



A *Batrachichnus salamandroides* trackway from the Minto Formation of central New Brunswick, Canada: Implications for alternative tracemaker interpretations

Traces de *Batrachichnus salamandroides* de la Formation de Minto dans le centre du Nouveau-Brunswick, Canada : répercussions sur les interprétations au sujet de producteurs de traces de rechange

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Article abstract

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A *Batrachichnus salamandroides* trackway from the Minto Formation of central New Brunswick, Canada: implications for alternative tracemaker interpretations

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ABSTRACT

A new specimen of *Batrachichnus salamandroides* was recovered from a recently discovered fossil-bearing site situated along the southern shore of Grand Lake, New Brunswick, among a diverse ichnofaunal assemblage from the Middle Pennsylvanian (upper Bolsovian; lower Moscovian), upper Minto Formation. The identity of the tracemaker of this ichnogenus is reinterpreted as a composite of various late Paleozoic tetrapod taxa, based on similarities of the postcranial skeletons, notably that of the manus and pes, of both temnospondyls and some “microsaurs”. These results indicate that the tracemaker of the monospecific ichnogenus *Batrachichnus* is not limited solely to a temnospondyl tracemaker, as previously interpreted, and that some “microsaurs” should also be considered among tracemaker candidates for this ichnotaxon.

RÉSUMÉ

Un nouveau spécimen de *Batrachichnus salamandroides* a été récupéré d'un emplacement fossilifère récemment découvert le long de la rive méridionale du Grand Lac, Nouveau-Brunswick, parmi un assemblage ichnofaunique diversifié remontant au Pennsylvanien moyen (Bolsovien supérieur, Moscovien inférieur) de la partie supérieure de la Formation de Minto. On a réinterprété l'identité de l'auteur des traces de cet ichnogène y voyant un composite de divers taxons tétrapodes du Paléozoïque tardif d'après des similarités des squelettes postcrâniens, notamment ceux des paumes et des pieds, des deux temnospondyles et de certains « microsauriens ». Ces résultats révèlent que l'auteur des traces de l'ichnogène monospécifique *Batrachichnus* ne se limite pas seulement à un producteur de traces temnospondyle, comme l'avaient supposé des interprétations antérieures, et que certains « microsauriens » devraient également être considérés parmi les producteurs de traces possibles de cet ichnotaxon.

[Traduit par la rédaction]

INTRODUCTION

The Maritimes Basin of Atlantic Canada has yielded the most complete record of Carboniferous fossil tetrapod footprints in the world (Lucas *et al.* 2005, 2022), spanning the

interval from the earliest Mississippian (Tournaisian) of Nova Scotia and New Brunswick to the early Permian (Artinskian) strata of Prince Edward Island (Lucas *et al.* 2022; Figs. 1 and 2). However, the occurrence of “middle” Carboniferous (late Bashkirian to early Moscovian) terrestrial

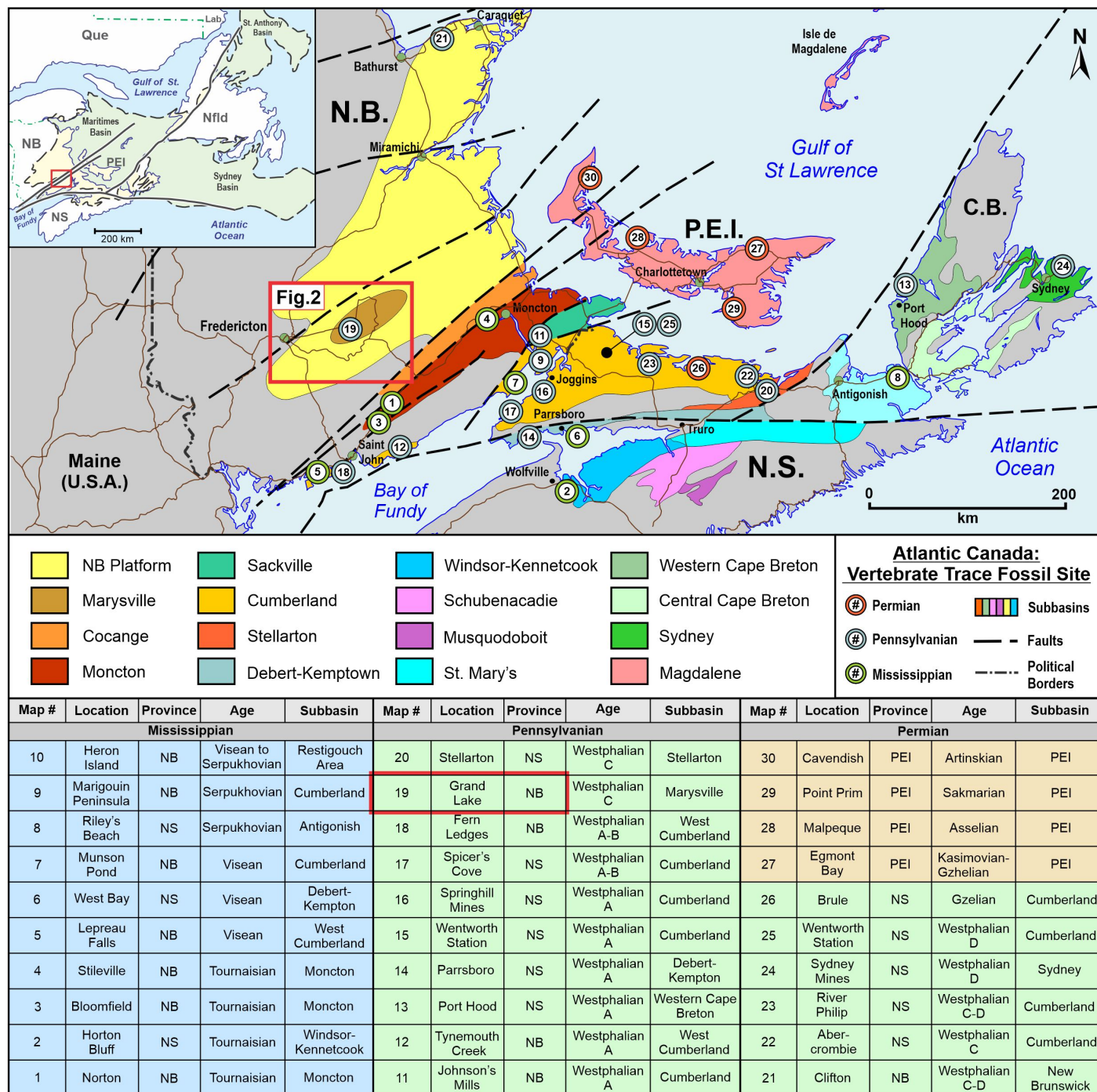


Figure 1. Map of the Atlantic Provinces of Canada and adjacent areas showing the extent of the latest Devonian to earliest Permian Maritimes Basin (after St. Peter and Johnson 2009; Gibling *et al.* 2019; and Bethoux *et al.* 2021). Subbasins are colour-coded as indicated in the upper legend. Fossil sites are numbered as indicated in the lower legend. In the lower legend, blue = Mississippian (1–10), green = Pennsylvanian (11–26), and pink = Permian (27–30); NB = New Brunswick, NS = Nova Scotia, and PEI = Prince Edward Island. Inset map shows broader geographic context.

ichnofossil localities in Atlantic Canada was unknown prior to the present study. Previously documented records of tetrapod tracks from the Bashkirian of the Maritimes Basin are from: the Joggins Formation in Nova Scotia (Dawson 1863; Matthew 1903, 1904; Sternberg 1933; Sarjeant and Mossman 1978; Lucas *et al.* 2005; Cotton *et al.* 1995; Stimson *et al.*

et al. 2012; Stimson *et al.* 2015; Prescott *et al.* 2014); the Tynemouth Creek Formation of New Brunswick (Falcon-Lang *et al.* 2010); the Lancaster Formation at Fern Ledges, Saint John, New Brunswick (Matthew 1910; Falcon-Lang and Miller 2007; Stimson *et al.* 2016a); and the Grand Anse Formation at Johnstons Mills, New Brunswick (Falcon-Lang *et al.*

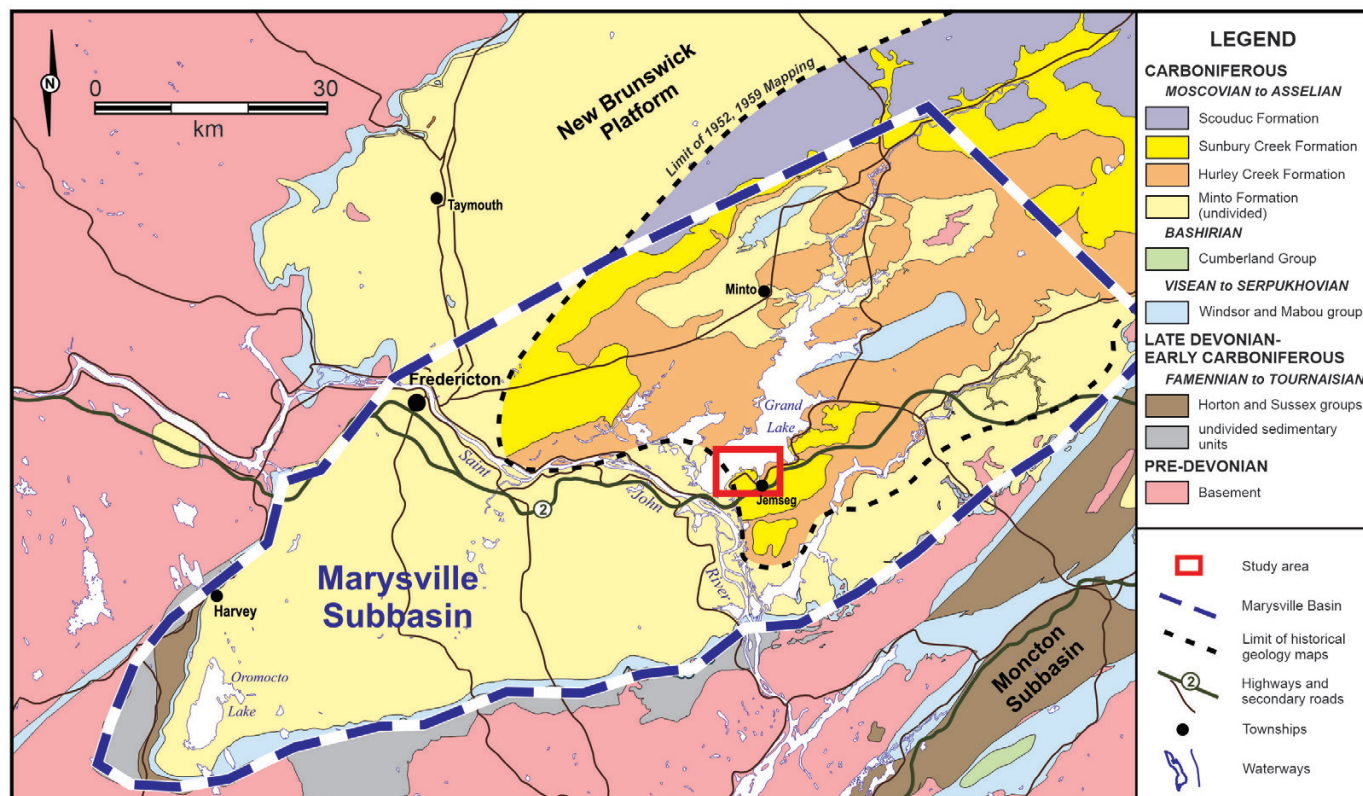


Figure 2. Geological map of part of the Maritimes Basin known as the Marysville Subbasin. (after Dyer 1926; Muller 1951, Hamilton 1960, 1962a, b, c; van de Poll *et al.* 1995). Study area outlined with a red box.

al. 2007). Tracks from Moscovian–Kasimovian strata have been found in the Clifton Formation of New Brunswick (Keough *et al.* 2020) and the Sydney Mines Formation of Cape Breton Island, Nova Scotia (Matthew 1903; Fig. 3).

