



An enigmatic, diminutive theropod footprint in the shallow marine Pliensbachian Hasle Formation, Bornholm, Denmark

JESPER MILÀN AND FINN SURLYK

LETHAIA



Milàn, J. & Surlyk, F. 2015: An enigmatic, diminutive theropod footprint in the shallow marine Pliensbachian Hasle Formation, Bornholm, Denmark. *Lethaia*, Vol. 48, pp. 429–435.

A well-preserved three-toed footprint, measuring 34 mm in length from a very small predatory dinosaur with an estimated hip height of 153 mm and a total body length around 50 cm including tail, is reported from the type section of the marine Lower Jurassic (Pliensbachian), Hasle Formation on the Danish island of Bornholm in the Baltic Sea. The morphology of the footprint is similar to the ichnogenus *Stenonyx* Lull 1904 from the contemporaneous Pliensbachian Szydłówek site in Poland. Apart from the Polish material, footprints from diminutive dinosaurs are rare and reported from few other localities around the world. The occurrence of a diminutive dinosaur footprint in a shallow marine sandstone is enigmatic. The well-defined morphology of the footprint, together with the very small size of the trackmaker, excludes the possibility that the track was emplaced by a swimming or wading animal. At the type locality where the footprint was found the formation consists of ferruginous coarse siltstone and very fine-grained sandstone, showing hummocky and swaley cross-stratification and rare large-scale trough cross-bedding and planar lamination. Deposition took place mainly in the upper shoreface in a storm-dominated environment 1 km west of the N–S-oriented faulted coastline. The formation becomes thinner and finer grained with heterolithic intercalations towards the south, indicating coast-parallel transport in this direction. The extreme uniformity in sedimentary facies as seen in two nearby fully cored boreholes shows that the accommodation space created by rapid subsidence along the fault was continuously filled in to upper shoreface level by rapid long-shore sediment influx from the north. In quiet periods with easterly winds and extreme low-water low tide, the small dinosaur creating the newly found footprint is interpreted to have walked in shallow beach pools, thus explaining the strange occurrence of the footprint in a marine deposit. □ *Bornholm, dinosaur track, ichnology, Lower Jurassic, marine sandstone, Pliensbachian, Stenonyx.*

Jesper Milàn [jesperm@oesm.dk], Geomuseum Faxe/Østsjællands Museum, Østervej 2 DK-4640 Faxe, Denmark; Finn Surlyk [Finns@ign.ku.dk], Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10DK-1350 Copenhagen K, Denmark; manuscript received on 09/05/2014; manuscript accepted on 29/09/2014.

The Mesozoic record of terrestrial vertebrates from southern Scandinavia is scarce with only a few localities known from southern Sweden and the Danish island Bornholm. The Upper Triassic–Lower Jurassic (Rhaetian–Hettangian) Höganäs Formation in southern Sweden has yielded large tracks and trackways of theropods and possible thyreophorean dinosaurs as well as sparse skeletal remains (Börlau 1952, 1954; Pleijel 1975; Ahlberg & Siverson 1991; Gierlinski & Ahlberg 1994; Milàn & Gierlinski 2004).

On Bornholm, dinosaur tracks are reported from the Lower Jurassic (Hettangian) Sose Bugt Member of the Rønne Formation (Clemmensen *et al.* 2014). The Middle Jurassic Bagå Formation has yielded tracks from large and small sauropods, thyreophoreans and theropods preserved as natural casts of sandstone (Milàn & Bromley 2005; Milàn 2011).

