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Late Jurassic theropod dinosaur bones from the Langenberg Quarry (Lower Saxony, Germany) provide evidence for several theropod lineages in the central European archipelago

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Marine limestones and marls in the Langenberg Quarry provide unique insights into a Late Jurassic island ecosystem in central Europe. The beds yield a varied assemblage of terrestrial vertebrates including extremely rare bones from theropod dinosaurs, which we describe here for the first time. All of the theropod bones belong to relatively small individuals but represent a wide taxonomic range. The material comprises a neovenatorid small pedal ungual and pedal phalanx, a ceratosaurian anterior chevron, a left fibula of a megalosauroid, and a distal caudal vertebra of a tetanuran. Additionally, a small pedal phalanx III-1 and the proximal part of a small right fibula can be assigned to indeterminate theropods. The ontogenetic stages of the material are currently unknown, although the assignment of some of the bones to juvenile individuals is plausible. The finds confirm the presence of several taxa of theropod dinosaurs in the archipelago and add to our growing understanding of theropod diversity and evolution during the Late Jurassic of Europe.

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Abstract

Marine limestones and marls in the Langenberg Quarry provide unique insights into a Late Jurassic island ecosystem in central Europe. The beds yield a varied assemblage of terrestrial vertebrates including extremely rare bones from theropod dinosaurs, which we describe here for the first time. All of the theropod bones belong to relatively small individuals but represent a wide taxonomic range. The material comprises a neovenatorid small pedal ungual and pedal phalanx, a ceratosaurian anterior chevron, a left fibula of a megalosauroid, and a distal caudal vertebra of a tetanuran. Additionally, a small pedal phalanx III-1 and the proximal part of a small right fibula can be assigned to indeterminate theropods. The ontogenetic stages of the material are currently unknown, although the assignment of some of the bones to juvenile individuals is plausible. The finds confirm the presence of several taxa of theropod dinosaurs in the archipelago and add to our growing understanding of theropod diversity and evolution during the Late Jurassic of Europe.

Introduction

Late Jurassic terrestrial sediments have seen a long history of fossil exploration (e.g. Close *et al.*, 2018; Tennant, Chiarenza & Baron, 2018), which led to the discovery of an amazingly high number of dinosaur bearing formations (e.g. McAllister Rees *et al.*, 2004). Despite the great dinosaur diversity known from that age (e.g. Lloyd *et al.*, 2008; Barrett, McGowan & Page, 2009; Mannion *et al.*, 2011), regional gaps in our knowledge of Late Jurassic dinosaur faunas still do exist. For example, most of Northern Germany was submerged during the Late Jurassic, resulting in an almost exclusively marine fossil record (Ziegler, 1990). A very rare exception is the Langenberg Quarry at the northern rim of the Harz Mountains where a variety of terrestrial vertebrates have been washed into the marine depositional environment from a nearby island (e.g. Sander *et al.*, 2006, Wings & Sander, 2012, Wings, 2015). The diverse tetrapod fauna of the Langenberg Quarry is particularly famous for the occurrence of the dwarf sauropod *Europasaurus holgeri*, but also includes mammals, pterosaurs, turtles, crocodylians, and squamates (e.g., Wings & Sander, 2012; Wings, 2015). The theropod bones from the Langenberg Quarry have so far received limited attention (but see Gerke & Wings, 2016), because of the general rarity and incompleteness of theropod material. Here, we describe the exceptionally rare theropod bones from that locality for the first time. Although much of the fragmentary material can only be classified on higher taxonomic levels, the new occurrences reported herein add to our understanding of the regional tetrapod fauna and to theropod diversity in general.

Locality, Geology and Stratigraphy

The Langenberg Quarry near the town of Goslar, Lower Saxony, northern Germany (Figure 1) is a classic and well-studied locality exposing large sections of Late Jurassic shallow marine strata (Fischer 1991; Lotze 1968; Pape 1970; Zuo *et al.* 2017). The layers consist of impure carbonates grading into marls. Tilted to a nearly vertical, slightly overturned position, the beds are quarried along strike, exposing them only in cross section and not along bedding planes. Sediment composition and invertebrate faunal content record changes in water depth and clear brackish influences, but there is no evidence of subaerial exposure (Lotze 1968; Pape 1970). The well dated sediments in the quarry range from late Oxfordian to late Kimmeridgian in age (Fischer 1991; Lotze 1968; Pape 1970; Zuo *et al.* 2017). After the stratigraphic subdivision of Fischer (1991), most of the terrestrial vertebrate remains (including the sauropod dinosaur *Europasaurus holgeri* and all theropod bones) were found in bed 83, not in bed 93 as erroneously stated in some publications (Carballido & Sander 2013; Marpmann *et al.* 2014; Sander *et al.* 2006). This bed is a light grey-greenish marly limestone. It has been assigned to the “Mittleres Kimmeridge”, a northwest-German equivalent to the lower part of the upper Kimmeridgian of the international chronostratigraphic time scale (Lallensack *et al.* 2015; Schweigert 1999). During the Late Jurassic, the Langenberg Quarry was located in the Lower Saxony Basin that covered much of northern Germany and that was surrounded by several paleo-islands (Ziegler 1990), the source of the clastic components in the sediment.

Fossil Vertebrates from the Langenberg Quarry

The Langenberg Quarry is the only locality where the abundant and exquisitely three-dimensionally preserved material of the dwarfed sauropod dinosaur *Europasaurus holgeri* has been found (Carballido & Sander 2013; Marpmann *et al.* 2014; Sander *et al.* 2006). The quarry also yielded a number of isolated teeth which belong to several different groups of theropod dinosaurs (Gerke & Wings 2016) as well as natural track casts of large theropods *(Lallensack et al.* 2015).

Beds 83 and 73 also have produced a variety of non-dinosaurian vertebrate remains. Among them are the only known Jurassic mammals from Germany, the pinheirodontid multituberculate *Teutonodon langenbergensis* (Martin *et al.*, 2016), the paulchoffatiid multituberculate *Cimbriodon multituberculatus* (Martin *et al.*, 2019), and the large morganucodontan mammaliaform *Storchodon cingulatus* (Martin *et al.*, in press). Additionally, a three-dimensionally preserved articulated skeleton of a small pterosaur (Fastnacht 2005), teeth and skeletons of the small non-marine atoposaurid crocodilian *Knoetschkesuchus langenbergensis* (Schwarz *et al.* 2017), various remains of marine crocodylians (Karl *et al.*, 2006; 2008) and the partial skeleton of a paramacellodid lizard (Richter *et al.* 2013) have been reported. Diverse marine turtle material (including several skulls) comprises cf. *Thalassemys* sp., *Plesiochelys* sp., and possibly a new taxon (Jansen & Klein 2014). Microvertebrate remains from the Langenberg yield beside many reptilian teeth (Wings, pers. obs.) a diverse fish fauna represented mainly by isolated teeth of marine chondrichthyans and osteichthyans (Mudroch 2001; Mudroch & Thies 1996; Thies 1995).

