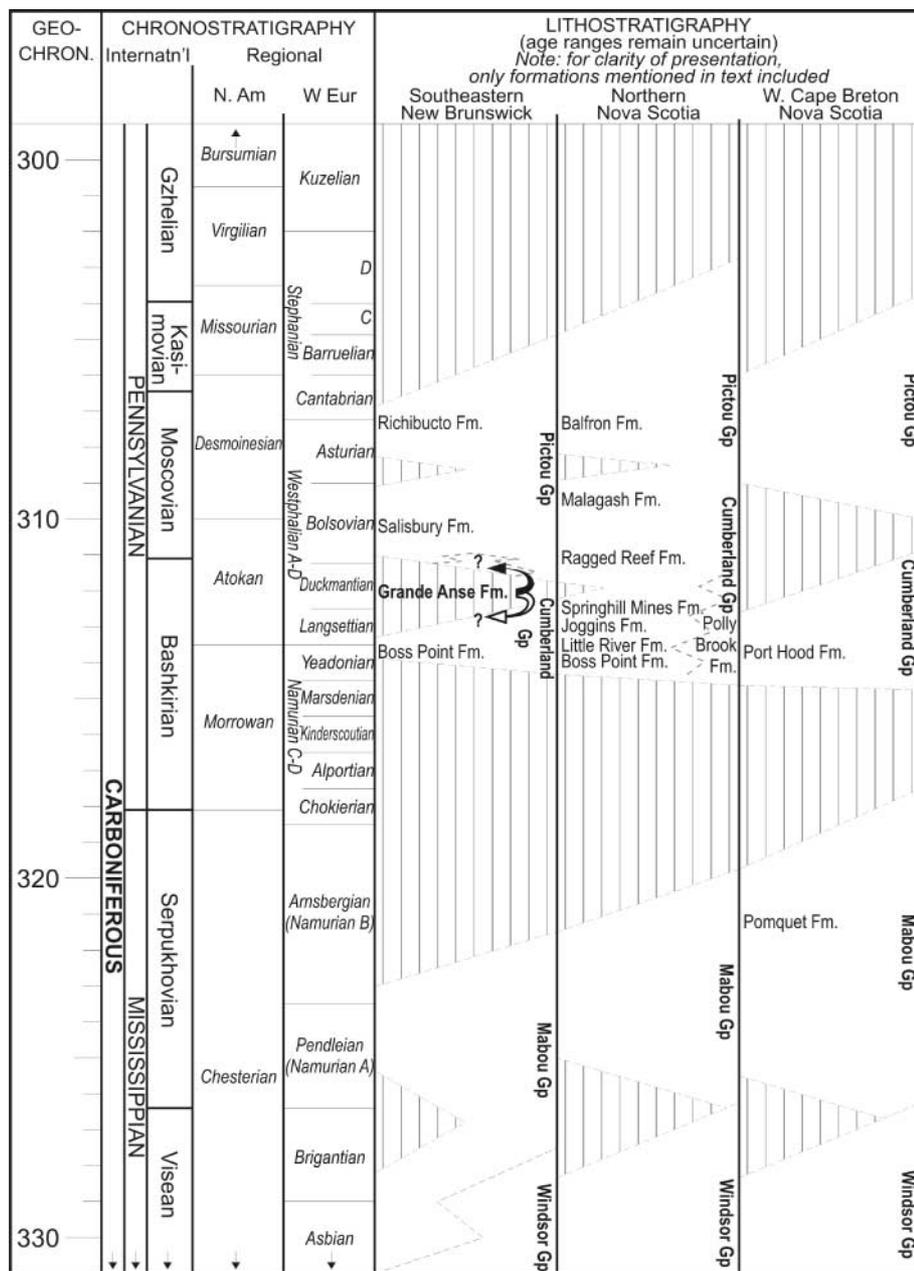


Fig. 2. Summary of mid-upper Carboniferous stratigraphy for the Maritime Provinces. For brevity and clarity, only formation and group names from this discussion have been included. Data are a compromise of numerous sources and so, although the stratigraphic succession is accurate, age ranges and boundaries are approximate.

strata that Keighley & Pickerill (2003) interpreted as dry flood-plain–ephemeral sheetflood. Palynology and stratigraphic relationships suggest an age no younger than Namurian C (J. Utting, pers. comm.). Certainly, print morphologies of these examples are less clear, but they should have been worthy of discussion as the facies interpretation would similarly suggest that the producers existed ‘in water-stressed environments, where the cleidoid egg would have presumably conferred reproductive advantage’ (Falcon-Lang *et al.* 2007, p. 1113).

In conclusion, we dispute the claim of Falcon-Lang *et al.* (2007) to have discovered the earliest evidence of amniotes based on any one of several criteria: the palynological dating of the rocks in which their trackways were found is equivocal; the field relationships better suggest correlation with a younger stratigraphic unit; the trackways do not have a comprehensive set of

features that are distinctly amniote in form; several previously described trackways in older rocks might alternatively be regarded as the earliest evidence of amniotes.