A rich fauna of micro-vertebrates including crocodiles, dinosaurs, birds, turtles, amphibians, sharks, other fish and mammals has been retrieved by screen washing of samples from the lowermost Cretaceous Rabekke Formation, in the coastal cliff east of Arnager (Lindgren *et al.* 2004, 2008; Rees *et al.* 2005; Schwarz-Wings *et al.* 2009), and large dinosaur tracks up to 70 cm in length associated with aestivation burrows are exposed in cross-section (Surlyk *et al.* 2008). Inland quarries in the overlying Jydegård Formation have produced remains of dinosaurs, turtles, crocodiles, fish scales, shark teeth and coprolites (Noe-Nygaard *et al.* 1987; Noe-Nygaard & Surlyk 1988; Bonde & Christiansen 2003; Christiansen & Bonde 2003; Bonde 2004, 2012; Milàn *et al.* 2012). Finally, remains of a neoceratopsian dinosaur have been found in Upper Cretaceous deposits at Åsen in the Kristianstad Basin, southern Sweden (Lindgren *et al.* 2007).

Recently, a slab with a small theropod footprint was found at the type locality of the marine Lower Jurassic (Pliensbachian) Hasle Formation on the island of Bornholm in the Baltic Sea. Previously, the formation has yielded skeletal remains of marine reptiles and sharks in addition to a rich invertebrate fauna found mainly in the southern more mud-dominated part of the succession (Surlyk & Noe-Nygaard 1986; Milàn & Bonde 2001; Donovan & Surlyk 2003; Smith 2008; Bonde 2012). The slab with the footprint is now in the collection of The Natural History Museum of Denmark (MGUH – 30889). The aim of this study is to interpret the enigmatic and rare occurrence of a footprint of a diminutive dinosaur in a marine deposit.

Geological setting, sedimentology and stratigraphy

The island of Bornholm in the Baltic Sea is a complex fault block situated adjacent to the N–S-oriented Rønne Graben forming a N–S-oriented dogleg in the NW–SE-trending Sorgenfrei–Tornquist Zone, which limits the Danish Basin from the Baltic Shield. This zone exerted a major role on sedimentation throughout the Mesozoic, and the eastern border fault is located a short distance inland from the west coast of Bornholm (Fig. 1). During much of the Jurassic the N–S and WNE–ENE-trending faults limiting the Bornholm horst controlled the position of the coastlines. During the Pliensbachian, the western coastline was thus controlled by the eastern N–S-oriented border fault of the Rønne Graben. The type section and track locality is located circa 1 km to the west of the fault, which controlled the position of the coastline during deposition (Surlyk & Noe-Nygaard 1986).

The Hasle Formation is about 135 m thick in the type area, and two cored boreholes at nearby localities penetrated 118 and 65 m of the lowest and uppermost parts of the formation, respectively, showing the same lithology as the 15-m-thick succession exposed in a low coastal cliff (Koppelhus & Nielsen 1994; Michelsen *et al.* 2003). The cored succession consists of hummocky and swaley cross-stratified coarse-grained siltstone and very fine-grained sandstone. A few levels show trough cross-bedding or planar lamination. The erosion surfaces at the base of the individual swales are draped with pebble lags with clasts of basement rocks, poorly preserved gastropods and bivalves, and rare plesiosaur teeth and bones (Surlyk & Noe-Nygaard 1986). Early Jurassic subsidence rates were high, as reflected

by the up to 135-m-thick lower Pliensbachian succession. However, sedimentation managed to keep pace with creation of new accommodation space, which was continuously filled in to upper shoreface and occasionally foreshore level. Deposition was strongly storm-influenced as indicated by the dominance of hummocky and swaley cross-stratified fine-grained sandstone, and mudstones are absent in the type area (Surlyk & Noe-Nygaard 1986; Koppelhus & Nielsen 1994; Michelsen *et al.* 2003; Nielsen 2003). The high-energy conditions along the fault-controlled coast explain why the accommodation space only rarely was infilled with sediments from above shoreface level as more proximal sediments were eroded during major storms (Fig. 2).

Fossiliferous clays are intercalated towards the south along the fault zone, and a rich early Pliensbachian fauna including 11 ammonite species has been found in clay pits in the town of Rønne and close to the south coast along the stream Stampe Å (Malling & Grönwall 1909; Malling 1911, 1914, 1920; Höhne 1933; Donovan & Surlyk 2003). Malling (1911) listed a marine fauna with 38 species of bivalves, gastropods, scaphopods, belemnites, ammonites, *Hybodus* and plesiosaur teeth and rib bones from the low coastal cliff of the type locality south of Hasle. The ammonites indicate the presence of all subzones of the lower Pliensbachian *Uptonia jamesoni* Zone together with the *Acanthopleuroceras valdani* Subzone of the overlying *Tragophylloceras ibex* subzone (Donovan & Surlyk 2003).

