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Article abstract

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Reassignment of vertebrate ichnotaxa from the Upper Carboniferous 'Fern Ledges', Lancaster Formation, Saint John, New Brunswick, Canada

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ABSTRACT

Vertebrate ichnotaxa described by George Frederic Matthew in 1910 from the Upper Carboniferous (Lower Pennsylvanian) 'Fern Ledges' of Saint John, New Brunswick, were dismissed as dubious trackways by previous authors. Thus, three new ichnospecies Matthew described appeared in the 1975 *Treatise on Invertebrate Paleontology* as "unrecognized or unrecognizable" and were mostly forgotten by vertebrate ichnologists. These traces include *Hylopus* (?) *variabilis, Nanopus* (?) *vetustus* and *Bipezia bilobata*. One ichnospecies, *Hylopus* (?) *variabilis*, here is retained as a valid tetrapod footprint ichnotaxon and reassigned to the ichnogenus *Limnopus* as a new combination, together with other poorly preserved specimens Matthew labeled, but never described. *Nanopus* (?) *vetustus* and *Bipezia bilobata* named by Matthew in the same paper, have been reexamined and remain as nomina dubia.

RÉSUMÉ

Les ichnotaxons vertébrés de Fern Ledges du Carbonifère supérieur (Pennsylvanien inférieur) de Saint John, au Nouveau-Brunswick, décrits par George Frederic Matthew en 1910 avaient été rejetés par des auteurs précédents les considérant comme des séries de traces douteuses. Trois nouvelles ichnoespèces décrites par Matthew sont ainsi apparues dans le *Treatise on Invertebrate Paleontology* (Traité sur la *paléontologie des invertébrés*) de 1975 à titre d'espèces « non identifiées ou non identifiables » et ont principalement été laissées aux ichnologues des vertébrés. Les traces en question comprennent des traces d'*Hylopus* (?) *variabilis,* de *Nanopus* (?) *vetustus* et de *Bipezia bilobata*. L'une de ces ichnoespèces, l'*Hylopus* (?) *variabilis*, est retenue ici comme spécimen valide d'ichnotaxon se rapportant à une empreinte de pas de tétrapode et a été rattachée à nouveau à l'ichnogenre *Limnopus* en tant que nouvelle combinaison, conjointement avec d'autres spécimens mal conservés auxquels Matthew avait donné un nom, mais qu'il n'avait jamais décrits. Le *Nanopus* (?) *vetustus* et le *Bipezia bilobata,* cités par Matthew dans le même article, ont été réexaminés et leurs désignations nomina dubia.

[Traduit par la redaction]

INTRODUCTION

In the early 1900s, George Frederic Matthew (1837–1923) identified and reviewed tetrapod footprints and trackways from the Maritimes region of Canada in an attempt to provide some organization to the classification of vertebrate ichnotaxa (Matthew 1903a–e, 1904, 1905). In the process, Matthew became a pioneer in the study of Carboniferous tetrapod ichnology (Leonardi 1987; Cotton *et al*. 1995; Haubold *et al*. 2005). The specimens he examined and described were mostly collected at Joggins (Cotton *et al*. 1995; Calder 2006; Stimson *et al*. 2012) and at other Carboniferous localities in Nova Scotia. In his final paper on tetrapod ichnofossils, Matthew (1910) described three new ichnospecies, *Hylopus* (?) *variabilis, Nanopus* (?) *vetustus* and *Bipezia bilobata*, from the Upper Carboniferous Lancaster Formation at 'Fern Ledges', Saint John, New Brunswick (Fig. 1). He published the first two ichnotaxa with the question marks suggesting he recognized the poor preservation of the fossils. Matthew stated in the paper that

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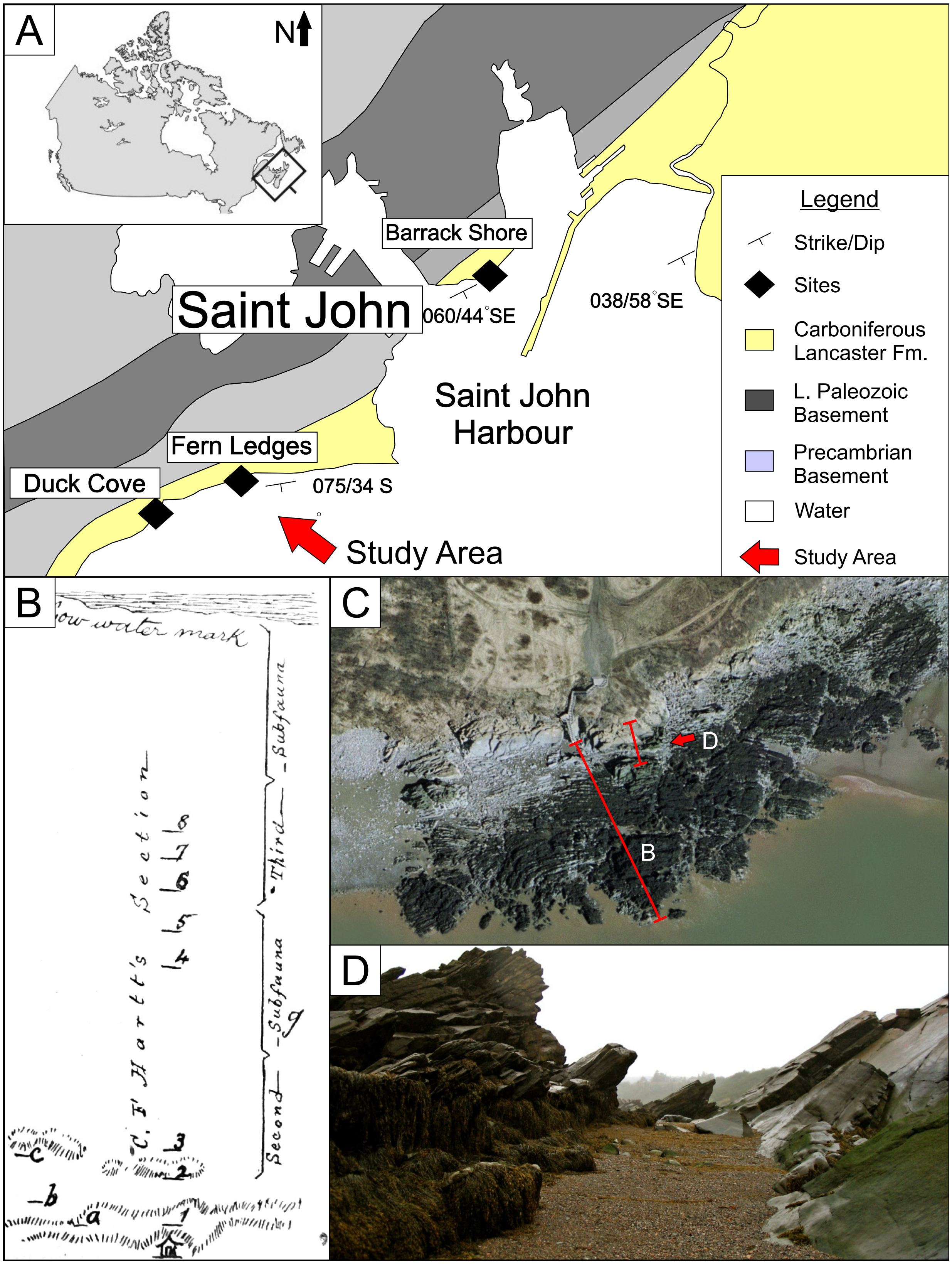

