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Milàn, J, Falkingham, PL and Mueller-Töwe, IJ (2020) Small ornithopod dinosaur tracks and crocodylian remains from the Middle Jurassic Bagå Formation, Bornholm, Denmark: Important additions to the rare Middle Jurassic vertebrate faunas of Northern Europe. Bulletin of the Geological

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Small ornithopod dinosaur tracks and crocodylian remains from the Middle Jurassic Bagå Formation, Bornholm, Denmark: Important additions to the rare Middle Jurassic vertebrate faunas of Northern Europe

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Geological Society of Denmark
<https://2dgf.dk>

Received 15 May 2020
 Accepted in revised form
 26 October 2020
 Published online
 17 November 2020

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Milàn, J., Falkingham, P.L. & Mueller-Töwe, I. J. 2020. Small ornithopod dinosaur tracks and crocodylian remains from the Middle Jurassic Bagå Formation, Bornholm, Denmark: Important additions to the rare Middle Jurassic vertebrate faunas of Northern Europe. *Bulletin of the Geological Society of Denmark*, Vol. 68, pp. 245–253. ISSN 2245-7070. <https://doi.org/10.37570/bgds-2020-68-11>

Two new small tridactyl dinosaur tracks are found in the Middle Jurassic Bagå Formation of Bornholm and are interpreted as ornithopodian in origin. A skeletal fragment is identified as a crocodylian skull fragment. Previous finds of dinosaur tracks from the locality consist of two sizes of sauropods, a medium sized theropod and thyreophorans. The addition of tracks from ornithopod dinosaurs and skeletal evidence of crocodylians now give a broader picture of a diverse Middle Jurassic vertebrate fauna. This is an important addition to the understanding of the terrestrial Mesozoic ecosystem of Denmark, and a valuable addition to the scarce Middle Jurassic vertebrate record of Europe.

Keywords: Dinosaur, ornithopod, crocodile, ichnology, Middle Jurassic, Bathonian, Bajocian.

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Mesozoic terrestrial vertebrates are rare in Denmark, as terrestrial outcrops are limited to a few geographically restricted exposures on the west and southwest coast of the Baltic island of Bornholm (Kear *et al.* 2016) (Fig. 1). The oldest evidence of terrestrial vertebrates consists of cross-sections through footprints in the Lower Jurassic (Hettangian) Sose Bugt Member of the Rønne Formation (Clemmensen *et al.* 2014), and a diminutive theropod footprint known from the Pliensbachian Hasle Formation (Milàn & Surlyk 2015), together with a small fragment of a femur from a juvenile sauropodomorph (Milàn & Cuny 2019). The Middle Jurassic (Bajocian – Bathonian) Bagå Formation has hitherto yielded tracks from theropod, thyreophoran and sauropod dinosaurs, preserved as natural casts of sandstone (Milàn & Bromley 2005; Milàn 2011).

An extensive vertebrate fauna including crocodiles, dinosaurs, birds, turtles, amphibians, sharks, other fish and a single mammal tooth 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 lungfish aestivation burrows are exposed in cross-section (Surlyk *et al.* 2008). Inland quarries in the overlying Jydegaard 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). After the initial report of dinosaur tracks

from the Middle Jurassic Bagå Formation (Milàn & Bromley 2005), which included tracks attributed to large sauropods and thyreophorans, new tracks from theropods, thyreophorans and small sauropods were described by Milàn (2011). This paper describes new tracks from ornithopod dinosaurs as well as the first skeletal evidence of a crocodylian skull fragment from the Bagå Formation.

Geological setting

The Bagå Formation is located on the west coast of the Danish Island of Bornholm situated in the Baltic Sea, and the type section is the Bagå Graven clay pit of the now closed Hasle Klinkefabrik at the small town of Sorthat (Gravesen *et al.* 1982; Michelsen *et al.* 2003; Nielsen *et al.* 2010) (Fig. 1). Today quarrying has ceased, and the clay pit is water-filled and known as Pyritsøen (pyrite lake). 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 Bagå Formation is palynologically dated to Middle Jurassic, Bajocian – Bathonian (Gry 1969; Koppelhus & Nielsen 1994). The formation contains abundant plant fossils

including ferns, cycads and conifers (Bartholin 1892; Florin 1958; Gry 1969; Hoelstad 1985), and vertebrate trace fossils are known from tracks of sauropod, theropod, and thyrophorean dinosaurs (Milàn 2011; Milàn & Bromley 2005).

