

Redescription of tetrapod trackways from the Mississippian Mabou Group, Lepreau Falls, New Brunswick, Canada

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Article abstract

Red-bed strata exposed at Lepreau Falls, southern New Brunswick, were originally interpreted as belonging to the Triassic Lepreau Formation. Poorly preserved tetrapod trackways within the strata were previously assigned to two ichnospecies; one to a new Triassic ichnospecies, *Isocampe lepreauense* Sarjeant and Stringer, and the other to *Rhynchosauroides* cf. *R. franconicus* (Heller). Both were attributed to reptiles. Subsequent mapping of the rocks and reassignment of the exposed strata at Lepreau Falls to the Mississippian Mabou Group prompted our re-examination of the trackway fossils. *Isocampe lepreauense* was described from a specimen block preserving three trackways and the original description was based on erroneous interpretation of extramorphological digit drags. *Rhynchosauroides* cf. *R. franconicus* was a tentative assignment in a letter accompanying a cast in the New Brunswick Museum, but was never formally published. We redescribe and re-interpret all the trackways as gait variations produced by temnospondyls, and most closely resemble the Carboniferous ichnotaxon *Matthewichnus*.

Redescription of tetrapod trackways from the Mississippian Mabou Group, Lepreau Falls, New Brunswick, Canada

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ABSTRACT

Red-bed strata exposed at Lepreau Falls, southern New Brunswick, were originally interpreted as belonging to the Triassic Lepreau Formation. Poorly preserved tetrapod trackways within the strata were previously assigned to two ichnospecies; one to a new Triassic ichnospecies, *Isocampe lepreauense* Sarjeant and Stringer, and the other to *Rhynchosauroides* cf. *R. franconicus* (Heller). Both were attributed to reptiles. Subsequent mapping of the rocks and reassignment of the exposed strata at Lepreau Falls to the Mississippian Mabou Group prompted our re-examination of the trackway fossils. *Isocampe lepreauense* was described from a specimen block preserving three trackways and the original description was based on erroneous interpretation of extramorphological digit drags. *Rhynchosauroides* cf. *R. franconicus* was a tentative assignment in a letter accompanying a cast in the New Brunswick Museum, but was never formally published. We redescribe and re-interpret all the trackways as gait variations produced by temnospondyls, and most closely resemble the Carboniferous ichnotaxon *Matthewichnus*.

RÉSUMÉ

Au départ, on croyait que les strates de couches rouges exposées aux chutes Lepreau, dans le sud du Nouveau-Brunswick, appartenaient à la formation de Lepreau, qui était datée du Trias. Des empreintes de tétrapode mal conservées présentes dans les strates avaient d'abord été attribuées à deux ichnoespèces, soit à une nouvelle ichnoespèce du Trias, *Isocampe lepreauense* (Sarjeant et Stringer), et à *Rhynchosauroides* cf. *R. franconicus* (Heller). Les deux étaient attribuées à des reptiles. Une cartographie ultérieure des roches et la réattribution au groupe Mabou du Mississippien des strates exposées des chutes Lepreau nous ont amenés à réexaminer les fossiles. La description d'*Isocampe lepreauense* a été effectuée au moyen d'un bloc de spécimen contenant trois empreintes, tandis que la description d'origine se fondait sur une interprétation erronée d'empreintes extramorphologiques. *Rhynchosauroides* cf. *R. franconicus* a été attribué de façon provisoire dans une lettre accompagnant une contre-empreinte conservée au Musée du Nouveau-Brunswick, qui n'a toutefois jamais été officiellement publiée. Nous redécrivons et réinterprétons toutes les empreintes comme des variations de la démarche de temnospondyles, qui ressemblent davantage à l'ichnotaxon du Carbonifère *Matthewichnus*.

[Traduit par la rédaction]

INTRODUCTION

Tetrapod trackways discovered at Lepreau Falls Provincial Park, New Brunswick (Fig. 1), in rocks thought to be Triassic in age, formed the basis for a new ichnospecies, *Isocampe lepreauense* (Sarjeant and Stringer 1978). The authors concluded that the track-maker was a small lepidosaur, lacertoid, or rhynchosauroid, based in part on the interpreted age of the rocks. A second trackway discovery from the same location several years later was not described formally in the literature, but notes that accompanied the cast repositied in the New Brunswick Museum tentatively identified it as *Rhynchosauroides* cf. *R. franconicus* (Heller 1956).

Subsequent research on the complex geology of the Lepreau Falls area (Park *et al.* 1994; Park 2001), including palynology (NBM Palaeontology file NBMG 3044; Dolby 1997; Utting 1987) and field mapping (Barr and White 2005) has resulted in reassignment of the trackway-bearing rocks to the Mississippian Mabou Group (Fig. 1).

MATERIALS AND METHODS

M.A. McNally discovered the first trackways at Lepreau Falls in October 1974, during a University of New Brunswick, Department of Geology student field trip (Figs. 2, 3). Preliminary identification was followed by a description and identification (Sarjeant and Stringer 1978). Plaster casts were made of the trackways because “The tracks could not be extracted without quarrying that would have probably damaged the tracks” (Sarjeant and Stringer 1978, p. 594). We have respected the original decision not to remove the trackways, due in part to the outcrop location within Lepreau Falls Provincial Park. New Brunswick’s Heritage Conservation Act enforced in 2010 requires a permit to collect the fossil or to alter the fossil site.

The original plaster cast was repositied in the New Brunswick Museum palaeontology collection (NBM Palaeontology file NBMG 3044) and designated as the holotype specimen of *Isocampe lepreauense* (NBMG 3044; Figs. 3, 4, 5, 6) by Sarjeant and Stringer (1978). However, we note that a plaster cast cannot be a holotype, according to the International Code of Zoological Nomenclature (Ride *et al.* 1999). The actual holotype of *Isocampe lepreauense* is the original tracks in the field.

A second trackway was discovered by P. Stringer on 22 October 1977 (Figs. 3, 7, 8). Stringer assumed that it had been exposed since the discovery of the first trackways in 1974 and noted that both sets of trackways occur on the same bedding plane (Fig. 3) and we confirm that they are adjacent to each other. A plaster cast was sent to W.A.S. Sarjeant for identification and repositied at the New Brunswick Museum on 22 August 1978. Documents accompanying the specimen indicated that Sarjeant and

Stringer were preparing a second written report, but it was never published (NBM Palaeontology file NBMG 3047).

Although both sets of trackways have been re-examined in the field, and latex moulds made in 1989, the two original plaster casts repositied in the New Brunswick Museum (NBMG 3044 and NBMG 3047) preserve better detail and were used for the descriptions herein. The specimen cast NBMG 3044 preserves three separate trackways. The specimen cast NBMG 3047 preserves a single trackway, even though accompanying original documents suggested multiple trackways might be present.

GEOLOGICAL CONTEXT

The tetrapod trackways described by Sarjeant and Stringer (1978) at Lepreau Falls (45°10'11.58"N; 66°27'43.15"W; Fig. 1) occur on the margin of an incising sandstone-filled channel body (Fig.2). All strata preserved at Lepreau Falls are highly oxidized and presumed to represent arid to semi-arid conditions, as was typical of the Visean to Serpukhovian Mabou Group in New Brunswick (St. Peter and Johnson 2009). The trackways are preserved in a siltstone that is part of a succession of red mudstones and sandstones. These strata occupy a WSW-trending strip of outcrops from West Branch Reservoir and Joshua Lake to Barnaby Head, via a continuous section from Lepreau Falls to Maces Bay, then outcropping sporadically along the coast through Haggertys Cove (also known as Fieldings Cove). This strip is bounded to the north and south by faults against the late Precambrian crystalline rocks of the Brookville terrane (Barr and White 1996, 2005).