Previous paleontological work on the Minto Formation is restricted to paleofloral assemblages documented by Bell (1962). A single trigonotarbid invertebrate body fossil (Miller and Forbes 2001) and a diverse faunal assemblage of aquatic vertebrates, which included undescribed tetrapod skeletal remains (Ó Gogáin *et al.* 2016), represent the only known evidence of terrestrial biota from the Minto Formation of central New Brunswick. Prior to the present study, ichnofossils had not been documented from the Minto Formation.

The absence of upper Bashkirian to lower Moscovian terrestrial tetrapod material represents an apparent gap in the fossil record of Atlantic Canada as, in contrast to other regions in North America (i.e., Mazon Creek, Illinois, and Five Points and Linton, Ohio; Fig. 3). This gap is due to poor surface exposure of strata from that time interval available for study. In addition, a major turnover in ecological conditions has been postulated during the Kasimovian, when the classic tropical ecosystems that made up the iconic image of “Coal-Age” ecosystems collapsed as a result of the formation of Pangea (Sahney *et al.* 2010; Pardo *et al.* 2019). Dunne *et al.* (2018) also suggested that the “Coal Age” collapse was likely more of a gradual transition. Taking into consideration the extensive Mississippian to Pennsylvanian rocks throughout

New Brunswick, the lack of fossil tetrapod localities is surprising when comparison to the situation in neighbouring Nova Scotia. However, a newly discovered fossil tetrapod footprint assemblage from the Minto Formation represents a high-diversity population comprising several ichnotaxa interpreted to be of both reptilian and amphibian affinity. This material occurs alongside various invertebrate ichnotaxa and a classic Pennsylvanian flora, and can be used as a proxy for biodiversity. The Minto assemblage is preserved within a mudstone interval on the flanks of an incised channel body backfilled with sandstone and conglomerate, and is interpreted as the floodplain interdistributary deposits of the broader New Brunswick Platform fluvial sedimentary depositional setting (Kalkreuth *et al.* 2000; St. Peter and Johnston 2009). Furthermore, this site offers a hitherto unavailable window into Middle Pennsylvanian paleoecology and aids in providing a more comprehensive understanding of the Carboniferous evolution of Atlantic Canada. However, we plan to discuss the full extent of this assemblage in future work. Here, we present and evaluate a tetrapod trackway of the ichnospecies *Batrachichnus salamandroides* (collected by RN and LA). This discovery offers new insights into tracemaker candidates for the ichnotaxon, expanding the traditional interpretation of a temnospondyl tracemaker to encompass particular “microsaur” tetrapod genera. (“Microsaurs” are further discussed below.)

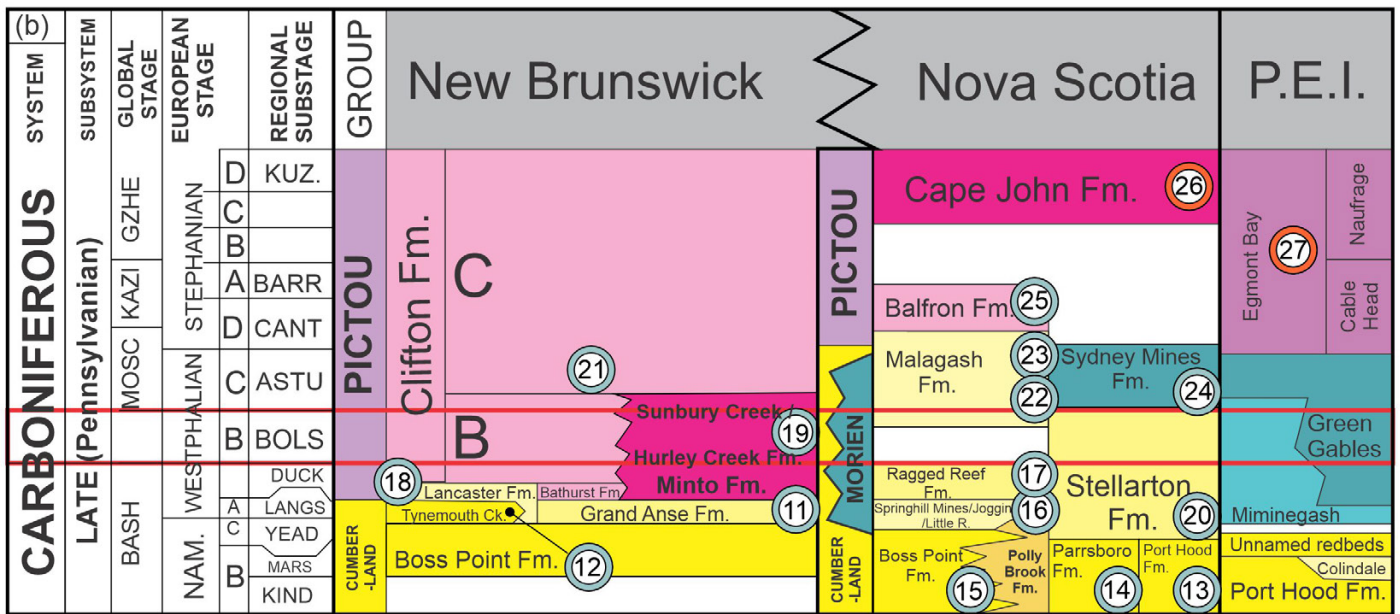
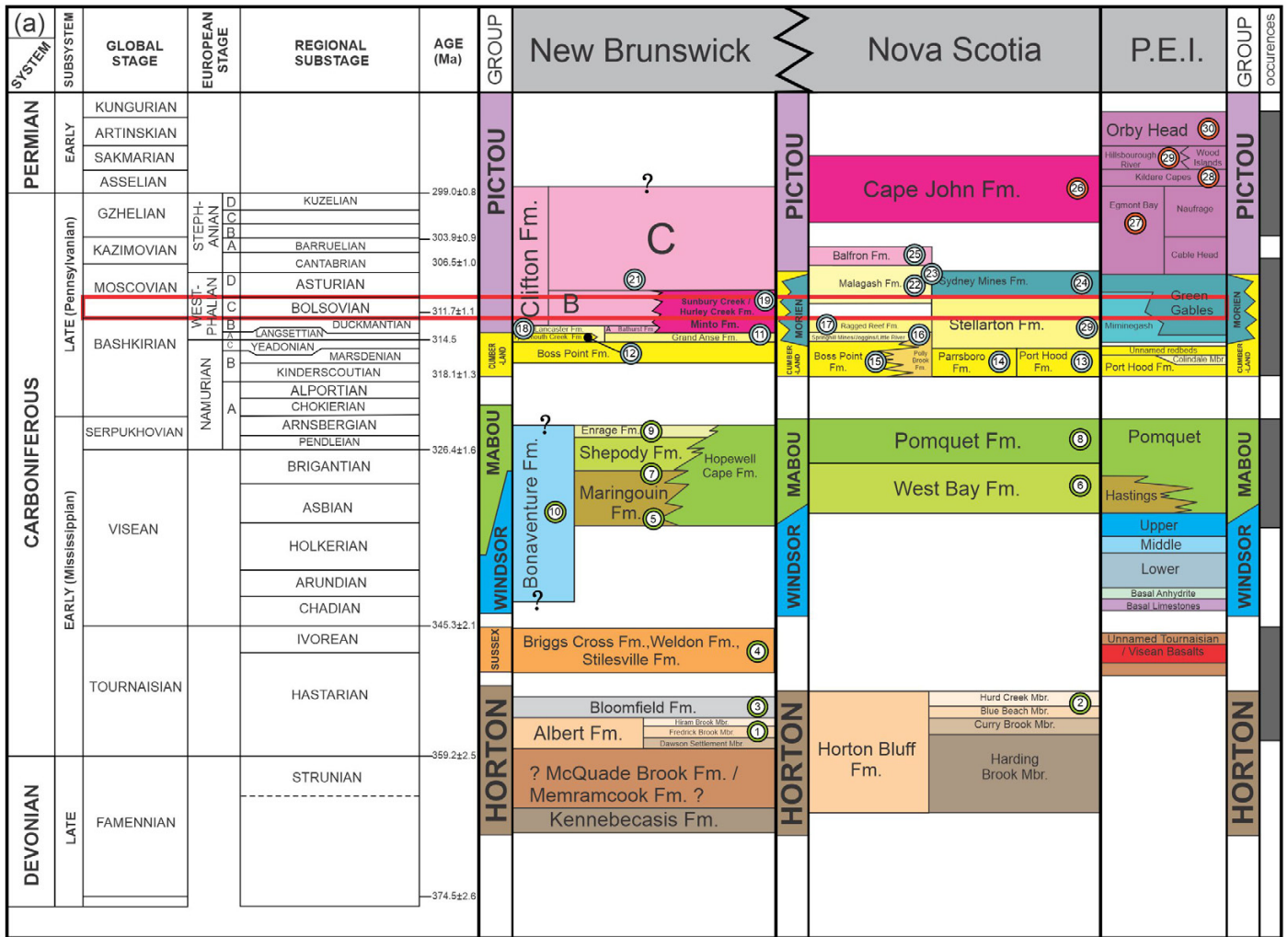


Figure 3. (a) Maritimes Basin stratigraphy for New Brunswick, Nova Scotia, and Prince Edward Island with the known Carboniferous-Permian tetrapod tracks plotted; for key to numbers see Fig. 1. Red box indicates the approximate stratigraphic horizon of the Minto Formation tetrapod tracks (NBMG 21591). After Lucas *et al.* (2022). (b) Detail of Cumberland and Pictou Group stratigraphy.

