

A PENNSYLVANIAN TETRAPOD TRACKWAY FROM JOGGINS, NOVA SCOTIA: THE SIZE CONTINUUM OF *BATRACHICHNUS SALAMANDROIDES*

LAWRENCE H. TANNER

Department of Biological Sciences, Le Moyne College, Syracuse, New York 13214, USA, email: tannerlh@lemoyne.edu

Abstract—A tetrapod trackway from the Lower Pennsylvanian at the historic section at Joggins, Nova Scotia, preserves 13 pairs of impressions with a possible partial tail drag. Although overstepping and poor preservation obscure many of the diagnostic features, the pes is plantigrade to semi-plantigrade and distinctly pentadactyl, with digit length increasing sequentially I-III. The manus may be tetradactyl, but no single impression allows this to be stated confidently. The size of the tracks is within the known range of *Batrachichnus salamandroides*, which is known from the same location, and so these tracks are assigned to this ichnospecies. The trackmaker was a small temnospondyl, although multiple candidates are known from body fossils in this section.

INTRODUCTION

The stratigraphic section at Joggins, Nova Scotia, is one of the best-exposed and most widely studied Carboniferous sections in the world. The locale has long been famous for the preservation of lycopsid trees in growth position, and more so for the diversity of tetrapod fossils, particularly those preserved within the stumps of those trees (Lyell and Dawson, 1853; Owen, 1862; Dawson, 1862, 1863, 1870, 1876, 1882, 1891a, 1891b, 1892a, 1892b, 1894, 1895; Steen, 1933; Carroll, 1964, 1966, 1967, 1972, 1988, 2009). These remains are an important record of tetrapod evolution, and include a demonstration of the diversity of temnospondyl amphibians, microsaur, anthracosaurs (Carroll, 1966; Holmes et al., 1998; Holmes et al., 2010), and the oldest known amniotes (*Hylonomus lyelli*; Dawson, 1895; Carroll, 1970, 1972, 1988, 2009). Most of the tetrapod body fossils at Joggins are small, due in part, undoubtedly, to the preferential mode of preservation, i.e., within tree stumps (Carroll, 1988).

The section at Joggins also produces a rich ichnofauna, with approximately a dozen tetrapod ichnogenera named thus far (Hunt et al., 2004; Lucas et al., 2005). Most recently, Stimson et al. (2012) described a trackway of *Batrachichnus salamandroides* from this site that they present as the smallest tetrapod tracks yet discovered. This paper describes a similar trackway from the same location in which the tracks are also quite small, although not so small as documented by these authors.

SETTING

The 1.5 km-thick section of the Joggins Formation at Joggins, Nova Scotia, is one of the best-known exposures of non-marine Carboniferous strata. The Joggins Formation, Cumberland Group, was deposited during the Namurian through Stephanian stages (Pennsylvanian) in the Maritimes Basin, Atlantic Canada, a region well known for its Pennsylvanian-age coal deposits, including the historically important location of Joggins. The Maritimes Basin is a complex of depocenters centered over the Bay of Fundy and Gulf of Saint Lawrence that includes the Cumberland, Minas, Moncton, and Sydney basins. It originated in the Middle Devonian as a structural and erosional remnant of an earlier depocenter of unknown size (Gibling et al., 1992).

The Devonian and Lower Carboniferous basin fill comprises alluvial and lacustrine deposits of the Horton and Canso groups and evaporitic marine deposits of the Windsor Group. Alluvial deposition dominated from Namurian to Early Permian time during accumulation of the Riversdale, Cumberland, and Pictou groups. Sedimentation was notably rapid during deposition of the Joggins Formation as withdrawal from the underlying Windsor Group (Mississippian) evaporites accelerated sediment accommodation (Waldron and Rygel, 2005). Deposition of the Joggins Formation was characterized by cyclical sequences of coastal wetland

deposits, including coastal plain, deltaic plain and distributary channel facies comprising fine-grained siliciclastics, sandstones, coals and limestones. Cyclicity was potentially controlled by eustatic changes (parasequences: Davies and Gibling, 2003).

MATERIAL AND PROVENANCE

The slab studied here was collected from the backshore of the beach at Joggins immediately below the cliff about 250 m north of the access from Main Street (Fig. 1). Matching the lithology and bedding of the slab to the cliff face suggests that it derived from just below a channel-fill sandstone at about 597 m above the formation base, between coals 16 and 17 in cycle 9 (after Davies et al., 2005); this is approximately the same location that produced the trackway described by Stimson et al. (2012). The specimen described herein was collected in the summer of 1988 (before passage of the Nova Scotia Special Places Protection Act) while the author conducted graduate research elsewhere in the province. The specimen is housed in the Department of Biological Sciences fossil collection at Le Moyne College, in Syracuse, New York.