Taphonomy

Almost all of the fossil material from terrestrial vertebrates (including all material described herein) was recovered after regular blasting operations in the quarry. Despite the large number of bones and teeth known from the sauropod *Europasaurus holgeri*, the general distribution of bones and teeth in bed 83 is rare. All of the extremely rare theropod bones were found intermingled with the mostly disarticulated *E. holgeri* material. All skeletal remains were accumulated in certain areas, probably lenses or channels. The bone-bearing sections of bed 83 were usually 30-50 cm thick and contained in all bone-rich areas a large number of well-rounded micritic intraclasts. The combination of bone material and intraclasts is also important for recognizing blocks of this specific layer in the quarry heap after the blasting. Because the blocks were not found *in situ*, it remains possible, although very unlikely, that the finds come from another bed nearby. In any case, they clearly belong to the lower part of the upper Kimmeridgian.

Abbreviations

BSPG Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany
BYU Brigham Young University, Provo, Utah, USA
DfmMh/FV Dinosaurier-Freilichtmuseum Münchehagen/Verein zur Förderung der niedersächsischen Paläontologie, Rehburg-Loccum, Germany
IVPP Institute of Vertebrate Paleomntology and Paleoanthropology, Beijing, China
JM SCHA Juramuseum Eichstätt, Eichstätt, Germany
MNN Museé National du Niger, Niamey, Niger
OUMNH Oxford University Museum of Natural History, Oxford, UK
SMNS Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
UC University of Chicago, Chicago, Illinois, USA
UMNH Utah Museum of Natural History, Salt Lake City, Utah, USA

Materials and Methods

The present work is based on several isolated bones, which have been morphologically examined by the authors. Comparisons have been made on the basis of first hand observation on relevant material by one of us (SWE), as well as literature comparisons.

Results

In the following section, we describe each specimen, provide its systematic identification, and justify the latter in a remarks section by comparative notes.

Dinosauria Owen, 1842
Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Avetheropoda Paul, 1988
Allosauroidea (Marsh, 1878) Currie & Zhao, 1993
cf. Neovenatoridae Benson, Carrano & Brusatte, 2010

Material: DfMMh/FV1/19, small pedal ungual (Figure 2A–D).

Description: DfMMh/FV1/19 is an ungual that measures 23 mm in a straight line from the extensor tubercle to the distal tip. DfMMh/FV1/19 is relatively slender, and ventrally only moderately broader than dorsally. The ungual has a transversely expanded proximal surface for the articulation with the preceding phalanx, and a moderately recurved body that extends distally into a sharp tip.

The proximal surface of DfMMh/FV1/19 is vaguely triangular in shape, transversely narrow, and dorsoventrally taller than wide. Its maximal height is 8 mm, and the maximal width is 6 mm. The proximal surface is slightly damaged at the ventral rim, but the overall shape is discernible as only the surface of the element seems to be superficially broken. The margin around the proximal surface is developed as a salient rim ventrally to the extensor tubercle. While the surface of the ungual is generally smooth, the surface around this proximal rim is roughened. The extensor tubercle forms a short a proximally overhanging tip at the dorsal margin of the proximal surface, and bears weak longitudinal striations on its dorsal surface (Figure 2A–D). The latero- and medioventral edges of the proximal surface form protruding flanges, expanding the ventral part of the proximal surface transversely in relation to the dorsal margin (Figure 2B). The articulation facet for the preceding phalanx on the proximal surface is dorsoventrally only weakly concave and lacks a distinct vertical median ridge, although the central portion of the facet is slightly raised in comparison to the parts of the facet near the outer margins. The dorsolateral and dorsomedial portions of the proximal facet are gently deepened, indicating that the distal surface of the preceding phalanx was slightly ginglymoid.

The body of the ungual is ventrally curved, and tapers to a sharp distal tip (Figure 2C–D). The dorsal surface of the body of the ungual is continuous with the surface of the extensor tubercle. This surface is transversely strongly convex and smooth. On the lateral and medial side, the body of the ungual is separated from the proximal surface by a low depression, which gives the claw a slightly constricted morphology just distal to the proximal articulation.

Distal to this constriction, the ventral surface of the body of the ungual is weakly broader than the dorsal surface. The ventral surface is also slightly less ventrally curved than the dorsal margin, and is transversely almost flat for most of its length. In the proximal part, immediately distal to the proximal facet, the ventral surface of the claw exhibits a small mount-like structure, the flexor tubercle (Figure 2B–D). As parts of the ventral surface of the claw are damaged toward the proximal articulation, the distal and left side of the flexor tubercle cannot be described. On the right side, however, there seems to be a small oblique groove or elongate depression that separates the flexor tubercle from the margin of the proximal facet.

The lateral and medial surface of the ungual are each incised by a deep groove (Figure 2C–D), which separates the body of the ungual into a broadened ventral part and a dorsal part. The collateral grooves parallel the ventral margin of the claw, and are therefore ventrally concavely rounded. At its proximal end, each groove merges with the medial and lateral depression, respectively. Each collateral groove starts proximally on a central position on the lateral and medial surface, respectively, but continues distally to a slightly dorsoventrally higher position, so that the broad ventral part of the claw is relatively prominent distally.

Remarks: Precise identification of DfMMh/FV1/19 is difficult, as unguals are generally not described in detail in the literature. We tentatively identify DfMMh/FV1/19 as belonging to a theropod dinosaur. Unfortunately, unguals of alternative taxa, such as crocodiles, lizards, and testudinids, all groups for which fossils have been found and described from the Langenberg Quarry (Thies, Windorf & Mudroch, 1997; Karl *et al.*, 2006; Karl *et al.*, 2008; Jansen & Klein, 2013; Richter *et al.*, 2013; Schwarz *et al.*, 2017), are even less described in the literature than theropod unguals, so that the following comments are largely based on personal observations.

Testudinid taxa that appear in the Lower Saxony Basin, including the Langenberg Quarry (e.g. Jansen & Klein, 2013), and that are common more generally in coastal and shallow marine settings in the Late Jurassic belong to an enigmatic array of eucryptodiran taxa known as eurysternids, plesiochelyids, and thalassemydids (Anquetin, Püntener & Joyce, 2017; Evers & Benson, 2018). Eurysternids, a eucryptodiran group of Late Jurassic, secondarily marine turtles are known from many relatively complete specimens that often include manual and pedal unguals. Eurysternids generally have manual and pedal unguals that are more robust, i.e. anteroposteriorly short but transversely broad (e.g. *Eurysternum wagleri* BSPG AS I 921, BSPG 1600 VIII 43, SMNS 59731; *Solnhofia parsoni* JM SCHA 70; Joyce, 2000; Anquetin & Joyce, 2014).

