Journal of Vertebrate Paleontology 30(2):521–527, March 2010

ARTICLE

PALEOCENE TRACKS OF THE MAMMAL PANTODONT GENUS *TITANOIDES* IN COAL-BEARING STRATA, SVALBARD, ARCTIC NORWAY

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ABSTRACT—We discuss large tracks recently discovered in Paleocene coal deposits from Svalbard. The age, large size, and excellent preservation of the tracks allows them to be identified to the pantodont *Titanoides*. This is the earliest evidence of a large mammal on the Arctic islands and the northernmost record from the Paleocene. The traces are described in detail and named *Thulitheripus svalbardii*, gen. et sp. nov. Large Paleocene pantodonts are previously only known from North America. The presence of pantodonts in the Paleocene strata of Svalbard confirms the postulated DeGeer route for migration of mammals in the Paleocene/Eocene.

INTRODUCTION

This is the first discovery of fossil mammal tracks on Spitsbergen in the Svalbard archipelago, Arctic Norway. Size and excellent quality of the tracks make them unique and makes it possible to identify the track maker and its implication for understanding the regional geology. The tracks were discovered on the 20th December 2006 by the miners Håvard Dyrkollbotn and Kent Solberg, in the roof of the coal mine (Gruve 7) in Longyearbyen. This coal is in the Todalen Member of the Firkanten Formation (Fig. 1), of Paleocene age (Manum and Throndsen, 1986). Svalbard has previously yielded some of the northern-most evidence of dinosaurs in the form of several track-bearing layers from the Lower Cretaceous (Lapparent, 1960; Lockley and Meyer 2000; for discussion and additional references, see Hurum et al., 2006).

The track record of Paleocene mammals is scarce and so far only a handful of tracks and trackways have been described worldwide (e.g., McCrea et al., 2004; Lucas, 2007). There are no known skeletal remains of mammals from the Paleocene of Svalbard and the adjacent Paleocene deposits of Greenland. The only vertebrate fossil ever recorded from this unit on Svalbard is an amiid fish (Lehman, 1951). The size of the tracks implies they were made by a large mammal.

GEOLOGICAL BACKGROUND

In the Paleogene, Svalbard was situated close to the northern part of Greenland and Ellesmere Island, Canada (Blythe and Kleinspehn, 1998). The convergence with Greenland due to plate movement in connection with the opening of the Northern Atlantic created the western fold and thrust belt and the related flexural basin (Blythe and Kleinspehn, 1998; Lüthje, 2008).

The main Paleogene succession on Svalbard is in the Central Tertiary Basin consisting of 1.9 km of clastic strata (Dallmann, 1999) deposited in the flexural basin (Lüthje, 2008). The Todalen Member of the Firkanten Formation is the lowest stratigraphic unit and is separated from the underlying Carolinefjellet Formation (Albian/Aptian) by an unconformity representing more than 35 million years (Fig. 1). The Firkanten and Basilika Formations (Fig. 1A) form a general transgressive succession (Lüthje, 2008) from continental and marginal marine coastal plain to shoreface and offshore transition (Steel et al., 1981; Dallmann, 1999; Lüthje, 2008). The Todalen Member was deposited in a marginal marine to coastal plain setting, characterized by tidally influenced lagoons protected by sandy barrier bars (Lüthje, 2008). The terrestrial vegetation has been characterized as the “Paleocene and Eocene polar, broad leaved, deciduous forests” (Collinson and Hooker, 2003). These forests were present in the Greenland Region (Greenland, Svalbard, Ellesmere Island, and Scotland) and characterized by the genera *Trochodendroides*, *Corylites*, and *Metasequoia* (Collinson and Hooker, 2003). The climate on Svalbard during the Paleocene and Early Eocene has been interpreted to be warm-temperate, with a high humidity equally distributed over the year based on fossil plant material (Golovneva, 2000; Cepek and Kruttzsch, 2001). It was a very favorable climate for plant production even though plate reconstruction places Svalbard at 65–68° N at this time (Cepek and Kruttzsch, 2001). In the Late Eocene, the climate changed to almost cool-temperate. The mean annual temperature has been estimated to be around +12°C in the Paleocene and only +8°C in the Late Eocene (Golovneva, 2000). On the coastal plain, large peat mire complexes built up the thick coal seams being mined today. The tracks were found at the boundary between the coal and overlying sandy deposits.