The material is a single trackway preserved on a roughly triangular-shaped slab, 15 cm by 24 cm, consisting of light brown, rippled siltstone with gray clay drapes (Fig. 2). The upper and lower surfaces of the slab are thin claystone coatings of the siltstone. The upper surface



FIGURE 1. Location of the sample collection site on the shore of Chignecto Bay, Bay of Fundy, by the village of Joggins, Nova Scotia, Canada (image adapted from Google Earth®).

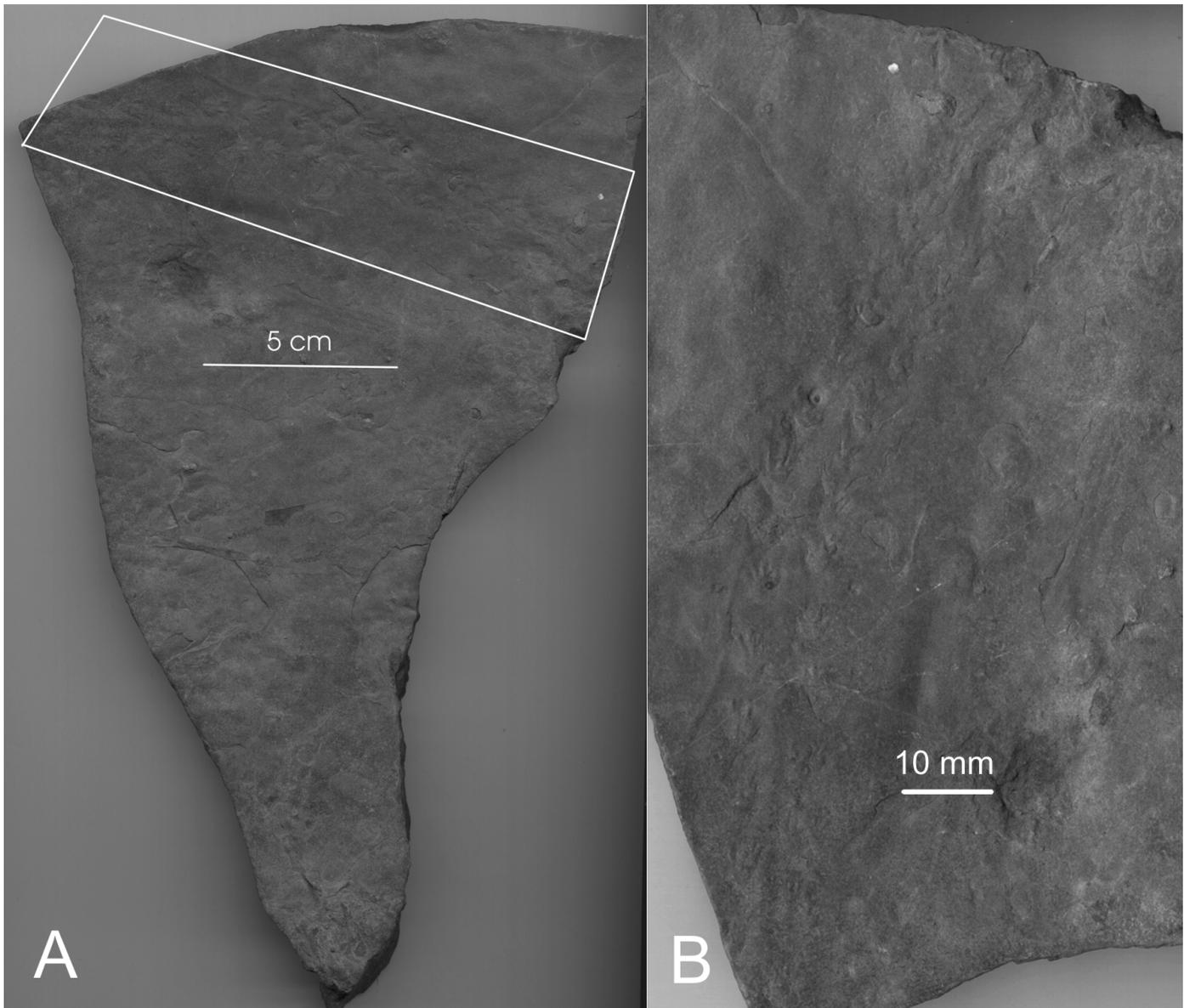


FIGURE 2. Specimen slab collected at Joggins. **A**, View of the underside of the entire slab, with **B**, detail of the trackway (view rotated with proximal end of trackway at bottom).

preserves circular impressions, presumably of raindrops. The trackway described below is preserved on the lower surface of the slab.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Batrachichnus* Woodworth, 1900

