Archosaur footprints (cf. *Brachychirotherium*) with unusual morphology from the Upper Triassic Fleming Fjord Formation (Norian–Rhaetian) of East Greenland

HENDRIK KLEIN[1]*, JESPER MILÀN[2,3], LARS B. CLEMMENSEN[3],
NICOLAJ FROBØSE[3], OCTÁVIO MATEUS[4,5], NICOLE KLEIN[6],
JAN S. ADOLFSSEN[2], ELIZA J. ESTRUP[7] & OLIVER WINGS[8]

[1]*Saurierwelt Paläontologisches Museum, Alte Richt 7, D-92318 Neumarkt, Germany*

[2]*Geomuseum Faxe/Østsjællands Museum, Østervej 2, DK-4640 Faxe, Denmark*

[3]*Department for Geosciences and Natural Resource Managements, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark*

[4]*Department of Earth Sciences, GeoBioTec, Faculdade de Ciências e Tecnologia, FCT, Universidade Nova de Lisboa, 2829-516 Caparica, Portugal*

[5]*Museu da Louriñha, Rua João Luis de Moura 95, 2530-158 Lourinhã, Portugal*

[6]*Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany*

[7]*Geocenter Møns Klint, Stengårdsvej 8, DK-4791 Borre, Denmark*

[8]*Niedersächsisches Landesmuseum Hannover, Willy-Brandt-Allee 5, 30169 Hannover, Germany*

**Corresponding author (e-mail: Hendrik.Klein@combyphone.eu)*

Abstract: The Ørsted Dal Member of the Upper Triassic Fleming Fjord Formation in East Greenland is well known for its rich vertebrate fauna, represented by numerous specimens of both body and ichnofossils. In particular, the footprints of theropod dinosaurs have been described. Recently, an international expedition discovered several slabs with 100 small chirotheriid pes and manus imprints (pes length 4–4.5 cm) in siliciclastic deposits of this unit. They show strong similarities with *Brachychirotherium*, a characteristic Upper Triassic ichnogenus with a global distribution. A peculiar feature in the Fleming Fjord specimens is the lack of a fifth digit, even in more deeply impressed imprints. Therefore, the specimens are assigned here tentatively to cf. *Brachychirotherium*. Possibly, this characteristic is related to the extremely small size and early ontogenetic stage of the trackmaker. The record from Greenland is the first evidence of this morphotype from the Fleming Fjord Formation. Candidate trackmakers are crocodylian stem group archosaurs; however, a distinct correlation with known osteological taxa from this unit is not currently possible. While the occurrence of sauropodomorph plateosaurs in the bone record links the Greenland assemblage more closer to that from the Germanic Basin of central Europe, here the described footprints suggest a Pangaea-wide exchange.

Supplementary material: Three-dimensional model of cf. *Brachychirotherium* pes–manus set (from MGUH 31233b) from the Upper Triassic Fleming Fjord Formation (Norian–Rhaetian) of East Greenland as pdf, ply and jpg files (3D model created by Oliver Wings; photographs taken by Jesper Milàn) is available at https://doi.org/10.6084/m9.figshare.c.2133546

During the Geocenter Møns Klint Dinosaur Expedition in July 2012, a new site with archosaur footprints was discovered by one of the authors (OW) in the lowermost part of the Ørsted Dal Member of the Upper Triassic Fleming Fjord Formation in mountain slopes facing the Carlsberg Fjord in East Greenland (Fig. 1). These archosaur footprints add to the knowledge of vertebrate life in the ancient lake and steppe system, and supplement previous descriptions of tetrapod footprints and other vertebrate trace fossils from the Upper Triassic deposits (Jenkins *et al.* 1994; Clemmensen *et al.* 1998; Milàn *et al.* 2004, 2006, 2012; Milàn & Bromley 2006; Niedźwiedzki *et al.* 2014; Sulej *et al.* 2014). They increase the diversity of tetrapod footprint assemblages from the Fleming Fjord Formation, reflecting a typical Late Triassic community with dinosaur and stem-crocodylian

From: Kear, B. P., Lindgren, J., Hurum, J. H., Milàn, J. & Vajda, V. (eds) *Mesozoic Biotas of Scandinavia and its Arctic Territories*. Geological Society, London, Special Publications, **434**, http://doi.org/10.1144/SP434.1

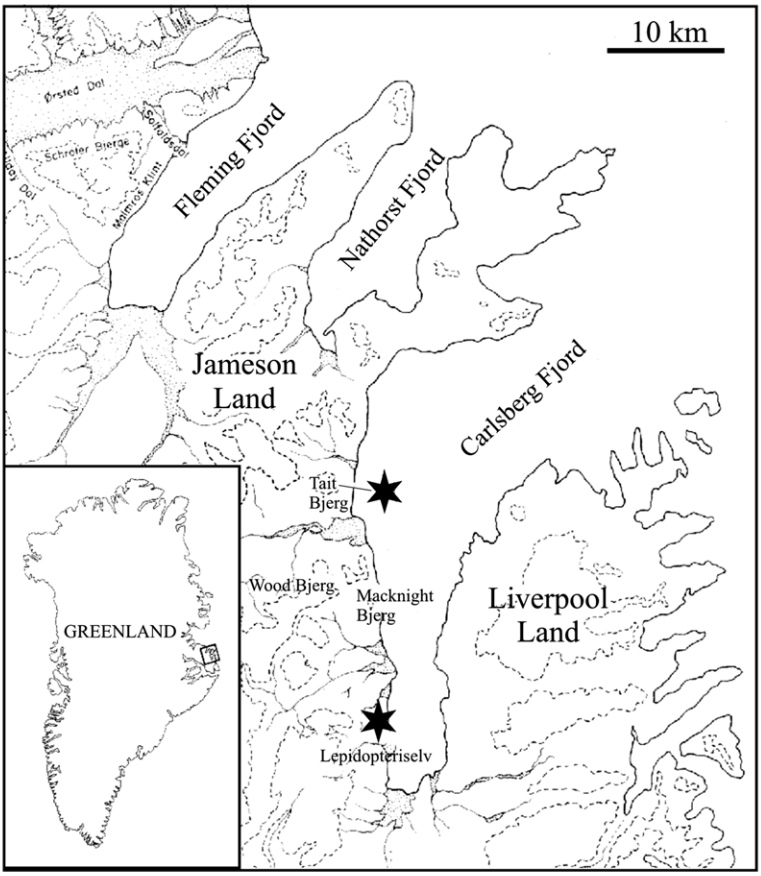

Fig. 1. Map showing the study area and the position of the footprint localities.

archosaurs. This is in congruence with the osteological record, which has an equivalent in assemblages of the Germanic Basin of central Europe (Jenkins *et al.* 1994). The new material, consisting of abundant and well-preserved imprints of identical shape, shows an anatomically based morphological peculiarity, and therefore requires a detailed discussion of the ichnotaxonomy and the possible trackmaker.

Geology and the depositional environment

The Jameson Land Basin lies in central East Greenland at 72° N (Fig. 1). The basin contains a seemingly complete (up to 300 m thick) Upper Triassic succession of lake deposits (Clemmensen *et al.* 1998). Stratigraphically, these sediments belong to the Fleming Fjord Formation, which is composed of a lower Edderfugledal Member, a middle Malmros Klint Member and an upper Ørsted Dal Member (Fig. 2) (Clemmensen 1980*a*, *b*). The latter is divided into a lower unit of red mudstones and sandstones (the Carlsberg Fjord beds), and an upper unit of light greyish dolomitic limestones and variegated mudstones (the Tait Bjerg Beds) (Clemmensen *et al.* 1998).

When the sediments of the Fleming Fjord Formation were deposited, the Jameson Land Basin lay at about 40° N, at the margin of the dry interior of the supercontinent Pangaea (Kent & Clemmensen 1996; Clemmensen *et al.* 1998; Kent & Tauxe 2005). Lake deposition was likely to have been influenced by seasonal, as well as orbitally controlled, precipitation changes (Clemmensen *et al.* 1998). The lake sediments record a gradual, long-term (a few million years) change in climate from semi-arid to humid, probably reflecting a slow northwards drift of the continent in latest Triassic times (Clemmensen *et al.* 1998; Kent & Tauxe 2005).

