New theropod, thyreophoran, and small sauropod tracks from the Middle Jurassic Bagå Formation, Bornholm, Denmark

JESPER MILÀN

Milàn, J. 2011. New theropod, thyreophoran, and small sauropod tracks from the Middle Jurassic Bagå Formation, Bornholm, Denmark © 2011 by Bulletin of the Geological Society of Denmark, Vol. 59, pp. 51–59. ISSN 0011–6297. (www.2dgf.dk/publikationer/bulletin) https://doi.org/10.37570/bgsd-2011-59-06

Three new dinosaur tracks are described from the Middle Jurassic Bagå Formation of Bornholm, Denmark. The tracks are all preserved as natural casts on the underside of fluvial sandstone blocks originating from the old Hasle Klinkefabrik's clay pit, now called Pyritsøen. The new tracks are from a medium-sized theropod, a thyreophoran, and a small sauropod. Together with a thyreophoran track and large sauropod tracks described in 2005, the Middle Jurassic dinosaur fauna of Bornholm now comprises theropods, two sizes of sauropods and at least one type of thyreophoran dinosaur. This is important additional data for the very scarce Middle Jurassic dinosaurian skeletal record of Europe.

Received 22 November 2010
Accepted in revised form
21 September 2011
Published online
30 September 2011

Key words: Dinosaur fauna, trace fossils, Middle Jurassic, theropod, thyreophoran, sauropod.

Jesper Milàn [jesperm@oesm.dk], GeomuseumFaxe, Østsjællands Museum, Østervej 2, DK-4640 Faxe, Denmark. Also Department of Geography and Geology, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.

Remains of Mesozoic terrestrial vertebrates are scarce in Denmark and have so far only been found in the few Mesozoic outcrops along the west and southwest coast of the Baltic island of Bornholm (Fig. 1). Loose teeth of small and large dromaeosaurs (Bonde & Christiansen 2003; Lindgren *et al*. 2008), and a possible sauropod tooth (Christiansen & Bonde 2003) have been found in the Lower Cretaceous (Berriasian) Rabekke, Robbedale and Jydegaard Formations together with a rich microvertebrate fauna comprising remains of turtles, crocodilians, amphibians, primitive lizards, and a tooth from a multituberculate mammal (Bonde 2004; Lindgren *et al*. 2004, 2008; Rees *et al*. 2005; Schwarz-Wings *et al*. 2009). Turtle fragments together with fish remains are known from the Berriasian Jydegård Formation (Noe-Nygaard *et al*. 1987; Noe-Nygaard & Surlyk 1988).

Tracks of a large sauropod and a small thyreophoran dinosaur were found in the Middle Jurassic Bagå Formation in 2004 (Milàn & Bromley 2005) and recently a dinosaur trampleground and possible lungfish aestivation burrows were described from the lowermost Cretaceous Rabekke Formation (Surlyk *et al*. 2008).

Dinosaur remains are more commonly encountered in the southern part of Sweden, where numerous dinosaur tracks and trackways of theropod dinosaurs, a single thyreophoran dinosaur track, and a few skeletal remains are known from the Rhaetian – Hettangian Höganäs Formation (Bölau 1952, 1954; Pleijel 1975; Ahlberg & Siverson 1991; Gierlinski & Ahlberg 1994; Milàn & Gierlinski 2004). The Campanian Åsen locality in the Kristianstad Basin has yielded remains of neoceratopsian dinosaurs (Lindgren *et al*. 2007).

After the initial discovery of dinosaur tracks in the Bagå Formation in 2004 (Milàn & Bromley 2005), the area has on several occasions been thoroughly searched for more track material. A large block with three distorted, superimposed tracks was originally found together with the other tracks in 2004 but was not described at that time. During 2005–2006 two new partially preserved tracks were found, and in 2010 a third new track was found. This paper describes the new track material from the Middle Jurassic Bagå Formation, which adds important new information about the composition of the Middle Jurassic dinosaur fauna of Bornholm and Scania.

Geological setting

The type section of the Bagå Formation is the Bagå Graven of the Hasle Klinkefabrik at Sorthat (Gravesen *et al*. 1982; Michelsen *et al*. 2003; Nielsen *et al*. 2010) (Fig. 1), and 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 beds (Gry 1969). During a revision partly based on well-core material (Michelsen *et al*. 2003), the lower part of the Bagå Formation, showing evidence of marine influence, was separated as the Sorthat Formation, thereby leaving the revised Bagå Formation entirely composed of non-marine sediments.

The Bagå Formation comprises thick grey clay, dark to black coaly clays with rootlets, coal beds, and medium- to fine-grained, cross-bedded or laminated sandstone. In the upper part, poorly sorted, muddy and pebbly sandstone beds locally contain boulders of weathered granite, and deposition is interpreted to have taken place in lakes and swamps, small crevasse channels, lacustrine deltas and fluvial channels (Gravesen *et al*. 1982; Koppelhus & Nielsen 1994; Michelsen *et al*. 2003; Nielsen *et al*. 2010). The age of the Bagå Formation is Middle Jurassic, Bajocian–Bathonian (Gry 1969; Koppelhus & Nielsen 1994).

The dinosaur tracks described by Milàn & Bromley (2005) and the new tracks described here were found as natural casts (sensu Lockley 1991) on the underside of slabs of coarse-grained sandstone beds that were broken up and dumped on the adjacent beach during quarrying for clay. Today quarrying has ceased and the clay pit, now known as Pyritsøen, has become water-filled hindering in situ studies of the track-bearing layers.

New dinosaur tracks from the Bagå Formation

In the following, the institutional abbreviation MGUH means the Natural History Museum of Denmark.

