Transition from swimming to walking preserved in tetrapod trackways from the Late Carboniferous of Bjørnøya, Svalbard

Keywords:

- Tetrapod
- Footprints
- Swimming
- Bjørnøya
- Svalbard
- Limnopus
- Carboniferous
- Ichnology

Seán Thór Herron¹, Edward James Fleming², & Michael John Flowerdew²

¹Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, UK, CB2 3EQ

²CASP, West Building, Madingley Rise, Madingley Road, Cambridge, UK, CB3 0UD

E-mail corresponding author (Seán Thór Herron): sth30@cam.ac.uk

Received:
11. April 2020

Accepted:
2. July 2020

Published online:
8. September 2020

The Late Carboniferous was a crucial interval for the establishment of terrestrial ecosystems. A dramatic change in tetrapod distribution and ecology is coupled with an ongoing transition from amphibian to amniote domination. Presented here is a new set of tetrapod footprints from a single slab discovered on the island of Bjørnøya in the Norwegian High Arctic. A three-dimensional photogrammetric model was constructed to allow analysis of the trackway, and palaeoenvironmental observations were taken to provide context to the ichnological determinations. The slab appears to preserve the transition from swimming to walking. Statistical tests provide indication that there is a significant change in locomotive behaviour (swimming to walking) present on the slab ($p = 0.0026$, $n = 15$). This coincides with a change in the preservation style and an apparent change in the depth of water traversed by the tracemaker. Two trackways can be assigned to the ichnogenus *Limnopus* Marsh, 1894 (temnospondyl amphibians). They consist of 36 and 24 prints, respectively, and have widths and lengths of 151 mm x 2149 mm and 166 mm x 1226 mm. Two other trackways represent the traces of indeterminate tetrapods. Palaeoenvironmental analysis suggests that the trackways had lain in a fluvial floodplain setting in a palaeo-river valley system, in agreement with regional-scale analyses. Locomotion analysis suggests that on moving from submerged walking and swimming to terrestrial walking, this large Late Carboniferous temnospondyl increased its pace angulation and lengthened its stride. At ~30°N, these tracks may be the farthest north *Limnopus* trackways yet found in terms of palaeolatitude. They are the first Carboniferous tetrapod traces discovered from Svalbard and are probably among the oldest examples of *Limnopus* yet found.

Introduction

The Late Carboniferous was an important time for the evolution of tetrapods and the environments in which they lived. During the formation of Pangaea, an unprecedented expansion in the ability of tetrapods to exploit ecological niches took place. Herbivory and carnivory (tetrapod-eating) evolved in tetrapods for the first time, adding to insectivory and piscivory (Sues & Reisz, 1998; Sahney et al., 2010). As Pangaea drifted

© Copyright the authors.

This work is licensed under a Creative Commons Attribution 4.0 International License.

Herron, S. T., Fleming, E. J. & Flowerdew, M. J. 2020: Transition from swimming to walking preserved in tetrapod trackways from the Late Carboniferous of Bjørnøya, Svalbard. *Norwegian Journal of Geology* 100, 202012. <https://dx.doi.org/10.17850/njg100-2-6>.

north in the Late Carboniferous, a rainforest collapse and subsequent transition to arid environments at palaeoequatorial to palaeotropical latitudes caused notable changes in tetrapod extinction rates and the distribution of taxa (Sahney et al., 2010; Brocklehurst et al., 2018). This event is referred to as the Carboniferous Rainforest Collapse or the Kasimovian revolution (Lucas, 2019).

Presented in this study is the description and ichnotaxonomic analysis of a new set of large tetrapod trackways discovered from a site of Late Carboniferous age on the Norwegian Arctic island of Bjørnøya (Figure 1). The palaeoenvironmental context is also provided. Few such trackways of this age have been described outside North America, and it is believed this is the first such find from Svalbard. We investigate the possibility that the transition from submerged walking and/or swimming to land-walking is preserved. There is currently limited data concerning the locomotive style of tetrapods during this interval, especially tetrapods of this large size.

Material and methods

The fossil tetrapod footprints in this study were found preserved in convex hyporelief on the underside of a slightly curved, overhanging slab of fine-grained sandstone from the Late Carboniferous Kapp Hanna Formation on Bjørnøya. A total of 785 photographs were combined to produce digital photogrammetric models using Agisoft Photoscan. The models were scaled using targets of known sizes placed on the slab when the photographs were taken. The scaled model chosen for taking measurements and drawing outlines used 96 photographs, and the error in the scale of the model was ± 3.5 mm. Outline sketches of imprints were drawn from the photogrammetric model using Adobe Illustrator. Standard methods

Figure 1. Location of trackways. (A) Simplified geological map of Bjørnøya focusing on the formations relevant to this study. Major faults are shown as black lines, with dashes on the downthrown side. Based on the map by Dallman (1999). For a detailed map of study area (red box), see Figure 2. (B) Location of Bjørnøya in the Svalbard archipelago. (C) Image showing the trackway site. Tracks on underside of bed indicated with arrow. The trackway site is located in the Kapp Hanna formation (yellow) at 74.386N, 18.939E.

were used to take measurements along the trackway (Haubold, 1971; Leonardi, 1987; Voigt, 2005). Sedimentary logs and palaeoflow measurements were taken at the field site to provide the palaeoenvironmental context.