Deposits of the Fleming Fjord Formation are particularly well exposed in mountain slopes facing the Carlsberg Fjord. The tracks in question were found in the lowermost part of the Carlsberg Fjord beds in the Ørsted Dal Member at the Lepidopteriselv and Tait Bjerg sections (Fig. 2). The Carlsberg Fjord beds are here composed of red mudstones repeatedly interbedded by thin silt- and sandstones with wave and current ripples. The sedimentary characteristics of these deposits indicate deposition in a relatively shallow lake that frequently dried up (Clemmensen *et al.* 1998). The base of the unit contains two fluvial sheet sandstones and one lenticular-shaped channel sandstone. The tracks from Lepidopteriselv locality were found in loose blocks at the base of the fluvial channel sandstone, and the sedimentary characteristics of the blocks indicate that they belong to the uppermost part of the composite channel sandstone (Figs 2 & 3).

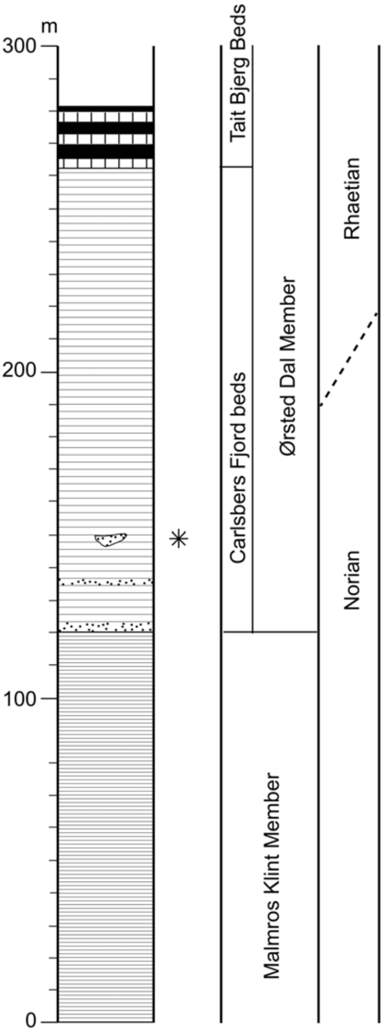

Fig. 2. Stratigraphic section of the Triassic of Greenland with the position of footprints described here marked with an asterisk. Stratigraphic section based on observations at Lepidopteriselv. The boundary between the Norian and the Rhaetian was placed at about 208.5 Ma in the middle of the Carlsberg Fjord beds in a nearby section by Clemmensen *et al.* (1998). New evidence from high-precision U–Pb geochronology, however, places this boundary at about 205.5 Ma (Wotzlaw *et al.* 2014), suggesting that the Norian–Rhaetian boundary should be moved upwards in the East Greenland section.

Magnetostratigraphical investigation of the Fleming Fjord Formation suggests that the tracks from the basal part of the Ørsted Dal Member are about 210 myr old and, hence, of Norian age (Clemmensen *et al.* 1998). A diverse assemblage of fossil vertebrates also indicates that the main part of the Ørsted Dal Member is of Norian age (Jenkins *et al.* 1994).

Material and methods

Three slabs with footprints have been recovered (Fig. 1). Two of them have been found at a locality (Lepidopteriselv) at the eastern margin of the Jameson Land Basin in East Greenland (Fig. 1). These are loose blocks (consisting of several pieces), but sedimentological data indicate that they originate from the topmost part of a fluvial channel sandstone in the lowermost part of the Ørsted Dal Member of the Fleming Fjord Formation (Fig. 3). The third sample was collected at Tait Bjerg (Fig. 1). These footprints were seen *in situ* at the top of a fluvial sheet sandstone in the lowermost part of the Ørsted Dal Member. The material is stored in the collection of the Natural History Museum of Denmark (Copenhagen) (MGUH) under catalogue numbers MGUH 31233a–c, MGUH 31234 and MGUH 31235. Concave imprints were outlined with chalk, drawn onto transparency film and digitized using Adobe Illustrator CS3 software. Sillicone moulds

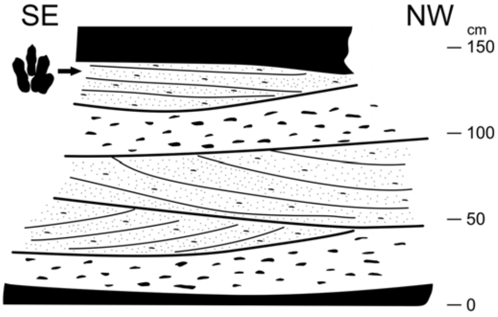

Fig. 3. Sketch of sedimentology at the Lepidopteriselv footprint locality with the position of the track level.

Table 1. *Measurements of cf.* Brachychirotherium *footprints described in this study compared with selective data from characteristic Upper Triassic* Brachychirotherium *of different localities*

Ichnotaxa	cf. *Brachychirotherium* (this study)	*B. hassfurtense**		*B. thuringiacum*†		*B. parvum*‡	
pl	4.0–4.5	**24.1**	14.4–20.5	**18.0–19.0**§	14.0–17.0	13.0	**13.5**
pw	4.0–4.5	**25.6**	16.9–23.9	**18.0–19.0**§	14.0–17.0	14.6	–
ml	2.0–2.2		–	**5.8–9.7**	6.0–8.0	5.9	–
mw	2.0–2.2		–	**7.3–11.0**	8.0–9.0	8.2	–
p I–IV	44		50	40–55		74	–
SL	–		–	**–**		**–**	92
PA	–		–	–		–	153

*†From the Hassberge Formation (Carnian) of northern Bavaria, Germany (*Brachychirotherium* type locality and horizon) (from Karl & Haubold 1998).

‡From the Redonda Formation (Chinle Group, Norian–Rhaetian) of New Mexico, USA (from Lucas *et al.* 2010). Notice all imprints being as wide as long, or wider than long.

pl, pes length (in cm); pw, pes width (in cm); ml, manus length (in cm); mw, manus width (in cm); p I–IV, divarication between pedal digits I and IV (in °); SL, stride length (in cm); PA, pace angulation (in °).

§Mean values. Length and width of imprints refers to anterior digit group I–IV only, except values in bold that include digit V.

and plaster casts were taken from the best-preserved footprints. Photographs were taken under artificial and natural light from both original slabs and casts, and all measurements were made from the original material only (Table 1).

Untextured 3D models from the slabs and high-resolution models from the best-preserved tracks were produced with photogrammetry. Digital photographs were subsequently processed using the methods described by Mallison & Wings (2014) using the photogrammetric software Agisoft PhotoScan Professional 1.0.4 build 1847 (64 bit) with generally high settings.

Tetrapod footprints

Formerly known material

The Ørsted Dal Member of the Fleming Fjord Formation has provided a rich tetrapod ichnofauna, including trackways of theropods with tridactyl footprints up to 28 cm long that can be assigned to the *Eubrontes–Anchisauripus–Grallator* plexus (Olsen *et al.* 1998; Gatesy *et al.* 1999; Milàn *et al.* 2004, 2006; Lucas *et al.* 2006; Milàn & Bromley 2006). Large imprints of a quadruped, up to 53 cm in length, were also described (Jenkins *et al.* 1994; Clemmensen *et al.* 1998; Lockley & Meyer 2000). Recently, Niedźwiedzki *et al.* (2014) and Sulej *et al.* (2014) reported new discoveries of trackways of large quadrupeds (up to 50 cm pes length) from the Malmros Klint Member of the Fleming Fjord Formation and attributed them to sauropodomorph dinosaurs. These large tracks from Greenland have been compared with *Eosauropus*, a purported sauropodomorph ichnotaxon known from Upper Triassic deposits of North America and Europe (Lockley & Meyer 2000; Lockley *et al.* 2006, 2011; Niedźwiedzki *et al.* 2014). Until now, they were figured without details or only symbolically on a map of the track surface (Jenkins *et al.* 1994; Sulej *et al.* 2014). Details of their morphology and documentation using close-up photographs and sketches were not given by these authors, and their identification as large chirotheres, therefore, cannot presently be excluded.

Jenkins *et al.* (1994, p. 19) also mentioned trackways of a smaller quadruped from the Ørsted Dal Member and small (2.5–5 cm) tetradactyl imprints showing ‘four relatively short digits with rounded ends’ from the Malmros Klint Member. The latter they consider as probable amphibian tracks. Again, no figures were provided and these authors did not indicate the whereabouts of the material. Probably, these footprints were left in the field.

