

The oldest record of the genus *Torvosaurus* (Theropoda: Megalosauridae) from the Callovian Ornatenton Formation of north-western Germany

Oliver W. M. Rauhut, Achim H. Schwermann, Tom R. Hübner & Klaus-Peter Lanser

Oliver W. M. Rauhut
SNSB, Bayerische Staatssammlung
für Paläontologie und Geologie
Sektion Paläontologie und
Geobiologie, Department für Geo-
und Umweltwissenschaften
Ludwig-Maximilians-Universität;
GeoBioCenter
Ludwig-Maximilians-Universität;
Richard-Wagner-Str. 10
80333 München
Germany

Achim H. Schwermann &
Klaus-Peter Lanser
LWL-Westfälisches Museum für
Naturkunde
Westfälisches Landesmuseum mit
Planetarium
Sentruper Str. 285
48161 Münster
Germany
(Current address for K.-P. Lanser:
Langebusch 9, 48159 Münster,
Germany)

Tom R. Hübner
Stiftung Schloss Friedenstein
Gotha
Schloss Friedenstein
Schlossplatz 1
99867 Gotha
Germany

Corresponding author:
rauhut@snsb.de

Manuscript
Received: 03.06.2020
Accepted: 07.09.2020
Available online: 06.10.2020

© LWL-Museum für Naturkunde

Abstract

A fragmentary maxilla from the middle Callovian Ornatenton Formation of the Wiehengebirge, north-western Germany, shows two autapomorphies of the theropod dinosaur genus *Torvosaurus*, a maxilla fenestra that is developed as a large and shallow but not sharply defined depression and an anteroposteriorly oriented ridge transversing the ventral part of the maxillary fenestra. This specimen represents the first occurrence of this genus from Germany and the oldest record of *Torvosaurus*, which is otherwise securely known from the Kimmeridgian-Tithonian of Portugal and the western USA. Given that the two closest relatives of *Torvosaurus*, *Megalosaurus* and *Wiehenvenator*, are known from the Bathonian of England and the Callovian of Germany, respectively, an evolutionary origin of derived megalosaurines in north-central Europe is indicated. The records of *Torvosaurus* in the Kimmeridgian-Tithonian of Portugal and the Morrison Formation of the western USA most probably represent dispersal of the genus from this area in the Late Jurassic.

Key words: Middle Jurassic, Europe, Germany, Tetanurae, Megalosauridae, *Torvosaurus*

Kurzfassung

Eine fragmentarische Maxilla aus der mittel-callovischen Ornatenton-Formation aus dem Wiehengebirge (nördliches Nordrhein-Westfalen, Deutschland) zeigt zwei Autapomorphien der theropoden Dinosaurier-Gattung *Torvosaurus*, ein Maxillarfenster, das nur als große, flache, aber nicht scharf begrenzte Depression entwickelt ist, und einen schräg von posteroventral nach anterodorsal verlaufenden Grat im unteren Teil des Maxillarfensters. Dieser Rest stellt somit den ersten Nachweis dieser Gattung aus Deutschland und den ältesten Fund von *Torvosaurus* generell dar, der bisher nur aus dem Kimmeridgium-Tithonium von Portugal und der USA bekannt ist. Da die beiden nächsten Verwandten von *Torvosaurus*, *Megalosaurus* und *Wiehenvenator*, aus dem Bathonium von England und dem Callovium von Norddeutschland stammen, weist dies auf einen Ursprung der fortschrittlichen Megalosaurinen im nördlichen Mitteleuropa hin. Die Vorkommen von *Torvosaurus* im Kimmeridgium-Tithonium von Portugal und der Morrison Formation Nordamerikas dürfte somit durch eine Einwanderung dieser Gattung im oberen Jura erklärt werden.

Schlüsselwörter: Mittlerer Jura, Europa, Deutschland, Tetanurae, Megalosauridae, *Torvosaurus*