Theropod tracks

The specimens are preserved as natural casts on the underside of a sandstone slab measuring 40×43 cm, with an average thickness of 11 cm (MGUH 29290). The slab was found by Stig Peberholm in 2010 and was lying loose on the beach at Pyritsøen (Fig. 1). The cast of the track is 25 cm long, 19 cm wide and about 3 cm deep. The track is mesaxonic, tridactyl and almost complete except for the tip of one toe (Fig. 2). The casts of the digits are long and terminate in impressions of sharp claws. A faint indication of digital pads is visible on the digits. The divarication angles between the middle and outer digits are 19° and 17°, giving at total divarication angle of 36° (Fig. 2B). The middle digit protrudes forward relative to the outer digits, and the

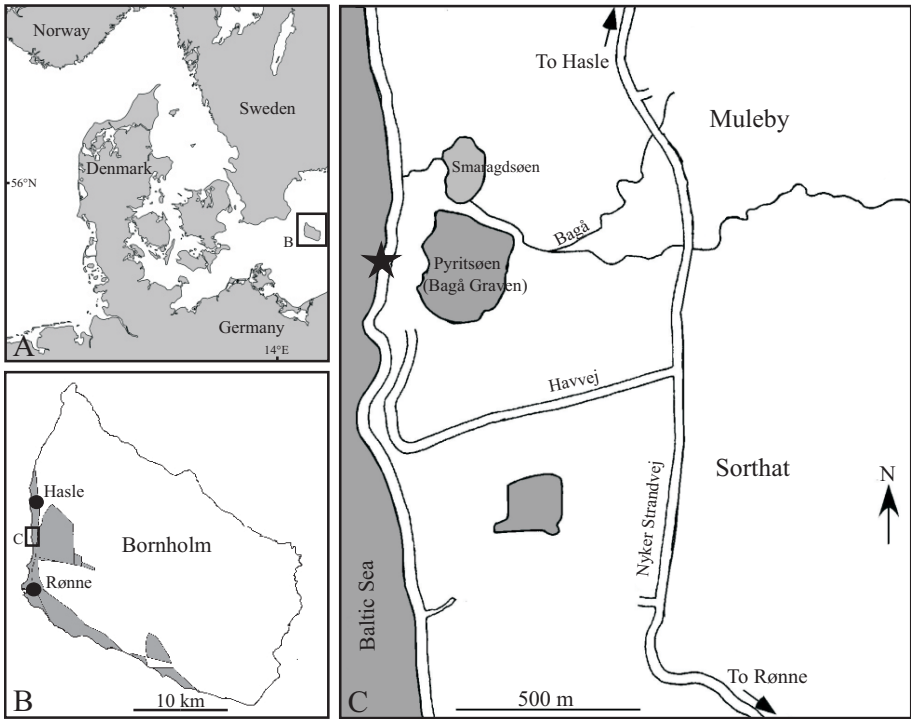

Fig. 1. Location maps. **A**, Bornholm is situated in the Baltic Sea south of Sweden. **B**, map of Bornholm with Mesozoic outcrops indicated in grey, based on Jensen & Hamann (1989). Rectangle marks the location of the Bagå Formation by Pyritsøen, between Hasle and Rønne. **C**, dinosaur track locality at Pyritsøen, sited near the villages of Muleby and Sorthat. Asterisk marks the position on the beach where the specimens were collected. After Milàn & Bromley (2005).

cast of its claw is slightly directed to the left. One of the outer digits extends further backwards than the middle digit and the outer digit on the opposite side (Fig. 2B). The track walls of the digit casts are sharply defined relative to the tracking surface. A second vaguely defined tridactyl track is present besides it, but due to its shallowness and poorly defined outline it is hard to get exact measurements from it.

Interpretation. Theropod tracks are generally longer than wide, with elongated narrow digits terminating in sharp claw impressions and a low divarication angle between the outer digits. The proximal pad impressions of digit IV extend further back than those of digits III and II, giving the tracks a distinct asymmetric 'heel' area. The claw impression of the middle digit III is in many cases directed inward toward the midline of the trackway (Moratalla *et al.* 1988; Thulborn 1990; Lockley 1991; Farlow *et al*. 2000). This identifies the new-found track as the cast of a left foot of a theropod dinosaur.

The hip height of the track maker can be estimated from the foot length. Thulborn (1990) estimated the hip height of theropods with a foot length less than 25 cm to be 4.5 times the foot length and for theropods

