The vertebrate-bearing Late Triassic Fleming Fjord Formation of central East Greenland revisited: stratigraphy, palaeoclimate and new palaeontological data

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Abstract: In Late Triassic (Norian–Rhaetian) times, the Jameson Land Basin lay at 40° N on the northern part of the supercontinent Pangaea. This position placed the basin in a transition zone between the relatively dry interior of the supercontinent and its more humid periphery. Sedimentation in the Jameson Land Basin took place in a lake–mudflat system and was controlled by orbitally forced variations in precipitation. Vertebrate fossils have consistently been found in these lake deposits (Fleming Fjord Formation), and include fishes, dinosaurs, amphibians, turtles, aetosaurs and pterosaurs. Furthermore, the fauna includes mammaliaform teeth and skeletal material. New vertebrate fossils were found during a joint vertebrate palaeontological and sedimentological expedition to Jameson Land in 2012. These new finds include phytosaurs, a second stem testudinatan specimen and new material of sauropodomorph dinosaurs, including osteologically immature individuals. Phytosaurs are a group of predators common in the Late Triassic, but previously unreported from Greenland. The finding includes well-preserved partial skeletons that show the occurrence of four individuals of three size classes. The new finds support a late Norian–early Rhaetian age for the Fleming Fjord Formation, and add new information on the palaeogeographical and palaeolatitudinal distribution of Late Triassic faunal provinces.

Late Triassic (Norian–Rhaetian) lake sediments of the Fleming Fjord Formation are very well exposed along the eastern margin of the Jameson Land Basin in East Greenland (Fig. 1). These lake deposits have been the subject of detailed stratigraphical, sedimentological and palaeontological studies since the late 1970s (e.g. Clemmensen 1980*a*, *b*; Jenkins *et al.* 1994; Kent & Clemmensen, 1996; Clemmensen *et al.* 1998; Milàn *et al.* 2004).

The vertebrate fauna of the Fleming Fjord Formation is both abundant and diverse, and includes fishes, dinosaurs, amphibians, turtles, aetosaurs and pterosaurs (Jenkins *et al.* 1994; Sulej *et al.* 2014). Furthermore, the fauna includes both teeth and skeletal elements of mammaliforms (Jenkins *et al.* 1994, 1997), such as *Haramiyavia clemmenseni*, *Brachyzostrodon* and *Kuehneotherium*. The association of several vertebrate groups is shared with well-known

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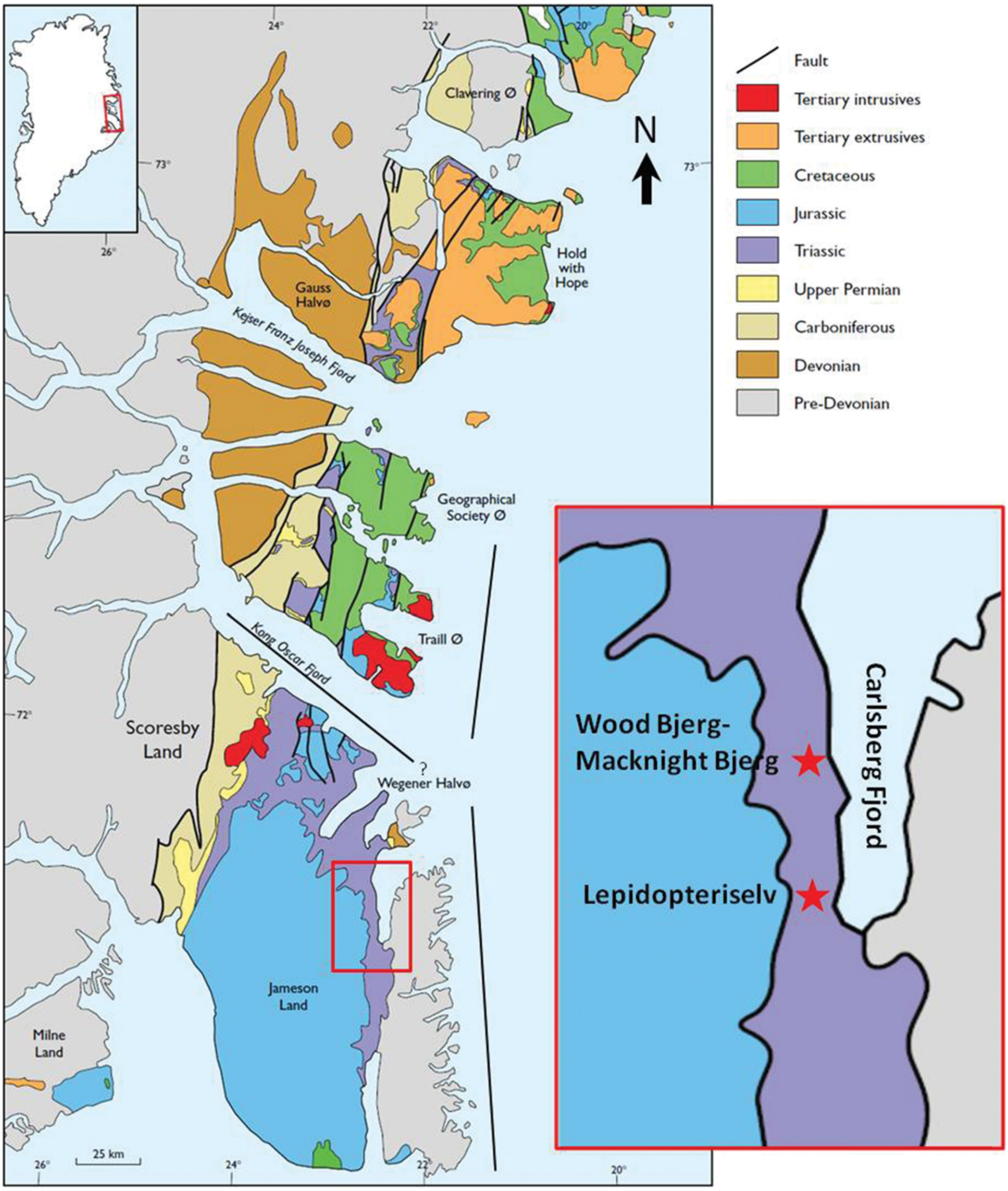

Fig. 1. Location map of East Greenland showing the Mesozoic deposits in the Jameson Land Basin. Small inset: Greenland. Large inset shows a close-up of the eastern part of the basin near Carlsberg Fjord, and the two localities with Upper Triassic sediments at Lepidopteriselv and Wood Bjerg–Macknight Bjerg. Figure modified from Stemmerik *et al.* (1997).

European Norian faunas, and the Greenland material adds new information to our understanding of the palaeogeographical distribution of Late Triassic fauna provinces. The vertebrate assemblage constrains the Jameson Land fauna in the Norian (Jenkins *et al.* 1994).

The published reptile taxa from the Late Triassic of Greenland are cf. *Proganochelys* (Testudinata), *Aetosaurus ferratus* and *Paratypothorax andressi* (Aetosauria: Stagonolepididae), *Plateosaurus engelhardti* (Dinosauria: Sauropodomorpha: Plateosauridae), Theropoda? indet., and *Eudimorphodon* *cromptonellus* (Pterosauria: Eudimorphodontidae: Eudimorphodontinae). This list is largely based on the brief descriptions by Jenkins *et al.* (1994), except for *Eudimorphodon cromptonellus*, which was the focus of a later monographic work (Jenkins *et al.* 2001). Therapsids are represented by the cynodont *Miltredon cromptoni* (Shapiro & Jenkins 2001), and amphibians represented by *Gerrothorax pulcherrimus* and *Cylcotosaurus* cf. *posthumus* (Jenkins *et al.* 1994, 2008). Classification of the remains attributed to theropods is not supported by any clear diagnostic theropodan feature and might alternatively be phytosaurian in origin.