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Howard Falcon-Lang & Mike Benton reply: Keighley *et al.* write that various ‘inaccuracies’ in our paper and ‘other lines of evidence’ bring into dispute our claim to have discovered the earliest known evidence for the evolution of reptiles based on

trackways (Falcon-Lang *et al.* 2007). They argue that (1) our preferred age for the trackways is incorrect and (2) our tracks cannot be unequivocally attributed to reptiles, and other older reptile tracks have already been reported in the literature. Here we respond to each concern and offer some suggestions for further research that could resolve the issues highlighted by Keighley *et al.*

Age of the trackways. Our trackways occur in the Grande Anse formation of New Brunswick, Canada. Keighley *et al.* dispute our view that this unit is (1) time-equivalent to the Little River Formation of Nova Scotia (Calder *et al.* 2005), (2) stratigraphically below reptile-bearing strata of the Joggins Formation of Nova Scotia (Falcon-Lang *et al.* 2006), and (3) of late Namurian to early Langsettian age (Falcon-Lang *et al.* 2007). We note that in our paper we did not conduct our own studies of the age and stratigraphic position of the Grande Anse formation, but merely reported the findings of the most up-to-date literature.

Our preferred age for the disputed formation is based on Calder *et al.* (2005, p. 43), who concluded that, 'palynological assemblages indicate that the Little River Formation is of probable late Namurian to basal Westphalian (basal Langsettian) age, and is a likely time-equivalent of the informal Grand-Anse Formation of southeast New Brunswick'. We highlight the fact that the lead author of Calder *et al.* (2005) is also an author of the Keighley *et al.* discussion. Although Calder has the right to change his mind about the age of the Grande Anse formation, we maintain that we provided an accurate summary of the published literature in Falcon-Lang *et al.* (2007).

That said, Keighley *et al.* are right to point out uncertainties concerning the palynological evidence used for biostratigraphic zonation. However, these difficulties extend to both the Grande Anse and Joggins formations, the two units whose relationship is herein disputed. Contrary to the view of Keighley *et al.*, palynological evidence suggests that the lowermost part of the Grande Anse formation, as understood at present, is as old as late Namurian age (G. Dolby in Johnson & St. Peter 2005) whereas the uppermost part is not younger than mid- to late Langsettian (Dolby 1999). As our fossils came from the lower part of the Grande Anse formation we favour the earlier age. In comparison, the Joggins Formation is thought to be of mid- to late Langsettian age. Given that reptile body fossils occur near the top of this unit (Falcon-Lang *et al.* 2006), a late Langsettian age is probable. We therefore reiterate that, on the basis of available palynological data, our reptile trackways (Falcon-Lang *et al.* 2007) are older than the earliest known reptile body fossils.

To better resolve the contentious age of the Grande Anse formation and its stratigraphic relationship to the Joggins Formation of Nova Scotia we would welcome a critical review of all relevant biostratigraphic evidence from these units, much of which is in the form of unpublished provincial government reports, along with a critical assessment of the palynological dataset that explicitly states its biostratigraphic rationale. Similarly, regarding their inferences about the lithostratigraphic position of the Grande Anse formation, the statements of Keighley *et al.* need to be supported by the publication of detailed maps, structural observation, and lithology. If undertaken, this work would provide a solid foundation for future research in a way that is open to the critical scrutiny of the international community.

Earliest evidence for reptiles from trackways. The second prong of the critique by Keighley *et al.* is that amniotes ('reptiles') cannot be unambiguously recognized from their trackways (or

feet) alone. We broadly agree, but note that one of the aims of our paper was to quantitatively assess the differences among the feet of difference groups of Carboniferous tetrapods, and to test to what extent discrimination was possible. We refer readers to table 2 of Falcon-Lang *et al.* (2007) to judge whether the characters we highlight are sufficient to distinguish Carboniferous reptiles from other contemporaneous tetrapods. We emphasize that no single character can be used to recognize reptile tracks (or feet) but where many characters are available and well preserved, we maintain that a strong case can be made for distinguishing amniote tracks from those of non-amniotes.

This discussion leads us on to the final point of Keighley *et al.*, that older examples of reptile tracks (than ours) have already been described in the literature. In particular, they cite Keighley & Pickerill (1998), who briefly described poorly preserved footprints in the Port Hood Formation of Nova Scotia, some of which are pentadactyl. Keighley *et al.* are correct that these tracks are probably older than our own (although their precise age is uncertain). We also broadly agree that some of the Port Hood trackways of Keighley & Pickerill (1998) could be of reptilian origin, as could even older early Namurian trackways recently reported from New Brunswick (Wood & Miller 2007). However, in the absence of good preservation and detailed description, we consider their position as yet unproven. In their original paper, Keighley & Pickerill (1998) did not make a case for their trackways being of reptilian origin, nor crucially did they show that both manus and pes were pentadactyl. We therefore recommend that Keighley *et al.* conduct a multivariate analysis of the characters preserved in their Port Hood trackways to better constrain the phylogenetic position of the trackmaker.

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