Geological context

Bjørnøya is the southernmost island in the Svalbard archipelago, and is entirely covered by sedimentary rocks ranging from Precambrian to Triassic in age. The ichnological material is contained within the Kapp Hanna Formation, comprising 145 m of fluvial sediments cropping out on the western half of the island (Worsley et al., 2001; Mørk et al., 2014). The Kapp Hanna Formation has tentatively been dated using palynology to the Late Carboniferous, specifically the Moscovian or Kasimovian (Worsley & Edwards, 1976; Worsley et al., 2001). The study area is situated at a section of yellow sandstones, brown mudstones and orange conglomerates along a beach in southwestern Bjørnøya, immediately north of Kapp Kåre (Figures 1 and 2). The trackways are located on the underside of an overhanging slab at 74.386N, 18.939E. Presently, the slab is attached to its bed (remains in situ) and its traces are accessible. The tracks were discovered on a CASP expedition in 2017, and documented during a second CASP expedition in 2018.

Figure 2. Photomosaic overlay on map of the study area. Location of the logs shown in Figures 4 and 5 marked by green stars, moving north to access stratigraphically higher beds. Point 2 is the trackway site (location of photograph in Figure 1C).

Palaeogeography

Palaeolatitudinal information for Bjørnøya is sparse, but a tentative middle Carboniferous location of 30°N is available (Turner & Tarling, 1975), placing Bjørnøya in the Euramerican palaeotropics (Figure 3). More recently, Torsvik & Cocks (2017) confirmed this palaeolatitude for the Late

Figure 3. Palaeogeographic reconstructions showing the location of Bjørnøya (white circle) at 303 Ma (Kasimovian–Gzhelian). Generated using GPlates with data from Matthews et al. (2016). Bjørnøya is located on the tectonic unit of West Svalbard near Euramerica. The upper image (A) shows tectonic subdivisions, whilst the lower image (B) shows regions coloured according to their modern continental affiliation.

Carboniferous, if Bjørnøya is assumed to form part of the West Svalbard tectonic unit (Figure 3). Orogenic activity also peaked during the Late Carboniferous, with the union of Gondwana and Euramerica (also called Laurussia) complete by the earliest Permian to form the Pangaeon supercontinent.

The Carboniferous rainforest collapse that began in the Moscovian and continued into the Kasimovian reduced the extent of rainforest biomes, and could have affected late Carboniferous tetrapod diversity (Sahney et al., 2010). Late Carboniferous wetlands thus gave way to ‘dryland terrestrial ecosystems’ (Falcon-Lang et al., 2006) commonly consisting of red mudstone and sandstone successions accumulated on well-drained alluvial plains, increasingly stabilised by vegetation (Davies & Gibling, 2011). Recent work has proposed that this ‘collapse’ may have been more gradual (Dunne et al., 2018) and is closely linked to an intensification of global warming and cooling cycles in the Late Carboniferous (Falcon-Lang et al., 2018).

Results and discussion

A Late Carboniferous river valley – Palaeoenvironmental context

Two formations are exposed in the studied area: the Bashkirian–Moscovian Kapp Kåre Formation, and the stratigraphically overlying Moscovian–Kasimovian Kapp Hanna Formation, which contains the trackways. Previous authors have noted that these formations represent a complex and highly variable interplay of depositional environments (Worsley et al., 2001). Both formations were examined to give an indication of the depositional history and palaeoenvironmental context of the trackway site.

The Kapp Kåre Formation is dominated by cherty limestone. It is exclusively marine and, in the upper part of the Formation, is thought to have been deposited by debris flows triggered by syndepositional tectonism (Worsley et al., 2001; Mørk et al., 2014). The Kapp Hanna Formation is composed of a series of conglomerates, sandstones and mudstones. The conglomerates become increasingly mature up-section. Angular limestone clasts (lithology suggesting reworked clasts from the underlying Kapp Kåre limestone) become less frequent, giving way to a greater abundance of rounded, multi-coloured cherts and extrabasinal clasts owing to the erosion of pre-Devonian material from the eastern topographic highs of the island (Gradstein et al., 2013).