Age of Sediments

The age of the Firkanten Formation is poorly controlled because of the sparse fossil record but a Paleocene age can be concluded. The Paleocene to Eocene boundary is in the overlying Frysjaodden Formation (Fig. 1) (Manum and Throndsen, 1986; Dallmann, 1999; Nagy et al., 2000). Sequence stratigraphic

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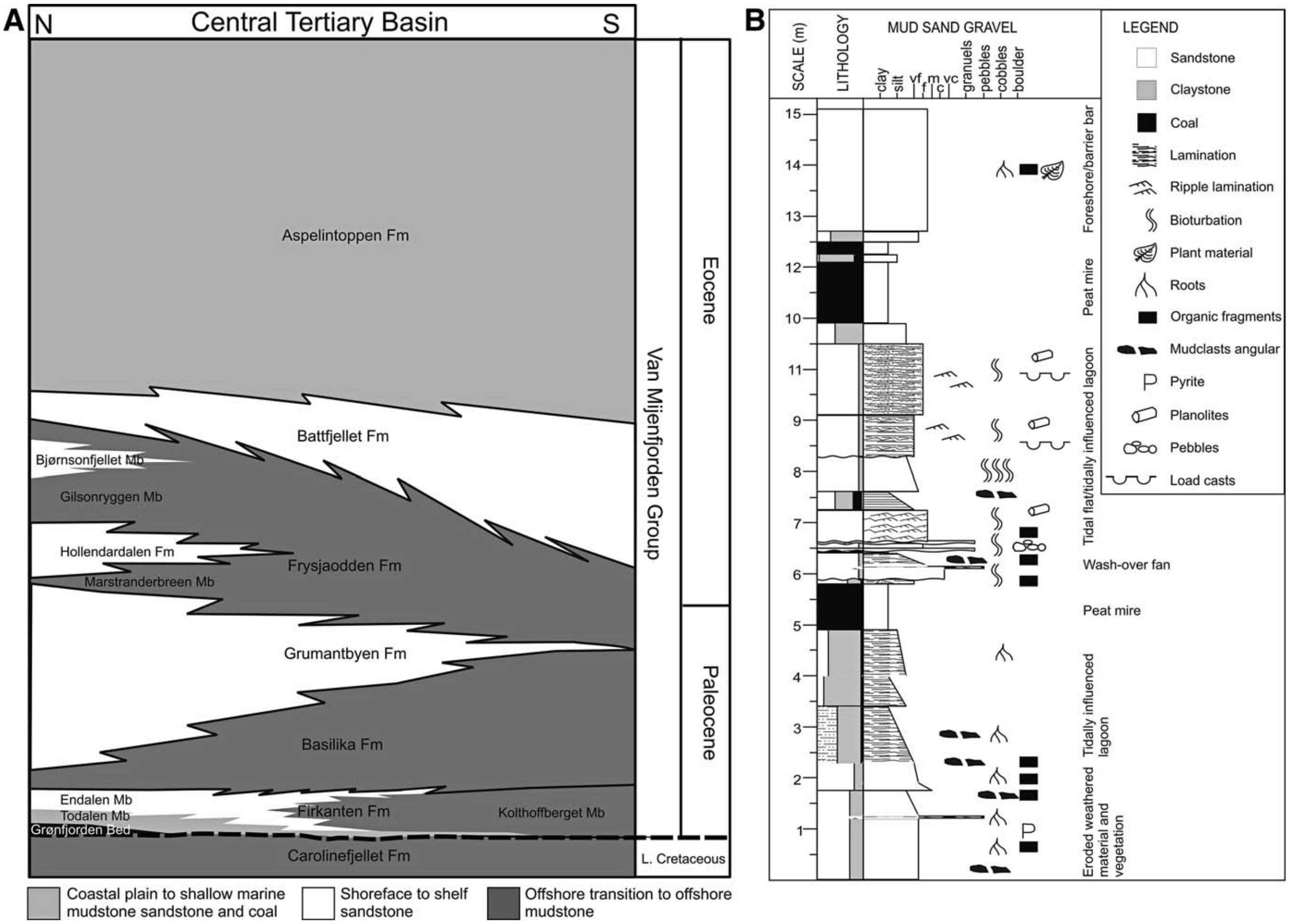

