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First record of tetrapod footprints from the Carboniferous Mesters Vig Formation in East Greenland

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A single slab with Late Palaeozoic tetrapod footprints from East Greenland has been housed at the Natural History Museum of Denmark for decades without scientific notice. The specimen comes from the Mesters Vig Formation of northern Scoresby Land in East Greenland and contains a monospecific assemblage of tetrapod footprints that we assign to *Limmopus* Marsh 1894. As there is no significant morphological difference from other records of this ichnogenus from North America, Europe and North Africa, the described tetrapod footprints can be referred to eryopoid temnospondyl trackmakers. *Limmopus* is well-known from Upper Carboniferous and Lower Permian continental deposits of palaeoequatorial Pangea. Identification of *Limmopus* tracks is in agreement with the supposed Late Carboniferous age of the Mesters Vig Formation and thereby also the first evidence of Carboniferous tetrapods from Greenland.

Keywords: Carboniferous, vertebrate tracks, *Limmopus*, Temnospondyli, Traill Ø Group, Mesters Vig Formation.

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A small sandstone slab was recently noted in the Greenland exhibition hall of the Natural History Museum of Denmark in Copenhagen, where it was on display labelled as “Permian reptile tracks” without further information. According to the original label, the specimen comes from Upper Carboniferous strata of East Greenland and was collected by E. Witzig during field work in 1950. Though the provenance and story of their discovery are supported by a firsthand account (Gilberg 1992), the fossil footprints have never been addressed in any scientific report. Thus, we present the first detailed description and ichnotaxonomic evaluation of the fossil vertebrate tracks and briefly discuss the biostratigraphy and depositional environment of the track-bearing strata. Other aspects discussed are palaeobiogeography and palaeoecology because this is the first evidence of Carboniferous tetrapods from Greenland.

Material and methods

This work is based on fossil tetrapod footprints preserved in convex hyporelief on the lower surface of a slab of dark-brown, fine- to medium-grained sandstone from Upper Carboniferous strata of East Greenland. The specimen consists of two well-fitting pieces that measure about 50 cm in total length, 23.5 cm in total width and 1.5 cm in average thickness. It is stored at the Natural History Museum of Denmark in Copenhagen and catalogued as MGUH 31556. In order to study the fossil tetrapod tracks, the track-bearing slab was photographed under obliquely incident artificial light. Outline sketches of all imprints were drawn on transparency film and digitised with vector-based drawing software. A digital photogrammetric model was generated from 134 close-range photographs using Agisoft Photoscan. Measurements of fossil

tetrapod tracks were taken using standard methods (Haubold 1971; Leonardi 1987; Voigt 2005).

Institutional abbreviations used are: MGUH, Natural History Museum of Denmark; YPM, Yale Peabody Museum, New Haven, Connecticut, USA; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA.

Geological Setting

MGUH 31556 was found about 400 m above sea level on the slopes of the Langelinie mountain (72°09' N, 24°07' W) in the vicinity of the former lead mine at Mesters Vig, northern Scoresby Land, East Greenland (Fig. 1). In this part of East Greenland, the Carboniferous succession is up to 2000 m thick and composed of continental sediments that were deposited in a N–S trending, at least 350 km long rift basin extending

from Jameson Land in the south to Clavering Ø in the north (Fig. 1; Witzig 1954; Kempter 1961; Vigran *et al.* 1999).

The Carboniferous deposits of northern Scoresby Land are referred to the Mesters Vig Formation of the Traill Ø Group. The Mesters Vig Formation is subdivided into five members (Fig. 2; Witzig 1954; Kempter 1961; Perch-Nielsen *et al.* 1972). The base of the formation is not exposed in northern Scoresby Land, but elsewhere the continental Carboniferous sediments are seen to rest unconformably on Devonian and older rocks (Vigran *et al.* 1999). The formation is unconformably overlain by marine deposits of the Upper Permian Foldvik Creek Group.

