

Dinosaur footprints from the Middle Jurassic Bagå Formation, Bornholm, Denmark

JESPER MILÀN & RICHARD G. BROMLEY



Milàn, J. & Bromley, R.G. 2005–11–15: *Dinosaur footprints from the Middle Jurassic Bagå Formation, Bornholm, Denmark*. Bulletin of the Geological Society of Denmark, Vol. 52, pp. 7–15, Copenhagen. © 2005 by the Geological Society of Denmark. ISSN 0011–6297.

Dinosaur footprints have been found preserved on sandstone blocks discarded from the flooded clay pit Pyritsøen, south of Hasle, Bornholm. The sandstone belongs to the Middle Jurassic Bagå Formation, but the exact horizon is not known. Palynological studies confirm that the sandstone blocks originate from the Bagå Formation. Two specimens were collected, one showing two footprints from a sauropod dinosaur having a foot length of 68 cm, and a small pentadactyl footprint, 26 cm long, interpreted as deriving from an armoured dinosaur. These are the first dinosaur footprints recorded from Denmark.

Key-words: Dinosaur footprints, sauropod, Middle Jurassic, Bornholm, Denmark.

Jesper Milàn [milan@geol.ku.dk], University of Copenhagen, Geological Institute, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark. Richard G. Bromley [rullard@geol.ku.dk], University of Copenhagen, Geological Institute, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.

Terrestrial Mesozoic sediments in Denmark are exposed along the west and south-west coasts of the Baltic island of Bornholm and in small inland quarries (Fig. 1). Only few of them are now open as quarrying has ceased.

The Lower Cretaceous sediments from the Nyker Group at Robbedale have revealed a diverse vertebrate fauna comprising fish, turtles, crocodiles and lizards (Bonde 2004), and a multituberculate mammal (Lindgren *et al.* 2004). Remains of marine reptiles have been found in the Lower Jurassic Hasle Formation (Milàn & Bonde 2001). In the year 2000, a tooth from a small carnivorous dinosaur, *Dromaeosauroides bornholmensis*, was found in the Lower Cretaceous Jydegård Formation, at Robbedale (Christiansen & Bonde 2003), and two years later, a probable sauropod tooth was found at the same locality (Bonde & Christiansen 2003).

Over many years, especially in connection with the mining of brown coal from the Höganäs Formation, numerous Late Triassic and Early Jurassic dinosaur footprints and trackways have been found in southern Sweden (Bölau 1952; Pleijel 1975; Ahlberg & Siveson 1991; Gierlinski & Ahlberg 1994). Footprints of dinosaurs are abundant in the Höganäs Formation, whereas the record of body fossils is

scarce and consists of only a series of indeterminate dinosaurian vertebrae (Bölau 1954). All dinosaur footprints from the Höganäs Formation have been described as footprints from theropod dinosaurs, of the ichnogenus *Grallator*, but at least one footprint from the formation, (on display at the Geological Museum, Copenhagen (MGUH 27219)), represents the footprint of an early Ornithischian dinosaur (Milàn & Gierlinski 2004).

The first hints that dinosaur footprints might be present on Bornholm, came when studying the detailed lithological logs by Gravesen *et al.* (1982) that depict horizons showing peculiar steep-walled deformation structures in the Tornhøj Member of the Lower Cretaceous Jydegård Formation, exposed at Skrædderbakken sand pit at Robbedale. Such steep-walled deformation structures are in many cases cross sections through vertebrate footprints (Loope 1986). Recent attempts by the authors to locate these horizons were unsuccessful, as the quarry has been filled with water and the walls partly levelled.

The lithology and depositional environment of the Bagå Formation were recognized as a highly likely setting for the preservation of tetrapod footprints and the authors made a search for such trace fossils in the summers of 2002 and 2003. Poorly preserved foot-



Fig. 1. A. Bornholm is situated in the Baltic Sea south of Sweden (KMS G15-Ø). B. Map of Bornholm with the outcrops of Mesozoic sediments indicated with grey, based on Jensen & Hamann (1989). Asterisks marks the location of Pyritsoen, between Hasle and Rønne. C. Dinosaur footprint locality at Pyritsoen, sited near the villages of Muleby and Sorthat. Asterisks marks the position where the specimens were collected (UTM koordinater 55.15N 14.70E).

prints were indeed found, but they were not convincingly distinguishable from slump structures or results of local concretionary diagenesis. In 2004, however, the senior author found unquestionable footprints on the beach beside the old clay-pit Bagå Graven. This pit is now flooded and has been re-named Pyritsoen (Pyrite Lake; Fig. 1). The pit had yielded clay from the Middle Jurassic Bagå Formation for the manufacture of hard-fired floor-tiles, bricks, pipes etc., by the Hasle Clinker Factory, which ceased production twenty years ago.

