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Dinosaur tracks and possible lungfish aestivation burrows in a shallow coastal lake; lowermost Cretaceous, Bornholm, Denmark

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ABSTRACT

The Mesozoic succession of the island of Bornholm in the Baltic Sea has hitherto yielded only very few remains after vertebrate life. We describe a new find of a well-exposed vertebrate trample ground and large, densely spaced, vertical to inclined burrows from shallow lake deposits belonging to the Berriasian Skyttegård Member of the Rabekke Formation. The succession is terrestrial, but a coastal setting is indicated by the great abundance of pyrite concretions and framboidal pyrite. Organic geochemical and palynological data show that the lake was surrounded by a low-diversity gymnospermous vegetation. The trampling ground is exposed in a vertical section at the boundary between light grey, structureless or trough cross-bedded fluvial sand and dark brown, organic-rich lacustrine mud with densely spaced vertical rootlets, wood fragments and large pyrite concretions. The tracks are bowl-shaped, have an irregular flat or slightly conical base, are on average 22 cm deep and on average 43 cm wide in the upper part and 23 cm in the lower part, but some reach widths up to about 1 m and have a highly irregular shape. The underlying sand in some cases shows a faint stratification that is bent downwards adjacent to the mud-filled tracks, which have near-vertical and commonly overhanging margins. The morphology of the bowl-shaped depressions suggests that they were made by dinosaurs, most likely sauropods. They were clearly emplaced after deposition of the dark brown mud. Long, vertical to inclined, commonly slightly curved, J-shaped or spiraling cylindrical burrows with a diameter averaging 4.4 cm and lengths up to 45 cm occur densely spaced in the mud. They are unbranched, have no mud or lag linings. The top of the burrows is indistinct or not preserved, whereas the base is rounded, concave-up, commonly with a slightly enlarged chamber. The length is difficult to estimate precisely because of the missing top and because the burrows cross-cut and go in and out of the plane of exposure. The burrows have a passive infill of dark mud and, at some levels, of irregularly alternating laminae of white sand and mud. The sand may be of aeolian origin or may represent distal crevasse splays or washovers from adjacent rivers or the nearby sea. Skeletal remains have not been found in or associated with the burrows, which are similar to burrows referred to lungfish or crayfish, and they are with hesitation interpreted as representing lungfish aestivation burrows based on the morphological characteristics.
This is only the second report of dinosaur tracks in Denmark and the first in-situ find where environmental conditions can be interpreted with some confidence. Possible lungfish burrows are here reported for the first time from the Danish Mesozoic. The overall rarity of vertebrate remains in the Mesozoic succession of Bornholm may reflect that the area was a horst island or submerged shoal during much of the Jurassic and Cretaceous and may not always have had direct land connection with surrounding land areas of the Baltic Shield or mainland Europe.

1. Introduction

Only very few dinosaur remains are known from the Mesozoic of Denmark. On the island of Bornholm in the Baltic Sea a few dromaeosaurid teeth and a possible sauropod tooth have been described from the lowermost Cretaceous, Berriasian Rabekke and Robbedale Formations (Bonde and Christiansen, 2003; Christiansen and Bonde, 2003; Lindgren et al., 2004). An intense hunt for dinosaur tracks in the Mesozoic succession recently resulted in the find of two sauropod tracks and one probable thyreophorean track in loose blocks derived from the Middle Jurassic Bagå Formation (Milàn and Bromley, 2005). Other vertebrate remains include turtle fragments, the fresh water shark *Lepidotes* and the holostean fish *Hybodus* from the Berriasian Jydegård Formation (Noe-Nygaard et al., 1987; Noe-Nygaard and Surlyk, 1988) and plesiosaur teeth and bone fragments from the Pliensbachian Hasle Formation (Surlyk and Noe-Nygaard, 1986; Bonde and Christiansen, 2003). Washing of 300 kg bulk samples of light-grey and brick-red lenses in dark-grey mud of the Berriasian Skyttegård Member of the Rabekke Formation (Gravesen et al., 1982) has recently

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yielded a relatively rich micro-vertebrate fauna. It comprises abundant teeth from crocodiles and fragments of turtle carapaces, scales and jawbone fragments of actinopterygians, skeletal remains of amphibians and primitive lizards, dromaeosaurid teeth and a single tooth of a multituberculate mammal (Lindgren et al., 2004, 2008).

The overall rarity of dinosaur remains and tracks in the Mesozoic of Denmark reflect that outcrops of terrestrial and paralic deposits are known only from the Hettangian, Bajocian–Bathonian and Berriasian of the Baltic island of Bornholm. Outcrops are rather small and most quarries are now abandoned. More importantly, the Bornholm horst was probably an island or a submerged high during much of the Mesozoic and successful immigration from the Baltic Shield or mainland Europe was not always possible. Lindgren et al. (2008, p. 260) in a paper published, after this paper was submitted noted that “One interesting aspect of the Rabekke dinosaur fauna is the apparent absence of large theropods, sauropods, ornithopods and other ornithischian dinosaurs” and suggested that “the marshy terrain and dense vegetation might have been an unsuitable habitat for large and heavy animals”.

Here we describe a remarkable lowermost Cretaceous succession from the same formation, containing structures that we interpret as representing dinosaur tracks associated with a high density of possible lungfish burrows. It is placed in an environmental context by facies analysis, palynology, coal petrography, organic geochemistry

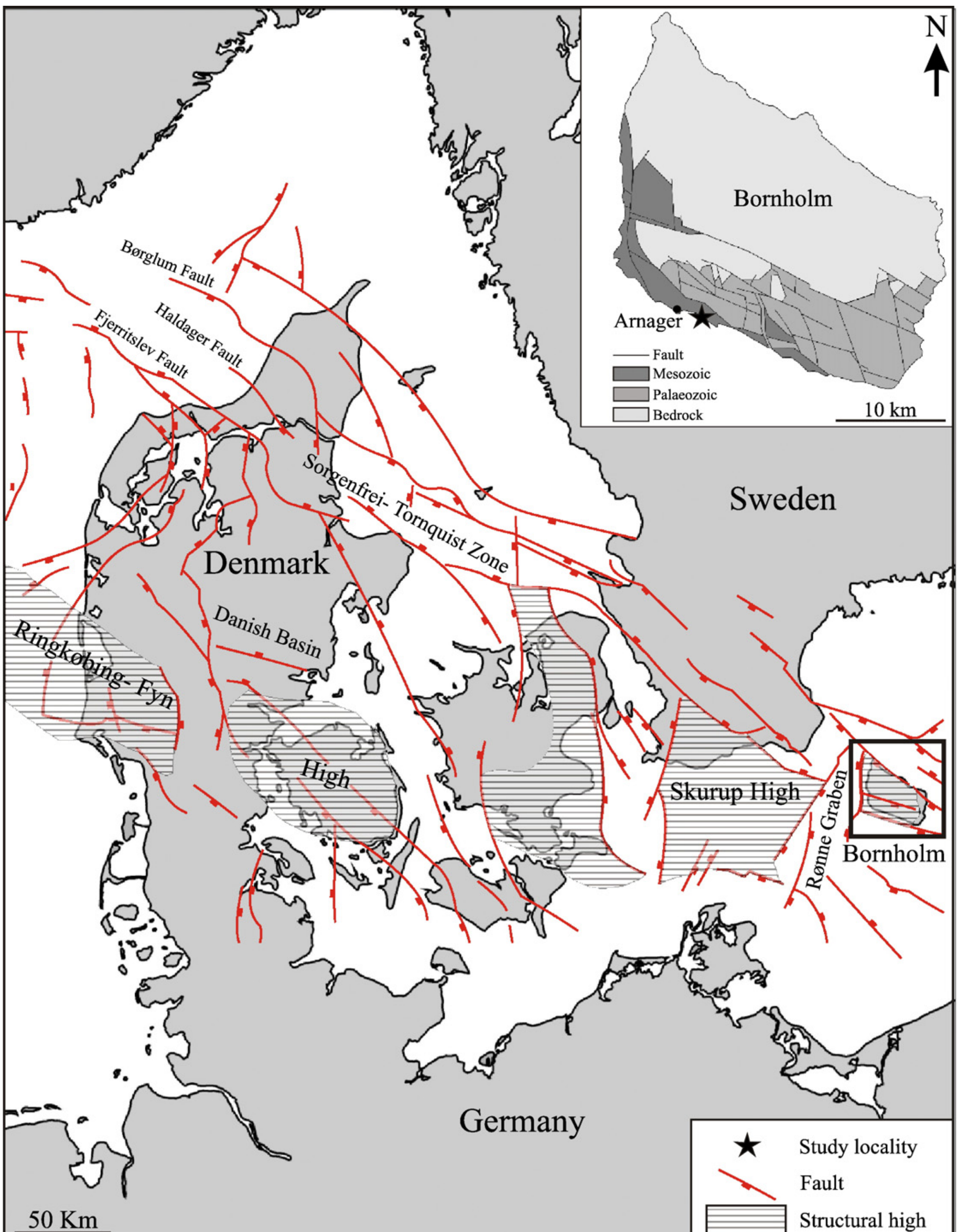

Fig. 1. Map showing the location of the Bornholm horst in the regional structural framework. Inset map shows the location of the studied locality.