Material and Methods

Two tracks are described here. The first specimen is a small track preserved as track and naturally formed cast (Track 1) found in a sandstone boulder in the Bagå clay pit. (Fig. 2A). The boulder was split along a thin clay seam, revealing the impression and naturally formed cast of a small tridactyl track. To enhance the features of the track, the infilling clay was mechanically removed in some parts of the track. The specimen was found by amateur geologist Christian Bach Hansen in the summer of 2018. The specimen was declared Danekræ (National treasure) (DK-1007) and stored in the collection of the Natural History Museum of Denmark (NHMD 625523).

A second track (Track 2) is larger and was brought to our attention by Rene Vilsholm from the exhibition centre NaturBornholm. The cast is preserved in coarse sandstone (Fig. 2B). The specimen is stored in the collection of the Natural History Museum of Denmark (NHMD 676864).

Both tracks were digitized via photogrammetry, using photos taken with a 16mp FujiFilm FinePix XP80, and processed using AliceVision Meshroom 2019.1.0 (<https://alicevision.github.io>) (Moulon *et al.*

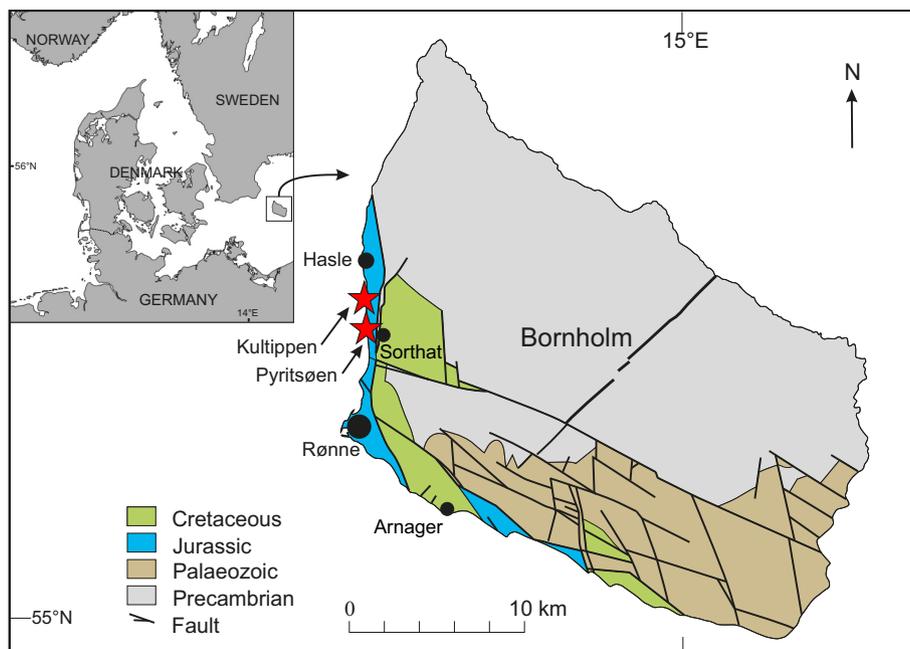


Fig. 1. Map of Bornholm with Mesozoic and Palaeozoic outcrops indicated. The type locality of the Bagå Formation is the water-filled clay-pit, Pyritsøen, between Hasle and Rønne towns, located at 55.150816°N, 14.704770°E. Kultippen is situated further north along the coast just south of Hasle at 55.170088°N, 14.705822°E. Bagå Graven and Kultippen are indicated by red stars. Modified from Gravesen (2009).