New data from an expedition in 2012 (briefly reported in Milàn *et al.* 2012) shows the presence of phytosaurs, a second testudinatan specimen and new material of sauropodomorph dinosaurs. Phytosaurs are an archosaurian group of top predators common in the Late Triassic, but previously unreported from Greenland. The finds include well-preserved partial skeletons that show the occurrence of four individuals of three size classes (Mateus *et al.* 2014).

The aims of this paper are to redescribe the stratigraphical, palaeoenvironmental and palaeoclimatic setting of the vertebrate-bearing lacustrine succession, to provide a first description and classification of the new vertebrate finds from the Late Triassic of East Greenland, and to briefly discuss the palaeogeographical and chronological implications of the vertebrate assemblage.

Geological setting

During Triassic times, East Greenland was located at the northern rim of the Pangaean supercontinent and bounded to the north by the Boreal Sea (Nøttvedt *et al.* 2008). Triassic sediments are well exposed in the Jameson Land Basin, which is located in central East Greenland at about 71° N at the present-day land areas of Jameson Land and Scoresby Land (Fig. 1). The basin was situated at the southern end of the East Greenland rift system, which formed part of a larger rift complex separating Greenland from Norway prior to the opening of the Atlantic (Ziegler 1988). It was bounded to the west by a major north–south-trending fault and to the east by the Liverpool Land structural high. A possible NW–SE-trending cross-fault in Kong Oscar Fjord defined the northern boundary of the basin. The southern boundary is unknown; however, the basin may have extended south of Scoresby Sund (Clemmensen 1980*a*, *b*; Surlyk 1990).

The Triassic succession in East Greenland has thicknesses of between 1.0 and 1.7 km (Nøttvedt *et al.* 2008). During the earliest Triassic, the Jameson Land Basin was a marine bay (Boreal Sea), but underwent regression and continental emergence later in the early Triassic (Clemmensen 1980*a*, *b*; Nøttvedt *et al.* 2008). Continental sediments comprised alluvial fan, floodplain, aeolian dune, saline lake and freshwater lake deposits (Clemmensen 1980*a*; Clemmensen *et al.* 1998). The freshwater lake deposits in the uppermost part of the Triassic succession (the Fleming Fjord Formation) are particular well exposed in steep cliff sides facing the Carlsberg Fjord (Fig. 2).

Methods

The area around Lepidopteriselv (Fig. 1; Jenkins *et al.* 1994, area II) was intensively prospected, revealing many isolated bones, bone fragments and tracks; all suitable material on the surface was collected. After several bone fragments were found at the *Plateosaurus* site described by Jenkins *et al.* (1994), two trenches, each several metres long and about 50 cm deep, were excavated in the unsuccessful search for more articulated bones. Work focused during the first half of the expedition on several dinosaur tracksites and a new site on the mountain slopes east of the camp, which was named the ‘Phytosaur Bone Bed’ (71° 15.584′ N, 22° 31.785′ W). A few teeth and bones were found on the surface near a small ledge, and cleaning of the surface over an area of several square metres was commenced in order to identify the bone-bearing layers. Prospecting, surface collection and excavation was continued at Wood Bjerg and Macknight Bjerg (Fig. 1) close to area V of Jenkins *et al.* (1994). Excavation here focused at the old Jenkins quarry (71° 22.262′ N, 22° 33.381′ W), which was named ‘Iron Cake’ due to the iron-rich matrix of the bone-bearing sediment. The concretion-like iron-rich matrix was impossible to remove via field preparation and, hence, entire blocks of sediment were excavated.

Sediment grain size, depositional structures, bed geometry, and the relationship to the over- and underlying facies were investigated for each bone- and track-bearing layer. Special attention was given to beds with wave ripples as they contain information on the palaeoclimatic events that brought rain to the basin (cf. Clemmensen *et al.* 1998). Sedimentological logs on the scale of 1:10 were measured in the uppermost Carlsberg Fjord beds and the lowermost Tait Bjerg Beds in the two study areas, and the stratigraphical positions of track-bearing horizons noted (see later).

Stratigraphy and study area

The Fleming Fjord Formation (Norian-Rhaetian) is the uppermost unit in the Triassic Scoresby Land

Fig. 2. Mountain slope at Macknight Bjerg showing the 100 m thick Malmros Klint Member (steep cliff face) overlain by the Carlsberg Fjord beds of the Ørsted Dal Member (more gentle cliff slope). Carlsberg Fjord to the left.

Group (Clemmensen 1980*b*). The formation is composed of cyclically bedded lacustrine deposits and is subdivided into three members: a lowermost Edderfugledal Member, a middle Malmros Klint Member and an uppermost Ørsted Dal Member. The latter Ørsted Dal Member is composed of a lowermost unit of red mudstones, the Carlsberg Fjord beds, and an overlying unit of variegated mudstones and light grey dolomitic limestones, the Tait Bjerg Beds (Fig. 3) (Jenkins *et al.* 1994); these are in turn overlain by deltaic and lacustrine deposits of the early Rhaetian–Sinemurian Kap Stewart Formation (Dam & Surlyk 1993). In most places, however, the boundary between these two units is obscured by scree and solifluction deposits.

Vertebrate fossils have consistently been reported from the Fleming Fjord Formation, with most finds deriving from the eastern part of the basin along the Carlsberg Fjord (Clemmensen 1980*a*, *b*; Jenkins *et al.* 1994, 1997, 2001, 2008; Shapiro & Jenkins 2001). New vertebrate fossils were found during a joined vertebrate palaeontological and sedimentological expedition to Jameson Land from 12 July–2 August 2012. This expedition was conducted by the Geocenter Møns Klint and the Department of Geosciences and Natural Resource Management, Denmark, and was staffed by 12 researchers and technicians from Denmark, Germany and Portugal.

The fieldwork in 2012 focused on two areas: Lepidopteriselv and Wood Bjerg–Macknight Bjerg, (Fig. 1) both located in mountain slopes along Carlsberg Fjord within the Malmros Klint and Ørsted Dal members of the Fleming Fjord Formation. On the western coast of Carlsberg Fjord, the Malmros Klint Member crops out in spectacular cliffs and forms a 100–130 m succession of lacustrine deposits (Fig. 2). The member consists of a number of red-coloured, siliciclastic facies, the most common of which are intraformational conglomerate, brownish red massive siltstone, greyish red laminated siltstone, reddish grey muddy sandstone with wave-generated structures and bioturbation, and yellowish disrupted dolomitic sediment. Large-scale planar cross-bedding is occasionally displayed in the sandstones, and wave ripples and desiccation cracks are ubiquitous (Clemmensen *et al.* 1998). New finds of prosauropod dinosaurs, phytosaurs, dipnoic fishes, temnospondyls and theropod tracks were made in this member.