The red beds are continuously exposed along the Lepreau River. A 45 m thick stratigraphic package that preserves the tetrapod tracks was measured by the authors along the eastern limb of a syncline that is exposed at Lepreau Falls (Fig. 2). The measured section commences in a dominantly fine sandstone to siltstone unit with occasional mudstone horizons. These strata are heavily overprinted by pedogenic features such as caliche nodules (1–5 mm) and reduction halos around rooting structures. The beds are generally featureless, with only occasional planar laminated beds and rare 0.5–1 m scale cross-bedding. This basal unit is incised by a 20 m thick medium sandstone unit that is exposed in the face and floor of Lepreau Falls. The base of this unit is in erosional contact with the underlying fine sandstones, with soft sediment deformation along the contact. Conglomerate lags are frequently observed at the base of channel incisions within this unit and contain dominantly red mudstone intraclasts, although rare extraformational pebbles also occur. Metre-scale cross-bedding is common within the sandstone channels and is interpreted as representing lateral accretion bars. The measured section is capped by a mudstone and siltstone unit with common caliche nodules up to 10 cm across, and shallow (10–20

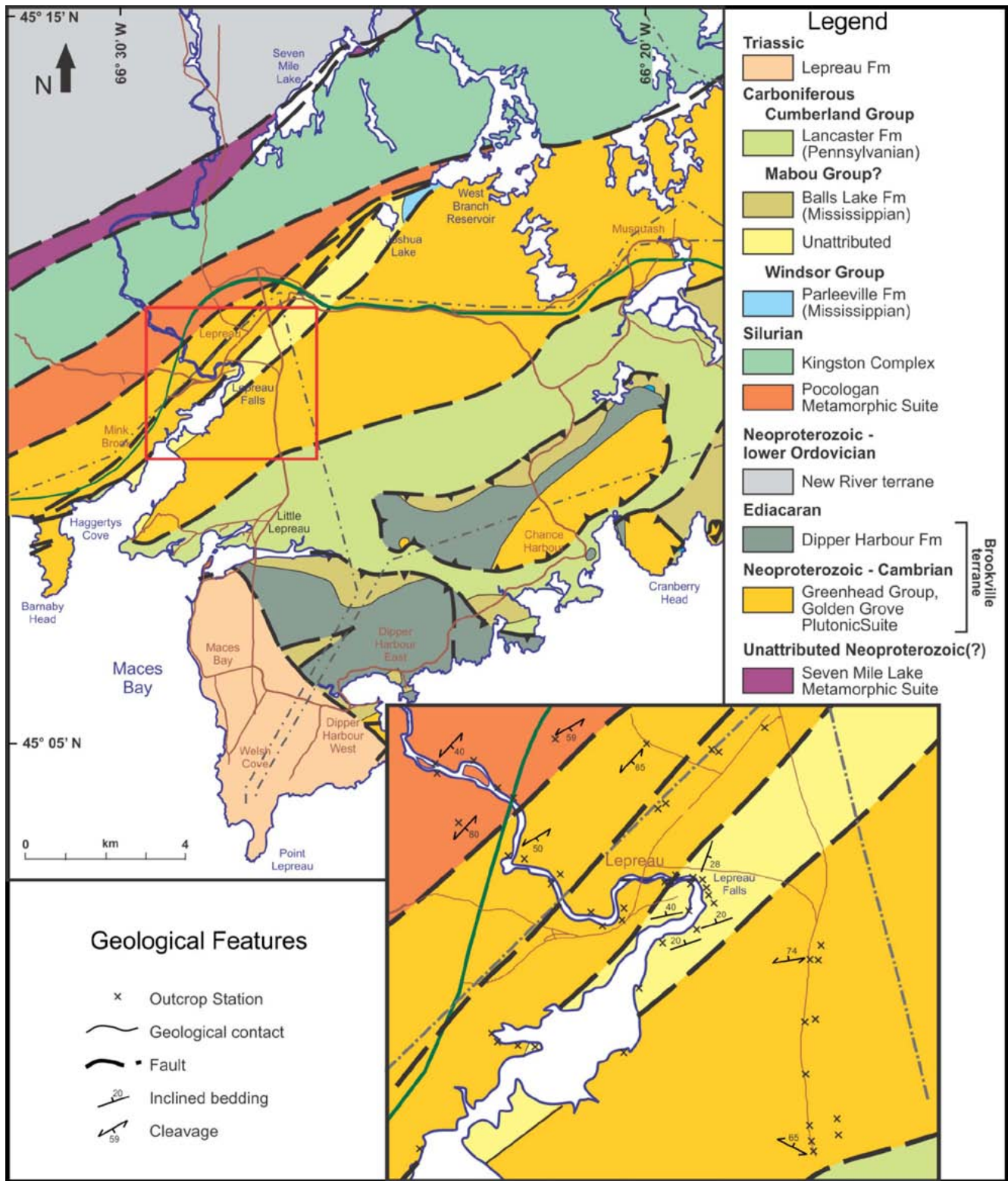


Figure 1. Geological map of the Lepreau Falls, New Brunswick (after Barr and White 2005, with modifications after Park *et al.* 1994).

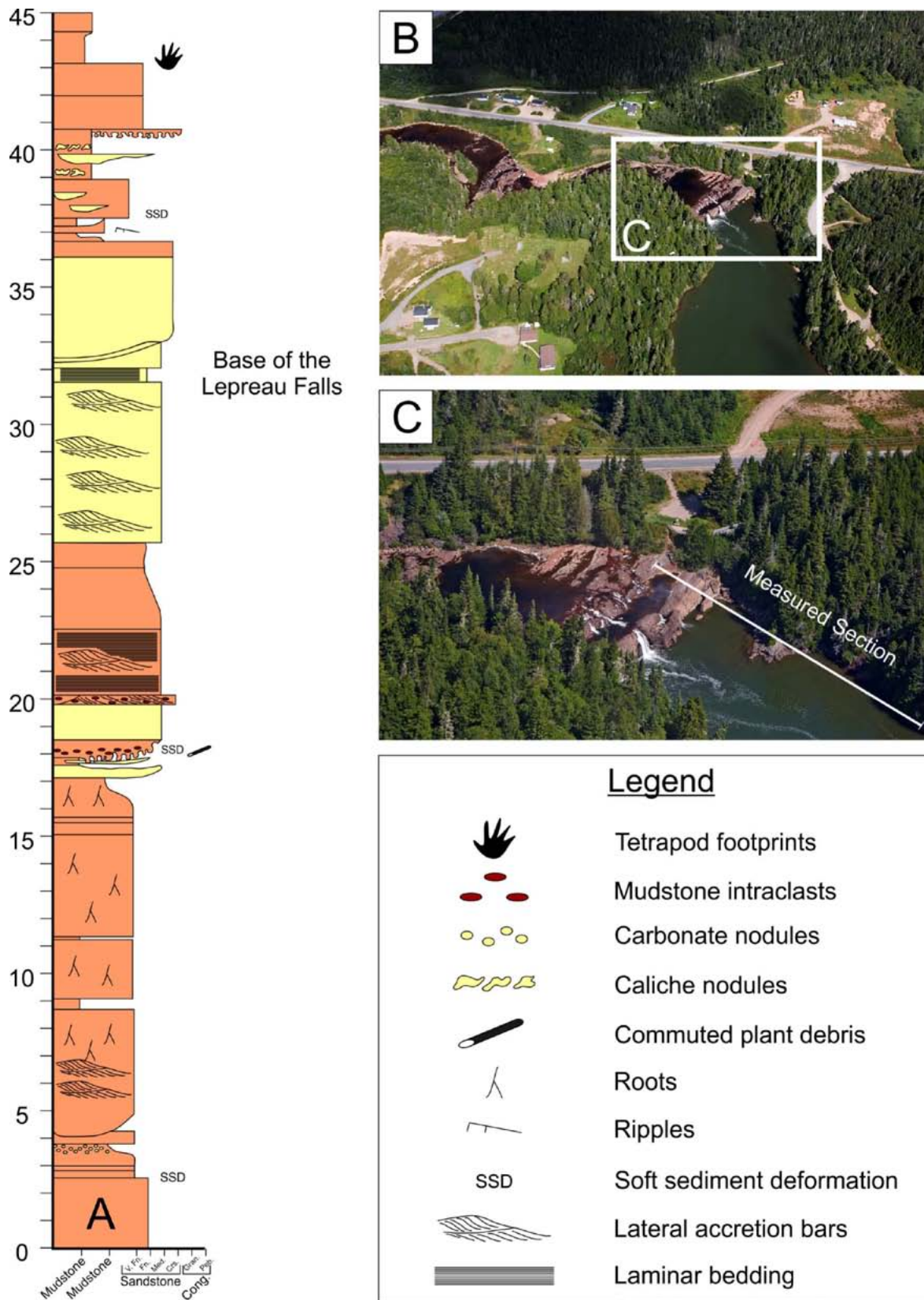


Figure 2. (A) Stratigraphic log of a portion of the exposed strata at Lepreau Falls that preserves tetrapod trackways. (B and C) Aerial photographs showing the location of the measured section.



Figure 3. Aerial Photo of Lepreau Falls. Backfilled channel annotated in white. Trackway site shown by red ellipse. Photograph courtesy of Stonehammer Global Geopark.

cm deep) channel incisions with common asymmetric cross-bedding and localized soft-sediment deformation. It is in this unit, at 43 m above the base of the measured section (Fig. 2), that the tetrapod tracks are preserved.

According to Sarjeant and Stringer (1978), the sandstone-mudstone sequence at Lepreau Falls correlates to the Triassic Lepreau Formation to the south, along the eastern shore of Maces Bay. Although this interpretation generally held (see, for instance, Currie 1988) until extensive remapping of the area in the early 1990s (see McLeod and Johnson 1998; Barr and White 2005), there were some early hints at a re-interpretation. On the basis of cleavage in sandstone-mudstone rocks near Haggertys Cove, Stringer and Lajtai (1979) suggested that some of the rocks in the outcrop strip were actually Pennsylvanian red beds; and spore evidence (Stringer and Burke 1985) suggested an Early Pennsylvanian age. The latter evidence was based on palynological analyses of samples submitted by P.