The footprints occurred in the sandstone beds that were unusable by the quarrymen. These sandstone beds were broken up and discarded by throwing them onto the adjacent beach, where they have been lying for over two decades. On discovery of the footprints, the best specimens were collected by crane

and transported to the Geological Museum in Copenhagen for closer study. Dinosaur footprints had not been found previously on Bornholm and were unfamiliar to the local geologists, and remained unnoticed. The aim of this paper is to describe the newly found dinosaur footprints from the Bagå Formation, their preservation and taphonomy and to place them in context with other finds of dinosaurs from Scania.

Geological setting

The Bagå Formation (Gravesen *et al.* 1982) includes the coal-bearing clays and sands in the Rønne-Hasle Fault Block of southwest Bornholm. These beds had been traditionally named the Levka, Sorthat and Bagå

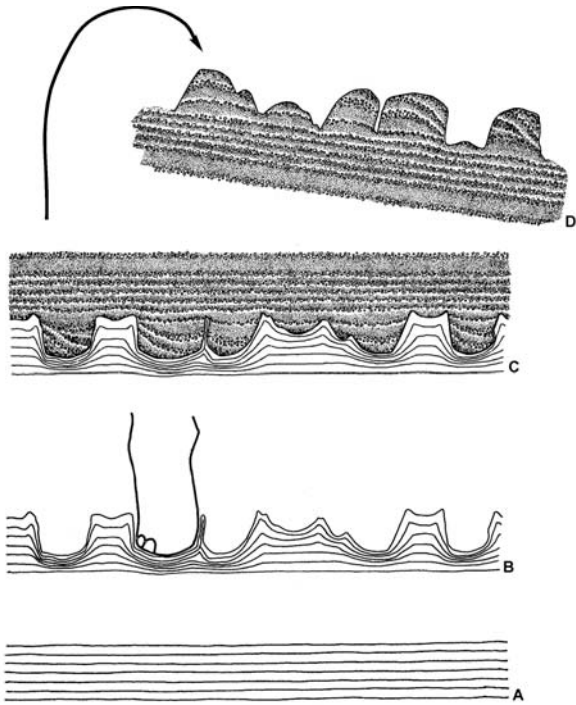


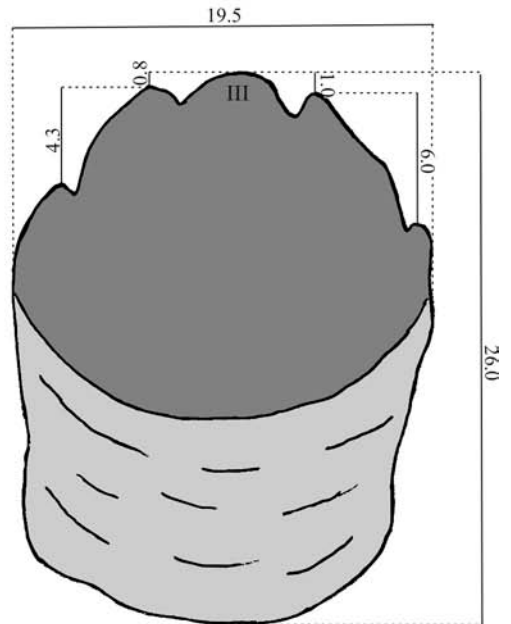
Fig. 2. Processes leading to the preservation of dinosaur footprints in the Bagå Formation. A. Deposition of laminated clay. B. Trampling by dinosaurs causing intense disturbance of the laminated clay layers. C. Deposition of fluvial sand filling and protecting the biogenic topography of the clay surface. D. Break-up of the sandstone by quarrymen and dumping on the nearby beach.