New discoveries

The material described here consists of about 100 distinct pes and manus imprints made by similarly sized individuals distributed on three main slabs (Figs 4–10). The dimensions of the largest slab (broken into three pieces) are 93 × 76 × 4 cm, displaying about 60 imprints (Figs 4, 5, 7a & 8). The two other slabs are 55 × 45 × 1 cm (Figs 6, 7b, c & 9) and 35 × 20 × 5.7 cm (Fig. 7d) in size, each showing about 20 imprints.

Description

Two slabs (MGUH 31233a–c (Figs 4, 8) and MGUH 31234 (Fig. 7d)) showing an upper surface with footprints preserved as concave epireliefs. Another slab (MGUH 31235 (Figs 6, 9)) displays footprints preserved as natural casts (convex hyporeliefs) and probably represents a partial counterplate that

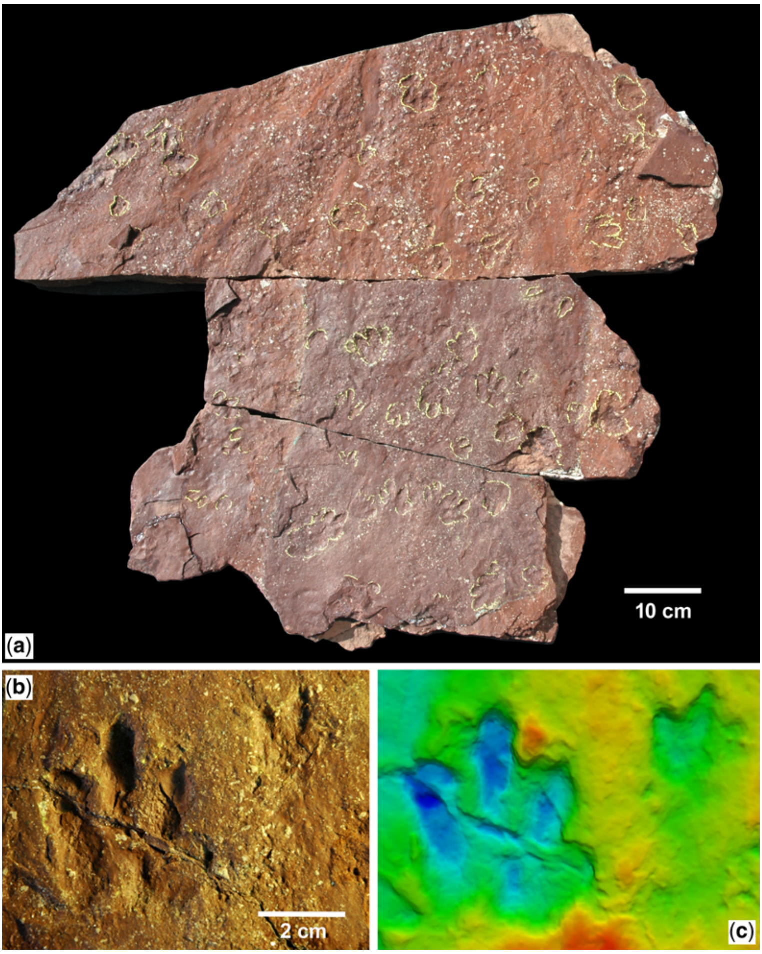

Fig. 4. Archosaur footprints cf. *Brachychirotherium* from the Ørsted Dal Member of the Fleming Fjord Formation (Upper Triassic, Norian–Rhaetian) of eastern Greenland. (**a**) Overview of slab MGUH 31233a–c (broken into three pieces: 31233a is the lower, 31233b the middle and 31233c the upper part) with numerous small pes and manus imprints of cf. *Brachychirotherium* preserved as concave epireliefs and outlined with chalk. (**b**) & (**c**) Detail of a pes–manus set from the middle part of the slab (MGUH 31233b): (b) photograph of natural mould and (c) a 3D model.

belongs to the same track level as MGUH 31233a–c but does not match the footprints on the slabs with the concave traces. Pes imprints are tetradactyl with moderate spread digits (the angle between digits I and IV is 44°). The digits are relatively broad and short, and show rounded phalangeal pads and small thin claws (Figs 4, 5, 10). Their lengths and widths are within the same size range (i.e. at 4–4.5 cm). Digit proportions are III > II > IV > I. A distinct metatarsophalangeal area is visible, sometimes showing well-developed rounded pads (Figs 4b, c & 10a). The proximal margin can be variable, appearing as posteriorly concave, convex or straight owing to different preservation and imprint depth. The smaller manus imprints are 2–2.2 cm in length and width, respectively, and mostly show only three (II–IV), but occasionally four (I–IV), digits (Fig. 10a–c, e). Digit proportions of the manus are similar as in the pes, with III > II > IV > I. Even in deeper (5 mm) imprints, all pes and manus tracks lack digit V. The manus imprints are inwardly rotated relative to the pes. The position of the manus relative to the pes is variable, appearing antero-medial, anterior or even antero-lateral (Fig. 10a–c, e). The well-preserved specimen from slab MGUH 31233b in Figures 4b, c and 10a shows a lateral overstep of the manus by the pes. Some imprints display structures related to scale impressions

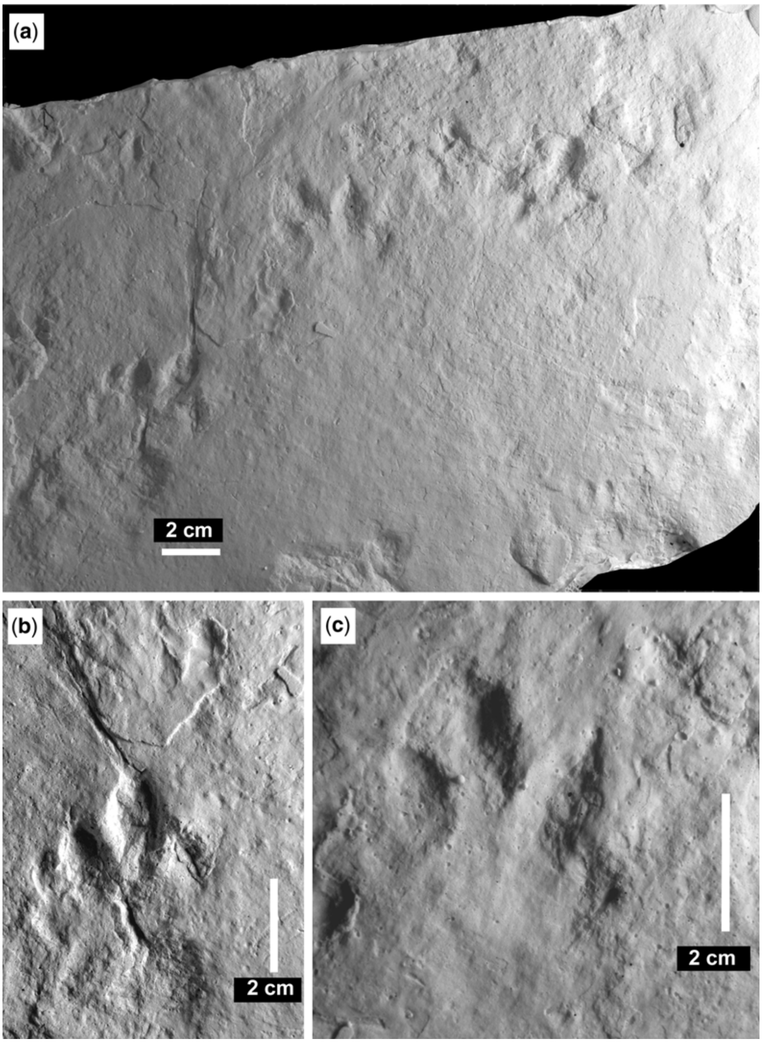

Fig. 5. Plaster replica of the lower portion of the slab in Figure 4 (MGUH 31233a). (**a**) Several pes and manus imprints; (**b**) & (**c**) detail of (a).

and/or scale drag marks (MGUH 31235: Fig. 6b). These are indistinctly preserved polygons and striations on the lateral sides of digits and along the sole surface, reflecting the dynamics of the pes when being pushed into the substrate and slipping backwards. However, no distinct scale pattern can be observed.