Stringer to M.S. Barss at the Geological Survey of Canada and recorded in an unpublished GSC report (Barss 1983). Stringer's samples were collected along the Lepreau River downstream from the Lepreau Falls on the east side of Fielding Cove (PS-23-82) and at North Bank (PS-25-82). In an unpublished letter to P. Stringer (NBM Palaeontology file NBMG 3044), Barss (1983) reported that the samples were poorly preserved, but strongly resembled "Assemblage zone II" of Utting (1980), and were thus of Late Visean age.

Re-mapping by McLeod and Johnson (1998) identified carbonates of Windsor Group age (Parleeville Formation) at the northeast end of the outcrop strip, between Joshua Lake and West Branch Reservoir; and Park *et al.* (1994) reported similar rocks with red breccias lying with non-conformity on the Carrying Cove granite immediately west of Haggertys Cove (McLeod *et al.* 2005). This granite is part of the Golden Grove plutonic suite (White *et al.* 2002) that was intruded into the Brookville terrane during the

Ediacaran to Cambrian interval (Barr and White 1996). Coarse grey sandstone and pebble conglomerate with plant debris and macrofossils, correlated with the Lower Pennsylvanian Lancaster Formation, is exposed on Barnaby Head (western side at Raspberry Cove; see Park *et al.* 1994, and Rast *et al.* 1979), and a faulted panel of similar rocks lies on the north side of the outcrop strip along the east side of Haggertys Cove (Stringer and Lajtai 1979). However, the relationships of the predominantly red succession above the Windsor Group carbonates in most of the Lepreau Falls belt remains ambiguous. At Lepreau Falls there is neither the coarse red conglomerate of the Balls Lake Formation, nor the grey conglomerate-sandstone of the Lancaster Formation with its abundant (Langsettian) flora (Falcon-Lang and Miller 2007). Flint and van der Poll (1982) interpreted the Balls Lake and Lancaster formations as laterally equivalent conglomerate and braid-plain deposits. However, the age of the Balls Lake Formation is ambiguous, and has also been considered Visean (van der Poll 1995).

Correlations of Carboniferous rocks in the area are complicated by the tectonic setting. The outcrop strip containing the Lepreau Falls section constitutes a cover sequence to the local Brookville terrane basement, and it represents the upper part of the basal member of a tectonic stack that has younger units to the south. On Barnaby Head, and south of Little Lepreau, two thrust-nappes carry crystalline basement over Carboniferous cover (Rast *et al.* 1979; Park 2001; Barr and White 2005), and locally the Carboniferous successions are inverted (Park *et al.* 1994).

Although the exact age of the stratigraphic package at Lepreau Falls remains in question, studies in recent decades confirm that the section is not Triassic, but rather can be assigned to the latest Mississippian (Visean–Serpukhovian) Mabou Group. The trackway-bearing sandstone-mudstone sequence at the falls seems to lie conformably near the top of a red-bed succession directly overlying Windsor Group carbonates. This relationship strongly suggests that this sequence belongs to the upper part of the Visean–Serpukhovian Mabou Group, and may be a local representation of the Shepody or Enrage formations.

SYSTEMATIC ICHNOLOGY

Genus *Matthewichnus* Haubold 1970

REMARKS: In this work we reassign multiple trackways preserved on two specimen casts from Lepreau Falls, New Brunswick, to *Matthewichnus*. We describe the two specimens separately.

Matthewichnus? lepreauense (Sarjeant and Stringer 1978)
Figures 4–7, 10

1978 *Isocampe lepreauense*: Sarjeant and Stringer, p. 598; nomen dubium.

MATERIAL: Plaster cast representing the holotype of *Isocampe lepreauense*, repositied at the New Brunswick Museum, Saint John, New Brunswick, Canada, NBMG 3044.

AGE AND HORIZON: Mississippian Mabou Group.

DESCRIPTION: Three trackways of a quadruped tetrapod are preserved. The most complete crosses the sandstone surface with a straight trackway length of 266.8 mm (Figs. 5, 6A). The specimen exhibits extensive extramorphological variability in the form of digit extensions (toe drags). Despite the interpretive sketches in Sarjeant and Stringer (1978, figs. 5–6), the trackway is digitigrade rather than plantigrade, lacking any clear sole or palm impressions (Fig. 7). The outer and inner widths of the trackway measure 67.11 mm and 14.90 mm (Fig. 5B), respectively. The manus and pes pace angles measure 90.4° and 91.3°, respectively (Fig. 6B).

Stride and pace were measured from the base of the most deeply impressed digits, where repeat morphologies are recognized. The stride was measured at 65.63 mm and the pace measured at 49.11 mm (Fig. 6B). The footprints are arranged in loose manus and pes sets and are barely recognizable from the digitigrade imprints, in which extramorphological digit extensions frequently create overlap of the manus and pes impressions.

The manus is smaller than the pes, and both are longer than wide, although this may be an artifact of (or exaggerated by) the extramorphological digit extensions. The manus is tetradactyl, and the pes is pentadactyl (Fig. 7). Pes imprints are oriented parallel to the midline, whereas the manus impressions are oriented slightly oblique to the midline. Digits of both manus and pes are thin, elongated, and sinuous to curvilinear, curving slightly away from the midline; they commonly taper at their terminations. Digits II–IV appear to be the longest, with digits II and III being roughly equal in length and digit IV being the longest (Fig. 7). Digits are roughly subparallel, with digits I and V being shorter and set back. Relative digit lengths are estimates as much of the true morphology is obscured by digit extension extramorphology. A continuous linear median tail (or body) drag is present in this specimen. The glenoacetabular distance was measured from successive footprint impressions to be 48.52 mm along the midline (Fig. 10A).

REMARKS: Two additional partial trackways are preserved on the surface (Figs. 6C–D). These trackways are pointing in opposing directions, parallel to the one described above. These additional trackways obscure one another, and for this reason we do not describe them in detail. The manus described by Sarjeant and Stringer (1978) was described from one of these two partial trackways. Given similarities to the already described trackway, we also assign these to *Matthewichnus?*

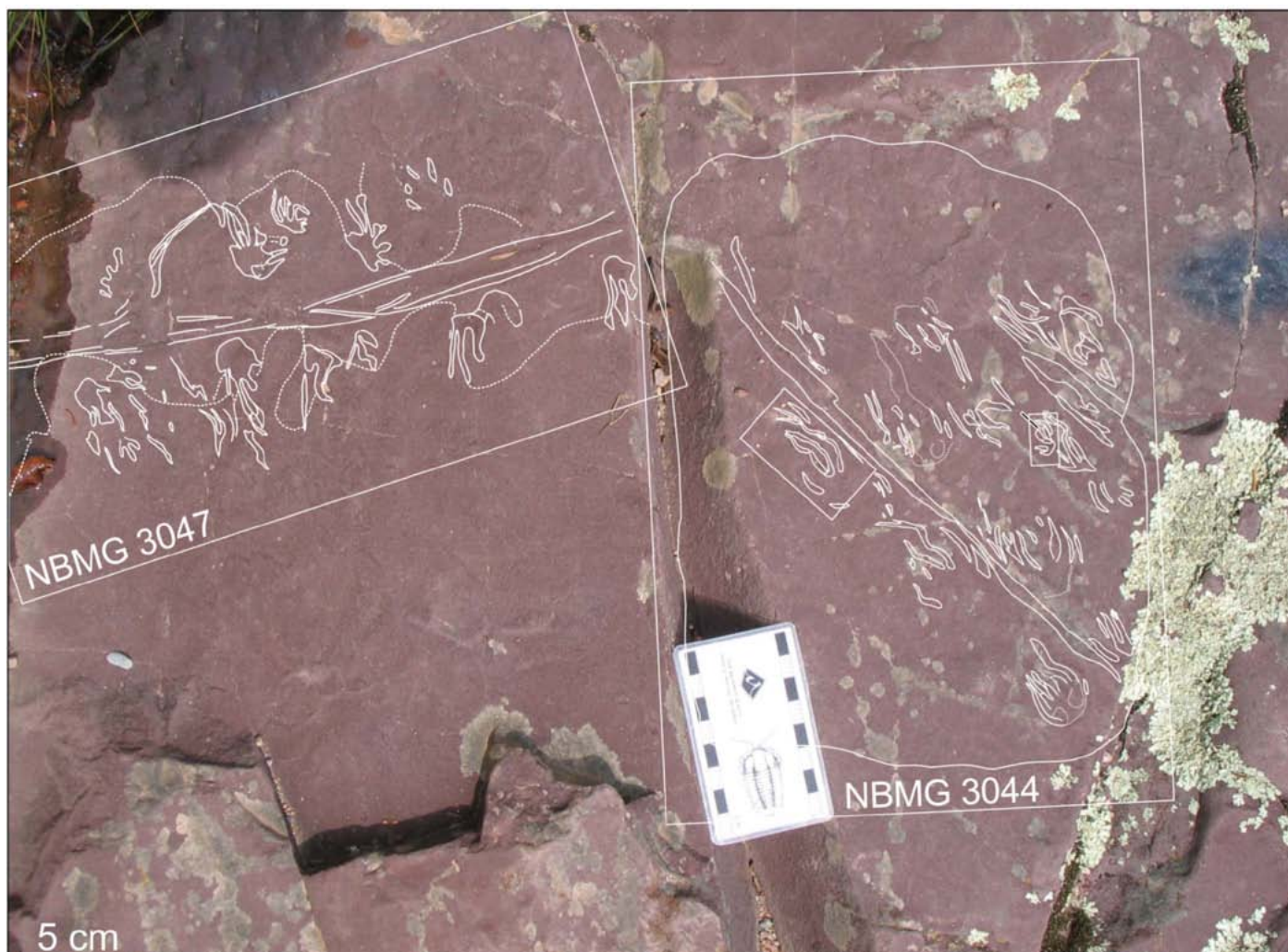


Figure 4. Type specimens, in situ, of *Isocampe lepreauense* (cast as NBMG 3044) and *Rhynchosauroides* cf. *R. franconicus* (cast as NBMG 3047), both reassigned herein tentatively to *Matthewichnus*.