GEOLOGICAL BACKGROUND

In New Brunswick, Devonian–Carboniferous strata are deposited within a triangular region that covers roughly 25 900 km² within the approximate 250 000 km² area of the Maritimes Basin (Ball *et al.* 1981; St. Peter and Johnston 2009; Lavoie *et al.* 2009; Williams 1974; Dietrich *et al.* 2011; Gibling *et al.* 2019; Fig. 1). Of the seven lithostratigraphic groups within the New Brunswick portion of the Maritimes Basin, only the Pictou Group (Middle Pennsylvanian to early Permian strata) will be discussed (Fig. 3). Traditionally in New Brunswick the Pictou Group has included strata as old as the Pennsylvanian Bolsovian (early Moscovian) stage, which sit conformably above the underlying Cumberland Group, or unconformably on crystalline basement rocks or older Mississippian sedimentary rocks. More recently, Jutras *et al.* (2007) reassigned the formations of the Pictou Group in central New Brunswick to the Cumberland Group. Bethoux *et al.* (2021) used the traditional stratigraphic classification — i.e., the Pictou Group (Bell 1944; Dyer 1926; Muller 1951; St. Peter 2000) — an approach we follow here pending further study. The Minto Formation sits at the base of the Pictou Group within the New Brunswick Platform (Dyer 1926; Muller 1951). Muller (1951) reassigned the Grand Lake Formation of Dyer (1926) to the Pictou Group of Bell (1944) and upgraded the Minto, Hurley Creek and Sunbury Creek members to formation status (Fig. 3).

Using the traditional stratigraphic nomenclature, the Minto Formation is defined as a 200–230-m-thick section of grey to reddish-brown and locally maroon strata exposed in central New Brunswick (Dyer 1926; Muller 1951). Conformably above the Minto Formation is the Hurley Creek Formation, defined as a 45–60-m-thick stratigraphic package containing abundant redbeds that coarsen upwards as a whole. Lithologies consist dominantly of red and grey mudstones with fine-grained sandstones in the lower strata and red (locally green–grey), coarse feldspathic and lithic sandstones with polymictic conglomerates in the upper strata (Muller 1951). Muller (1951) estimated the overlying Sunbury Creek Formation to have a maximum thickness of approximately 90 m and is lithologically similar to the basal Minto Formation, but is stratigraphically younger than the Minto and the Hurley Creek formations. The interpreted similarity of the Minto and Sunbury formations led St. Peter (1997a, b) to informally incorporate the Sunbury Creek into the Minto Formation and downgrade the Hurley Creek Formation to member status. The member status of the three subdivisions of the Minto Formation is currently being revised and will be the subject of a future publication by some of the present authors. The stratigraphic descriptions of Muller (1951) were recently used by Bethoux *et al.* (2021), and will be followed here as the fossil reported in this study was discovered from the same fossil locality.

Robertson Point locality

The footprint locality discussed here is situated at Rob-

ertson Point along the southern shoreline of Grand Lake, Queens County, central New Brunswick (~45°52'11.64" N, ~66°05'37.40" W; Figs. 1 and 2, 4a–c). The outcrop extends 860 m along the southern shore of Grand Lake (between 45°52'7.77" N, 66° 5'46.03" W and 45°52'12.88" N, 66° 5'7.65" W), where a total of 18 m of strata are exposed. These strata have a strike of 150° and a shallow dip of 5° to the southwest. They are subdivided into two distinct sedimentary units: a lower 6.5-m-thick redbed unit interpreted below as belonging to the Hurley Creek Formation and an upper 11.5-m-thick unit composed dominantly of grey to red shales and buff-coloured sandstones that are interpreted below as belonging to the basal Sunbury Creek Formation. The contact between these two formations at this locality is erosive, with the basal deposits of the Sunbury Creek Formation (exposed along the shoreline for roughly 500 m) filling eroded hollows cut in the underlying Hurley Creek Formation. The basal Sunbury Creek Formation at the fossil locality is composed of coarse pebble conglomerates that form a wave-cut platform and, locally, raised sandstone platforms (Figs. 4 and 5, unit 2).

The fossil locality is thus in a shoreline section composed of resistant sandstone headlands and actively eroding embayments of mudstone and shale. Recent erosion of the shale units within coves adjacent to the sandstone headlands has exposed the three-dimensional nature of the channel body and the paleo-erosional cut banks at the channel margin. The outcrop exhibits the channel incision into the shales completely, demonstrating that the shales and resistant sandstone that comprise the headlands are lateral equivalents (Fig. 4c). This observation suggests that the shales represent the interdistributary zone of a fluvial channel system, whereas the incised sandstones and conglomerates may be interpreted as the backfilled channel thalweg of the distributary system. The *Batrachichnus* trackway (NBMG 21591) described below is preserved in the interdistributary shales.

Sedimentology

The sedimentology of the Robertson Point site was first described by Bethoux *et al.* (2021). The lower redbed unit, which they assigned to the Hurley Creek Formation, consists of ~6.5 m of maroon to buff-coloured, fine-grained sandstones; the sediments were deposited in backfilled channel thalwegs locally incised by, or lateral to, red to maroon mudstones and siltstones that represent interdistributary floodplain deposits with localized paleosols. Macrofloral elements of *Cordaites principalis*, *Calamites* sp. and cf. *Pecopteris* suggest a Pennsylvanian age, which is consistent with determinations from the Hurley Creek Formation fossils (Muller 1951).

Bethoux *et al.* (2021) assigned the overlying 11.5 m of grey to buff-coloured strata to the Sunbury Creek Formation of Muller (1951). This formation includes a basal ~6 m thick extraformational polymictic conglomeratic unit has localized coarse sandstone lenses at the base (Figs. 4 and 5, unit 1). The conglomerates locally incise up to 2 m into

the underlying redbeds of the Hurley Creek Formation. The basal conglomerates of the Sunbury Creek Formation are overlain by 2.5 m of buff-coloured, coarse to very fine-grained sandstones that locally exhibit trough cross-beds and form sheet sandstone beds (Figs. 4 and 5, unit 2). This sandstone, the basal portion of which locally contains reworked pebbles derived from the conglomerate underneath, locally incises the underlying conglomerate unit a depth of to 2.5 m. A specimen of a new genus of odonate wing (Bethoux *et al.* 2021) was described from the upper part (~9 m above the base of the measured section) of these incising sandstone strata; it occurred with transported plant stems and constituted the first fossils documented from the Sunbury Creek Formation. The top of unit 2 is 13.5 m above the base of the measured section at Robertson Point. The upper 2 m of unit 2 (Fig. 4) comprise heterolithic strata that locally incise the strata below. These heterolithic sedimentary beds are composed of thinly bedded siltstone and mudstones and very-fine trough cross-bedded sandstones.

A fossil-rich unit is located between 12.0 and 15.0 m above the base of the measured section (at 45°52'11.68"N, 66° 5'37.45"W; Figs. 4 and 5, unit 3). This unit is a 3 m thick section of light to medium grey fine-grained siltstone that laterally grades to a maroon colour. This unit contains abundant well-preserved plant fossils (i.e., transported and in situ *Calamites*, cf. *Sphenopteris*, and *Cordaites principalis*); abundant vertebrate and invertebrate ichnofossils; and a yet-undescribed forewing of a stem-relative of cockroaches and mantids (family Archimylacridae according to J. Schneider, personal communication to MS 2021). The unit varies locally from coarser siltstones at the base to claystone with centimetre scale bedding in the middle; both variations contain tetrapod and invertebrate ichnofossils, including the trackway described in this paper.

The fossil-bearing shales (Figs. 4 and 5, unit 3) are incised 2 m by a 6.5 m thick channel body composed of buff to grey extraformational polymictic conglomerates and coarse-grained sandstones (Figs. 4 and 5, unit 4). These channel bodies preserve abundant carbonized plant axes, likely of pteridosperm and cordaitalean affinities (Figs. 4 and 5, unit 4). The uppermost sandstone strata of unit 4 is locally incised by a 1.5-m-thick, mud-filled channel that is backfilled with maroon-coloured mudstone with very fine sandstone lenses 5–10 cm thick (Figs. 4 and 5, unit 5).

Age

The Minto Formation (lower Minto Formation of St. Peter 2000) is assigned a latest Bashkirian age, whereas the overlying Hurley Creek Formation (middle Minto Formation of St. Peter 2000) straddles the Bashkirian–Moscovian boundary. The overlying Sunbury Creek Formation (upper Minto

Formation of St. Peter 2000) has been considered Bolsovian (late Bashkirian to early Moscovian; St. Peter and Johnson 2009). With the lack of volcanic rocks or ash beds throughout these formations, ages were determined through palynological analysis. Palynomorph assemblages were analyzed by Hacquebard (1972) and Hacquebard and Barss (1970), who determined that the Minto Formation is within the *Vestispora* Palynomorph Zone — of Bolsovian age (late Bashkirian to early Moscovian). This assignment corroborated the paleobotanical age assignment of Bell (1962), whose work was focused on the coal resources of the lower Minto Formation, stratigraphically below the Hurley Creek and Sunbury Creek formations as used in this study.