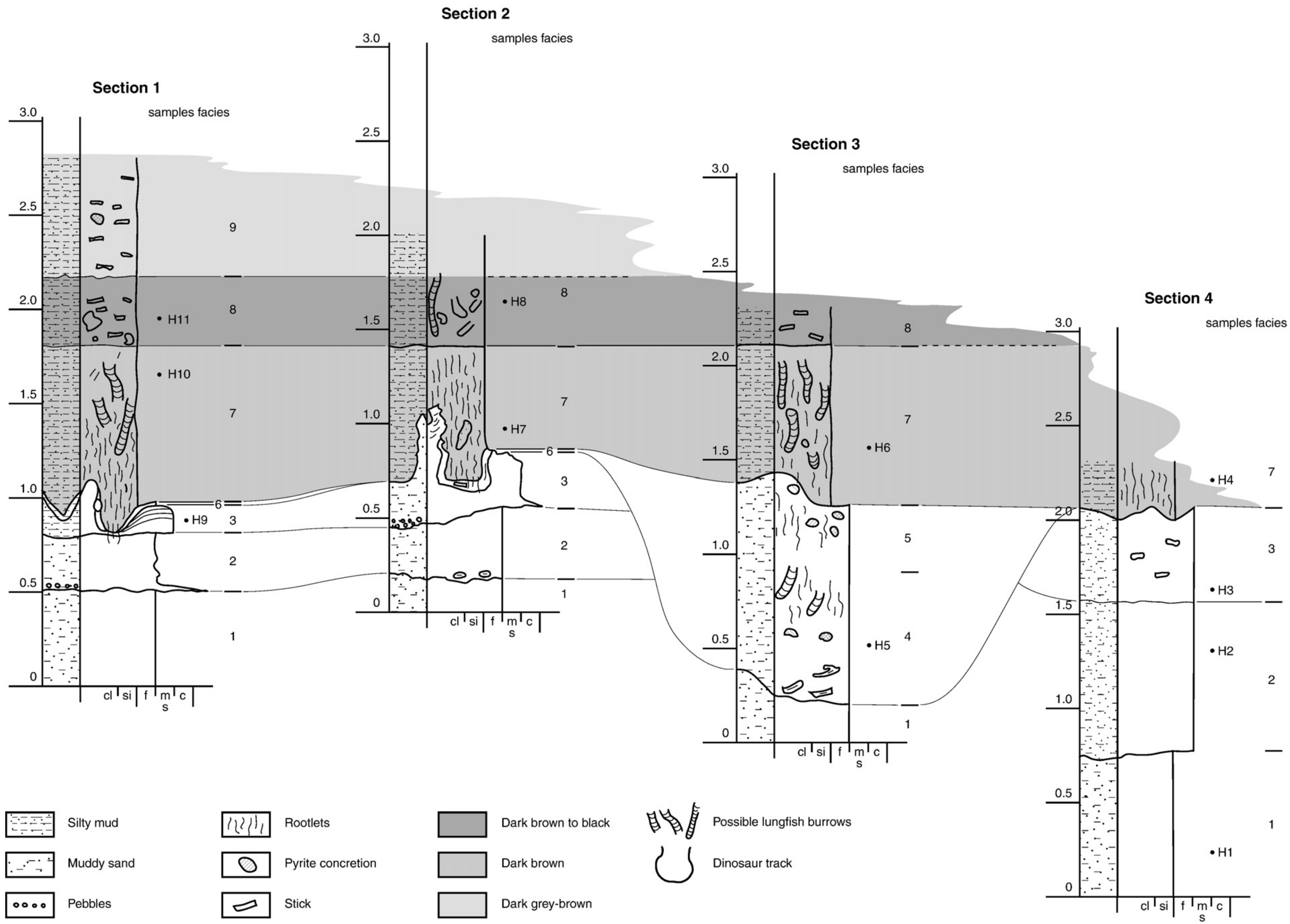

Fig. 2. Sedimentological logs through the Skyttegård Member. Positions of the logs are shown on Fig. 3. The level of the dinosaur trackway is indicated. The logs are hanged on the boundary between units 7 and 8 which is assumed to represent an originally horizontal surface.

and stable isotope analyses. These are the first in-situ dinosaur tracks and possible lungfish burrows documented from the Danish Mesozoic and as such add considerably to our knowledge of the life and ecosystems in the earliest Cretaceous of the region.

2. Geological setting and stratigraphy

Bornholm is a horst in a right-stepping dogleg between the Sorgenfrei–Tornquist Zone and the Polish Trough, separating the basement areas of the Baltic Shield from the subsiding Danish and North German Basins (Fig. 1). The Mesozoic succession of Bornholm comprises continental Triassic redbeds overlain by an overall transgressive Lower Jurassic lacustrine–paralic fully marine succession of clay, sand and thin coals (Surlyk et al., 1995). A major regression started at the end of the Early Jurassic and in early Middle Jurassic, Toarcian–Aalenian times, culminated in mid-Jurassic uplift and erosion of large areas (Ziegler, 1982; Koppelhus and Nielsen, 1994; Andsbjerg et al., 2001; Michelsen et al., 2003). Renewed subsidence is marked by fault-controlled deposition of sand, clay and peat in rivers, lakes and swamps belonging to the Bajocian–Bathonian Bagå Formation. Late Jurassic uplift resulted in erosional removal of about 500 m of sediment in the study area (Petersen et al., 1996) before the area was gradually transgressed in the earliest Cretaceous (Gravesen et al., 1982).

The lowermost Cretaceous succession is placed in the Nyker Group (Gravesen et al., 1982), comprising the Berriasian Rabekke Formation of mainly terrestrial origin overlain by the interfingering Berriasian–Valanginian(?), Robbedale and Jydegård Formations of barrier and lagoonal origin (Noe-Nygaard et al., 1987; Noe-Nygaard and Surlyk, 1988). These formations are unconformably overlain by the fully marine Cenomanian Arnager Greensand Formation containing Albian ammonites in phosphatic pebbles in the complex basal conglomerate.

The dinosaur tracks and possible lungfish burrows described here are from the type locality of the Skyttegård Member, which forms the upper, relatively fine-grained part of the Rabekke Formation. The section is exposed in a low coastal cliff on the south coast of Bornholm between Madsegrav and the small bluff, Homandshald (Figs. 1–3). The micro-vertebrate fauna recently listed by Lindgren et al. (2004) was found in lenses of light-grey to brick-red silty claystone in the member, but similar lenses do not occur in the nearby studied section.