Ichnospecies *Batrachichnus salamandroides* (Geinitz, 1861)

Diagnosis: This ichnospecies is represented by quadrupedal trackways that are typically small and narrow, and commonly show alternating manus-pes sets with little divergence of manus and pes axes, and a pace angulation that rarely exceeds 90° . The individual impressions are elongate, the distal ends of the soles and digits are rounded, and the soles narrow posteriorly. Pes prints are pentadactyl and plantigrade to semi-plantigrade, with lengths up to 35 mm long (Voigt, 2005). Digits I–III are grouped closely together and increase in length sequentially, digit IV is the longest and somewhat separated from the others and digit V is directed laterally and set somewhat posteriorly. Manus prints are tetradactyl and semi-plantigrade; they are smaller than the pes prints and digits increase from I–III; digit IV diverges outward from the grouping of

I–III. A tail or body drag may be present (Haubold, 1971, 1996; Melchor and Sarjeant, 2004; Lucas et al., 2011; Stimson et al., 2012).

Description: The trackway consists of 27 impressions arranged as roughly 13 left-right pairs. All tracks are preserved as undertracks in convex hyporelief. The entire trackway is 149 mm long and has a mean width (=outer left pes to outer right pes) of 13 mm. The proximal end of the trackway is straight, but bends 23° to the right (relative to the direction of travel) after 70 mm (Figs. 2A, 3). There is no distinct tail drag, although there is a subdued convex linear feature between the left and right sides of the trackway at the proximal end extending to about 50 mm from the trackway start that suggests a tail or body drag impression (Fig. 4).

In general, preservation is better for the proximal tracks, particularly 2 through 6, in which features of individual tracks are more clearly recognizable. However, consistent partial overstepping severely compromises the ability to measure these quantitatively. Among the proximal tracks, the best preserved pes (e.g. LP5; Fig. 4) is pentadactyl, measuring 5.2 mm long by 5.0 mm wide. On this print, digits I–III are seen to increase serially and IV–V diverge from the first three. Only one manus

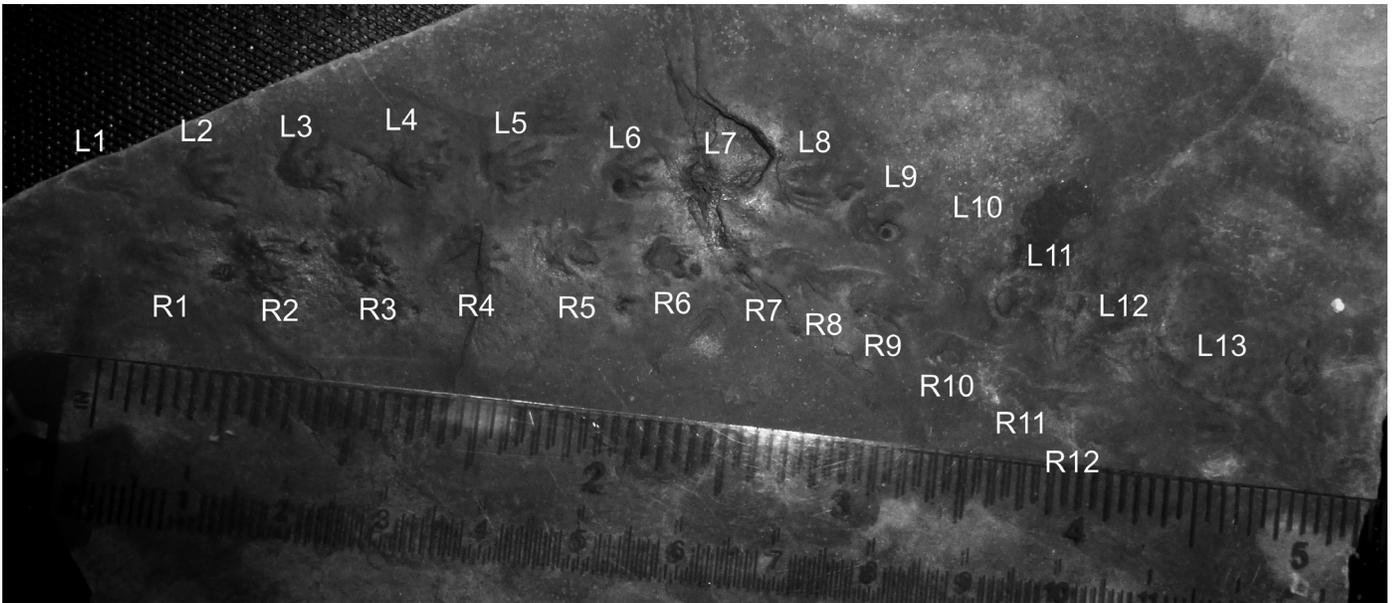


FIGURE 3. Detail of trackway with tracks numbered serially from proximal to distal.