2012; Jancosek & Pajdla, 2011). Models of track 1, its natural cast, and track 2 were constructed using 21, 18, and 20 photos respectively. Digital models are presented as textured and false colour images (Fig. 3), and all photos and models are made available at <https://doi.org/10.6084/m9.figshare.7994216.v1> following the protocol set out by Falkingham *et al.* (2018).

The hip height of the track makers was estimated using the relations between foot length and hip height. Alexander (1976) proposed that hip-height could be approximated as $4 \times$ foot length, while Thulborn (1990) expanded upon this by suggesting that hip-height could be more accurately predicted from 4.5, 4.8 or $4.6 \times$ foot length for respectively theropods, ornithopods and bipeds in general with foot length < 25 cm.

A small bone fragment (Fig. 4) was found at the locality Kultippen north of Bagå Graven in the summer of 2016, by amateur geologist Christian Rasmussen. Kultippen is the locality where excess excavated material from Bagå Graven was dumped near the beach. The specimen is declared Danekræ (DK-869) and is stored in the collection of the Natural History Museum of Denmark (NHMD 625420).

New finds

Track 1

Description. Tridactyl track measuring 8.4 cm in length and with a maximum width across the impressions of the outer digits of 8.9 cm. The impression of the track is 1.1 cm deep at the deepest part (Fig. 2A). The track is preserved as track and naturally formed cast in a block of coarse sandstone. The block was split along a thin seam of clay, revealing both the natural cast and impression of the track. The track has preserved impressions of three short, blunt digits, with indications of short claws at the terminations of the digits. One digit impression is sufficiently well-preserved to reveal the presence of one large digital pad covering the length of the digit. The proximal part of the track representing the impressions of the metatarsal-phalangeal joint is broad and rounded. The track is laterally deformed with gently sloping track walls on one side and steep to vertical track walls on the other side (Fig. 2A). The divarication angle between the outer digits is 65° . The natural cast was mostly composed of clay and deteriorated after the block was split apart, leaving very limited anatomical details to be revealed, even on digitally enhanced photos (Fig. 3A).

Track 2

Description. Cast of a tridactyl track preserved in coarse sandstone. The cast is 20.7 cm long and 16.0 cm

wide, however, part of one of the outer digits is missing and we estimate that the total width would have been around 18 cm. The cast is 2.9–4.1 cm deep. Each digit cast shows the presence of one large, rounded pad encapsulating the whole digit (Fig. 2B). The two complete digit casts terminate in casts of short blunt claws. The casts of the digits are separated from the cast of the metatarsal-phalangeal pad by a shallower area (Fig. 3B). The metatarsal-phalangeal pad is broad with a wide proximal part. The divarication angle between the outer digits is estimated to be about 75° .

Bone fragment

Description. Small, elongated bone fragment measuring 53 mm in length and 31 mm in the widest end and 22 mm in the thinnest end (Fig. 4). The bone is roughly oval to D-shaped in cross section. The thinnest end is broken but the broad end has preserved the suture for the adjacent bone. The flatter surface of the bone is strongly ornamented by closely spaced, oval to rounded pits, 3–6 mm wide and up to 2 mm deep,