A theropod footprint from the marine Hasle Formation

A small slab, 13 × 7 cm, of the marine Hasle Formation containing a small tridactyl footprint (MGUH – 30889), was found by Marcel Tomiola in January 2014, at the beach at the type section of the Hasle Sandstone south of Hasle harbour, in the southern end of the exposure (N55° 10' 39.369"–E14° 42' 9.548"). Due to the small size of the slab, no further footprints from the same animal are preserved. The slab is clearly derived from the succession exposed at the cliff which extends about 1 km from the north to the south.

A prominent erosion surface draped with pebbles separates two types of fine-grained sandstone with different diagenetic histories (Larsen & Friis 1991). The sediments below the surface are poorly cemented and contain concretionary siderite, whereas the overlying sandstone is hard and cemented by various carbonate minerals. The

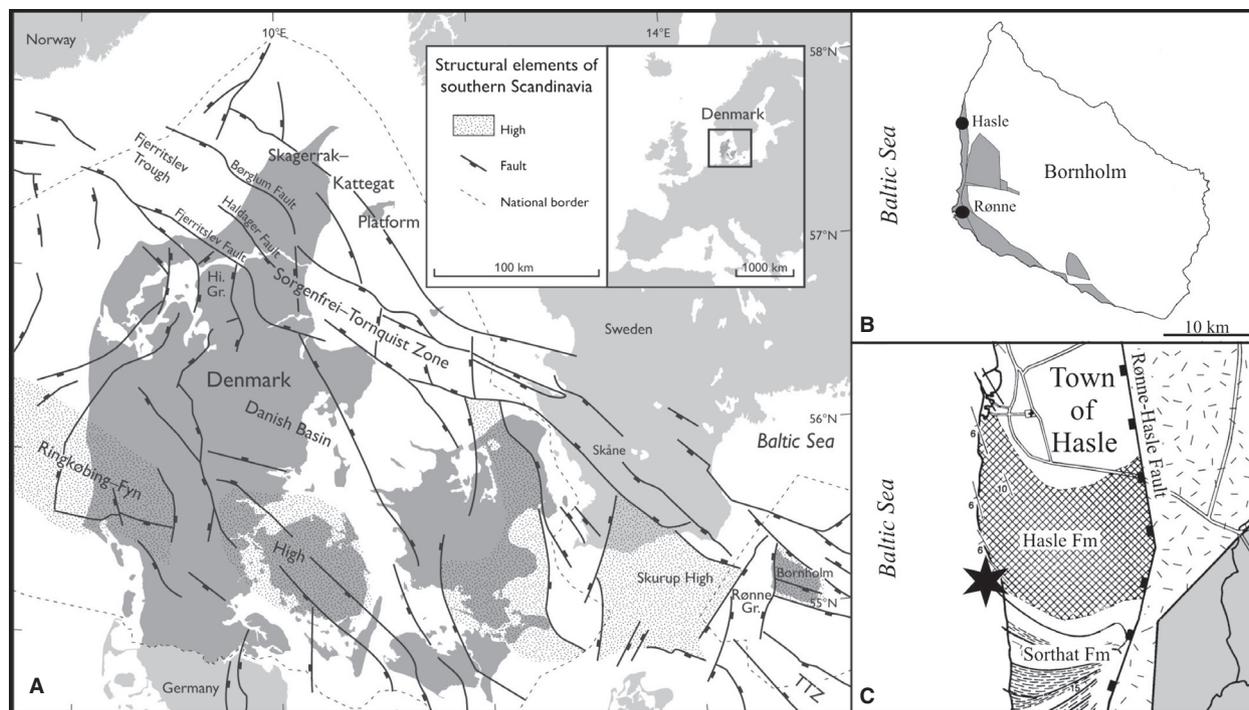


Fig. 1. A, location map showing the main structural features in the area around Bornholm and southern Scandinavia. B, Mesozoic outcrops are found along the south-western margin of Bornholm, indicated by grey. C, the type locality of the Pliensbachian Hasle Formation is situated immediately south of the town Hasle, approximately 1 km west of the main border fault, limiting the Rønne Graben to the east. The dinosaur footprint was found in the southern part of the exposure (indicated by asterisk), approximately 1 km south of Hasle Harbour. Modified from Nielsen *et al.* (2010).

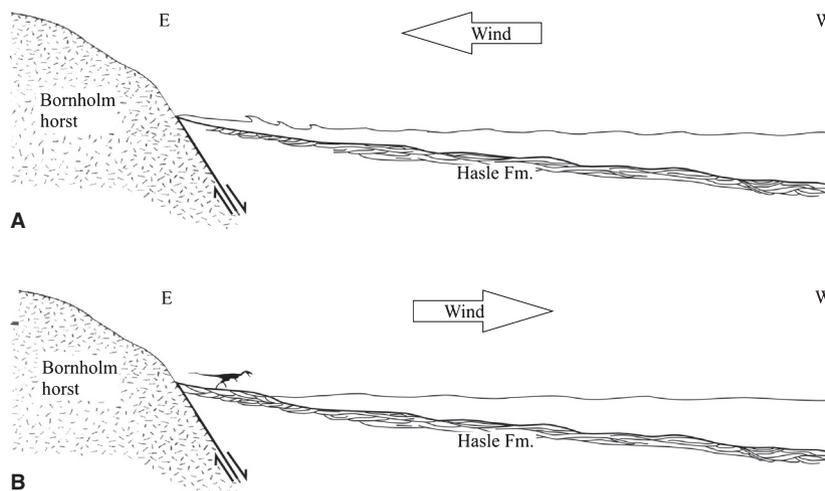