The Carlsberg Fjord beds, which have a thickness of 80–140 m, are composed of siliciclastic sediments of mudflat and lake origin. The Carlsberg Fjord beds crop out in more gentle slopes. The

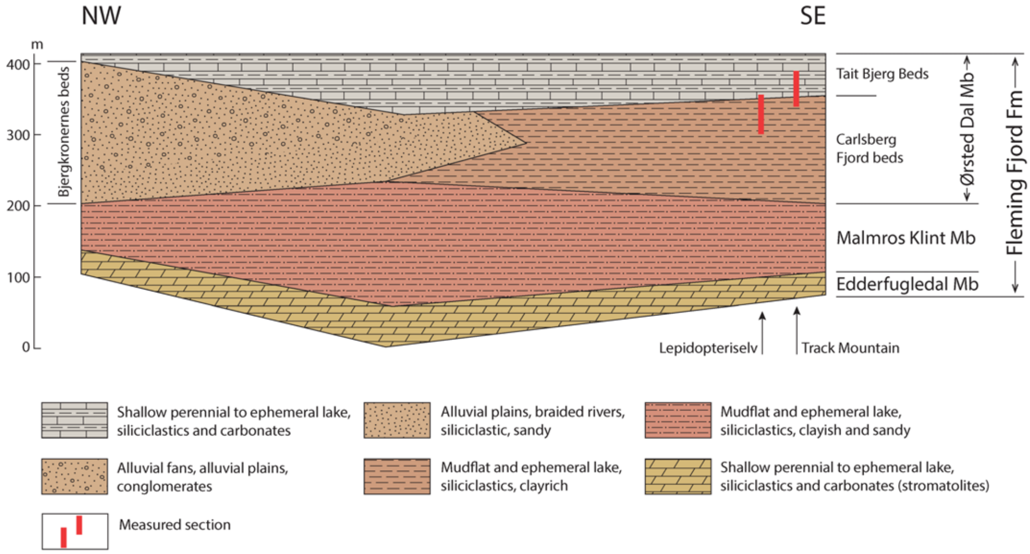

Fig. 3. Stratigraphy and depositional environments of the Late Triassic Fleming Fjord Formation, Jameson Land Basin, East Greenland. The investigated sections of the Carlsberg Fjord beds and the Tait Bjerg Beds are indicated. Figure modified from Jenkins *et al.* (1994).

most common facies are intraformational conglomerates, red-brown to purple massive mudstone, light reddish or greenish grey mud–peloid siltstone with wave-ripple cross-lamination and light greyish, fine- to medium-grained sandstone with current-formed cross-stratification (Clemmensen *et al.* 1998). Slabs with archosaur tracks were found in a fluvial sandstone bed in the lowermost part of the Carlsberg Fjord beds at Lepidopteriselv (see Klein *et al.* 2015). Numerous *Grallator* theropod tracks were observed in the upper part of this unit both at Lepidopteriselv and at Wood Bjerg–Macknight Bjerg ('Track Mountain'). The *Grallator* tracks are primarily seen on the upper surfaces of the relatively thin (2–5 cm thick) wave-rippled siltstones (see also Jenkins *et al.* 1994; Clemmensen *et al.* 1998). Testudinatan remains were found in poorly exposed Carlsberg Fjord beds at Wood Bjerg–Macknight Bjerg (at 71° 22.965′ N, 22° 33.216′ W: 462 m above sea level).

The Tait Bjerg Beds, which have a thickness of 50–65 m, in contrast to the underlying units are composed of both siliciclastic beds and limestones of lake origin. The unit is formed by a number of facies including intraformational conglomerate, massive to faintly laminated red-brown and purple mudstone, faintly laminated greenish mudstone, partly laminated greyish mudstone, thin wave-rippled silt- or sandstone and dolomitic limestone. *Grallator* tracks are common on exposed bedding planes in the lower part of the unit; in the transition zone between the Carlsberg Fjord beds and the Tait Bjerg Beds at 'Track Mountain', three trackways of sauropodomorph dinosaurs were observed (see also Jenkins *et al.* 1994).

Sparse invertebrate fossils and land-derived palynomorphs suggest that the Malmros Klint Member is of Carnian–Norian age, and that the Ørsted Dal Member is of Norian–early Rhaetian age (Clemmensen 1980*b*). Palaeomagnetic data indicate that the Malmros Klint and Ørsted Dal members are of late Norian–early Rhaetian age, and most probably represent a time span of between 212 and 207 myr (Kent & Clemmensen 1996; Clemmensen *et al.* 1998).

Palaeoclimate and lake environments

In Late Triassic times, the Jameson Land Basin lay at 40°N (Kent & Clemmensen 1996; Kent & Tauxe 2005). This position placed the basin in a transition zone between the relatively dry interior of the supercontinent Pangaea and the more humid peripheral part of this continent (Clemmensen *et al.* 1998; Sellwood & Valdes 2006), or well inside the humid temperate belt (Kent *et al.* 2014).

The sedimentary characteristics of the Malmros Klint Member indicate deposition in shallow-lake and mud-flat environments during a relative dry steppe-like climate probably influenced by seasonal rain. The overlying Carlsberg Fjord beds also represent shallow-lake and mud-flat deposition in a dry steppe-like climate, but during deposition of this unit the overall precipitation appears to have been very limited. The basal part of Tait Bjerg Beds formed in ephemeral to semi-perennial lakes, while the upper part of this unit was deposited in perennial lakes recording a more humid climate (Clemmensen *et al.* 1998).

Variations in precipitation on longer timescales are largely overprinting seasonal variations in precipitation and sedimentation, resulting in a composite sedimentary cyclicity. This is evidenced in the field by systematic variations in lithology and colour, which were interpreted by Clemmensen *et al.* (1998) as orbital controls on precipitation. Samples for colour determination were taken in the uppermost part of the Carlsberg Fjord beds and the lowermost Tait Bjerg Beds. Preliminary frequency analysis of rock colour time series (lightness, as well as green/red and blue/yellow values) and magnetic susceptibility variation shows significant peaks (cycles) with thicknesses of 0.9, 1.6 and 5.5 m. The ratios between the sedimentary cycles (1:1.8:6.1) suggest that the 0.9 m cycle records the 20 kyr precession cycle, the 1.6 m cycle records the 36 kyr obliquity cycle and the 5.5 m cycle records the 100 kyr eccentricity cycles (Frobøse & Clemmensen 2014). A cyclicity of around 20 m detected in the magnetic susceptibility variation and gamma-ray data could be the long 413 kyr eccentricity cycle. Frequency analysis of facies variation supports this interpretation and, if the observed facies variation is fitted with sinusoidal curves, the composite cyclicity of the sedimentary succession is clear (Fig. 4). However, refined statistical analysis may indicate an additional significant sedimentary cycle with a thickness of 2.6 m. This cyclicity could, alternatively, be viewed as the 100 kyr eccentricity cycle, indicating a slower accumulation rate in the basin.

The Late Triassic lake succession also contains clear evidence of long-term shifts in climate. The studied part of the sequence (the uppermost Carlsberg Fjord beds and lowermost Tait Bjerg Beds) is composed of three depositional systems (Figs 4 & 5):

- A – thought to record an ephemeral lake system with limited precipitation; we propose that rainfall was linked to the relatively weak summer monsoons;
- B – lacustrine conditions varying from ephemeral to semi-perennial; precipitation had increased and may partly have been brought to the basin by Westerlies;
- C – semi-perennial to perennial lake system with increased precipitation primarily influenced by Westerlies.

The uppermost part of the Tait Bjerg Beds forms a fourth deposition system and records deposition in a perennial lake that seemingly deepens with time due to increased precipitation (Clemmensen *et al.* 1998). The increasing influence of the relatively humid Westerlies with time cannot be supported by data on palaeowind directions, but is suggested by the increased abundance of perennial lake facies in depositional systems B and C. This long-term shift in climate towards being more humid revealed in the uppermost part of the Fleming Fjord succession has been explained by the slow northwards drift of the continent in the Late Triassic (Clemmensen *et al.* 1998; Kent & Tauxe 2005). It is possible that this gradually shifted the lake system from the relatively dry part of the supercontinent to an area influenced by the Westerlies and, thereby, increased precipitation. A northwards drift of up to 15° over the Late Triassic (Kent & Tauxe 2005; Kent *et al.* 2014) could, according to Sellwood & Valdes (2006), have significantly increased winter precipitation across the basin.