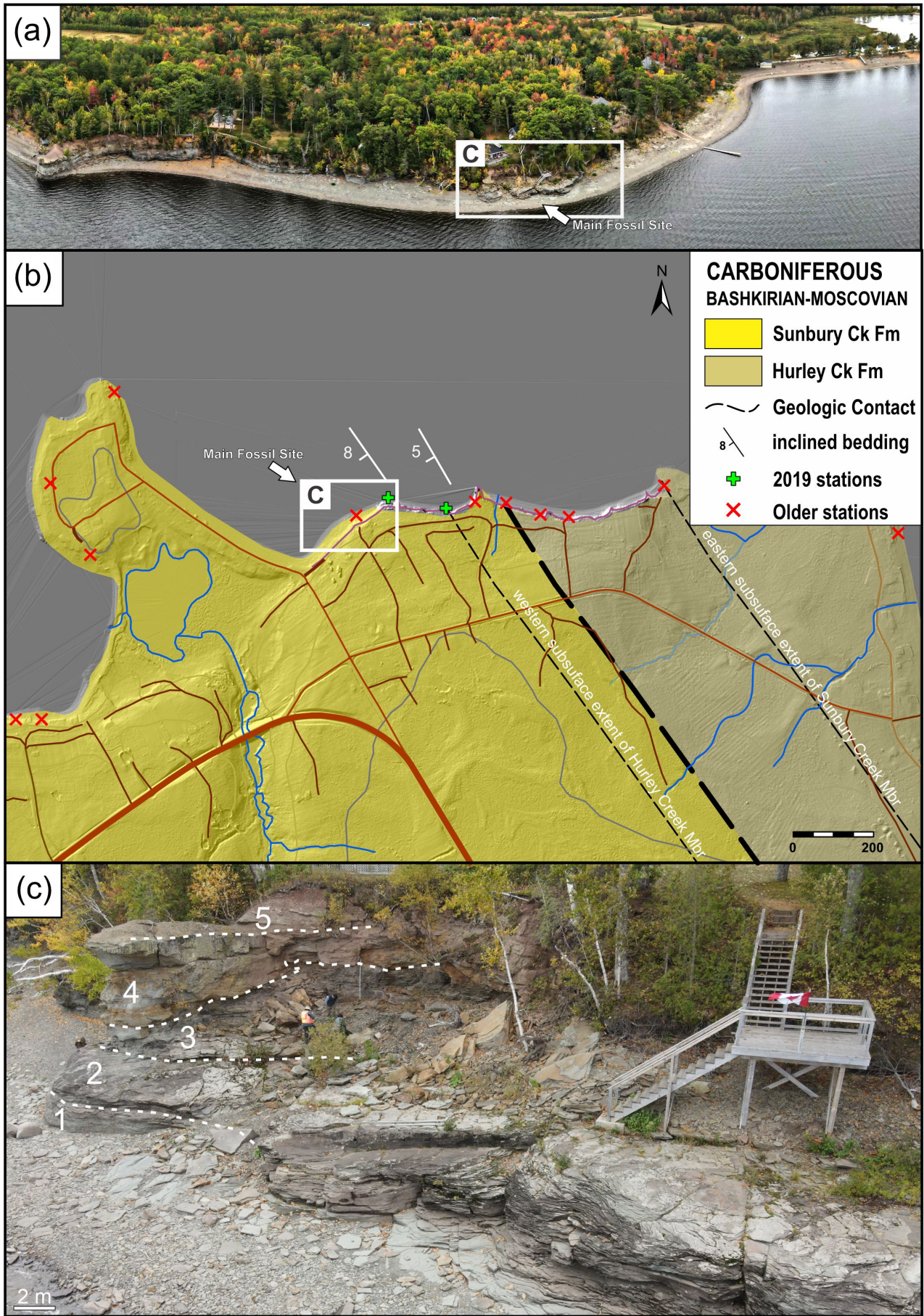
More recently, samples of grey shale from the present study site (13.5 m above the base of the measured section) were processed for palynology. The results, as reported in Bethoux *et al.* (2021), showed that the palynomorph assemblage at Robertson Point belonged to the *Torispora* Biozone (Bethoux *et al.* 2021). The Bolsovian stage of the Pennsylvanian (latest Bashkirian and early Moscovian) is divided into two palynomorph biozones: the older (late Bashkirian) *Vestispora* Biozone and the younger (early Moscovian) *Torispora* Biozone. The miospore assemblage is dominated by *Calamospora* spp. with subdominant *Florinites pumicosus* and *Punctatisporites* spp. This age determination is based on the presence of the palynomorphs *Vestispora fenestrata* and ? *Thymospora pseudothiessenii*. The Robertson Point outcrop is thus considered to be of earliest Moscovian age (i.e., early Westphalian C), which conforms with the youngest determination of Hacquebard (1972) and Hacquebard and Barss (1970), agreeing with the relative stratigraphic position of the Sunbury Creek Formation of Muller (1951).

METHODS

The Robertson Point fossil site was documented using both standard digital photography and drone imaging. Three drones with 40 megapixel cameras were used to document the fossil site from high altitudes and beyond the water's edge, locations that would otherwise be inaccessible. The cliffs were photographed at various elevations to capture the 3D details of the broader shoreline as well as close-up images of the fossil site using a 48 megapixel camera mounted on a Mavic Air 2 Drone (Fig. 4a). The local stratigraphy was logged by hand at centimetre scale using metre sticks and later drafted digitally using CorelDraw 2019.

The trackway specimen (NBMG 21591) under discussion was coated in ammonium chloride at Saint Mary's University, Halifax, to accentuate the vertical relief of the footprints during specimen photography. Low-angled illumination from 6000 lumen work lamps were used to cast shadows and

Figure 4. (next page) Fossil site on Grand Lake, NB. (a) Aerial drone images of the fossil site. (b) Geological map plotted against LIDAR images for Robertson Point. (c) Aerial Drone images of the fossil site, where numbers correspond to the different sedimentary units plotted on Figure 5.



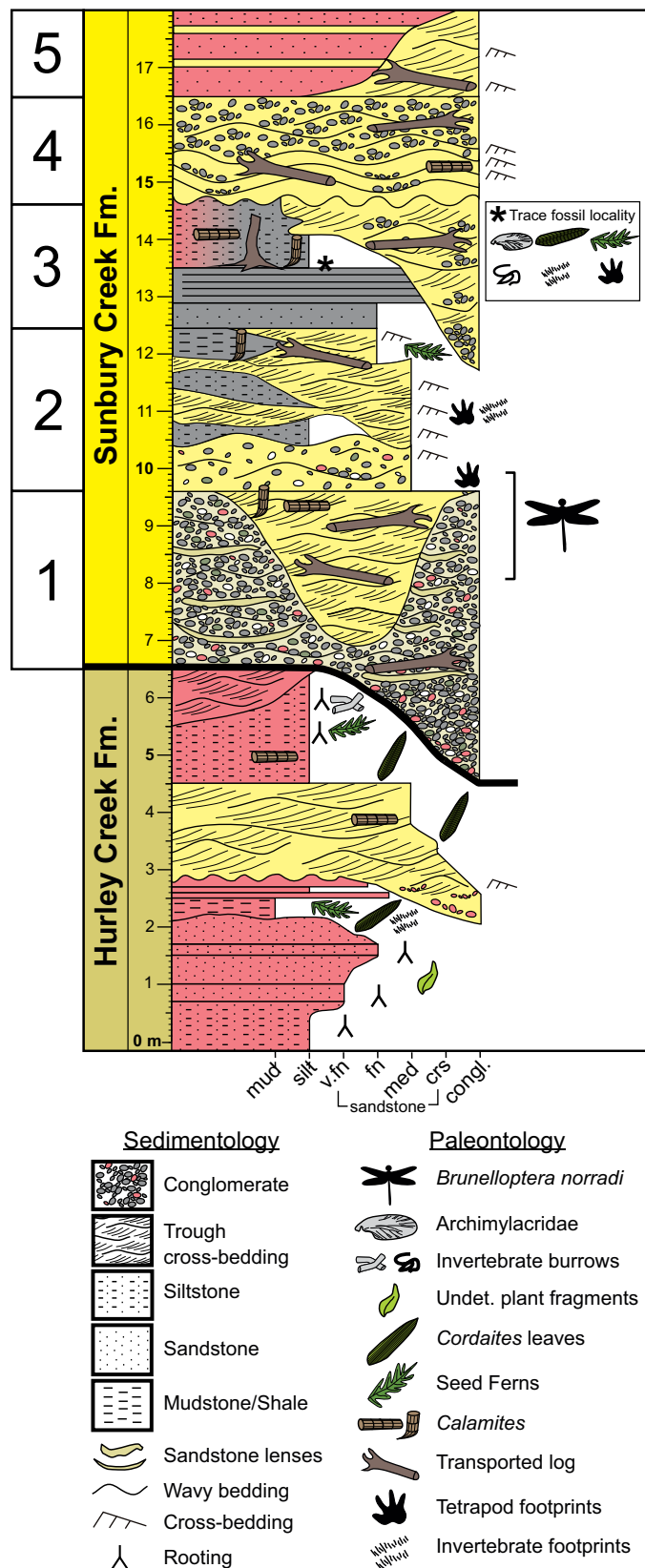


Figure 5. Stratigraphic log of the Hurley Creek and Sunbury Creek formations exposed at Robertson Point, New Brunswick.

highlight the footprint morphology (Teichert 1948; Grabau and Shimer 1910; Ulrich and Bassler 1923; Stimson *et al.* 2012; Stimson *et al.* 2016a, b). False colour topographic relief maps of the trackway were generated by photographing the specimen in a tiled pattern with the same zoom factor and 50–80% overlap. Images were then rendered as a 3D photogrammetry model using the digital software Agisoft PhotoScan. The digital model was subsequently modified into a false colour relief map using the digital software packages of Metlab, Cloud Compare, and Paraview. The digital software program ImageJ was used to record morphometric data of the footprints, which were then verified using digital vernier calipers. Standard vertebrate ichnotaxonomy measurements were collected following the work of Leonardi (1987), Stimson *et al.* (2012), and Marchetti *et al.* (2020). The footprint impressions are considered underprints, yet they express the most distal impressions of the digits and sole impressions. The morphological quality of the footprints was evaluated based on Marchetti *et al.*'s (2019) numerical preservation scale. Measurements were taken using the most distal and proximal expressions of the tracks, eliminating extramorphological distortion where appropriate.

Figures were drafted using digital drafting and photo editing software (e.g., CorelDRAW). This specimen of *Batrachichnus salamandroides* has been accessioned into the New Brunswick Museum Geology/Paleontology Collection under the specimen number NBMG 21591.

Previous published literature was extensively consulted for vertebrate comparative anatomy. Manus and pes reconstructions, as well as skeletal reconstructions (Carroll 1967, 1968; Holmes *et al.* 1998; Carroll and Gaskill 1978; Mann *et al.* 2020), were used to obtain glenoacetabular distance measurements; published images of fossil specimens were also used where available. Following the work of Stimson *et al.* (2012, 2016b), skeletal reconstructions of temnospondyl and “microsauro” candidates were used as models to estimate the length of the potential cranial and postcranial skeletons of the tracemaker of NBMG 21591. Measurements of the skull (tip of the premaxilla to the base of the skull), presacral vertebral series (the cervical vertebrae to the base of the pelvic girdle), and caudal vertebral series of each tetrapod were recorded and calculated as percentages of the respective glenoacetabular distance (GAD). To maintain consistency, the caudal vertebral series is inferred to be roughly equal in length to the GAD.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Batrachichnus* (Woodworth 1900)

Ichnospecies *Batrachichnus salamandroides*
(Geinitz 1861)
(Figs. 6–7, 8a)

Referred Materials. NBMG 21591a and b.