FIGURE 1. **A**, The stratigraphy of the Paleogene Van Mijenfjorden Group in the Central Tertiary Basin of Spitsbergen, from (Lüthje, 2008), based partly on Bruhn and Steel (2003) and Steel et al. (1985). Geometries are based on relative thickness variations (Dallmann, 1999) over the basin. **B**, Sedimentary log of core BH05-2004, from a location near Gruve 7.

analysis indicates a general stepwise but overall transgressive succession, with no relative sea level fall detected in the Firkanten Formation (Lüthje, 2008), indicating that it was deposited in a period with no major eustatic sea level falls, arguing for a Late Paleocene age for the Firkanten Formation (Lüthje, 2008).

Locality Gruve 7, Longyearbyen

The tracks were found at the boundary between the coal and overlaying muddy, organic-rich fine-grained sandstone (Fig. 1B). The coal, which is highly bituminous, accumulated as peat in extensive mire complexes on the coastal plain and has been mined from several places on Svalbard the last 100 years.

Normally tracks would not be expected to be preserved in coal because coal originates from peat, which is not expected to keep an imprint. However, tracks and trackways are commonly encountered in the top surface of coal seams because the lithological differences between the coal and the overlying sediments are optimal for track preservation (e.g., Peterson, 1924; Brown, 1938; Lockley and Jennings, 1987; Parker and Balsby, 1989; Parker and Rowley, 1989; Lockley and Hunt 1995; Hurum et al., 2006). Furthermore, the worldwide commercial coal quarrying helps to expose large, potentially track-bearing surfaces.

The tracks in Gruve 7 are also situated in a 2–5 cm thick layer of sapropelic coal on top of the ombrotrophic coal. Sapropelic coal is normally produced by algal, bacterial, or fungal organic production in stagnant swamps under anaerobic conditions (McCabe, 1984) and greatly improves the possibilities for preservation of the tracks. The tracks show that the animals sank deeply into the sticky substrate, leaving a good imprint, because an algal mat does not have the same elastic properties as peat. Some of the tracks were found to have been imprinted in the sandstone on top of the coal. This suggests that they are either of a slightly later time (hours) and/or the surface area was mud/algae covered in places and sandy in others.

The preservation of the tracks was also improved by being covered shortly after by fine-grained sandstone from the marine transgression that was already ongoing. The sapropelic coal indicates a base level rise where the environment became too waterlogged for peat production and therefore became a swamp. The mire was flooded by raised ground water level, which is characteristic for swamps. Swamps can be influenced by both fresh and marine salt water. In this case, the following marine transgression on top of the coal indicates that the swamp was created by marine flooding from a rising relative sea level.

The sandstone on top of the tracks is organic-rich, with poor structural development and pebbly layers (Fig. 1B). The section is interpreted to represent part of a wash-over fan deposited on top of the swamp and the mire by the marine transgression. *Teredolites* trace fossils found in the overlying sandstone were created by