Figure 1. (A) Location of outcrops exposed at 'Fern Ledges', Duck Cove and Barrack Shore in the Upper Carboniferous Lancaster Formation, Saint John, New Brunswick, Canada; (B) reproduction of a sketch of the 'Fern Ledges' in Matthew (1906) showing C.F. Hartt's plant beds (1–8) and collections by W.J. Wilson (a–c); (C) aerial view of the 'Fern Ledges', line B approximates Matthew's (1906) sketch. The arrow at D indicates the direction of view in D; (D) view of the tilted beds at 'Fern Ledges'.

tetrapod tracks had been previously recognized in situ on the surfaces of hard sandstone beds in the 'Little River group' (Lancaster Formation), but that they were not collected, nor were any specimens described. In this study we re-examine the published specimens that Matthew did collect. We also document additional poorly preserved footprints found among plant fossils in the collections of the Natural History Society of New Brunswick that were discovered by Matthew, C.F. Hartt (1840–1878), W.J. Wilson (1857–1920) and others. Although Matthew recognized *Hylopus* and *Nanopus* as Devonian–Carboniferous ichnogenera, by the early 1900s Matthew was convinced that at 'Fern Ledges' the rocks were Silurian (Matthew 1910), older than the Devonian age he and others originally proposed. The 'Fern Ledges' site is known mostly for its plant and invertebrate assemblages (Dunlop and Miller 2007; Falcon-Lang and Miller 2007a), and for a late nineteenth to early twentieth century controversy concerning the age of the rocks (Falcon-Lang and Miller 2007b), which was ultimately resolved by Marie Stopes in her classic palaeobotanical memoir on the Upper Carboniferous plants of the site (Stopes 1914).

All three of Matthew's ichnospecies have remained misunderstood orphans in tetrapod ichnology, in part because Matthew's description was published just a few years prior to the demise of the Natural History Society of New Brunswick, where Matthew conducted most of his research activities. The Society collections became difficult to access, even after they were acquired by the New Brunswick Museum in 1932. By 1917, the Society had ceased publication of its Bulletin, and by 1921 Matthew had retired and moved to New York to live with his son William Diller Matthew (Colbert 1992). Matthew's collection was largely inaccessible when Abel (1935) reviewed *Hylopus* (?) *variabilis* and *Nanopus* (?) *vetustus*. Even though he had not seen the specimens, Abel concluded that they are not vertebrate tracks. Both ichnotaxa appeared in Part W of the *Treatise on Invertebrate Paleontology* dealing with Trace Fossils and Problematica (Häntzschel 1975; Miller 1996), where they were treated as 'unrecognized and unrecognizable' based on Abel's (1935, p. 78) judgment. Thus, subsequent workers have also not regarded them as tetrapod track ichnotaxa (e.g., Sundberg *et al.* 1990). *Bipezia bilobata* was also reported in Part W of the *Treatise* (Häntzschel 1975) as a dubious tetrapod trace based on Glaessner (1957), who considered it a possible arthropod trace synonymous with *Isopodichnus*.

Matthew's specimens of all three ichnotaxa were relocated in 1987 during re-organization of the New Brunswick Museum palaeontology collection (Miller 1988). Falcon-Lang and Miller (2007a) published the fossils as (?)*Hylopus variabilis* and (?)*Nanopus vetustus* and concluded they were possibly poorly preserved vertebrate undertracks, but that assignment to *Hylopus* or *Nanopus* was questionable. The fossils are re-evaluated and re-illustrated here as part of a project to examine tetrapod tracks from New Brunswick and are accordingly reassigned. Hereafter we simply refer to the species as *Hylopus variabilis* and *Nanopus vetustus*. Also included in our study are previously unrecognized examples of *Hylopus variabilis* and other putative tetrapod tracks found in the New Brunswick Museum collections that had not been previously described.

In summary, the purpose of this paper is to reassess the validity of Matthew's three tetrapod ichnotaxa from the Lancaster Formation. We demonstrate that Häntzschel (1975) was correct in his assessment that *Nanopus vetustus* and *Bipezia bilobata* are indeed nomina dubia. We also reinstate Matthew's ichnospecies *Hylopus variabilis* as a tetrapod footprint and reassign the ichnospecies to the ichnogenus *Limnopus*; the only ichnogenus treated systematically herein.

GEOLOGIC SETTING

The 'Fern Ledges' section belongs to the Upper Carboniferous Lancaster Formation of the Cumberland Group. The Lancaster Formation is found along the Bay of Fundy coast of southern New Brunswick from Saint John to Lepreau (Fig. 1A). It is exposed along coastal sections, much of it in the intertidal zone. In the type locality at 'Fern Ledges' to Duck Cove, the Lancaster Formation consists of grey to greenish-grey quartzose sandstone and dark grey, greenish-grey or black shale. The Formation also includes units of coarse-grained sandstone, quartz-pebble conglomerate, minor red mudstone, and fine-grained sandstone. Falcon-Lang and Miller (2007a) reviewed the palaeoenvironments and palaeoecology of the 'Fern Ledges' section, with the emphasis on the invertebrate fauna and ichnofossils. A review of the Lancaster Formation flora is underway, with revisions of several taxa completed (Wagner 2001, 2005a, b). An Early Carboniferous (Langsettian) age is currently assigned to the formation (Falcon-Lang and Miller 2007a).

Matthew (1910) recorded the tetrapod ichnofossils as coming from the 'Lower Cordaite' shale at 'Fern Ledges'. C.F. Hartt made the first comprehensive collections at the site (Fig. 1B) and used the term 'Cordaite Shale' (in Bailey 1865, p. 131; in Dawson 1868, p. 514, 516) probably to describe the plant-rich shale beds, which he divided into plant beds 2–8 (in Bailey 1865, p. 134–140; in Dawson 1868, p. 517–523; Matthew 1906). More precise information was not recorded with the fossils. Almost all of the historical fossil collections from the Lancaster Formation at 'Fern Ledges', including diverse plant compressions and remains of terrestrial and aquatic fauna, were likely derived from Facies 3 of Falcon-Lang and Miller (2007a). They described Facies 3 as lenticular, upward-coarsening sheets of sediment 0.12–2.97 m thick. Mudstone beds, 0.02–0.71 m thick, grade upward into fine- to medium-grained, horizontally bedded sandstone 0.10–2.26 m thick, with symmetrical ripple marks. Some sandstone beds may show low-angle, mutually erosive cross-beds, or localized channel fills. Upward-coarsening units are usually capped by palaeosols. Fossils are most abundant in the mudstone beds overlying palaeosols. Facies 3 was interpreted as either representing wave-reworked mouth-bar deposits associated with small channels, or with linear clastic shorelines in which rhythmic bedding in mudstones may result from weak tidal influence. Falcon-Lang and Miller (2007a) concluded that the 'Fern Ledges' sediments were deposited on a tectonically influenced coastal plain where braided channels drained into a shallow brackish bay.

ICHNOTAXONOMIC ASSESSMENT OF *HYLOPUS VARIABILIS*

A fossil found by William Logan in 1841 from rocks at Horton Bluff, Nova Scotia, was the first Mississippian tetrapod footprint specimen to be discovered in North America (Logan 1842; Dawson, 1882). Logan's specimen was not given much attention until it was named and described as *Hylopus hardingi* by Dawson (1882). Fillmore *et al*. (2012) revised the diagnosis of *Hylopus*, in the process reviewing all three known ichnospecies of that genus. *Hylopus* was considered monospecific with the only valid ichnospecies being *Hylopus hardingi* Dawson 1882. *Hylopus variabilis* was not considered in the revision by Fillmore *et al*. (2012), presumably as it was considered a nomen dubium by Abel (1935) and in the *Treatise* (Häntzschel 1975). In their emended diagnosis, Fillmore *et al*. (2012, p. 58) described *Hylopus* as follows:

> Footprints of a quadrupedal tetrapod in which the manus is tetradactyl and the pes is pentadactyl. The manus and pes are of approximately equal size (especially in widths), generally plantigrade and may be overstepped. The digits are often thin and curved medially, and digit IV is much longer than the rest (digit IV> digit III >digitV>digit II). In the pes, the digits are straight to slightly curved medially and are more nearly of subequal length than in the manus (digit II> digit I = digit III > digit IV > digit V).