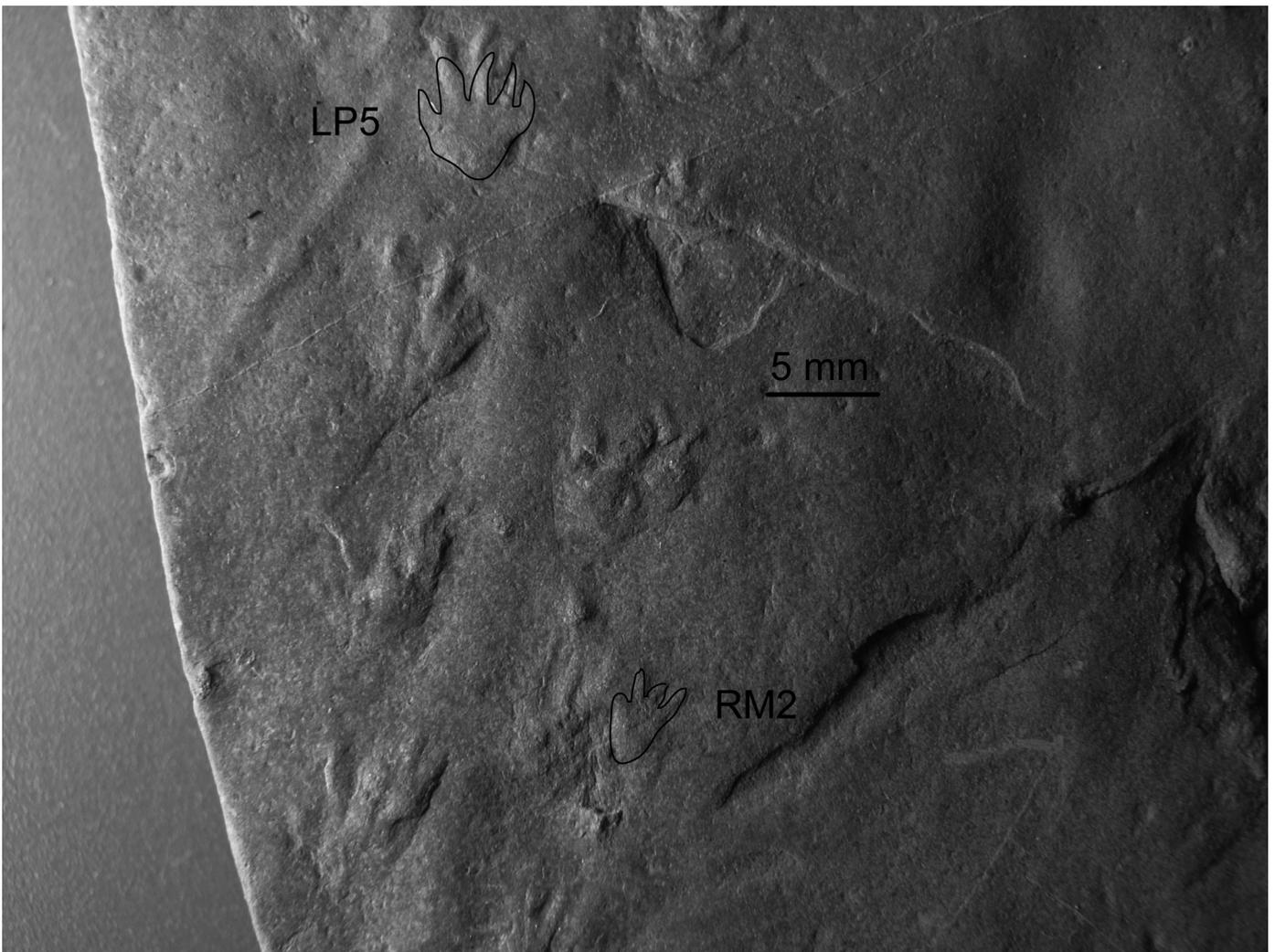


FIGURE 4. Detail of the proximal portion of the trackway, illustrating potential tail drag impression between left and right prints. Partial overstepping of pes on manus present in most tracks, with lateral offset between manus and pes visible in tracks. LP5 and RM2 discussed in text.