Introduction

Megalosaurids represent the first successful radiation of the Tetanurae, the most important lineage of theropod dinosaurs, which also includes modern birds (Benson 2010a; Carrano et al. 2012; Rauhut et al. 2016; Rauhut & Pol 2019). The oldest representatives of this clade appear in the fossil record in the earliest Bajocian (Benson 2010b), and the family is taxonomically diverse, especially in Europe, in the late Middle Jurassic (Bathonian–Callovian; Carrano et al. 2012; Rauhut et al. 2016). However, if a Middle Jurassic age is assumed for the African taxon *Afrovenator* (Sereno et al. 1994; Rauhut & López-Arbarello 2009), only few megalosaurids have been identified from the Late Jurassic. Apart from the Callovian–Oxfordian taxon *Streptospondylus* (Allain 2001) and the so far only preliminarily described *Leshansaurus* from China (Li et al. 2009), the best known Late Jurassic megalosaurid is the genus *Torvosaurus*, with two species, the North American *Torvosaurus tanneri* (Galton & Jensen 1979; Britt 1991) and the European *Torvosaurus gurneyi* (Hendrickx & Mateus 2014). The occurrences of *Torvosaurus* in the Tithonian of the Morrison Formation and the Lusitanian Basin are the youngest records of megalosaurids; the clade apparently went extinct at the end of the Jurassic.

Other Late Jurassic occurrences of megalosaurids are usually fragmentary, undiagnostic at species or genus level, and/or of questionable affinities (see overview in Rauhut et al. 2018). An exception to the fragmentary nature of most remains is the excellently preserved type specimen of *Sciurumimus*, which was found to be a megalosaurid in at least one of the analyses carried out by Rauhut et al. (2012). However, as this taxon is based on an early post-hatchling individual and possible ontogenetic changes in basal tetanurans are poorly understood, the exact affinities of this taxon should be regarded as uncertain at the moment. Some fragmentary remains, such as a poorly preserved maxilla fragment and a tibia from the Kimmeridgian Kimmeridge Clay Formation of England show megalosaurid affinities and are similar to *Torvosaurus* and thus might represent the same genus (Benson & Barrett 2009; Carrano et al. 2012). The Gondwanan Late Jurassic theropod fossil record is exceedingly poor (Rauhut & López-Arbarello 2008), and remains of a large, robustly built megalosauroid from the Tendaguru Formation (Rauhut 2011) might represent either a megalosaurid, or a spinosaurid. Recently, Soto et al. (2020) identified the genus *Torvosaurus* from the Tendaguru Formation and the Tacuarembó Formation of Uruguay on the basis of isolated teeth. However, even though these teeth might be referable to megalosaurids, an identification on lower taxonomic levels, such as genera, should be seen with caution. With the possible

exception of *Leshansaurus* (Carrano et al. 2012), no megalosaurids have so far been reported from the Late Jurassic of Asia.

Torvosaurus is one of the most recently recognized, but at the same time one of the largest taxon of theropod from the Morrison Formation (Galton & Jensen 1979; Britt 1991). As noted by Hanson & Makovicky (2014), the genus is not only recognizable because of its large size, but also because of the massiveness of its bones, a feature that it shares with its closest relatives *Megalosaurus* and *Wiehenvenator* (Benson 2010a; Rauhut et al. 2016). Although Foster (2007) noted that *Torvosaurus* is the second most abundant theropod taxon in the Morrison Formation, few specimens have been recorded so far, and the vast majority are fragmentary and occur in multi-taxon bonebeds in association with the much more abundant *Allosaurus* (Hanson & Makovicky 2014). Likewise, the European species of *Torvosaurus* is also the largest and most massive theropod dinosaur from the Late Jurassic of this continent, but, although megalosaurids seem to have been less rare in the European Late Jurassic than in North America (Rauhut et al., 2018), all specimens recorded so far are fragmentary (Antunes & Mateus 2003; Mateus et al. 2006; Malafaia et al. 2008, 2017a; Hendrickx & Mateus 2014).

The occurrence of shared taxa in the Morrison Formation and the Lusitanian Basin has been recognized repeatedly recently (e.g., Pérez-Moreno et al. 1999; Antunes & Mateus 2003; Mateus 2006; Escaso et al. 2007; Malafaia et al. 2007, 2015), but the direction of faunal exchange is largely unclear. Mateus (2006) considered it to be more likely that the shared taxa in the Lusitanian Basin result from immigration events from North America, whereas Hendrickx & Mateus (2014) noted that the close relationship between *Torvosaurus* and the Middle Jurassic English taxon *Megalosaurus* might indicate a dispersal of this genus from Europe to North America.

Here we report a fragmentary theropod specimen from the Callovian Ornatenton Formation of Westphalia, north-western Germany, which can be referred to the genus *Torvosaurus* and thus represents the oldest record of this genus.