DfMMh/FV1/19 exhibits some features that are comparable to claws of theropod dinosaurs. Manual and pedal unguals in theropod dinosaurs generally vary relatively strongly in morphology. Pedal unguals usually exhibit a weaker degree of curvature, are transversely broader and ventrally flatter than their manual counterparts. They also have less strongly developed extensor and flexor tubercles, and often lack a distinct median vertical ridge on the proximal articulation facet (e.g. *Allosaurus fragilis*: Madsen, 1976; *Eustreptospondylus oxoniensis*: Sadleir *et al.*, 2008; *Australovenator wintonensis*: Hocknull *et al.*, 2009). In manual unguals, the median ridge is generally well developed, and separates a medial and lateral surface for the respective cotyles on the strongly ginglymoid distal articulation surfaces of penultimate manual phalanges (e.g. *Australovenator wintonensis*: White *et al.*, 2012). These surfaces are dorsoventrally usually quite tall, and the entire proximal surface is laterally and medially not much expanded in respect to the distal part of the claw so that manual unguals appear laterally compressed. Additionally, the flexor tubercle is pronounced in manual unguals (Rauhut, 2003*a*). The features described above for DfMMh/FV1/19 are congruent with the generalised features of theropod pedal unguals, and thus we interpret DfMMh/FV1/19 to represent such an element. However, it remains unclear if DfMMh/FV1/19 represents a right or left element, and we are also uncertain about the digit identity of DfMMh/FV1/19.

Isolated teeth of Late Jurassic theropod dinosaurs from the Lower Saxony Basin in Northern Germany, including material from the Langenberg Quarry, have been identified by multivariate and cladistics analyses as belonging to basal Tyrannosauroidea, Allosauroidea, Megalosauroidea, and Ceratosauria (Gerke & Wings, 2016). These taxa therefore provide potential comparative clues about the taxonomic identification of DfMMh/FV1/19.

Pedal unguals of non-abelisaurid ceratosaurs, such as *Limusaurus inextribacilis* (IVPP P 15923), are more robust, less recurved, and dorsoventrally more flattened as well as transversely broader than seen in DfMMh/FV1/19. DfMMh/FV1/19 also does not compare well with abelisaurid ceratosaurs. Pedal unguals reported for abelisaurids commonly show a broad triangular depression on the ventral surface (e.g. *Majungasaurus crenatissimus:* Carrano, 2007; *Eoabelisaurus mefi*: Pol & Rauhut, 2012), and at least some forms have a pair of collateral grooves on either side of the claw body (e.g. *Masiakasaurus knopfleri*: Carrano, Sampson & Forster, 2002). All of these features are absent in DfMMh/FV1/19.

Pedal unguals of basal tyrannosauroids also differ substantially from DfMMh/FV1/19. The proceratosaurid tyrannosauroid *Guanlong wucaii* (IVPP 14532) has relatively large extensor tubercles, collateral grooves that deepen dorsoventrally toward the proximal end of the ungual, and proximal articulations that are much more strongly concave than seen in DfMMh/FV1/19. In the basal tyrannosauroid *Dilong paradoxus* (IVPP V 11579), the pedal unguals are proximally dorsoventrally much deeper than in DfMMh/FV1/19, right and left sub-facets are separated by a moderately strong median ridge, and flexor tubercles are much more prominent, significantly expanding the depth of the proximal part of the unguals ventrally.

In megalosauroid theropods, pedal unguals are general more robust that seen in DfMMh/FV1/19. For instance, *Eustreptospondylus oxoniensis* has a preserved pedal ungual that is transversely broader in regard to DfMMh/FV1/19 both at the dorsal and ventral margins of the ungual body (OUMNH.J 13558: Sadleir *et al.*, 2008). Additionally, the extensor tubercle is more prominent and the proximal articulations facet is oval rather than triangular.

DfMMh/FV1/19 has superficial similarities to *Allosaurus fragilis*, in that the degree of curvature is similar, weak flexor tubercles and relatively flat ventral surfaces are present, and right and left sub-facets on the proximal articulation are only weakly differentiated (e.g. UMNH VP 5355, 5365, 5368, 6771). However, in *Allosaurus fragilis* pedal unguals are generally dorsoventrally higher than in DfMMh/FV1/19, have slightly more expanded extensor tubercles, somewhat more laterally compressed proximal articulation facets, and the collateral grooves are positioned more dorsally on the claw body.

DfMMh/FV1/19 is closest in both overall similarity as well as detailed aspects of morphology to material described for the neovenatorid *Australovenator wintonensis* (Hocknull *et al.*, 2009; White *et al.*, 2012). It should be noted that the unguals of *Australovenator wintonensis* are likely the best described unguals for any theropod dinosaur, as all ungual elements are described separately, figured, and 3D models that were created on the basis of CT scans were made available (White *et al.* 2012). The pedal unguals of the fourth digit (IV-5) of *Australovenator wintonensis* but also *Neovenator salerii* (Brusatte, Benson & Hutt, 2008) are very similar to DfMMh/FV1/19: ~~The~~ respective specimens share a similar degree of curvature; a relatively flat ventral surface; a short extensor tubercle and rim around the proximal articulation facet; a gently concave facet with incomplete separation of medial and lateral sub-facets by a shallow central tubercle; a mediolaterally slightly constricted area between the proximal surface and the body of the claw; and shallow ~~a~~ depression to either side of the flexor tubercle. *Australovenator* *wintonensis* and *Neovenator salerii* have a more prominent extensor tubercle than DfMMh/FV1/19 and a ventral part of the claw body that is transversely broader in relation to the dorsal portion of the claw. DfMMh/FV1/19 is also similar to the pedal ungual of the second digit (II-3) of *Australovenator wintonensis*. In this element, the ventral surface of the claw is less expanded transversely than in IV-5, which is more like the morphology of DfMMh/FV1/19. However, in II-3, the collateral grooves on the claw body are less deep than in both the IV-5 of *Australovenator wintonensis* or DfMMh/FV1/19. The pedal ungual of the first digit (I-2) of *Australovenator* does not match the morphology of DfMMh/FV1/19 well, as this element has a more prominent extensor tubercle, and a dorsoventrally high ovoid proximal surface as well as only faintly developed collateral grooves. The ungual of the third digit (III-4) of *Australovenator wintonensis* seems proximally distorted, so that the degree of similarity to DfMMh/FV1/19 is harder to establish.

Based on these observations, a tentative identification of DfMMh/FV1/19 as a pedal ungual of a neovenatorid theropod seems plausible. However, DfMMh/FV1/19 is relatively small in general terms for this group of dinosaurs, which commonly achieve body masses of more than one metric ton and femoral lengths of around 750 mm (e.g. *Neovenator salerii*; Benson *et al.*, 2014), so that it is highly likely that DfMMh/FV1/19 represents a juvenile.