Fig. 2. Reconstruction of the depositional conditions of the Pliensbachian Hasle Formation. A, the normal depositional conditions for the shallow marine Hasle Formation. B, during times of high sediment influx, combined with low tide and easterly wind, the upper shoreface sand may become subaerially exposed, allowing animals to venture out on the surfaces. Modified from Surlyk & Noe-Nygaard (1986).

hardness, lithology and discovery site show that the footprint is derived from the latter unit. This unit is estimated to correlate with a depth of roughly 90–100 m in the Hasle-1 borehole, which penetrated the lower part of the Hasle Formation and the top of the underlying Rønne Formation

(Koppelhus & Nielsen 1994; Michelsen *et al.* 2003; Nielsen *et al.* 2003).

The track is preserved in concave epirelief, that is a natural impression of the foot in the surface of the slab. The track is tridactyl, mesaxonic, with clear impressions of all three digits (Fig. 3A). The dimen-

sions of the track are 34 mm along the length axis of the middle digit and 25 mm at the widest point between the outer digits. The impressions of the digits are long and slender, terminating in impressions of short triangular claws. A faint indication of digital pads is visible on the digits. The divarication angle between the outer and middle digits is 20° and 23° , respectively, giving a total divarication angle of 43° (Fig. 3B). The middle digit protrudes forward relative to the outer digits, and the impression of its claw is slightly directed to the left. A shallow rim of laterally displaced sediment is present around the impressions of the digits (Fig. 3C).