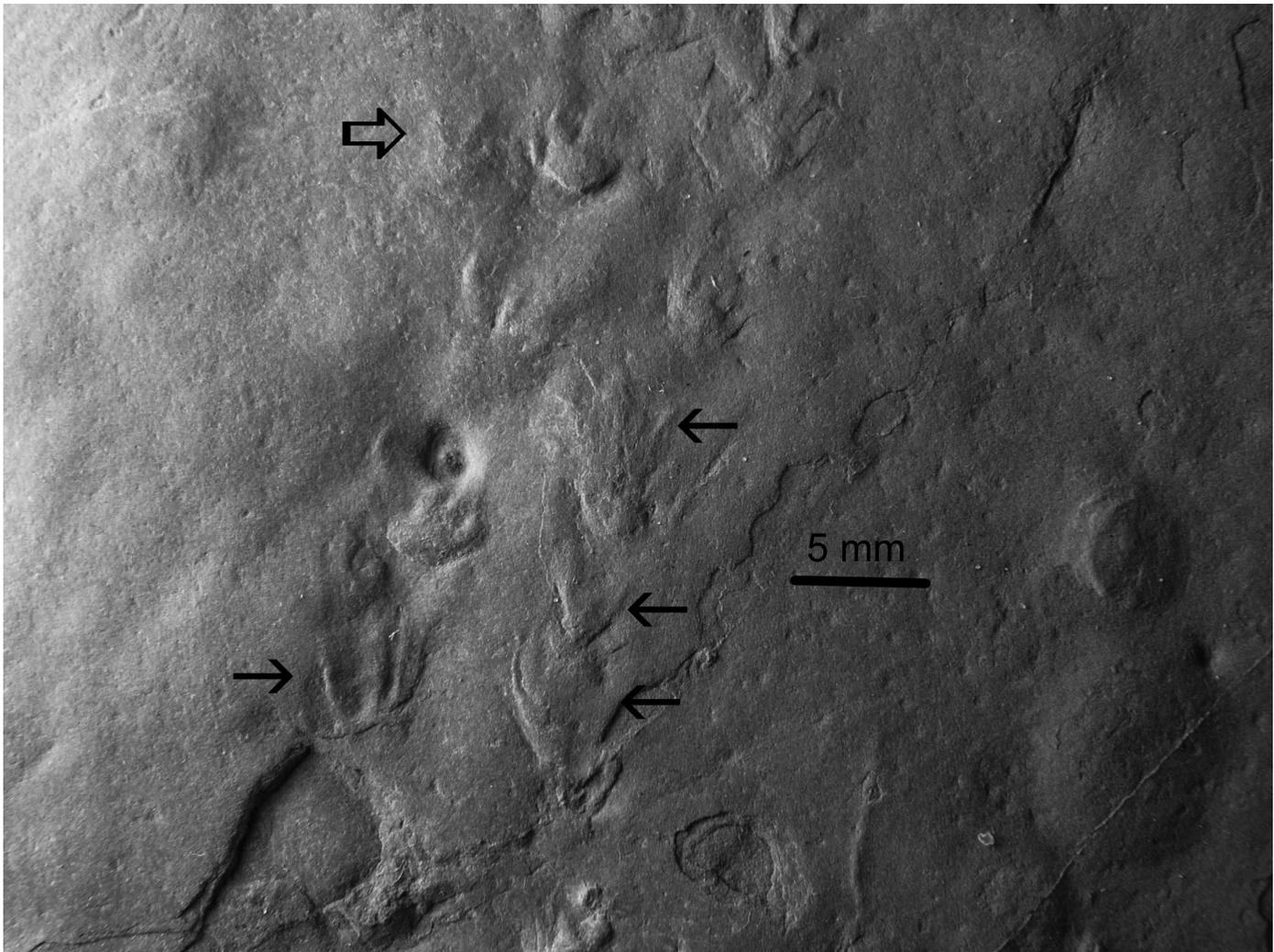


FIGURE 5. Distal portion of the trackway exhibits poorer detail. Elongated digits (*Gracilichnium* preservation) visible in some tracks, indicated by closed arrows. An isolated tridactyl impression appears to the left of the trackway near the top of the photograph (open arrow).

(RM2) approximates a tetradactyl morphology, measuring 4.5 mm long by 4.2 mm long, but this impression is not sufficiently distinct to assess confidently. All other manus impressions have reduced digits (typically three), where the digits are distinct from the overstepping pes impression. The impressions (pes and manus) in the proximal trackway are mostly plantigrade to semi-plantigrade, with posteriorly rounded soles and rounded to pointed digits. The direction of overstepping of the manus by the pes varies from directly in-line (e.g., LP5 over LM5 in figure 3), to offset, with the manus to the right of the pes in both right and left pairs (LM2, LM3, RM2, RM3). The pace measures 4.7 to 6.0 mm, and stride length varies from 9 to 11 mm. Pace angulation varies from 61° to 74°.