Dinosauria Owen, 1842
Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Avetheropoda Paul, 1988
Allosauroidea (Marsh, 1878) Currie & Zhao, 1993
cf. Neovenatoridae Benson, Carrano & Brusatte, 2010

Material: DfMMh/FV/343, small pedal phalanx (Figure 2E–J).

Description: DfMMh/FV/343 is a small proximal pedal phalanx that measures 11 mm in length. The proximal articular facet of the phalanx is 7 mm wide, narrows from ventral to dorsal and is 3 mm tall. A small extensor turbercle is developed at the dorsal surface of the proximal end (Figure 2E, H). The phalangeal shaft of DfMMh/FV/343 is somewhat more slender than the articular ends of the element, and the ventral surface of the shaft is flattened. Proximally, a broad flexor fossa is well-developed (Figure 2F). The anterior end of the element is developed as a 6 mm wide trochlea that is not subdivided into distinct left and right cotylar facets (Figure 2J). Ligament pits are developed on each of the lateral cotyle surfaces. These pits are relatively deep in DfMMh/FV/343, and do not occupy the entire lateral surface of the cotyles.

Remarks: Similarly to the pedal ungual, interpretation of DfMMh/FV/343 is complicated by the fact that the phalangeal morphology of many taxa occurring in the Langenberg Quarry is not well described. However, the general morphology of DfMMh/FV/343 is consistent with that of a pedal phalanx of a theropod dinosaur. The relatively broad overall shape of DfMMh/FV/343, as well as the presence of a singular proximal articulation facet that is not divided by a vertical ridge in subfacets or the presence of only moderately development extensor tubercles is generally typical for proximal pedal phalanges of theropods (e.g., Madsen, 1976). Although little has been explicitly published on pedal phalanx morphology for theropods, a few details of the anatomy narrow the taxonomic identification of DfMMh/FV/343 down to neovenatorids. For instance, the collateral ligament pits of DfMMh/FV/343 are deep but relatively small, as for instance in *Australovenator wintonensis* (White *et al.*, 2012), whereas the pits occupy the entire cotylar surface and are smore shallowly sloping, funnel like depressions in *Eustreptospondylus oxoniensis* (Sadleir, Barrett & Powell, 2008).

DfMMh/FV/343 was found in the same block of matrix as the pedal phalanx DfMMh/FV1/19, although not in articulation or particularly close association with it (pers. comm., Nils Knötschke). Both specimens have are relatively small, with the ungual being somewhat longer than the non-ungual phalanx. In neovenatorid theropods, unguals are equally long or longer than more proximally positioned phalanges in the fourth digit (e.g. Brusatte, Benson & Hutt, 2008), which is consistent with one of the possibly identifications of the ungual. Therefore, it is possible (but highly speculative) that both elements belong to the same individual.

Dinosauria Owen, 1842
Theropoda Marsh, 1881
cf. Ceratosauria Marsh, 1884

Material: DfMMh/FV/776, anterior chevron (Figure 3A–E).

Description: DfMMh/FV/776 is a chevron from an anterior position within the caudal vertebral series. The chevron consists of a well-preserved haemal arch and an incompletely preserved haemal spine. The haemal spine is crushed in the distal third of its preserved length, and the distal tip is broken and not preserved. The preserved parts of DfMMh/FV/776 measure c. 110 mm.

The haemal arch consists of two lateral processes that border the haemal canal, and a proximal articular surface that is buttressed by the lateral processes. The lateral chevron processes and the haemal spine are angled strongly posteriorly in respect to the articulation surface (Figure 3B, D). The haemal canal is vaguely triangular and proximally broader than distally (Figure 3A, C). It measures 12 mm across its widest part, and is 16 mm high. The lateral processes are anteriorly expanded to convex flanges that expand the lateral wall of the haemal canal anteriorly. These flanges are relatively small, and form symmetrically rounded anterior margins (Figure 3B, D). A similar, yet much less prominent posterior expansion of the lateral processes is present. The articulation surface of DfMMh/FV/776 is anteroposteriorly narrow, measuring 11 mm, and transversely broad, measuring 35 mm. The articulation facet is not subdivided into interior and posterior subfacets for the preceding and successive caudal vertebral articulations, but the topology of the surface is also not uniform (Figure 3E). Instead, the articulation surface is convexly rounded to either side laterally and concavely depressed centrally. The margin surrounding the articulation surface is gently elevated, which is particularly prominent on the posterior side.

The haemal spine is elongate and slender, and has approximately parallel anterior and posterior margins. It forms a straight process that is not posteriorly kinked or curved. The transverse width of the haemal spine decreases from 8 mm proximally, to 4 mm at its broken distal end. DfMMh/FV/776 has a low but prominent medial keel on the anterior surface of the haemal spine (Figure 3A). The keel has a sharp margin and is deepest proximally, where it forms a low anteriorly projecting flange. The proximal part of the posterior surface of the haemal spine shows a broad groove, which is continuous with the posterior opening of the haemal canal. This groove gets shallower distally and is replaced by a low median keel in the central parts of the haemal spine. The posterior keel becomes more prominent distally, and develops to a ridge-like posterior margin in the distal third of the preserved haemal spine length.

Remarks: DfMMh/FV/776 can be identified as an anterior chevron of a large theropod dinosaur, because of the presence of anterior flanges of the lateral process, which are only present in theropods (Rauhut, 2003*a*). Because of its rod-like haemal spine, DfMMh/FV/766 is a chevron from the anterior part of the caudal axial series. Theropod chevrons are not well described in the literature, making a precise taxonomic assessment of DfMMh/FV/776 difficult. However, a few general comparisons can be made. The relatively robust, weakly posteriorly oriented haemal arch is widespread among neotheropods, including non-tetanurans (e.g. *Dilophosaurus wetherilli*: Welles, 1984; *Ceratosaurus* sp.: Madsen & Welles, 2000) and tetanurans (e.g. *Allosaurus fragilis*: Madsen, 1976). Most theropods show a subdivision of the articular facet into an anterior and a posterior subfacet, which are usually separated by a transverse ridge. DfMMh/FV/766 lacks such a subdivision, and instead has a single articular facet. Carrano, Benson & Sampson (2012) found chevrons without a subdivided facet but low lateral mounds on each side as a putative synapomorphy of Megalosauroidea (e.g. present in *Torvosaurus tanneris*, *Baryonyx walkeri*, *Afrovenator abakensis*). However, undivided articulation facets have also been described for chevrons of ceratosaurs (Bonaparte, Benson & Coria, 1990; Coria & Salgardo, 1998; O'Connor, 2007), some of which show this feature only in the first chevron (e.g. *Majungasaurus crenatissimus*: O'Connor 2007). This indicates that the character has a wider distribution than recognized by Carrano, Benson & Sampson (2012). The relatively small size of the anterior flanges of DfMMh/FV/776 matches the condition ~~for~~ described ceratosaurs better than for megalosauroids, in which the flanges are either absent altogether (e.g. *Baryonyx walkeri*: Charig & Milner, 1998), or relatively pointed (e.g. *Torvosaurus tanneri*: Britt, 1991). Allosauroids usually have more prominent and anteriorly pointed anterior flanges (e.g. Madsen, 1976; Zanno & Makovicky, 2013; Malafaia *et al.*, 2016), making it unlikely that DfMMh/FV/776 represents an allosauroid. The straight haemal arch of DfMMh/FV/776 is also compatible with ceratosaurian affinities (e.g. *Ceratosaurus* sp.: Madsen & Welles, 2000; *Carnotaurus sastrai*: Bonaparte, Benson & Coria, 1990), but is also observed in some megalosaurs such as *Torvosaurus tanneri* (Britt, 1991). Based on these limited comparisons, DfMMh/FV/776 is most compatible with the chevron morphology observed in ceratosaurs, although megalosauroid affinities cannot be ruled out entirely.