Hylopus variabilis does not conform to this ichnogenus concept for *Hylopus.* It differs from the emended diagnosis in that the manus is smaller than the pes. The digits on the manus of *Hylopus variabilis* are of subequal length, increasing only slightly in length from digits I–III from 4 mm to 6.2 mm. However, digit IV in *Hylopus hardingi* is much longer than the other digits in the manus. The digits on the pes of *Hylopus hardingi* are subequal whereas in *Hylopus variabilis* they increase in length from I–IV, with digit IV being the longest. Given these differences, *Hylopus variabilis* requires reassignment.

Lucas and Dalman (2013) re-examined Pennsylvanian trackways described by King (1845) from western Pennsylvania. In the process, King's ichnospecies, *Thenaropus heterodactylus*, was reassigned to the ichnogenus *Limnopus* and considered to be the senior subjective synonym of the type ichnospecies, *Limnopus vagus.* They thus concluded that *Limnopus* is monospecific and that *Limnopus heterodactylus* is the valid name for the single species, all other names being synonymous with *Limnopus heterodactylus*. Lucas and Dalman (2013, p. 236) emended the genus concept, providing a diagnosis of *Limnopus* for quadrupedal tetrapod tracks consisting of as follows:

> … a pentadactyl pes and tetradactyl manus; pes digits that increase in length from I to IV, with digit V subequal in length to digit II; relatively thick pes and manus digits with blunt/rounded distal tips; broad and rounded sole imprints; manus just in front of pes; manus digits I–III obliquely set (turned) toward the trackway midline; and manus digits that increase in length from I to III, with digit IV subequal in length to digit II (cf. Baird, 1952; Haubold, 1970, 1971; Voigt, 2005).

Hylopus variabilis does not easily conform to any other known ichnotaxon, but is not sufficiently well preserved to justify a new ichnogenus. *Hylopus variabilis* most closely resembles *Limnopus.* However, that genus was described by Lucas and Dalman (2013) as having thick digits with blunt or rounded digit terminations, whereas *Hylopus variabilis* has thin and short digits. The morphology of *Hylopus variabilis* likely reflects shallow underprints, and for reasons discussed below should not at this time be considered a junior synonym of *Limnopus heterodactylus.* Thus, Matthew's form is here transferred to *Limnopus* but retained as a separate ichnospecies, at least until better specimens are discovered to either confirm it as a separate ichnospecies or more confidently establish its synonymy with *Limnopus heterodactylus*. We suggest a revision of the ichnogeneric concept of *Limnopus* to better accommodate Matthew's species.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Limnopus* Marsh 1894

1894 *Limnopus* Marsh, p. 82, pl. 2 (2), pl. 3 (2).
1912 *Permomegatherium* n. g.; Delage, p. 241.
1963 *Opisthopus* n. g; Heyler & Lessertisseur, p. 177, figs. 25–31.
1973 *Limnopus* Marsh; Haubold, p. 8; fig. 13.
1973 *Opisthopus* Heyler & Lessertisseur; Haubold, p. 30.
1973 *Permomegatherium* Delage; Haubold, p. 30.
1973 *Limnopus* Marsh; Haubold & Sarjeant, p. 900, fig. 2 (4), pls. 3–4.
2005 *Limnopus* Marsh; Voigt p. 73, figs. 21 D–F, 22 H–N, 24.
2013 *Limnopus* Marsh; Lucas and Dalman, p. 236, figs. 3, 6, 11.

EMENDED DIAGNOSIS: Quadrupedal tetrapod tracks consisting of a pentadactyl pes and a tetradactyl manus; pes digits increase in length from I–IV, with digit V subequal in length to digit II; commonly with relatively thick manus and pes digits with blunt to rounded distal tips, but may be short and slender; broad rounded sole imprints; manus just in front of pes; manus digits I–III obliquely set toward the trackway midline; and manus digits that increase in length from I–III, with digit IV subequal in length to digit II (Modified from Lucas and Dalman 2013).

REMARKS: Prior to this study *Limnopus* has been considered monospecific. Voigt (2005) provided a comprehensive review of *Limnopus* with all previous species included in the genus and species concept for *Limnopus vagus* Marsh. *Limnopus* was reviewed by Lucas and Dalman (2013) who reassigned all known species to *Limnopus heterodactylus*, considering the genus to be monospecific. We have expanded the generic concept to accommodate minor morphological variation at the species level, thus including *Hylopus variabilis* (discussed below).

***Limnopus heterodactylus* (King 1845)**

1844 Batrachia; King, p. 179.
1845 *Thenaropus heterodactylus* n. sp.; King, p. 348–352, figs. 7–9.
1873 unnamed; Mudge, p. 71.
1894 *Limnopus vagus* n. sp.; Marsh, p. 82, pl. 2 (2), pl. 3 (2).
1894 *Allopus littoralis* n. sp.; Marsh, p. 83, pl. 2 (4, 4a).
1894 *Baropus lentus* n. sp.; Marsh, p. 83, pl. 2 (5).
1903b *Theranopus* (?) *mcnaughtoni* n. sp. Matthew, p. 103, pl. 2, fig. 1.
1903e *Thenaropus heterodactylus* King; Matthew, p. 112, fig. 1 (1, 2).
1903e *Limnopus vagans* Marsh; Matthew, p. 112, fig. 3 (2).
1903e *Baropus lentus* Marsh; Matthew, p. 113, fig. 3 (6).
1910 unnamed; Hausse, p. 3–19, pls. 2–7.
1912 *Permomegatherium zeilleri* n. sp.; Delage. p. 241, 8 pls.
1926 unnamed; Tilton, p. 389, pl. 2 (A–E).
1931 *Baropus waynesburgensis* n. sp.; Tilton, p. 551, fig. 4.
1932 *Allopus littoralis* Marsh; Branson & Mehl, p. 390, text fig. 2, pl. 10, fig.2.
1952 *Limnopus vagus* Marsh; Baird, p. 835, text figs. 1–2, pl. 122.
1952 *Limnopus littoralis* Marsh; Baird, p. 836, text fig. 3, pls. 123, 124, figs 1–3.
1952 *Limnopus waynesburgensis* (Tilton); Baird, p. 837, text fig. 4, pl. 124, fig. 4.
1959 *Limnopus vagus* Marsh; Schmidt, p. 78, fig. 32e.
1959 *Baropus haussei* n. sp.; Schmidt, p. 81, fig. 33d.
1965 *Limnopus cutlerensis* n. sp.; Baird, p. 47, figs. 14 (B–C).
1970 *Limnopus vagus* Marsh; Haubold, p. 96, fig. 5B.
1970 *Limnopus littoralis* Marsh; Haubold, p. 96, fig. 5H.
1970 *Limnopus waynesburgensis* (Tilton); Haubold, p. 96, fig. 5G.
1970 *Limnopus cutlerensis* Baird; Haubold, p. 96, fig. 5D.
1970 *Limnopus heterodactylus* (King); Haubold, p. 96, fig. 5.
1970 *Limnopus haussei* (Schmidt); Haubold, p. 99, fig. 5E.
1971 *Limnopus vagus* Marsh; Haubold, p. 17, figs. 12 (5), 13 (2).
1971 *Limnopus littoralis* Marsh; Haubold, p. 17, fig. 13 (4).
1971 *Limnopus waynesburgensis* (Tilton); Haubold, p. 17, fig. 13 (3).
1971 *Limnopus cutlerensis* Baird; Haubold, p. 17, fig. 12 (4).
1971 *Limnopus heterodactylus* (King); Haubold, p. 17, fig. 13 (5).
1971 *Limnopus haussei* (Schmidt); Haubold, p. 17, fig. 13 (6).
1971 *Theranopus*? *mcnaughtoni* Matthew; Haubold, p. 17.
1983 *Limnopus palatinus* n. sp.; Fichter, p. 46, figs. 28–35.
1988 *Limnopus zeilleri* (Delage); Gand, p. 98, figs. 28, 29 (A–I), 30 (A–E), 31.
1991 *Limnopus glenshawensis* n. sp.; Martino, p. 960, figs. 4–13.
1995 *Limnopus vagus* Marsh; Hunt *et al*., p. 264, figs. 2F, 4 [non figs. 2E, 3].
1996 *Limnopus vagus* Marsh; Haubold, p. 48.
1996 *Limnopus waynesburgensis* (Tilton); Haubold, p. 48.
1996 *Limnopus cutlerensis* Baird; Haubold, p. 48.
1996 *Limnopus zeilleri* (Delage); Haubold, p. 48.
2000 *Limnopus cutlerensis* Baird; Haubold, p. 12.
2000 *Limnopus zeilleri* (Delage); Haubold, p. 12.