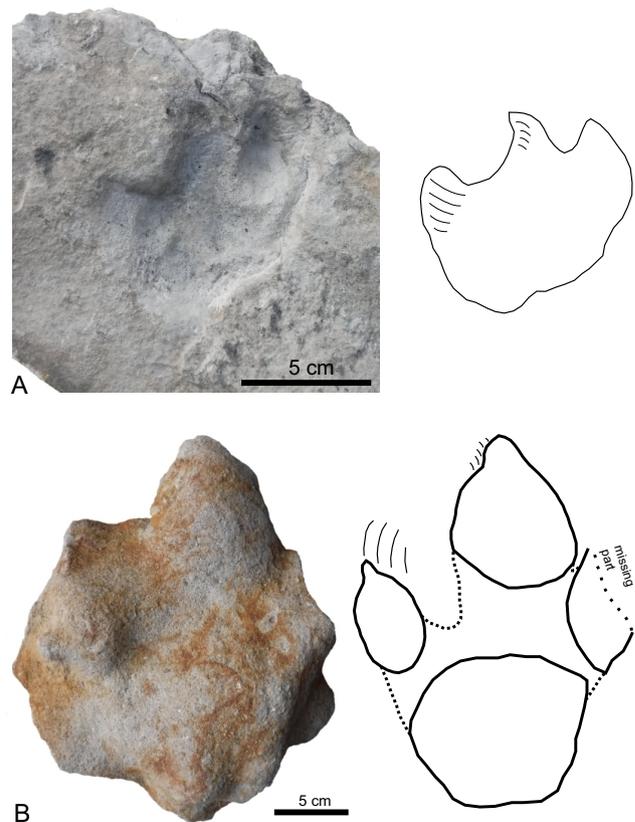


Fig. 2. The two new ornithopod tracks. **A:** Small track (MGUH 625523) and interpretive drawing. **B:** Natural cast of larger specimen (MGUH 676864) and interpretive drawing, highlighting the division into digital pads and metatarsal-phalangeal pad. Parallel curved lines indicate areas with evidence of sliding of the foot.

forming a honeycomb-like pattern with the pits being separated by thin bony ridges. The rounded side is smooth except for a rough area on the medial side.

Discussion

Tracks

Both theropod and ornithopod dinosaurs are functionally tridactyl, and both leave tridactyl tracks that can be of very similar appearance. However, several features make it possible to distinguish between them. Theropod tracks are characterized by being longer than they are wide, with long, narrow, often tapering, digits ending in long, sharp claw impressions, and an asymmetrical, narrow “heel” part consisting of a prolonged projection of digit IV (Moratalla *et al.* 1988; Thulborn 1990; Lockley 1991). The divarication angle

between digits II and IV is normally 50–60° but can be as low as 35° and up to 75° (Thulborn 1990). In contrast, ornithopod tracks are generally as wide, or wider, than they are long, the digits are short and rounded, and when present the imprints of the claws are blunt and rounded. The divarication angle between digits II and IV are normally in excess of 60° (Moratalla *et al.* 1988; Thulborn 1990; Lockley 1991).

Identifying small-sized Early to Middle Jurassic footprints as ornithopod is a bit tricky. In the ichnological literature, “ornithopod” is generally applied to tridactyl ornithischian tracks that are not ceratopsian or thyreophoran. However, when looking at body fossils, ornithopods are united by features in their skull and dentition (e.g. Butler *et al.* 2008; Boyd 2015), and there are many non-ornithopod ornithischians with a functionally tridactyl foot structure that could potentially produce small ornithopod-like tracks, e.g. *Scelidosaurus* (Norman 2020). For ease of comparison with other fossil track faunas and the earlier ichno-