Dinosauria Owen, 1842
Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
cf. Megalosauroidea (Fitzinger, 1843) Walker, 1964

Material: DfMMh/FV/287, left fibula (Figure 4A–E).

Description: DfMMh/FV/287 is a partially preserved left fibula, in which the distal end is missing. The proximal part of the fibula is expanded anteroposteriorly to form the fibular head, and distally the element forms a slender shaft (Figure 4A–E). The expansion of the fibular head relative to the shaft is asymmetric, and proportionally stringer on the posterior side: The posterior margin of the fibular head forms a convexly rounded process, which is separated from more distal parts of the fibula by a gentle notch. The posterior margin of the fibular head is formed as a transversely thin edge. In contrast, the anterior side of the fibular head expands more gradually, and forms a relatively thick and rounded margin. The fibular head is inflected medially (i.e. toward the tibia) at its anterior side, giving the proximal articular surface a crescentic outline (Figure 4C). On the medial surface, the fibular head bears a shallow, concave fossa (Figure 4E). The fossa is limited to the anterior and central parts of the medial surface, and does not extend onto the thin posterior expansion of the fibular head. Anteriorly, the fossa is well defined by a vertically projecting anteromedial ridge. The fossa extends distally to the level of the tubercle for the *M. iliofibularis*, and is developed as a deep trough just proximally to the tubercle. It remains unclear, if the present depth of the fossa is natural in this part of the bone, ~~of~~ if slight crushing hypertrophied this structure.

The proximal part of the fibula tapers distally to the level of the notch, until it reaches the tubercle for the *M. iliofibularis*. This tubercle is developed as a bulbous swelling with a rugose surface texture, which makes the fibula appear expanded in this part (Figure 4E). The tubercle is located on the anteromedial side of the bone, but covers most of the medial surface of the fibula as well.

Distally to the tubercle for the *M. iliofibularis*, the fibular shaft extends as a slender and rod-like structure. The fibular shaft is kinked posteriorly on respect to the proximal third of the fibula, but is ~~itself~~ straight. The shaft retains its width and depth along the rest of its preserved length. The fibular shaft is slightly longer anteroposteriorly than it is transversely wide, and it is conspicuously concavo-concex, whereby the lateral surface of the ~~cone~~ is strongly convexely rounded. The medial surface of the shaft is furrowed by a longitudinal groove. The distal end of the fibula is broken off, so that it is unclear if and how the bone expands to articulate with the tarsus.

Remarks: The fibula DfMMh/FV/287 can be assigned to the Theropoda because of the presence of a marked M. iliofibularis tubercle, which is only found in theropods among dinosaurs (Rauhut, 2003*a*). Within Theropoda, DfMMh/FV/287 represents a member of the Averostra, because of the presence of the fossa on the medial surface of the fibular head, which is absent in earlier branching lineages such as coelophysids (Rauhut, 2003*a*). It is unlikely that DfMMh/FV/287 belongs to a ceratosaur, because the fossa on the medial surface ~~of ceratosaurs~~ is usually very deep and anteriorly and posteriorly bound by well-defined ridges (e.g. *Ceratosaurus* sp.: UMNH VP 5278, Madsen & Welles, 2000; *Eoabelisaurus mefi*: Pol & Rauhut, 2012; *Elaphrosaurus bambergi*: Rauhut & Carrano, 2016). Additionally, the medial surface of the shaft is not concave in ceratosaurs such as *Ceratosaurus* (UMNH VP 5278), whereas this is the case in basal tetanurans, including allosauroids (e.g. *Allosaurus fragilis*: UMNH VP 7949) or megalosauroids (e.g. *Afrovenator abakensis*: UC OBA 1). Among the Tetanurae, DfMMh/FV/287 is most similar to megalosauroids, some of which share the unusually shallow medial fossae with DfMMh/FV/287 (e.g. *Suchomimus tenerensis*: MNN GDF501; *Torvosaurus tanneri*: BYU VP 9620; Britt, 1991; Benson, 2010). In allosauroids, such as *Allosaurus fragilis* (Madsen, 1976), *Neovenator salerii* (MIWG 6348; Brusatte *et al.*, 2008), or *Australovenator wintonensis* (White *et al.*, 2013), the medial fossae are usually deeper, and proximally well bound by a sharp margin, whereas the fossa on DfMMh/FV/287 simply becomes shallower proximally.

Dinosauria Owen, 1842
Theropoda Marsh, 1881
cf. Tetanurae Gauthier, 1986

Material: DfMMh/FV/105, distal caudal vertebra (Figure 3F–K).

Description: DfMMh/FV/105 is identified as a distal caudal vertebra based on its general centrum dimensions and development of neural arch processes. The vertebra is incomplete, as the posterior intervertebral articulation is ventrally splintered and transversely incomplete, and the prezygapophyses are broken at their bases. However, the delicate postzygapophyses are preserved.

The centrum of DfMMh/FV/105 is anteroposteriorly elongate and measures 33 mm in length. The intercentral articulations are thus broader than high (12 mm wide and 9 mm high for the anterior facet; Figure 3H), and reniform in shape. The facets are slightly concave, and the vertebra is accordingly amphyplatian/amphicoelous. The exposed anterior intercentral articulation is dorsoventrally and transversely expanded in relation to the mid-centrum, so that the centrum is centrally gently constricted. The lateral surface of the centrum bears a longitudinal ridge on either side, which is sometimes observed in posterior caudal vertebrae past the transition point, i.e. the vertebral position after which the transverse processes are fully reduced in theropod dinosaurs. A cross-section through the central part of the centrum would be hexagonal because of the lateral ridge on either side.