The distal section of the trackway differs from the proximal in the generally indistinct preservation of the tracks (Figs. 3,5), most likely due to a change in substrate; the clay layer containing the tracks is less than 1 mm thick at the edge of the slab on the proximal end, but about 2 mm thick at the distal edge. Thus, the track maker walked across a firmer substrate initially and encountered deeper, softer material farther on. The distal tracks are mainly semi-plantigrade, and the digits are typically too indistinct to count or measure. Several of the distal impressions exhibit “*Gracilichnium*-type” preservation (Fig. 5; *sensu* Haubold, 1970), consistent with a deeper, softer substrate.

Two isolated impressions occur exterior to the distal portion of the trackway, 2 to 3 mm to the left of the outer edge of the nearest

impression (Fig. 5). These appear to be semi-digitigrade impressions displaying at most three digits. The relief and clarity differ from the adjacent impressions of the trackway, and therefore represent tracks made at a different time.

Remarks: As well-reviewed by Stimson et al. (2012), the ichnospecies *Batrachichnus plainvillensis*, erected by Woodworth (1900), is a junior synonym of *Saurichnites salamandroides*, initially erected by Geinitz (1861). Because small trackways are readily subject to significant extramorphological variations, due in part to differences in grain size and water content of the substrate, as well as mode of preservation (Melchor and Sarjeant, 2004), multiple ichnotaxa were introduced to account for the variable morphologies of small temnospondyl footprints, but these were recognized as junior synonyms of *B. delicatulus* (Lull, 1918). Subsequent comparisons of *Anthichnium salamandroides* indicated that it also conforms to the ichnogenus *Batrachichnus* (Woodworth, 1900). Tucker and Smith (2004), in contrast, synonymized *Batrachichnus* and *Limnopus* based on similarities of morphology and the size continuum, but Falcon-Lang et al. (2010) retained *Batrachichnus* to describe the traces at the smaller end of the size range. The present work follows Lucas et al. (2011) in recognizing *Batrachichnus* as a mono-specific ichnogenus that includes only *B. salamandroides*.

DISCUSSION

Assignment of the described specimen to *B. salamandroides* is

based on the presence of most of the diagnostic features described above, in combination with the size of the individual impressions. In clear specimens, the pentadactyl pes and tetradactyl manus, with distinct separation between digits I-III and IV, are considered diagnostic. The specimen described here does not present a manus sufficiently clear to describe as tetradactyl, due largely to overstepping, although at least one impression suggests this morphology. Otherwise, the tracks conform to the general features of *B. salamandroides*. Haubold et al. (1995) present 20 mm as the typical pes length for *Batrachichnus delicatulus*, with smaller impressions (4 to 5 mm) referred to *B. obscurus*. Lucas et al. (2011), however, suggest 20 mm as the upper range of size of *Batrachichnus*, and describe pes lengths of 5 to 15 mm as typical for the ichnogenus. Falcon-Lang et al. (2010), for example, described tracks of *Batrachichnus* sp. from the Lower Pennsylvanian of New Brunswick (equivalent to the Joggins Formation) and measured manus lengths of 5 to 8 mm. Stimson et al. (2012) extend the size range of this ichnogenus significantly, measuring pes lengths of 1.7 to 3.2 mm. Consequently, size and morphological conformity of the herein described tracks is consistent with attribution to *B. salamandroides*.

Haubold (1971, 1996) favored a small temnospondyl as the *Batrachichnus* trackmaker, possibly a juvenile eryopid, but as noted by others (Yates and Warren, 2000; Ruta et al., 2003; Falcon-Lang et al., 2006), there are no synapomorphies of the manus and pes other than the

four-digit manus. Falcon-Lang et al. (2006) suggest the temnospondyl *Dendrerpeton*, known from body fossils in the Joggins Formation, as a likely candidate. Stimson et al. (2012), in comparing the tracks they describe with potential trackmakers, acknowledge *Dendrerpeton* as one possibility, but also acknowledge other temnospondyls (branchiosaur, *Eryops*) that might produce similar tracks.

SUMMARY

The Lower Pennsylvanian tetrapod trackway collected at Joggins displays many of the features typical of the ichnogenus *Batrachichnus*, such as a pentadactyl pes and the size distribution of the digits on the pes. Overstepping and lack of detailed preservation prevent confident description of the manus as tetradactyl, however. The size of the tracks is within the range known for the ichnospecies *B. salamandroides*, which is well-described from this locality, and so these tracks are assigned to this ichnospecies. Potential trackmakers known from body fossils at this section include a variety of small temnospondyls.