Abbreviations

BYU	Brigham Young University, Provo, USA
ML	Museu da Lourinhã, Lourinhã, Portugal
OUMNH	Oxford University Museum of Natural History, Oxford, England, UK
SHN	Sociedade de História Natural, Torres Vedras, Portugal
UC	University of Chicago, Chicago, USA
UMNH	Utah Museum of Natural History, Salt Lake City, USA
WMNM	LWL-Museum für Naturkunde, Münster, Germany

Geological and paleontological context

The specimen comes from the Ornatenton Formation of the locality of Lutternsche Egge in the Wiehengebirge, close to the city of Minden (Fig. 1), from the same locality where the megalosaurid *Wiehenvenator albatii* was reported by Rauhut et al. (2016). The specimen is stored at the paleontological collection of the LWL-Museum für Naturkunde, Münster, Germany (WMNM).

The Ornatenton Formation is a shallow marine sequence dominated by dark, mainly pelitic or fine sandy sediments that crops out both in northern and southern Germany (Rieggraf 1994). In northern Germany, the Ornatenton Formation has three members, from bottom to top the Lower Siltstone Series, the Upper Siltstone Series, and the Phosphoritic Clay Member. The latter is missing in many outcrop areas, thus the Upper Siltstone Series being capped by a condensation horizon that represents a sedimentation gap, followed by the hard sandstones of the Oxfordian Heersumer Beds (Mönning 1993). In the area of Minden, the Ornatenton Formation crops out on the crest of the Wiehengebirge and Weserberge, a chain of low hills with a NW-SE orientation that represents the northernmost outlier of the central German mountain ranges. For details of the section of the locality Lutternsche Egge see Rauhut et al. (2016). The current specimen was found in 1999 some 28 m away from the site that yielded the remains of the only known *Wiehenvenator*-specimen, and most remains were found weathered in the float, with only one piece found in situ just below the condensation horizon. Apart from *Wiehenvenator* and the specimen described here, the vertebrate fauna of the locality Lutternsche Egge includes isolated vertebrae and teeth of the pliosaur *Liopleurodon*.

Nearby outcrops of the Ornatenton have documented other vertebrates in the past. These include various chondrichthyes and osteichthyes, sparse evidence of ichthyosaurs, various plesiosaur remains, as well as skulls, mandibles and postcranial elements of teleosaurid and metriorhynchid crocodiles (Michelis et al. 1996, Waskow et al. 2018). The identification of *Lexovisaurus* could not be confirmed, corresponding finds have rather been assigned to *Leedsichthys* (Liston 2010). Furthermore, a long bone was identified as a possible dryosaurid (Michelis et al. 1996), but this identification is questionable.

Systematic palaeontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Megalosauroida (Fitzinger, 1843)

Megalosauridae Fitzinger, 1843

Torvosaurus Galton & Jensen, 1979

Torvosaurus sp.

Description

The material includes several fragmented remains of a left maxilla (Fig. 2) and a pedal phalanx. Most fragments of the maxillary body were found in the float and are strongly weathered and poorly preserved, but the base of the ascending process, which was found in situ, is well-preserved and shows important anatomical details.

Maxilla

Several fragments represent the maxillary body anterior to and below the anterior end of the antorbital fenestra (Fig. 2, 3). One of these fragments (WMNM P27690 and P27691, which represent the separate, but fitting



Figure 1: Map of north-eastern North Rhine-Westphalia, showing the geographic location of the locality Lutternsche Egge.



Figure 2: Fragments of a left maxilla of *Torvosaurus* from the Ornatenton Formation of Lutternsche Egge, superimposed on the left maxilla of *Torvosaurus tanneri* to show approximate position of preserved parts. Scale bar is 5 cm.

labial and lingual wall of the alveoli of the same part of the maxillary body) fits onto the base of the ascending process (WMNM P80969; Fig. 3A-E) and thus shows the height of the maxillary body below the anterior end of the antorbital fossa (Fig. 2), which was approximately 110 mm. The total height of the maxilla up to the dorsal break of the ascending process is thus c. 250 mm. Two other large fragments (WMNM P 27685 and 27686; Fig. 3F-I) might represent the maxillary body directly in front of the fragment that fits to the base of the ascending process. Although their breaks do not fit exactly, the shapes are close, and fitting them together results in alveoli of congruent sizes. If these two fragments fit in front of WMNM P27690 and P27691, the height of the anterior process of the maxilla right in front of the base of the ascending process can be estimated to be approximately 18 cm.