The neural arch is low and elongate (Figure 3F–K), but does not cover the centrum from end to end. Instead, the neural arch is removed from the dorsal margin of the anterior and posterior intercentral articulations, exposing a broad floor of bone anterior to the entry and posterior to the exit of the neural canal. The prezygapophyses are broken off, but their remaining pedicles suggest that they were larger than the postzygapophyses, and diverged slightly from the midline, as commonly found in theropods. The neural arch between the pre- and postzygapophyses is a continuously low table of bone, which is transversely narrower than the centrum.

The postzygapophyses are delicate processes (Figure 3J–K), which are only weakly diverged from the midline. They overhang the posterior end of the centrum by a few millimetres. The postzygapophyses are slightly twisted, so that their articulation facets point progressively more ventrally as they are approaching their distal tip; while the articulation facets are basically laterally oriented at the base of the postzygapophyses, the facets have a strongly lateroventral inclination at their tips. This suggests, that the (unpreserved) prezygapophyses reached far onto preceding vertebrae, as is the case for many theropods.

The dorsal surface of the neural arch is completely flat in the anterior and central part of the vertebra, but a small, ridge-like protrusion can be found in between of the postzygapophyses. This protrusion likely represents a low neural spine, which gets progressively reduced along the caudal vertebral series of theropods.

Remarks: DfMMh/FV/105 is identified to be a theropod, and most likely a basal tetanuran, primarily on the basis of relatively elongate prezygapophyses (indicated by the position and shape of the postzygapophyses). In non-theropod dinosaurs, as well as more basal theropods such as *Dilophosaurus wetherilli* or *Ceratosaurus* sp., the prezygapophyses are generally much shorter in distal caudal vertebrae and do not extend far beyond the preceeding vertebra (Rauhut, 2003*a*).

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Material: DfMMh/FV2/19, a small pedal phalanx III-1 (Figure 2K–P).

Description: DfMMh/FV2/19 is nearly completely preserved phalanx, with minor damage near the extensor groove, the right dorsal margin of the proximal facet, and around the ventral surface near the proximal end of the bone. The small phalanx is identified as a first pedal phalanx of the third digit of a theropod dinosaur, because of its broad and ventrally relatively flat proximal end, the non-saddle shaped proximal articulation surface, relatively long phalangeal shaft, and ginglymoid distal joint. It is unlikely that the phalanx represents a manual element, as the combination of a broad proximal end and a concave proximal joint surface are usually not found in manual phalanges (the first phalanx of the first manual digit usually has a saddle-shaped joint to mirror the condition of the first metacarpal, and the first phalanx of the manual second digit is usually relatively slender and less broad; e.g. *Allosaurus fragilis*: Gilmore, 1920, Madsen, 1976).

DfMMh/FV2/19 is relatively elongate and slender: It measures 10 mm proximodistally and a ~~true~~ phalangeal shaft separates the proximal and distal joints. This morphology is consistent with a first or second phalangeal position of the second or third digit, as other phalanges are usually stout and lack long phalangeal shafts (e.g. *Allosaurus fragilis*: Madsen, 1976). The phalangeal shaft of DfMMh/FV2/19 is transversely constricted in respect to the proximal and distal articulations, and is near circular in cross-section.

The proximal surface of DfMMh/FV2/19 is dorsally rounded and ventrally flat, therefore being 'D'-shaped (Figure 2M). It is 5 mm wide transversely, and 3 mm high dorsoventrally. The proximal articular surface is a single deep concavity. This is typical of first phalanges, which articulate with the broad trochlea of the metatarsalia, while more distally positioned phalanges usually have a saddle-shaped proximal joint that receives the condyles of preceding ginglymoid articulations typical for phalanges. The right dorsal margin of the proximal joint is unfortunately partly broken, but it seems that an extensor tubercle was very small if present at all. This again fits the morphological expectations for a first pedal phalanx.

The distal joint is ginglymoid, with a lateral and medial condyle (although it is not sure, which side is medial and which is lateral as it is currently not known whether the phalanx represents a left or right element) (Figure 2P). Both condyles are subequal in size, and are separated from one another by a vertical intercondylar sulcus, that curves around the distal end of the bone. The condyles are slightly rotated anteriorly, so that they are ventrally stronger expanded than dorsally, and inclined outwards, so that the intercondylar sulcus gets broader anteroventrally. The sulcus opens into a shallow flexor groove posteriorly and ventrally. On the dorsal surface, just proximally to the condyles, there is a relatively deep extensor groove present, but its depth might be exaggerated by minor breakage around this part. Collateral ligament pits are hard to discern on the phalanx; on one side, it appears that no pit is present at all, and on the other side there is only a minor depression near the dorsal surface of the condyle (Figure 2O).

Remarks: The phalanx DfMMh/FV2/19 is herein identified as belonging to an indeterminate theropod dinosaur. The relatively strongly ginglymoid distal articulation and 'D'-shaped proximal articulation, combined with a relatively narrow and long phalangeal shaft are consistent with this interpretation. Phalanges of Jurassic turtles such as thalassochelydians have flatter shafts, often more broadly expanded proximal and distal ends, and the articular surfaces are less pronounced than in DfMMh/FV2/19 (e.g. *Eurysternum wagleri*, BSPG 1960 VIII 43). Pseudosuchian phalanges, for example from the Late Jurassic crocodyliform *Alligatorellus* sp., are usually more elongate and gracile than observed for DfMMh/FV2/19 (e.g. Tennant & Mannion, 2014).

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Material: DfMMh/FV3/19, proximal part of a small right fibula (Figure 4F–J).

DfMMh/FV3/19 is a small fragment of a long bone, as it preserves parts of a shaft and one expanded terminal end. This specimen is herein identified as the proximal end of a right fibula of a theropod. The expanded proximal end of the specimen is relatively thick on one side, and thin-edged on the other side. The thicker side is interpreted to be the transversely expanded anterior side of the fibula (Figure 4F), and the thin-edged side is interpreted to be the posterior margin of the fibula (Figure 4I). However, fibulae are usually posteriorly stronger expanded than anteriorly, which is not the case in DfMMh/FV3/19. The presence of a large but shallow depression on what is interpreted as the medial side is consistent with the gross anatomy of a fibula.

The anterior and posterior sides of DfMMh/FV3/19 are slightly arched inwards towards the proximal end of the bone, so that the fibular head is gently crescentic. The surface of the articular facet is domed in its central part, and dips ventrally on the anterior side (Figure 4H). The anterior margin of the articular facet forms a small lip that protrudes slightly anteriorly. The lateral surface of the fibular head is convexly rounded but becomes relatively flat towards the posterior side of the specimen. Just beneath the articular surface, the rounded anterior margin of DfMMh/FV3/19 is raised to a short tubercle or protuberance with slightly rugose surface texture that indicates the origin or insertion of some soft tissue structure. Posteriorly, the sharp-edged margin of the bone extends ventrally toward the shaft, and levels off reaching before the shaft.