Discussion

Morphologically, the imprints described here show a strong similarity with chirotheriid footprints, in particular with the ichnogenus *Brachychirotherium* Beurlen, 1950 from the Late Triassic of Europe (Beurlen 1950; Karl & Haubold 1998, 2000; Petti *et al.* 2009), North America (Baird 1957; Silvestri & Szajna 1993; Lockley & Hunt 1995; Szajna & Silvestri 1996; Szajna & Hartline 2003; Klein *et al.* 2006; Hunt & Lucas 2007*a*, *b*; Lucas *et al.* 2010; Lucas & Heckert 2011), South America (Melchor & De Valais 2006), North Africa (Hminna *et al.* 2013) and southern Africa (Ellenberger 1972; D'Orazi Porchetti & Nicosia 2007). The short and broad digits with small, thin claws, and the digit proportions with digit IV $<$ digit II in the Greenland tracks are diagnostic of *Brachychirotherium* (Karl & Haubold 1998).

Problematic is the lack of a fifth digit in all (about 100) imprints. Even more deeply impressed footprints show no digit V impression.

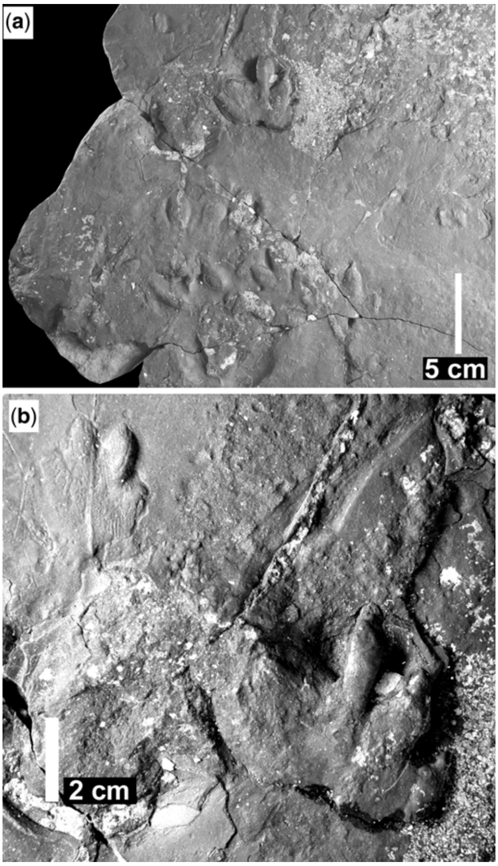

Fig. 6. Slab MGUH 31235 with several pes and manus imprints of cf. *Brachychirotherium* preserved as natural casts (convex hyporeliefs): (**a**) overview of the larger section; and (**b**) detail with a possible pes–manus set. Note dragmarks of scales in the manus.

This is unusual for *Brachychirotherium* and for all chirotheriids, especially in the pes imprint. *Brachychirotherium* occasionally lacks a trace of digit V due to substrate conditions and pes posture (Karl & Haubold 1998), but the large number of tracks from Greenland suggests a relationship of this feature to the pes anatomy of the trackmaker, which obviously had a functionally tetradactyl pes. However, the compact digit group I–IV in the Greenland tracks is typically chirotheriid. The only non-chirotheriid tracks of a quadruped that are similar to *Brachychirotherium* but show a functionally tetradactyl pes imprint is *Batrachopus*, mainly known from the Lower Jurassic but also from the Late Triassic (Fig. 11g). *Batrachopus* is considered to be a crocodylomorph track (Olsen & Padian 1986; Klein & Lucas 2010*b*). However, the manus imprint of *Batrachopus* is strongly rotated outwards relative to the pes imprint: whereas, in the material from Greenland, the manus imprint is inwards or slightly rotated outwards with respect to the pes imprint (cf. Fig. 11f & g). In typical *Brachychirotherium* tracks from the Late Triassic, the manus imprint is turned slightly more outwards than the pes (Fig. 11b–d).

Considering the overall congruence of the Greenland tracks with the ichnogenus *Brachychirotherium*, as well as the morphological peculiarity and lack of a (diagnostic) fifth digit trace, we tentatively refer the material described here to archosaur footprints cf. *Brachychirotherium*. Possibly, the lack of digit V generally characterizes juvenile *Brachychirotherium* (see below), requiring an emendation of the diagnosis of the ichnogenus. Late Triassic *Brachychirotherium* footprints of small size (<5 cm) are hitherto known only from a few imprints with a preserved fifth digit from a single locality in Argentina, South America (Fig. 11e). Small '*Brachychirotherium*' tracks from the Middle Triassic of Germany (Haubold 1967, 1971*a*, *b*) also show a fifth digit, but the correct identification of the ichnogenus in these strata (originally Late Triassic) is doubtful (Karl & Haubold 1998; Klein & Haubold 2004). Alternatively, the tracks from Greenland could represent a new ichnotaxon, but this cannot be demonstrated here with confidence. Establishing a new ichnotaxon would require the presence of a juvenile *Brachychirotherium* and early ontogenetic stage to be excluded, and, instead, the presence of a small adult form to be proven. However, a new ichnotaxon would be based weakly on the lack of a fifth digit only.

Trackmakers

Brachychirotherium footprints have most probably been left by stem-crocodylian archosaurs (*sensu* Brusatte *et al.* 2010; Nesbitt 2011). The pes of the latter is distinguished from that of dinosaur bird-line archosaurs (Avemetatarsalia *sensu* Benton 1999) by the broader configuration of the metatarsals. This feature is reflected in the typically broad pes imprints of *Brachychirotherium*. An exception to this rule is the pes of the stem-crocodylian *Poposaurus* from the Late Triassic of North America, which has a slender shape developed convergent with that of dinosauromorphs (Farlow *et al.* 2014). *Brachychirotherium* has been attributed to rauisuchians, crocodylomorphs and aetosaurs by different authors (Klein *et al.* 2006; Avanzini *et al.* 2010; Heckert *et al.* 2010; Lucas & Heckert 2011; Desojo *et al.* 2013).

Small *Brachychirotherium* from Upper Triassic deposits are uncommon, and the tracks from Greenland thus far could represent the smallest known. A detailed study of different-sized specimens and

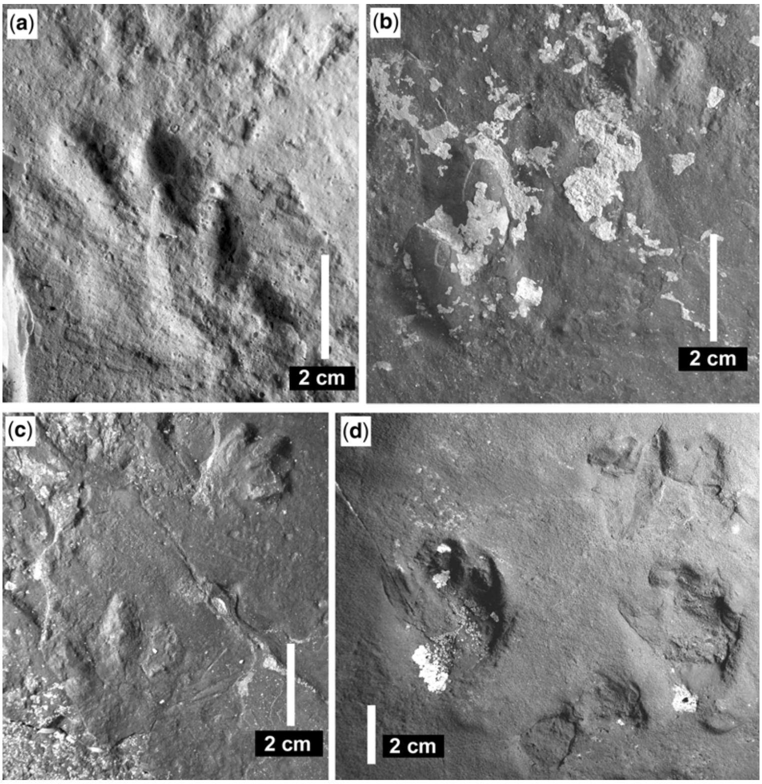

Fig. 7. Pes and manus imprints of cf. *Brachychirotherium*: (**a**) plaster replica taken from slab MGUH 31233a with two overprinted pes impressions; (**b**) & (**c**) natural casts from slab MGUH 31235; and (**d**) natural mould from a different slab (MGUH 31234).