Description. Specimen NBMG 21591 consists of a single tetrapod trackway associated with a single *Undichna* trail, and is preserved as part and counterpart on a dark grey, ~1 cm thick siltstone slab that measures 15 by 27 cm (concave epirelief) and 30 by 12 cm (convex hyporelief). The trackway consists of 13 shallow underprints preserved in concave epirelief with the counterpart preserving 12 prints in corresponding convex hyporelief. Manus and pes imprints are paired, resulting in an approximately evenly spaced trackway pattern. Minimal extramorphological distortion is present in the trackway with the exception of faint, shallow digit drags. Manus and pes sets are positioned approximately 2.65 cm apart, with the manus and pes oriented parallel to the midline, and the manus situated much more medially in relation to the trackway midline.

Manus prints are slightly wider than long with average measurements of 1.07 by 0.83 cm, width and length, respectively. Footprints are preserved as semi-digitigrade tracks with faint diminutive sole pads. The manus is tetradactyl. Digits increase in length from I–III with digit IV being subequal in length to digit II. The relative digit lengths of the manus are thus 1-2-3-2. Digits are evenly and well-spaced with digit I and IV diverging laterally in relation to the trackway midline. Digits I and IV exhibit greater curvature in their distal portions. Digits II and III display arcuate curvature in opposite directions to form a “pincer-like” morphology and are oriented approximately parallel to each other. Digits are long and appear elongated, with more deeply impressed rounded digit terminations likely associated with toe pads.

Pes imprints are wider than long, measuring 1.31 by 0.92 cm, length and width, respectively. Footprints are preserved as digitigrade tracks likely associated with undertrack preservation. Pes is pentadactyl with only the digit tips impressed. Digits increase in length from I–IV with digit V being subequal to digit II. The relative digit lengths of the pes are thus 1-2-3-4-2. Digits I–IV are evenly and closely spaced, and digit V is somewhat divergently spaced. Digit terminations appear rounded/blunt, with deeply impressed digits III and IV exhibiting terminal curvature.

The trackway extends in a semi-straight path until the part of the slab where a change in direction occurs, veering to the left on the original concave epirelief surface. Measurements taken from this section of trackway were not incorporated into the averages due to the alteration of the following values. The average external trackway width is 5.5 cm, decreasing to 4.7 cm during the turn. The average internal trackway width is 1.83 cm, decreasing to 1.29 cm on the turn. The average manus pace is 3.8 cm. The manus pace angulation averages 74.3°, increasing during the change in direction to 98.91°. The average pace for the pes measures 5.2 cm. Average pes pace angulation is 66.5°, increasing to 78.5° during the turn. The manus stride measures approximately 4.65 cm and increases to 5.98 cm during the change in direction. The average stride for the pes is 5.22 cm and increases during the change in direction to 6.45 cm.

Following the model of Baird (1952) and Stimson *et al.*

(2012, 2016b), the glenoacetabular distance (GAD) was measured to be 5.4 cm (Figs. 9a, b); however, given the spacing between the manus and pes impressions, this GAD measurement is equivocal. A second GAD interpretation is also possible if an elongated body form is considered, following Haubold (1971; fig. 4D). This longer body form would result in a longer GAD, which can be measured as 9.9 cm in length (Fig. 9c).

Remarks. The ichnotaxonomy of the ichnogenera *Batrachichnus* and *Anthichnium* was studied in detail by Voigt (2005). Voigt agreed with the observations made by Haubold *et al.* (1995) that the multiple ichnospecies of *Batrachichnus* and *Anthichnium* were morphologically similar, and that these ichnotaxa encompassed a wide range of morphological variability. Voigt (2005) synonymized several ichnotaxa under the new combination *Batrachichnus salamandroides*. *Batrachichnus* is common in the Pennsylvanian strata of Atlantic Canada (Stimson *et al.* 2012; Lucas *et al.* 2005; Lucas *et al.* 2022) and elsewhere (Lucas *et al.* 2022 and references therein). In Atlantic Canada, the stratigraphic range of *Batrachichnus* extends from the lowest Mississippian (lower Tournaisian age) strata of the Albert Formation in New Brunswick (Stimson *et al.* 2018; Stimson *et al.* 2019) and the Horton Bluff Formation in Nova Scotia (Mansky and Lucas 2013) to the lower Permian Cape John Formation at Brule, Nova Scotia.

Baird (1952) and Tucker and Smith (2004) recognized the morphological similarities and size continuum between *Batrachichnus* and *Limnopus*, the only difference being the size of the footprints. Tucker and Smith (2004) thus recognized the *Limnopus*–*Batrachichnus* spectrum with an ~2.1 cm pes length boundary to distinguish the two ichnogenera on dimensions (i.e., *Batrachichnus* pes length less than 2.1 cm, *Limnopus* greater). Some authors propose that *Batrachichnus* and *Limnopus* are ontogenetic variants (Haubold 2000; Tucker and Smith 2004; Stimson *et al.* 2012), the smaller *Batrachichnus* size suggesting that it was produced by juveniles. Haubold (1971, 1996, 2000), Fichter (1979), Voigt (2005), Stimson *et al.* (2012) and others assigned *Batrachichnus* to small temnospondyl tracemakers, and this interpretation has been widely accepted in the literature. However, some authors have also informally postulated and speculated that “microsaurs” were potential tracemakers of *Batrachichnus* (e.g., Stimson *et al.* 2012; Petti *et al.* 2014; Cisneros *et al.* 2020).

The Minto trackway exhibits several diagnostic characteristics of *Batrachichnus salamandroides*: (i) tetradactyl manus, pentadactyl pes; (ii) manus and pes wider than long; (iii) manus slightly smaller than pes; (iv) small size (pes length <35 mm); and (v) relative digit lengths (manus:1-2-3-2; pes:1-2-3-4-2). Following the parameters developed by Marchetti *et al.* (2019), the footprint preservational value of the Minto trackway is 2.0 (semi-optimal), permitting a confident assignment to the ichnogenus. The trackway pattern of NBMG 21591 differs from other trackways of *Batrachichnus* in its evenly spaced arrangement and

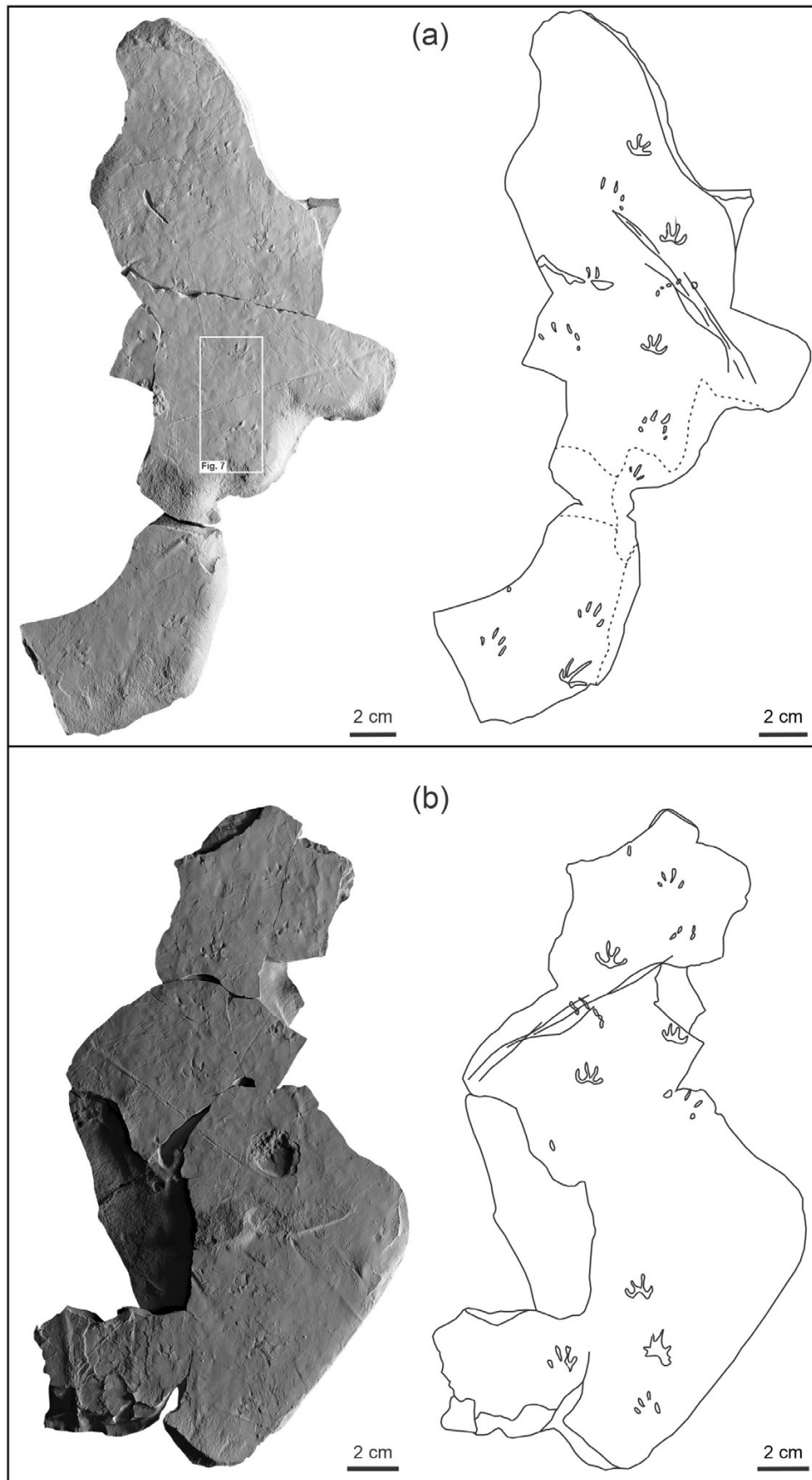


Figure 6. Trackway specimen NBMG 21591. (a) Photograph of NBMG 21591a (left) and interpretive sketch of the same (right). (b) Photograph of counter part of NBMG 21591b (left) and interpretive sketch of the same (right).