MGUH 31556 was found loose and its exact stratigraphic position is unknown, although it most likely belongs to either the Blyklippen or Profilbjerget Member of the Mesters Vig Formation. All sediments of the Mesters Vig Formation contain a palynoflora dominated by *Potonieisporites* and have been correlated to

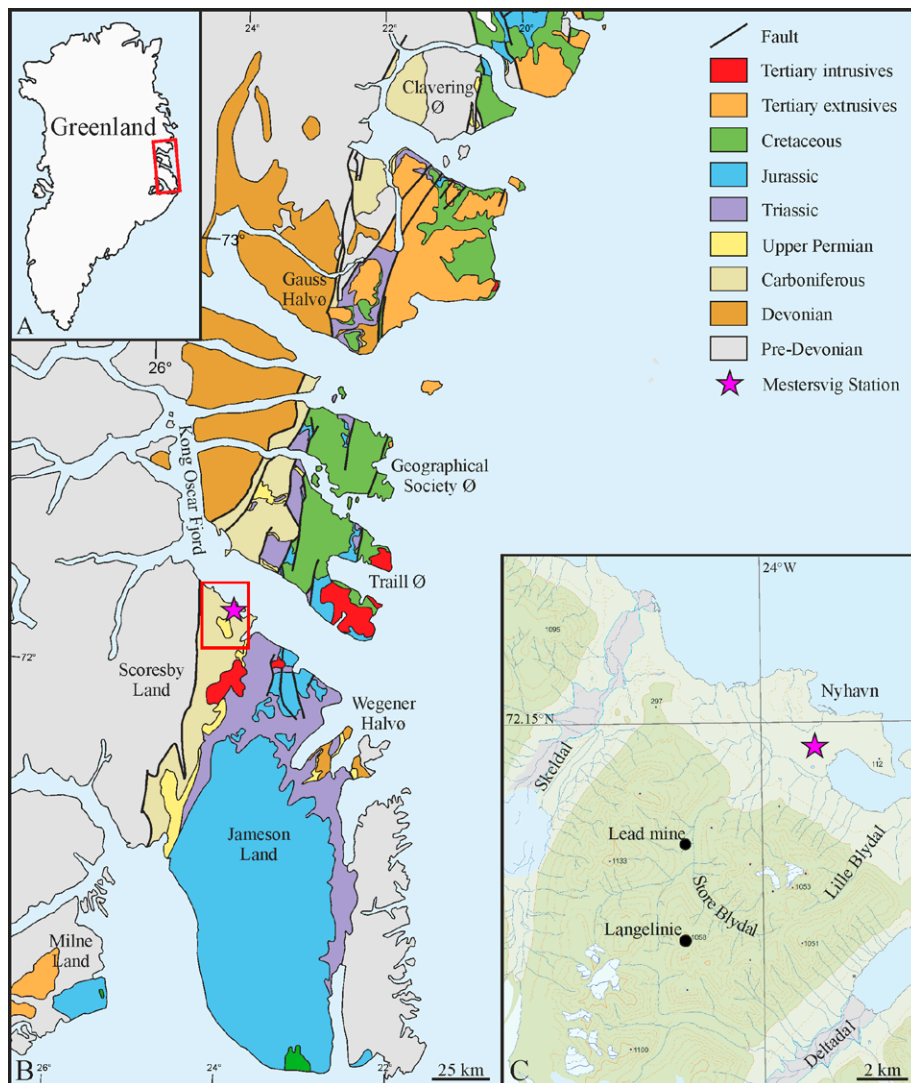


Fig. 1. Maps showing the locality on the east coast of Greenland where the track-bearing slab was found. **A:** Index map. **B:** Simplified geological map of the area between Jameson Land and Clavering Ø showing the distribution of Carboniferous non-marine sediments in central East Greenland. **C:** Detailed map showing the location of Langelinie in northern Scoresby Land where the track-bearing slab was found by E. Witzig in 1950. Maps modified from Stemmerik *et al.* (1997) and Higgins (2010).

the lower Cisuralian ('Autunian') of Europe (Piasecki 1984). Based on correlation to other Arctic microfloras, Vigran *et al.* (1999) concluded that this palynoflora is of Late Carboniferous rather than Early Permian age and correlated it with the Westphalian A RA Miospore Zone sensu Clayton *et al.* (1977), which corresponds to the upper Bashkirian to lower Moscovian stages (Fig. 2).