their morphologies has never been undertaken. Chirotheriid footprints reflecting juvenile individuals have been described from the Middle Triassic (Anisian) of Germany (Haubold 1967, 1971*a*, *b*). Avanzini & Lockley (2002) gave a detailed analysis of different *Isochirotherium* size classes from the Middle Triassic of the Southern Alps (Italy), with some specimens having a pes length of 2.7 cm. However, these very small imprints show all features diagnostic of the ichnogenus *Isochirotherium* and of chirotheriids in general, including an impression of the fifth pedal digit. The Greenland tracks represent the second occurrence of small-sized cf. *Brachychirotherium* footprints from Upper Triassic deposits. They could possibly represent juveniles and ontogenetic stages with a still less-developed (not impressed) digit V or functionally tetradactyl pes. The wide variation in the position and orientation of the manus imprint (Fig. 10) might reflect the still unconsolidated gait of juvenile individuals of basal archosaurs. Possibly, juveniles also walked with a more digitigrade posture of the pes, where the short fifth digit did not touch the ground and therefore left no impression. During growth and increase in body weight, this might have changed towards a semi-plantigrade or plantigrade posture, leaving footprints with distinct sole and digit V impressions. Allen *et al.* (2009, 2010) demonstrated the shift of the centre of mass (COM) during ontogeny in extant crocodylians and birds. Crocodylians show a craniodorsal shift of the COM and an increase in loading on the hip joints that essentially influence locomotor mechanics (Allen *et al.* 2009). For extant crocodylians, Farlow & Britton (2000) showed that during growth the autopodia become shorter relative to the glenoacetabular length. However, comparing the lengths of the toe region and the plantar/palmar portion of the feet relative to total leg length, the digits show slightly negative allometric growth, whereas values for the sole indicate isometric growth (Farlow & Britton, 2000). This would mean that the sole becomes slightly longer relative to the digit portion. For the theropod dinosaur *Allosaurus*, Foster & Chure (2006) showed negative allometric growth of metatarsal IV relative to the tibia. In any case, the increase in weight on the

Fig. 8. Overview sketch of slab MGUH 31233a–c with archosaur footprints of cf. *Brachychirotherium*. Letters (a, b, d & f) indicate the position of footprints outlined in Figure 10.

hind limbs, combined with the relative shortening of metatarsals, as in some digitigrade bipeds, or the elongation of the palmar/plantar portion in more plantigrade quadruped forms, affect the biomechanics and function of the pes. Whether the same patterns observed in extant archosaurs were present

Fig. 9. Overview sketch of slab MGUH 31235 with archosaur footprints of cf. *Brachychirotherium*. Letters (c & e) indicate the position of footprints outlined in Figure 10.

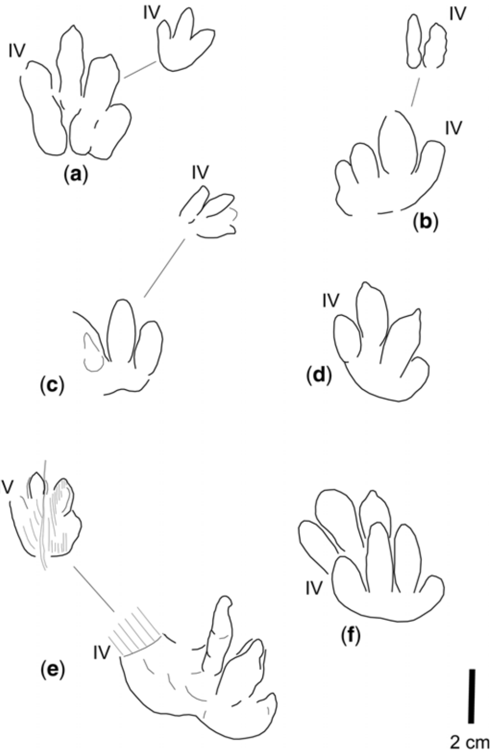

Fig. 10. (**a**)–(**f**) Sketches of footprints of cf. *Brachychirotherium* from the Ørsted Dal Member. The outlines refer to specimens in the following figures: (a) Figure 4b–c; (b) Figure 5b; (c) Figure 7c; (d) Figure 5c; (e) Figure 6b; and (f) Figure 7a. Their position on the slabs is indicated by corresponding letters in Figures 8 and 9. Note tetradactyl preservation and lack of digit V.

in the Greenland trackmakers cannot be proved with certainty, but the degree of contact of pedal digit V with the substrate, and the preservation of its impression, was probably controlled by differential growth of limb parts.

The osteological tetrapod record of the Fleming Fjord Formation thus far yields temnospondyls, possible sphenodonts and lepidosaurs, turtles, phytosaurs, a possible rauisuchian, aetosaurs, pterosaurs, prosauropods, theropods, and mammals (Jenkins *et al.* 1994; Mateus *et al.* 2014; Sulej *et al.* 2014). From these, only stem-crocodylian archosaurs (rauisuchians, aetosaurs) might be cautiously considered as potential trackmaker candidates (Karl & Haubold 1998; Heckert *et al.* 2010; Lucas & Heckert 2011). An affinity of *Brachychirotherium* to aetosaurs was suggested by Lucas & Heckert (2011), who found several synapomorphies of footprints and pes skeletons. Skeletal remains of aetosaurs are known from the Fleming Fjord Formation by the taxa *Aetosaurus ferratus* and *Paratypothorax andressi* (Jenkins *et al.* 1994). The size of the pes of *Aetosaurus* is in the range of the tracks described (Schoch 2007): however, the skeleton shows a relatively long digit IV in the pes and manus, whereas the tracks have a short pedal and manual digit IV (IV < II). Unfortunately, no trackway is preserved in the chirotheriid material from Greenland, and a comparison with the pattern of *Brachychirotherium* trackways from other localities is not possible. It is important to mention that the occurrence of body fossils and footprints in the same stratigraphic unit does not necessarily indicate a relationship. For example, the Olenekian–Anisian (Lower–Middle Triassic) Moenkopi Formation/Group is dominated by amphibian body fossils, whereas the tetrapod footprint record shows only a few amphibian, but abundant reptile, tracks (Peabody 1948; Klein & Lucas 2010*a*). This is probably due to alternating ecological conditions with different precipitation and water supply under a semi-arid climate and/or a taphonomic effect due to the different conditions under which skeletons or footprints can be preserved.

Biostratigraphy, palaeobiogeography, palaeoecology

If the footprints from Greenland represent the ichnogenus *Brachychirotherium*, then they match characteristic tetrapod footprint assemblages from Upper Triassic deposits in the global record (Klein & Haubold 2007; Klein & Lucas 2010*c*). Klein & Lucas (2010*c*) proposed a *Brachychirotherium* biochron for Carnian–Rhaetian assemblages that, similar to those from Greenland, contain abundant tridactyl footprints of the *Grallator–Eubrontes* type (see above).