REMARKS: The synonymy list above for *Limnopus heterodactylus* is updated from Voigt's (2005) list of material that he considered belonged to the genus *Limnopus*; here we include Lucas and Dalman's (2013) work.

***Limnopus variabilis* (Matthew 1910)**
(Figs. 2–3)

1910 *Hylopus* (?) *variabilis* Matthew, p. 120, pl. 2, figs. 1–3.
1935 *Hylopus* (?) *variabilis* Matthew; Abel, p. 78.
1975 *Hylopus*? *variabilis* Matthew; Häntzschel, p. W185.
2007a (?)*Hylopus variabilis* Matthew; Falcon-Lang and Miller, p. 949.

MATERIAL: NBMG 3041, 3042, 3043, reposited at the New Brunswick Museum. 'Lower Cordaite' shales, 'Fern Ledges', Lancaster Formation, Saint John, New Brunswick

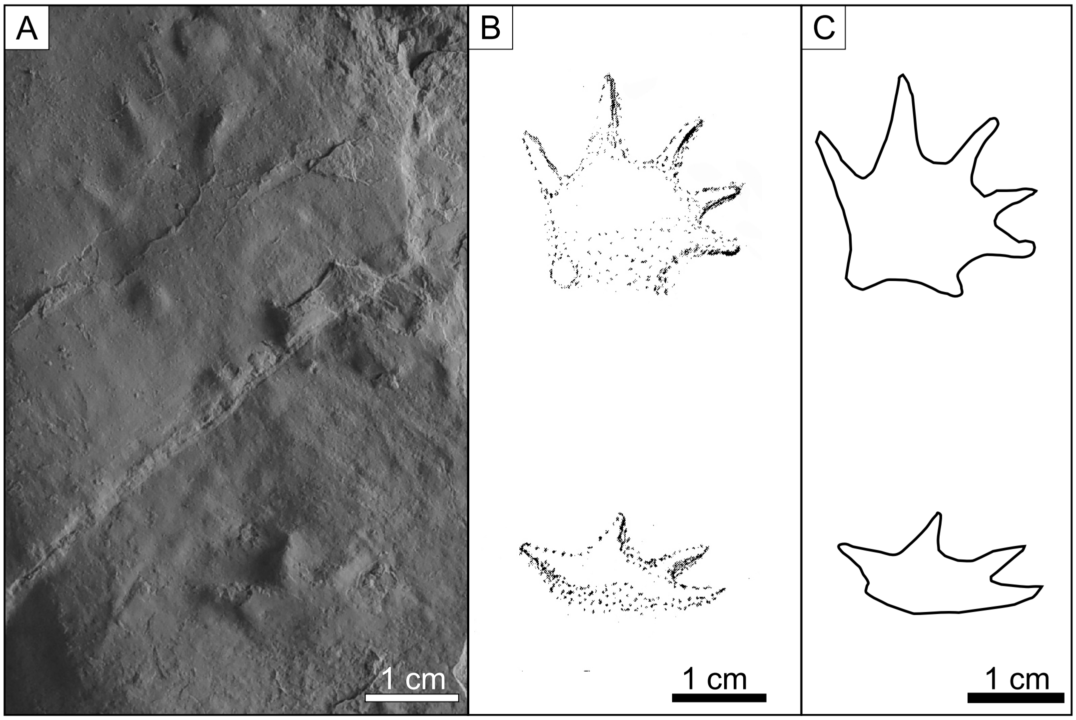

Figure 2. **(A) Photograph (coated) of the lectotype of *Limnopus variabilis* NBMG 3041; (B) Matthew's (1910) drawing of *Hylopus* (?) *variabilis* (NBMG 3041); (C) line drawing of *Limnopus variabilis* (NBMG 3041).**

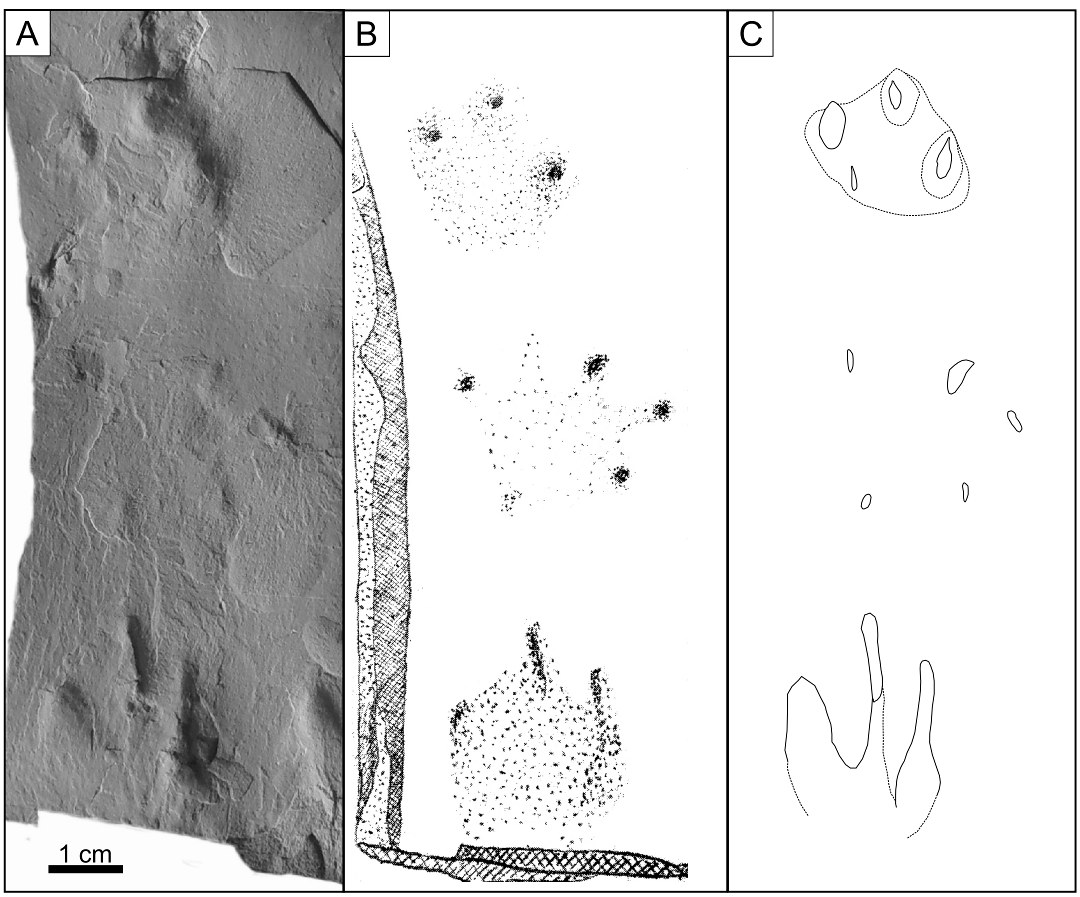

Figure 3. **(A) Photograph (coated) of the paralectotype (pes and manus impressions) of *Limnopus variabilis* (Matthew) NBMG 3042; (B) Matthew's (1910) drawing of Hylopus (?) variabilis (NBMG 3042); (C) line drawing of *Limnopus variabilis* (NBMG 3042).**

(approximately 45°14’42.39”N; 66°04’56.83”W). As Matthew (1910) did not select a holotype, we here select specimen NBMG 3041 and its counterpart NBMG 3043 as the lectotype with specimen and designate NBMG 3042 as a paralectotype.