Systematic ichnology

Ichnogenus Limmopus Marsh 1894

Type ichnospecies. Limmopus vagus Marsh 1894.

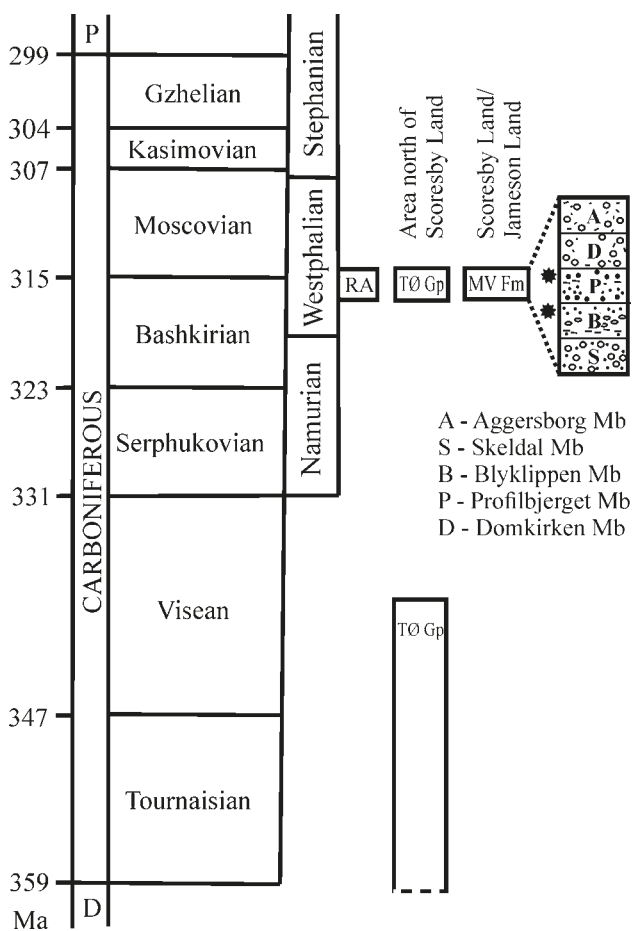


Fig. 2. Stratigraphy of the Carboniferous non-marine succession in East Greenland showing the age of the Traill Ø Group (TØ Gp) and the Mesters Vig Formation (MV Fm). Modified from Vigran *et al.* (1999). Ages in Ma from Gradstein *et al.* (2012). RA: *Radizonates aligerens* Miospore Zone of Clayton *et al.* (1977). Subdivision of the Mesters Vig Formation according to Perch-Nielsen *et al.* (1972). Asterisk marks the most likely stratigraphic position of the investigated material.

Diagnosis (after Haubold 1971, 1996; Voigt 2005). Trackways of a quadrupedal tetrapod with plantigrade to semiplantigrade imprints, pace angulation 80°–96°, stride : pes length = 3–5.5 : 1; pes impressed closely behind manus, pentadactyl, digits increasing in length from I–IV, digit IV longest, digit V as long as digit II and occasionally missing, short and broad oval sole, in deeply impressed imprints with proximolateral 'heel', robust basal pad of digit I, distal ends of digits rounded; manus tetradactyl with short broad, distally rounded digits, digits increasing in length from I–III, digit III longest, digit IV slightly shorter (80–90% of digit III), mostly longer than digit II, digit I with deeply impressed proximal pad similar to that in the pes.

Description. MGUH 31556 shows at least 12 tetrapod tracks that range in preservation from a very shallow impression of some digit tips to a very deep imprint lacking any anatomically controlled feature. The majority of traces are moderate to deep, more or less distinctly preserved imprints with stout and distally rounded digits (Figs 3–4). This kind of imprint measures 50–55 mm in length and 55–70 mm in width. The number of preserved digits varies between two and four to maybe five. Palm and sole impressions are poorly defined and show an approximately straight, slightly convex or slightly concave proximal margin. The digits increase in length from I to III. Digit IV, if present at all, is either longer or shorter than III. Most of the imprints show a well developed pad proximal to digit I, imitating an additional digit. Close to the centre and the edge of the slab, there is the only impression that preserves five digits. The digits of this imprint increase in length from I to IV and digit V is about as long as digit II (Fig. 4A, C–D, 5A).