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REFERENCES

- Carroll, R.L., 1964, The earliest reptiles: Zoological Journal of the Linnean Society, v. 45, p. 61-83.
- Carroll, R.L., 1966, Microsaur from the Westphalian B of Joggins Nova Scotia: Proceedings of the Royal Society of London, v. 177, p. 63-97.
- Carroll, R.L., 1967, Labrynthodonts from the Joggins Formation: Journal of Paleontology, v. 4, p. 111-142.
- Carroll, R.L., 1970, The ancestry of reptiles: Philosophical Transactions of the Royal Society of London Series B. Biological Sciences, v. 257, p. 267-308.
- Carroll, R.L., 1988, Vertebrate Paleontology and Evolution: W.H. Freeman and Company, New York.
- Carroll, R.L., 2009, The rise of amphibians: 365 million years of evolution: The John Hopkins University Press, Baltimore.
- Davies, S.J., and Gibling, M.R., 2003, Architecture of coastal and alluvial deposits in an extensional basin: The Carboniferous Joggins Formation of eastern Canada: Sedimentology, v. 50, p. 415-439.
- Davies, S., Gibling M.R., Calder, J.H. and Rygel, M. 2005, The Pennsylvanian Joggins Formation of Nova Scotia: Sedimentological log and stratigraphic framework of the historic fossil cliffs: Atlantic Geology, v. 41, p. 115-142.
- Dawson, J.W., 1862, Notice of the discovery of additional remains of land animals in the Coal Measures of the South Joggins, Nova Scotia: Quarterly Journal of the Geological Society of London, v. 18, p. 111-113.
- Dawson, J.W., 1863, Notice of a new species of *Dendrerpeton* and of the dermal covering of certain Carboniferous reptiles: Quarterly Journal of the Geological Society of London, v. 19, p. 469-473.
- Dawson, J.W., 1870, Notes on some new animal remains from the Carboniferous and Devonian of Canada: Quarterly Journal of the Geological Society of London, v. 40, p. 75.
- Dawson, J.W., 1876, On a recent discovery of Carboniferous batrachians in Nova Scotia: American Journal of Science, v. 12, p. 440-447.
- Dawson, J.W., 1882, On the results of recent explorations of erect trees containing reptilian remains in the Coal Formation of Nova Scotia: Proceedings of the Royal Society, v. 33, p. 254-256.
- Dawson, J.W., 1891a, Note on *Hylonomus lyelli*, with photographic reproduction of skeleton: Geological Magazine, v. 8, p. 258-259.
- Dawson, J.W., 1891b, On new specimens of *Dendrerpeton acadianum*, with remarks on other Carboniferous amphibians: Geological Magazine, v. 8, p. 145-156.
- Dawson, J.W., 1892a, Supplementary report on explorations of erect trees containing animal remains in Coal Formation of Nova Scotia: Proceedings of the Royal Society of London, v. 54, p. 4-5.
- Dawson, J.W., 1892b, On mode of occurrences of remains of land animals in erect trees at the South Joggins: Transactions of the Royal Society of Canada, v. 9, p. 127-128.
- Dawson, J.W., 1894, Preliminary note on recent discoveries of Batrachians and other air-breathers in the Coal Formation of Nova Scotia: Ex. Canadian Record of Science, v. 6, p. 1-7.
- Dawson, J.W., 1895, Synopsis of the air-breathing animals of the Paleozoic in Canada up to 1894: Transactions of the Royal Society of Canada, v. 12, p. 71-88.
- Falcon-Lang, H.J., Benton, M. J., Braddy, S.J., and Davies, S.J., 2006, The Pennsylvanian tropical biome reconstructed from the Joggins Formation of Nova Scotia, Canada: Journal of the Geological Society of London, v. 163, p. 561-576.
- Falcon-Lang, H.J., Gibling, M.R., Benton, M.J., Miller, R.F. and Bashforth, A.R., 2010, Diverse tetrapod trackways in the Lower Pennsylvanian Tynemouth Creek Formation, near St. Martins, southern New Brunswick, Canada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 296, p. 1-13.
- Geinitz, H.B., 1861, Dyas oder die Zechsteinformation und das Rhotliegende, Heft I Wilhelm: Engelmann, Leipzig.
- Gibling, M.R., Calder, J.H., Ryan, R., Van De Poll, H.W. and Yeo, G.M., 1992, Late Carboniferous and Early Permian drainage patterns in Atlantic Canada: Canadian Journal of Earth Sciences, v. 29, p. 338-352.
- Haubold, H., 1970, Versucheiner Revision der Amphibien-Fährten des Karbon und Perm: Freiburger Forschungshefte Reihe C, 260, Leipzig, p. 83-117.
- Haubold, H., 1971, Ichnia Amphibiorum et Reptiliorum fossilium: Handbuch der Paläoherpologie, v. 18, p. 1-124.
- Haubold, H., 1996, Ichnotaxonomie und Klassifikation von Tetrapodenfährten aus dem Perm: Hallesches Jahrbuch für Geowissenschaften, B18, p. 23-88.
- Haubold, H., Hunt, A.P., Lucas, S.G. and Lockley, M.G., 1995, Wolfcampian (Early Permian) vertebrate tracks from Arizona and New Mexico: New Mexico Museum of Natural History and Science, Bulletin 6, v. 135-165.
- Holmes, R.B., Carroll, R.L. and Reisz, R.R., 1998, The first articulated skeleton of *Dendrerpeton acadianum* (Temnospondyli, Dendrerpetontidae) from the Lower Pennsylvanian locality of Joggins Nova