Fig. 3. The small footprint (MGUH 27754) seen in oblique frontal angle, as it was found on the beach. The footprint is preserved as a natural sandstone cast. In this view the digit impressions appear as grooves running down the front of the footprint. Scale on knife handle in centimetres.



↓ Fig. 4. A. The small footprint (MGUH 22754) seen from above. The footprint is almost symmetrical along the length axis. Knife handle represents 10 cm. B. Interpretative drawing of the small footprint, with measurements in centimetres. The footprint is 26 cm long and 19.5 cm wide. The oval front part of the footprint, showing the five digit impressions, is 13–15 cm deep, indicated by dark grey. The proximal part of the footprint, indicated by light grey, shallows proximally to a depth of 6 cm.



B



Fig. 5. Latex mould of the small footprint. This allows the footprint to be seen in negative relief, exactly as when it was originally impressed into the tracking surface. Notice how the five toes have been dragged down through the sediment and formed ridges in the track wall at the front of the footprint. Scale bar 10 cm.

beds (Gry 1969). The Bagå Formation was revised, partly on the basis of well-core material, by Michelsen *et al.* (2003). In this revision, a series of beds showing evidence of marine influence was separated as the Sorthat Formation, thereby leaving the Bagå Formation entirely composed of nonmarine sediments. Marine trace fossils from the Sorthat Formation were recently studied by Bromley & Uchman (2003). The age of the Bagå Formation is Middle Jurassic, Bajocian–Bathonian (Gry 1969; Koppelhus & Nielsen 1994).

The type section of the Bagå Formation is the Bagå Graven of the Hasle Clinker Factory at Sorthat (Graversen *et al.* 1982; Michelsen *et al.* 2003) (Fig. 1). The formation includes thick, grey clay units, dark to black coaly clays containing rootlets, coal beds, and medium- to fine-grained, cross-bedded or laminated sand beds. In the upper part, poorly sorted, muddy and pebbly sand beds locally contain boulders of weathered granite.

According to Graversen *et al.* (1982), Koppelhus & Nielsen (1994), Nielsen (1995) and Michelsen *et al.*

(2003), deposition took place in lakes and swamps, small crevasse channels, lacustrine deltas and fluvial channels. Today, quarrying has ceased and the Bagå pit and other, smaller clay pits are filled with water, hindering detailed new studies of the footprint-bearing layers (Gravesen 1996).

The footprints

Two large blocks were collected; one containing a small well-defined footprint and several eroded footprint-like structures, and one bearing two large footprints, *c.* 70 cm long. Additionally, two blocks showing footprint-like deformation structures were collected, but the erosion of these blocks was too extensive for the structures to be confirmed as footprints. The two blocks with well-preserved footprints are curated by the Geological Museum, Copenhagen (MGUH 27754 and MGUH 27755) and are on display at the museum NaturBornholm, Aakirkeby, Bornholm.

Pinched between the two large footprints, some of the original clay in which the footprints were emplaced has escaped weathering. A palynological study, conducted by Eva Koppelhus (personal communication 2004), confirmed that the palynological assemblage identified in the clay between the footprints, belongs to the assemblage known from the Bagå Formation (Koppelhus & Nielsen 1994), and thus confirming the origin of the blocks.

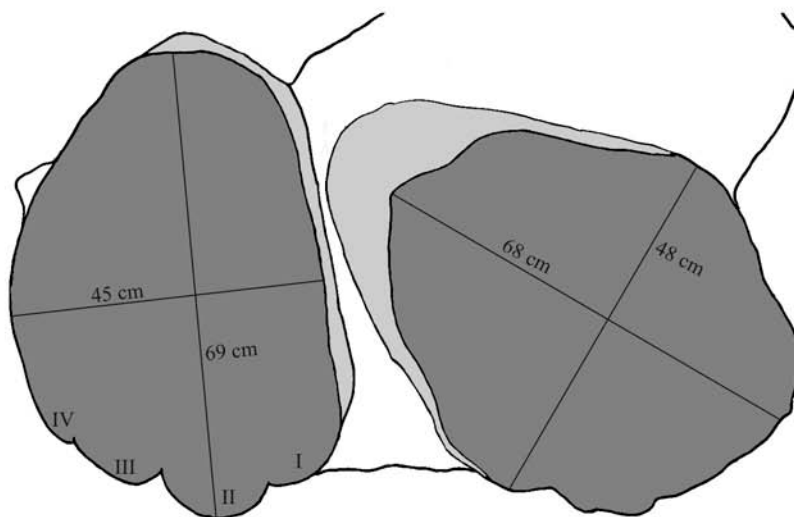
The small footprint (MGUH 27754). The small footprint is preserved as a natural cast on the underside of a large block of sandstone (Fig. 2). The footprint is 26 cm long and 19.5 cm wide (Fig. 3) and the distal part with the digit impressions is impressed to a depth of 15 cm. The distal part shows impressions of the digits. The proximal part deepens gradually to a depth of 6 cm at the ‘heel’ of the footprint.