AGE: Late Carboniferous, Early Pennsylvanian (Langsettian), Lancaster Formation, Cumberland Group.

EMENDED DIAGNOSIS: *Limnopus variabilis* differs from the only other currently recognized ichnospecies of the genus, *Limnopus heterodactylus* (=*Limnopus vagus*), in having slender digits in both the manus and the pes, and digit distal tips that taper sharply. Both manus and pes digits are shorter in length than in *Limnopus heterodactylus*, but otherwise follow the emended ichnogenus concept described in this paper.

DESCRIPTION: *Hylopus variabilis* was described from a single manus and pes that are not clearly distributed into manus and pes sets (Matthew 1910). Tracks have low relief and may represent shallow underprints, but retain their footprint plantigrade morphology. The deepest impressions are the digit terminations. Digits are well spaced at regular intervals, with wide hipices between digits. The pes is plantigrade with short, broad sole impressions. The pes is only slightly wider than long, measuring 25 mm by 28 mm for length and width, respectively. The pes is pentadactyl with regularly spaced digits that increase in length from I to IV and are set forward. Digit V is shorter than digit IV and set to the side. Matthew described a callus or lump on the side of the palm of dubious validity.

The manus is wider than long, measuring 13 mm by 24 mm for length and width, respectively. The manus is tetradactyl with regularly spaced digits. Digits I to III are roughly equal in length, only increasing slightly from 4.0 mm to 5.3 mm to 6.2 mm. Digits I to II are directed inward towards the midline, whereas digit III is directed forward. Digits I to III are closely grouped with digit IV and directed away from the midline and slightly set back. Matthew (1910) described the stride, however, with only a single manus and pes with no repeated footfalls present on the specimen, measuring other morphometrics such as stride, pace, and inner and outer trackway widths is not possible.

DISCUSSION

Limnopus from ‘Fern Ledges’

Matthew (1910) described three specimens of *Hylopus variabilis* from ‘Fern Ledges’. *Hylopus variabilis* was considered a non-tetrapod track by Abel (1935) and Häntzschel (1975). Although the lectotype specimen (NBMG 3041) was illustrated in a New Brunswick Museum newsletter (Anonymous 1987), it has only rarely been mentioned elsewhere (e.g., Sundberg *et al*. 1990), and has undergone no systematic reassessments. Indeed, the comprehensive tetrapod footprint compendia of Kuhn (1963) and Haubold (1971) do not list the ichnotaxon. Falcon-Lang and Miller (2007a) tentatively vindicated Matthew’s ichnospecies, stating that it may represent “possible poorly preserved undertracks of a tetrapod emplaced in soft sediment”, but they provided no further detailed study of its ichnological features; they added that assignment to *Hylopus* is questionable. From our reassessment, we conclude that the specimens represent actual tetrapod tracks, which we reassign to *Limnopus*. One of the three specimens labeled as *Hylopus variabilis* by Matthew (NBMG 3043) in the NBM collection has been recognized as the counterpart to the Matthew’s figured specimen of *Hylopus variabilis* (NBMG 3041). Matthew assigned a third specimen (NBMG 3042) to *Hylopus variabilis*; we consider this specimen to be a deep underprint of *Limnopus variabilis*.

Subsequent explorations of the New Brunswick Museum collections have identified three additional, previously undescribed and unillustrated specimens with putative tetrapod tracks from the Lancaster Formation. Two of these specimens (NBMG 12926, Fig.4A; and NBMG 2191, Fig.4B) were collected and labeled by Matthew for associated plant remains but contain previously unrecognized tetrapod tracks, both tentatively interpretable as strongly extramorphologically distorted deep underprints of *Limnopus variabilis*; these specimens do not warrant further description.

A third specimen with tetrapod tracks (NBMG 3494) was labeled as the type specimen for the plant *Odontopteris crassa*, but had associated tetrapod tracks that were labeled simply as ‘Batrachian tracks?’ (Fig. 4C). Matthew (presumably), using red circles, identified 13 individual but unconvincing footprints on the surface; they may represent the tracks of a small amphibian with a short stride. On the specimen label, Matthew indicated the toes are distinct in the last footfalls. Deep, elliptical impressions arranged in groups of up to three are present at the anterior of the ‘trackway’. Given the short blunt digits measuring a maximum of 4.7 mm in length, the tracks may represent deep, digitigrade underprints of a tetrapod trackway. The putative trackway is digitigrade at best, with no clear diagnostic features to assign it to an existing vertebrate ichnotaxon with confidence.

Limnopus variabilis differs from the other valid species of the ichnogenus, *Limnopus heterodactylus* (which incorporates the type ichnospecies originally named *Limnopus vagus*). As defined by Lucas and Dalman (2013), *Limnopus heterodactylus* has thick digits with blunt to rounded terminations (Fig. 5). These authors used this concept to synonymize all previously described *Limnopus* forms into a monospecific ichnogenus (Figs. 5A–D). In contrast, *Limnopus variabilis* has short, slender digits with sharp, tapering digit terminations that are well spaced with wide interdigit hipicies (Fig. 5E). The lectotype of *Limnopus*