The differences in the relative length of digit IV are interpreted to refer to manual and pedal tracks, respectively. A short fourth digit may characterize tetradactyl manual tracks, whereas a long fourth digit may belong to (originally pentadactyl, but in most cases preservationally tetradactyl) pedal tracks. Following this interpretation, MGUH 31556 shows three or four pedal and at least five manual tracks. Three manus–pes couples can be differentiated that all point to an inwardly rotated manual track (Fig. 3C).

Discussion

The described tracks from MGUH 31556 are most similar to *Limmopus* Marsh 1894. This assignment is mainly based on the tetradactyl manus imprint and the relatively short, broad and clawless digits. Another characteristic feature of *Limmopus* is the presence of a

well developed basal pad proximal to digit I of both manus and pes imprints (Baird 1952; Voigt 2005).

The ichnogenus *Limnopus* was introduced for Pennsylvanian tetrapod footprints from Kansas (Marsh 1894). Since then, numerous other records have been mentioned from Upper Carboniferous and Lower Permian strata of Europe, North America and North Africa (Baird 1952, 1965; Haubold 1973; Martino 1991; Haubold *et al.* 1995; Voigt 2005; Voigt *et al.* 2011a, b; Marchetti *et al.* 2013, 2015; Lagnaoui *et al.* 2014; Lucas *et al.* 2015; Voigt and Haubold 2015; Voigt and Lucas 2015a, b). *Limnopus* tracks are remarkably similar to the ichnogenus *Batrachichnus* first described from Pennsylvanian strata of Pennsylvania (Woodworth 1900).

The discrimination of *Batrachichnus* and *Limnopus* tracks has been extensively discussed but is still an unresolved issue (Baird 1952; Haubold 1970, 1971, 1996; Tucker & Smith 2004; Voigt 2005). According

to Haubold (1996), tracks of both ichnogenera differ in the imprint proportions, relative length of digits, the trackway width as well as the imprint size (e.g., *Batrachichnus* pedal tracks are shorter than 30 mm). Voigt (2005) proposed the following distinguishing features: (1) relative length of manual digit IV, which is considered to reach 80–90 % of digit III in *Limnopus*, but only 60–70 % in *Batrachichnus*, giving manual tracks of *Batrachichnus* a more bilaterally symmetrical shape; (2) plantar surface of *Limnopus* with broad-oval pad and occasional proximolateral extension, whereas the sole of *Batrachichnus* pedal tracks is structureless; (3) *Limnopus* manual tracks are strongly inwardly rotated with respect to the midline and the pedal tracks, whereas the inward rotation of the manual track is less significant in *Batrachichnus*; (4) *Batrachichnus* pedal tracks range in size from less than 10 mm up to almost 40 mm, *Limnopus* pedal tracks may well