The footprint is pentadactyl, showing short but well-defined impressions of five digits. It is close to symmetrical along the medial axis, and thus it is not possible to determine whether it is a left or a right footprint (Fig. 4A). The impressions of the three middle digits are almost of equal length, and the middle digit, digit III, is only 1.0 cm and 0.8 cm longer than the adjacent digits. The impressions of the two outer digits are 4.3 and 6.0 cm behind the neighbouring digit impressions (Fig. 4B). Recent erosion has rounded the tips of the digits, preventing exact measurements of their lengths. The footprint is preserved in positive relief as a natural cast of the dinosaur’s foot. A cast was made of the surface of the block in order

Fig. 6. A. The sandstone block containing the two large, sauropod footprints (MGUH 27755). The left footprint is the better preserved and the impressions of four short rounded digits are visible in the lower part of the footprint. The handle of the knife is 10 cm.



B. Interpretative drawing of the block with the two footprints including measurements in centimetres. The bottom of the footprints is shaded in dark grey and the parts forming the track walls to the tracking surface are light grey. Digit numbers are indicated by Roman numerals.



to obtain a view of the footprint in negative relief, as it appeared when it was impressed in the tracking surface. It is apparent by doing this, that the foot had sunk to a considerable depth, and the short toes formed vertical ridges and grooves in the mud as they were pressed into and passed through the soft substrate (Fig. 5).

The two large footprints (MGUH 27755). Two large and well-defined footprints are preserved as sandstone casts on the underside of the block (Fig. 6A). The better preserved footprint, 69 cm long and 45 cm

wide, is oval to pear-shaped in outline and includes the impressions of four short blunt digits. The other less well-preserved footprint measures 68 cm in length and 48 cm in width (Fig. 6B). The cast of the better preserved footprint varies in depth from 25 to 29 cm, and that of the other footprint varies from 10 to 20 cm. The bottoms of the two footprints are flat and appear to lie at the same level. The digit impressions are preserved as ridges extending from the tracking surface to the bottom of the footprint (Fig. 7).



Fig. 7. The better preserved sauropod footprint in frontal view. The impressions of the digits, indicated by Roman numbers, are preserved as ridges formed as they were dragged through the mud. Part of the mud from the tracking surface is preserved between the two footprints, indicated by finger. Palynological examination of this mud confirms the Middle Jurassic age for the footprints (Eva Koppelhus, personal communication 2004).

Discussion

This first report of dinosaur footprints from Denmark is important because a number of potential alternative explanations for the origin of the structures may be considered. Alternative scenarios for the origin of the structures are that the structures are random slump structures, or that they are products of erosion by the sea, as the blocks were found on the beach. A number of observations, however, disqualify this.

Although the blocks containing the footprints have been exposed to erosion on the beach for years, clay from the original tracking surface is still present between the two large footprints (Fig. 7). The clay layers have been disturbed and display an almost vertical lamination in the parts preserved, suggesting extreme deformation caused by compression by the trackmaker's feet. Deposition of the sand post-dates the formation of the footprints, as the clay around the footprint is highly deformed, whereas the sandstone infilling is horizontally bedded and lacks indications of subsequent disturbance. Thus the configuration of the clay-sand interface, where the surface layer of the clay contains large concave structures directly related to deformation of the lamination, clearly demonstrates a tetrapod trample-ground in soft substrate. The preservation of the sculptured clay surface topography demonstrates that it was overlain a short time after trampling by a unit of sand, which protected its highly sculptured topography. The sand shows primary lamination that has not been

subsequently deformed. Gravitational slumping at this level would cause correlative deformation of both clay and sand. This detailed topography and deformation scenario also negates the possibility of the structures having been created by modern marine erosion or by concretionary diagenesis.