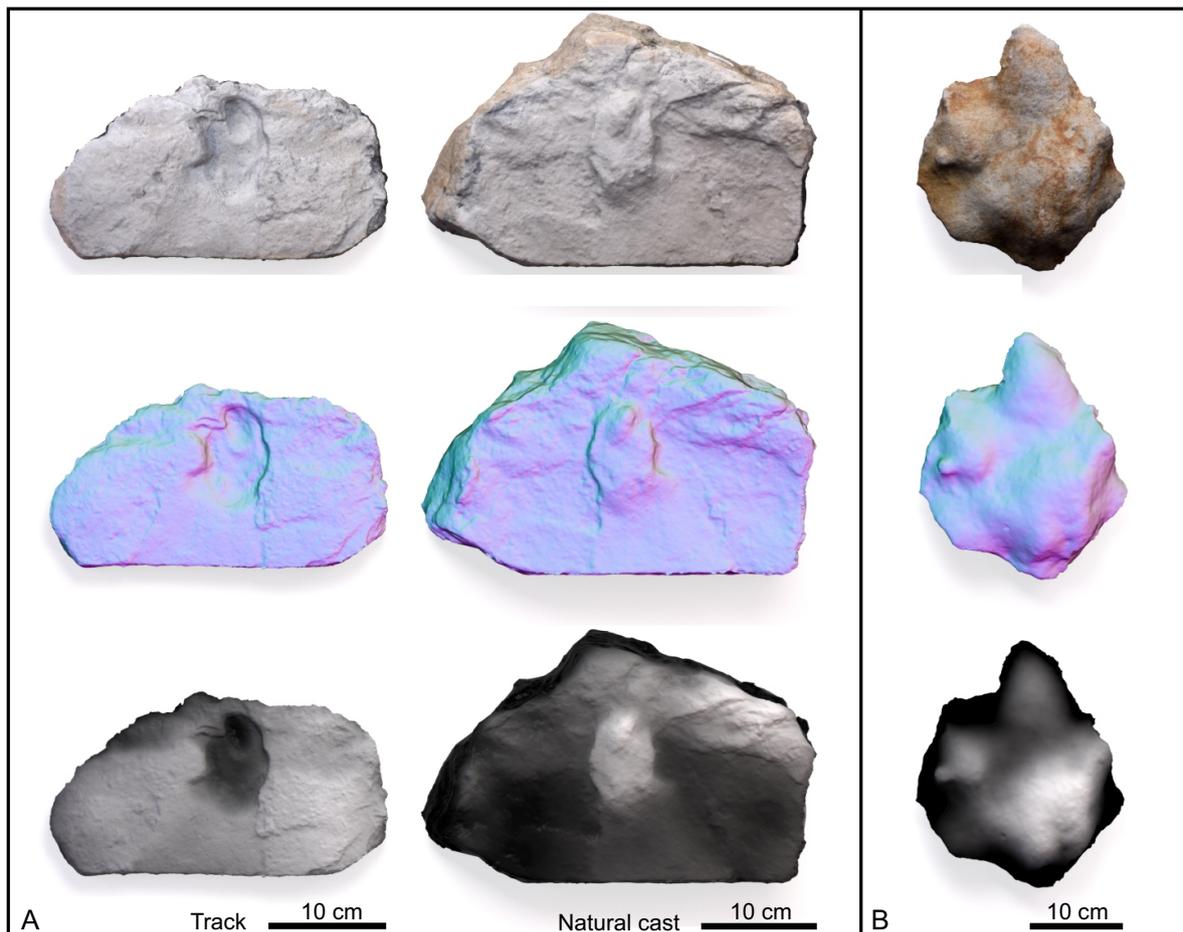


Fig. 3. Digital models of tracks. **A:** Track 1. **B:** Track 2. From top to bottom presented as textured, normal mapped to enhance contrast, and height mapped photogrammetric models to display 3D topography more clearly. Track 1 is shown as track (left) and convex natural cast (right).

logical literature, we choose to refer to these tracks as ornithopod tracks, while the possibility that they are made by a non-ornithopod ornithischian exists.

Track 1. The small track (NHMD 625523) (Figs. 2A, 3A): The overall dimensions of the track, being wider than long, with short blunt digits, a broad metatarsal-phalangeal joint and a high angle of divarication between digits II and IV, falls within the morphology of typical ornithopod tracks (Moratalla *et al.* 1988; Thulborn 1990; Lockley 1991). The track is deformed sideways, but the measurements are made in the bottom of the track, bringing them as close to the original dimensions as possible. Based on these dimensions, we interpret MGUH 625523 to be ornithopodian in origin. The preservation of the tracks is too poor to determine whether the track is from a right or left foot. By applying the foot length/hip height ratio for ornithopod dinosaurs with a foot length less than 25 cm (Alexander 1976; Thulborn 1990), the hip height of the trackmaker is estimated to be between 40 and 48 centimetres, indicating a very small animal.