On the medial side, the fibular head is characterised by a low, vaguely triangular concavity (Figure 2J). The concavity is not well defined to either side, and spans more or less the entire space of the fibular head. The concavity narrows distally where it approaches the shaft, and finally vanishes just prior to a medial thickening of the fibular shaft.

The fibular shaft is broken shortly distal to the fibular head. The cross section of the break shows that the fibular shaft was circular in its proximal part.

Remarks: The described morphology of DfMMh/FV3/19 is consistent with its identification of an indeterminate theropodan fibula.

Discussion

Most German finds of Late Jurassic theropods are confined to the lagerstätten deposits of the Solnhofen area in Southern Germany, and include coelurosaurian theropods such as *Juravenator starki* (Göhlich & Chiappe, 2006), *Archaeopteryx lithographica* and closely related avian theropods (e.g. Foth, Tischlinger & Rauhut, 2014; Foth & Rauhut, 2017; Rauhut *et al.*, 2019), as well as the megalosauroid *Sciurumimus albersdoerferi* (Rauhut *et al.*, 2012). Relatively complete theropod material from Northern Germany has been found in about 10 Ma older deposits from the Callovian, and belongs to the megalosauroid *Wiehenvenator albati* (Rauhut, Hübner & Lanser, 2016). On the basis of isolated teeth, Gerke & Wings (2016) found evidence for the presence of tyrannosauroids, allosauroids, megalosauroids, and ceratosaurs in the Langenberg

Quarry. However, the findings of van der Lubbe, Richter & Knötschke (2009), who reported on the presence of velociraptorine teeth from the Langenberg Quarry, could not be confirmed (Gerke & Wings, 2016). The fossils described in this contribution, interpreted as belonging to allosauroid, megalosauroid, ceratosaurian, and indeterminate theropods, represent the first body fossil evidence of theropods for the Langenberg Quarry. All of our material belongs to relatively small individuals. The ontogenetic stages of the material are currently unknown, but the presence of large theropod tracks in the Langenberg Quarry (Lallensack *et al.*, 2015) demonstrates that large-bodied individuals were at least temporarily present in the habitat of today's Langenberg Quarry. The fossil tooth, body fossil, and track record from Langenberg indicates a relatively high diversity of basal averostrans (i.e. ceratosaurs and basal tetanurans), which are rare elements of the Solnhofen archipelago limestone deposits. Despite the regional differences in faunal composition between different German basins, and although the Late Jurassic theropod fauna of Germany remains patchy, it is clear that all major groups of theropods that lived during the Late Jurassic were also present in Germany.

The Late Jurassic theropod dinosaur record in other parts of Europe is mostly similarly patchy, but also confirms the presence of several theropod lineages in Europe during the Late Jurassic. From the United Kingdom, diagnostic material is known from several formations and several stages of the Late Jurassic. For instance, the tyrannosauroid *Juratyrant langhami* is known from the Tithonian Kimmeridge Clay (Benson, 2008; Brusatte & Benson, 2013), whereas the allosauroid *Metriacanthosaurus parkeri* and the megalosauroid *Eustreptospondylus oxoniensis* are known from the older, Callovian–Oxfordian, Oxford Clay (Sadleir, Barrett & Powell, 2008; Carrano, Benson & Sampson, 2012).

Some of the best and most complete theropod material in Europe comes from Late Kimmeridgian–Tithonian formations in the Lusitanian Basin of Portugal, including the Lourinhã and Alcobaça Formations. The Portuguese theropod fauna includes the allosauroid *Allosaurus europaeus* (Mateus, Walen & Antunes, 2006), the ceratosaur *Ceratosaurus* sp. (Mateus & Antunes, 2000), the megalosauroid *Torvosaurus gurneyi* (Hendrickx & Mateus, 2014; Malafaia *et al.*, 2017), the allosauroid *Lourinhanosaurus ~~antuneso~~* (Mateus, 1998; Benson, 2010), the tyrannosauroid *Aviatyrannis jurassica* (Rauhut, 2003*b*). The faunal composition of the Portuguese record has been interpreted to be very similar to the much better documented equivalent North American fauna from the Morrison Formation (Mateus, 2006; Mateus, Walen & Antunes, 2006; Pol & Rauhut, 2012; Hendrickx & Mateus, 2014).

Conclusions

We present new occurrences of theropod dinosaurs from the Late Jurassic Langenberg Quarry of northern Germany. The incomplete material can be assigned to certosaurian, megalosauroid, and allosauroid theropods. These identifications agree with previous reports of the presence of these theropod groups in the Late Jurassic of Northern Germany based on teeth. Although the

Langenberg theropod fauna is not as rich as some other European localities, such as the Lourinhã Formation of Portugal, our findings confirm a varied dinosaur fauna in central Europe and add to our incomplete understanding of theropod diversity and evolution during the Late Jurassic of Europe.

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Figure 1

Geographic location of the Langenberg Quarry in the Harz Mountains of Germany.

(A) Map of Germany with the Harz Mountains highlighted in grey and Langenberg Quarry (LQ) indicated by star. (B) Close-up of the Harz Mountain area with Langerberg Quarry and nearby towns indicated.