3. Methods

3.1. Facies analysis

The Skyttegård Member consists of unlithified but hard and rather compact sediments that were cleaned with shovels, trowels, and knives for the finer details. A digital photomosaic was subsequently made and four vertical sections were measured along the profile (Fig. 3). Lithology, grain-size, primary sedimentary structures, tracks, burrows, rootlets, wood fragments, sticks, branches and pyrite nodules were recorded. Special emphasis was placed on the study of the tracks and burrows. All the main lithologies were sampled for analysis of grain-size, organic content, Total Organic Carbon (TOC), palynology, stable isotopes, and macrofossils. A detailed coal petrographic and organic geochemical analysis of the track-bearing bed was

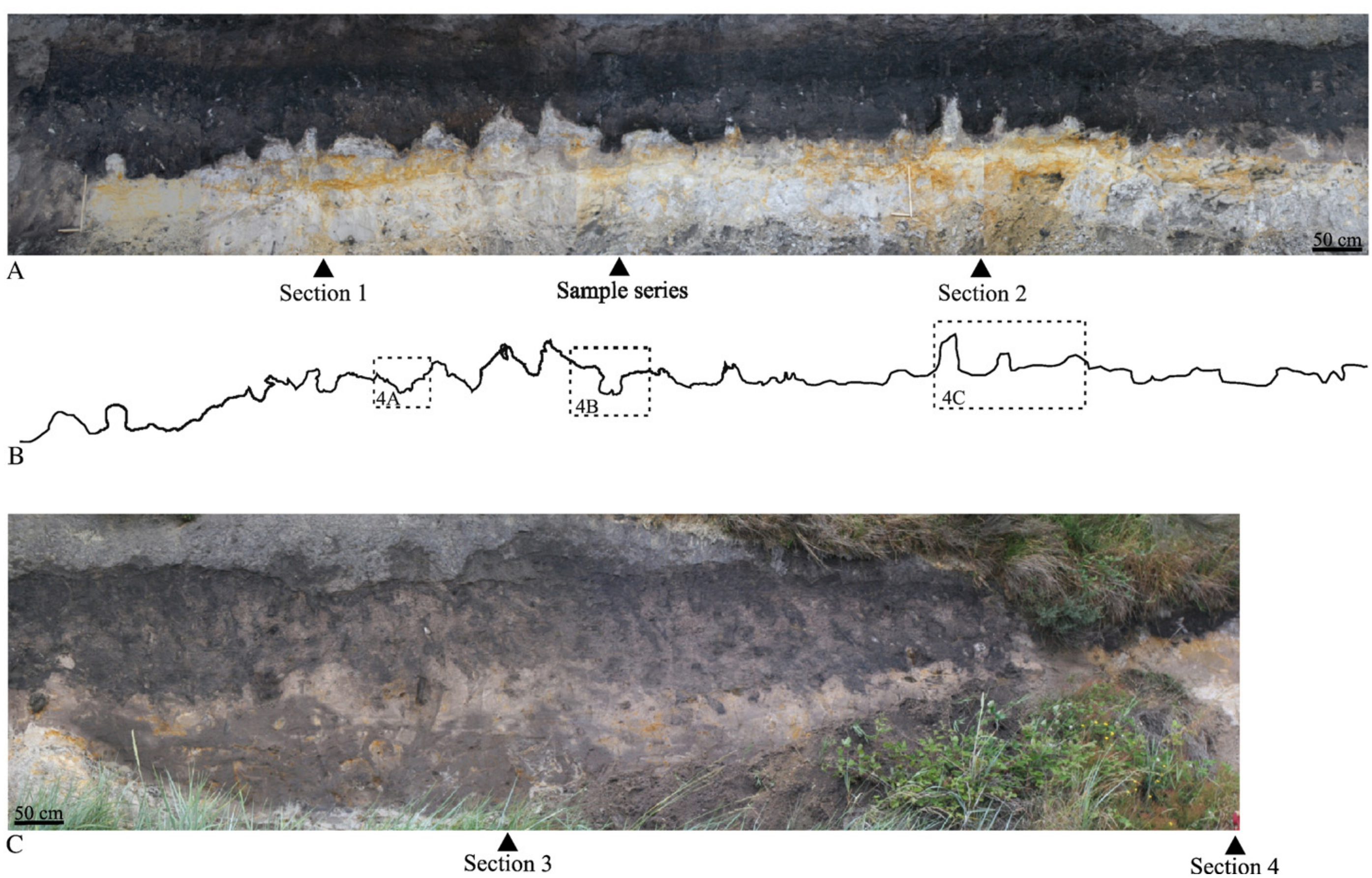

Fig. 3. A. Photomosaic of the type locality of the fluvial-lacustrine Skyttegård Member. The dinosaur trample ground is situated at the irregular base of the dark brown lake mud of unit 7. B. Line drawing of the trackway based on A. Positions of Fig. 4A, B and C indicated. C. Continuation of A towards the right, showing grey fill of abandoned fluvial channel. Note the great density of interpreted lungfish burrows, especially in the dark lacustrine mud of unit 7 overlying the channel fill. The position of the measured Sections 1–4 (Fig. 2) indicated in A and C.

undertaken by Petersen et al. (1996) and a number of samples collected by us were analyzed for TOC, total sulphur (TS) and organic matter (OM) (H.I. Petersen, pers. comm. 2007) and a densely spaced sample series through the trace fossil-bearing beds was analyzed for TOC,TS, magnetic susceptibility (SUS), δ^{13}C, and $CaC0_3$ (Fig. 4).

4. Results

4.1. Sedimentology

A total of seven facies units are recognized (Fig. 2) and are described below in ascending stratigraphic order and an environmental interpretation is presented in the Discussion.

4.1.1. Unit 1 — light grey massive mud

This unit comprises at least 1 m of structureless silty mud. It was deposited out of suspension, probably in a well-oxygenated lake.

4.1.2. Unit 2 — white structureless sand

This unit is up to about 0.8 m thick and consists of light grey somewhat argillaceous, structureless fine-grained sand. It overlies unit 1 having an erosional boundary with a small-scale relief of a few centimetres. Small clasts of the silty, light-grey clay of unit 1 occur scattered in the sand.

The depositional mechanism cannot be interpreted with any certainty due to the virtually complete absence of primary sedimentary structures. The structureless appearance, the erosional base and the scattered rip-up clasts suggest, however, emplacement by a high-energy event such as a crevasse splay from a nearby river or a wash-over from the sea.

4.1.3. Unit 3 — white sand containing clay clasts, wood fragments, and scattered rootlets

This unit is up to 50 cm thick but the upper boundary is strongly modified by the bowl-shaped depressions at the base of unit 7 interpreted here as dinosaur tracks. It consists of white to light-grey, medium-grained sand that is commonly coloured with yellow stripes and bands of recent ground-water origin. The base of the bed is strongly erosional and is draped by a thin, discontinuous, normally graded lag of mainly quartzite pebbles, up to 1 cm in diameter. The unit is structureless except for ghosts of scour-and-fill cross-bedding with a set thickness of about 10 cm occurring in a few places, and the upper part of the unit shows diffuse lamination that has been deformed by the tracks at the base of the overlying unit.