Furthermore, it shows that the sedimentary infilling of each of the footprints was passive filling of a pre-existing depression. If the footprints had been emplaced during the deposition of the sand, the filling would have been convoluted or disturbed (Nadon 1993, 2001). The palynological examination confirms the presence of Middle Jurassic clay *in situ* between the footprints, dismissing the argument that the footprints are the result of modern sea-erosion.

Elsewhere on the beach from which the blocks were collected, there are blocks of Bagå sandstone that are not connected with the top surface of the clay. Some of these show cross-bedding (containing wood clasts) that is undisturbed, whereas others show extreme deformation of the bedding. In the light of the collected material described here, this deformed bedding within the sandstone probably belongs to other dinosaurian trampling events.

Interpretation

The large footprint is 69 cm long, pear-shaped in outline and have impressions of four short rounded digits, which is consistent with hind-foot prints from

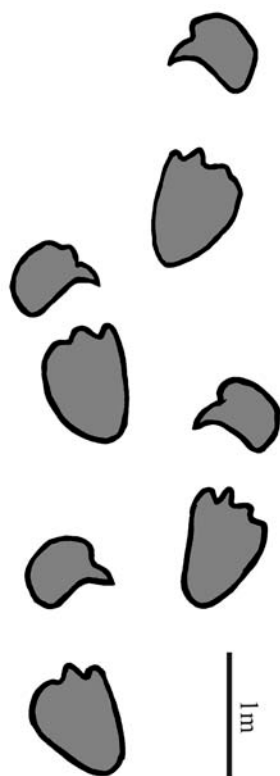


Fig. 8. Tracing of part of a sauropod trackway from the Middle Jurassic Galinha tracksite near Fatima, Portugal. The manus imprints are hoof-like, having only one inward-facing claw impression. The pes prints have impressions of three to four short blunt digits. This pes morphology is consistent with the better preserved of the two sauropod footprints from Bornholm (Fig. 6). Figure modified from Santos *et al.* (1994).

sauro pod dinosaurs. This better preserved of the two footprints is the impression of a left foot. The other footprint lacks any distinct digit impressions, but instead the bottom seems to be divided into a number of 'pads', similar to what is observed in Middle Jurassic sauropod footprints from the Yorkshire coast (Romano & Whyte 2003). As distinct digit impressions are lacking in the footprint, it is not possible to determine if it represents the impression of the right foot, connected to the left footprint beside it, i.e. a pair, or if it is unrelated.

The two footprints are impressed to different depths relative to the tracking surface, but the bottoms of the two impressions are at the same level. This apparent difference in depth is due to the uneven and trampled topography of the tracking surface. The depth of the two footprints thus may represent the maximum depth the softness of the mud allowed the feet to sink to, beneath which the mud was too rigid to allow further penetration by the feet.

Sauropods have an extreme degree of heteropo-

dy. The sauropod forefoot (manus) is pentadactyl, with short reduced digits encapsulated by tissue to form hoof-like units, whereas only digit I, the pollex, is separate and bears a claw. In the most derived sauropods, the titanosaurs, even this claw is reduced (Bonnan 2003). The hindfeet (pes) of sauropods are pentadactyl and the digits are short and blunt. At least the inner two to three digits bear blunt but prominent claws (Christiansen 1997a, b).

Well-preserved sauropod trackways from around the world all show that the impressions of the inner three digits are the most prominent in the pes prints, and that the outer two digits rarely leave impressions. The impressions of the manus are hoof-shaped, sometimes showing impressions of the inwardly directed pollex claw (Meyer *et al.* 1994; Santos *et al.* 1994) (Fig. 8). Manus prints have not been identified in the material from Bornholm.