Discussion and conclusions

Theropod footprints are generally longer than wide, with elongated narrow digits terminating in sharp claw impressions and a low divarication angle

between the outer digits. The claw impression of the middle digit III in many cases is directed inward towards the midline of the trackway (Moratalla *et al.* 1988; Thulborn 1990; Lockley 1991; Farlow *et al.* 2000). This identifies the footprint as the impression from the right foot of a theropod dinosaur. The Early Jurassic, Pliensbachian age of the footprint excludes the possibility that the footprint could be from a bird, as the earliest birds first appear in the Middle–Late Jurassic, approximately 30 million years later (Godefroit *et al.* 2013). The foot length of bipedal dinosaurs relates closely to the hip height of the animal. Thulborn (1990) calculated the hip height of theropod dinosaurs with a foot length <25 cm to be 4.5 times the foot length and for theropods with a foot length in excess of 25 cm to be 4.9 times the foot length. With a foot length of 34 mm, the hip height of the track maker is estimated to 153 mm and an estimated total length of the animal about 50 cm including tail. Small sized non-avian

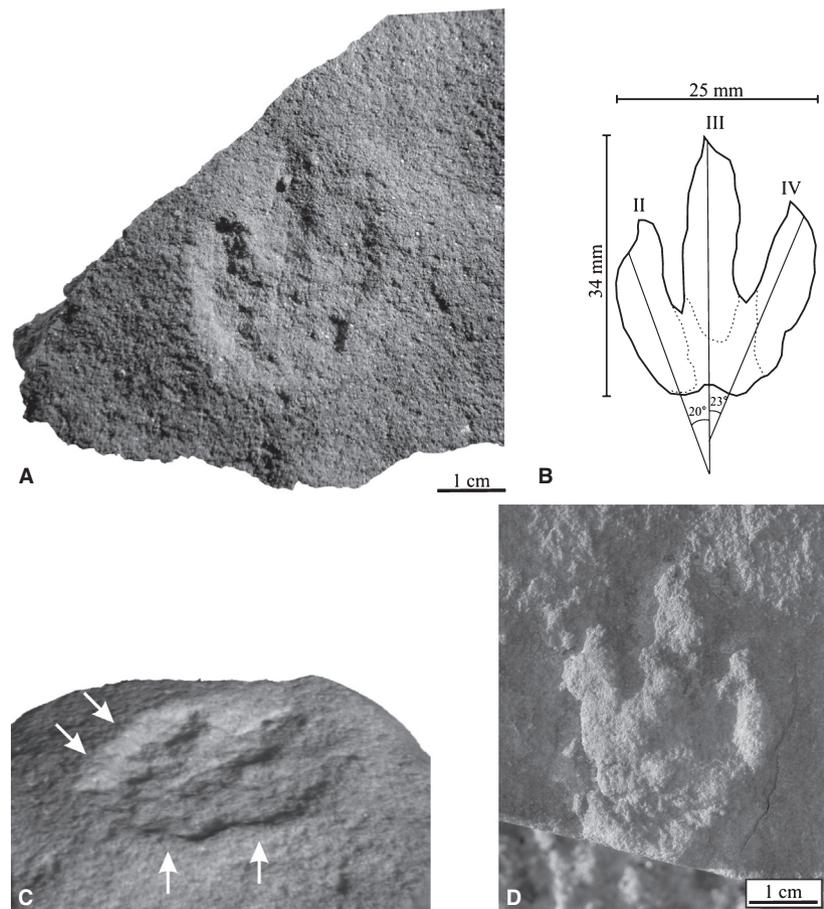


Fig. 3. A, the small theropod footprint (MGUH – 30889) as it appears on the surface of the slab of sandstone from the Hasle Formation. B, interpretative drawing of the track, with measurements and divarication angles indicated. C, 3D photogrammetry model shown in oblique view to show the footprint with the raised rims of displaced sediment indicated by arrows. Model by Oliver Wings. D, theropod footprint of the ichnogenus *Stenonyx* from the Pliensbachian Drzewica Formation of Szydłówek, Poland. Photograph by Gerard Gierlinski.