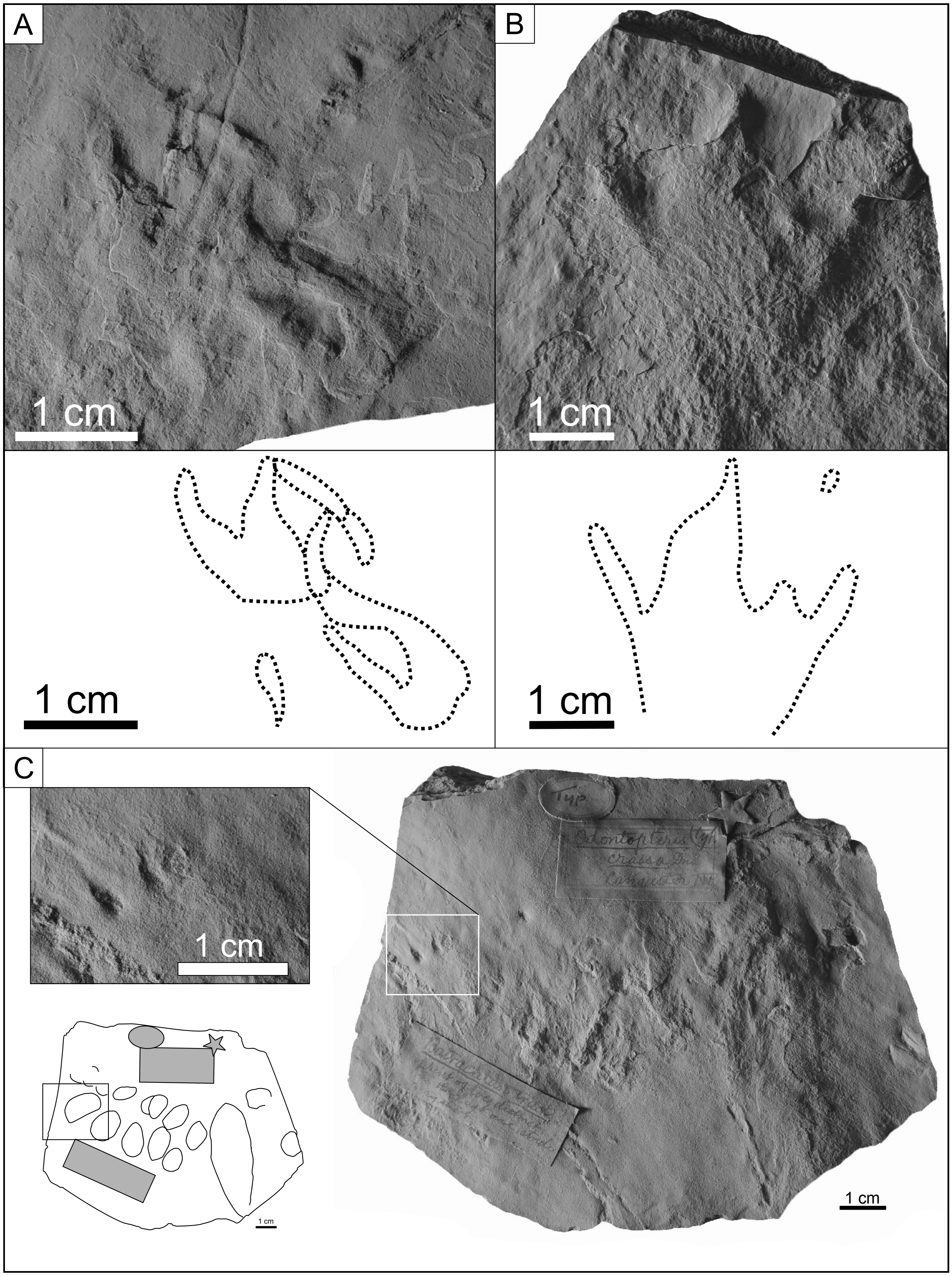

Figure 4. Photographs (coated) of additional possible tracks from the Upper Carboniferous Lancaster Formation (A) *Limnopus variabilis* (NBMG 12926); (B) *Limnopus variabilis* (NBMG 2191); (C) specimen labeled as "Batrachian tracks?" probably by G.F. Matthew, may represent poorly preserved vertebrate tracks (NBMG 3494).

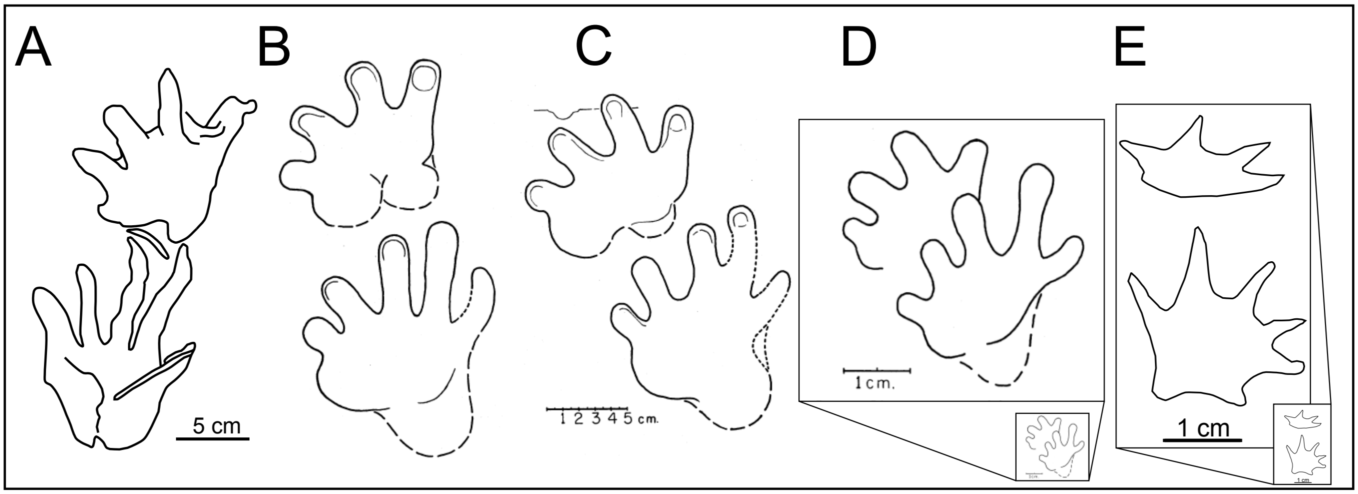

Figure 5. Line drawings illustrating morphology and size of: (A) *Limnopus heterodactylus* King 1845; (B) *Limnopus (Allopus) littoralis* Marsh 1894; (C) *Limnopus (Baropus) waynesburgensis* Tilton 1931; (D) *Limnopus vagus* Marsh 1894; and (E) *Limnopus variabilis* Matthew 1910. All line drawings are 25 percent of their natural size except the enlarged boxes provided in D and E for morphological comparison. Modified from Baird (1952) and Lucas and Dalman (2013).

heterodactylus has a manus that is longer than wide, which by strict definition is applicable to *Limnopus variabilis*. The pes of *Limnopus heterodactylus* has a length-to-width ratio of roughly 2:1, whereas *Limnopus variabilis* has a length-to-width ratio that is nearly 1:1, being only slightly longer in length by 3 mm in the lectotype specimen.

Given the low relief of the footprints, the type specimen of *Limnopus variabilis* is likely a shallow underprint, but it is plantigrade and displays the complete morphology of the manus and pes. If the digit impressions were preserved as underprint fallout, the sediment distortion around the digits would widen rather than be preserved as slender impressions. The digits do not exhibit extramorphological digit extensions or extractions, which would lengthen the digits; the digits preserved on the lectotype specimen are short. If digit extractions were present, the digit relief would shallow distally towards the anterior, as the foot was removed from the substrate. The digits are in fact deepest at their anterior, indicating they do not represent extramorphological toe drags.

Alternatively, the slender and short nature of the digits of *Limnopus variabilis* may be due to digit-impression wall collapse. Wall collapse is related to the cohesiveness of the sediments in which the footprint was emplaced. In poorly consolidated sediments that are not cohesive, sediment slumping occurs where the digit imprint walls are steeper than the angle of repose, allowing for sediment collapse into the imprint from either side. This would artificially narrow the base of the imprint. However, the loss of sediment from the trace wall would cause a widening of the digit imprint at the sediment surface. As the trace is probably a shallow underprint, it is unlikely that these surface features would be observed, and thus we are indeed seeing the true foot morphology within the shallow underprint fallout. If better examples were to be discovered, they might show that *Limnopus variabilis* is a minor morphological variant of *Limnopus heterodactylus*.

Limnopus versus *Batrachichnus*

Tucker and Smith (2004) recognized the close similarity between the ichnogenus of *Limnopus* and the variable ichnogenus *Batrachichnus* first described by Woodworth (1900). Using a multivariate taxonomic analysis of *Limnopus* and *Batrachichnus* specimens, Tucker and Smith concluded that size seems to be the only ichnotaxobase upon which to separate the two ichnogenera. They observed two separate but overlapping size distributions. Although size is not a major factor in distinguishing ichnotaxa, based on the possibility that *Batrachichnus* and *Limnopus* may be produced by separate biotaxa with separate stratigraphic ranges, as well as the fact the two names are well established in literature, Tucker and Smith retained both ichnotaxa. However, they reduced *Batrachichnus* to a subgenus of *Limnopus*, and the designation of *Limnopus* subgenus *Batrachichnus* automatically created a second subgenus, the autonym *Limnopus* subgenus *Limnopus*. *Limnopus vagus* was considered to be the only ichnospecies of *Limnopus (Limnopus)* at the time, while *Limnopus (Batrachichnus)* was composed of two ichnospecies, *Limnopus* (*Batrachichnus*) *salamandroides* and *Limnopus* (*Batrachichnus*) *plainvillensis*.