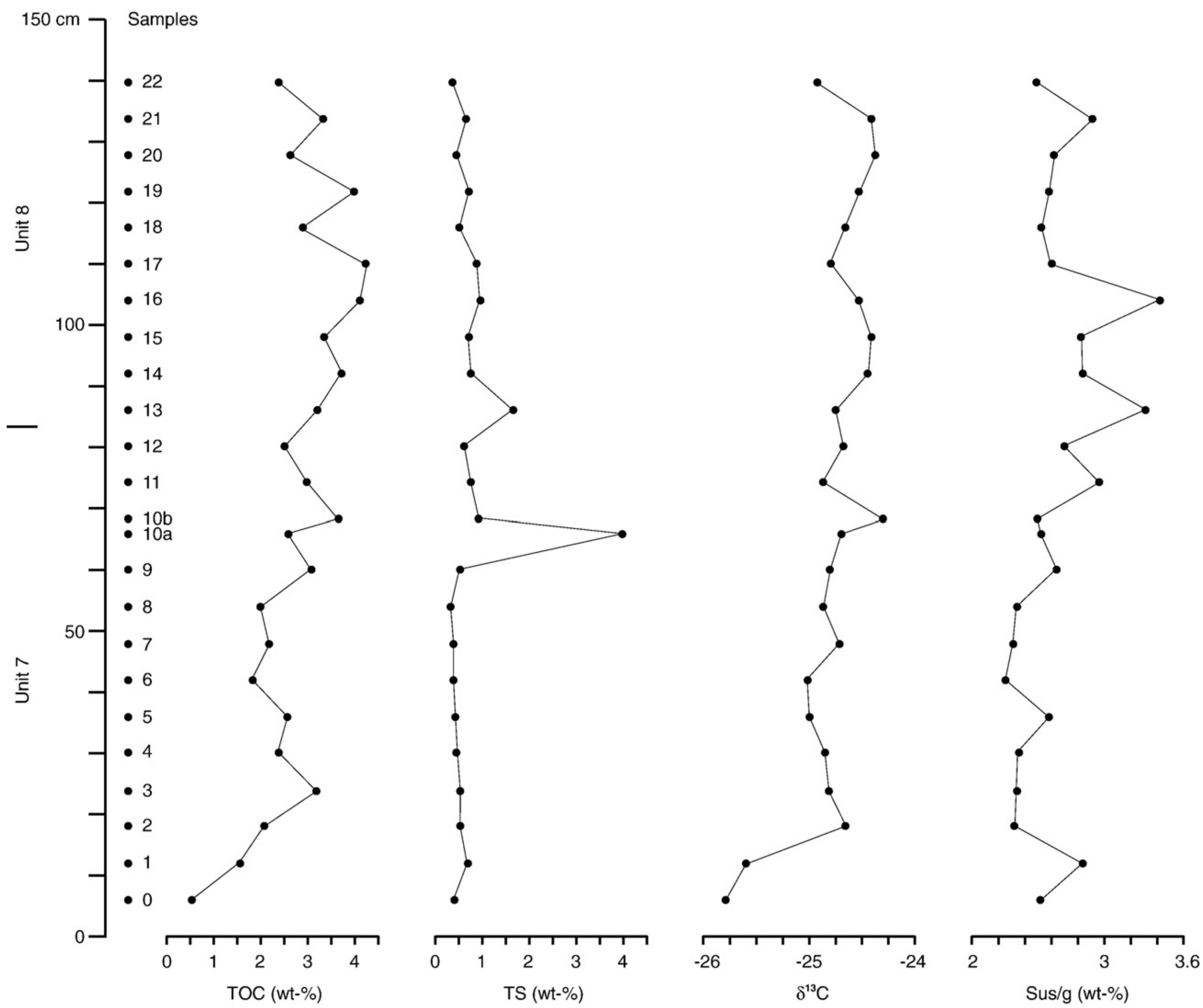

Fig. 4. Geochemical analyses based on a densely spaced sample series through units 7–8 (position indicated on Fig. 3A). The curves show weight percentages of Total Organic Carbon — TOC (actually TC, but samples are free of $CaCO_3$) and Total Sulphur — TS, δ^{13}C, and magnetic susceptibility — SUS. The TOC varies between 0.54 and 4.22 wt.%, showing an overall upwards increase towards the middle part of the dark unit 8. The TS varies between 0.32 and 3.95 wt.%, but it should be noted that most sulphur occurs in large pyrite concretions. The δ^{13}C varies between −24.64 and −25.84, indicating a terrestrial source for the organic matter. The magnetic susceptibility shows an overall upwards increase towards the middle part of the dark unit 8, reflecting a higher content of silt and clay in this unit compared to unit 7.

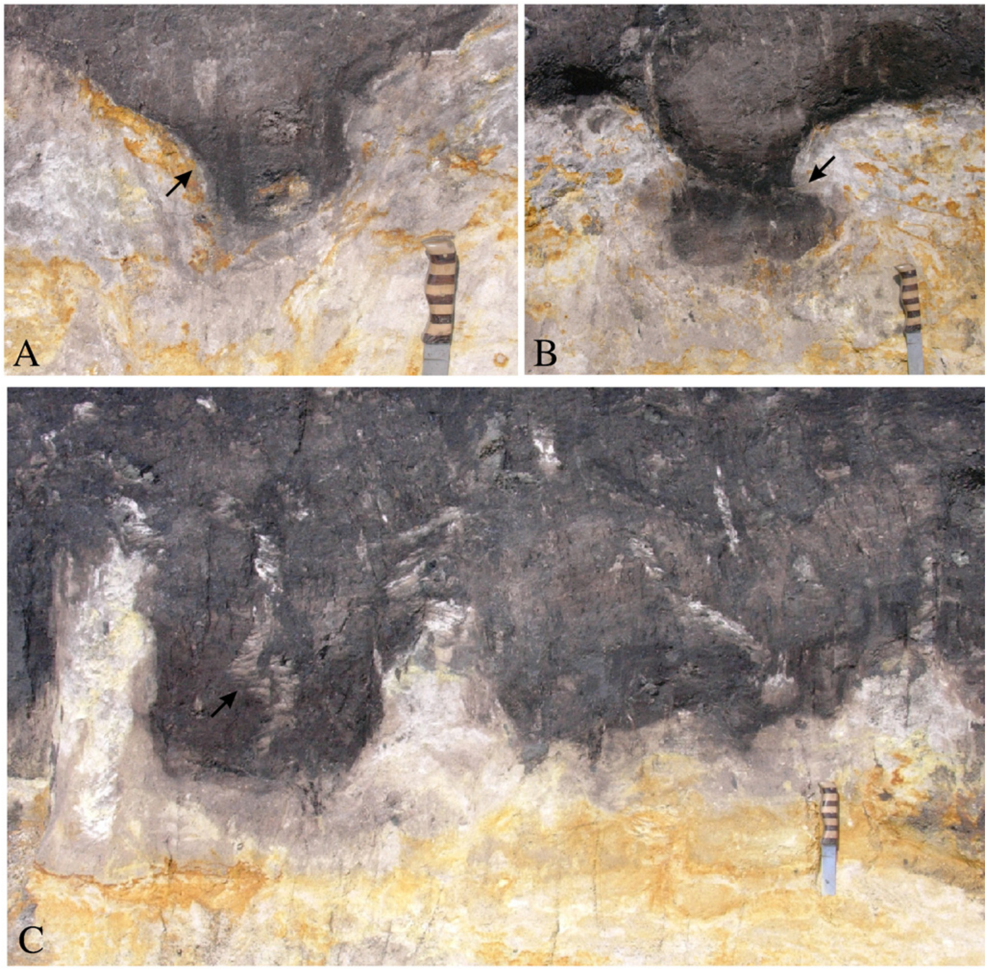

Fig. 5. Examples of tracks from the trample ground shown in Fig. 3. The dark lacustrine mud belongs to unit 7 (Fig. 2). Note the down-bending of the diffuse layering in the underlying sand in A (arrow), the overhanging walls of the track in B (arrow), and the slightly curved, oblique or spiraling possible lungfish burrows and densely spaced rootlets in C (arrow). Bands on knife handle are 1 cm wide.

The erosional base, the graded pebble lag, the structureless nature of the lower part, rare ghosts of scour-and-fill cross-bedding and top lamination suggest emplacement by one flow event, probably a crevasse splay or a washover as envisaged from the underlying unit 2. An alternative interpretation is that the sand was primarily trough cross-bedded throughout but was liquefied and almost completely homogenized possibly by the load of passing dinosaurs. The tracks described below were made in a shallow muddy lake, and the sand was sealed by the lake floor mud and completely water-saturated. This interpretation is preferred here because of the presence of ghosts of cross-bedding in a few places, covering areas of less than 0.5×0.5 m in the vertical outcrop wall, whereas the rest is structureless. This suggests that the unit was originally trough cross-bedded throughout.

4.1.4. Unit 4 — light grey-brown muddy channel fill sand

In the eastern part of the profile, a shallow channel cuts down from the top of unit 3, through unit 3 and the top of unit 2 (Figs. 2 and 3). The channel is about 13 m wide and up to about 1.5 m deep in the exposed profile, giving a width/depth ratio of about 9. The channel fill comprises a lower part, up to about 70 cm thick (unit 4) and an upper part (unit 5). The trend of the channel is not known and the width is probably smaller as it is rather unlikely that the channel axis cuts the exposure at a right angle. The lower part of the channel fill (unit 4) consists of light grey-brown to medium grey, structureless, muddy fine-grained sand, which becomes lighter coloured upwards. The unit contains scattered rootlets, wood fragments and pyrite concretions. Vertical to inclined, slightly curved or spiralling cylindrical burrows with a laminated passive fill also occur, especially in the middle part of the channel fill. One sample has a TOC content of only 0.30 wt.% and a TS of 0.04 wt.%. The OM is principally composed of textured huminite.

The structureless appearance and fine grain-size of the channel fill suggests that the channel represents an abandoned meander bend — an oxbow lake — filled mainly by fall out from a heavy suspension-loaded current. The abundance of pyrite concretions suggests some marine influence and the channel may represent an abandoned distributary of a small muddy river. A palynological screening of the pyrite bearing units has, however, only yielded well-preserved spores but no dinoflagellates (S. Piasecki, pers. comm. 2007).

The basal part of the channel fill is somewhat chaotic and strongly deformed, containing fragments of grey, muddy sand of the underlying unit 1. The fragments are angular and have not undergone any transport and are clearly not a lag. The strongly mixed basal channel fill resembles a seismite formed by in-place shaking and break-up of the layers at the base of the channel. Seismites are common in the Middle Jurassic Bagå Formation (Gry, 1969; Gravesen et al., 1982; F. Surlyk, unpublished data), and the faults delimiting the Bornholm horst were intermittently active throughout the Mesozoic, supporting a seismite interpretation.