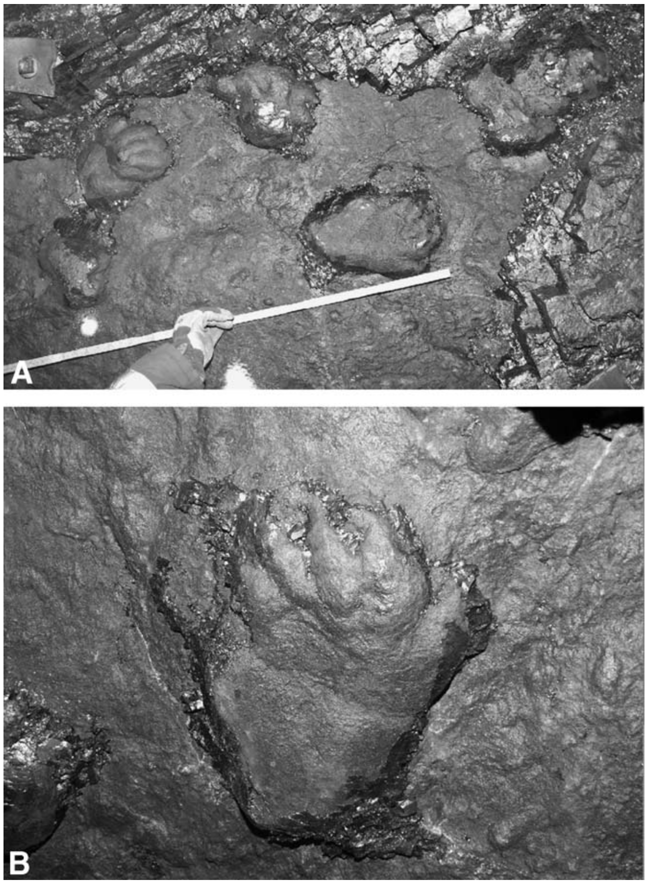

FIGURE 2. **A**, Photo of the tracks as they were discovered in the roof of the coal mine. The scale equals 1 m. **B**, Frontal view of track T3-2. The pes is partly overstepping the more deeply impressed manus print.

marine burrowing and dwelling bivalves that typically bore into organic deposits that are flooded (Pemberton et al., 1992).

THE TRACK ASSEMBLAGE

The track assemblage consists of 17 individual imprints exposed on a 5 m stretch along the roof of the coal mine. All tracks are preserved as natural casts of silty sandstone (Fig. 2).

Trackways

The tracks can de divided into three individual trackways, based on differences in size and trackway parameters. Four individual tracks cannot be readily assigned to any specific trackway (Fig. 3). The three trackways are numbered T1–T3, with each individual track within the trackway numbered in running order. The four unassigned tracks are designated ‘T?’ The trackways are set in a narrow gauge pattern, with the tracks from left and right side of the animal set close to the midline of the trackway. T1 has an average stride length of 85 cm and an average pace angulation of 113° (Fig. 4). The trackway width is on average 47 cm. T2 has a stride length of 98 cm and pace angulation of 118°, and is 44 cm wide. T3 have a stride length of 82 cm and a pace angulation of 125° and is 36 cm wide.

Manus (fore limb) and pes (hind limb) imprints are pentadactyl, with short, broad digits. The pes impressions are in most cases partly overstepping the manus impression, obscuring the details of the pedal digits, and hindering exact measurements of the dimensions of the pes. The size of the manus imprint is on