lepreauense (Sarjeant and Stringer 1978). Given the poor preservation of all three trackways, further identification of the ichnospecies is impossible and thus it should be restricted to the holotype. Consequently, we recommend that the name *Matthewichnus lepreauense* be abandoned.

Matthewichnus? sp.
Figures 4, 8–10

Rhynchosauroides cf. *R. franconicus*: Sarjeant and Stringer (NBM Palaeontology file NBMG 3047)

MATERIAL: Plaster cast reposit at the New Brunswick Museum, Saint John, New Brunswick, Canada, NBMG 3047.

AGE AND HORIZON: Mississippian, Mabou Group.

DESCRIPTION: The specimen exhibits a linear trackway that is 304.91 mm long (Fig. 8). The outer and inner widths of the trackway measure 108.6 and 29.32 mm, respectively (Fig. 8B). Manus and pes impressions are poorly preserved, demonstrating a high degree of extramorphological distortion in the form of toe drags. There are examples of both plantigrade and digitigrade imprints. The trackway has a stride of 72.57 mm and a pace of 27.6 mm, the latter measured from successive pes impressions (Fig. 8B). Pace angulations, which could be obtained only for the pes impressions, are 103.5° (Fig 10B).

The manus appears to be smaller than the pes. The pes is most often expressed, whereas the manus is very poorly preserved and often absent. The pes is oriented perpendicular to the midline of the trackway, with the deepest portion of the tracks on the inside (left side, anterior relative to the trackway). The tracks commonly display 3 digits with suggestions of up to 5 digits. Right Pes 4 (RP4;

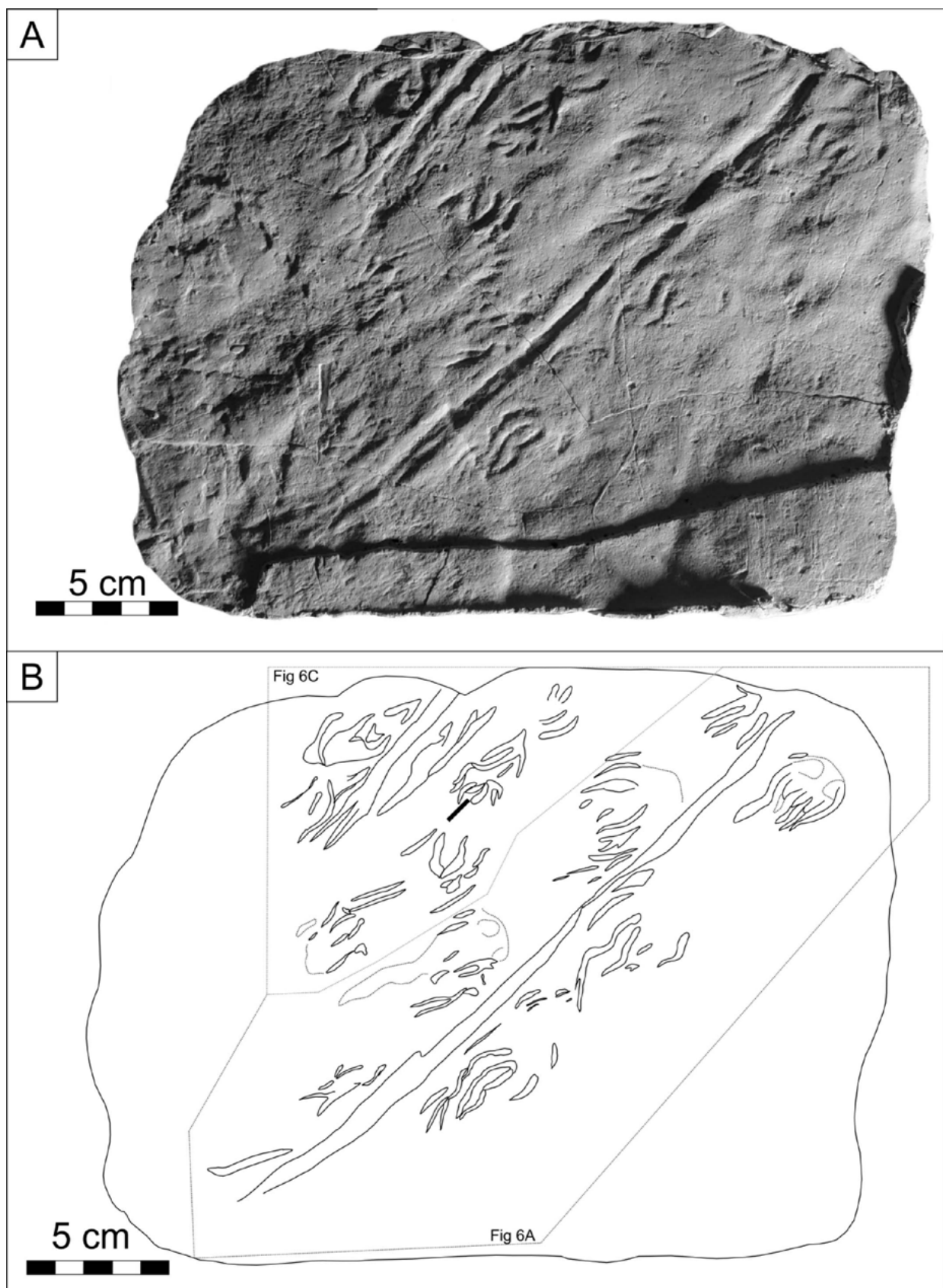


Figure 5. *Matthewichnus?* (formerly *Isocampe lepreauense*; NBMG 3044). (A) photograph of plaster cast repositated at the New Brunswick Museum. (B) Interpretive sketch.