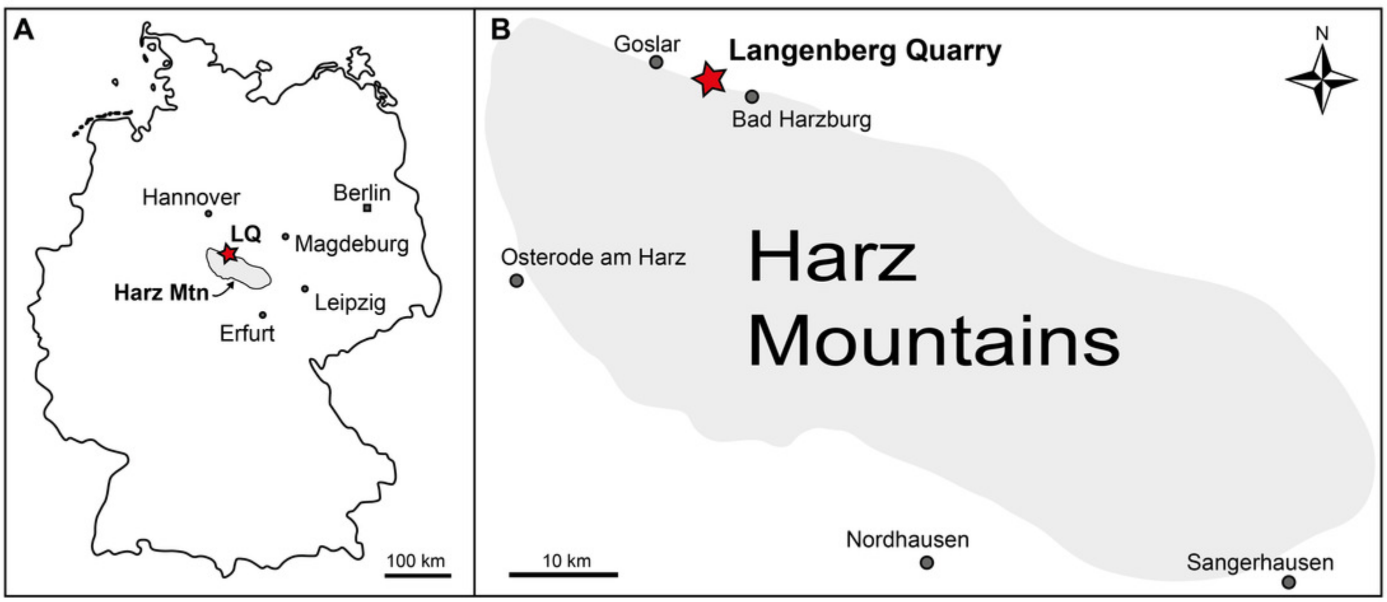

Figure 2

Isolated theropodan phalangeal elements from the Langenberg Quarry.

DfMMh/FV1/19, pedal ungual, in (A) dorsal view, (B) ventral view, (C) left lateral view, (D) right lateral view. DfMMh/FV/343, pedal phalanx, in (E) dorsal view, (F) ventral view, (G) distal view, (H) left lateral view, (I) right lateral view, (J) distal view. DfMMh/FV2/19, pedal phalanx, in (K) dorsal view, (L) ventral view, (M) distal view, (N) left lateral view, (O) right lateral view, (P) distal view. Abbreviations: cg, collateral groove; ext, extensor tubercle; fxf, flexor fossa; fxt, flexor tubercle; lp, ligament pit. All scale bars equal 5 mm.


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C
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cg
fxt
E
F
G
ext
fxf
H
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lp
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lp

Figure 3

Isolated theropoda axial elements from the Langenberg Quarry.

DfMMh/FV/776, chevron, in (A) anterior view, (B) left lateral view, (C) posterior view, (D) right lateral view, (E) anterodorsal view on proximal articular surface. DfMMh/FV/105, distal caudal vertebra, in (F), ventral view, (G) dorsal view, (H) anterior view, (I) posterior view, (J) left lateral view, (K) right lateral view. Abbreviations: ak, anterior keel; hc, hemal canal; poz, postzygapophysis. Scale bar in A–E equals 20 mm, scale bar in F–K equals 10 mm.

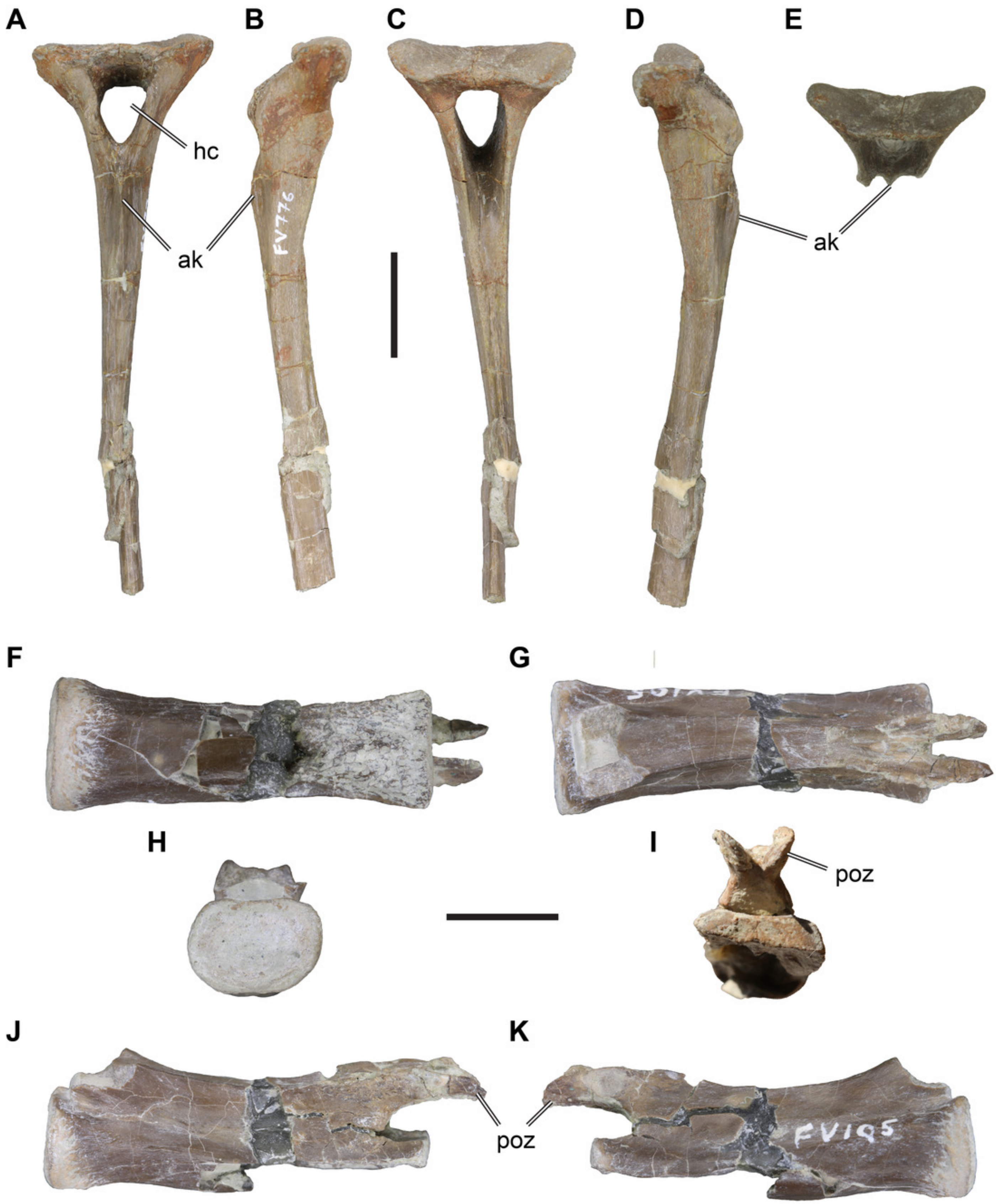
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Figure 4

Isolated theropodan fibulae from the Langenberg Quarry.

DfMMh/FV/287, left fibula in (A) anterior view, (B) medial view, (C) proximal view, (D) posterior view, (E) medial view. DfMMh/FV3/19, partial right fibula in (F) anterior view, (G) lateral view, (H) proximal view, (I) posterior view, (J) medial view. Abbreviations: g, groove; mf, medial fossa; pr, posterior ridge; tif, tubercle for the M. iliofibularis. All scale bars equal 20 mm.


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