Two fragments of the maxillary body show broken alveoli that extend high into the maxillary body (Fig. 3I, 4A), as in *Megalosaurus*, *Wiehenvenator* and *Torvosaurus*. The most informative piece of the alveolar border (WMNM P 27690 and 27691), representing a fragment of the mid-section of the maxilla below the base of the ascending process, is broken along the alveolar row, but preserves both the outer and inner surface of the maxillary body (Fig. 3J, K), as well as an unerupted replacement tooth (Fig. 4A, B). The outer surface is high and largely smooth over its entire preserved height (Fig. 3J), showing a very slight

medial inflection at the dorsal break towards the rim of the antorbital fossa. A large, ventrolaterally opening nutrient foramen with a well-developed groove extending ventrally from it is present some 3-4 cm above the alveolar margin at about the mid-width of each of the two preserved alveolous on the lateral side. At the level of the wall separating the alveoli, a smaller and slightly more ventrally placed foramen is found. The ventral margin of the lateral wall is broken off at the level of these foramina and slightly displaced ventrally and medially, being preserved with the medial side of the alveolar wall.

Medially, the interdental plates are poorly preserved (Fig. 3K). They seem to be partially fused, unlike the unfused plates in the megalosaurines *Duriavenator*, *Megalosaurus* and *Wiehenvenator* (Benson 2008, 2010a; Rauhut et al. 2016) and other megalosaurids (Allain 2002; Sadleir et al. 2008; Benson 2010b), but do not form a continuous interdental wall, as it is found in *Torvosaurus* (Britt 1991; Hendrickx & Mateus 2014; Malafaia et al. 2017a). Thus, the plates seem to be fused at about their mid-height, but are separated ventrally, where the more anterior plate preserved terminates in a broad, V-shaped tip, as in *Torvosaurus tanneri* (Britt 1991). Dorsally, there are large suprainterdental plate foramina (Britt 1991) between the interdental plates at the base of the alveoli. Fragments of the paradental lamina are preserved, and the lamina ascends anteriorly, indicating that this fragment probably represents approximately the mid-length