The small footprint is well preserved, showing clear impressions of five short, claw-bearing digits. However, the symmetrical configuration of the foot makes it hard to clearly assign it to any known dinosaurian ichnogenus. Furthermore, the symmetrical configuration of the digit impressions prevents it from even being identified as a right or left foot. The known pentadactyl pes configurations among Middle Jurassic dinosaurs are all asymmetrical like the sauropod footprints, in which digits I and II are the most prominent. A possibility is that the footprint is a manus print from an early thyreophoraen dinosaur, as these animals possessed pentadactyl mani, symmetrical around the middle digits (McCrea *et al.* 2001). However, the known manus prints from thyreophorean dinosaurs are crescent- to hoof-shaped and broader than long (Romano & Whyte 2003). The small footprint is longer than broad but is deeply impressed into the substrate. When an animal walks, its feet are not merely impressed and lifted vertically. If the foot is impressed deeply into a substrate, parts of the forward movement of the limb will be captured in the footprint. This causes a prominent elongation of the footprint, as demonstrated with Late Triassic theropod footprints by Gatesy *et al.* (1999) and Pleistocene artiodactyl footprints (Fornós *et al.* 2002). Additional footprints, and preferably trackway segments preserving both manus and pes impressions, are needed before the trackmaker responsible for the small footprint can be identified with certainty.

Correlation with previous finds

There is a wide temporal gap between the new footprints from the Bagå Formation, the footprints from

the Höganäs Formation of southern Sweden and the two teeth previously found on Bornholm. The footprints from Sweden are from the Late Triassic to Early Jurassic and are roughly 40 million years older than the new footprints from Bagå (Bölauf 1952; Pleijel 1975; Ahlberg & Siveson 1991; Gierlinski & Ahlberg 1994; Milàn & Gierlinski 2004). The two teeth found in Robbedale are from the Early Cretaceous (Bonde & Christiansen 2003; Christiansen & Bonde 2003), and thus around 30 million years younger than the Bagå footprints. The Middle Jurassic age of the new footprints from Bornholm, thereby fills in the 70 million years gap between the Late Triassic records of dinosaurs from Sweden to the Lower Cretaceous records from Bornholm. To date, no skeletal remains of dinosaurs have been found in the Bagå Formation, but this is not surprising as the preservation of footprints and bones is controlled by two widely different taphonomic processes.

Conclusions

Exploitation of clay of the Middle Jurassic Bagå Formation from the clay-pit Bagå Graven south of Hasle, Bornholm, produced waste material in the form of blocks of indurated sandstone layers. Large blocks of these were discarded from the clay-pit onto the nearby beach.

Two sandstone blocks containing well-preserved hind-foot prints of sauropods and a smaller footprint, interpreted as the footprint of a small armoured dinosaur, were found among the discarded blocks. Study of these loose sandstone blocks revealed deformed bedding, representing dinosaur footprints preserved at a clay-sand interface. The tracking surface was the top of a clay unit, that had been considerably deformed by dinosaur trampling to a depth of 20–30 cm. This surface was rapidly overlain by fluvial sand, thus preserving the footprints in considerable detail. The precise horizon within the Bagå Formation has not yet been identified, as the quarry is now flooded, but palynological examination of clay between the footprints confirms a Middle Jurassic age, and that the blocks originate from the Bagå Formation. It is to be expected that further dinosaur footprints can be found in the continental Mesozoic rocks of Bornholm and in future sedimentological studies, special attention should be paid to deformed bedding planes.

Danish Summary

De første forstenede dinosaur fodspor er blevet fundet i sandstens blokke der er blevet brudt og dumpet på stranden under lergravning i den gamle Hasle Klinkefabriks lergrav (Bagå Graven), syd for Hasle, Bornholm (Fig. 1). Leret der blev gravet i lergraven tilhørte den midt Jurassiske Bagå formation. I dag er lergravningen ophørt og graven er fyldt med vand og omdøbt til Pyritsøen.

To sandstens blokke med dinosaur fodspor, samt yderligere to blokke med spor-lignende strukturer er blevet indsamlet og studeret. De fundne spor er bevaret som sandstensudfyldninger af de oprindelige spor og fremstår derved i positivt relief (Fig. 2). På den ene blok ses et lille spor på 26 cm længde (Figs. 3–5) sandsynligvis fra en pansret dinosaur. Den anden blok indeholder to store, respektivt 69 og 68 cm lange spor fra en sauropod dinosaur. Det bedst bevarede af dem har aftryk af fire korte brede tæer (Figs. 6–8).