The Kapp Hanna Formation contains abundant trace fossils, with invertebrate traces and macrofloral impressions commonly found alongside physical sedimentary structures such as desiccation cracks. The logged sections correlated over 200 m in this study (Figures 4 and 5; logs taken at locations shown in Figure 2) show lateral variation in the thickness of the Kapp Hanna Formation. Beds can be followed and directly seen expanding from thin sand layers to interbedded mudstones and sandstones. Extensive lateral variation is observed in these southern exposures of the Kapp Hanna Formation, echoing the observations of Worsley et al. (2001).

The many internal minor erosion surfaces, mud drapes and intraclast-rich breccias imply frequent fluctuation in supply of material. This is consistent with variable (seasonal, monsoonal or ephemeral) flow (Miall, 1988). However, the environment must also have been calm enough for wood to bunch and settle and for its impressions to be preserved. Drying of puddles must have been common given the abundance of desiccation cracks. The red-to-brown colour of the sandstones and mudstones could imply the environment was oxidising and subaerial.

Bedding surfaces of the mudstone horizons commonly appear to show rain-pitting, and there appear to be isolated gley palaeosols present. Gley palaeosols are formed by soils subjected to long periods of waterlogging, preserved here as poorly consolidated grey clay. Such palaeosols are typical of Pennsylvanian delta plains (Kraus, 1999).

Collating these observations, the Kapp Hanna Formation is interpreted to represent a fluvial floodplain environment. Numerous lenses of sand and mud with evidence of variably wet and dry conditions (mud drapes, desiccation cracks), and terrestrial fauna (trackways) and flora (wood impressions), represent fluvial deposits and their surroundings. Intermittent debris flows, incorporating material from eastern topographic highs formed the conglomerates which in places scour and erode into the underlying strata. This agrees with the review from Mørk et al. (2014), based on the original work in Worsley et al. (2001), who suggested that the Kapp Hanna Formation is formed by floodplain and valley-fill deposits due to rivers draining to the northwest, as the island was tilted up in the east at this time. Similar facies have previously been interpreted as formed in a floodplain environment with a persistently high water table (Tucker & Smith, 2004; Hedge et al., 2018).

Figure 4. Sedimentary log 1, taken through the Kapp Kåre Formation—Kapp Hanna Formation contact. Locations of log sites are shown in Figure 2. Some beds follow continuously to log 2 (trackway site, approx. 175 m north), where the fluvial sequence is expanded and lenses of mud and fine sand are developed. The analogous sandstone to the fossiliferous bed at the trackway site is indicated by the arrow. The green line indicates analogous sequences constrained by beds continuous between log 1 and log 2. The “Top conglomerate” is a distinctive pink conglomerate found at the base or top of each of logs 1–3.

Without better age constraint on the Kapp Hanna Formation, its context regarding the Carboniferous rainforest collapse remains uncertain given that well-drained, seasonally dry environments were common even in the pre-collapse Pennsylvanian wetlands of the so-called coal age (DiMichele et al., 2010). However, despite the timing, there is no evidence of coal swamp (rainforest) deposits within the Kapp Hanna Formation. Whether surrounding rainforests were common and extensive or rare and receding, life in the immediate vicinity would have been inhabiting a drier, alluvial floodplain environment of the kind that became common toward the very end of the Carboniferous and completely dominant by the earliest Permian.

Figure 5. Sedimentary logs 2 and 3, taken in the Kapp Hanna Formation. Locations of log sites are shown in Figure 2. Log 2 is taken at the trackway site. The footprint and arrow indicate the location of the trackway slab. The green line indicates correlation between the logs, and the 'Top conglomerate' is a distinctive pink conglomerate found at the base or top of each of logs 1–3. Sandy and muddy layers are much thicker in log 2 than in log 1, indicative of the high along-strike variance in the Kapp Hanna Formation. No macrofossils or macrofloral impressions were found at log site 3. This could have been due to the dominance of conglomerate at this site, or due to the lack of exposed bedding surfaces in the area. Beds across the Kapp Hanna Formation show great internal variation.

Mud-rich and fine sandy channel bodies such as the bed containing the trackways likely represent waterholes formed by the seasonal cessation of flow (Falcon-Lang et al., 2004). The system may resemble the ephemeral drainages of modern-day central Australia (Davies & Gibling, 2003).

Systematic ichnology

The slab shows several trackways of a quadrupedal tetrapod with plantigrade to semiplantigrade imprints, preserved in convex hyporelief (as natural casts; Figures 6, 7 and 8). Quantitative data was taken from trackways 1 and 2 (see labels 't1' and 't2', respectively, in Figure 7). The mean pace angulation is 86–90 degrees. The pes is pentadactyl and impressed closely behind the manus but not overlapping. The mean pes length is 66 mm and the mean pes width is 51 mm. Digit length increases from I to IV with digit IV the longest. Digit II has the same length as digit V. The sole is commonly oval-shaped, short and broad, and deeply impressed. The manus is tetradactyl and has a mean length of 60 mm, and a mean width of 39 mm. Digit length increases from I to II and digit II is the longest digit overall. Digit III has almost the same length as digit II, and digit IV is slightly shorter (approximately 85% of digit III). Impressions of the palm are commonly well preserved and deeply impressed.