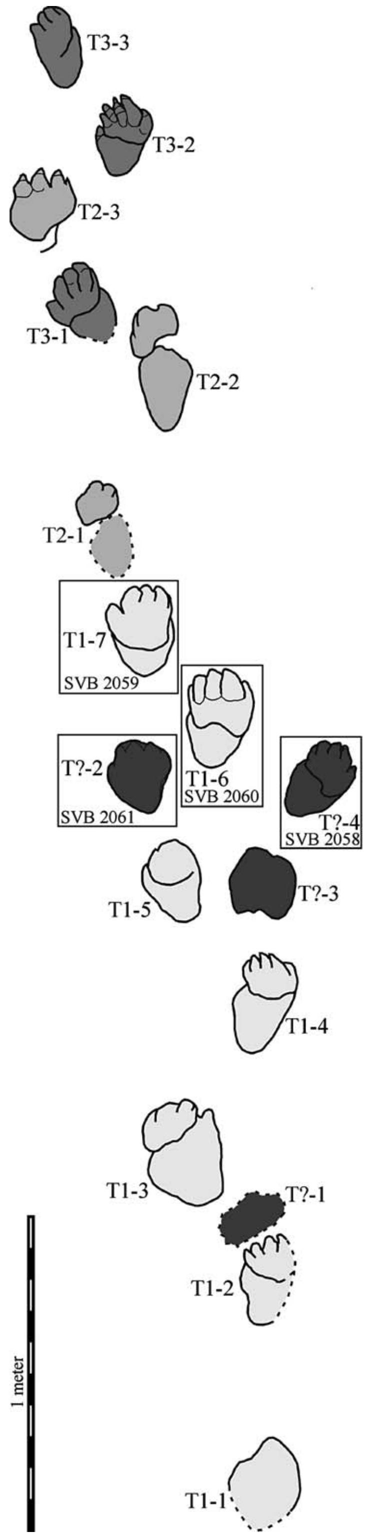

FIGURE 3. Sketch of the complete track assemblage from the mine. The sketch is redrawn from a photograph mosaic of the mine roof. The tracks belonging to the three different trackways are indicated by different shades of grey and each trackway is numbered T1–T3, with each consecutive track numbered. The four tracks designated ‘T?’ indicates tracks that cannot be assigned to the three trackways. Tracks indicated by broken lines are very badly preserved or damaged during mining. The holotype and collected specimens are indicated by boxes and museum numbers.

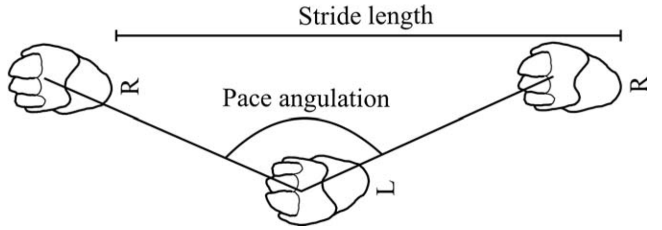

FIGURE 4. Stride length is defined as the distance between two successive right or left tracks in a trackway. Pace angulation is the angle between a left-right-left or right-left-right succession of tracks (Leonardi, 1987).

average half the size of pes imprints, ranging from one-third to two-thirds the size of the pes. The manus is typically more deeply impressed than the pes by several centimeters. However, a few pes tracks are found impressed behind the manus imprint showing the complete pedal imprint.

Manus

The manus imprints are pentadactyl. The impression of digits III and IV are the longest, with digits II–I of decreasing length and digit V of equal length to digit I. Each digit impression terminates in the impression of short, laterally compressed sharp claw. In the best-preserved specimens, a weak division of the digits into digital pads are present (Fig. 5).

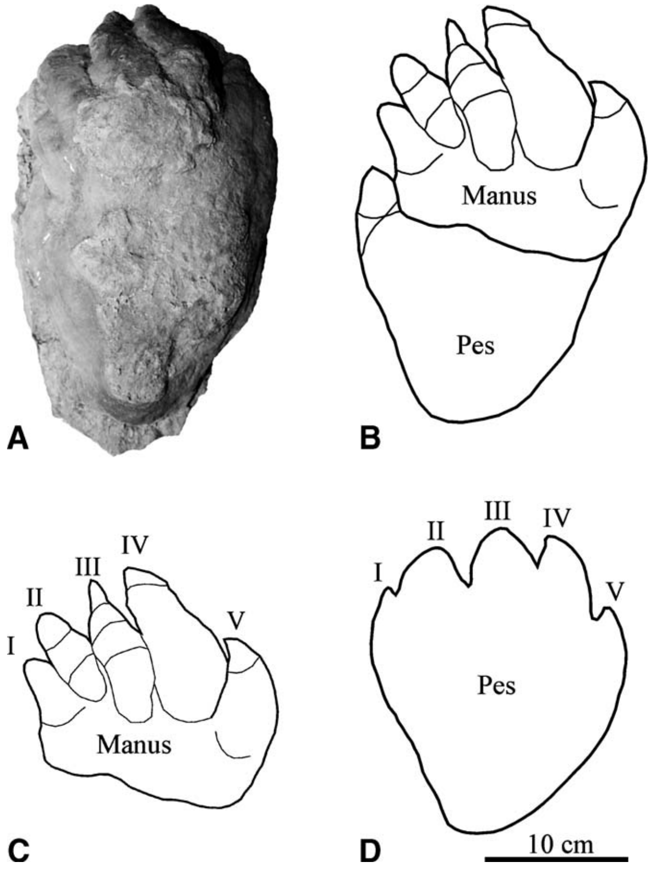

FIGURE 5. **A**, The holotype of *Thulitheripus svalbardii* (SVB 2058). **B**, Interpretative drawing of overlapping manus and pes couple, based on tracks T?-4 (SVB 2058) and T3-2. **C**, Isolated manus based on track T3-2. **D**, Isolated pes, based on track T?-2 (SVB 2061). All drawn to same scale.