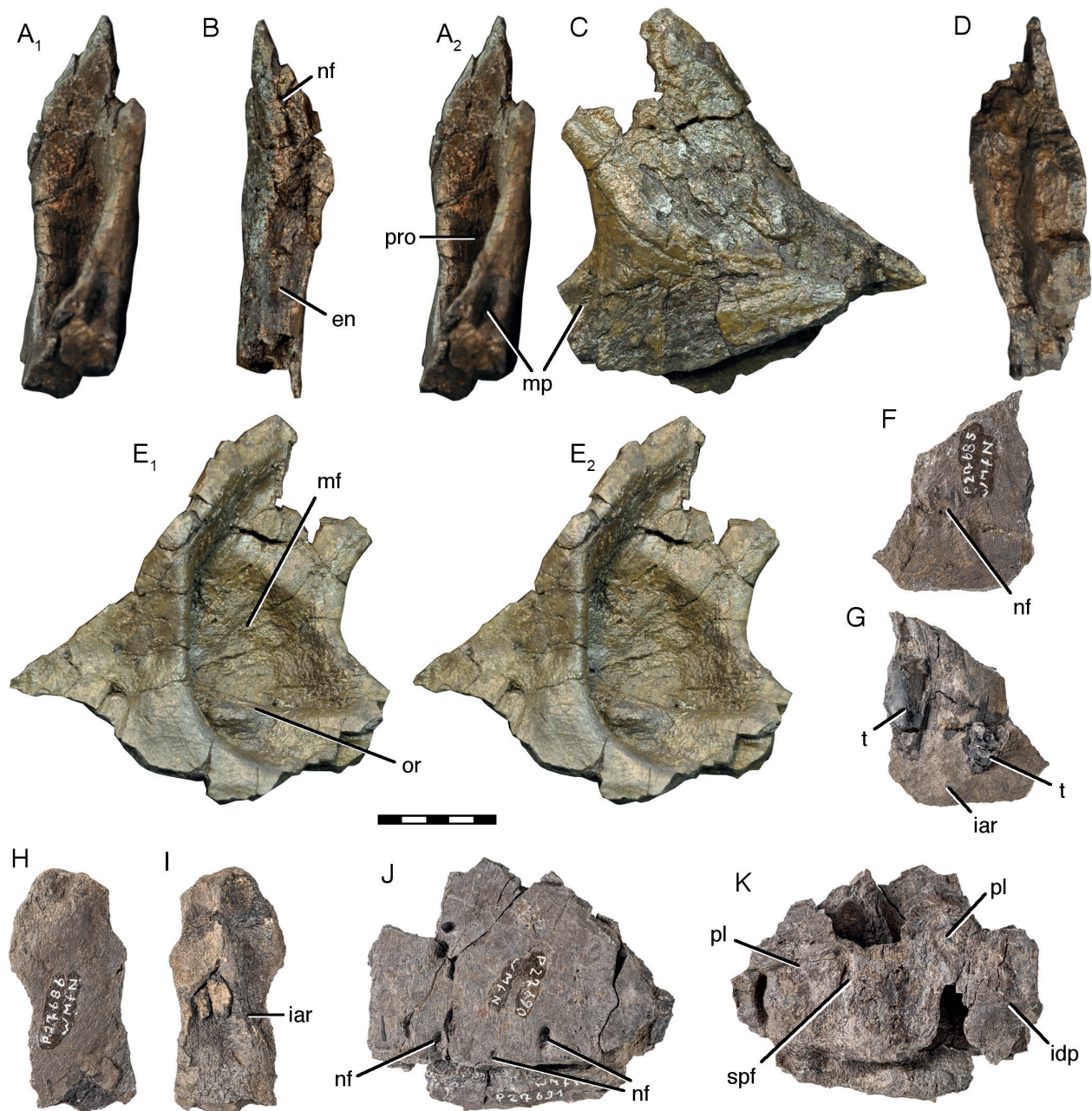


Figure 3: Fragments of a left maxilla of *Torvosaurus* from the Ornatenton Formation of the locality Lutternsche Egge. **A–E**, Base of the ascending process (WMNM P80969) in posterior (A, stereophotographs), anterodorsal (B), medial (C), ventral (D), and lateral (E, stereophotographs) views. **F, G**, Fragment of alveolar border (WMNM P27685) in lateral (F) and medial (G) views. **H, I**, Fragment of alveolar border (WMNM P2786) in lateral (H) and medial (I) views. **J, K**, Part of the maxillary body below the ascending process (WMNM P2690 and P2691) in lateral (J) and medial (K) views. Abbreviations: en, border of external nares; fn, facet for nasal; iar, interalveolar ridge; idp, interdental plate; mf, maxillary fenestra; mp, medial pneumaticity; nf, nutrient foramen; or, oblique ridge; pl, paradental lamina; pro, promaxillary recess; spf, suprainterdental plate foramen; t, tooth. Scale bar is 5 cm.

of the tooth row, as the lamina flexes ventrally in the anterior part in *Torvosaurus* and other megalosaurids (Benson 2010a; Carrano et al. 2012). Ventrally, the interdental plates do not reach the level of the lateral alveolar wall, but fall considerably short, as in *Torvosaurus* (Britt 1991), *Megalosaurus* (Benson 2010a) and *Wiehenvenator* (Rauhut et al. 2016).

The alveoli are elongate oval in outline, being slightly wider in their anterior than their posterior half, and closely spaced, being separated by thin, very slightly

posterodorsally flexed interalveolar walls. The alveoli in total are slightly inclined anteroventrally (Fig. 4A). The more anterior preserved alveolus is c. 40 mm long anteroposteriorly, whereas the second alveolus is considerably smaller, with an anteroposterior length of c. 32 mm.

The most informative fragment of the maxilla is certainly the base of the ascending process (WMNM P80969). Preserved is the base of the ascending process with anterior, anterodorsal, and anteroventral margin of the antorbital fossa as well as the anterior margin of the