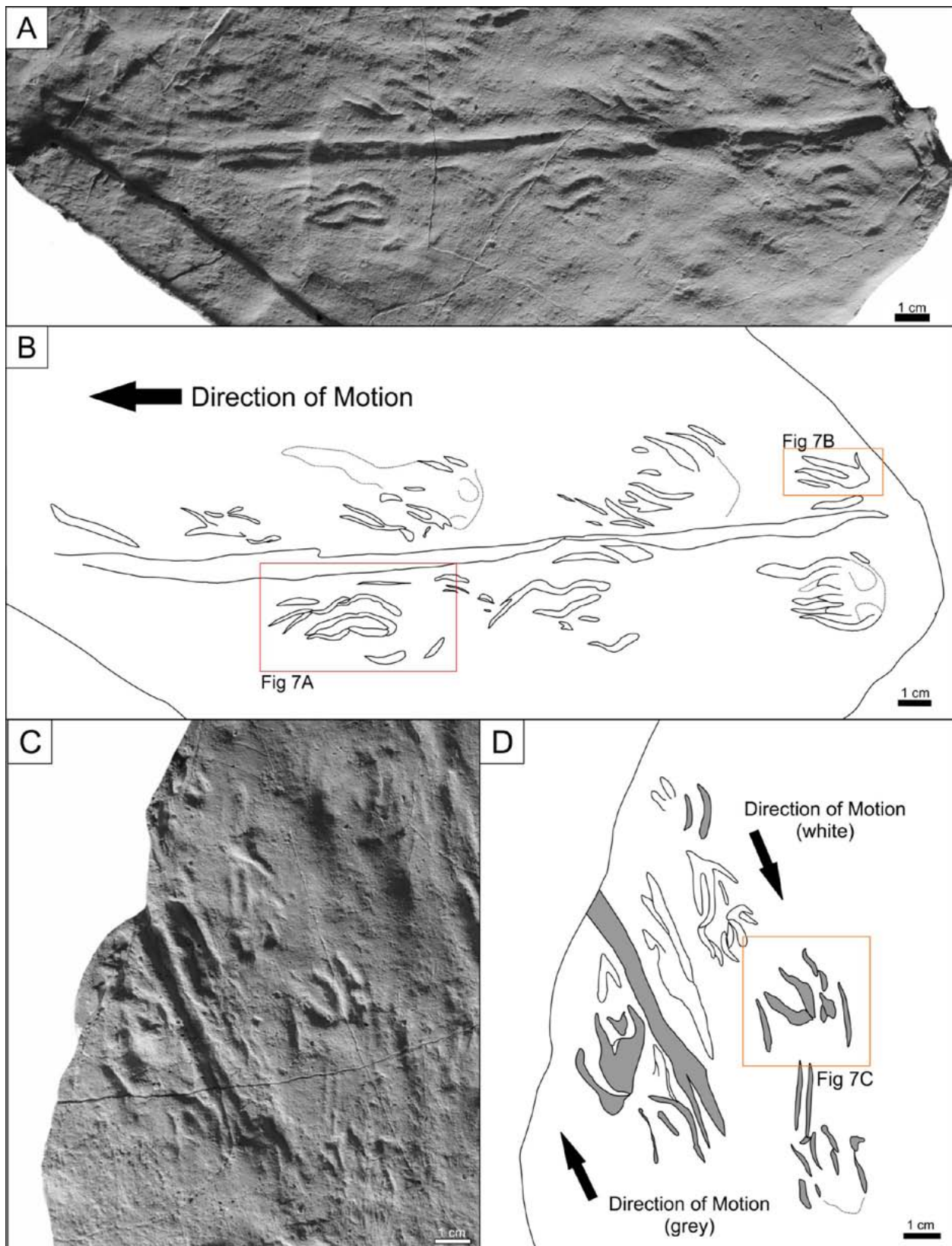


Figure 6. Close up images of *Matthewichnus?* trackways (formerly *Isocampe lepreauense*; NBMG 3044). (A and B): Trackway 1; red boxes indicate the best manus and pes, used for description. (C and D): overlapping trackways; Trackway 2 (grey) and Trackway 3 (white).

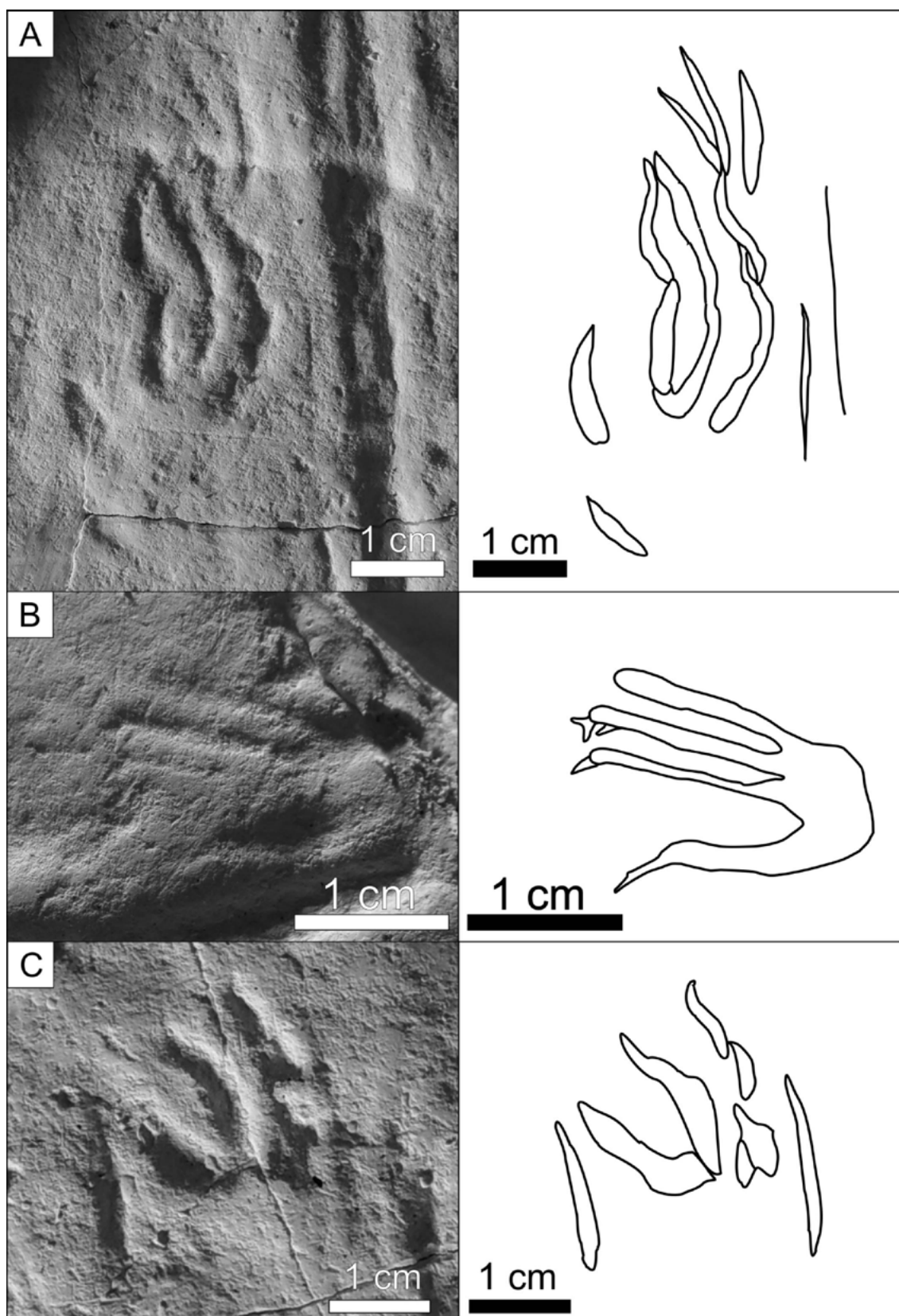


Figure 7. *Matthewichnus? lepreauense* (formerly *Isocampe lepreauense*; NBMG 3044). Close ups of select manus and pes: (A) manus and pes set; (B) best manus impressions; (C) pes impression previously interpreted as a manus by Sarjeant and Stringer (1978).

Fig. 9A and B) and Left Pes 4 (LP4; Fig. 9C and D) are the clearest imprints and are pentadactyl. The manus is poorly preserved and or often absent. When preserved the manus is represented by partial tracks and scratch marks. Although even the best manus (LM2) is too poorly preserved to be interpreted with confidence, it appears to show at least a tetradactyl arrangement with extensive extramorphology.

The pes is pentadactyl, with increasing digit length from digits I through IV, and IV being the longest. Digit V is slightly shorter than digit IV. Terminal digit pads are visible on left Pes 4, with little to no evidence of claw impressions (Fig. 9). Digits I and II are directed parallel to the midline whereas digits III–V are divergent to perpendicular to the midline. Exact digit lengths of the manus are unclear and impossible to ascertain due to a very high degree of extramorphological distortion. The glenoacetabular distance was measured from successive footprints. The resulting glenoacetabular distance measures 50.28 mm (Fig. 10B). A clear median (tail or body) drag is present, associated with the smoothing of the pitted substrate texture between the outermost margins of the trackway. The smooth patches swell near the tracks, thinning between successive impressions.

REMARKS: The specimen was previously interpreted to represent multiple individual trackways, informally identified as *Rhynchosauroides* cf. *R. franconicus* (NBM Palaeontology file NBMG 3047). Based on the above description, only a single trackway is preserved, here identified as *Matthewichnus?* sp. The poor preservation of the trackway prevents further ichnotaxonomic assignment to the ichnospecific level.

DISCUSSION

Isocampe strata Hitchcock 1858

Hitchcock (1858) erected the genus *Isocampe* to accommodate *Isocampe strata*, an ichnospecies of Early Jurassic tracks from the Turners Fall Formation in Massachusetts; he believed the tracks were made by an amphibian or a lizard. Lull (1904) considered *Isocampe strata* to represent a synapsid track, whereas Haubold (1971) considered *Isocampe strata* to be a lepidosaur track allied to the Triassic ichnogenus *Gwynnedichnium*. However, Rainforth (2005; see also Lucas *et al.* 2014) regarded *Isocampe strata* as a nomen dubium because it is based on insufficient material to be properly diagnosed. Indeed, the type material (syntypes) of *Isocampe strata* (Hitchcock 1858, pl. 20, fig. 5, pl. 36, fig. 5; Rainforth 2005, fig. 4.15) consists of mostly parallel and slightly curved digit marks up to 15 cm long, commonly interpreted as “swim tracks”. They resemble the common swim-track ichnogenus *Characichnos* (Whyte and Romano 2001). Similar to *Isocampe strata*, the Lepreau Falls trackway also

resemble *Characichnos*, except that manus and pes sets are clearly recognizable. However, beyond some slightly curved digits that are not associated with sole impressions, the Lepreau Falls specimens bear little resemblance to *Isocampe*.