At least 15 manus-pes couples and 52 prints from t1 and t2 can be assigned to this tracemaker. The digits are commonly rounded (i.e., claws were absent or are not preserved), though preservation of digit tips is generally imperfect. The fifth digit of the pes is not always visible, but the pes can still be identified

Figure 6. Orthomosaic image generated from the 3D model of the trackway slab, showing true colour. The dark spots in the centre of the image are artifacts of lighting conditions in the original photos. The spots have been artificially brightened.

Figure 7. Interpretive sketch of the impressions on the trackway slab. Trackways are colour-coded and numbered t1–t4. Arrows show the inferred direction of tracemaker movement. Trackways 1 (red) and 2 (green) are classified as *Limnopus* trackways. Note that the footprints are lost while the continuous tail trace undergoes no change in preservation quality. This may mean that the animal is swimming or jumping in this portion of the trackway. Trackways 3 (purple) and 4 (blue) lack the information for confident ichno-classification, but appear to represent the subaqueous locomotion of a tracemaker of the same size as trackways 1 and 2. Best manus (m) and pes (p) prints detailed in Figure 8 are highlighted. Error in the scale is ± 3.5 mm.

by the relative length of digit IV. Trackway 1 comprises 36 prints and a tail trace, with a mean width of 151mm and a length of 2149 mm. Trackway 2 shows 24 prints and has a mean width of 166 mm and a length of 1226 mm.

Trackways 3 and 4 (t3 and t4; Figure 7) represent the traces of indeterminate tetrapods and are not sufficiently well preserved for systematic description. Superficially, they appear to represent the subaqueous locomotion of a tracemaker of the same size as the tracemaker of trackways 1 and 2.

Figure 8. Information on the best manus (m) and pes (p) prints present on the slab. A and D are topographic heat maps for manus and pes, respectively. B and E are true colour images with the digits labelled with roman numerals. C and F are cross-sections taken through the lines of section indicated on B and E, respectively, drawn to best accentuate the digits. The vertical scale on the cross-sections and heat maps is relative to a best-fit plane drawn below the model.

Tracemakers

The better-preserved trackways closely resemble those of the ichnogenus *Limnopus* Marsh, 1894, which was first introduced for tetrapod footprints from the Pennsylvanian of Kansas (Marsh, 1894) and is thought to represent the pedal impressions of a temnospondyl amphibian (Haubold 1971; Voigt 2005). The impressions also bear similarity to *Batrachichnus* Woodworth, 1900 and it has been noted across the field that distinguishing *Limnopus* and *Batrachichnus* can be challenging (e.g., Voigt & Lucas, 2015).

There is no evidence of a basal pad proximal to digit I on either pes or manus, a characteristic feature of *Limnopus* (Voigt, 2005). However, preservation of such detailed features depends strongly on the substrate (Sarjeant & Leonardi, 1987). These tracks were likely laid in wet, muddy sand. This means the tracks were vulnerable to distortion as the foot left the print (the mud sticks to the foot) and as water left the substrate.

Tucker & Smith (2004) went as far as to synonymize *Batrachichnus* and *Limnopus*, based on similar morphology and a continuum of sizes between the two forms. Lucas et al. (2011) rejected this proposal, and continued to consider them separate ichnogenera based on size. More authors have

retained *Batrachichnus* as a useful term to describe very small footprints representing this morphotype (e.g., Falcon-Lang et al., 2010). The possibility that *Batrachichnus* could represent juvenile forms of *Limnopus* must also be considered. Voigt (2005) has proposed that the length of digit IV on the manus, which is considered to reach 80–90% of digit III in *Limnopus* but only 60–70% in *Batrachichnus*, could be a distinguishing feature. He also proposed that *Batrachichnus* pedal tracks range in size from less than 10 mm up to almost 40 mm, whereas the pedal tracks of *Limnopus* may well exceed 60 mm in length. This find cannot contribute to the question of synonymy between *Limnopus* and *Batrachichnus*, but due to their large size the tracks described in this work are more similar to the ichnological concept of *Limnopus* than that of *Batrachichnus*, and will be taken as such. However, the lack of a broad-oval pad and strongly inwardly rotated manual tracks -- both characteristic features of *Limnopus* according to Voigt (2005) -- are an unresolved cause for concern.