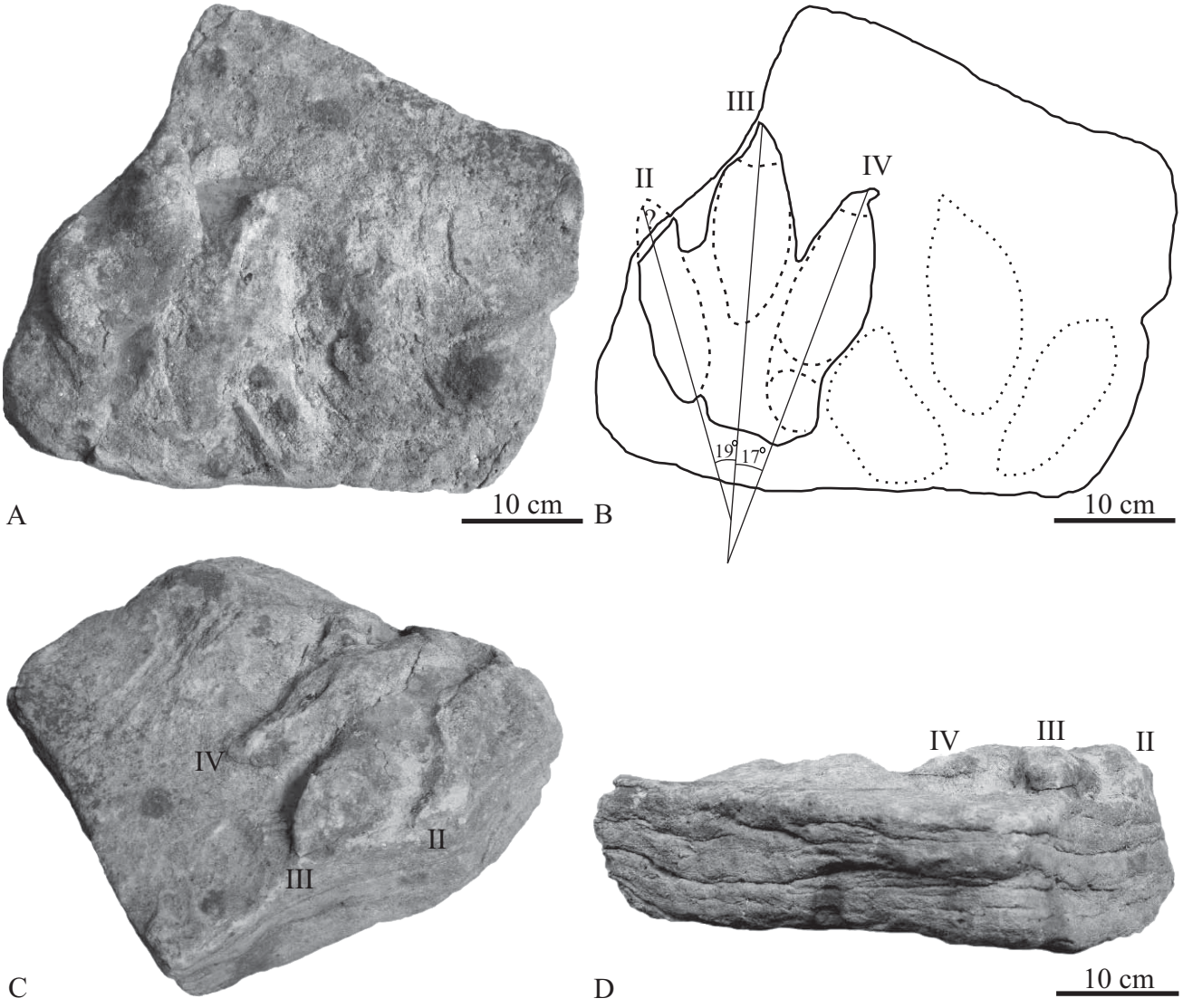

Fig. 2. Sandstone slab containing the natural cast of a well-preserved theropod track and a second poorly preserved track (MGUH 29290). **A**, the well-preserved track is complete except for the termination of digit II; the less well-preserved track is situated beside it. **B**, interpretative drawing of the block. Digital pads and the interpreted extension of digit II are indicated by broken lines. The second poorly defined track is indicated by dotted lines. **C**, oblique frontal view of the slab, with good view of the sharp claws of the digits. **D**, frontal view of the slab through the long axis of digit III. Notice the well-defined track walls of the digits, and that the cast of digit III is slightly deformed towards digit IV. The second less well-preserved track to the left has a much lower and poorly defined relief.

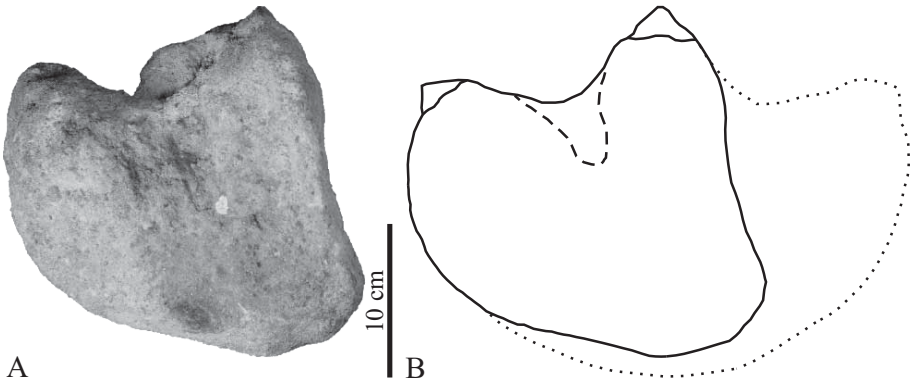

Fig. 3. Partial natural cast of a thyreophoran pes track (MGUH 29291). **A**, the preserved part comprises casts of two well-preserved digit impressions with short triangular claws. **B**, interpretative drawing of the specimen, where the missing digit is indicated by a broken line. The reconstruction is based on the shape of the thyreophoran ichnogenus *Stegopodus* (Gierlinski & Sabath 2008).

with a foot length in excess of 25 cm to be 4.9 times the foot length. As the specimen from Bornholm is 25 cm long, the estimated hip height of the animal is between 112 and 122 cm, and the estimated total body length is around 4 m. The cast of digit III is sideways deformed towards the right and the cast of digit II is deformed towards the left, as if the digits have diverged from the tracking surface to the bottom to the track. The outward deformation of digit III is similar to that found in Late Triassic, Early and Late Jurassic theropod tracks (Milàn *et al*. 2006), while the outward deformation of digit II is not typical of fossil tracks. However, this is observed in tracks of an extant emu, *Dromaius novaehollandiae*, when accelerating from a walk to a run. Here digits II and III diverge as the foot is pressed down through the sediment (Milàn 2006).