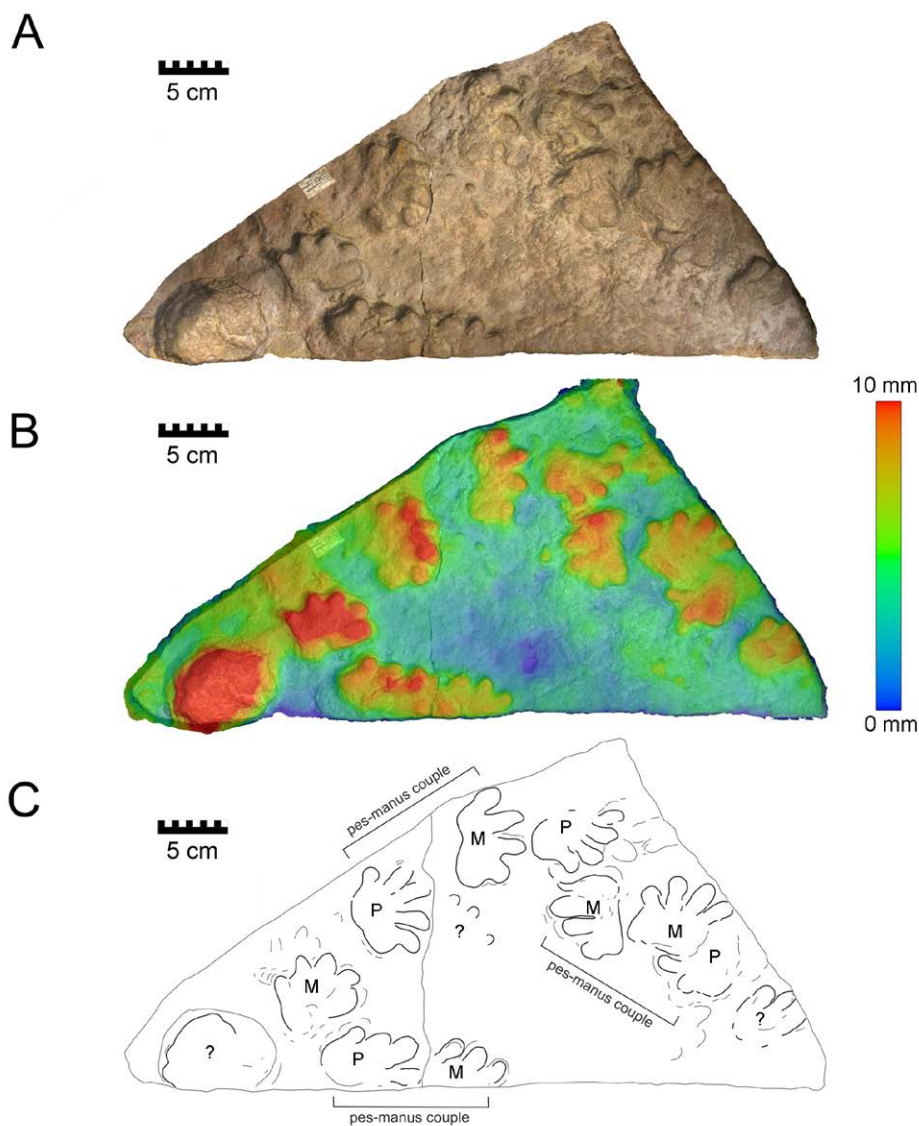


Fig. 3. Overview of slab MGUH 31556 from the Upper Carboniferous Mesters Vig Formation of East Greenland, with footprints preserved as convex hyporelief on the lower surface and assigned here to *Limnopus* isp. **A–B:** Photogrammetric models with B as coloured depth map. **C:** Interpretative drawing with demarcated pes (P) and manus (M). 3D models by Peter Falkingham.

exceed 60 mm in length. According to the imprint size, the relative length of the fourth digit of the manus, and the strongly inwardly rotated manus, the tracks of MGUH 31556 are much more similar to *Limnopus* than to *Batrachichnus*.

Numerous ichnospecies have been introduced for *Limnopus* or combined with this ichnogenus during the last century (Baird 1952, 1965; Haubold 1971, 1996, 2000; Voigt 2005; Lucas & Dalman 2013). With respect to anatomically controlled features of the imprint morphology and trackway pattern, hitherto discriminated *Limnopus* ichnospecies are not justified (Voigt 2005). *Limnopus heterodactylus* (King 1845) is the first named ichnospecies of *Limnopus* but is based on an isolated manus–pes imprint that, moreover, is ambiguous with respect to the relative length of pedal digit V (lectotype; Lucas & Dalman 2013). The second named *Limnopus* ichnospecies is *Limnopus vagus* Marsh 1894 that was designated the type ichnospecies. As it is known from full digit proportions and complete trackways, *L. vagus* is considered to be a valid ichnospecies. The most complete pedal track of MGUH 31556 shows a fifth digit that is about the same length as all other known *Limnopus* pedal tracks (Baird 1952; Haubold 1971; Voigt 2005; Fig. 5). As there is some degree of uncertainty regarding the quality of tracks and especially the lack of true trackways, we prefer to keep the described *Limnopus* tracks from Greenland in open nomenclature at the ichnospecies level.