Limnopus is most commonly considered to be the track of eryopoid temnospondyls (Baird, 1965; Haubold, 1971, 1996; Voigt, 2005). These Late Carboniferous amphibians were supposedly able to spend a considerable part of their life outside of water in sub-adult to adult ontogenetic stages (Haubold, 1996; Voigt, 2005).

Preserving a true substrate and the transition from swimming to walking

Sedimentary features on the slab surface demonstrate that the sedimentary surface seen in the present day represented the sediment-water or sediment-air interface at the time of deposition. That is, a 'true substrate' is preserved (Davies & Shillito, 2018). Reference here is to a 'true substrate' *sensu* Davies & Shillito (2018) rather than to the substrate in which the footprints were laid. That is, a record of the sediment—water or sediment—air interface rather than a random surface from within a sedimentary packet exposed by erosion. Strictly, a cast of the true substrate has been preserved (recall the footprints are in convex hyporelief on the underside of a slab). These sedimentary features include microbially induced sedimentary structures (MISS) and infilled burrows.

Evidence that the cast of the true substrate is preserved is presented in Figure 9. Circular features could be raindrop impressions or gas-escape structures related to microbial activity. Since the features are in convex hyporelief on the underside of the slab, raindrop impressions are more likely. 'Elephant-skin' texture (MISS) found on the slab is formed by the binding action of microbial mats at the sediment surface. These mats form on the bottoms of pools. Faint, connected linear traces represent either infilled horizontal burrows or mud-cracks. Infilled ends of vertical burrows are preserved, again indicating that the surface was in connection with either water or air at the time of preservation.

Because a cast of the true substrate is preserved, the trace fossil may be viewed as recording the true interaction of the tracemaker with the sediment-water interface. The varied preservation and deformation in the footprints can therefore be used to examine the subaqueous locomotion of the tracemaker.

The preservation style of the footprints does show a clear change across the slab. Scratch-like supposed 'swim' traces transition sharply to more pristinely preserved footprints. The irregular, scratch-like markings occur as the digits are dragged through sediment in relatively shallow water and/or mud is pooled behind the hands and feet as the animal propels itself forward (Niedźwiedzki, 2015). Regularly shaped footprints are presumably laid down in shallower water or at the sediment-air interface, during walking.

Because the slab appears to represent preservation of a true substrate, the curved bed on which the trackways are imprinted can be considered to represent a drape infill of the true palaeosurface (where the tracemaker walked). The surface preserves a 'true pool-bottom'. The convex curvature of the bed should therefore provide a proxy for the depth of the pool through which the tracemaker walked. That is, the bed surface near the bottom of the curvature should represent parts of the palaeosurface that were actually deeper underwater at the time the traces were made. A cross-section through trackway 1 is shown in Figure 10.

As Figure 10 shows, the portions of the trackway with 'swim-like' traces and scratches occur in the deeper parts of the pool. This portion of the slab also shows the footprints being lost while only the tail drag remains, suggesting a swim or subaqueous jump (compare Figure 7 and Figure 10). This presents independent evidence supporting a change in tracemaker locomotion across the slab. Furthermore, the mean manus pace angulation is statistically lower in the 'swimming' region of the trackway than in the walking part ($p = 0.0026$, $n = 15$), and the stride also lengthens. Only manus prints were used for this measurement as they are best preserved across the transition.

There are thus three lines of evidence for a transition from swimming to walking: the preservation style of the footprints changes; the quantitative trackway parameters show a statistically significant change; and both of these transitions apparently coincide with a transition from the deepest underwater to the shallower parts of the preserved slab.

It would seem then that on transition from swimming to walking, the behaviour of this large Late Carboniferous temnospondyl was to increase the pace angulation and lengthen the stride. The same behaviour is seen in modern salamanders, and the observations agree with studies on smaller tetrapod tracks of similar age preserving the transition (e.g., Petti et al., 2014).

Figure 10. Vertical section through the trackway showing evidence of subaqueous locomotion. (A) Topographic heat map of trackway slab showing line of section a—a' drawn through t1. (B) Vertical section along line a—a' with interpretation of tracemaker behaviour. Representative examples of the changing morphology along the trackway are shown (taken from the outlines in Figure 7). The change in footprint morphology and in pace angulation and stride length indicate a transition in locomotive style. These changes coincide with the change in apparent depth traversed by the tracemaker.

Significance and comparison with existing literature

The finds in Bjørnøya are the first Carboniferous tetrapod tracks reported from Svalbard, and join recent finds in Poland (Niedźwiedzki, 2015), Greenland (Milàn et al., 2016) and Italy (Marchetti et al., 2018) to expand the range and knowledge of Euramerican Late Carboniferous tetrapods. The Bjørnøya site shares many features with sites of a similar age. The environment apparently had a fluvial association, abundant flora, a relatively high water-table and possibly a relatively warm and humid climate.