En række sedimentologiske faktorer bekræfter at de fundne strukturer virkelig er dinosaur spor og ikke slumpstrukturer, konkretionsdannelse eller erosions fænomener. Underfladen af sandstens blokkene er formet efter en ujævn mudderflade. Dette mudder er bevaret *in situ* imellem de to store sauropod spor, og laminationen i det er her stærkt forstyrret. Sandet der udfylder sporene derimod, er horisontalt lagdelt, hvilket viser at udfyldningen er sket efter at mudderfladen er blevet deformeret, i dette tilfælde af dinosaurer. Palynologiske undersøgelser af leret fundet mellem sporene yderligere bekræfter at blokkene stammer fra Bagå Formationen og at sporene er dannet i Jura tiden, og derfor heller ikke kan være et resultat af erosion efter at sandstensblokkene var blevet tippet af på stranden.

Acknowledgements

We are grateful to the Geological Institute, University of Copenhagen for covering the cost of transportation of the footprints. Steen Lennart Jacobsen, Geological Museum Copenhagen, made the latex cast of the surface of the block containing the small footprint. Eva Koppelhus (Royal Tyrrell Museum, Canada) is thanked for applying her expertise in Jurassic palynological analysis to the clay samples. Phillip J. Currie, (Royal Tyrrell Museum, Canada) kindly commented on an early draft of the manuscript. Special thanks to Finn Hansen, NaturBornholm, for arranging for the footprints to be placed on permanent display there. The manuscript benefited from the criti-

cal reviews of Mike Romano, (University of Sheffield) and Gregers Dam, (Danish Oil and Natural Gas).