Track makers

Limnopus is most commonly considered to be the track

of eryopoid temnospondyls (Baird 1965; Haubold 1971, 1996, 2000; Voigt 2005). Although a four-digit manus is characteristic of both temnospondyls and microsaur, the latter can be ruled out because of their smaller size compared with the tracks of MGUH 31556. *Limnopus* may refer to amphibians that were able to spend a considerable part of their life outside the water in subadult to adult ontogenetic stages (Haubold 1996; Voigt 2005).

Biostratigraphy, palaeobiogeography and palaeoecology

Available biostratigraphic data suggest that the tetrapod footprints of MGUH 31556 were produced during the Late Carboniferous at a time when central East Greenland was located some 10–15° north of the palaeoequator. The sedimentary record indicates overall warm and humid conditions with floodplains dominating the central axis of active rift basins and better drained sediments along the margins (Vigran *et al.* 1999). Associated flora (e.g. *Lepidodendron* and *Calamites*; Witzig 1951) and fauna (e.g. ‘palaeoniscid’ fishes; Moy-Thomas 1942) support palaeoenvironmental conditions with sufficient rainfall and a relatively high groundwater table.

Limnopus tracks are hitherto exclusively known from palaeoequatorial regions of Pangea in North America (Marsh 1894; Baird 1952, 1965; Voigt & Lucas 2015a, b), Europe (Haubold 1971; Gand 1988; Voigt 2005; Marchetti *et al.* 2013, 2015), and North Africa

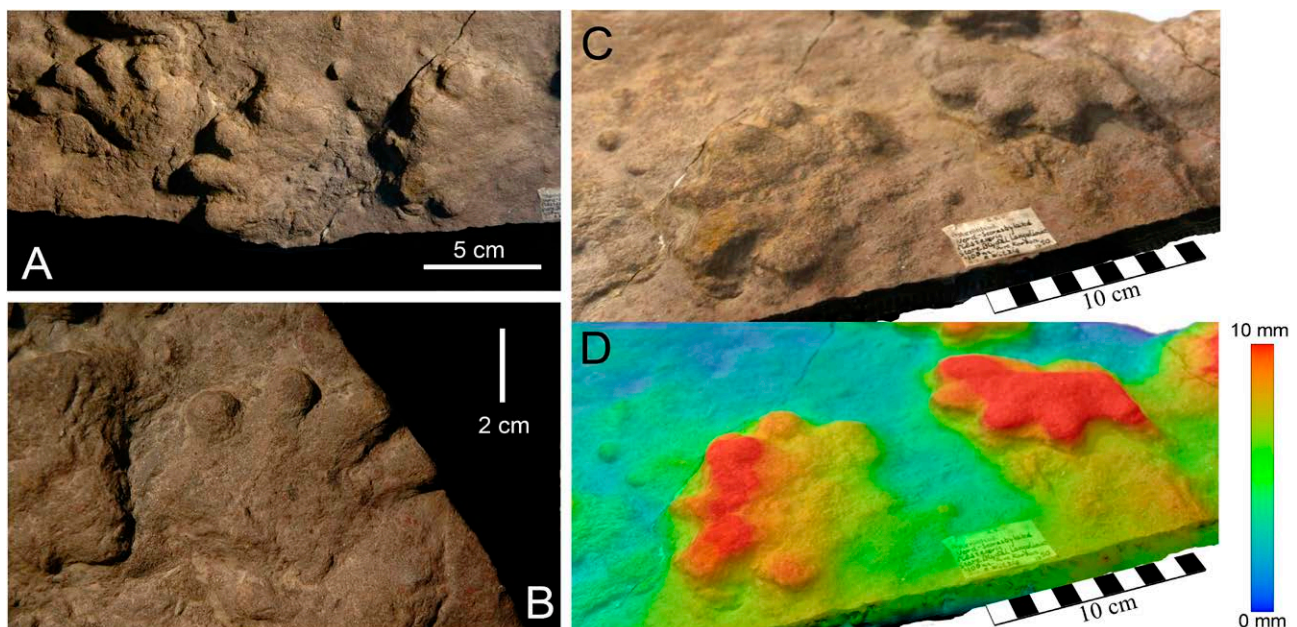


Fig. 4. Close-ups of selected tracks from slab MGUH 31556 from the Upper Carboniferous Mesters Vig Formation of East Greenland. **A:** Pes–manus couple corresponding to specimen in Fig. 5A and an isolated pes (left). **B:** Isolated manus. **C–D.** Photogrammetric models, with D as coloured depth map, of relatively well-preserved manus and pes imprints. 3D models by Peter Falkingham.