The taxonomic proposals of Tucker and Smith (2004) were rejected by Lucas *et al*. (2011) on the basis that a trinomial nomenclature is cumbersome and confuses the ichnotaxonomic assessment of *Batrachichnus* and *Limnopus*. Although technically valid, we concur that the use of subichnogenera and subichnospecies should be discouraged as confusing, cumbersome and ultimately unhelpful. Despite morphological similarities, *Batrachichnus* and *Limnopus* can be separated arbitrarily at the 20 mm pes-length size boundary. *Batrachichnus* is considered to extend from 2.38 mm (Stimson *et al*. 2012) to 20 mm (Lucas *et al*. 2011; Voigt 2005; Melchor and Sarjeant 2004) in pes length. *Limnopus* is considered to be morphologically similar but to occupy all size ranges above 20 mm in pes length up to 140 mm (DiMichele *et al*. 2012). With a pes length of 25 mm, *Limnopus variabilis* can thus be considered within the size range of *Limnopus*. If the two ichnogenera were to be considered synonymous, *Batrachichnus* would have priority; but a systematic review of that ichnogenus is beyond the scope of this manuscript. If the two ichnogenera are considered to be nearly identical and distinguished on size only, then much of the extramorphological variability included within the ichnospecies *Batrachichnus salamandroides* identified by Haubold *et al*. (1995) should also be included within the ichnogenus concept of *Limnopus*.

Both *Batrachichnus* and *Limnopus* are considered to have been produced by temnospondyls (Haubold 1971, 1984; Melchor and Sarjeant 2004; Van Allen *et al*. 2005; Stimson *et al*. 2012) or terrestrial microsaurs (Stimson *et al*. 2012) and may represent ontogenetic variations. Knowing the size ranges of *Limnopus* and *Batrachichnus*, *Limnopus variabilis* is a medium-sized footprint. It could be argued that *Limnopus variabilis* is an ontogenetic variation of either: an adult trackway to the smaller juvenile produced *Batrachichnus*; or a small example of *Limnopus* made by a juvenile of a larger animal that would produce larger footprints assigned to *Limnopus heterodactylus* (see Stimson *et al*. 2012 for detailed discussion of juvenile temnospondyl footprints). *Limnopus vagus* exhibits the typical morphology of *Limnopus heterodactylus* and is of similar size to some specimens of *Limnopus heterodactylus*. Given the wide range in size of *Limnopus heterodactylus*, we do not consider *Limnopus variabilis* to be an ontogenetic variation of this ichnospecies. If *Limnopus* and *Batrachichnus* are as similar as previous authors (e.g., Tucker and Smith 2004) would suggest, then the extensive research and treatment of *Batrachichnus* could stand as a model for the taxonomic treatment of *Limnopus*. The above-mentioned taxonomic work on *Batrachichnus* suggested a wide range of extramorphological variability that was included within the genus concept (Haubold *et al*. 1995). By comparison, the ichnotaxonomy for the ichnogenus concept for *Limnopus* should be handled in a similar manner and it would thus encompass a wide range of extramorphological variations. *Limnopus variabilis* redescribed here is at least a shallow underprint or a surface trace with low relief that preserves its original morphology that can be distinguished from *Limnopus heterodactylus* at the ichnospecies level. The morphological differences are minor enough that they should be considered variability under the genus concept by analogy to the treatment of *Batrachichnus*.

Nanopus (?) vetustus and *Bipezia bilobata*

Matthew (1910) described two other ichnotaxa; *Nanopus vetustus* (NBMG 3045) (Fig. 6) and *Bipezia bilobata* (NBMG 3037, 3038) (Fig. 6). *Nanopus vetustus* was considered by Abel (1935) and Häntzschel (1975) to be a nomen dubium; these authors thus discarded the ichnotaxon. Matthew

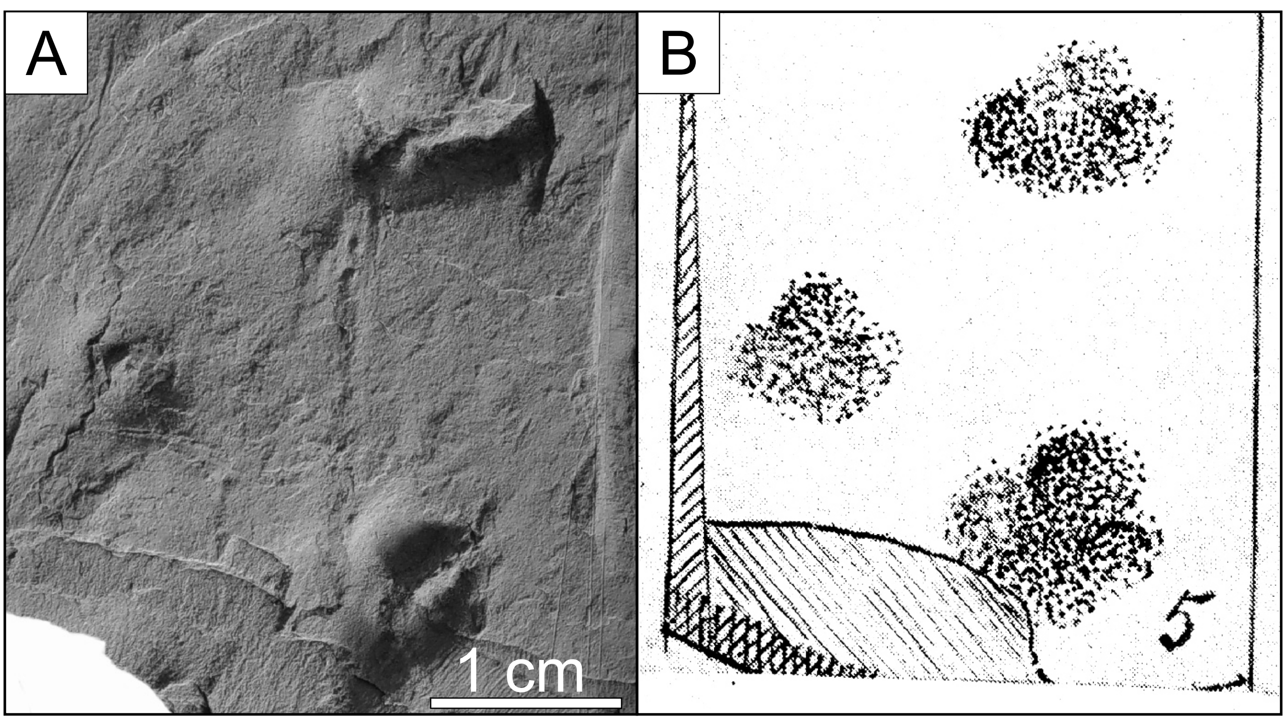

Figure 6. (A) Photograph (coated) of *Nanopus* (?) *vetustus* (NBMG 3045); (B) Matthew's (1910) drawing of *Nanopus* (?) *vetustus* (NBMG 3045).

described *Nanopus vetustus* (Figs. 6A, B) as a small footmark comparable to other examples of the genus, with maximum dimensions of 12 mm by 12 mm. He described digits as mere lobes, and none of the "footprints" exhibit more than three digits. Abel (1935) considered *Nanopus vetustus* to be an unrecognizable form and likely not footprints of a tetrapod. We agree that this form was incorrectly identified by Matthew as a tetrapod track and should be regarded as a nomen dubium.