4.1.5. Unit 5 — light-grey, muddy, fine-grained sand

This unit represents the upper 50–65 cm of the channel fill (Figs. 2 and 3). It is demarcated from the lower part of the fill by a subtle

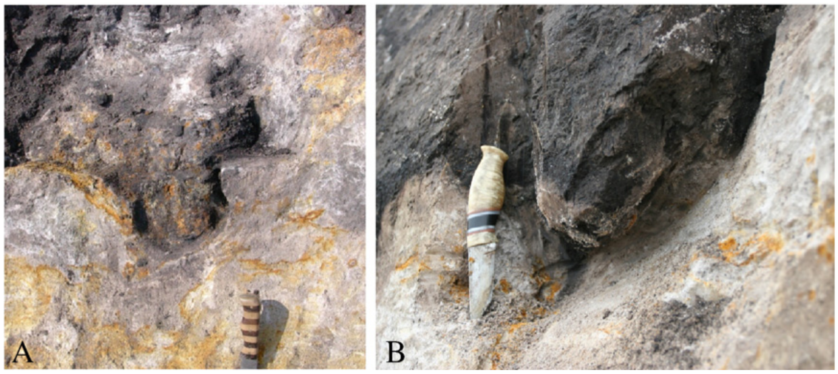

Fig. 6. Excavated tracks, showing the three-dimensional shape. A. Downwards oblique view where the boundary between the sand and the dark mud has been cleaned. Bands on knife handle are 1 cm wide. B. Rounded cone shape of a track seen obliquely from below. Knife is 20 cm long.

bedding plane and a change to lighter colours and fewer subvertical burrows than unit 4. It contains abundant vertical rootlets and pyrite concretions and is topped by the trackway at the base of units 6 and 7. The unit was deposited out of suspension as unit 4 and the lighter colour suggests better oxygenated conditions.

4.1.6. Unit 6 — light-grey or light-brown draping muddy sand

This unit is only a few centimetres thick and consists of light-grey or light-brown muddy sand (Figs. 2 and 3). It drapes the channel fill and extends laterally outside the channel, irregularly draping unit 3 in a highly irregular discontinuous way due to the disturbances of the tracks at the boundary to the overlying bed. It is thickest beneath the tracks and commonly wedges and smears out upwards along the track margins and has a wavy discontinuous appearance (Fig. 5).

4.1.7. Unit 7 — dark brown mud with basal tracks, burrows, rootlets and pyrite nodules

This is the main unit of the study as it contains what we interpret as dinosaur tracks at its base (Figs. 2 and 3). The unit is 65–70 cm thick and consists of dark brown mud, strongly mottled by large, subvertical to inclined burrows and containing long, densely spaced vertical rootlets. The base is sharp and stands out very clearly due to the strong colour contrast with the underlying light-grey sand. It is highly irregular with bowl-shaped more or less regular downward extensions, representing the tracks described below. The tracks occur along all of the western part of the profile but are absent above the channel where superficially similar rounded extensions from the base of the unit represent the ends of densely spaced vertical to inclined burrows (Fig. 3). The tracks recur farthest to the east outside the eastern channel margin. The unit is rich in finely disseminated organic detritus and the TOC is on average 2.86 wt.% and the TS 0.81 wt.% (three bulk samples; Figs. 2 and 3); a sample taken above the channel fill (unit 4) contains only 0.39 wt.% TOC and 0.14 wt.% TS. A dense sample series taken through units 7–8 was analyzed for TOC, TS, δ^{13}C and magnetic susceptibility, SUS (Fig. 4). The TOC varies between 0.54 and 4.22 wt.% and the TS varies between 0.32 and 3.95 wt.%, but most sulphur occurs in large pyrite concretions. The δ^{13}C varies between −24.64 and −25.84, and the magnetic susceptibility shows an overall upwards increase towards the middle part of the dark unit 8, reflecting a fining upwards grain-size trend with an increase in silt-sized grains which may be primary or formed by weathering in the plant-covered soil horizon.

The OM consists predominantly of angular inertinite particles derived from crushed fusinite (fossil charcoal) and huminite, and wood fragments, sticks and large pyrite concretions are common. The sediment is almost totally bioturbated and apparent remains of primary bedding are only represented by the passive infill of the subvertical, somewhat curved or spiraling cylindrical burrows. Parts of some burrow fills consist of irregularly alternating laminae of white, fine-grained sand and clay, giving the fill a heterolithic appearance with a superficial resemblance of a spreite.

Deposition took place in a shallow anoxic lake. The coal petrographic and biogeochemical data suggest that organic material was not transported very far and that the source was a low-diversity gymnospermous vegetation chiefly composed of Pinaceae and Cupressaceae around the margin of the lake (Petersen et al., 1996). This is corroborated by a recent palynological analysis which indicates that the lake was surrounded by a gymnospermous vegetation dominated by Taxodiaceae, with common pteridosperms, Auracariaceae and ferns (Lindgren et al., 2008). The abundant pyrite concretions may indicate some marine influence although dinoflagellates are absent and the white sand forming part of the fill of some of the burrows may be of aeolian origin or represent distal washovers from a river or the nearby sea into the shallow coastal lake.

4.1.8. Unit 8 — dark brown to black mud with burrows

The dark brown mud of unit 7 passes gradually into unit 8 which is about 35 cm thick (Figs. 2 and 3). This bed was the main subject of the study of Petersen et al. (1996). It has the highest TOC in the succession of 4.22 wt.% and TS values up to 1.65 wt.% (Fig. 4). Petersen et al. (1996) report TOC values of 5.4 up to 39.39 wt.% but most values are below

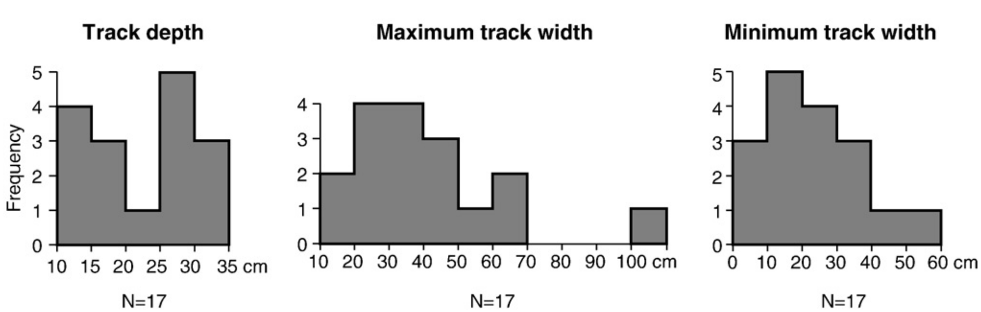

Fig. 7. Size-frequency histograms showing depth, maximum and minimum widths of the dinosaur tracks.

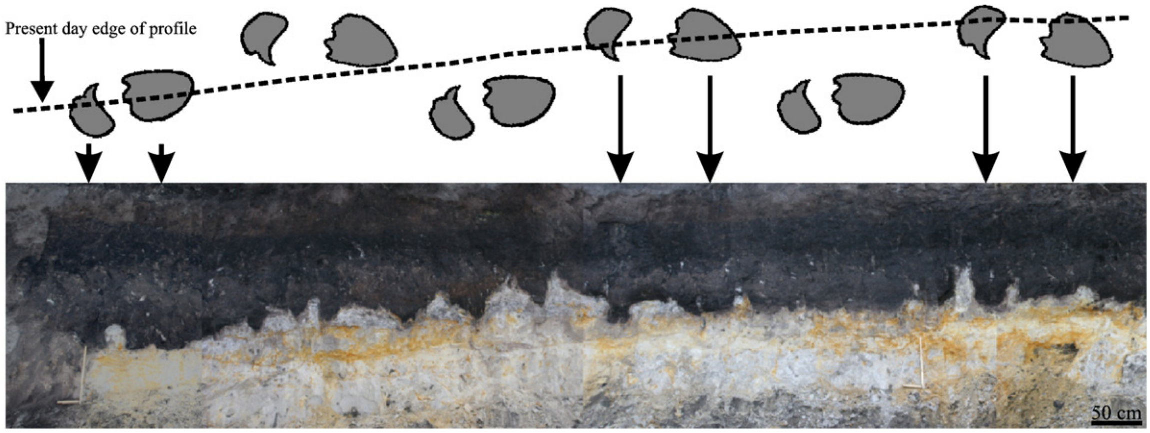

Fig. 8. Interpreted sauropod trackway correlated with the profile shown in Fig. 3.