(Voigt *et al.* 2011a, b). All records are restricted to Upper Carboniferous and Lower Permian strata (Haubold 1971; Gand 1988; Gand & Durand 2006; Voigt 2005; Voigt & Lucas 2015a, b, in press).

The oldest occurrence of *Limnopus* is from the Salop Formation of Great Britain currently correlated with the Kasimovian stage of the Upper Carboniferous (Haubold & Sarjeant 1973; Tucker & Smith 2004), whereas the last occurrence is from upper Lower Permian (Artinskian) strata of the Italian Southern Alps (Marchetti *et al.* 2013, 2015). Possibly, older (Lower Carboniferous) records are hidden behind similar footprints that have been assigned to the ichnogenus *Palaeosauropus*, and the latter could be a junior synonym of *Limnopus* (Hay 1902; Lucas *et al.* 2010). However, *Palaeosauropus* is not well enough known to be readily compared to *Limnopus* (Lucas *et al.* 2010; Fillmore *et al.* 2012). If the Bashkirian-Moscovian age of the Mesters Vig Formation is correct, MGUH 31556 from East Greenland would predate the first occur-

rence of *Limnopus* by *c.* 8–10 Ma. Irrespective of the exact chronostratigraphic position of the footprint-bearing beds, the identification of *Limnopus* is at least in agreement with a supposed Late Carboniferous age of the Mesters Vig Formation. The rift basins of East Greenland are composed of thick successions of Palaeozoic and Mesozoic terrestrial to marine sediments that locally contain significant vertebrate remains (Bendix-Almgreen 1976; Henriksen & Higgins 1976). The Devonian succession on Ymer Ø is the famous locality for the early tetrapods, *Ichthyostega* and *Acanthostega*, as well as numerous fishes (e.g. Jarvik 1952; Bendix-Almgreen 1976; Blom *et al.* 2005, 2007; Clack *et al.* 2012). The overlying Carboniferous deposits of this area have yielded a diverse palaeoflora (Witzig 1951, 1954; Halle 1953; Pedersen 1976) and fossil fishes (e.g. Nielsen 1932; Moy-Thomas 1942; Bendix-Almgreen 1975), but no tetrapod remains as yet. Therefore, the footprints of MGUH 31556 are also the first evidence of Carboniferous tetrapods from Greenland.