Following Lucas (1998, 2010), the vertebrate body fossil assemblage in Greenland belongs to the Revueltian land-vertebrate faunachron (LVF), which can be cross-correlated with the Carnian–Norian as it is similar to typical associations in Central Europe (e.g. from the German Keuper). In particular, the occurrence of the prosauropod *Plateosaurus* resembles assemblages from the Germanic Basin, whereas the Triassic bone record from North America lacks prosauropods. Against the background of the close proximity of what is today Greenland and North America in Late Triassic times, this can possibly be explained by the existence of larger barriers such as mountain ranges and/or climatic obstacles. In a reconstruction of climate belts on the Late Triassic supercontinent Pangaea, Kent *et al.* (2014) placed the Germanic Basin and the Jameson Land Basin in a relatively humid climate belt, while the North American

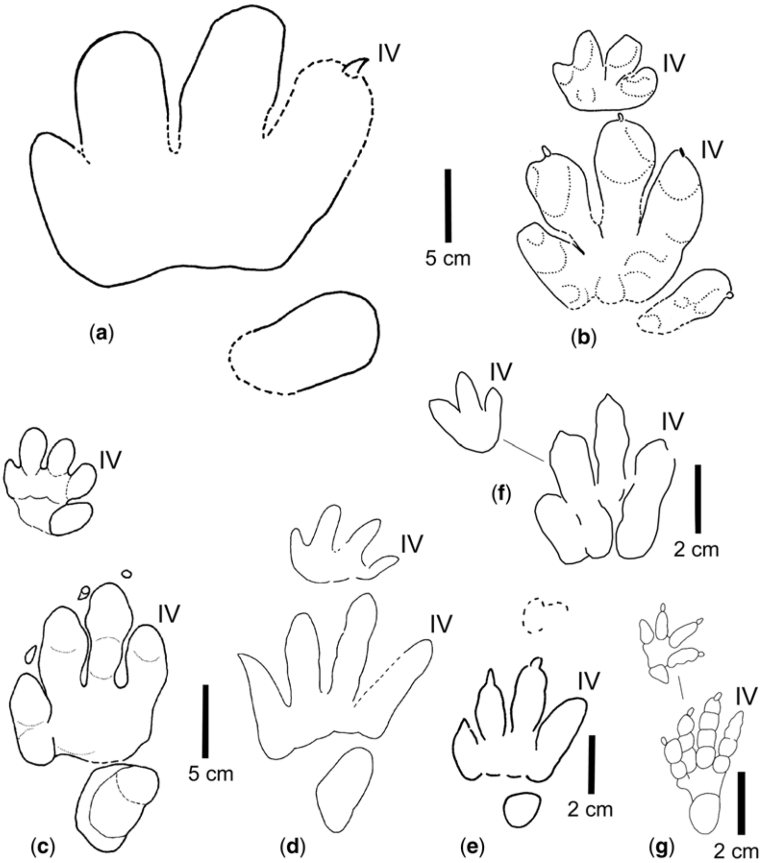

Fig. 11. (**a**)–(**e**) Sketches of *Brachychirotherium* pes and manus from different Upper Triassic localities. (a) *Brachychirotherium hassfurtense* (type ichnospecies, lectotype) from the Hassberge Formation (Late Carnian, Upper Triassic) of northern Bavaria, Germany. (b) *B. thuringiacum* from same stratum and locality as (a). (c) *B. parvum* (holotype) from the Passaic Formation (Norian, Upper Triassic) of New Jersey, USA. (d) *B. parvum* from the Redonda Formation (Norian–Rhaetian, Upper Triassic) of New Mexico, USA. (e) *B.* isp. from the Los Colorados Formation of NW Argentina. (**f**) cf. *Brachychirotherium* from the Ørsted Dal Member of the Fleming Fjord Formation (Upper Triassic, Norian–Rhaetian) of eastern Greenland. (**g**) *Batrachopus* from the Newark Supergroup (Lower Jurassic) of North America. From Klein & Lucas (2010*a*, *b*).

localities are situated in a relatively arid climate belt. This climatic zonation may have controlled faunal variation on the continent. However, tetrapod footprints of the ichnogenus *Eosauropus*, originally described from the Upper Triassic of North America and possibly present in the Flemingfjord assemblage (see above), have been attributed to sauropodomorphs (Lockley *et al.* 2001, 2006, 2011). Interestingly, the Late Triassic record of the Argana Basin of Morocco, which was positioned close to eastern North America prior to the Atlantic rifting, also lacks sauropodomorph body fossils. Purported prosauropods from Morocco (*Azendohsaurus*: Jalil 1999) have more recently been referred to basal archosauromorphs (Flynn *et al.* 2010). In any case, the footprint record, and the presence of the characteristic and widely distributed Upper Triassic morphotype *Brachychirotherium* in the Fleming Fjord Formation of Greenland, indicates a distinct faunal exchange of trackmakers within Triassic Pangaea.

In Late Triassic times, the Jameson Land Basin lay at 40° N in a transition zone between the relatively dry interior of the supercontinent Pangaea and the more humid peripheral part of this continent (Kent & Tauxe 2005). Much of the interior of the continent was influenced by monsoonal rain, and shallow lakes were formed. The archosaur footprints were found in a fluvial channel sandstone in the lowermost part of the Carlsberg Fjord beds during a period when the overall climate of the basin was relatively dry (Kent *et al.* 2014). The formation of a relatively thick channel sandstone may record intense monsoonal rain transporting sand into the marginal part of the lake system (Clemmensen *et al.* 2015).

The lake deposits have been shown to contain a high-resolution record of orbitally forced climate change controlling the intensity of monsoonal rain with time (e.g. Kemp & Coe 2007; Volmer *et al.* 2008). Previous studies of sedimentary cycles in the Late Triassic lake deposits of the Jameson Land Basin suggest that this lake system too was influenced by orbitally forced climate change (Clemmensen *et al.* 1998). Detailed studies of facies, colour variation, measurements of magnetic susceptibility, gamma-ray intensity and carbonate content were used in a recent study by Frobøse & Clemmensen (2014) to detect statistical cyclicity in the uppermost part of the Carlsberg Fjord beds. These new data indicate, in agreement with Clemmensen *et al.* (1998), the existence of a composite cyclicity in the Carlsberg Fjord beds, with significant cycles. This cyclicity matches well the theoretically expected cyclicity in a lake system that experienced orbitally controlled variation in precipitation and lake environment (Clemmensen *et al.* 2015).

The track-bearing Carlsberg Fjord beds form part of a lake succession that indicates a long-term shift in climate from semi-arid to humid at the transition from the Norian to the Rhaetian (Clemmensen *et al.* 1998, 2015). This long-term shift in climate has been explained by the slow northwards drift of the continent in the Late Triassic (Clemmensen et al. 1998; Kent & Tauxe 2005).

Conclusions and perspectives

Clarification of the question of whether the herein-described tracks represent a very unusual morphotype of *Brachychirotherium*, possibly an early ontogenetic stage or a new ichnotaxon, must await additional data. Studies of ontogenetic growth in the autopodia of basal archosaurs based on footprints are little known. Future discoveries of different-sized specimens in the Fleming Fjord Formation and a potential distinction of different size classes would be of great importance. They might shed light on the differential growth of chirotheriid trackmakers, and, furthermore, permit a re-evaluation of the extremely large forms reported by Jenkins *et al.* (1994), Niedźwiedzki *et al.* (2014) and Sulej *et al.* (2014) from the same unit (?*Brachychirotherium* or ?*Eosauropus*) that could possibly represent adult individuals.

We would like to thank Nils Natorp for organizing the funding for the expedition to Greenland in the summer of 2012. OW is currently funded by the Volkswagen Foundation. We are indebted to Hartmut Haubold (Halle, Germany) for his valuable comments and discussions on the material. Finally, we thank Spencer G. Lucas and an anonymous reviewer for their constructive comments and reviews.

References

Allen, V., Paxton, H. & Hutchinson, J. R. 2009. Variation in center of mass estimates for extant sauropsids and its importance for reconstructing inertial properties of extinct archosaurs. *The Anatomical Record*, **292**, 1442–1461.

Allen, V., Elsey, R. M., Jones, N., Wright, J. & Hutchinson, J. R. 2010. Functional specialization and ontogenetic scaling of limb anatomy in *Alligator mississipiensis*. *Journal of Anatomy*, **216**, 423–445.

Avanzini, M. & Lockley, M. 2002. Middle Triassic archosaur population structure: interpretation based on *Isochirotherium delicatum* fossil footprints (Southern Alps, Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **185**, 391–402.

Avanzini, M., Petti, F. M., Bernardi, M. & Tomasoni, R. 2010. Crocodile-like footprints from the Upper Triassic (Carnian) of the Italian Southern Alps. *In*: Milàn, J., Lucas, S. G., Lockley, M. G. & Spielmann, J. A. (eds) *Crocodyle Tracks and Traces*. New Mexico Museum of Natural History and Science Bulletin, **51**, 61–64.

Baird, D. 1957. Triassic reptile footprint faunules from Milford, New Jersey. *Bulletin of the Museum of Comparative Zoology*, **117**, 449–520.

Benton, M. J. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philosophical Transactions of the Royal Society of London*, **B354**, 1423–1446.

Beurlen, K. 1950. Neue Fährtenfunde aus der fränkischen Trias [New track discoveries in the Franconian Triassic]. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1950**, 308–320.

Brusatte, S. L., Benton, M. J., Desojo, J. B. & Langer, M. C. 2010. The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *Journal of Systematic Palaeontology*, **8**, 3–47.