Track 2. The larger track (NHMD 676864) (Figs. 2B, 3B): The track is slightly longer than wide. The short, rounded digit impressions are not divided into separate digital pads and the high angle of divarication between the outer digits is typical of ornithopod tracks (Moratalla *et al.* 1988; Thulborn 1990; Lockley 1991). It is not possible to determine whether the cast repre-

sents a right or left foot. Previous finds of theropod tracks from the same formation show typical theropod morphology in the digits and angle of divarication between the outer digits (Milàn 2011). Based on these proportions we interpret NHMD 676864 to be made by an ornithopod trackmaker. Using the foot length/hip height ratio for ornithopods with a foot length less than 25 cm (Thulborn 1990), the hip height of the trackmaker is estimated to be 1–1.2 m.

Bone fragment

The bone fragment (NHMD 625420) is roughly oval to D-shaped in cross section, widening towards one end (Fig. 4). The ornamentation on the dorsal side of the fragment consists of closely spaced, oval to rounded pits 2 to 5 mm in diameter (Fig. 4a), while the ventral rounded side is smooth (Fig. 4B, C). This kind of ornamentation is typical in the cranial parts and osteoderms of crocodylians (Romer 1956). Osteoderms are flat, thin, platy bones, oval to rectangular in shape. This excludes the possibility of NHMD 625420 being an osteoderm. By comparison with the skull of the extant Slender-snouted Crocodile, *Mecistops cataphractus*, the morphology of the fragment shows similarity to the distal part of the jugal (Milàn 2017). However, comparing the morphology to that of the most common Middle Jurassic crocodylians, the now extinct thalattosuchians, and more specifically Teleosauridae, the morphology of the skull fragment fits more

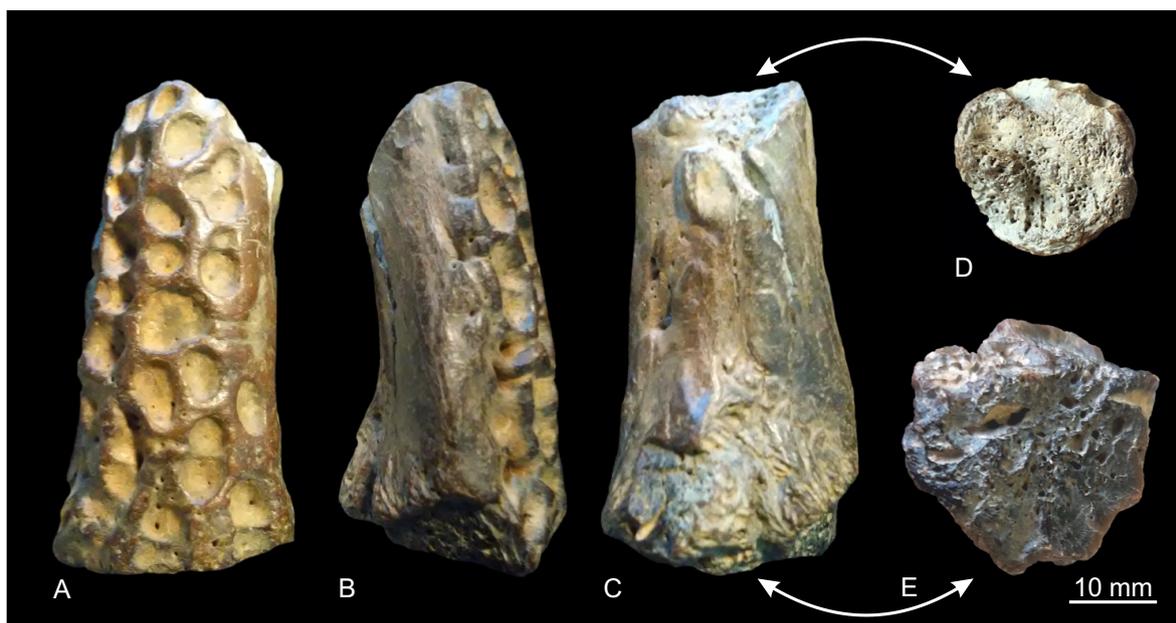


Fig. 4. Crocodilian skull fragment (MGUH 625420). **A:** Dorsal view showing the densely pitted surface of the bone. **B:** sideview showing the difference between the pitted surface and the smooth ventral side of the bone. **C:** Ventral view. **D:** Broken end of bone, note the sections through the pits in the top of the picture. **E:** Broad end of the bone with the suture to the adjacent bone.