theropod footprints are only reported from a few other localities around the world and differ significantly in size and morphology from each other. The ichnospecies *Minisauripus chuanzhuensis* Zhen *et al.* 1995, described from the Lower Cretaceous of China (Barremian–Albian) and Korea (Aptian–Albian), is typically between 25 and 40 mm in length, with sub-parallel, broad digits and a relative short digit III (Zhen *et al.* 1995; Lockley *et al.* 2008). *Grallator emeiensis* Zhen *et al.* 1995, which is of similar length, was found together with *Minisauripus* (Zhen *et al.* 1995), but has a wider angle approaching 80° between the outer digits, and a very elongated middle digit III (Zhen *et al.* 1995; Lockley *et al.* 2008). At the St. George Dinosaur Discovery Site at Johnson Farm in Utah, USA, several diminutive grallatorid footprints and trackways are recorded in a large exposure of the Upper Triassic–Lower Jurassic Moenave Formation (Milner *et al.* 2006). These footprints are 20 to 50 mm long and show morphologies in between *G. emeiensis* and *Minisauripus* Zhen *et al.* 1995. The ichnogenus *Wildeichnus* Casamiquela 1964 from the Middle Jurassic of Argentina has slender digits, an elongated middle digit, and typically a high angle of divarication between the outer digits (Casamiquela 1964; de Valais 2011). The footprint from the Hasle Formation differs from *Wildeichnus* and *Grallator emeiensis* in having broader digits and low angle of divarication between the outer digits, and a relatively short middle digit. The relatively long digit IV is similar to *Minisauripus*, but in *Minisauripus*, digits are usually less divaricated and nearly parallel. *Stenonyx* Lull 1904, *sensu lato* (Gierlinski *et al.* 2004), described from the Early Jurassic Soltków (Hettangien) and Szydłówek (Pliensbachian) track sites in the Holy Cross Mountains, southern Poland, shows an identical morphology to the specimen from the Hasle Formation (Fig. 3D; Gerard Gierlinski, personal communication 2014), until further specimens are found, we tentatively refer the specimen from Hasle to the ichnogenus *Stenonyx*. Southern Sweden, Bornholm and Poland were contiguous during the Early Jurassic (e.g. Ziegler 1990), and dinosaurs could thus freely roam this large area.

One possible explanation for the footprint in a shallow marine sandstone is that it could have been emplaced by a swimming or bottom-walking animal. Tracks made by swimming theropods scratching the bottom are well known (e.g. Ezquerro *et al.* 2007; Milner *et al.* 2007) and differ significantly in morphology from walking tracks in being extremely elongated, only consisting of imprints from the distal parts of the digits, and mostly consisting of curved parallel scratch marks created by the digits being dragged along the bottom substrate. The track

from the Hasle Formation is well-defined with all parts evenly impressed into the substrate, including the ‘heel’ area, indicating that it is a normal walking track. The diminutive size of the trackmaker, being only 15 cm over the hips, would require a water depth of <15 cm in order for the foot to be emplaced firmly on the bottom. No invertebrate trace fossils have ever been described from the type locality of the Hasle Formation, making an invertebrate origin of the structure unlikely.

The occurrence of a footprint of a small predator dinosaur in a marine sandstone is enigmatic. The mainly swaley cross-stratified nature of the succession points to deposition in the upper shoreface. However, the position of the type locality 1 km west of the border fault, which controlled the position of the coastline makes it likely that the actual beach area prograded away from the fault zone to the area of the type section during times of high sediment influx. A few beds with planar lamination thus occur in the upper part of the formation in the cores and are interpreted as deposited in a foreshore environment. Very low tide associated with strong winds from the east could have caused short-lived emergence of the inner part of the upper shoreface and formation of small very shallow beach pools (Fig. 2B). Following change in wind direction and associated rise in water level fine sand was washed into the pools and draped the footprints. In this way, the enigmatic occurrence of a footprint of a small dinosaur in a marine sediment can be explained. The footprint was made by the smallest non-avian theropod found in Scandinavia. The morphology is consistent with footprints found at a contemporaneous succession at Szydłówek Poland, reflecting the connection between the Danish and Polish faunas during the Early Jurassic. It is an important addition to the scarce Scandinavian record of Mesozoic vertebrate fossils and to the similarly scarce fossil record of footprints of diminutive dinosaurs worldwide.