- Scotia and a review of its relationships: *Journal of Paleontology*, v. 18, p. 64-79.
- Holmes R.B. and Carroll, R.L., 2010, An articulated embolomere skeleton (Amphibia: Anthracosauria) from the Lower Pennsylvanian (Bashkirian) of Nova Scotia: *Canadian Journal of Earth Sciences*, v. 47, p. 209-219.
- Hunt, A.P., Lucas, S.G., Calder, J.H., Van Allen, E.K., George, E., Gibling, M.R., Hebert, B.L., Mansky, C. and Reid, D.R., 2004, Tetrapod footprints from Nova Scotia. The Rosetta stone for Carboniferous tetrapod ichnology: *Geological Society of America Abstracts with Programs*, v. 36, p. 66.
- Lucas, S.G., Hunt, A.P., Calder, J.H., Reid, D.R., Hebert, B.L. and Stimson, M.R., 2005, Tetrapod footprints from Joggins Nova Scotia: A template for understanding Carboniferous tetrapod footprints: *Geological Association of Canada Annual Meeting, Halifax, Abstracts*, v. 30, p. 116-117.
- Lucas, S.G., Voigt, S., Lerner, A.J. and Nelson, W.J., 2011, Late Early Permian continental ichnofauna from Lake Kemp, north-central Texas, USA: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 308, p. 395-404.
- Lull, R.S., 1918, Fossil footprints from the Grand Canyon of the Colorado: *American Journal of Science, Series 4*, v. 45, p. 337-346.
- Lyell, Sir C. and Dawson, J.W., 1853, On the remains of a reptile (*Dendroperpeton acadianum*, Wyman and Owen) and of a land shell discovered in the interior of an erect fossil tree in the coal measures of Nova Scotia: *Quarterly Journal of the Geological Society of London*, v. 9, p. 58-63.
- Melchor, R.N. and Sarjeant, W.A.S., 2004, Small amphibian and reptile footprints from the Permian Carapacha basin, Argentina: *Ichnos*, v. 11, p. 57-77.
- Owen, R., 1862, Description of specimens of fossil reptilians discovered in the coal measures of the South Joggins, Nova Scotia: *Quarterly Journal of the Geological Society London*, v. 18, p. 238-244.
- Ruta, M., Jeffery, J.E. and Coates, M.I., 2003, A supertree of early tetrapods: *Proceedings of the Royal Society of London, Series B*, v. 270, p. 2507-2516.
- Steen, M.C., 1933, The amphibian fauna from the south Joggins Nova Scotia: *Proceedings of the Zoological Society of London*, v. 104, p. 465-504.
- Stimson, M., Lucas, S.G. and Melanson, G., 2012, The smallest known tetrapod footprints: *Batrachichnus salamandroides* from the Carboniferous of Joggins, Nova Scotia: *Ichnos*, v. 19, p. 127-140.
- Tucker, L. and Smith, M. P., 2004, A multivariate taxonomic analysis of the Late Carboniferous vertebrate ichnofauna of Alveley, southern Shropshire, England: *Palaeontology*, v. 47, p. 679-710.
- Voigt, S., 2005, Die Tetrapodenichnofauna des kontinentalen Oberkarbon und Perm im Thüringer Wald- Ichnotaxonomie, Paläoökologie und Biostratigraphie: Cuvillier, Verlag, Göttingen.
- Waldron, J.W.F. and Rygel, M.C., 2005, Role of evaporate withdrawal in the preservation of a unique coal-bearing succession: Pennsylvanian Joggins Formation, Nova Scotia: *Geology*, v. 33, p. 337-340.
- Woodworth, J.B., 1900, Vertebrate footprints on Carboniferous shales of Plainville, Massachusetts: *Geological Society of America Bulletin*, v. 11, p. 449-454.
- Yates, A.M. and Warren, A.A., 2000, The phylogeny of the "higher" temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli: *Zoological Journal of the Linnean Society*, v. 128, p. 77-121.