closely to the postorbital bar (Mueller-Töwe 2006). The morphology of the ornamentation of the bone shows strong similarity to that of thalattosuchians. Assuming NHMD 625420 is a fragment of a postorbital bar, the total length of the postorbital bar must have been more than 65 mm. That would result in a postorbital fenestra size of minimum 60 mm, which corresponds to a skull length of about 1 m in longirostrine thalattosuchians (Mueller-Töwe 2006). The total body length of the crocodile is hard to calculate, but in the extant mesorostrine saltwater crocodile, *Crocodylus porosus*, the total body length can be calculated from the head length (Fukuda *et al.* 2013). By applying their ratios a skull length of 1 m would give an animal with a body length about 6 m. However, taking into account the longirostrine condition in teleosaurids, which gives a proportionally longer skull, we tentatively suggest a total body length for NHMD 625420 of 4 to 5 m. While thalattosuchians are predominantly marine crocodylians, teleosaurid thalattosuchians are reported from freshwater environments in association with theropod, ornithopod and sauropod dinosaurs (Martin *et al.* 2019).

Comparison with European Middle Jurassic vertebrate faunas

The Middle Jurassic is known for a worldwide, and especially European, scarcity of dinosaurian body fossils, and as such any new finds help improve our understanding of this time period. Due to the scarcity of body fossils, ichnological data are becoming an increasingly important source of information about Middle Jurassic dinosaurian diversity and biogeography (Romano & Whyte 2003, 2010; Whyte *et al.* 2007, 2010; Romano *et al.* 2018; dePolo *et al.* 2018; Moreau *et al.* 2020). The new find of ornithopod tracks from the Bagå Formation, and a crocodylian skull fragment,

contribute to show a vertebrate fauna consisting of two sizes of sauropods, thyreophorans, theropods, crocodylians and two sizes of ornithopods (Fig. 5). This faunal composition is similar to the very diverse ichnofauna from the Middle Jurassic Cleveland Basin of the Yorkshire coast, England, which consists of 25 reported morphotypes of tracks from several sizes of sauropods, theropods, ornithopods, thyreophoreans, and crocodylians (Romano & Whyte 2003, 2010; Whyte *et al.* 2006, 2007, 2010; Romano *et al.* 2018).

The Middle Jurassic Hebrides Basin on the Isle of Skye, Scotland, has over recent years proved to contain a very diverse dinosaurian fauna comprised of both skeletal and ichnological material (e.g. Clark 2001; Clark & Barco-Rodriguez 1998; Clark & Gavin 2016; Romano *et al.* 2018; dePolo *et al.* 2018, 2020). Dinosaur footprints from the Isle of Skye include several sizes of sauropod tracks, which can be referred to as *Breviparopus*-like, thyreophorean tracks in the form of *Deltapodus*; three sizes of tridactyl tracks interpreted to be from large ornithopods with foot lengths between 30 and 40 cm, and several sizes of small to medium-sized theropods with foot lengths from 10 to 30 cm (Brusatte *et al.* 2016; Clark & Gavin 2016; dePolo *et al.* 2018, 2020; Romano *et al.* 2018). In addition to dinosaurs, the Isle of Skye fauna includes several neosuchian crocodiles (Young *et al.* 2016; Yi *et al.* 2017) and a possible Mesoeucrocodylian (Wills *et al.* 2014).