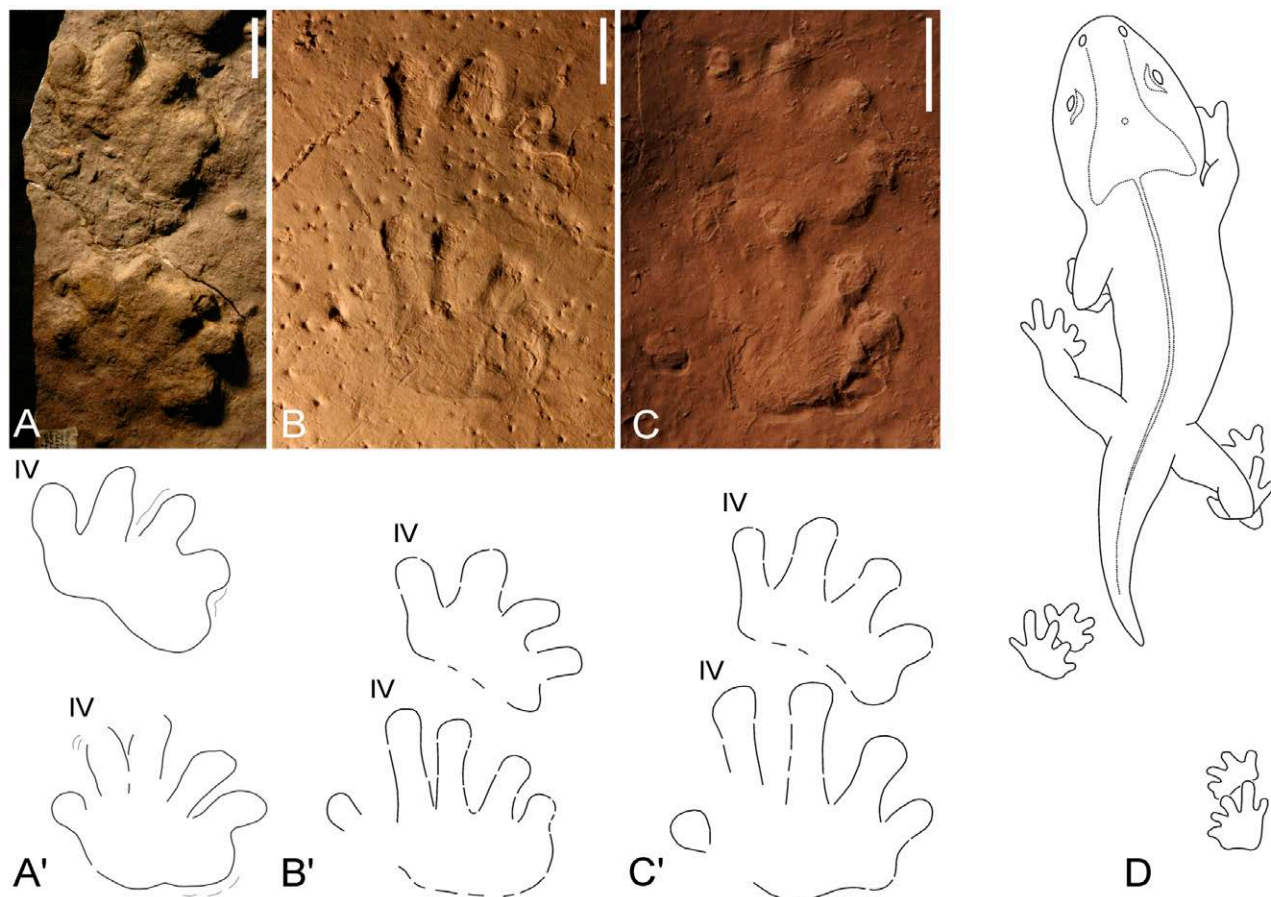


Fig. 5. Comparison of *Limnopus* tracks from various localities. **A, A'**: tracks from the Upper Carboniferous Mesters Vig Formation of East Greenland. **B, B'**: tracks from the Upper Carboniferous/Pennsylvanian of Kansas. **C, C'**: tracks from the Lower Permian of New Mexico. The pictures show a generally uniform morphology of pes and manus tracks. Material: (A, A') MGUH 31556; (B, B') YPM 405, Yale Peabody Museum New Haven, Connecticut; (C, C') NMMNH P-24603, New Mexico Museum of Natural History Albuquerque, New Mexico. Scale bars equal 1 cm. **D**: Hypothetical reconstruction of the *Limnopus* track maker and its gait, modified from Baird (1952).

Conclusions

The terrestrial Mesters Vig Formation of northern Scoresby Land, East Greenland, yields fossil tetrapod footprints, opening the potential for future investigations in the area.

A single slab and the only known specimen with fossil tetrapod footprints from the Mesters Vig Formation was collected in 1950 and is housed at the Natural History Museum of Denmark in Copenhagen.

Assignable tetrapod tracks on this specimen all correspond to medium-sized tracks of the ichnogenus *Limnopus*, considered to be made by eryopoid temnospondyls.

The biostratigraphic age of *Limnopus* is in agreement with a supposed Late Carboniferous age of the Mesters Vig Formation.

The find of *Limnopus* tracks in the Mesters Vig Formation is the first evidence of Carboniferous tetrapods from Greenland and an important biogeographical marker.

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Peter Falkingham from Liverpool John Moors University kindly provided 3D photogrammetric models of the tracks. Sten Lennart Jakobsen, Natural History Museum of Denmark, is thanked for practical help during the study of the specimen. Furthermore we thank Jennifer A. Clack and Spencer G. Lucas for their comments and constructive reviews.

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