Pes

The pes imprints partly overstep those of the manus in most of the observed specimens in the trackways, so only the rear end of the pes imprint is preserved, hindering descriptions of the digits. In two cases the pes is not overstepping the manus (Fig. 3, T2–1 and T2–2), but unfortunately the tracks are too indistinctly preserved to reveal any anatomical details.

One specimen, however, has preserved the complete pes imprint (Fig. 3, T?-2). The specimen was found detached from the sand layer on top of the coal seam. From below it appeared as a smooth sub-circular rounded depression filled with sandstone. When carefully excavated, the upper side of the cast revealed the perfect impression of a pes.

The pes imprint is pear-shaped and measures 24 cm in length and 22 cm in width. There are impressions of five short, triangular, forward-facing, hoof-like digits, with the middle digit being the longest, with a length of 4 cm, and the adjacent digits subsequently shorter (Fig. 5).

Interpretations of Tracks and Trackways

All the tracks are deeply impressed into the substrate but the manus prints are more deeply impressed than the pes prints. The impressions of the manual digits are preserved as elongated impressions, representing the movement of the digits first sinking deeply into the substrate and subsequently being lifted out of the substrate, which hinders the reconstruction of the exact manus shape. The pes impressions are in all but three specimens, partly overprinting the manus impressions. However, they have been shallowly impressed into the substrate, and therefore in most cases have not left any impressions of the pedal digits. In two examples, the pes impression is located behind the manus impressions, but in these cases the pes impressions are too poorly preserved to reveal anything but the gross shape of the pes. The only complete pes impression is the one preserved as part of the rounded depression.

The peculiar morphology of the sandstone depressions with the pes imprint is the result of the foot being emplaced on a relatively firm substrate, creating a rotated disc of material below the foot during the kick-off when the weight of the animal was transferred to the distal parts of the digits (Thulborn and Wade, 1989). This exercises a downward and backward force on the sediment subjacent to the foot, creating the rotated disc below the foot. Faint striations from the rotation are preserved on the underside of the disc. A condition similar to the formation of rotated discs is described from Middle Jurassic theropod tracks from the Entrada Sandstone in Utah (Graversen et al., 2007).

The majority of the tracks are preserved as natural casts of true tracks, and sapropelic coal is preserved squeezed between the casts of the digit impressions, demonstrating that the animals were walking directly on top of the mire/swamp deposit before it was covered. The two tracks preserved as rotated discs are emplaced later than the trackways, because the rotated disc itself is composed of the same sandstone that overlies the coal seam. The tracks have thereby been emplaced after deposition of the sand layer (Fig. 6).

SYSTEMATIC ICHNOLOGY

This is the first worldwide record of such large-sized, well-preserved tracks and trackways from the Paleocene, and we erect the following new ichnogenus and species to accommodate them, *Thulitheripus svalbardii*, gen. et sp. nov.

THULITHERIPUS, gen. nov.

Diagnosis—Narrow-gauge trackway of quadruped trackmaker, manus, and pes pentadactyl, with impressions of short, forward-facing digits. Digits III and IV are the longest, with digits

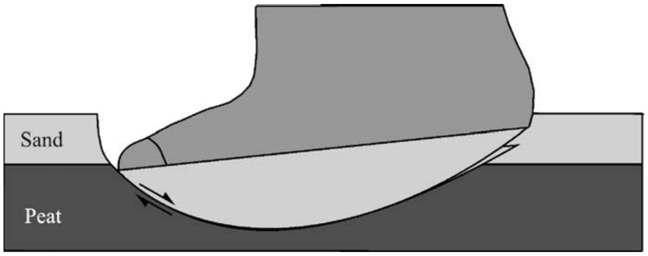

FIGURE 6. The tracks, preserved as rotated discs of sandstone, are formed when the animal walks on a few-centimeter-thin layer of sand deposited on top of the peat. When the weight of the animal is transferred forward during the stride, the sandlayer below the foot breaks and forms a rotated disc below the foot.