Bipezia bilobata was described from two specimens (Fig. 7A and Figs 7B–D), although only one of these was illustrated by Matthew (1910) (Fig. 7D). He described the ichnogenus as containing spindle-shaped footprints that were pointed at both ends, found usually in laterally coalescing pairs, one print opposite the other. Matthew noted that some imprints are short and round. Imprints are up to 10 mm in length and up to 3 mm in width. They were later considered by Glaessner (1957) to be a junior synonym of the invertebrate ichnotaxon *Isopodichnus*, and were included as such in Häntzschel (1975). Species of *Isopodichnus* are now considered junior synonyms of either *Cruziana* or *Rusophycus* (Keighley and Pickerill 1996).

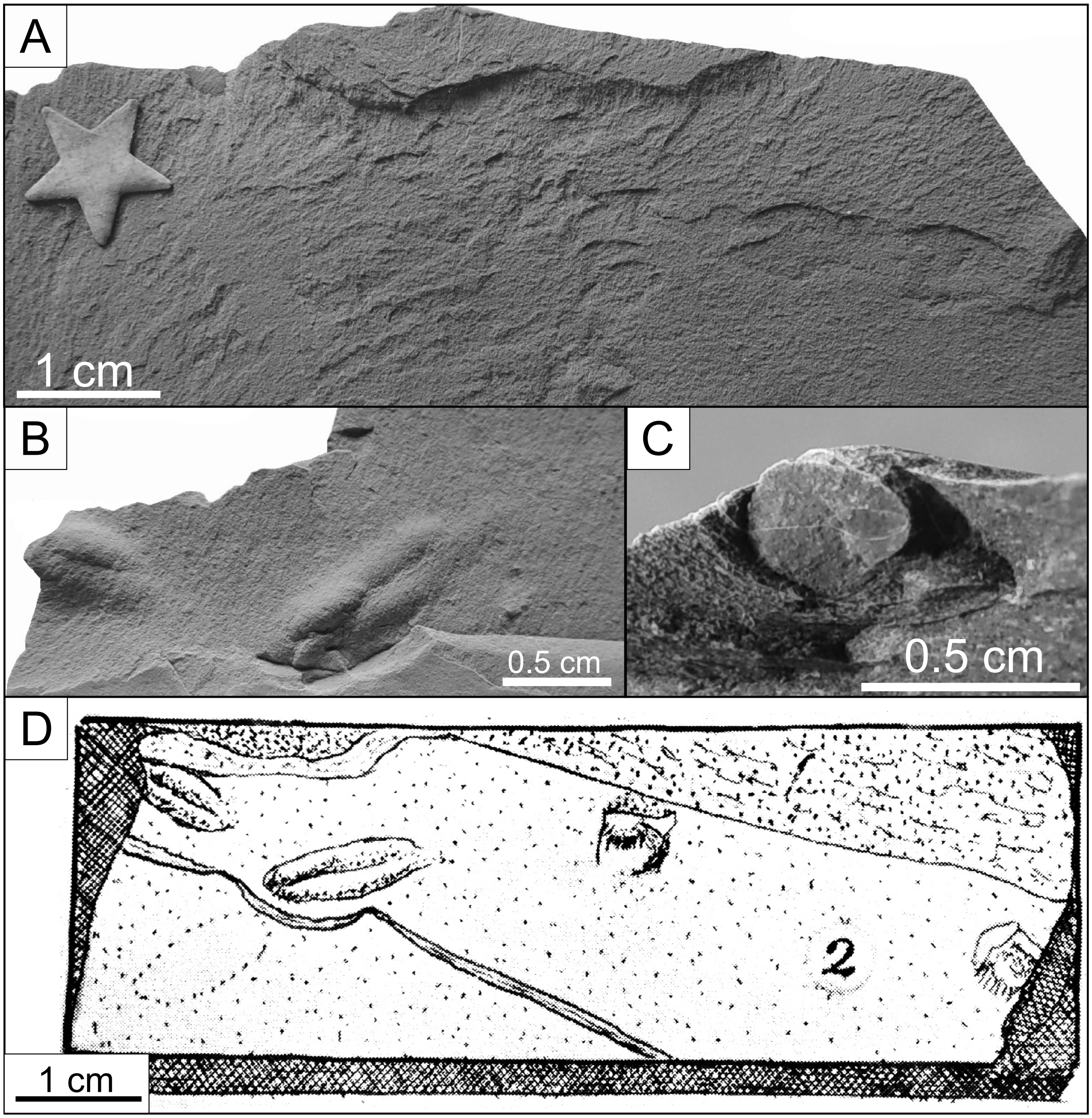

Figure 7. **(A) Photograph (coated) of *Bipezia bilobata* (NBMG 3037); (B–C) Photographs (coated) of Bipezia bilobata (NBMG 3038) showing bilobed feature interpreted by Glaessner (1957) as possible *Isopodichnus* and cross-section interpreted herein as vegetation-induced sedimentary structure; (D) Matthew's (1910) drawing of *Bipezia bilobata* (NBMG 3038).**

We have re-examined the type specimen of *Bipezia bilobata* (NBMG 3038). Indeed, we concur that the surface impression strongly resembles *Rusophycus*. However the three-dimensional nature of the fossil can be examined along the broken edge of the specimen (Fig. 7C). In cross section the 'trace' is a cylindrical tube with an organic rich rind, infilled by fine grey siltstone similar to the sediment encasing it. The surrounding sediment is deformed around the tube. The organic rind suggests that *Bipezia bilobata* is not a surface trace of either an invertebrate or vertebrate, and the deformed sediments are similar to those of Rygel *et al.*'s (2004) vegetation-induced sedimentary structures. These observations suggest that *Bipezia bilobata* represents a hollow tube that the sediments surrounded and encased, rather than any form of infaunal burrow. *Bipezia bilobata* likely represents the remains of a plant stem or root that has been cast in sediment rather than an ichnofossil; Matthew's other, unillustrated, specimen of *Bipezia bilobata* (NBMG 3037) shows that the bilobate impressions do not represent an ichnofossil but are broken fragments of shale that superficially resemble the type specimen. We thus agree with Glaessner (1957) and Häntzschel (1975) that *Bipezia bilobata* does not represent a vertebrate trackway and regard it as a nomen dubium.

CONCLUSION

As Matthew (1910) concluded, specimens he identified as *Hylopus* (?) *variabilis* are poorly preserved tetrapod footprints; we consider that they can now be assigned to *Limnopus.* Matthew published his vertebrate tracks amongst descriptions of arthropod body fossils and invertebrate ichnofossils found in the Upper Carboniferous Lancaster Formation at 'Fern Ledges' and a second locality at Barrack Shore (Fig. 1A). Certainly, some of the vertebrate ichnotaxa he described are indeed dubious as discussed above, but the dismissal of the entire assemblage by Abel (1935) and the subsequent assignment of the ichnotaxa to 'unrecognized or unrecognizable' in the *Treatise on Invertebrate Paleontology* (Häntzschel 1975) essentially removed *Hylopus* (?) *variabilis* from further review by vertebrate ichnologists. Dismissal by previous authors was based in part on the poor quality of preservation of the tracks, and lack of access to the type material. The detailed re-examination of the original material presented here vindicates Matthew's ichnotaxon *Hylopus* (?) *variabilis* as a vertebrate ichnotaxon and it is here reassigned to the ichnogenus *Limnopus* based on the similar ichnotaxobase of their ichnogeneric concepts. Although Lucas and Dalman (2013) considered *Limnopus* a monospecific ichnogenus, *Limnopus variabilis* can be distinguished from *Limnopus heterodactylus* (the other valid ichnospecies of *Limnopus*) in its ichnospecific diagnosis. Matthew's type specimen does not closely match the genus concept of *Hylopus*, nor does it conform to the species concept of *Limnopus heterodactylus* with its short, slender digits with sharply tapered digit terminations. Until further data is available, the ichnospecies *Limnopus variabilis* should be retained.

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