The recent Greenland find may represent the oldest *Limnopus* traces yet known (Bashikirian–Moscovian; Milàn et al., 2016). This means the Moscovian–Kasimovian age for the Kapp Hanna Formation places the Bjørnøya trackways among the oldest examples of this ichnogenus in the world.

Limnopus tracks are, to this point, known exclusively from palaeoequatorial regions of Pangea (Milàn et al., 2016). The palaeolatitude of approximately 30°N found here could, if correct, locate these the northernmost *Limnopus* trackways to the edge of the palaeotropics. Recent finds from the Devonian Antarctic circle (Gess & Ahlberg, 2018) imply that early tetrapods were probably not restricted to equatorial or tropical regions.

Traces of swimming tetrapods are common in the Carboniferous (Petti et al., 2014; Niedźwiedzki, 2015) but the preservation of the transition from swimming to walking is rare, and the Bjørnøya site provides the first such example for large amphibians.

Conclusions

At least four tetrapod trackways have been recorded on a single slab from the Late Carboniferous Kapp Hanna Formation in southwest Bjørnøya, Svalbard. Palaeoenvironmental observations suggest that the surrounding environment represents a palaeotropical river valley system, probably a relatively open environment with abundant flora. Extensive lateral and vertical variation in the Kapp Hanna Formation indicates that the valley was sporadically or seasonally flooded. The impressions were probably preserved when footprints lain in a wet substrate dried and hardened, only to be filled in a subsequent flood event by slowly settling suspended sediment. Sedimentary surface features such as infilled burrows indicate that the bed surface preserves a true substrate, and hence a snapshot of the true pool-bottom traversed by the tracemaker. This allows reconstruction of the depth of the pool through which the tracemaker was moving. A change in preservational style and the manus pace angulation and stride length combine with this changing pool depth to indicate a transition from swimming to walking.

The tracemaker for at least two of the trackways is probably *Limnopus* Marsh, 1894.. *Limnopus* is thought to represent the trace of an eryopoid temnospondyl amphibian.

The transition from swimming to walking has not previously been observed for large Late Carboniferous tetrapods. On moving from swimming to walking, this large Late Carboniferous temnospondyl increased its pace angulation and lengthened its stride. These tracks may also be the northernmost *Limnopus* trackways yet found in terms of palaeolatitude, showing for the first time that the eryopoids inhabited the northern reaches of the palaeotropics. They are the first Carboniferous tetrapod traces discovered from Svalbard, and are probably among the oldest examples of *Limnopus* yet found (Moscovian–Kasimovian).

Acknowledgements. Thanks to Neil Davies for comments and improvements, and to Alex Lipp for insight when the traces were first discovered in 2017. Thanks are also extended to Magdalena Bieszczuk for assistance with photogrammetric software. CASP provided the opportunity and funding for fieldwork and analysis of the specimens. The authors thank the reviewers Atle Mørk and Franz-Josef Lindemann for their comments, which greatly improved the clarity of the text, figures and arguments, and Trond Slagstad for help during the editorial process.