20 wt.%. The huminite occurs as relatively large particles of densinite, textinite/textoulminite and eu-ulminite. Massive pyrite crystals and large concentrations of framboidal pyrite are observed in the samples. Wood fragments and pyrite concretions are common and scattered quartzite pebbles occur. The vertical to inclined burrows are densely spaced as in units 5 and 7. The colour becomes lighter and the TOC

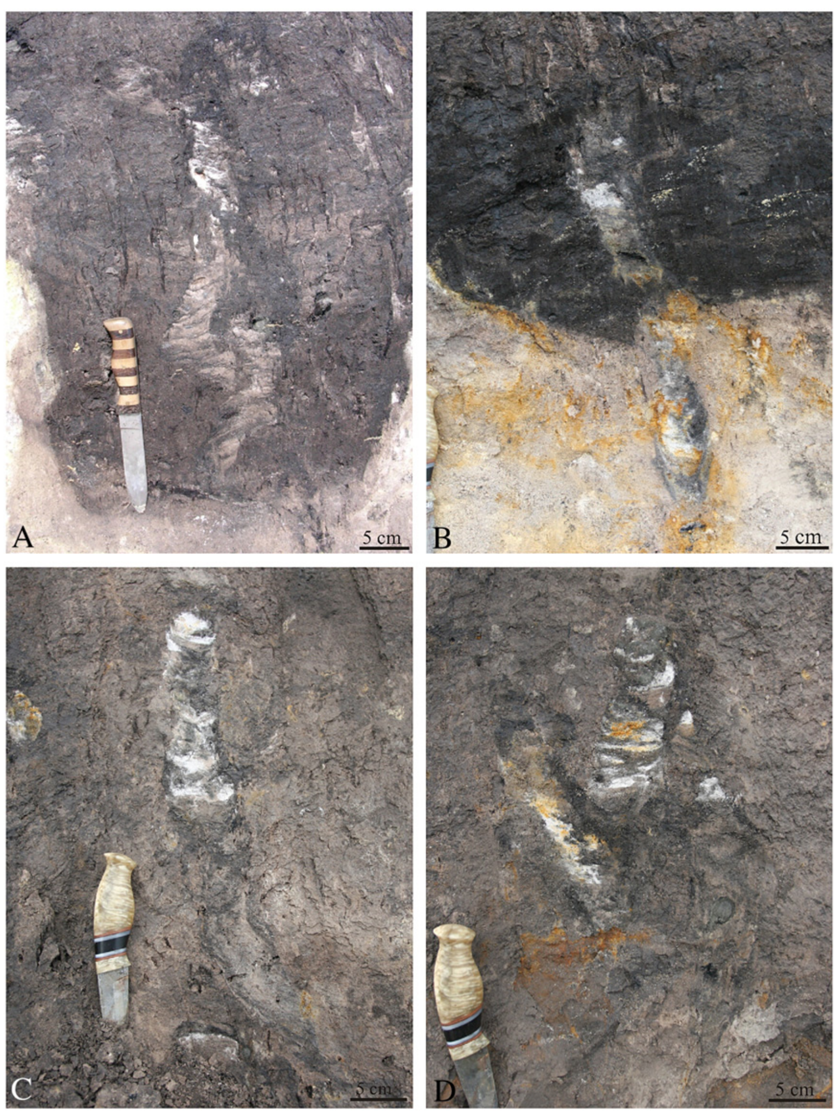

Fig. 9. Densely spaced, subvertical burrows interpreted as formed by lungfish. A. Curved and spiraling burrows with a passive heterolithic fill. White sand laminae are probably of aeolian origin. B. Rare example of a burrow passing down from the lake mud (unit 7) into the underlying sand. C (unit 3). J-shaped burrow. The lower part of the burrow fill is identical to the surrounding mud, whereas the upper part consists of heterolithic sand-mud. D. Two intersecting burrows both with heterolithic fill.

decreases towards the east above the channel, and the burrows are more clearly visible in this part.

This unit represents the most anoxic stage in the history of the shallow lake with a complete lack of oxygenation of the organic material. Marine influence is possible as reflected by the abundant pyrite concretions and framboidal pyrite but dinoflagellates are absent.

4.1.9. Unit 9 — dark grey silt with sticks and wood fragments

This unit forms the top of the succession and only about 65 cm are exposed (Figs. 2 and 3). It consists of dark grey, diffusely laminated silt with sticks, wood fragments, and scattered pyrite concretions.

It was deposited during the last stages of the lake under somewhat oxygenated conditions resulting in degradation of much of the organic material.

4.2. Ichnology

4.2.1. Bowl-shaped tracks

The horizon of particular interest in this study is the highly deformed base of unit 7 (Figs. 2, 3, 5 and 6). The bowl-shaped deformation structures have an average depth of 22 cm and maximum and minimum average widths of 43 and 23 cm, respectively (Fig. 7). The majority appears as steep-walled, irregular flat-bottomed or slightly concave-up depressions, whereas others have a more v-shaped profile (Figs. 3, 5 and 6). The sediment layers below the depressions are squeezed laterally, and where two depressions are situated close together, the sediment between them is displaced sideways and upwards between the depressions (Figs. 3, 5A and 6A). The thin unit 6 is squeezed out by the deformation, and appears as isolated units between, and especially below the depressions (Figs. 3 and 5). Excavation of several of the depressions shows them to be three-dimensional, highly irregular bowl-shaped depressions, with an irregular bottom and well-defined vertical, steeply inclined or even overhanging walls (Fig. 6).

Fossil vertebrate tracks and trackways are most easily recognized when encountered on exposed bedding planes, but a track is not only a two-dimensional bedding plane feature; it is a complex three-dimensional structure associated with deformation not only of the original tracking surface, but also of the subjacent layers, commonly to a considerable depth, depending on the weight and speed of the track maker and water content of the substrate. This makes it possible to recognize vertebrate tracks exposed in vertical cross-sections and in different erosional cuts through the original bedding planes (Loope, 1986; Allen, 1989, 1997; Fornós et al., 2002; Milàn et al., 2004, Milàn and Bromley, 2006). When a high density of tracks is emplaced in a soft but cohesive substrate, the result is a highly sculpted surface consisting of deep, bowl-shaped, irregularly flat-bottomed depressions divided by high rims of displaced mud.

The dinosaur tracks from the Middle Jurassic Bagå Formation on Bornholm were preserved as natural casts of sandstone (Milàn and Bromley, 2005). The surface of the sandstone blocks containing these tracks was moulded after an originally highly sculpted muddy floodplain surface with the largest of the tracks being 69 cm long and 29 cm deep. These tracks were emplaced in clay and filled with sand (Milàn and Bromley, 2005), opposite to the situation described here, but the morphology of the original trampled surfaces is similar.

Trampling by vertebrates is, however, not the only process capable of creating a sculpted surface consisting of pits and grooves. At least on one occasion has an alleged surface with dinosaur tracks been reinterpreted. Oval pits on average 34 cm long and 43 cm wide exposed with high density on an extensive Upper Cretaceous shallow marine sandstone surface at La Posa in Spain. were initially described as dinosaur tracks, because of their size (Santafé et al., 1997). However, closer examination of the pits showed them to be v-shaped in cross-section and the distribution of the structures was random and did not constitute recognizable tetrapod trackway patterns. This morphology and distribution was much more consistent with feeding traces of rays, which frequently inhabit shallow marine environments (Martinell et al., 2001).

The structures described here are evenly distributed along the profile and were formed in a shallow lake. The majority are flat-bottomed with steep, well-defined walls, resulting from a heavy load applied to the soft package of sediments. This is corroborated by the bending of the subjacent layers around the depressions. If the structures were feeding traces, they would have been dug out and would not have caused the extensive deformation of underlying beds. This is in line with the almost structureless appearance of the underlying sand of unit 3, which may have been caused by liquefaction due to the trampling load on the water-saturated sand that was sealed by lake mud.

The structures are thus interpreted as the result of trampling by large vertebrates, in this case most likely sauropod dinosaurs, as they were the only possible track makers for such large structures. Finds of teeth of small theropod dinosaurs, and crocodiles from the same

Fig. 10. A. J-shaped oblique burrow with a slightly enlarged basal chamber. B. Intersecting oblique, slightly curved or spiraling burrows all filled with the same type of mud as the surrounding host sediment.

member close to the section described here (Lindgren et al., 2004, 2008) and teeth of both theropod and sauropod dinosaurs from the slightly younger Jydegård Formation (Christiansen and Bonde, 2003; Bonde and Christiansen, 2003) prove that dinosaurs were indeed present at Bornholm during the earliest Cretaceous.