Clemmensen, L. B. 1980*a*. Triassic rift sedimentation and palaeogeography of central East Greenland. *Grønlands Geologiske Undersøgelse Bulletin*, **136**, 1–72.

Clemmensen, L. B. 1980*b*. Triassic lithostratigraphy of East Greenland between Scoresby Sund and Kejser Franz Josephs Fjord. *Grønlands Geologiske Undersøgelse Bulletin*, **139**, 1–56.

Clemmensen, L. B., Kent, D. V. & Jenkins, F. A., Jr., 1998. A Late Triassic lake system in East Greenland: facies, depositional cycles and palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **140**, 135–159.

Clemmensen, L. B., Milàn, J. et al. 2015. The vertebrate-bearing Late Triassic Fleming Fjord Formation of central East Greenland revisited: stratigraphy, palaeoclimate and new palaeontological data. *In*: Kear, B. P., Lindgren, J., Hurum, J. H., Milàn, J. & Vajda, V. (eds) *Mesozoic Biotas of Scandinavia* *and its Arctic Territories*. Geological Society, London, Special Publications, **434**. First published online December 16, 2015, http://doi.org/10.1144/SP434.3

Desojo, J. B., Heckert, A. B., Martz, J. W., Parker, W. G., Schoch, R. R., Small, B. J. & Sulej, T. 2013. Aetosauria: a clade of armoured pseudosuchians from the Upper Triassic continental beds. *In*: Nesbitt, S. J., Desojo, J. B. & Irmis, R. B. (eds) *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin*. Geological Society, London, Special Publications, **379**, 203–239, http://doi.org/10.1144/SP379.17

D'Orazi Porchetti, S. & Nicosia, U. 2007. Re-examination of some large early Mesozoic tetrapod footprints from the African collection of Paul Ellenberger. *Ichnos*, **14**, 219–245.

Ellenberger, P. 1972. *Contribution`a la classification des Pistes de Vertébrés du Trias: les types du Stormberg d'Afrique du Sud (I)*. Palaeovertebrata, Memoire Extraordinaire.

Farlow, J. O. & Britton, A. 2000. Size and body proportions in *Alligator mississippiensis*: implications for archosaurian ichnology. *In*: Lee, Y.-N. (ed.) *2000 International Dinosaur Symposium for Kosong County in Korea*. Paleontological Society of Korea, Special Publications, **4**, 189–206.

Farlow, J. O., Schachner, E. R., Sarrazin, J. C., Klein, H. & Curry, P. J. 2014. Pedal proportions of *Poposaurus gracilis*: convergence and divergence in the feet of archosaurs. *Anatomical Record*, **297**, 1022–1046.

Flynn, J. J., Nesbitt, S. J., Parrish, J. M., Ranivoharimanana, L. & Wyss, A. R. 2010. A new species of *Azendohsaurus* (Diapsida: Archosauromorpha) from the Triassic Isalo Group of southwestern Madagascar: Cranium and Mandible. *Palaeontology*, **53**, 669–688.

Foster, J. R. & Chure, D. J. 2006. Hindlimb allometry in the Late Jurassic theropod dinosaur *Allosaurus*, with comments on its abundance and distribution. *New Mexico Museum of Natural History and Science Bulletin*, **36**, 119–122.

Frobøse, N. & Clemmensen, L. B. 2014. Sedimentary rock colour and palaeoclimate: an example from a Late Triassic lake succession in East Greenland. Paper presented at the 19th International Sedimentological Congress, 18–22 August 2014, Geneva, Switzerland.

Gatesy, S. M., Middleton, K. M., Jenkins, F. A., Jr. & Shubin, N. H. 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature*, **399**, 141–144.

Haubold, H. 1967. Eine Pseudosuchier-Fährtenfauna aus dem Buntsandstein Südthüringens. *Hallesches Jahrbuch für Mitteldeutsche Erdgeschichte*, **8**, 12–48.

Haubold, H. 1971*a*. Die Tetrapodenfährten des Buntsandsteins. *Paläontologische Abhandlungen A*, **IV**, 395–548.

Haubold, H. 1971*b*. Ichnia Amphibiorum et Reptiliorum fossilium. *Encyclopedia of Paleoherpetology*, **18**, 1–124.

Heckert, A. B., Lucas, S. G., Rinehart, L. F., Celeskey, M. D., Spielmann, J. A. & Hunt, A. P. 2010. Articulated skeletons of the aetosaur *Typothorax coccinarum* Cope (Archosauria: stagonolepididae) from the Upper Triassic Bull Canyon Formation (Revueltian: early–mid Norian), eastern New Mexico, USA. *Journal of Vertebrate Paleontology*, **30**, 619–642.

Hminna, A., Voigt, S., Klein, H., Saber, H., Schneider, J. W. & Hmich, D. 2013. First occurrence of tetrapod footprints from the continental Triassic of Sidi Said Maachou area (Western Meseta, Morocco). *Journal of African Earth Sciences*, **80**, 1–7.

Hunt, A. P. & Lucas, S. G. 2007*a*. Late Triassic tetrapod tracks of western North America. *New Mexico Museum of Natural History and Science Bulletin*, **40**, 215–230.

Hunt, A. P. & Lucas, S. G. 2007*b*. The Triassic tetrapod track record: ichnofaunas, ichnofacies and biochronology. *New Mexico Museum of Natural History and Science Bulletin*, **41**, 78–87.

Jalil, N.-E. 1999. Continental Permian and Triassic vertebrate localities from Algeria and Morocco and their stratigraphical correlations. *Journal of African Earth Sciences*, **29**, 219–226.

Jenkins, F. A., Jr, Shubin, N. H. *et al*. 1994. Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland. *Meddelelser om Grønland Geoscience*, **32**, 1–25.

Karl, C. & Haubold, H. 1998. *Brachychirotherium* aus dem Coburger Sandstein (Mittlerer Keuper, Karn/Nor) in Nordbayern. *Hallesches Jahrbuch für Geowissenschaften*, **B20**, 33–58.

Karl, C. & Haubold, H. 2000. Saurierfährten im Keuper (Obere Trias) Frankens, die Typen von *Brachychirotherium. Berichte der Naturwissenschaftlichen Gesellschaft Bayreuth*, **XXIV**, 91–120.

Kemp, D. B. & Coe, A. L. 2007. A non-marine record of eccentricity forcing through the Upper Triassic of southwest England and its correlation with the Newark Basin astronomically calibrated geomagnetic polarity timescale from North America. *Geology*, **35**, 991–994.

Kent, D. V. & Clemmensen, L. B. 1996. Paleomagnetism and cycle stratigraphy of the Triassic Fleming Fjord and Gipsdalen formations of East Greenland. *Bulletin of the Geological Society of Denmark*, **46**, 121–136.

Kent, D. V. & Tauxe, L. 2005. Corrected Late Triassic latitudes for continents adjacent to the North Atlantic. *Science*, **307**, 240–244.

Kent, D. V., Malnis, P. S., Colombi, C. E., Alcober, O. A. & Martinez, R. N. 2014. Age constraints on the dispersal of dinosaurs in the Late Triassic from magnetochronology of the Los Colorados Formation (Argentina). *Proceedings of the National Academy of Sciences*, **111**, 7958–7963, http://doi.org/10.1073/pnas.1402369111

Klein, H. & Haubold, H. 2004. Überlieferungsbedingte Variation bei Chirotherien und Hinweise zur Ichnotaxonomie nach Beispielen aus der Mittel- bis Ober-Trias (Anisium–Karnium) von Nordbayern. *Hallesches Jahrbuch für Geowissenschaften*, **B26**, 1–15.

Klein, H. & Haubold, H. 2007. Archosaur footprints – potential for biochronology of Triassic continental sequences. *New Mexico Museum of Natural History and Science Bulletin*, **41**, 120–130.

Klein, H. & Lucas, S. G. 2010*a*. Review of the tetrapod ichnofauna of the Moenkopi Formation/Group (Early–Middle Triassic) of the American Southwest.

New Mexico Museum of Natural History and Science Bulletin, **50**, 1–67.

Klein, H. & Lucas, S. G. 2010*b*. The Triassic footprint record of crocodylomorphs – a critical re-evaluation. *In*: Milàn, J., Lucas, S. G., Lockley, M. G. & Spielmann, J. A. (eds) *Crocodyle Tracks and Traces*. New Mexico Museum of Natural History and Science Bulletin, **51**, 55–60.