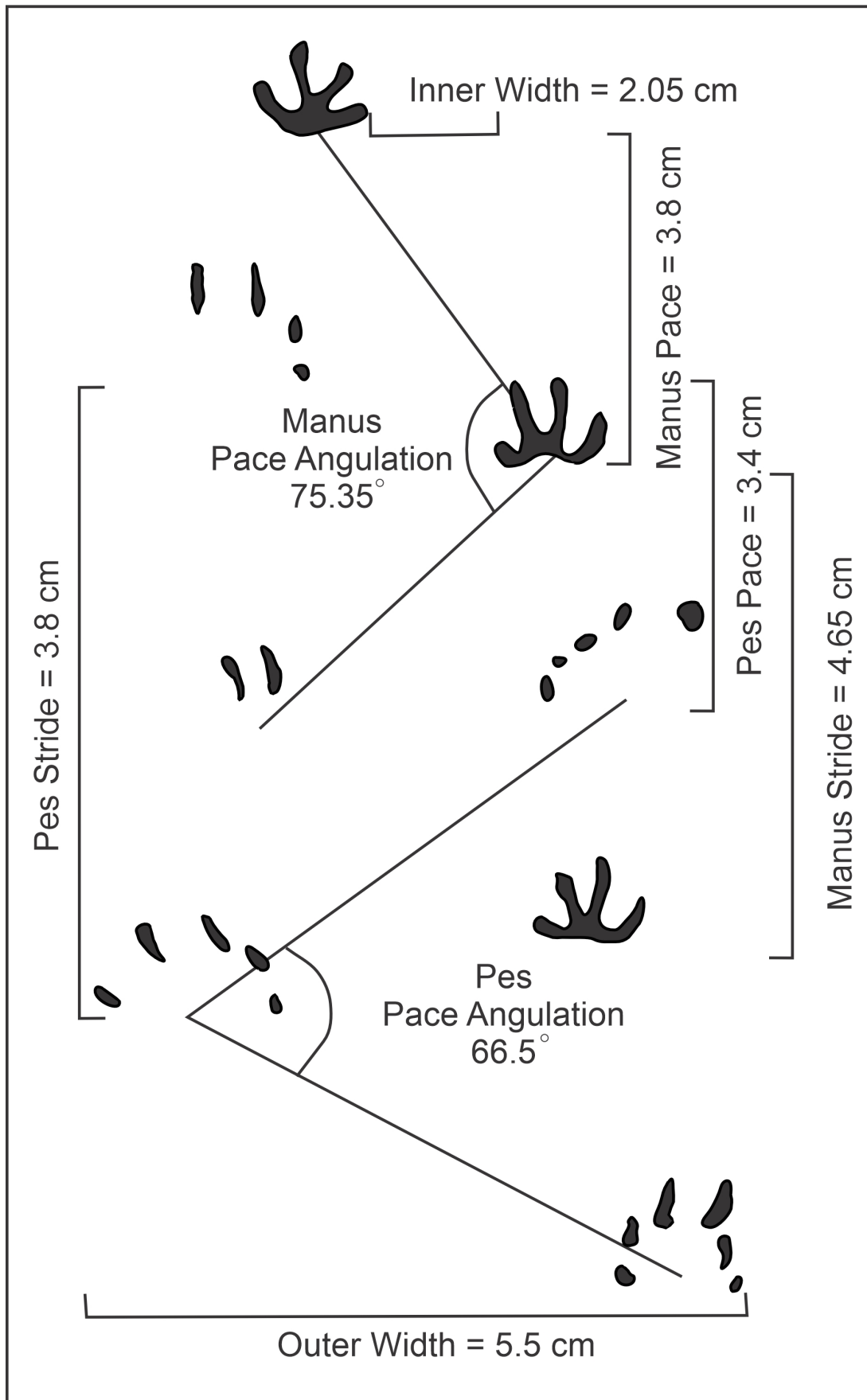


Figure 7. Interpretive sketch of NBMG 21591a with trackway measurements.

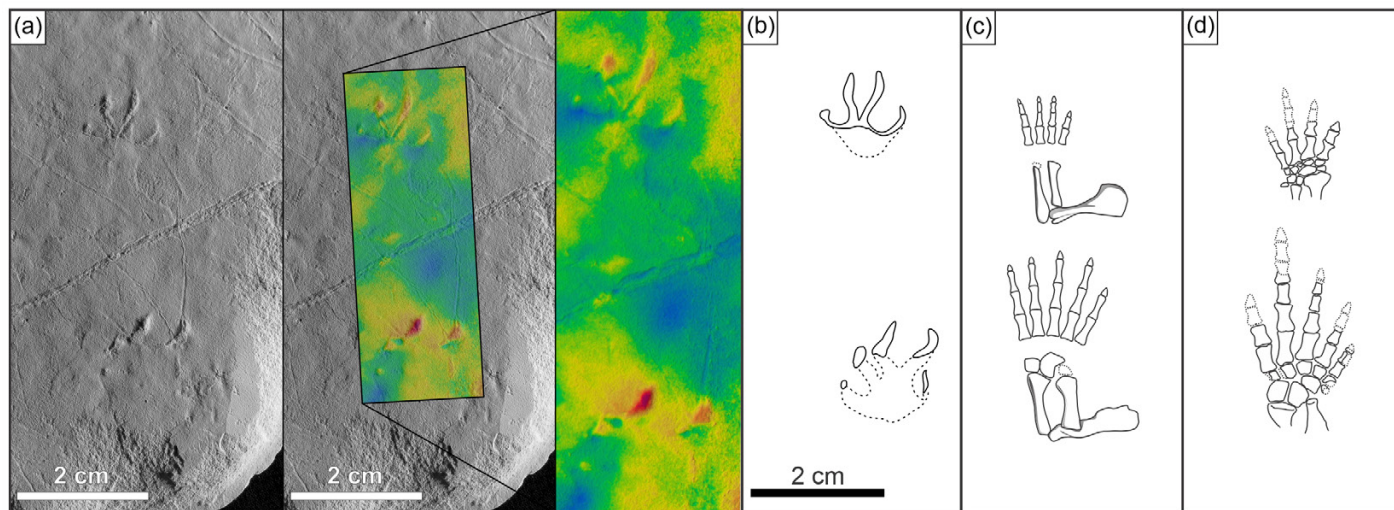


Figure 8. Details of best manus and pes set. (a) Photograph (left) and photogrammetry with false colour relief (middle and right); and (b) interpretive sketch of NBMG 21591a. (c and d) Comparisons with generic temnospondyl (c) and “microsaurian” (d) manus and pes based on reconstructions by Holmes *et al.* (1998) and Carroll (1968), respectively.

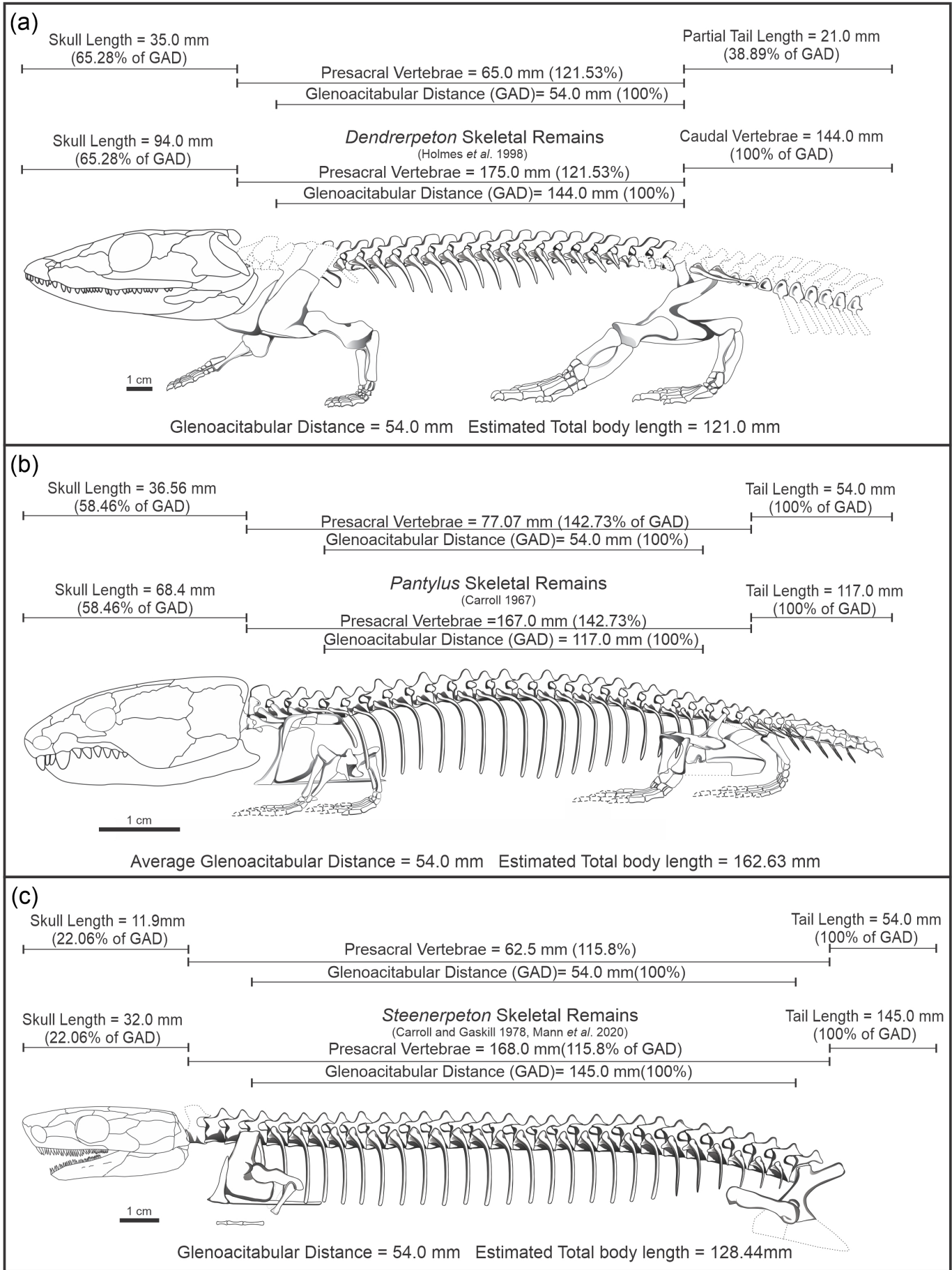
undefined manus–pes sets. The low pace angulation, long distance between manus and pes, short stride length, and wide trackway width are indicative of a slow-moving gait. Similar trackway patterns occur frequently in *Matthewichnus caudifur*, which have been attributed to more elongated tracemakers, most notably “microsaurs” (Kohl and Bryan 1994; Voigt and Lucas 2015). Furthermore, when experimenting with modern salamanders, Peabody (1959) noted that tracemaker size also affects trackway pattern. Taking a complementary approach to Kohl and Bryan (1994), we recognize two potential GAD measurements pertaining to both groups of Carboniferous tetrapods. Alongside temnospondyls, we therefore consider “microsaurs” as potential tracemakers of NBMG 21591 based on abnormal trackway parameters that are suggestive of an elongated bauplan commonly associated with “microsauria”.