The European record of Early Cretaceous dinosaurs includes sauropods, theropods, ornithopods, and thyreophoreans (Martill and Naish, 2001; Weishampel et al., 2004; Naish and Martill, 2007). The tracks described here are large, more-or-less flat-bottomed depressions, lacking indications of subdivisions into separate digits. This morphology is most consistent with the elephantine feet of sauropods. Seen in cross-section the tridactyl feet of theropods and ornithopods are unlikely to display the track morphology described here. Thyreophoreans had small compact feet with short blunt digits, normally with a crescent shaped manus and oval pes shape (Christiansen 1997a,b). In vertical cross-sections, tracks of thyreophoreans would also occur as flat-bottomed depressions, but the sheer size, up to 67 cm in length, of well-defined tracks strongly suggests that the tracks originate from sauropods. The water content of a sediment seriously alters the surface appearance of tracks, as increasing softness of the sediments causes the track walls to flow together leaving even a tridactyl track to appear as an indistinct rounded hole in the surface (Milàn, 2006). However, such tracks retain their original shape at the bottom of the tracks even if totally collapsed at the tracking surface. This is especially evident when the tracks are observed in vertical cross-section (Allen, 1997; Milàn et al., 2004; Milàn and Bromley, 2006).

A large flat-bottomed depression associated with an immediately adjacent smaller, deeper and more rounded depression occurs at three locations along the profile (Fig. 3). This constellation is consistent with the trackway morphology of sauropod dinosaurs, as sauropods had an extreme degree of heteropody, i.e. size difference between fore and hind feet, ranging from 1/5 to 1/2 with the hind feet being always the largest (Lockley et al., 1994). The hind feet of sauropods were oval to pear shaped, with short blunt digits; the fore feet were encapsulated in tissue to form a massive hoof, lacking free digits, except for an inward directed pollex claw (Lockley et al., 1994; Milàn et al., 2005). The presence of three consecutive sets of interpreted fore and hind foot impressions suggests that the present-day coastal profile has exposed the vertical section through a segment of a sauropod trackway, or manus-pes couples from several individuals (Fig. 8), as well as several smaller unidentifiable cross-sections of tracks from smaller dinosaurs or other terrestrial vertebrates.

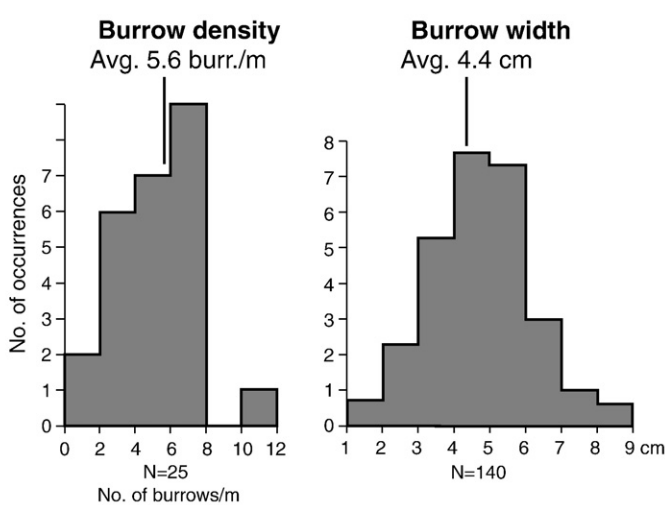

Fig. 11. Size-frequency histograms showing density of burrows, averaging 5.6 burrows per metre along a bedding parallel line transect in unit 7, and burrow widths, averaging 4.4 cm. Burrow depths cannot be measured due to indistinct tops, common cross-cutting relationships and because the burrows go in and out of the exposure.

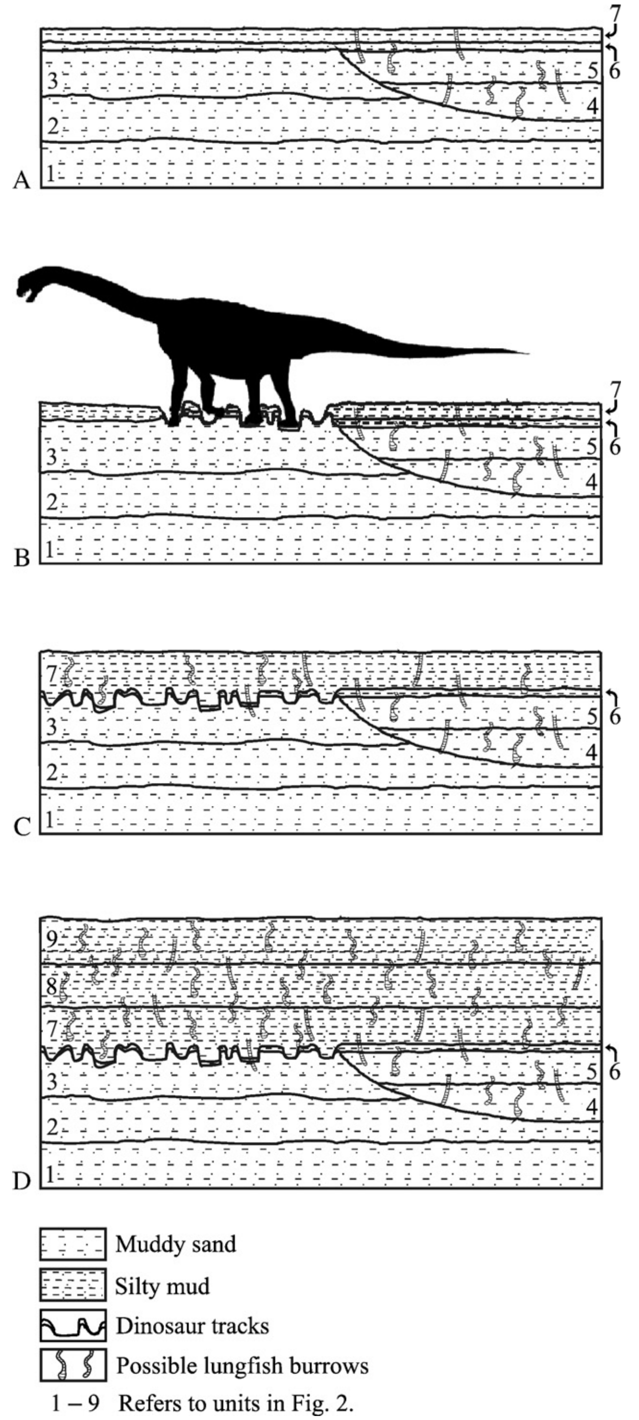

Fig. 12. Interpretation of the depositional history and formation of the dinosaur trample ground.

4.2.2. Large, vertical to inclined burrows

The channel fill (units 4 and 5) and the overlying dark brown, shallow lake mud (units 7 and 8) contain abundant large, vertical to inclined burrows (Figs. 9 and 10). They are cylindrical, straight, slightly spiraling, or J-shaped. The burrow tops are indistinct or not preserved, whereas the base is rounded and concave-up, giving the burrow a test-tube morphology. Chimneys have not been observed. The diameter averages 4.4 cm, ranging from 1 to 8.5 cm (Fig. 11). The length is difficult to assess because the burrows are rarely completely straight and vertical, and they cut in and out of the exposure surface. In addition they commonly have cross-cutting relationships or are partly reburrowed, but preserved lengths of about 30 cm are common and lengths up to 45 cm have been observed. Branching does not occur and there is no mud or lag linings of the burrow walls, but the burrow margins are commonly discoloured due to redox processes. The burrow shafts are generally parallel-sided throughout but a few examples show a slight swelling of part of the shaft and some have terminal chambers slightly wider than the shaft. These chambers are commonly subhorizontal or oblique to bedding, giving the burrow a sock-like appearance (Figs. 9C and 10A). Surficial wall ornament has not been observed, but this may be due to the main lithology which consists of stiff, somewhat crumbling mud, making it impossible to isolate individual burrows. However, preparation of numerous clean vertical sections through burrow margins show them to be even lacking signs of furrows, scratch traces, hummocky or knobby texture. The burrows were passively filled with the same mud as the surroundings or by irregularly alternating layers of white sand and mud, giving the fill a heterolithic appearance superficially resembling a spreite. The passive fill is somewhat similar to the fill of *Psilonichnus* burrows (Gingras et al., 2000) and like these provides the only evidence of episodic sedimentation in the otherwise dark muddy sediment.