Vertebrate remains

Sauropodomorph dinosaurs

Prospecting and surface collecting revealed numerous bone fragments and smaller isolated bones, of which most could be tentatively assigned to sauropodomorph dinosaurs, cf. *Plateosaurus*, due to morphology (Huene 1926) and/or characteristic bone microstructure visible at breakages (Klein & Sander 2007).

The richest locality for dinosaur remains is a sheet sandstone–mudstone in the uppermost part of the Malmros Klint Member at Macknight Bjerg (Fig. 6a) – the Iron Cake Site (71° 22.262′ N, 22° 33.381′ W). This locality was found in 1991 and reported by Jenkins *et al.* (1994). We discovered numerous broken cf. *Plateosaurus* vertebrae and some long bones scattered over several square metres, and assume that these were discarded by the 1991 expedition. The best-preserved pieces were collected from the surface. The original bone-bearing layer was located and excavation on approximately 5 m^3 of matrix with *in situ* bones commenced. The fossils were encased in very hard iron-stained red sandstone. Frost heaving and solifluction had severely affected that layer, partially destroying many elements and relocated several blocks, complicating the taphonomical reconstruction.

Dinosaur material was found in several horizons within a stratigraphical thickness of about 1.0 m (Fig. 6a–e). The lateral extent of this bone accumulation was approximately 2 × 3 m. The bone-bearing sediments are mostly massive, strongly cemented by iron-rich solutions, but contain a few mud-cracked surfaces near its top. The bed is topped

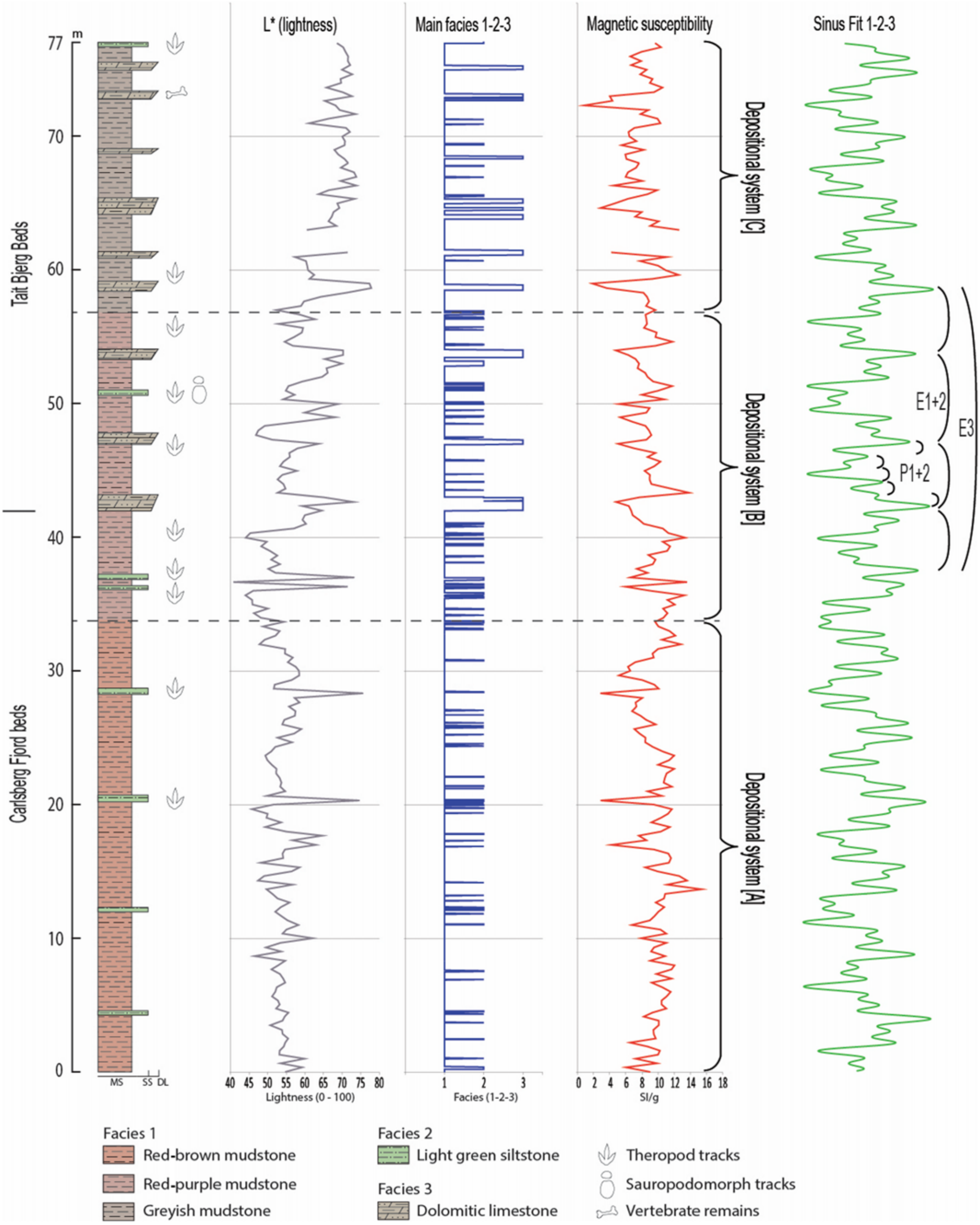

Fig. 4. Sedimentary log with main facies, colour variation (lightness), magnetic susceptibility variation and deduced climatic variation. P1+2 denotes precession cycles of about 20 kyr; E1+2 denotes eccentricity cycles of about 100 kyr; E3 denotes eccentricity cycles of 413 kyr. Levels with dinosaur tracks and vertebrate remains are indicated. The vertical distribution of the facies defines three depositional systems: (A) an ephemeral lake system; (B) an ephemeral to semi-perennial lake system; and (C) a semi-perennial to perennial lake system. The sinus Fit 1–2–3 (green) reflects the average peak distribution of the frequency analysis based on primarily the main facies 1–2–3. Log is compiled by data from the two study sites.