Analysis of candidate tracemakers. No terrestrial vertebrates have yet been documented from New Brunswick, making it necessary to make interpretations from material found elsewhere in Atlantic Canada and other coeval localities in Euramerica. Traditionally, the ichnogenus *Batrachichnus salamandroides* was interpreted to have been produced by temnospondyl amphibians (Fichter 1979; Voigt 2005; Stimson *et al.* 2012). An articulated specimen of *Dendrerpeton* described from Joggins, Nova Scotia (Holmes *et al.* 1998), provides the only articulated temnospondyl skeleton found in the Pennsylvanian succession of Atlantic Canada (Fig.10a). Measurements extracted from this articulated

specimen of result in a GAD of 144 mm. The skull measures 94 mm in length (65.28% of the GAD), the presacral vertebral series measures 175 mm (121.53% of the GAD), the caudal vertebral series, though incomplete, is estimated as 144 mm (100% of the GAD), and the complete body length is thus estimated to be 413 mm (Fig.10a). The GAD of *Dendrerpeton* can subsequently be represented as 34.87% of the total body length. *Amphibamus grandiceps* from the early Moscovian of the Mazon Creek Lagerstätte (Bolt 1979; Mann and Gee 2019) and *Platyrrhinops lyelli* from Linton, Ohio (Clack and Milner 2009), are additional examples of the classic (short-bodied) temnospondyl bauplan. When the 54 mm GAD interpretation of trackway NBMG 21591 is implemented, a total tracemaker body length of 155 mm is estimated.

Though typically rare in comparison to temnospondyl amphibians, numerous disarticulated “microsaur” remains have been discovered from Nova Scotia. The famous Joggins Fossil Cliffs have yielded a diverse “microsaur” fauna within the interiors of hollow lycopsid trunks (Dawson 1894; Steen 1934; Carroll 1966; Carroll and Gaskill 1978). However, recent work (Mann *et al.* 2020) reduced the faunal list to only four accepted “microsaur” taxa: *Hylerpeton dawsoni* and *Leiocephalikon problematicum* (gymnarthrids), *Steenerpeton silvae* (ostodolepid or rhynchonkid), and *Trachystegos megalodon* (pantylid). All other “microsaur” material at Joggins represent either indeterminate tetrapods or have been reassigned to a different tetrapod lineages. A less diverse “microsaur” assemblage is found at the slightly

Figure 9. (next page) Quantitative comparison of skeletal proportions between the inferred measurements of NBMG 21591 (top measurements in each panel) with estimated glenoacetabular distances (GAD) plotted as temnospondyl (a) and “microsaur” (b and c) body morphologies. (a) Following a short-bodied temnospondyl (*Dendrerpeton* sp.) using an interpreted 54 mm GAD; (b) following a short-bodied “microsaur” (*Pantylus*) using an interpreted GAD of 54 mm; (c) following a longer-bodied “microsaur” (*Steenerpeton*) using a long interpreted GAD of 99 mm.



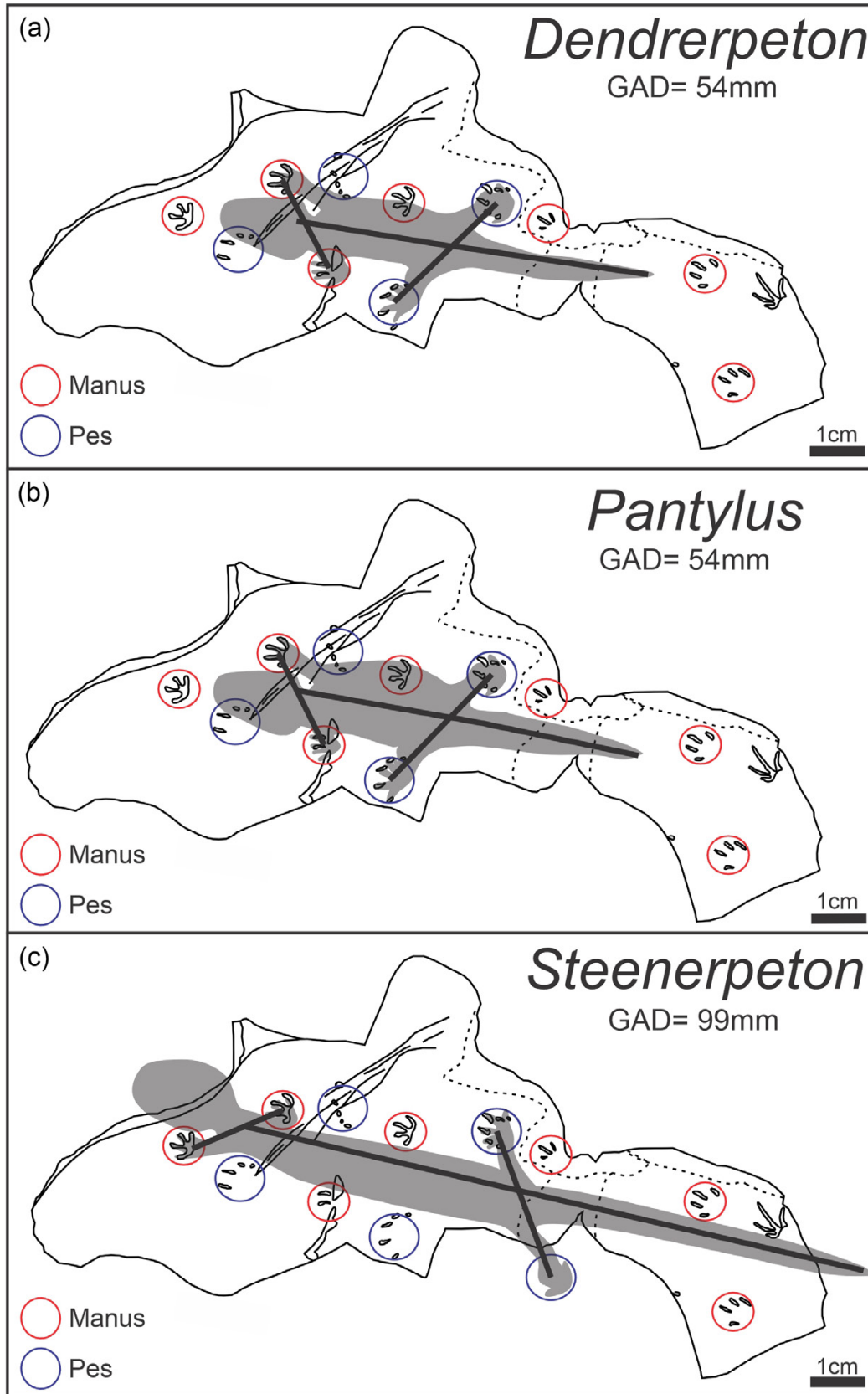


Figure 10. Skeletal measurements of a temnospondyl and select “microsaurs”, calculated as percentages of their respective GADs to estimate potential tracemaker body sizes. The short-bodied temnospondyl *Dendrerpeton* (a) using a GAD of 54 mm; (b) The short-bodied “microsaur” *Pantylus*, using an interpreted GAD of 54 mm; and (c) the elongated “microsaur” *Steenerpeton* using an interpreted GAD of 99 mm.

younger (late Moscovian) Florence locality in Nova Scotia (Carroll 1969; Reisz 1971). The rare taphonomy associated with the Joggins tree fauna is also observed at Florence, and involves the remains of temnospondyls (Rieppel 1980; Holmes *et al.* 1995), embolomeres (Klembara 1985), synapsids (Reisz 1971; Mann and Paterson 2020; Mann and Reisz 2020), a “protorothyridid” eureptile (Carroll 1969), and a “microsauro” (Carroll and Gaskill 1978) preserved within in-situ *Sigillaria* stumps. The only “microsauro” taxon recognized from this site is an unidentified gymnarthrid (Carroll and Gaskill 1978). Outside of Atlantic Canada, the Mazon Creek Lagerstätte in Illinois, USA, contains one of the most diverse “microsauro” assemblages of similar age to the Minto Formation (Moscovian). Diverse “microsauro” faunas from the Middle Pennsylvanian are present in the upper Moscovian deposits of Linton, Ohio, and Nyrany in the Czech Republic (Hook and Baird 1986, 1988; Carroll and Gaskill 1978). We do not regard “microsauros” occurring outside the Maritimes Basin as relevant tracemaker candidates for specimen NBMG 21591. However, the ichnological record reveals the presence of tetrapod taxa in the Minto Formation that are currently not known from the skeletal records, the latter being incomplete due to taphonomic factors (Lucas *et al.* 2022). Furthermore, no tetrapod remains have yet been discovered at Robertson Point, leaving candidates from these nearby assemblages open to consideration.

Based on their relative geographic proximity and stratigraphic position to the Minto Formation, pantylids (*Trachystegos megalodon*) and ostodolepids/rhynchonkids (*Steenerpeton silvae*) are possible “microsaurian” tracemakers for specimen NBMG 21591. Carroll (1968) observed a notable correlation between disarticulated remains of *Trachystegos* from Joggins and the postcranial skeleton of the Permian pantylid, *Pantylus*, from Texas. Based on the availability of skeletal reconstructions, for this study we use *Pantylus* as a skeletal archetype for short-bodied “microsauros”. Lesser-known, short-bodied “microsauros” include *Diablorotter bolti* (Mann and Maddin 2019) and *Batropetes* (Carroll 1991). *Pantylus* is described from the Wichita Group (lower Permian) of Texas and represents a fully terrestrial form with a short trunk length (24 presacral vertebrae) and robust fore- and hindlimbs (Carroll 1968; Carroll and Gaskill 1978). Measurements taken from the articulated skeletal reconstruction of *Pantylus* (Carroll 1968) provide a GAD of 117 mm. The skull measures 68.4 mm (59% of the GAD), the presacral vertebral series measures 167 mm (142% of the GAD), and the caudal vertebral series, though lacking several elements, is estimated as 117 mm (100% of the GAD). Assuming the reconstruction was correctly interpreted and to scale, the total body length of *Pantylus* is consequently 352.4 mm. The GAD can thus be represented as 33.2% of the total body length. By applying this GAD value to the potential trackway GAD of 54 mm, a total body length of the tracemaker of 162.65 mm is estimated (Fig. 10b).