The second vaguely defined track on the slab is also tridactyl, and the general dimensions also suggest a theropod origin. However, the low relief and undefined digit impressions of the track, plus the fact that one of the digit impressions disappear below the other track, suggest the second track to be an undertrack (Milan & Bromley 2006, 2008) originating from a stratigraphically higher level.

Thyreophoran track

The specimen was found by Gunver Krarup Pedersen in 2005 and consists of an isolated, partial natural cast consisting of two well-preserved digit impressions (MGUH 29291). The cast is 19 cm wide and 21.5 cm long. A fresh break limits the cast along the outer edge of the right digit. The casts of the digits are well-defined, very short and broad and have preserved evidence of short triangular claws (Fig. 3). Between the two digits casts is preserved a sandstone cast of a part of the original tracking surface. Here the angle

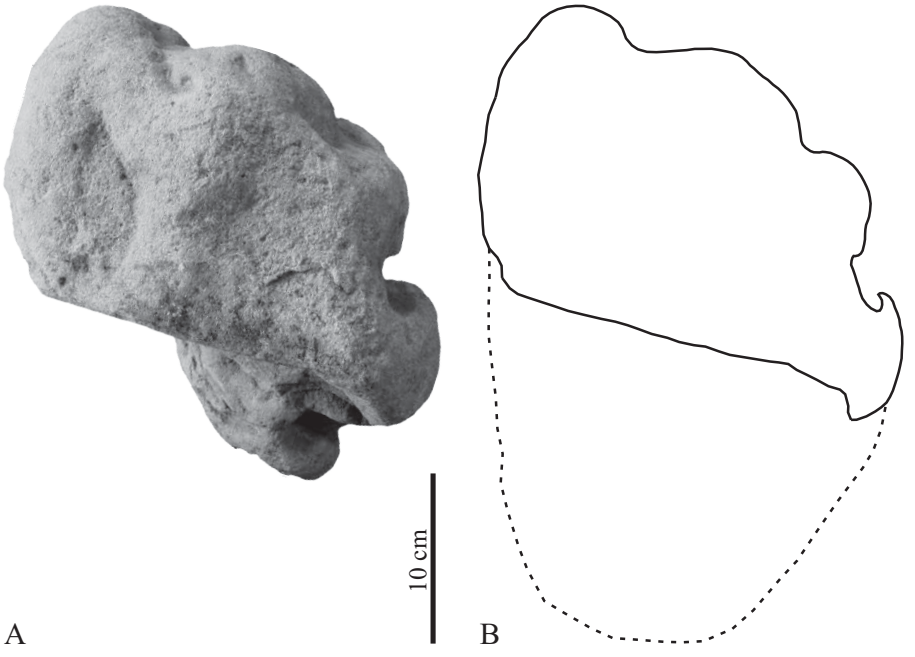

Fig. 4. Natural cast of a small sauropod track (MGUH 29292). **A**, only the front half with the casts of four short, blunt digits is preserved. **B**, interpretative drawing of the track, with the extent of the missing part indicated by a broken line. The reconstruction is based on an average of the two sauropod pes tracks from the same locality previously described by Milàn & Bromley (2005).

between the original tracking surface and the track walls is sharply defined.

Interpretation. The morphology of the two complete, broad digits with short triangular claws (Fig. 3) fits the morphology of the thyreophoran ichnogenus *Stegopodus* from the Middle Jurassic of Morocco and Upper Jurassic of Utah (Lockley & Hunt 1998; Gierlinski & Sabath 2008; Gierlinski *et al*. 2009). *Stegopodus* is tridactyl, with very short, broad and rounded digits, and assuming the cast is broken and the missing part represents another digit, the track can be interpreted as a *Stegopodus* specimen and thus represents a pes from a thyreophoran dinosaur. The sharply defined outline of the track and the well-defined casts of the claws demonstrate that it is a cast of a true track, and not an undertrack (Milàn & Bromley 2006, 2008).

Sauropod track

The specimen is a natural cast representing the front half of a track which is entaxonic and displays four short, blunt casts of digits (MGUH 29292). Without the missing part, the cast measures 17.5 cm in length and 31 cm at the widest across the digit impressions (Fig. 4). The impressions of the digits are outward rotated relative to the orientation of the foot. The cast has an average depth of 11 cm, deepest at the digit impressions.

Interpretation. The short blunt digits, and the shape of the cast, with the interpreted missing heel part added, are consistent with the morphology of a sauropod pes track, which is characterized by being elongated, entaxonic, and can display from three to five short