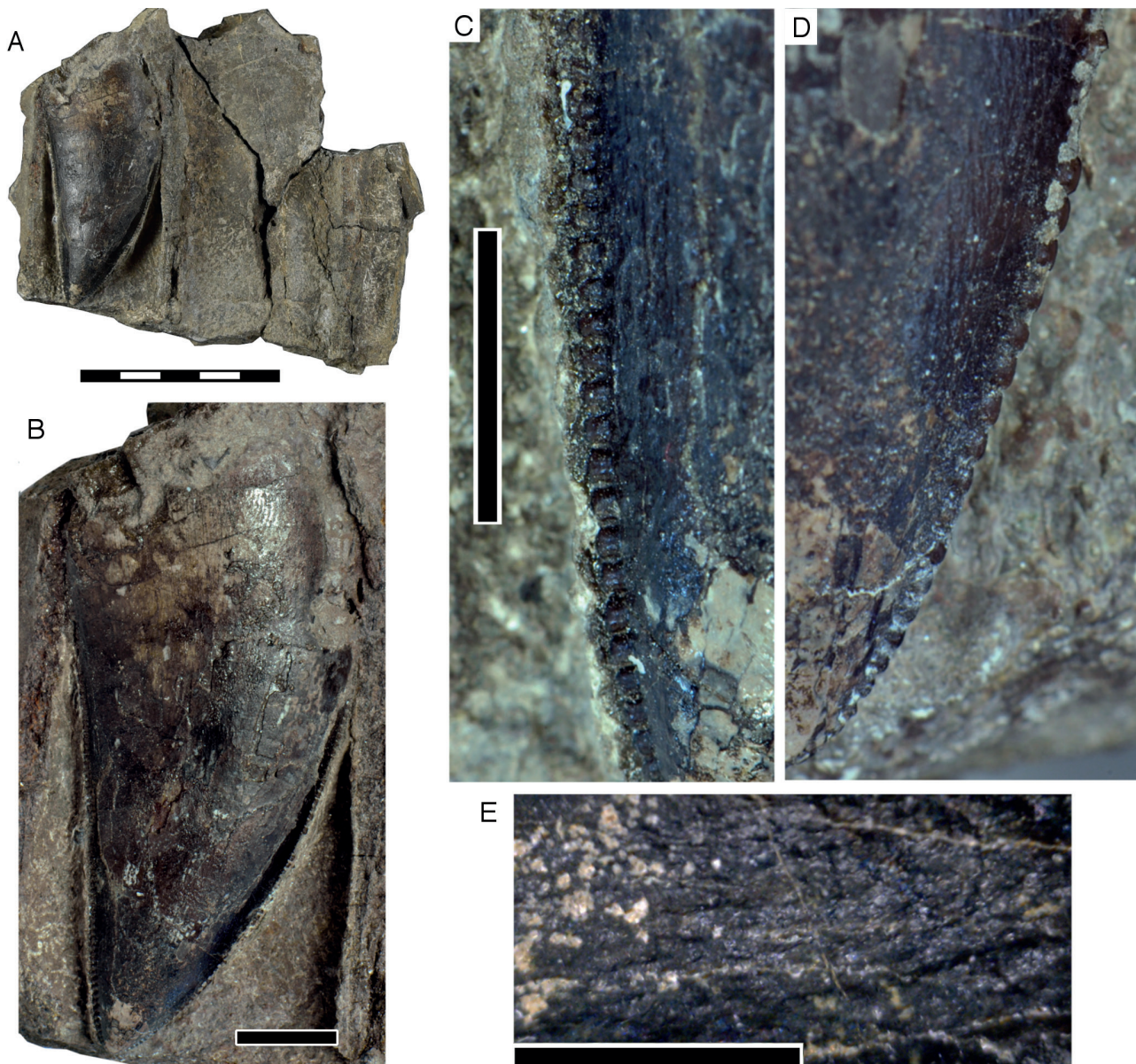


Figure 4: Replacement tooth in the maxillary body (WMNM P27690). **A**, Maxillary body broken along the alveoli in medial view. **B**, Replacement tooth in the posterior alveolus in medial view. **C**, Detail of the distal serrations of replacement tooth. **D**, Detail of the mesial serrations of replacement tooth. **E**, Enamel ornamentation close to the carina. Scale bars are 5 cm (A), 1 cm (B), 5 mm (C, D), and 1 mm (E).

antorbital fenestra and the posterior margin of the narial cavity (Fig. 3A-E). The base of the process is robust transversely, being up to c. 45 mm wide, indicating a generally robust maxillary bone, as in other megalosaurines (Britt 1991; Benson 2010a; Rauhut et al. 2016). The base of the ascending process between the anteriormost margin of the antorbital fenestra and the point where the anterior margin flexes notably dorsally is c. 85 mm long, and the maximum thickness of the base below the anterior end of the antorbital fossa is c. 43 mm.

The anterior margin of the base of the ascending process is generally concave, but with a marked kink in the anterior rim at about a third of the preserved length of the margin. In the dorsalmost preserved part, the anterior margin of the ascending process becomes

convex. The transversely thick anterior margin of the base of the ascending process is poorly preserved, and so nothing can be said about the possible presence of a facet for the posterodorsal process of the premaxilla or the ventral process of the nasal, so that it is unclear whether the maxilla took part in the rim of the external nares. However, the surface seems to have been slightly concave transversely, which might indicate the presence of such a facet.