Isocampe lepreauense—Specimen NBMG 3044

Sarjeant and Stringer (1978) provided an elaborate description and interpretation of the trackway. In their description, they concluded that the trackway constituted a new species of the reptile ichnogenus *Isocampe* Hitchcock 1858 on the basis of its digitigrade morphology and the supposed Triassic age of the hosting Lepreau Formation.

Much of Sarjeant and Stringer’s (1978) description is based on extramorphological digit extensions, which they interpreted as true digit impressions. In vertebrate ichnology, many ichnotaxobases that were used for ichnospecific assignment are no longer considered to be valid criteria to assess vertebrate trackways (i.e. digit divarication) and are ignored here. Stringer and Sarjeant described the trackway as having four toes on the manus and on the pes. They followed with a description of a fifth digit, starting the digit count at II rather than I on their interpretive sketch. This suggests that Sarjeant and Stringer (1978) suspected that a fifth digit was present; but this was not clear from their description. The manus and pes set used in Sarjeant and Stringer’s description were in fact two separate pes impressions taken from two separate trackways going in opposing directions. We reinterpret the carpals and metacarpals described by Sarjeant and Stringer as representing the sinuous and undulose nature of the extramorphological digit drags. They also thought that the manus was oriented slightly towards the midline, but in our view the manus is oriented obliquely away from the midline.

A further problem is that Sarjeant and Stringer (1978, p. 600) designated a plaster replica as the holotype of their new species, *Isocampe lepreauense*. According to the International Code of Zoological Nomenclature (ICZN, Article 72.5.3), the eligibility of a name-bearing type specimen is restricted to “In the case of fossils, a natural replacement, natural impression, natural mould or natural cast of an animal or colony or part of either.” According to the Code, the plaster replica assigned as the holotype in their paper, cannot be designated as such and invalidates the name. The fossil remains in outcrop, but is unrecoverable and is highly weathered.

The trackways, as identified by Sarjeant and Stringer (1978), were used by those authors as palaeontological supporting evidence for the Triassic age of the Lepreau Formation, even though the type material of *Isocampe* is Early Jurassic. More recent field mapping summarized above has refuted the age assignment of Triassic in favour of a Mississippian (Visean to Serpukhovian) age. Assuming a Triassic age, it is reasonable that Sarjeant and Stringer did not explore Carboniferous ichnotaxa as nomenclatural

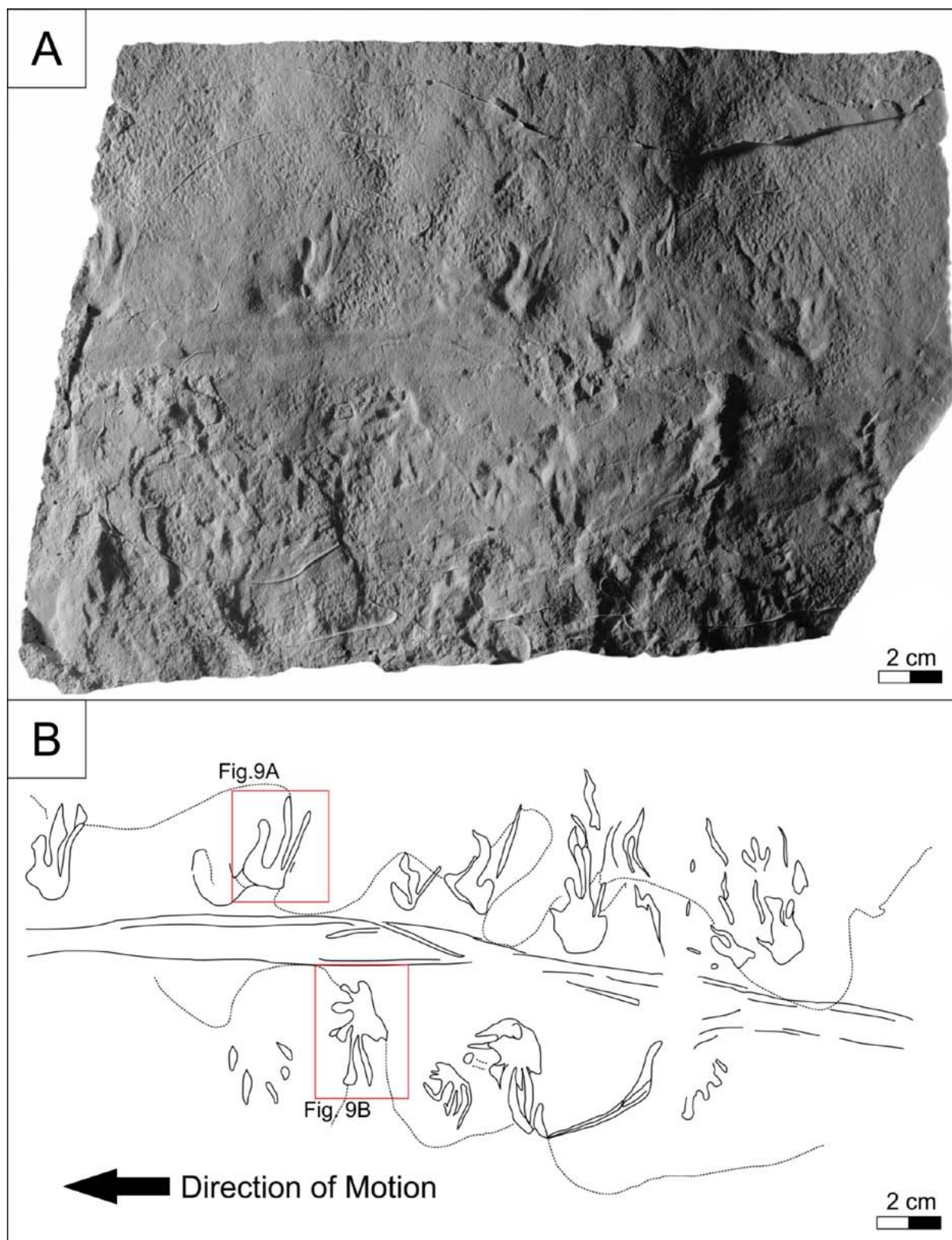


Figure 8. *Matthewichmus?* sp. (formerly *Rhynchosauroides* cf. *R. franconicus*; NBMG 3047). (A) photograph of plaster cast repositated at the New Brunswick Museum; (B) interpretive sketch. Box outlines indicate the best preserved manus and pes impressions.

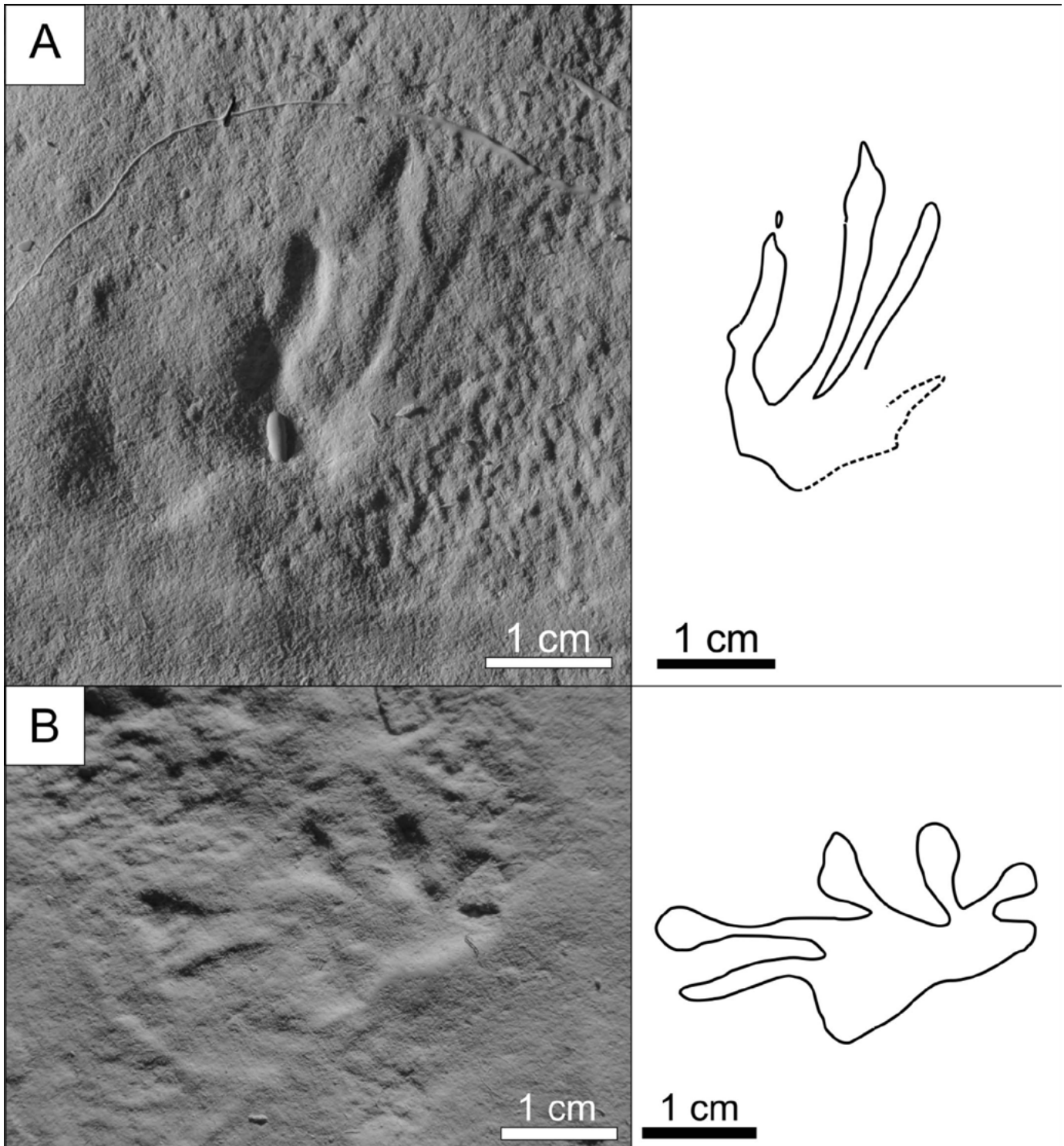


Figure 9. *Matthewichnus?* sp. (formerly *Rhynchosauroides* cf. *R. franconicus*; NBMG 3047). (A and B): close ups of the best pes impressions.