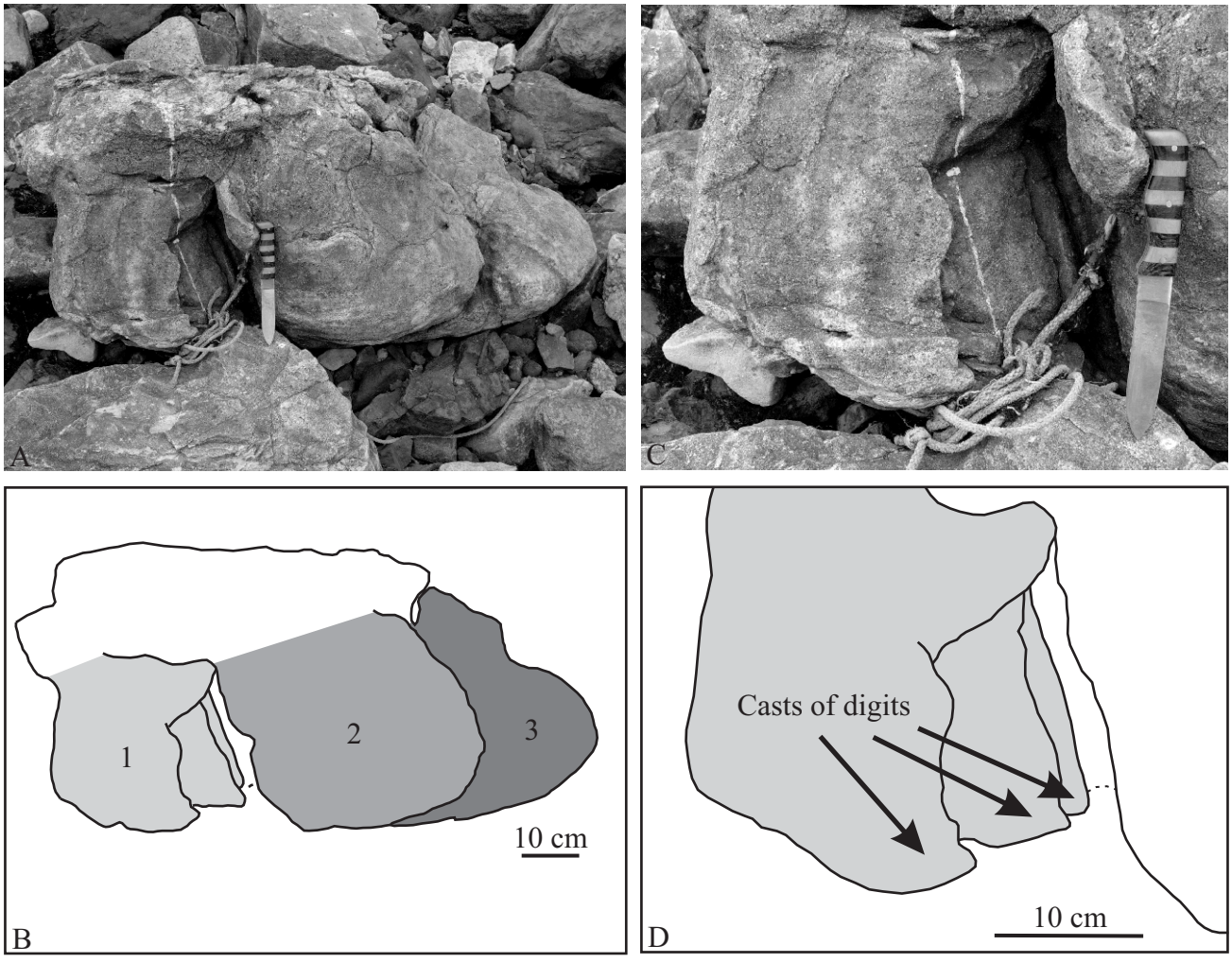

Fig. 5. Block with the natural casts of three partly superimposed tracks. **A**, photo of the whole block. The casts are seen from the side and are directed downwards. Two of the tracks only appear as indistinct, flat-bottomed casts. **B**, interpretative drawing of the block, with the three casts indicated by different shades of grey. Cast number 1 is better preserved than 2 and 3. **C**, close up photo of cast 1, showing the well-defined casts of three short, sharp digits being dragged deep down through the sediment. **D**, interpretative drawing of cast 1 with arrows indicating the casts of the digits. Scale bar on knife handle equals 10 cm.

outward rotated digit impressions (Thulborn 1990; Lockley 1991; Lockley *et al.* 1994; Wright 2005). The two previously described sauropod pes tracks (Milàn & Bromley 2005) measured respectively 68 and 69 cm in length and 48 an 45 cm in width, which gives a length/width ratio of approximately 1.5. When this ratio is applied to the new track it gives an estimated length of 46 cm, showing that the track originates from a significantly smaller individual.

Block with superimposed tracks

A large block consisting of natural casts of three partly superimposed tracks was found on the beach in 2005 (Fig. 5). Two of the track casts appear as featureless, flat-bottomed casts approximately 40 and 50 cm in diameter. A third cast of a track is better preserved, showing steep, well-defined trackwalls and the visible side of the cast shows clear casts of two short, sharp digits being dragged through the sediment (Fig. 5B). The outline of the track cast is elliptical, 28 cm long and approximately 40 cm wide. Unfortunately, the block broke up during transportation, destroying most of the preserved features and hindering further measurement. The remains of the block are stored at the visitor centre NaturBornholm.

Interpretation. The two poorly defined casts do not show any features that can easily attribute them to any specific dinosaur group, however, it is possible that they represent sauropod manus tracks. The morphology of the third, well-preserved track resembles the purported thyreophoran manus track described by Milàn & Bromley (2005), especially in its broad, elliptical outline and the short, but sharp digits. This track, however, is significantly larger, 28 cm long, than the track described by Milàn & Bromley (2005) which measured 15.5 cm in length and was 19.5 cm wide.