The Middle Jurassic cliffs of the Vache Noirs in Normandy, France, show a vertebrate fauna heavily dominated by many sizes of theropods, and less frequent sauropods and thyreophoran remains (Buffetaut & Tabouelle 2019). Sauropod trackways are found in a mine roof in the Causses Basin, Southern France (Moreau *et al.* 2020). Sauropod and theropod tracks are also known from the Middle Jurassic of Oxfordshire, England (Day *et al.* 2004), and the Middle Jurassic of Portugal has preserved extensive monospecific track

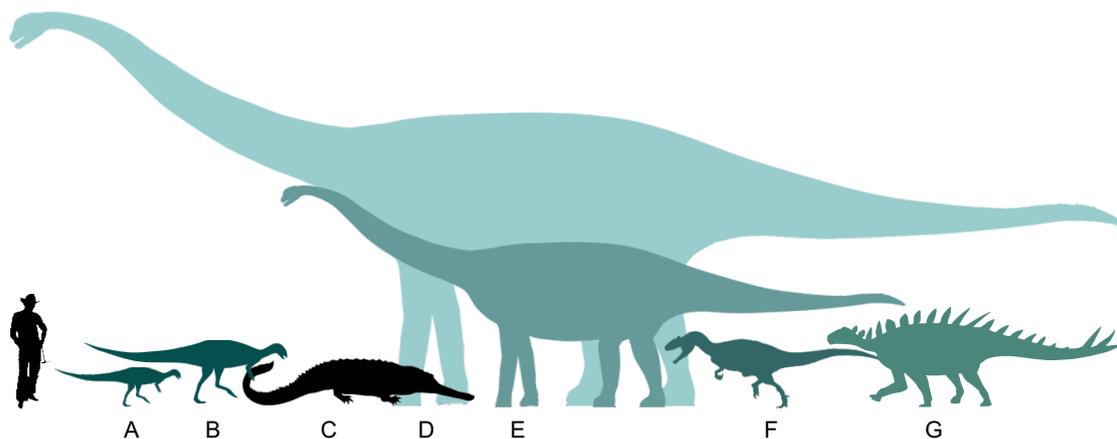


Fig. 5. Schematic representation of the Middle Jurassic vertebrate fauna of the Bagå Formation, with a 180 cm human as scale. A and B: Small ornithopods. C: Crocodylian. D and E: Sauropods. F: Theropod. G: Thyreophoran. Modified after Milàn (2011).

sites with abundant trackways of sauropods (Santos *et al.* 2009), and theropods (Razzolini *et al.* 2016).

Despite the limited sample size known from the Bagå Formation, consisting of so far of only eight footprint specimens and one skeletal fragment, the reported types of tracks count at present three sauropod tracks, where two are 68–69 cm in length (Milàn & Bromley 2005) and one is a significantly smaller specimen with an estimated total length of 56 cm (Milàn 2011), two different sizes and morphologies of tracks assigned to thyreophorans (Milàn & Bromley 2005; Milàn 2011), and one track from a medium-sized theropod with a foot length of 25 cm (Milàn 2011). Together with the crocodylian bone fragment and the ornithopod tracks, this makes the fauna of the Bagå Formation (Fig. 5), comparable in faunal diversity to the faunas from the Cleveland and Hebridean Basins and thus an important addition to the scarce Middle Jurassic vertebrate record of Europe.

Conclusion

Two new tracks from the Middle Jurassic Bagå Formation are interpreted as being made by small ornithopod dinosaurs, one with an estimated hip height of 40–48 cm and one with an estimated hip height of 100–120 cm. A bone fragment is identified as skull fragment of a thalattosuchian crocodylian and most likely represents a postorbital bar. Together with previous finds of tracks from theropods, thyreophorans and sauropod dinosaurs, these specimens provide evidence of a diverse Middle Jurassic dinosaurian fauna when the Bagå Formation was deposited. Compared to other European Middle Jurassic dinosaur faunas, the Bagå Formation is among the most diverse in Europe and is thus an important addition to the sparse record of Middle Jurassic vertebrates from Europe. The presence of preserved bone material in the Bagå Formation suggest that more skeletal material can be found in the future.

Acknowledgements

We are grateful to the eager amateur geologists Christian Rasmussen who found the crocodile bone and Christian Bach Hansen who found the small track, and to Rene Vilsholm from NaturBornholm for bringing the large track to our attention. The critical and constructive comments from Paige dePolo and an anonymous reviewer helped to improve the paper significantly.

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