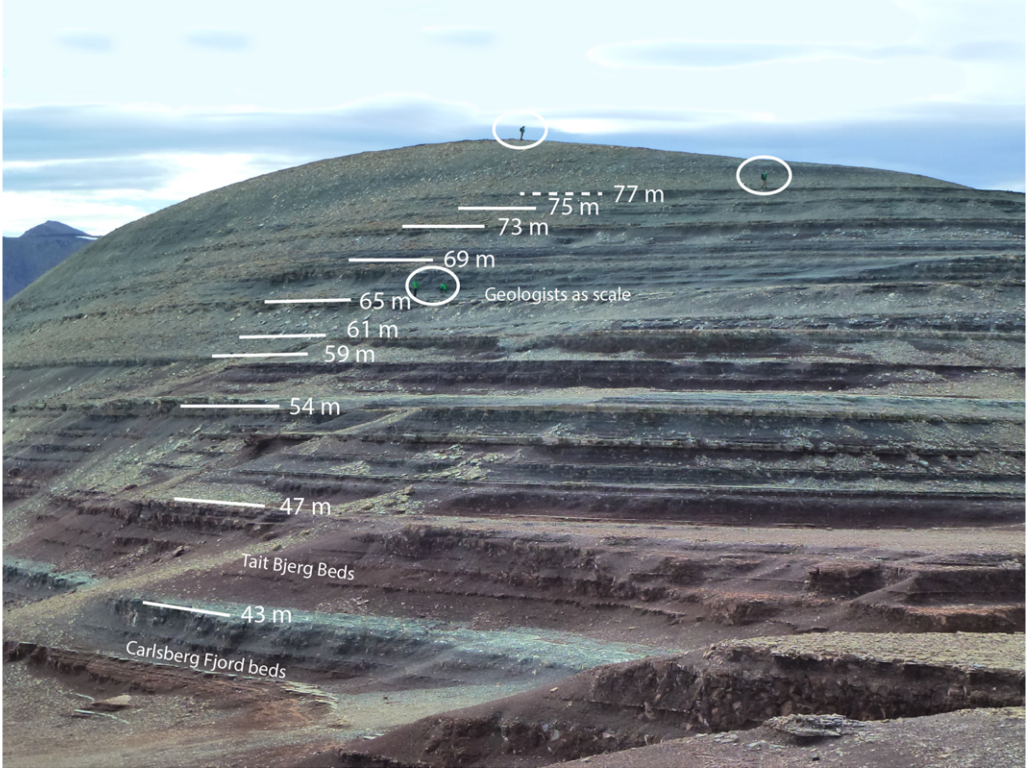

Fig. 5. The Track Mountain outcrop showing the uppermost Carlsberg Fjord beds and the main part of the overlying Tait Bjerg Beds. Depositional system B (33–57 m) at the base of the picture is overlain by depositional system C (57–77 m). This evolution of the lake system is thought to reflect increasing precipitation with time. The 10 level indicators correspond to the nine dolomitic limestone beds in the Tait Bjerg Beds and the top boundary (dotted line) of the measured sections as seen in Figure 4. The geologists are for scale.

by a wave-rippled sandstone. Large-scale deformation structures are present in parts of the bed. The bones seem to have been confined to several layers, some of which contained fully articulated three-dimensionally preserved specimens with minimal diagenetic deformation (Fig. 6c–e). The number of bones and their relative size indicate that more than one individual is present. Elements damaged before burial were rarely observed, indication parautochthonous deposition of the carcasses. Owing to the lack of diagnostic sedimentary structures, the bone-bearing sediment can only tentatively be interpreted as representing deposition in a lakeshore environment.

Skull components are very rare but comprise a lower jaw fragment with three teeth exhibiting leaf-like shape and serrations typical for *Plateosaurus* (Fig. 6d): these are possibly associated with cranial elements in the same block. Commonly articulated axial material includes two cervical vertebrae (Fig. 6a–c), dorsals with ribs and caudal vertebrae. The elongated cervical vertebrae are low and strongly compressed transversely (i.e. hourglass-shaped), as in *Plateosaurus* (Galton & Upchurch 2004). Only the more anteriorly situated cervical is complete enough to estimate the length/height ratio (95/35 mm) of the centrum at 2.7, indicating a rather anterior position (C3 or C4). The articulation surfaces of the centra are not yet prepared and it is currently unclear whether they show the amphicoelous condition of *Plateosaurus*. The preserved neural spine of the more anteriorly situated cervical is long and relatively low. The left cervical ribs are preserved *in situ*: they are thin and delicate, again consistent with *Plateosaurus* (Galton & Upchurch 2004; Huene 1926).

The dorsal vertebrae with articulated ribs (Fig. 6e) belong probably to at least two individuals of small (length of vertebra: 4–5 cm) to medium body size (length of vertebra: *c.* 6 cm), possibly representing not yet fully grown individuals when compared to the maximal known size of *Plateosaurus*

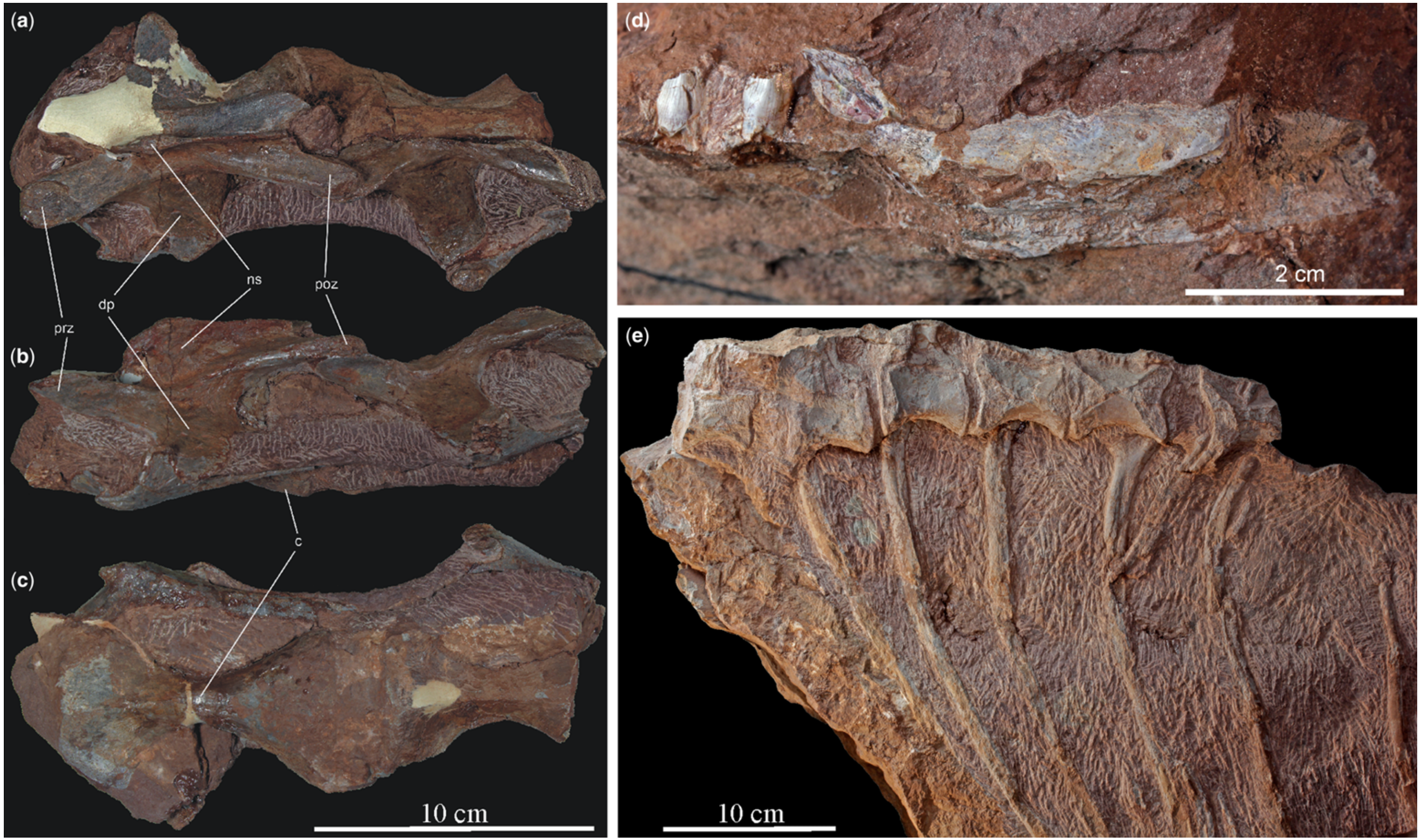

Fig. 6. Two articulated cervical vertebrae of cf. *Plateosaurus* from the Iron Cake Site in (**a**) dorsal, (**b**) left lateral and (**c**) ventral aspect. The more posteriorly situated vertebra is partially missing. Field number: III D. c, centrum; dp, diapophysis; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis. (**d**) Unprepared, partially preserved jaw of cf. *Plateosaurus* from the Iron Cake Site. Note the three teeth on the left upper side of the photograph and the serration on the left tooth. Field number: VII B 1. (**e**) Photograph of six articulated dorsal vertebrae of cf. *Plateosaurus* in left lateral aspect. The block is currently under preparation. Note the articulated right ribs and the unfused neurocentral sutures, indicating a juvenile individual. Field number: VI A 23.