II–I of decreasing length and digit V is of equal length to digit I. The pes is trapezoid in outline and almost symmetrical along the midline, and has an elongated triangular heel (Fig. 5). The digits are triangular in shape, digit III being the longest, with the adjacent digits being subsequently shorter. The manus impression is on average half the size of the pes impression, and has a transverse posterior margin (Fig. 5). Trackway widths range from 36 to 47 cm, stride lengths from 82 to 98 cm, and pace angulations from 113° to 125°.

THULITHERIPUS SVALBARDII, gen. et sp. nov.

Diagnosis—As for *Thulitheripus*, with manus having impressions of sharp, laterally compressed claws on the manual digits. Pedal digits terminate in impressions of blunt hoof-shaped claws.

Holotype—A double track showing manus and pes (Fig. 5A) in the collection of Svalbard Museum (SVB 2058), Longyearbyen, Norway.

Additional Material—two double tracks showing manus and pes (SVB 2059, 2060), and a track showing pes (SVB 2061).

Etymology—*Thulitheripus*, Thulitheri, meaning great beast from the north and Pus, a foot. Species *svalbardii* after the Arctic island Svalbard where the tracks are found.

Type Locality—Ceiling of the coal mine Gruve 7, 12 km southeast of Lonyearbyen in the mountain Breinosa, on Svalbard, Arctic Norway, in Paleocene strata of the Todalen Member, Firkanten Formation, Van Mijenfjorden Group.

DISCUSSION

Taxonomic Identification: Pantodonta, Titanoideidae

The detailed preservation of the tracks enables a unique identification of the track maker on a high taxonomic level. The late Palaeocene age, the size, and the morphology of the tracks strongly suggests that the tracks have been made by pantodonts, which were the only known mammals with a sufficient body size during the Palaeocene (Rose, 2006). The configuration of blunt claws on the hind feet and sharp, laterally compressed claws on the forefeet suggests that the tracks are made by a member of the pantodont family Titanoideidae, which so far only comprises the Paleocene, North American genus *Titanoides* (Coombs, 1983; Lucas, 1998, Rose 2006). Titanoideids are the only large pantodonts in the Paleocene that possessed laterally compressed claws on the manus (Fig. 7). The claws of the pes are unknown in *Titanoides*, but based on the track evidence, it is suggested that Titanoideidae possessed blunt hoofs on the pes. All other known pantodonts with preserved manus and pes had blunt hoofs on both (Rose, 2006).

Purported pantodont tracks have previously been reported from the Eocene Checkanut Formation, Northeastern Washington, but these tracks are only preserved as indistinct rounded depressions, without any anatomical details about the foot morphology of the track maker, and were only suggested to be of pantodont origin due to their size (Mustoe, 2002).

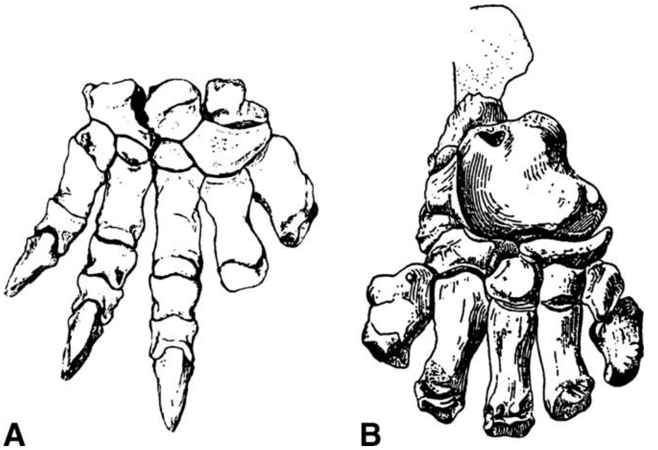

FIGURE 7. Pedal skeleton of the pantodont *Titanoides*. **A**, The manus of *Titanoides* bears sharp laterally compressed claws. **B**, The unguals of the pes are unknown in this genus. After Simons (1960).