Acknowledgements. – The slab with the footprint was found by Marcel Tomiola, Bornholm, who kindly brought it to the attention of the staff at NaturBornholm. Gerard Gierlinski is thanked for constructive discussion and photographs of Polish tracks. Oliver Wings kindly produced a 3D photogrammetry model of the track. We thank Lars Henrik Nielsen for critical reading and suggestions to an early manuscript version, and the reviewers Spencer G. Lucas and Octavio Mateus for constructive comments.

References

- Ahlberg, A. & Siverson, M. 1991: Lower Jurassic dinosaur footprints in Helsingborg, southern Sweden. *Geologiska Föreningens i Stockholm Förhandlingar* 113, 339–340.

- Böläu, E. 1952: Neue Fossilfunde aus dem Rhät Schonens und ihre paläogeographisch-ökologische Auswertung. *Geologiska Föreningens i Stockholm Föreläsningar* 74, 44–50.
- Böläu, E. 1954: The first finds of dinosaurian skeletal remains in the Rhaetic-Liasic of N. W. Scania. *Geologiska Föreningens i Stockholm Föreläsningar* 76, 501–502.
- 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. 2012: Danish dinosaurs: a review. In Godefroit, P. (ed.): *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems*, 434–451. Indiana University Press, Bloomington, 464 pp.
- Bonde, N. & Christiansen, P. 2003: New dinosaurs from Denmark. *Comptes Rendus Palevol* 2, 13–26.
- Casamiquela, R.M. 1964: *Estudios ichnológicos. Problemas y métodos de la icnología con aplicación al estudio pisadas mesozoicas (reptilia, mammalia) de la Patagonia*. Colegio Industrial Pío IX, Buenos Aires, Argentina, 229 pp.
- Christiansen, P. & Bonde, N. 2003: The first dinosaur from Denmark. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 227, 287–299.
- Clemmensen, L.B., Milàn, J., Pedersen, G.K., Johannesen, A.B. & Larsen, C. 2014: Dinosaur tracks in Lower Jurassic delta plain sediments (Sose Bugt Member, Rønne Formation), Bornholm, Denmark. *Lethaia* 47, 485–493.
- Donovan, D.T. & Surlyk, F. 2003: Lower Jurassic (Pliensbachian) ammonites from Bornholm, Baltic Sea, Denmark. In Ineson, J.R. & Surlyk, F. (eds): *The Jurassic of Denmark and Greenland. Geological Survey of Denmark and Greenland Bulletin, volume 1*, 555–583.
- Ezquerro, R., Doublet, S., Costeur, L., Galton, P.M. & Pérez-Lorente, F. 2007: Were non-avian theropod dinosaurs able to swim? Supportive evidence from an Early Cretaceous trackway, Cameros Basin (La Rioja, Spain). *Geology* 35, 507–510.
- Farlow, J.O., Gatesy, S.M., Holtz, T.R., Hutchinson, J.R. & Robinson, J.-M. 2000: Theropod locomotion. *American Zoologist* 40, 640–663.
- 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., Pienkowski, G. & Niedzwiedzki, G. 2004: Tetrapod track assemblages in the Hettangien of Soltykow, Poland and its paleoenvironmental background. *Ichnos* 11, 195–213.
- Godefroit, P., Cau, A., Dong-Yu, H., Escuillie, F., Wenhao, W. & Dyke, G. 2013: A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds. *Nature* 498, 359–362.
- Höhne, R. 1933: Beiträge zur Stratigraphie, Tektonik und Paläogeographie des südbaltischen Rhät-Lias, insbesondere auf Bornholm. *Abhandlungen aus dem Geologisch-Paläontologischen Institut der Universität Greifswald* 12, 1–105.
- 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.
- Larsen, O. & Friis, H. 1991: Petrography, diagenesis and pore-water evolution of a shallow marine sandstone (Hasle Formation, Lower Jurassic, Bornholm, Denmark). *Sedimentary Geology* 72, 269–284.
- 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*. Cambridge University Press, New York, 238 pp.
- Lockley, M.G., Kim, J.Y., Kim, K.S., Kim, S.H., Matsukawa, M., Rihui, L., Jianjun, L. & Yang, S.-Y. 2008: *Minisauripus* – the track of a diminutive dinosaur from the Cretaceous of China and South Korea: implications for stratigraphic correlation and theropod foot morphodynamics. *Cretaceous Research* 29, 115–130.
- Malling, C. 1911: Hasle-Sandstenens alder. *Meddelelser fra Dansk Geologisk Forening* 3, 629–631.
- Malling, C. 1914: De Jespersenske Buelag i Lias paa Bornholm. *Meddelelser fra Dansk Geologisk Forening* 4, 265–270.
- Malling, C. 1920: De marine Lias og Wealden-Aflejringer paa Bornholm. *Meddelelser fra Dansk Geologisk Forening* 5, 55–57.
- Malling, C. & Grönwall, K.A. 1909: En Fauna i Bornholms Lias. *Meddelelser fra Dansk Geologisk Forening* 3, 271–316.
- Michelsen, O., Nielsen, L.H., Johannesen, 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, volume 1*, 147–216.
- Milàn, J. 2011: New theropod, thyreophoran, and small sauro-pod tracks from the Middle Jurassic Bagå Formation, Bornholm, Denmark. *Bulletin of the Geological Society of Denmark* 59, 51–59.
- Milàn, J. & Bonde, N. 2001: Svaneøgler, nye fund fra Bornholm. *VARV* 2001, 3–8.
- 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. & 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., Rasmussen, B.W. & Bonde, N. 2012: Coprolites with prey remains and traces from coprophagous organisms from the Lower Cretaceous (Late Berriasian) Jydegaard Formation of Bornholm, Denmark. *New Mexico Museum of Natural History and Science Bulletin* 57, 235–240.
- Milner, A.R.C., Lockley, M.G. & Johnson, S.B. 2006: The story of the St. George Dinosaur Discovery Site at Johnson Farm: an important new Lower Jurassic Dinosaur Tracksite from the Moenave Formation of southwestern Utah. *New Mexico Museum of Natural History and Science Bulletin* 37, 329–345.
- Milner, A.R.C., Lockley, M.G. & Kirkland, J.I. 2007: A large collection of well-preserved theropod dinosaur swim tracks from the Lower Jurassic Moenave Formation, St. George, Utah. *New Mexico Museum of Natural History and Science Bulletin* 37, 315–328.
- 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. 2003: Late Triassic – Jurassic development of the Danish Basin and the Fennoscandian Border Zone, southern Scandinavia. In Ineson, J.R. & Surlyk, F. (eds): *The Jurassic of Denmark and Greenland. Geological Survey of Denmark and Greenland Bulletin, volume 1*, 459–526.
- 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.
- 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.