(Huene 1926; Hofmann & Sander 2014), but note that size differences in *Plateosaurus* can also represent developmental plasticity (Sander & Klein 2005; Hofmann & Sander 2014). An articulated part of a trunk is associated with gastralia, pelvic bones and limb bones. Several more lower-limb bones, together with a femur, humerus and pes incorporating the phalanges, were found above and below the axial material, respectively. Because it is unprepared, the taxonomic attribution of this material is uncertain.

Close to the top of the Macknight Bjerg in the Carlsberg Fjord beds, at least three sites yielded isolated bones or numerous associated, but heavily weathered, bone fragments, which indicated the presence of another cf. *Plateosaurus* individual (71° 25.118′ N, 22° 32.494′ W and 71° 23.040′ N, 22° 32.508′ W).

Phytosaurs

Phytosaur bones were found in the in the middle part of the Malmros Klint Member at Lepidopteriselv (Fig. 7a–d). The elements were derived from the uppermost section of a fine-grained sandstone, which is about 0.2 m thick and contains scattered mud clasts. This bed contains rare wave-generated structures, possibly formed in a sandy lake-shore environment. Closely associated fluvial channel sandstones indicate that the lake was supplied

Fig. 7. Phytosaur material from the site at Lepidopteriselv. (**a**) Anatomical mounting of the collected material from one of the large individuals, now on display in the exhibition at the Geocenter Møns Klint. Notice the small juvenile specimen below for comparison. (**b**) Three articulated dorsal vertebrae. (**c**) Three humeri, two left and one right, from two adult individuals. (**d**) Partial dentary, with two teeth preserved. (b)–(d) are reproduced to the same scale. Pictures by Verena Régent.

(intermittently) with water and sandy sediments from nearby uplands. The Phytosaur Bone Bed was exposed for about 7 m in the sandstone and excavated over 30 m^2, yielding about 130 individual bones or fragments.

The fossils were generally well preserved with a muddy coating on the surface due to frost heaving. Disarticulated skull material consisted of the mandible (Fig. 7d), jugals, postorbital, angular and quadrate. Vertebrae, gastralia, ribs and appendicular bones were also collected. Considering size ranges and duplication of bones, the phytosaur material pertains to at least four individuals and three size classes. Most represented individuals with an estimated body length of 3.8 m. The full body sizes are obtained by placing the fossil bones over the skeleton illustration of *Angistorhinus* by Stocker & Butler (2013, fig 3a) that was printed to real-size to fit the Greenland specimen (Fig. 7a). To fit the print to the bones, the skull drawing was reduced by about 20% when compared to the skeleton. Most of the bones pertain to individuals of this size range (3.8 m long), including three nearly identical humeri of the same size (two left and one right side, between 255 and 264 mm) that provide evidence for at least two individuals (Fig. 7c).

Three complete dorsal neural arches and one centrum, all with unfused open neurocentral suture (Fig. 7b) and an anterior part of a dentary about 63 mm long, show the additional presence of an animal with a body length of 1–2 m. The third and smallest body size is deduced from a complete left scapula only 34 mm in length, corresponding to a body length of 45–55 cm. These are the first well-documented phytosaurs in Greenland. Bones of previous expeditions assigned to phytosaurs belong to temnospondyls (Mateus *et al.* 2014).

The outline of the collected phytosaur jaw resembles the type specimen (UCMP26699: Camp 1930, fig. 41) of *Machaeroprosopus*/*Smilosuchus adamanensis*, in particular the minute teeth, subhorizontal surangular, dorso-ventral thin dentary and short posterior part of the jaw (distance between the last tooth and the articular is less than one-third of the jaw length). Note that the '*Machaeroprosopus' adamanensis* Camp, 1930 type specimen was re-identified as *Smilosuchus adamanensis* by Stocker (2010).

Testudinatan

The fragmentary carapace of a basal testudinatan was collected in the Carlsberg Fjord beds at Macknight Bjerg at 71° 22.965′ N, 22° 33.216′ W, 462 m above sea level. The suture patterns of the carapace show a basal condition of imbricated overlapping osteoderms rather than derived side-by-side fusion as seen in most turtles, including modern forms. Proganochelys was previously documented to the area (Jenkins *et al.* 1994).

Temnospondyl amphibians

The locality used in Jenkins *et al.* (1994) on the southern flank of Macknight Bjerg (the lower part of the Carlsberg Fjord beds of the Ørsted Dal Member: 71° 22.30′ N, 22° 33.14′ W) was revisited. The intensively excavated quarry during former expeditions produced an abundant tetrapod fauna, including temnospondyls, pterosaurs, dinosaurs and mammals (Jenkins *et al.* 1994), indicating that the bone bed represents a taphocoenosis. A 1 day survey during the 2012 field campaign revealed numerous temnospondyl vertebrae and girdle bones, as well as some hollow long bone material, which could represent pterosaur and/or theropod remains. Smaller bones had been weathered out and were collected from the surface. The large temnospondyl girdle bones were excavated in the old quarry. A lower jaw fragment collected on the surface can be assigned to a temnospondyl.

The isolated vertebral centra are platycoelous. Their shape is cubic with a U-shaped cross-section and a 'flat' dorsal surface incised by a shallow notochord depression (in sagittal axis). The parapophyses is located very high, almost dorsally. All features are typical for *Gerrothorax* (D. Konietzko-Meier pers. comm.; Konietzko-Meier *et al.* 2014). Some of the interclavicle, clavicle and lower jaws can also be assigned to *Gerrothorax*, while a second interclavicle and clavicle show affinity with *Cyclotosaurus*; this is mainly based on the sculpturing of the bones – *Gerrothorax* has a tubular or pustulated pattern, whereas *Cyclotosaurus* displays longitudinal striations that are deeper and more massive.

One bone bed comprising disarticulated small temnospondyl remains was found in the Carlsberg Fjord beds at 71° 24.686′ N, 22° 33.619′ W, 515 m above a steep cliff face. The palaeontological potential of this bone bed is promising if safety conditions are secured. One temnospondyl bone (probably a girdle element) was collected in the Tait Bjerg Beds at 71° 29.194′ N, 22° 36.705′ W, 683 m above sea level, but a more detailed identification has not yet been conducted.

In the lowermost part of the Kap Stewart Formation ('Burned Paper-Shale' locality at 71° 24.800′ N, 22° 34.417′ W, 572 m above sea level: Milàn *et al.* 2012) shark coprolites, pterosaur bones, phytosaur scutes, bivalves and capitosaurid temnospondyl bones were found in dark, parallel-laminated lacustrine mudstone. Temnospondyls were tentatively identified based on the labyrinthodont dentine, large size and the presence of large anterior tusk teeth.

Tetrapod tracks

Numerous tracks and trackways were found at both main camps and on the short visit to the nearby Tait Bjerg Mountain. Four main kinds of tracks were recognized: (1) abundant theropod tracks and trackways of different sizes, but morphologically similar; (2) one sauropod-like trackway; (3) basal sauropodomorph-like trackways; and (4) archosaur tracks.