The anterior rim of the antorbital fenestra is notably concave over its preserved portion. Most of the base of the ascending process anterior to the fenestra is occupied by the antorbital fossa, the margin of which curves from its ventral rim abruptly dorsally at about the anterior third of the base of the ascending process

(Fig. 3E). It extends straight for some 6 cm, until it curves posterodorsally and becomes less conspicuous towards the anterior rim of the ascending process. Anterior to the antorbital fossa, a triangular surface of the lateral side of the ascending process is slightly concave both antero-posteriorly and dorsoventrally.

The antorbital fossa is deeply depressed, especially in the area of the maxillary fenestra, which is developed as a shallow, but large, and not sharply defined depression, which occupies almost the entire ventral part of the base of the ascending process. Anteriorly, the maxillary fenestra is deeply excavated into the anterior rim of the ascending process, forming a promaxillary recess, but without a promaxillary foramen. Ventrally, a stout, dorso-laterally directed and slightly anterodorsally curving ridge transverses the ventral part of the antorbital fossa.

Medially, the base of the antorbital fossa is slightly convex anteroposteriorly. Posteriorly, close to the posterior break, the maxillary body bifurcates below the antorbital fenestra to form a higher and more sharply defined ridge delimiting the antorbital fossa laterally, and a lower, more rounded medial ridge. In between the two ridges, a posterodorsally directed, narrow depression is present (Fig. 3A), the medial pneumaticity of the ascending process of Carrano et al. (2012).

Dentition

Four teeth are at least partially preserved, including two strongly broken replacement teeth in a small alveolar fragment (WMNM P27685; Fig. 3G), a large replacement tooth in the maxillary body (WMNM P27690) below the anterior end of the antorbital fossa (Fig. 4), and two poorly preserved isolated tooth crowns (WMNM P27683 and P27684). Only the replacement tooth in the maxillary body (WMNM P27690) is informative, so most of the description of the dentition is based on this element, but the other tooth fragments confirm the morphology seen in this tooth, as far as this can be established. The terminology used follows Hendrickx et al. (2015a, 2019).

The teeth are ziphodont, as in the vast majority of non-maniraptoriform theropods (Hendrickx et al. 2019), and large, in absolute terms, but also in relation to the size of the maxilla, as already indicated by the large size of the alveoli. The isolated tooth crown has a Crown Base Length (CBL) of approximately 40–45 mm and an estimated Crown Height (CH) of c. 95 mm, although both measures should be seen with caution, since the poor preservation of this crown makes an evaluation of its completeness difficult. The replacement tooth in the more posterior alveolous of the fragment of the maxillary body below the anterior end of the antorbital fossa (Fig. 4) has a CBL of c. 30 mm (the basal part of the mesial carina is hidden by bone), a CH of c. 60 mm and a Crown

Base Width (CBW) of 11 mm as preserved, but as this tooth is a replacement tooth, these values are minimal estimates for the size of the functional tooth. The tooth is thus strongly labiolingually compressed, with a Crown Base Ratio (CBR) of 0.37. This value is similar to the very strongly compressed teeth of *Carcharodontosaurus* (see Hendrickx et al. 2015b), but it should be kept in mind that this is not necessarily the ratio at the base of the functional tooth.

Whereas the apical part of the isolated crown is recurved so that the distal carina is concave apically, the distal carina of the replacement tooth is almost straight, being only very slightly concave apicobasally (Fig. 4B). In contrast, the mesial carina of the tooth is strongly convex. Both carinae seem to be more or less centrally placed on their respective sides and continue to where they are hidden by bone basally. Both mesial and distal carinae are serrated, but in contrast to *Wiehenvenator* and a well-preserved replacement tooth in *Megalosaurus* (Rauhut et al. 2016), the denticles are not continuous over the apex of the tooth, which bears only a very low, unserrated carina; as the tooth is a replacement tooth, it seems unlikely that this might be due to wear. The denticles are rectangular, chisel-shaped, and are clearly separated from another by well-developed, narrow interdental slits (Fig. 4C, D). The mesial denticles remain of approximately equal size over the entire preserved length of the carina, only diminishing rapidly in size on the last c. two mm towards the apex. On the distal carina, denticle size is also more or less constant over most of the preserved length of the carina, but diminishes similarly rapidly towards the apex, and more gradually towards the basal end of the preserved crown. There are eight denticles per five mm on the central part of the distal carina, but only 6–7 on the mesial carina. However, whereas denticle length is slightly higher on the mesial than the distal carina, the opposite is true for denticle height. Thus, whereas denticle height is slightly less than denticle length on the mesial carina, it is slightly more on the distal carina.