- Schwarz-Wings, D., Rees, J. & Lindgren, J. 2009: Lower Cretaceous Mesoeucrocodylians from Scandinavia (Denmark and Sweden). *Cretaceous Research* 30, 1345–1355.
- Smith, A.S. 2008: Plesiosaurs from the Pliensbachien (Lower Jurassic) of Bornholm, Denmark. *Journal of Vertebrate Paleontology* 28, 1213–1217.
- Surlyk, F. & Noe-Nygaard, N. 1986: Hummocky cross-stratification from the Lower Jurassic Hasle Formation of Bornholm, Denmark. *Sedimentary Geology* 46, 259–273.
- 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*. Chapman & Hall, London, 410 p.
- de Valais, S. 2011: Revision of dinosaur ichnotaxa from the La Matilde Formation (Middle Jurassic), Santa Cruz Province, Argentina. *Ameghiniana* 48, 28–42.
- Zhen, S., Li, J., Chen, W. & Zhu, S. 1995: Dinosaur and bird footprints from the Lower Cretaceous of Emei County, Sichuan. *Memoirs of the Beijing Natural History Museum* 54, 105–120.
- Ziegler, P. 1990: *Geological Atlas of Western and Central Europe*. Shell Internationale Petroleum Maatschappij B.V, The Hague.