Theropod tracks

Most theropod tracks were found at Lepidopteriselv and Track Mountain (Fig. 8a, b), and all could be identified as grallatorid-type. The quantity of theropod tracks is overwhelming and can be safely estimated at up to 1000 tracks in multiple horizons.

At Tait Bjerg, some well-preserved theropod tracks were found, but not collected, at 71° 28.838′ N, 22° 36.492′ W, 592 m above sea level. At Track Mountain one theropod track with a skin impression was collected from 71° 24.938′ N, 22° 33.038′ W. One theropod trackway observed nearby (71° 24.839′ N, 22° 32.939′ W), but not collected, with four footprints, preserved the imprints of metatarsus and hallux. Each track measured between 21 and 25 cm in length, and 7.5–8.5 cm in width. The pace was 61 cm, while the step was 119 cm long (Fig. 8c, d).

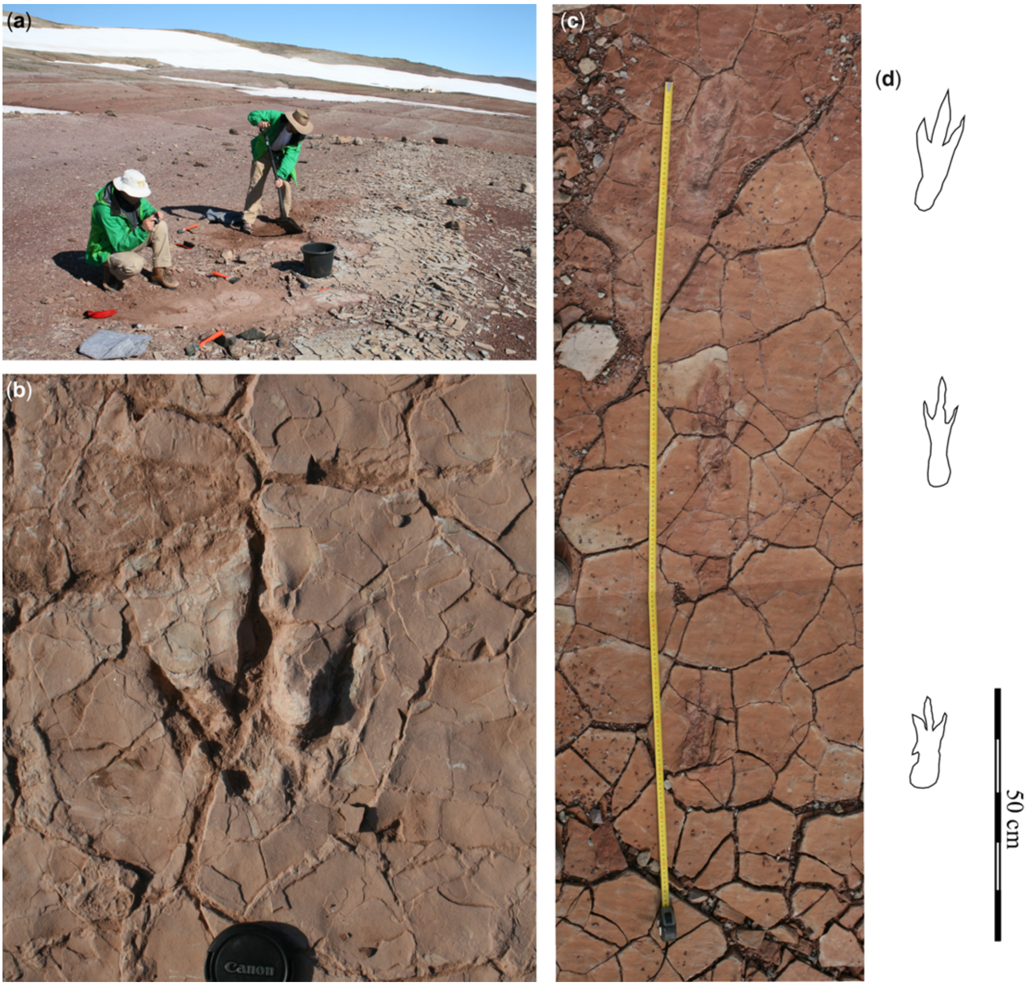

Fig. 8. (**a**) Investigation of one of the track-bearing layers from the Lepidopteriselv site. (**b**) Close-up of a typical grallatorid theropod track. (**c**) Theropod trackway with metatarsal impressions. (**d**) Interpretative sketch of the trackway in (c).

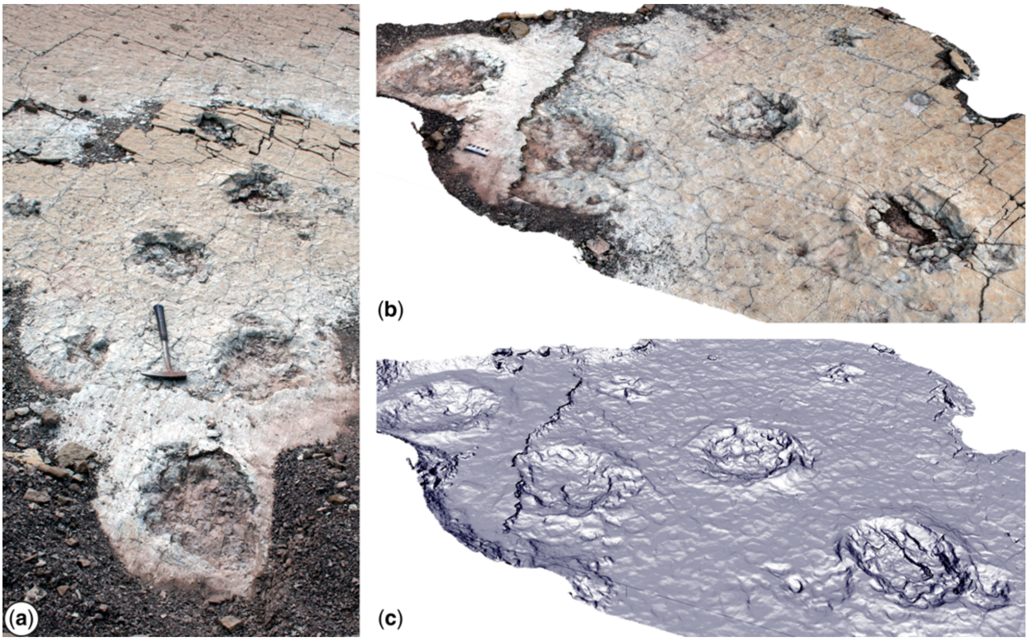

Fig. 9. Sauropodomorph tracks from the Track Mountain locality: (**a**) bipedal trackway set in a relatively narrow gauge; (**b**) photogrammetric 3D model of the trackway, enhancing the shape and features of the track; and (**c**) the same trackway without texture enhancing the profile of the tracks.

Sauropodomorph tracks

Three different sauropodomorph trackways were partly excavated and measured at the Track Mountain locality (Figs 9 & 10). The first type of trackway is bipedal with rounded pes and weak indications of outwards-rotated claws. One shows a weak impression in front of the pes that could indicate the presence of a thin semilunate-shaped manus. The pes length is around 38 cm long and 35 cm wide (Fig. 9). The second type is quadrupedal, with an extreme degree of heteropody. The pes is elongated, on average 42 cm long and 15 cm wide, with indications of outwards-rotated, short claws. The manus prints are situated immediately in front of the pes and measure about 11 cm long and 16 cm wide. The pattern is narrow gauge (Fig. 10a). The third track type is bipedal, with tetradactyl pes prints. The digits are inwards rotated, are long and narrow, and terminate in impressions of sharp claws (Fig. 10b, c).