The burrow density was measured along a bedding-parallel line transect in the middle of unit 7. The density ranges from 1 to 11 burrows per metre with an average of 5.6/m (Fig. 11). Burrows originate from all levels of the units and the high density does not necessarily reflect a high density at any one time. The burrows may have been seasonal and the same animal thus may have constructed a number of burrows during its life time.

Skeletal remains which could have revealed the nature of the burrower have not been found undoubtedly due to dissolution in the acid boggy lake mud (carbonate has not been detected in any of the samples). It is noteworthy that the micro-vertebrate fauna from the Skyttegård Member (Lindgren et al., 2004) was only found in light-grey and brick-red lenses which are absent from the section described here.

The burrows are closely similar to burrows interpreted as made by lungfish or crayfish, and the originator of such burrows has been subject to much discussion (Dubiel et al., 1987, 1988; McAllister, 1988; Dubiel et al., 1989; Hasiotis and Mitchell, 1989, 1993; Miller et al., 2001). Both groups are poorly known from Mesozoic deposits and skeletal remains are only rarely found in the burrows and, even in the few lucky cases, there is no guarantee that the fossil actually represents the primary burrower. Attempts at identifying distinguishing characters was made by Hasiotis et al. (1993), and Miller et al. (2001, Table 3) who list the characteristics of burrows made by lungfish, Triassic and modern crayfish, and Permian and Triassic therapsids. Gobetz et al. (2006) interpreted burrows from the Upper Triassic Chinle Group that are closely similar to the burrows described here as lungfish aestivation burrows. They based their interpretation on the basis of the hemispherical, test-tube-like base, distinct sides and base, indistinct top, circular cross-section, smooth surface except for occasional faint spiraling striations, following McAllister (1979, unpublished thesis, not seen). The Chinle burrows have a diameter of 4.7–7.5 cm within the range of previously published lungfish burrows.

The burrows described here have a vertical to inclined, straight, gently helical, or curved to J-shaped morphology, a circular to slightly oval cross-section with a diameter of the shaft ranging from 1–8.5 cm, averaging 4.4 cm, common presence of terminal chambers and fit well with described characteristics of simple lungfish burrows.

The burrows differ from most crayfish burrows in their shape and surface architecture. However, they superficially resemble the simple crayfish burrows termed type IIIA by Hasiotis et al. (1993). These are simple, subvertical and have surficial ornamentation such as scrape and scratch traces, mud and lag liners, knobby surfaces and chimney structures. Type IIIA burrows were made by so-called tertiary crayfish (Hobbs, 1981), which spent most of their lives in open water, and only burrowed to escape desiccation and to reproduce (Hobbs, 1981; Hasiotis et al., 1998). The anoxic nature of the floor of the lake or swamp described here does not fit well with a bottom-living mode of life, although the occasional presence of redox discoloration indicates fluctuations in water table and short periods of desiccation. The lack of branching, chimney, burrow linings, surficial traces and the relatively uniform depth of burial also fit well with lungfish burrows, and speak against a crayfish origin. The burrows are thus, with some reservation, interpreted as lungfish aestivation burrows.

Fig. 13. Modern analog of the dinosaur tracks found at the marsh-like margin of Mariager Fjord in NW Denmark. Trampling of cows in shallow muddy, flat-bottomed creeks is reflected by tracks varying from well-defined with clear impressions of the hoofs to deep, completely smeared-out depressions depending on the consistency and wetness of the mud.

Burrows of lungfish are the oldest recognized vertebrate burrows, and have been used as an indication of seasonal droughts (Romer and Olson, 1954). The modern lungfish *Protopterus annectens* lives in floodplain swamps along the Gambia River in Africa. The climate has wet and dry seasons and large areas of the floodplain are flooded during the five-month-long rainy season. The lungfish burrow into the floor of shallow lakes and swamps at the end of the rainy season and aestivate (Greenwood, 1986). They burrow by biting bits of the moist muddy substrate and force the material out through the gills. Useful overviews of lungfish burrowing are given by Hasiotis et al. (1993, 2007). The common spiraling or helical burrow morphology has been attributed to the anguilliform movements of the fish as it burrowed into the substrate (Gobetz et al., 2006).

5. Discussion

All data point towards a terrestrial environment of deposition for the whole succession although a coastal position is suggested by the high amount of large pyrite nodules and of framboidal pyrite. The environment appears to have been a mosaic of rivers, crevasse splays, cut-off channels similar to billabongs or oxbow lakes, well-oxygenated organic-poor lakes, organic-rich poorly oxygenated to anoxic lakes with a dense, low-diversity gymnospermous vegetation. The two-dimensional nature of the low outcrops does not allow a detailed interpretation of the nature of the fluvial system although there is no evidence for lateral accretion and the total distribution of facies is highly similar to anastomosing fluvial systems as defined by Nadon (1994). This is corroborated by the presence of numerous, densely spaced possible lungfish aestivation burrows which indicate a highly seasonal water budget with a strongly seasonal rainfall distribution. Interestingly, dinosaur tracks which are highly similar to those described here occur in the uppermost Cretaceous, Maastrichtian, North Horn Formation of Utah which is interpreted as also deposited in anastomosed fluvial environments (Difley and Ekdale, 2002).

The history of events leading to the preserved dinosaur tracks and possible lungfish burrows is reconstructed on the basis of the sedimentological–stratigraphical evidence (Fig. 12). The light-grey, structureless mud (unit 1) at the base of the succession was deposited out of suspension in a quiet, well-oxygenated lake. A crevasse splay or a washover from the nearby sea deposited the erosionally-based white structureless sand (unit 2). The white, equally erosionally-based structureless sand with clay clasts, wood fragments and ghosts of trough cross-bedding (unit 3) may have been deposited by a second flow event but it is considered more likely that it represents fluvial bars where the structureless appearance is secondary, caused by liquefaction of the sand due to the trampling load of the dinosaurs. A fluvial channel was cut down through unit 3 and partly down into unit 2. The channel was abandoned and was subsequently filled-in by fine-grained muddy sand from suspension during flooding events (units 4 and 5) and finally the channel and its surroundings were draped by a thin veneer of light grey-brown muddy sand (unit 6).

A shallow anoxic lake was formed above the channel fill and its margins and dark organic-rich mud (unit 7) was deposited on the lake floor. During deposition of the mud, the area was trampled by dinosaurs, probably sauropods, causing strong deformation of the interface between the lowermost lake mud (unit 7) and the underlying muddy sand of unit 3 and the thin drape of unit 6. Subsequent to the trampling event, deposition of mud continued and the lake was partly overgrown. Numerous large, subvertical burrows tentatively interpreted as lungfish aestivation burrows were formed (units 7 and 8). The gradual change to dark brown and black mud of unit 8 marks the most anoxic state in the lake history but the burrowing activity of lungfish continued. Finally, the dark grey silt with wood fragments and pyrite concretions (unit 9) represents a change to a more oxygenated stage in the lake development, and this unit does not contain any lungfish burrows.

A modern analog of the trample ground was found at the marsh-like margin of Mariager Fjord in NW Denmark (Fig. 13). Shallow, muddy, flat-bottomed creeks were trampled by cows and the morphology of their tracks varied from well-defined with clear impressions of the hoofs to deep, completely smeared-out depressions depending on the consistency and wetness of the mud. This compares extremely well with the Berriasian trample ground where some tracks are very well-defined — although not preserving imprints of the digits, whereas others are highly irregularly formed by sliding of the animal (Fig. 3).

6. Conclusions

1. The lowermost Cretaceous, Berriasian Skyttegård Member of the Rabekke Formation on the island of Bornholm in the Baltic Sea was deposited in rivers and shallow lakes, probably close to the coast.
2. A horizon showing evidence of intense trampling by dinosaurs occurs at the boundary between light-coloured fluvial sand and dark brown lake mud.
3. The tracks were probably made by sauropods as judged by their size and common association of what is interpreted as hind and fore feet impressions.
4. This is the first find of in-situ dinosaur tracks in the Mesozoic successions of Bornholm and of Denmark in general. The rarity probably reflects the fact that the Bornholm horst constituted and island or a shallow shoal during much of the Mesozoic and was not in direct land connection with the surrounding landmasses.
5. The lake mud contains large, densely spaced, vertical to inclined, straight, or commonly spiraling or J-shaped burrows interpreted as made by lungfish, although a crayfish origin cannot be completely dismissed.
6. Burrows referred to the activity of lungfish are generally very rare in Mesozoic deposits and this is the first find in the Mesozoic of Denmark.

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