Klein, H. & Lucas, S. G. 2010*c*. Tetrapod footprints – their use in biostratigraphy and biochronology of the Triassic. *In*: Lucas, S. G. (ed.) *The Triassic Timescale*. Geological Society, London, Special Publications, **334**, 419–446, http://doi.org/10.1144/SP334.14

Klein, H., Lucas, S. G. & Haubold, H. 2006. Tetrapod track assemblage of the RedondaFormation (Upper Triassic, Chinle Group) in east-central New Mexico – reevaluation of ichnofaunal diversity from studies of new material. *New Mexico Museum of Natural History and Science Bulletin*, **37**, 241–250.

Lockley, M. G. & Hunt, A. P. 1995. *Dinosaur Tracks and other Fossil Footprints of the Western United States*. Columbia University Press, New York.

Lockley, M. G. & Meyer, C. A. 2000. *Dinosaur Tracks and other Fossil Footprints of Europe*. Columbia University Press, New York.

Lockley, M. G., Wright, J. L., Hunt, A. P. & Lucas, S. G. 2001. The Late Triassic sauropod track record comes into focus: old legacies and new paradigms. *New Mexico Geological Society Guidebook*, **52**, 181–190.

Lockley, M. G., Lucas, S. G. & Hunt, A. P. 2006. *Eosauropus*, a new name for a Late Triassic track: further observations on the Late Triassic ichnogenus *Tetrasauropus* and related forms, with notes on the limits of interpretation. *New Mexico Museum of Natural History and Science Bulletin*, **37**, 192–198.

Lockley, M. G., Hups, K., Cart, K. & Gerwe, S. 2011. A zone of sauropodomorph footprints in the basal Wingate Sandstone (Latest Triassic) of western Colorado and eastern Utah: is *Eosauropus* a common ichnogenus in this region? *New Mexico Museum of Natural History and Science Bulletin*, **53**, 337–343.

Lucas, S. G. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **143**, 347–384.

Lucas, S. G. 2010. The Triassic timescale based on nonmarine tetrapod biostratigraphy and biochronology. *In*: Lucas, S. G. (ed.) *The Triassic Timescale*. Geological Society, London, Special Publications, **334**, 447–500, http://doi.org/10.1144/SP334.15

Lucas, S. G. & Heckert, A. B. 2011. Late Triassic aetosaurs as the trackmaker of the tetrapod footprint ichnotaxon *Brachychirotherium*. *Ichnos*, **18**, 197–208.

Lucas, S. G., Klein, H., Lockley, M. G., Spielmann, J., Gierlinski, G. D., Hunt, A. P. & Tanner, L. H. 2006. Triassic–Jurassic stratigraphic distribution of the theropod footprint ichnogenus *Eubrontes*. *New Mexico Museum of Natural History and Science Bulletin*, **37**, 68–93.

Lucas, S. G., Spielmann, J. A., Klein, H. & Lerner, A. J. 2010. Ichnology of the Upper Triassic Redonda Formation (Apachean) in east-central New Mexico. *New Mexico Museum of Natural History and Science Bulletin*, **47**, 1–75.

Mallison, H. & Wings, O. 2014. Photogrammetry in paleontology – a practical guide. *Journal of Paleontological Techniques*, **12**, 1–31.

Mateus, O., Clemmensen, L. B. *et al.* 2014. The Late Triassic of Jameson Land revisited: New vertebrate findings and the first phytosaur from Greenland. *In*: Maxwell, E. & Miller-Camp, J. (eds) *Society of Vertebrate Paleontology, 74th Meeting, Program and Abstracts*, 5–8 November 2014, Berlin, Germany. Society of Vertebrate Paleontology, Bethesda, MD, 182.

Melchor, R. N. & De Valais, S. 2006. A review of Triassic tetrapod track assemblages from Argentina. *Palaeontology*, **49**, 355–379.

Milàn, J. & Bromley, R. G. 2006. True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **231**, 253–264.

Milàn, J., Clemmensen, L. B. & Bonde, N. 2004. Vertical sections through dinosaur tracks (Late Triassic lake deposits, East Greenland) – undertracks and other surface deformation structures revealed. *Lethaia*, **37**, 285–296.

Milàn, J., Avanzini, M., Clemmensen, L. B., Garciá-Ramos, J. C. & Piñuela, L. 2006. Theropod foot movement recorded by Late Triassic, Early Jurassic and Late Jurassic fossil footprints. *New Mexico Museum of Natural History and Science Bulletin*, **37**, 352–364.

Milàn, J., Clemmensen, L. B. *et al.* 2012. A preliminary report on coprolites from the Late Triassic part of the Kap Stewart Formation, Jameson Land, East Greenland. *New Mexico Museum of Natural History and Science Bulletin*, **57**, 203–206.

Nesbitt, S. J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, **352**, 1–292.

Niedźwiedzki, G., Bonde, N., Błażejowski, B., Tałanda, M., Wolniewicz, A. & Sulej, T. 2014. Early sauropodomorph footprints in the Late Triassic of East Greenland. *In*: *4th International Palaeontological Congress Abstract Volume: The History of Life: A View from the Southern Hemisphere*, 28 September–3 October 2014, Mendoza, Argentina. International Palaeontological Association, Lawrence, KS & CONICET, Mendoza, 242.

Olsen, P. E. & Padian, K. 1986. Earliest records of *Batrachopus* from the southwestern United States, and a revision of some early Mesozoic crocodylomorph ichnogenera. *In*: Padian, K. (ed.) *The Beginning of the Age of Dinosaurs*. Cambridge University Press, Cambridge, 259–273.

Olsen, P. E., Smith, J. B. & McDonald, N. G. 1998. Type material of the type species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, and *Grallator* (Early Jurassic, Hartford and Deerfield Basins, Connecticut and Massachusetts, U.S.A.). *Journal of Vertebrate Paleontology*, **18**, 586–601.

Peabody, F. E. 1948. Reptile and amphibian trackways from the Moenkopi Formation of Arizona and Utah. *University of California Publications, Bulletin of the Department of Geological Sciences*, **27**, 295–468.

Petti, F. M., Avanzini, M. *et al.* 2009. Late Triassic (Early–Middle Carnian) chirotherian tracks from the Val Sabbia Sandstone (eastern Lombardy, Brescian Prealps, northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, **115**, 277–290.

Schoch, R. 2007. Osteology of the small archosaur *Aetosaurus* from the Upper Triassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **246**, 1–35.

Silvestri, S. M. & Szajna, M. J. 1993. Biostratigraphy of vertebrate footprints in the Late Triassic section of the Newark Basin, Pennsylvania: reassessment of stratigraphic ranges. *New Mexico Museum of Natural History and Science Bulletin*, **3**, 439–444.

Sulej, T., Wolniewicz, A., Bonde, N., Błażejowski, B., Niedźwiedzki, G. & Tałanda, M. 2014. New perspectives on the Late Triassic vertebrates of East Greenland: preliminary results of a Polish–Danish palaeontological expedition. *Polish Polar Research*, **35**, 541–552.

Szajna, M. J. & Hartline, B. W. 2003. A new vertebrate footprint locality from the Late Triassic Passaic Formation near Birdsboro, Pennsylvania. *In*: Le Tourneau, P. M. & Olsen, P. E. (eds) *The Great Rift Valleys of Pangaea in Eastern North America*. Columbia University Press, New York, **2**, 264–272.

Szajna, M. J. & Silvestri, S. M. 1996. A new occurrence of the ichnogenus *Brachychirotherium*: implications for the Triassic–Jurassic mass extinction event. *Museum of Northern Arizona Bulletin*, **60**, 275–283.

Volmer, T., Ricken, W., Weber, M., Tougiannidis, N., Röhling, H.-G. & Hambach, U. 2008. Orbital control on Upper Triassic playa cycles of the Steinmergel–Keuper (Norian): a new concept for ancient playa cycles. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **267**, 1–16.

Wotzlaw, J.-F., Guex, J. *et al.* 2014. Towards accurate numerical calibration of the Late Triassic: high-precision U–Pb geochronology constraints on the duration of the Rhaetian. *Geology*, **42**, 571–574.