References

- Ahlberg, A. & Siverson, M. 1991: Lower Jurassic dinosaur footprints in Helsingborg, southern Sweden. *Geologiska Föreningens i Stockholm Förhandlingar* 113, 339–340.
- Bonde, N. 2004: An Early Cretaceous (Ryazanian) fauna of “Purbeck-Wealden” type at Robbedale, Bornholm, Denmark. *In* Arratia, G. & Tintori, A. (eds): *Mesozoic Fishes 3 – systematics, palaeoenvironments and biodiversity*, 507–528. Verlag Dr. Friedrich Pfeil, München, Germany.
- Bonde, N. & Christiansen, P. 2003: New dinosaurs from Denmark. *Comptes Rendus Palevol* 2, 13–26.
- Bonnan, M.F. 2003: The evolution of manus shape in sauropod dinosaurs: implications for functional morphology, forelimb orientation, and phylogeny. *Journal of Vertebrate Paleontology* 23, 595–613.
- Bölau, E. 1952: Neue Fossilfunde aus dem Rhät Schonens und ihre paläogeographisch-ökologische Auswertung. *Geologiska Föreningens i Stockholm Förhandlingar* 74, 44–50.
- Bölau, E. 1954: The first finds of dinosaurian skeletal remains in the Rhaetic-Liassic of N. W. Scania. *Geologiska Föreningens i Stockholm Förhandlingar* 76, 501–502.
- Bromley, R.G. & Uchman, A. 2003: Trace fossils from the Lower and Middle Jurassic marginal marine deposits of the Sortehat Formation, Bornholm, Denmark. *Bulletin of the Geological Society of Denmark* 52, 185–208.
- Christiansen, P. 1997a: Locomotion in sauropod dinosaurs. *Gaia* 14, 45–75.
- Christiansen, P. 1997b: Hindlimbs and feet. *In* Currie, P.J. & Padian, K. (eds): *Encyclopedia of Dinosaurs*, 320–328. Academic Press, New York.
- Christiansen, P. & Bonde, N. 2003: The first dinosaur from Denmark. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 227, 287–299.
- Fornós, J.J., Bromley, R.G., Clemmensen, L.B. & Rodríguez-Perea, A. 2002: Tracks and trackways of *Myotragus balearicus* Bate (Artiodactyla, Caprinae) in Pleistocene aeolianites from Mallorca (Balearic Islands, Western Mediterranean). *Palaeogeography, Palaeoclimatology, Palaeoecology* 180, 277–313.
- 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.
- Gierlinski, G. & Ahlberg, A. 1994: Late Triassic and Early Jurassic dinosaur footprints in the Höganäs Formation of southern Sweden. *Ichnos* 3, 99–105.
- Gravesen, P., Rolle, F. & Surlyk, F. 1982: Lithostratigraphy and sedimentary evolution of the Triassic, Jurassic and Lower Cretaceous of Bornholm, Denmark. *Danmarks Geologiske Undersøgelse Serie B* 7, 51 pp.
- Gravesen, P. 1996. *Geologisk set Bornholm, en beskrivelse af områder af national geologisk interesse*. Miljø- og Energiministeriet Skov- og Naturstyrelsen, Geografforlaget, Brenderup, 209 pp.
- Gry, H. 1969: Megaspores from the Jurassic of the island of Bornholm, Denmark. *Meddelelser fra Dansk Geologisk Forening* 19, 69–89.
- Jensen, J.B. & Hamann, N.E. 1989: Geological mapping of Mesozoic deposits along the eastern margin of the Rønne Graben, offshore Bornholm, Denmark. *Bulletin of the Geological Society of Denmark* 37, 237–260.
- Koppelhus, E.B. & Nielsen, L.H. 1994: Palynostratigraphy and palaeoenvironments of the Lower to Middle Jurassic Bagå Formation of Bornholm, Denmark. *Palynology* 18, 139–194.
- Lindgren J., Rees J., Siverson M. & Cuny G. 2004: The first Mesozoic mammal from Scandinavia. *GFF* 126, 325–330.
- Loope, D.B. 1986: Recognizing and utilizing vertebrate tracks in cross section: Cenozoic hoofprints from Nebraska. *Palaios* 1, 141–151.
- McCrea, R.T., Lockley, M.G. & Meyer, C.A. 2001: Global distribution of purported ankylosaur track occurrences. *In* Carpenter, K. (ed.): *The Armoured Dinosaurs*, 413–454. Indiana University Press, Bloomington.
- Meyer, C.A., Lockley, M.G., Robinson, J.W. & Santos, W.F. 1994: A comparison of well-preserved sauropod tracks from the Late Jurassic of Portugal and the western United States: evidence and implications. *Gaia* 10, 57–64.
- Michelsen, O., Nielsen, L.H., Johannessen, P.N., Andsbjerg, J. & Surlyk, F. 2003: Jurassic lithostratigraphy and stratigraphic development onshore and offshore Denmark. *In* Ineson, J.R. & Surlyk, F. (eds): *The Jurassic of Denmark and Greenland*, 147–216. Geological Survey of Denmark and Greenland Bulletin 1.
- Milàn, J. & Bonde N. 2001: Svaneøgler: nye fund på Bornholm. *Varv* 2001 (4), 3–8.
- Milàn, J. & Gierlinski, G. 2004: A probable thyreophorean (Dinosauria, Ornithischia) footprint from the Upper Triassic of southern Sweden. *Bulletin of the Geological Society of Denmark* 51, 71–75.
- Nadon, G.C. 1993: The association of anastomosed fluvial deposits and dinosaur tracks, eggs and nests: Implications for the interpretation of floodplain environments and a possible survival strategy for ornithopods. *Palaios* 8, 31–44.
- Nadon, G.C. 2001: The impact of sedimentology on vertebrate track studies. *In* Tanke, D.H. & Carpenter, K. (eds) *Mesozoic Vertebrate Life*, 395–407. Indiana University Press, Bloomington.
- Nielsen, L.H. 1995: Genetic stratigraphy of the Upper Triassic – Middle Jurassic deposits of the Danish Basin and Fennoscandian Border Zone 2, 3. 162 pp. Unpublished Ph.D. thesis, University of Copenhagen, Denmark.
- Pleijel, C. 1975: Nya dinosauriefotspår från Skånes Rät-Lias. *Fauna och Flora* 3, 116–120.
- Romano, M. & Whyte, M.A. 2003: Jurassic dinosaur tracks and trackways of the Cleveland Basin, Yorkshire: preservation, diversity and distribution. *Proceedings of the Yorkshire Geological Society* 54, 185–215.
- Santos, V.F., Lockley, M.G., Meyer, C.A., Carvalho, J. Galopim de Carvalho, A.M. & Moratalla, J.J. 1994: A new sauropod tracksite from the Middle Jurassic of Portugal. *Gaia* 10, 5–13.