References

- Baird, D. 1965: Footprints from the Cutler Formation. U.S. *Geological Survey Professional Paper* 503, 47–50.
- Brocklehurst, N., Dunne, E.M., Cashmore, D.D. & Fröbisch, J. 2018: Physical and environmental drivers of Paleozoic tetrapod dispersal across Pangaea. *Nature Communications* 9, 1–12. <https://doi.org/10.1038/s41467-018-07623-x>.
- Dallmann, W. 1999: Upper Palaeozoic lithostratigraphy. *Lithostratigraphic Lexicon of Svalbard*. Norsk Polarinstitut, Tromsø, pp. 127–214.
- Davies, S.J. & Gibling, M.R. 2003: Architecture of coastal and alluvial deposits in an extensional basin: the Carboniferous Joggins Formation of eastern Canada. *Sedimentology* 50. <https://doi.org/10.1046/j.1365-3091.2003.00553.x>.
- Davies, N.S. & Gibling, M.R. 2011: Evolution of fixed-channel alluvial plains in response to Carboniferous vegetation. *Nature Geoscience* 4, 629–633. <https://doi.org/10.1038/ngeo1237>.
- Davies, N.S. & Shillito, A.P. 2018: Incomplete but intricately detailed: The inevitable preservation of true substrates in a time-deficient stratigraphic record. *Geology* 46, 679–682. <https://doi.org/10.1130/G45206.1>.
- DiMichele, W.A., Cecil, C.B., Montañez, I.P. & Falcon-Lang, H.J. 2010: Cyclic changes in Pennsylvanian paleoclimate and effects on floristic dynamics in tropical Pangaea. *International Journal of Coal Geology* 83, 329–344. <https://doi.org/10.1016/j.coal.2010.01.007>.
- Dunne, E.M., Close, R.A., Button, D.J., Brocklehurst, N., Cashmore, D.D., Lloyd, G.T. & Butler, R.J. 2018: Diversity change during the rise of tetrapods and the impact of the ‘Carboniferous rainforest collapse’. *Proceedings of the Royal Society B: Biological Sciences* 285. <https://doi.org/10.1098/rspb.2017.2730>.
- Falcon-Lang, H.J., Rygel, M.C., Calder, J.H. & Gibling, M.R. 2004: An early Pennsylvanian waterhole deposit and its fossil biota in a dryland alluvial plain setting, Joggins, Nova Scotia. *Journal of the Geological Society* 161, 209–222. <https://doi.org/10.1144/0016-764903-109>.
- Falcon-Lang, H.J., Benton, M.J., Braddy, S.J. & Davies, S.J. 2006: The Pennsylvanian tropical biome reconstructed from the Joggins Formation of Nova Scotia, Canada. *Journal of the Geological Society, London* 163, 561–576. <https://doi.org/10.1144/0016-764905-063>.
- Falcon-Lang, H.J., Gibling, M.R., Benton, M.J., Miller, R.F. & Bashforth, A.R. 2010: Diverse tetrapod trackways in the Lower Pennsylvanian Tynemouth Creek Formation, near St. Martins, southern New Brunswick, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 296, 1–13. <https://doi.org/10.1016/j.palaeo.2010.06.020>.
- Falcon-Lang, H.J., Nelson, W.J., Heckel, P.H., DiMichele, W.A. & Elrick, S.D. 2018: New insights on the stepwise collapse of the Carboniferous Coal Forests: Evidence from cyclothems and coniferopsid tree-stumps near the Desmoinesian–Missourian boundary in Peoria County, Illinois, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 490, 375–392. <https://doi.org/10.1016/j.palaeo.2017.11.015>.

- Gess, R. & Ahlberg, P.E. 2018: A tetrapod fauna from within the Devonian Antarctic Circle. *Science* 360, 1120–1124. <https://doi.org/10.1126/science.aag1645>.
- Gradstein, F.M., Davydov, V.I. & Hammer, Ø. 2013: Carboniferous cyclic sedimentation and micropaleontology of Bear Island, Arctic Norway. *Newsletters on Stratigraphy* 46, 303–317. <https://doi.org/10.1127/0078-0421/2013/0036>.
- Haubold, H. 1971: Ichnia amphibiorum et reptiliorum fossilium. *Encyclopedia of Paleoherpétology* 18, 1–124.
- Haubold, H. 1996: Ichnotaxonomie und Klassifikation von Tetrapodenfährten aus dem Perm. *Hallesches Jahrbuch für Geowissenschaften B* 18, 23–88.
- Hedge, J., Shillito, A.P., Davies, N.S., Butler, R.J. & Sansom, I.J. 2018: Invertebrate trace fossils from the Alveley Member, Salop Formation (Pennsylvanian, Carboniferous), Shropshire, UK. *Proceedings of the Geologists' Association* 130, 103–111. <https://doi.org/10.1016/j.pgeola.2018.10.002>.
- Kraus, M.J. 1999: Paleosols in clastic sedimentary rocks: their geologic applications. *Earth-Science Reviews* 47, 41–70. [https://doi.org/10.1016/S0012-8252\(99\)00026-4](https://doi.org/10.1016/S0012-8252(99)00026-4).
- Leonardi, G. 1987: *Glossary and Manual of Tetrapod Footprint Palaeoichnology*. Ministerio Minas Energie, Departamento Nacional da Produção Mineral, Brasília.
- Lucas, S.G. 2019: An ichnological perspective on some major events of Paleozoic tetrapod evolution. *Bollettino della Società Paleontologica Italiana* 58, 223–266.
- Lucas, S.G., Voigt, S., Lerner, A.J. & Nelson, W.J. 2011: Late Early Permian continental ichnofauna from Lake Kemp, north-central Texas, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 308, 395–404. <https://doi.org/10.1016/j.palaeo.2011.05.047>.
- Marchetti, L., Petti, F.M., Zoboli, D. & Pillola, G.L. 2018: Vertebrate and Invertebrate Trace Fossils in the Late Pennsylvanian (Carboniferous) Fluvio-Lacustrine San Giorgio Basin (South-West Sardinia): Remarks on the Oldest Continental Ichnoassociation of Italy. *Ichnos: An International Journal for Plant and Animal Traces* 25, 94–105. <https://doi.org/10.1080/10420940.2017.1337572>.
- Marsh, O.C. 1894: Footprints of vertebrates in the Coal Measures of Kansas. *American Journal of Science* 48, 81–84. <https://doi.org/10.2475/ajs.s3-48.283.81>.
- Matthews, K.J., Maloney, K.T., Zahirovic, S., Williams, S.E., Seton, M. & Müller, R.D. 2016: Global plate boundary evolution and kinematics since the late Paleozoic. *Global and Planetary Change* 146, 226–250. <https://doi.org/10.1016/j.gloplacha.2016.10.002>.
- Miall, A.D. 1988: Architectural elements and bounding surfaces in fluvial deposits: Anatomy of the Kayenta Formation (Lower Jurassic), Southwest Colorado. *Sedimentary Geology* 55, 233–262. [https://doi.org/10.1016/0037-0738\(88\)90133-9](https://doi.org/10.1016/0037-0738(88)90133-9).
- Milàn, J., Klein, H., Voigt, S. & Stemmerik, L. 2016: First record of tetrapod footprints from the Carboniferous Mesters Vig Formation in East Greenland. *Bulletin of the Geological Society of Denmark* 64, 69–76.