Pantodonts were omnivorous and herbivorous large mammals that lived in the Northern hemisphere, except one pantodont-type from South America (Muizon and Marshall, 1992), in the Paleocene and Eocene. Primitive forms were small and some of them with a body weight of about 10 kg. More derived forms were large and some exceeded 500 kg. The pantodonts on Svalbard were comparable to the largest pantodonts found so far and have presumably migrated from Northern America. This is the northernmost identified evidence of pantodonts from this period.

Migration Routes

The Central Tertiary Basin of Svalbard was formed as a flexural basin to the West Spitsbergen fold and thrust belt (Steel et al., 1985; Bruhn and Steel, 2003; Lüthje, 2008) due to convergence between the Eurasian plate and Greenland. In the Paleocene, there was a land contact from Svalbard to Northern Greenland and Ellesmere Island, Canada (Blythe and Kleinspehn, 1998). Even a narrow sound would probably have prevented the pantodonts from migrating from the American continent, implying that the opening of the Greenland Svalbard strait seaway must have taken place after the deposition of the Firkanten Formation.

The postulated DeGeer route for migration of mammals from North America to an isolated Fennoscania in the Paleocene/Eocene via Northeastern Canadian Arctic, Greenland, Svalbard, and the Barents shelf (Janis, 1993) is supported by the pantodont tracks. The late Paleocene Cernaysian mammal age of Europe lacks evidence of large herbivores like pantodonts. However, pantodonts are preserved in deposits of the same age in North America (Lofgren et al., 2004). The younger Eureka Sound Formation (early Eocene) at Ellesmere Island in the Canadian Arctic with its vertebrate assemblage is the only other high Arctic finding of this age (Dawson et al., 1976; Rose et al., 2004). Unfortunately no pantodonts has yet been described from the locality (Dawson, 1990).

The sedimentary record in the thrust belt indicates substantial erosion. The most important factor creating the Central Tertiary Basin is suggested to be compressional folding (Lüthje, 2008). When the basin was established, flexural loading and isostasy would have had some effect on further basin development. The compressional folding model suggests that the orogeny did not necessarily create a mountain belt with high elevation (Zhang and Bott, 2000). The uplift and erosion of thick sediments could still have taken place without the formation of great mountain belt (Lüthje, 2008) if the uplift and erosion were in balance. Any great orogenic belt would have been a natural obstruction for the pantodonts to cross.

CONCLUSION

The Paleocene tracks from Svalbard are a unique discovery. There are no previous records of Paleogene terrestrial mammals from Svalbard and the excellent quality of preservation allows the tracks to be identified as belonging to a titanoideid pantodont like *Titanoides*. This is the earliest discovery of pantodonts this far north and east, and the tracks are formally named *Thulitheripus svalbardii*, gen. et sp. nov. The tracks are found in sapropelic coal deposited in a swamp later covered by marine fine-grained sandstone as a result of a marine transgression. The presence of pantodont tracks in the Firkanten Formation suggests that during the Paleocene, there was no seaway between Svalbard and Greenland/Ellesmere Island and the topography of the thrust belt was probably limited, because this would otherwise have implied an obstruction for the migrating pantodonts.

ACKNOWLEDGMENTS

SNSK (Store Norske Spitsbergen Kulkompani) is thanked for providing access to the mine in Longyearbyen, and especially Terje Carlsen and Malte Jochmann for contacting Jørn H. Hurum when the tracks were found. Charlotta Lüthje would also like to thank SNSK for providing funding for a Ph.D. project carried out at UNIS, Royal Holloway University of London, and at the University of Bergen. Jesper Milàn was supported by the Danish Natural Science Research Council. An early version of the manuscript was thoroughly reviewed by Gary Nichols and Mikael Lüthje is acknowledged for careful reading of the manuscript, and the comments and suggestions from two anonymous reviewers helped improve and narrow the focus of the manuscript. David L. Bruton corrected language in the last version.

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Submitted October 28, 2008; accepted May 4, 2009.