candidates for the Lepreau Falls specimens. The assignment of the trackways to *Isocampe* is also understandable given that that genus is a digitigrade trace strongly resembling the extramorphological digit extensions interpreted here for the

Lepreau Falls specimen. Based on our re-evaluation of the morphology of this specimen, we here re-interpret these trackways as highly distorted underprints (digitigrade) most closely similar to the ichnogenus *Matthewichnus*.

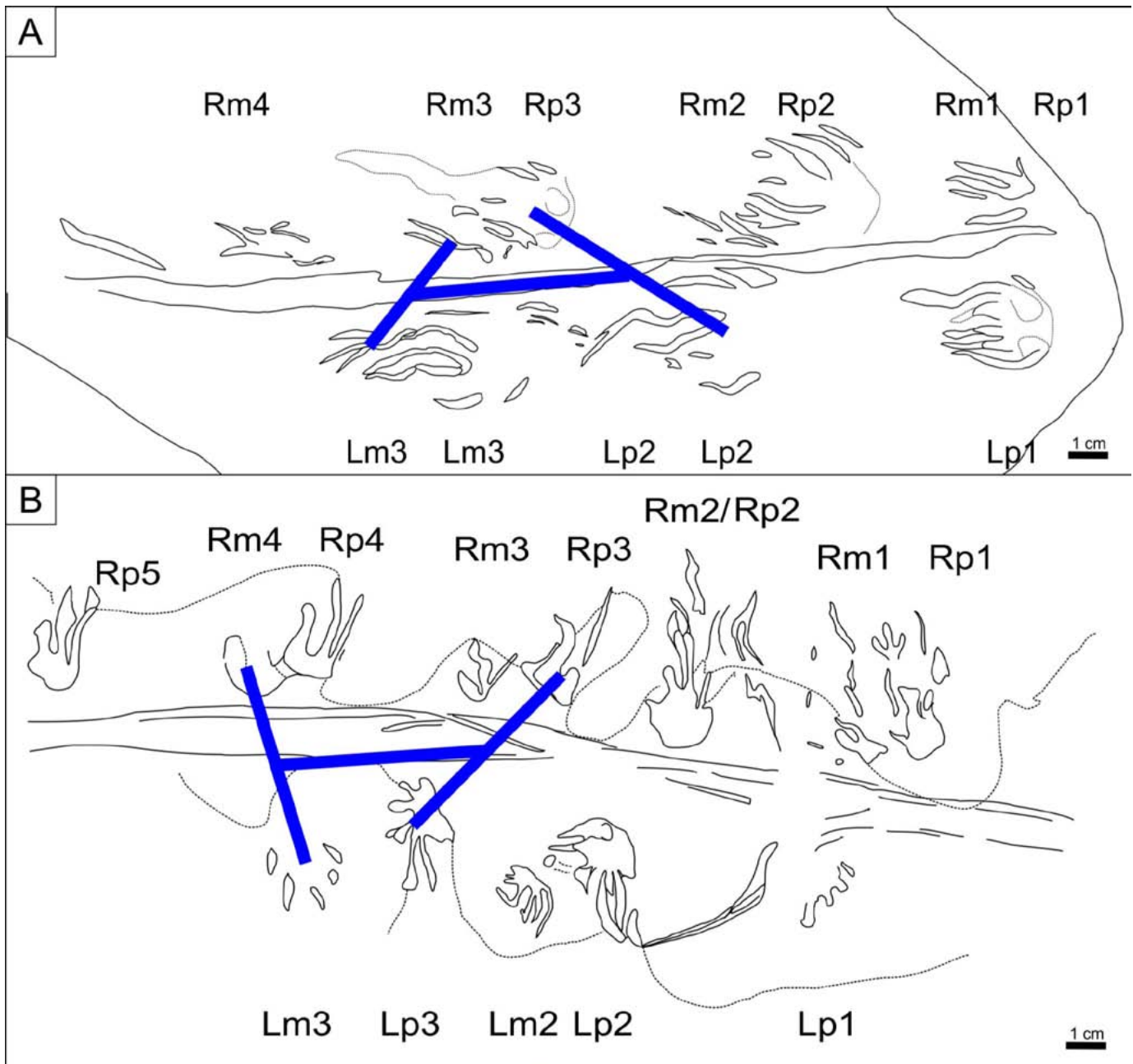


Figure 10. Glenoacetabular distance: (A) *Matthewichnus?* *lepreauense* (formerly *Isocampe lepreauense*; NBMG 3044) of Left Manus 2 (Lp2), Right Pes 3 (Rp3), Left Manus 3 (Lm3), Right Manus 3 (Rm3); (B) *Matthewichnus?* sp. (formerly *Rhynchosauroides* cf. *R. franconicus*; NBMG 3047) of Left Pes (Lp3), Right Pes 3 (Rp3), Left Manus 3 (Lm3), Right Manus 4 (Rm4).

At present, three ichnospecies of *Matthewichnus* are known (*Matthewichnus caudifer*, *Matthewichnus velox* and *Matthewichnus woodworthii*), but their separation has been questioned by Fillmore *et al.* (2012). The presence of a tail and body drag has been used to distinguish *Matthewichnus caudifer*, as its name suggests. However, as noted by Haubold

et al. (2005) and Fillmore *et al.* (2012), tail and body drags are not good ichnotaxabases as they are variably present. The elongated manus of *Matthewichnus velox* separates it from *Matthewichnus caudifer* and *Matthewichnus woodworthii*. However *M. woodworthii* is distinguished only by very large size, and size is also not a good ichnotaxabase. Based on

the characteristics noted above, the Lepreau Falls trackways loosely conform to the diagnosis of *Matthewichnus caudifer* (Kohl and Bryan 1994) as currently defined. However, given the poor preservation of the present material and the taxonomic problems associated with ichnospecies of *Matthewichnus*, the trackways from Lepreau Falls are assigned only at the ichnogenus level as *Matthewichnus*?

Matthewichnus caudifer has been described from the Serpukhovian (Mississippian) by Kohl and Bryan (1994) and from the uppermost Visean to Serpukhovian Mauch Chunk Formation of Pennsylvania (Fillmore *et al.* 2012) which extended the range of the ichnogenus into the Mississippian. The specimens described here from the Mabou Group are latest Visean to Serpukhovian in age, well within the temporal range established for *Matthewichnus*.

In conclusion, there are good morphological reasons not to assign the Lepreau Falls tracks to *Isocampe*, which is in any case an ichnogenus of questionable status. We consider the criteria used by Sarjeant and Stringer (1978) to distinguish *Isocampe lepreauense* to be erroneous. Given the ambiguity of the generic type ichnospecies, *Isocampe strata*, and the false ichnotaxobase used to distinguish the very poorly preserved type of *Matthewichnus lepreauense*, we recommend that this name be abandoned.

Rhynchosauroides cf. *R. franconicus*— Specimen NBMG 3047

A specimen collected as a plaster cast with a single tetrapod trackway tentatively assigned to *Rhynchosauroides* cf. *R. franconicus* (Heller 1956) is here reassigned questionably to *Matthewichnus*. The trackway was never formally published, but its historical account and a preliminary assessment and description of it are preserved in a letter from William Sarjeant to Peter Stringer (NBM Palaeontology file NBMG 3047).

The trackway was first observed by Stringer on 22 October 1977, and later a cast was made by R.H. Grant of the University of New Brunswick. In his letter, Sarjeant proposed that there were multiple trackways produced by at least two, if not several track makers, but he claimed he could not unravel the trackway patterns to match manus and pes morphologies in order to assign them to individual trackways. Sarjeant concluded that the manus was pentadactyl with a very long thin digit IV, and is much smaller than the pes. The trackways were assigned to the lactertoid ichnogenus *Rhynchosauroides* based on the morphology of the traces and the supposed Triassic age of the red beds exposed at Lepreau Falls.