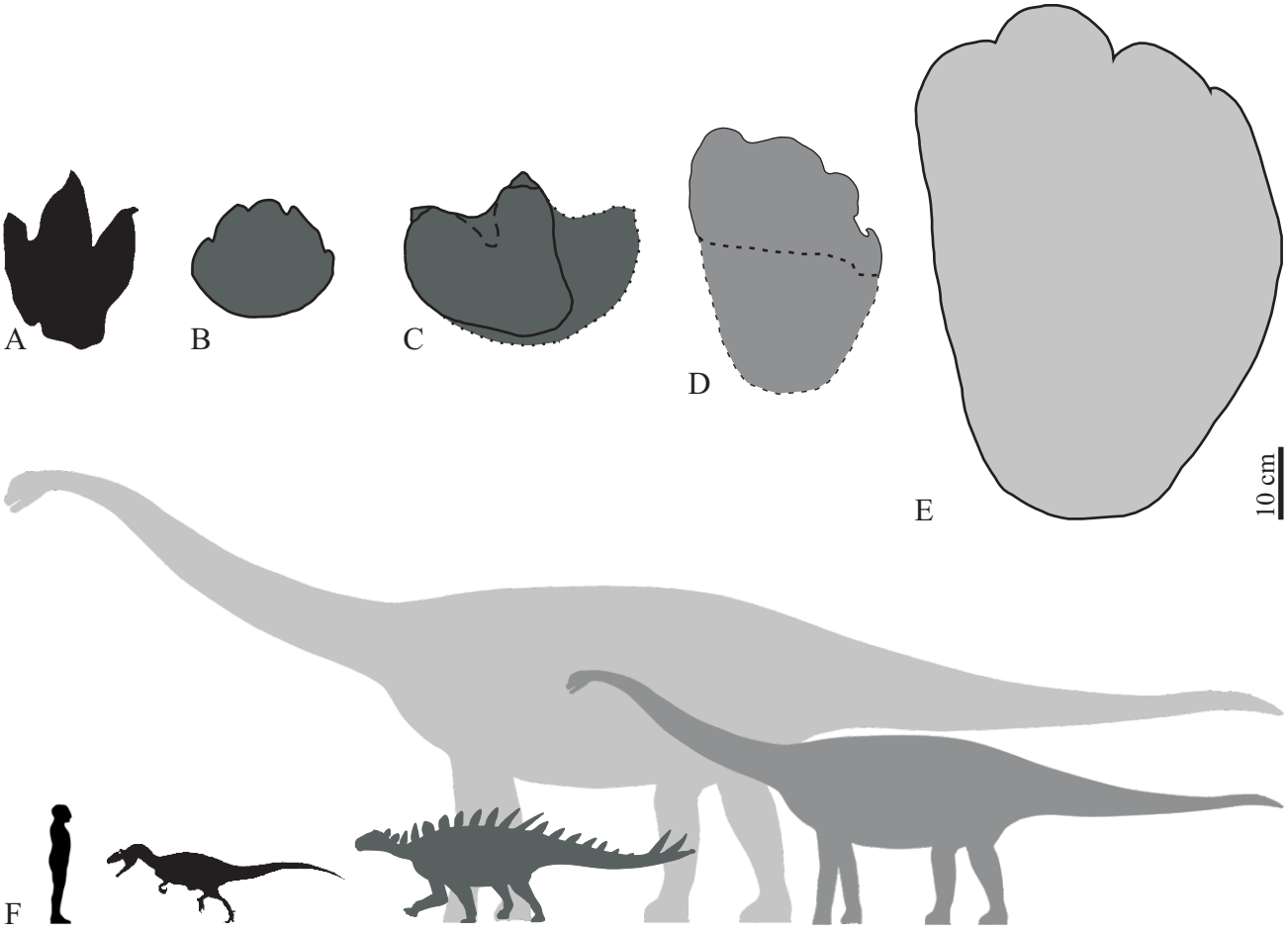

Fig. 6. Schematic representation of the different dinosaur tracks known from the Middle Jurassic Bagå Formation. All tracks reproduced to same scale. **A**, pes track from a medium-sized theropod with a footlength of 25 cm. **B**, manus track from a thyreophoran dinosaur, from Milàn & Bromley (2005). **C**, pes track from a thyreophoran dinosaur. **D**, small sauropod pes track. **E**, large sauropod pes track, from Milàn & Bromley (2005). **F**, silhouettes demonstrating the relative size of the track makers of the tracks with a human silhouette for scale. The Middle Jurassic dinosaur fauna on Bornholm comprised large and small sauropods, thyreophorans, and theropods. The colour of the silhouettes corresponds to the colour of the tracks.

Discussion

The Middle Jurassic is characterized by a worldwide scarcity of dinosaurian body fossils (Romano & Whyte 2003, 2010; Whyte *et al*. 2007, 2010). In Europe the scarcity of body fossils is especially pronounced and ichnological data thus become an important source of information about the dinosaurian diversity and biogeography during the Middle Jurassic. As an example, the Middle Jurassic Cleveland Basin of the Yorkshire coast has preserved one of the most diverse track assemblages from the Middle Jurassic of Europe, with abundant tracks from theropods, ornithopods, stegosaurians, sauropods, and crocodilians (Romano & Whyte 2003, 2010; Whyte *et al*. 2006, 2007, 2010). In contrast, skeletal material is only represented by a few scattered, often badly preserved bones (Romano & Whyte 2003; Whyte *et al*. 2010). Middle Jurassic sauropod tracks are known from Portugal (Santos *et al*. 1994), sauropod tracks together with tracks from theropods are known from Oxfordshire in England (Day *et al*. 2004), and theropod tracks and trackways are found on the Isle of Skye, Scotland (Clark *et al*. 2005). The sauropod and thyreophoran tracks from the Middle Jurassic of Bornholm (Milàn & Bromley 2005) are from a formation where, to date, no skeletal remains have been discovered. The new finds, although fragmentary, are important new information about the Middle Jurassic dinosaur fauna of Bornholm (Fig. 6) and add to our knowledge about the poorly known Middle Jurassic dinosaur distribution in Europe.