Steenerpeton silvae is a newly recognized “microsauro” from the Joggins Fossil Cliffs described by Mann *et al.* (2020), following the re-examination of material previously assigned

to *Asaphestera intermedium* (Steen 1934; Carroll 1966). The fine-toothed recumbirostran was described as being possibly related to ostodolepids or rhynchonkids (Mann *et al.* 2020), and likely occupied a terrestrial to semi-terrestrial habitat (Carroll and Gaskill 1978). The limbs are relatively large and well-ossified; however, the body length is currently indeterminate due to inadequate preservation of the vertebral column. Following the approach of Carroll and Gaskill (1978), the presacral vertebral count of *Tudititanus* (29) is used to estimate that of *Steenerpeton silvae*. Although largely conjectural, this interpretation, supported by a mosaic of anatomical features shared between the two ‘tuditanimorphs’, reveals *Steenerpeton* to be of a more elongated body plan. Other examples of “microsauros” with semi-elongated bodies include *Joermungandr bolti* from Mazon Creek, Illinois (Mann *et al.* 2021), *Trihecaton howardinus* from the Late Pennsylvanian of Colorado (Vaughn 1972; Carroll and Gaskill 1978), and *Pelodosotis* from the lower Permian of Texas (Carroll and Gaskill 1978). The GAD of *Steenerpeton silvae* (Mann *et al.* 2020) is found to be 144 mm. The skull measures 44.1 mm (30.63% of the GAD), the presacral vertebral series, possessing 29 elements, measures 171 mm (118.8% of the GAD), and the caudal vertebral series, not included in the reconstruction due to the paucity of preserved elements, is estimated to be 144 mm (100% of the GAD). The GAD can thus be represented at 40.1% of the total body length of 359.1 mm (Fig. 10c). The formula was subsequently applied to the potential trackway of 99 mm resulting in a total tracemaker body length of 246.9 mm (Fig. 10c).

DISCUSSION

Tracemaker candidates for the ichnogenus *Batrachichnus* have hitherto been attributed to temnospondyl amphibians (Haubold *et al.* 1995, 2005; Voigt 2005; Stimson *et al.* 2012). This consensus was made through recognition of a tetradactyl manus and pentadactyl pes corresponding with autopodium reconstructions of contemporaneous temnospondyl amphibians in close proximity to known *Batrachichnus* localities, for example Joggins (Dawson 1863, 1895; Holmes *et al.* 1998; Stimson *et al.* 2012). Though assigning zoological correlatives to a fossil trace is commonly a challenging task, Voigt (2005) suggested that the temnospondyl *Dendrerpeton* was the most likely tracemaker for *Batrachichnus* due to morphological congruence. However, the significant morphological variability attributed to small amphibian footprints has been noted (Haubold *et al.* 1995), raising the possibility of *Batrachichnus* having been produced by multiple late Paleozoic tetrapod taxa. For example, some authors (Stimson *et al.* 2012; Petti *et al.* 2014; Cisneros *et al.* 2020) proposed that *Batrachichnus* could have additionally been produced by other groups of tetrapods, namely “microsauros”. However, this hypothesis has received little attention subsequently in the literature.

“Microsauros” represent a taxonomically problematic group of small-bodied tetrapods that first appeared in the

Mississippian (Carroll *et al.* 1991; Lombard and Bolt 1999; Clack 2011), diversified during the Pennsylvanian (Mann *et al.* 2020; Mann and Maddin 2019; Mann *et al.* 2019; Mann *et al.* 2021; Carroll and Gaskill 1978), and persisted through to the early Permian (Carroll 1968; Daly 1973; Carroll and Gaskill 1978). Traditionally “microsaurs” have been considered to be stem-amniotes and part of the group Lepospondyli (Zittel 1888; Romer 1950; Baird 1965; Carroll 1966, 1998; Carroll and Chorn 1995); however, recent taxonomic and phylogenetic studies have found this group to be a polyphyletic assemblage (Anderson 2007; Pardo *et al.* 2017; Pardo and Mann 2018; Clack *et al.* 2019). Study of the anatomy and systematics of “microsaurs” has recently undergone a revival, using new imaging techniques (micro-CT) and methods to reveal stereotypical fossorial adaptations among the group (Maddin *et al.* 2011; Huttenlocker *et al.* 2013; Pardo *et al.* 2015; Szostakiwskyj *et al.* 2015; Pardo and Anderson 2016; Mann and Maddin 2019; Mann *et al.* 2019.) These studies have led to the emergence of a well-supported, fossorially adapted clade called Recumbirostra (Anderson 2007), which includes a core-group of some “microsaurs” and lysorophians (Pardo and Anderson 2016; Pardo *et al.* 2017; Mann *et al.* 2019). The most recent phylogenetic analyses including recumbirostrans retrieve the clade within crown-group amniotes, specifically as early-diverging reptiles (Pardo *et al.* 2017; Mann and Maddin 2019; Mann *et al.* 2019; Mann *et al.* 2021). Despite the recent surge in research on recumbirostran “microsaurs”, further work is still needed to confirm the exact phylogenetic placement of the group (involving some or all of its members).

Limitations concerning trackway preservation restrict the production of small tetrapod tracks, including *Batrachichnus*, to terrestrial, semi-aquatic paleoenvironments. Tetrapod footprints preserved in shallow, subaqueous conditions exhibit morphological inaccuracies consisting of a reduced number of digits, distorted digit position, and a parallel digit orientation attributed to the fact that the tracemaker would have been buoyed up by the water (Brand and Kramer 1996). Distortions generated under these conditions hinder the ability to confidently distinguish between walking ichnotaxa (*Batrachichnus salamandroides*) and swimming variants (*Characichnos*, *Lunichnium*). Aside from a rare instance where the limbs were used as stabilizers when swimming directly above the substrate (Minter and Braddy 2006), diagnostic tetrapod trackways produced in deep-water contexts are seldom preserved in the late Paleozoic fossil record. The presence of the fish ichnotaxon *Undichna* on the same surface as the *Batrachichnus salamandroides* trackway studied here suggests a close proximity, at least periodically, to aquatic environments.

The paleoenvironmental constraints on *Batrachichnus* footprints exclude the aquatic microbrachomorph “microsaur” groups such as Hyloplesiontidae and Microbrachidae. The tetrapod trackway under discussion is a shallow underprint of plantigrade impressions that are spaced at regular intervals (stride and pace) on the same surface as a surface impression of *Undichna*. The co-occurrence of these

two ichnogenera does not suggest that this tetrapod trackway was registered into sediments that were deposited under subaqueous settings. Instead, the traces were registered on different sedimentary surfaces, with tetrapod trackway being registered into a slightly younger stratum at millimetre scale above the exposed surface. The tetrapod trackway penetrated into an underlying surface that preserved the *Undichna*, which was obviously deposited under subaqueous conditions. On this basis, it is feasible to narrow down “microsaur” candidates to terrestrially adapted recumbirostrans (e.g., pantylids, hapsidopariieds, gymnarthrids, brachystelechids, ostodolepids, and rhynchonkids) and the currently unrevised forms, such as *Tuditonus* and *Trihecaton*. Some of these terrestrial “microsaurs” bear significant resemblance to small-bodied temnospondyls in bauplan, and can be found in similar environmental settings (Carroll and Gaskill 1978). These settings include coal swamps (Lyell and Dawson 1853; Dawson 1894, 1896; Calder 1998; Calder *et al.* 2006; Davies *et al.* 2005), shallow lakes or ponds (Rayner 1971), channel flanks (Vaughn 1972; Hook and Ferm 1985, 1988), and delta floodplains (Rayner 1971). They are thus viable contenders as producers of *Batrachichnus* footprints.

This conclusion is additionally supported by observations that the autopodium of terrestrial “microsaurs” and temnospondyls share a similar morphology (Carroll 1968; Stimson *et al.* 2012; Fig. 10). The diagnostic tetradactyl manus of *Batrachichnus* is consistent with both groups, as are identical digit proportions (e.g., 1-2-3-2 in the manus), and slightly wider than long dimensions. The Minto trackway exhibits a slightly longer digit IV; however, morphological variation within the ichnogenus is quite extensive, dismissing this feature as a viable extramorphological discrepancy (Haubold *et al.* 1995). Furthermore, the factors relevant in the evaluation of footprint morphology, as discussed by Milàn and Bromley (2006, 2007), have been erected to compensate for some of the extramorphological variability that occurs during trackway registration. The effects of substrate condition, water saturation, taphonomy, erosion, and undertrack preservation must all be taken into consideration as factors that influence footprint morphology (Haubold *et al.* 1995; Melchor and Sarjeant 2004). It is thus interpreted that the footprints produced by “microsaurs” and temnospondyls could be rendered virtually indistinguishable on an ichnotaxonomic level.

The diversity in recumbirostran “microsaur” body proportions, particularly that of the trunk region, provides the potential for high levels of variation in certain aspects of trackway morphology, specifically the estimated GAD. Furthermore, Haubold (1971) noted that the trackway pattern will alter in respect to the tracemaker’s body size. The body size of the tracemaker of NBM 21591 is equivocal, as two GAD interpretations are considered valid: (1) a GAD measuring 99 mm, attributed to an overstepping gait of a semi-elongated recumbirostran “microsaur”, and (2) GAD measuring 54 mm consistent with known temnospondyls in the region, but also consistent with short-bodied “microsaurs” (e.g., *Pantylus*, *Tuditonus*, and brachystelechids). The

latter interpretation is favoured based on the cogent trackway parameters discussed above. “Microsaur”-produced trackways are thus interpreted to encompass a range of GAD values ranging from lengths only achievable by elongated recumbirostran “microsaurs” to those of temnospondyl affinity. This observation raises the possibility of past tracemaker misidentifications, as the GAD of temnospondyls and short-bodied “microsaurs” would overlap, resulting in a dubious zone of tracemaker identity. Despite being helpful in determining potential tracemaker candidates, the GAD of specimen NBMG 21591 is open to various measurements and cannot be heavily relied on to distinguish between a temnospondyl or “microsaur” tracemaker. Furthermore, additional discoveries of tetrapod body fossils are needed to aid in resolving the true identities of Carboniferous trackways.

CONCLUSIONS

Based on prior studies, the original interpretation that *Batrachichnus* was produced by temnospondyls is regarded as a valid hypothesis. However, the results of this study support those of Stimson *et al.* (2012) in expanding possible tracemakers for *Batrachichnus* to include terrestrial recumbirostran “microsaurs”. “Microsaurs” frequented the equatorial regions of Pangea during the Pennsylvanian and were a common component in the terrestrial ecosystems alongside temnospondyls (Carroll and Gaskill 1978). The body lengths of terrestrial recumbirostran “microsaurs” and temnospondyls overlap, and together with indistinguishable manus and pes morphology, complicate the process of discerning between the two groups as potential tracemakers. A more equivocal approach to selecting associated tracemakers for the ichnogenus is encouraged, which may inspire subsequent re-examinations of biota inferred from *Batrachichnus* populated ichnoassemblages. This approach pertains especially to fossil localities where either tetrapod skeletal remains are absent and tetrapod communities are being inferred solely from the ichnological record, or where both “microsaurs” and temnospondyls are present in the skeletal record in addition to tetrapod ichnofossils, for example at Joggins (Dawson 1882, 1896; Carroll 1964, 1966, 1967; Stimson *et al.* 2012; Mann *et al.* 2020; Calder *et al.* 2006).

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