We interpret the fossil to only preserve a single trackway. Sarjeant's assessment was likely based on the direction of the individual footprints, assuming they were oriented in the direction of motion. In contrast, we interpret the footprints as being oriented perpendicular to the midline of the trackway (Fig. 8). A very clear tail drag impression with body drags bifurcates the two oppositely oriented rows

of footprints, giving credence to the new interpretation that the trackway was produced by a single individual with an obliquely oriented pes. The manus is very poorly preserved, often being expressed as a few scratch marks or an irregular depression on the surface; thus the number of digits is difficult to assess, but at least four are visible. The trackway exhibits extensive extramorphological variation in the form of digit extensions very similar to specimen NBMG 3044. The pes is indeed significantly larger than the manus, and the pes are pentadactyl. Posterior to each pes impression, an elliptical to semi-lunate impression the width of the trackway is observed. The sedimentary surface texture is pitted, perhaps reflecting bioturbation, some form of adhesion sedimentary structure, or the original presence of a thin biofilm caused by microbial activity. This texture is absent in the elliptical impression that likely represents a body drag that smoothed the sediment surface (Fig. 11).

Based on the morphological similarities to the previously described trackways on specimen NBMG 3044, we here assign this specimen to a gait variation of *Matthewichnus*, exhibiting a slow gait with outwardly oriented, perpendicular pes impressions and low relief body impressions.

Track maker

Matthewichnus was originally classified as an indeterminate amphibian trackway (Haubold 1971) based on the lack of knowledge of the manus morphology. The discovery of a better preserved species of *Matthewichnus* (*Matthewichnus caudifer*) by Kohl and Bryan (1994) allowed the assignment of these traces to temnospondyls based on the diagnostic tetradactyl manus (Haubold *et al.* 2005). *Limnopus* and *Batrachichnus* have also been assigned to temnospondyls (Voigt 2005; Stimson *et al.* 2012). In an attempt to classify trackways of the Union Chapel Mine site in Alabama to the known skeletal remains of Pennsylvanian tetrapods, the temnospondyl *Dendrerpeton* was specifically named, together with *Amphibamus*, by Haubold *et al.* (2005) as possible trace makers of *Matthewichnus caudifer* and *Nanopus reidiaae*. Stimson *et al.* (2012) used the only known articulated *Dendrerpeton* specimen, from the Joggins Fossil Cliffs, Nova Scotia, as a model for juvenile temnospondyl trackways assigned to *Batrachichnus*, also found at Joggins. Stimson *et al.* (2012) concluded that *Dendrerpeton* or some other temnospondyl was the most likely candidate for the trace maker of *Batrachichnus*, although terrestrial microsaur, which also have a tetradactyl manus (Carroll and Gaskill 1978), may also be considered.

The age range of *Dendrerpeton* (Serpukhovian to Bashkirian) overlaps with the age of the Mabou Group (Visean to Serpukhovian). Temnospondyls are abundant during the Mississippian to Pennsylvanian transition, especially within the Maritimes Basin (Carroll and Gaskill 1978; Carroll 1988, 2009). The tetradactyl manus and



Figure 11. Interpretive artwork of *Matthewichnus* and tracemaker to illustrate pes directed outwards, perpendicular to the trackway midline, and a body impression that involved a smoothing of the sediment surface. Illustration by Alexina LePage.

pentadactyl pes of the Lepreau Falls trackways conform to interpretations by Haubold *et al.* (2005) of the Union Chapel Mine trackways as being of temnospondyl origin. Voigt and Lucas (2015) examined trackways from the Permian Robledo Formation of New Mexico assignable to *Matthewichnus*. In their examples, trackway patterns were very irregular, with no manus and pes sets. They determined that the glenoacetabular distance must be elongate and considered microsaur as the makers of *Matthewichnus caudifer*. The trackways described from Lepreau Falls show manus and pes sets, and thus microsaur with elongated bodies can be ruled out as the trackmakers. Some microsaur with shorter bodies that resemble temnospondyls are still possible candidates (Stimson *et al.* 2012). Voigt and Lucas (2015) also noted strong similarities between their *Batrachichnus* (and *Limnopus*) and *Matthewichnus* specimens, the regularity in trackway patterns being the only distinguishing ichnotaxobase. Given that these ichnotaxa are produced by similar biotaxa, it stands to reason that the ichnotaxa would be similar as

well. No Carboniferous tetrapod skeletal remains have been described from New Brunswick. Many early tetrapods have similar digit counts and morphologies, so assigning the Lepreau Falls trackways to a specific tetrapod is not possible.

Stimson *et al.* (2012) examined a specimen of *Batrachichnus* alongside an articulated temnospondyl (*Dendrerpeton acadianum*) from Joggins, Nova Scotia, assuming the body morphometrics of the trace maker are similar for Carboniferous terrestrial temnospondyls. Baird (1952) measured the distance between successive manus and pes sets as a proxy for the relative trunk length of a quadrupedal tetrapod (the glenoacetabular distance — i.e. the horizontal distance between the glenoid cavity and the acetabulum). Stimson *et al.* (2012) used this convention to compare the glenoacetabular distance (GAD) of their trackways to the known morphometrics described from an articulated *Dendrerpeton* skeleton described by Holmes *et al.* (1998). With a known GAD, comparable on both trackways and skeletal remains, Stimson *et al.* (2012) realized that all other known measurements from the articulated skeleton

could be scaled as a percent of the GAD to determine the total body length of a temnospondyl amphibian. This model assumed similar body form and no ontogenetic variability. They concluded that the presacral vertebra measured a length of 121.53% of the GAD. The skull length, measured from the premaxilla to the first vertebra, was 65.28% of the GAD, and the caudal vertebra length was 38.89% of the GAD. Applying this formula and a measured GAD of 48.52 mm, the trace maker of specimen NBMG 3044 had a skull length of 31.67 mm, a presacral vertebral column length of 58.97 mm, and a caudal vertebral column length of 18.87 mm. This tetrapod thus has a total estimated body length of 109.55 mm (10.955 cm; Fig. 10A). Applying the same formula and a measured GAD of 50.28 mm, specimen NBMG 3047 has a skull length of 32.82 mm, presacral vertebral column length of 61.11 mm and a caudal vertebral column length of 19.55 mm. This tetrapod thus had an estimated total body length of 113.48 mm (11.35 cm; Fig. 10B). Sarjeant and Stringer (1978) considered that the GAD cannot be calculated based on their interpretation of the manus and pes sets, though this is clearly not the case (see below). Sarjeant and Stringer also raised the valid point that a broad tail impression indicates a relatively long tail. Assuming that tail length is at least the same as trunk length, as is the case for many terrestrial tetrapods, the total estimated body length for the Lepreau Falls track makers could be adjusted to 139.16 mm and 144.21 mm, respectively.

The outward directed pes impressions of specimen NBMG 3047, peculiar for temnospondyls, is more commonly observed in the reptilian ichnogenera *Notalacerta* and *Cincosaurus* (Haubold *et al.* 2005). We consider specimens NBMG 3044 and NBMG 3047 to be gait variations of the same ichnotaxon, *Matthewichnus*. All footprint impressions in specimen NBMG 3044, a linear trace with a longer stride than NBMG 3047, are directed forward. Specimen NBMG 3047 has a shorter stride, broader outer width, and pes impressions directed outwards perpendicular to the trackway midline; these features are in association with a body impression whose formation involved a smoothing out of the textured sediment surface. We conclude that the track maker for specimen NBMG 3047 was moving slowly in a semi-resting motion similar to that shown in Fig. 11, whereas the track maker for specimen NBMG 3044 was in full locomotion, with no associated body drag for forward oriented impressions.

CONCLUSIONS

The Lepreau Falls strata have been re-dated on the basis of recent mapping from a Triassic to a Mississippian (Visean-Serpukhovian) age and assigned to the Mabou Group. This revised status prompted our re-study of the vertebrate ichnotaxa *Isocampe lepreauense* and *Rhynchosauroides*

cf. *R. franconicus*. The ichnogenus *Isocampe* is likely a nomen dubium based on poorly preserved material, as is *I. lepreauense*. The original description of the Lepreau tracks did not reflect the extensive extramorphological toe drags, resulting in a misinterpretation of the traces. The specimen previously designated as *Rhynchosauroides* cf. *R. franconicus* was originally thought to have been produced by two or more tetrapods, but we interpret it as having been generated by a single track maker. Despite the digitigrade extramorphological preservation, both specimens have enough characteristics to ascribe them to gait variations of a single ichnogenus that, because of poor preservation, we tentatively assign to *Matthewichnus*. The trackways were previously attributed to reptiles, but based on the tetradactyl manus, we interpret them as having been produced by temnospondyl amphibians with a total body length of at least 113.48 mm and 114.21 mm respectively.

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