As in the case with the first tracks from the Bagå Formation (Milàn & Bromley 2005), the tracks described here are preserved as natural casts in coarse-grained fluvial sandstone. The sediment constituting the casts is horizontally laminated, demonstrating passive infill from suspension of an existing void. None of the original tracking surface is preserved in the new tracks, but Milàn & Bromley (2005) described distorted clay layers between the tracks found in 2004, originating from the original tracking surface, and palynological analysis of the sediment between the tracks confirmed that the tracks originated from the Bagå Formation (Milàn & Bromley 2005).

The track walls on all track casts are steep and well defined, and are at a steep angle to the surrounding sediment where present, showing that the natural casts are casts of the true tracks and not cast of undertracks (sensu Lockley 1991). Undertracks tend to be shallower, less well-defined and with a broader outline than the true tracks (Manning 2004; Milàn & Bromley 2006, 2008). The type of track preservation found on Bornholm is typical of tracks preserved in siliciclastic sediments and is very similar to tracks found in floodplain deposits in the Middle Jurassic of England (Romano & Whyte 2003; Whyte *et al*. 2007), the Upper Jurassic of Asturias, Spain (Garcia-Ramos *et al*. 2006; Lockley *et al*. 2008), the Upper Jurassic Morrison Formation of Utah (e.g. Lockley & Hunt 1995; Platt & Hasiotis 2006) and the Upper Jurassic Lourinhã Formation of Portugal (Mateus & Milàn 2010).

Conclusion

Three new dinosaur tracks are interpreted as tracks from a theropod, a thyreophoran, and a small sauropod. Together with previously described tracks, they are the only evidence of a Middle Jurassic dinosaur fauna of Bornholm that comprised theropods, small and large sauropods and at least one type of thyreophoran dinosaur (Fig. 6). This is important data, as the Middle Jurassic of Europe is characterized by a pronounced scarcity of skeletal material.

All the tracks from the Bagå formation are found as natural casts on the underside of blocks of fluvial sandstone that were dumped on the beach from the nearby Hasle Klinkefabrik's abandoned clay pit, now flooded and named Pyritsøen. A systematic investigation and excavation of the sandstone blocks from the clay pit might expose more tracks that add can further to the record.

Acknowledgements

This study was supported by Danish National Science Research Council. I am grateful to Stig Peberholm for finding and securing the theropod track by bringing it to the visitor centre NaturBornholm, and to Gunver Krarup Pedersen who found the thyreophoran track and kindly placed it at my disposition. Peter Haase, Jens Kofoed, Finn Hansen, and all the employees at NaturBornholm are thanked for their hospitality and cooperation. Gerard Gierlinski provided helpful discussions and references to literature, Finn Surlyk kindly read and made critical comments on an early version of the manuscript, and Christopher Alan Halewood helped to improve the language. The critical and constructive reviews of Martin A. Whyte and Mike Romano greatly helped to improve the manuscript.

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. München: Verlag Dr. Friedrich Pfeil.

Bonde, N. & Christiansen, P. 2003: New dinosaurs from Denmark. Comptes Rendus Palevol 2, 13–26.

Bölau, E. 1952: Neue Fossilfünde 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.

Christiansen, P. & Bonde, N. 2003: The first dinosaur from Denmark. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 227, 287–299.

Clark, N.D.L., Ross, D.A. & Booth, P. 2005: Dinosaur tracks from the Kilmalaug Formation (Bathonian, Middle Jurassic) of Score Bay, Isle of Skye, Scotland, UK. Ichnos 12, 93–104.

Day, J.J., Norman, D.B., Gale, A.S., Upchurch, P. & Powell, H.P. 2004: A Middle Jurassic dinosaur Trackway site from Oxfordshire, UK. Palaeontology 47, 319–348.

Farlow, J.O., Gatesy, S.M., Holtz, T.R., Hutchinson, J.R. & Robinson, J-M. 2000: Theropod locomotion. American Zoologist 40, 640–663.

Garcia-Ramos, J.C., Piñuela, L. & Lires, J. 2006: Atlas del Jurásico de Asturias. Ediciones Nobel, Oviedo. 225 pp.

Gierlinski, G. & Ahlberg, A. 1994: Late Triassic and Early Jurassic dinosaur footprints in the Höganäs Formation of southern Sweden. Ichnos 3, 99–105.

Gierlinski, G. & Sabath, K. 2008: Stegosaurian footprints from the Morrison Formation of Utah and their implication for interpreting other ornithischian tracks. Oryctos 8, 29–46.

Gierlinski, G., Menducki, P., Janiszewska, K., Wicik, I. & Boczarowski, A. 2009: A preliminary report on dinosaur track assemblages from the Middle Jurassic of the Imilchil area, Morocco. Geological Quarterly 53, 477–482.

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.

Gry, H. 1969: Megaspores from the Jurassic of the island of Bornholm, Denmark. Meddelelser fra Dansk Geologisk Forening 19, 69–89.

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.

Lindgren, J., Currie, P.J., Siverson, M., Rees, J., Cederström, P., & Lindgren, F. 2007: The first neoceratopsian dinosaur remains from Europe. Palaeontology 50, 929–937.

Lindgren, J., Currie, P.J., Rees, J., Siverson, M., Lindström, S. & Alwmark, C. 2008: Theropod dinosaur teeth from the lowermost Cretaceous Rabekke Formation on Bornholm, Denmark. Geobios 41, 253–262.

Lockley, M. 1991: Tracking Dinosaurs. 238 pp. New York: Cambridge University Press.

Lockley, M. & Hunt, A.P. 1995: Dinosaur tracks and other fossil footprints of the Western United States. 338 pp. New York: Columbia University Press.