Archosaur tracks

Several slabs with abundant small morphs of *Brachychirotherium* were recovered (see Klein *et al.* 2015), with well-preserved manus and pes tracks no larger than 2.2 and 4.5 cm, respectively.

Thrombolites/stromatolites

Up to 13 biochemical accretionary structures (thrombolites or stromatolites) were found and samples collected at 71° 24.906′ N, 22° 33.160′ W in uppermost Tail Bjerg Beds a few metres below the base of the Kap Stewart Formation (Fig. 11a). These cylindrical structures encrusted around tree branches or submerged roots, which are now dissolved and replaced by coarse sandstone preserving natural casts including branching twigs (Fig. 11b). The biomat growth was accretionary from the surface of the tree to the periphery. The largest thrombolite/stromatolite sample was 70 cm long and 18.5 cm in total diameter, and enclosed a tree trunk 8 cm in diameter (Fig. 11c). Some examples have the ends also covered with thrombolite/stromatolite. The layers suggest different original inclinations of the trees, from horizontal to subvertical. We interpret this preservation as a shallow water body that flooded a forest, creating favourable conditions for microbial mat growth.

Discussion and conclusions

The vertebrate fauna of the Fleming Fjord Formation is abundant and taxonomically diverse,

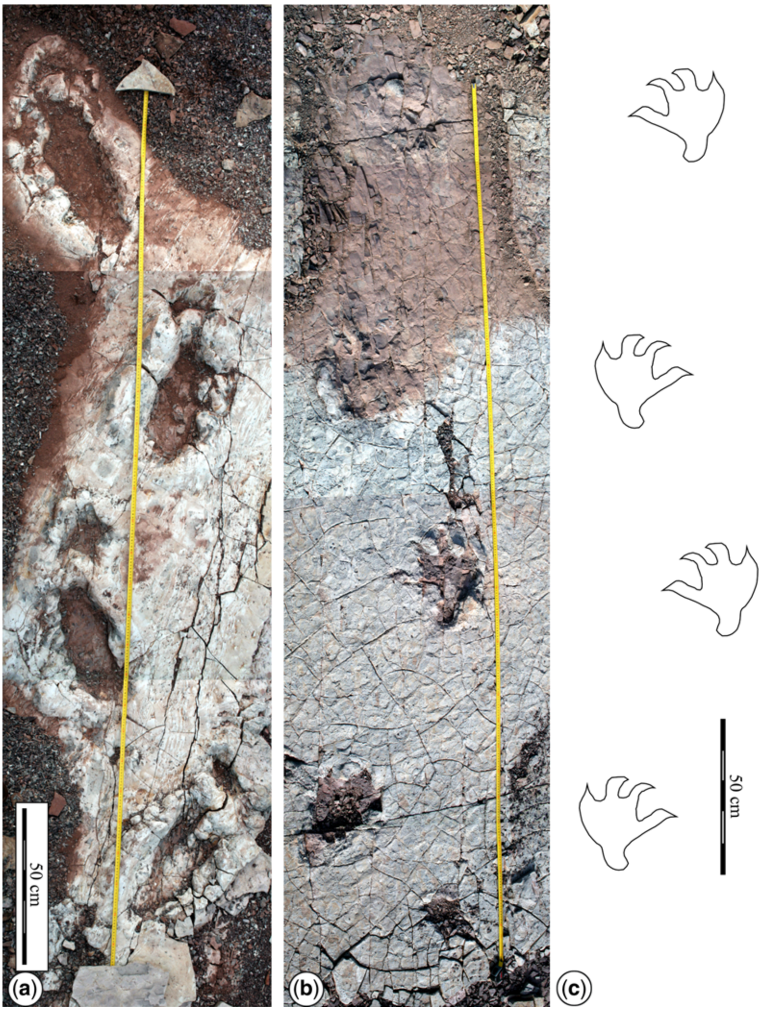

Fig. 10. (**a**) Quadrupedal trackway with extreme heteropody and large banana-shaped pes tracks, with outwards-rotated claw impressions. (**b**) Biped trackway with tetradactyl tracks with inwards-rotated digits. (**c**) Interpretative sketch of (b).

including fishes, amphibians, turtles, phytosaurs, an aetosaur, a pterosaur, dinosaurs and early mammaliforms (Jenkins *et al.* 1994, 1997, 2001, 2008; Gatesy *et al.* 1999). The association of several vertebrate genera (e.g. *Aetosaurus*, *Cyclotosaurus*, *Plateosaurus*) in the Fleming Fjord Formation matches that of well-known late Norian faunas from central Europe (i.e. Germany), but the Greenland material adds significant new information to our understanding of the palaeogeographical and palaeolatitudinal distribution of Late Triassic faunal provinces. The vertebrate fauna provides support for the inference of a late Norian–early Rhaetian age for the Fleming Fjord Formation. The Fleming Fjord vertebrates lived in and around a lake palaeoenvironment (Jenkins *et al.* 1994; Clemmensen *et al.* 1998).

A re-examination of the palaeontology and sedimentology of the Fleming Fjord Formation in 2012 provided new material of phytosaurs, a second turtle specimen and new specimens of cf. *Plateosaurus*. Phytosaurs are a group of aquatic predators common worldwide in the Late Triassic, but their occurrence in Greenland had previously been uncertain. The new discoveries include well-preserved partial skeletons that show the occurrence of four individuals in three size classes.

The number of theropod tracks encountered at the localities of Lepidopteriselv and Track

Fig. 11. (**a**) *In situ* stromatolite/trombolite orientated subvertically into the substrate. The central cavity is filled with sandstone. (**b**) The inner side of the stromatolite/trombolite has preserved an impression of the tree branch or root around which it was growing. (**c**) The specimens found were up to 70 cm in height and 18 cm in diameter.

Mountain can safely be counted in the thousands along several horizons up through the succession. Such high numbers are remarkable when compared with the fact that no unequivocal theropod bones or teeth have been recovered and/or identified in the Fleming Fjord Formation. This enigmatic disparity in the abundance of theropod tracks and the absence of bones is yet to be understood, but may, perhaps, be explained by two reasons: (1) theropods were truly scarce but very active, thus each individual produced thousands of tracks during its lifetime while patrolling the lake shore; and (2) the sedimentological and geochemical conditions for bones and track preservation are different. This second option is less supported owing to the presence of well-preserved skeletons of other clades, such as sauropodomorphs and phytosaurs. However, skeletal remains of prosauropods are relatively common compared to the few finds of sauropodomorph trackways in the area. Furthermore, all discovered sauropodomorph tracks derive from large individuals, whereas much smaller, not yet fully grown, individuals constitute a large part of the fossil bone record.

The investigations show the presence of at least three different sauropodomorph trackmakers, two of which had a bipedal stance and one quadrupedal with pronounced heteropody. Further findings suggest the presence of a fourth sauropodomorph, with rounded elephantine feet and a narrow trackway pattern (Niedźwiedzki *et al.* 2014). In comparison, all of the excavated skeletal material seems to belong to cf. *Plateosaurus*. (Jenkins *et al.* 1994; Mateus *et al.* 2014). This demonstrates that the Fleming Fjord dinosaur fauna is much more diverse than that which is known from the skeletal record, and that future excavations and investigations are needed in order to understand the complete picture of the Late Triassic continental ecosystem in Greenland.

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