Mørk, A., Gjelberg, J.G. & Worsley, D. 2014: *Bjørnøya – an Upper Paleozoic-Triassic window into the Barents Shelf*. Geological Society of Norway, Trondheim, 50 pp.

Niedźwiedzki, G. 2015: Carboniferous tetrapod footprints from the Lublin Basin, SE Poland. *GFF* 137, 57–65. <https://doi.org/10.1080/11035897.2014.945618>.

Petti, F.M., Bernardi, M., Ashley-Ross, M.A., Berra, F., Tessarollo, A. & Avanzini, M. 2014: Transition between terrestrial-submerged walking and swimming revealed by Early Permian amphibian trackways and a new proposal for the nomenclature of compound trace fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 410, 278–289. <https://doi.org/10.1016/j.palaeo.2014.05.032>.

Sahney, S., Benton, M.J. & Falcon-Lang, H.J. 2010: Rainforest collapse triggered Carboniferous tetrapod diversification in Euramerica. *Geology* 38, 1079–1082. <https://doi.org/10.1130/G31182.1>.

Sarjeant, W.A.S. & Leonardi, G. 1987: Substrate and Footprints. In Leonardi, G. (ed.): *Glossary and Manual of Tetrapod Footprint Palaeoichnology*, Ministerio Minas Energie, Departamento Nacional da Produção Mineral, Brasilia.

Sues, H.-D. & Reisz, R.R. 1998: Origins and early evolution of herbivory in tetrapods. *Trends in Ecology & Evolution* 13, 141–145. [https://doi.org/10.1016/S0169-5347\(97\)01257-3](https://doi.org/10.1016/S0169-5347(97)01257-3).

Torsvik, T.H. & Cocks, R.M. 2017: *Earth History and Palaeogeography*. Cambridge University Press. <https://doi.org/10.1017/9781316225523>.

Tucker, L. & Smith, M.P. 2004: A multivariate taxonomic analysis of the Late Carboniferous vertebrate ichnofauna of Alveley, southern Shropshire, England. *Palaeontology* 47, 679–710. <https://doi.org/10.1111/j.0031-0239.2004.00377.x>.

Turner, P. & Tarling, D.H. 1975: Implications of new palaeomagnetic results from the Carboniferous System of Britain. *Journal of the Geological Society of London* 131, 469–488. <https://doi.org/10.1144/gsjgs.131.5.0469>.

Voigt, S. 2005: *Die Tetrapodenichnofauna des kontinentalen Oberkarbon und Perm im Thüringer Wald – Ichnotaxonomie, Paläoökologie und Biostratigraphie*. Cuvillier Verlag Göttingen.

Voigt, S. & Lucas, S.G. 2015: Permian tetrapod ichnodiversity of the Prehistoric Trackways National Monument (south-central New Mexico, USA). *New Mexico Museum of Natural History and Science Bulletin* 65, 153–167.

Woodworth, J. 1900: Vertebrate footprints on Carboniferous shales of Plainville, Massachusetts. *Geological Society of America Bulletin* 11, 449–454. <https://doi.org/10.1130/GSAB-11-449>.

Worsley, D. & Edwards, M.B. 1976: The upper Palaeozoic succession of Bjørnøya. *Norsk Polarinstitutt Årbok* 1974, 17–34.

Worsley, D., Agdestein, T., Gjelberg, J.G., Kirkemo, K., Mørk, A., Nilsson, I., Olaussen, S., Steel, R.J. & Stemmerik, L. 2001: The geological evolution of Bjørnøya, Arctic Norway: implications for the Barents Shelf. *Norsk Geologisk Tidsskrift* 81, 195–234.