Lockley, M.G. & Hunt, A.P. 1998: A probable stegosaur track from the Morrison Formation of Utah. Modern Geology 23, 331–342.

Lockley, M.G., Farlow, J.O. & Meyer, C.A. 1994: *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. Gaia 10, 135–146.

Lockley, M.G., Garcia-Ramos, J.C., Lires, J., Piñuela, L. & Avanzini, M. 2008: A review of vertebrate track assemblages from the Late Jurassic of Asturias, Spain with comparative notes on coeval ichnofaunas from the western USA: implications for faunal diversity in association with siliciclastic facies assemblages. Oryctos 8, 53–70.

Manning, P. 2004: A new approach to the analysis and interpretation of tracks: examples from the dinosauria. In: McIlroy, D. (ed.): The application of ichnology to palaeoenviromental and stratigraphic analysis. Geological Society, London, Special Publication 228, 93–123.

Mateus, O. & Milàn, J. 2010: A diverse Upper Jurassic dinosaur ichnofauna from Central-west Portugal. Lethaia 43, 245–257.

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. Geological Survey of Denmark and Greenland Bulletin 1, 147–216.

Milàn, J. 2006: Variations in the morphology of emu (*Dromaius novaehollandiae*) tracks, reflecting differences in walking pattern and substrate consistency: ichnotaxonomical implications. Palaeontology 49, 405–420.

Milàn, J. & Bromley, R.G. 2005: Dinosaur footprints from the Middle Jurassic Bagå Formation, Bornholm, Denmark. Bulletin of the Geological Society of Denmark 52, 7–15.

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

Milàn, J. & Bromley, R.G. 2008: The impact of sediment consistency on track and undertrack morphology: experiments with emu tracks in layered cement. Ichnos 15, 18–24.

Milàn, J. & Gierlinski, G. 2004: A probable thyreophoran (Dinosauria, Ornithischia) footprint from the Upper Triassic of southern Sweden. Bulletin of the Geological Society of Denmark 51, 71–75.

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

Moratalla, J.J., Sanz, J.L. & Jimenez, S. 1988: Multivariate analysis on Lower Cretaceous dinosaur footprints: Discrimination between ornithopods and theropods. Geobios 21, 395–408.

Nielsen, L.H., Petersen, H.I., Dybkjær, K. & Surlyk, F. 2010: Lake-mire deposition, earthquakes and wildfires along a basin margin fault; Rønne Graben, Middle Jurassic, Denmark. Palaeogeography, Palaeoclimatology, Palaeoecology 292, 103–126.

Noe-Nygaard, N. & Surlyk, F. 1988: Washover fan and brackish bay sedimentation in the Berriasian–Valanginian of Bornholm, Denmark. Sedimentology 35, 197–217.
Noe-Nygaard, N., Surlyk, F. & Piasecki, S., 1987: Bivalve mass mortality caused by toxic dinoflagellate blooms in a Berriasian–Valanginian lagoon, Bornholm, Denmark. Palaios 2, 263–273.
Platt, B. & Hasiotis, S.T. 2006: Newly discovered sauropod dinosaur tracks with skin and foot-pad impressions from the Upper Jurassic Morrison Formation, Bighorn Basin, Wyoming, U.S.A. Palaios, 21, 249–261.
Pleijel, C. 1975: Nya dinosauriefotspår från Skånes Rät–Lias. Fauna och Flora 3, 116–120.
Rees, J., Lindgren, J. & Evans, S.E. 2005: Amphibians and small reptiles from the Berriasian Rabekke Formation on Bornholm, Denmark. GFF 127, 233–238.
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.
Romano, M. & Whyte, M.A. 2010: Crocodilian and other non-dinosaurian tracks and trackways from the Ravenscar Group (Middle Jurassic) of the Cleveland Basin, Yorkshire, UK. New Mexico Museum of Natural History and Science Bulletin 51, 69–81.
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.
Schwarz-Wings, D., Rees, J. & Lindgren, J. 2009: Lower Cretaceous Mesoeucrocodylians from Scandinavia (Denmark and Sweden). Cretaceous Research 30, 1345–1355.
Surlyk, F., Milàn, J. & Noe-Nygaard, N. 2008: Dinosaur tracks and possible lungfish aestivation burrows in a shallow coastal lake; lowermost Cretaceous, Bornholm, Denmark. Palaeogeography, Palaeoclimatology, Palaeoecology 231, 253–264.
Thulborn, T. 1990: Dinosaur Tracks. 410 p. London: Chapman & Hall.
Whyte, M.A., Romano, M. & Watts, W. 2010: Yorkshire dinoasaurs: a history in two parts. In: Moody, R.T.J., Buffetaut, E., Naish, D. & Martill, D.M. (eds). Dinosaurs and Other Extinct Saurians: A Historical Perspective. Geological Society, London, Special Publication 343, 189–207.
Whyte, M.A., Romano, M. & Elvidge, D.J. 2007: Reconstruction of Middle Jurassic dinosaur- dominated communities from the vertebrate ichnofauna of the Cleveland Basin of Yorkshire, UK. Ichnos 14, 117–129.
Whyte, M.A., Romano, M., Hudson, J.G., & Watts, W. 2006: Discovery of the largest theropod dinosaur tracks known from the Middle Jurassic of Yorkshire. Proceedings of the Yorkshire Geological Society 56, 77–80.
Wright, J.L. 2005: Steps in understanding sauropod biology. In: Curry Rogers, K.A. & Wilson, J.A. (eds): The Sauropods: Evolution and Paleobiology, 252–285. Berkeley: University of California Press.