Only the lingual side of the tooth crown is exposed, so the absence or presence of enamel ornamentation can only be evaluated for this side. No interdental sulci are present on either the mesial or distal serration, and the crown also lacks any flutes, ridges, grooves or undulations. The areas adjacent to the carinae are notably convex mesiodistally both mesially and distally. The enamel surface is poorly preserved in most parts of the crown, making it difficult to establish any pattern of enamel texture. In the few areas where enamel texture can be seen it seems to be irregular to braided (see Hendrickx et al. 2015a). However, the irregular structure might be due to weathering of an originally braided



Figure 5: Theropod pedal phalanx II-2 (WMNM P27698, P27693) from the same locality as the maxillary fragments. **A**, Dorsal view. **B**, Lateral view. **C**, Proximal view. Scale bar is 5 cm.

texture, as better preserved areas close to the carinae seem to show the latter (Fig. 4E).

Pedal phalanx

One piece of a pedal phalanx was found in the float in October of 1999 (WMNM P27693). It fits together perfectly with another piece (WMNM P29438), which was found also in the float in April of 2000, right below the point where the maxillary fragment was found in situ the year before. Although it thus seems likely that this phalanx represents the same individual as the maxilla, it cannot be completely excluded that this element belongs to the type of *Wiehenvenator*, which was found less than 30 m away and includes remains of the hindlimbs (Rauhut et al. 2016). As little is known about the pedal morphology of megalosaurine megalosaurids (or even megalosauroids in general), this phalanx has little diagnostic value and is thus not discussed further below, but it will be briefly documented here.

The element (Fig. 5) is rather short and broad, but retains a distinct neck between the proximal and distal end. Both the proximal and distal ends are damaged, so that no precise measurements can be given. However, the element is approximately 10 cm long proximodistally, 7 cm wide and 6 cm high proximally, and 5.5 cm wide and 3.5 cm high distally. The central part of the bone is constricted to a minimal width of 4.5 cm and a height of 3 cm, so the proximal end is strongly expanded, both mediolaterally as well as dorsally. The proximal end was obviously semioval in outline, with a flattened to slightly concave ventral margin. It is subdivided into a narrower medial and a wider lateral articular surface by a low medial dorsoventral ridge, but most of the articular surfaces are lost due to erosion. Whereas the dorsomedial margin of the articular end is convex, the dorsolateral margin is convex only dorsally, but then becomes straight towards a small lateroventral expansion of the articular end. Thus, the two articular surfaces were slightly asymmetrical not only in respect to their size, but also their shape.

The shaft of the phalanx rapidly descends distoventrally from the high dorsal margin of the articular surface,

its dorsal side being strongly convex mediolaterally. The ventral side is concave mediolaterally, being bounded by a broad, and slightly rugose swelling medially and a more sharply defined, low and broad ridge laterally. The latter flexes slightly medially towards its distal end and disappears at approximately one third of the length of the phalanx from the proximal end. The distal end is gynglimoidal, with the articular condyles extending further proximally on the ventral than on the dorsal side. The ventral side of the distal articular end is also wider than the dorsal side, especially due to the medial condyle flaring medioventrally. Both condyles are separated by a well-defined groove that extends slightly obliquely from dorsolateral to medioventral and continues between the condyles on the distal end of the ventral side. An extensor groove on the dorsal side seems to be absent (but the dorsomedial part of the medial condyle is strongly damaged), and the collateral ligament pits were obviously displaced dorsally from the mid-height of the distal end.

Several features of this element indicate that it is a pedal phalanx II-2 of the left pes, including the asymmetrically subdivided proximal articular surface, lack of an extensor groove, and the presence of a ventrolateral ridge at the proximal end of the ventral surface (see Madsen 1976; Currie & Zhao 1993; Malafaia et al. 2019).

Discussion

Taxonomic identification of the Ornatenton theropod

Given that the material comes from the same locality as the type material of *Wiehenvenator albatii*, just some 28 m away from the site of the excavation of the latter, and represents the other (left) maxilla than the one preserved with the *Wiehenvenator* specimen, the question arises whether it represents this taxon and might even be derived from the same individual. However, marked differences between the type maxilla of *Wiehenvenator albatii* and the material described here indicate that this is not the case. The maxilla of *Wiehenvenator* has a tunnel-like promaxillary foramen that leads into a large promaxillary antrum within the base of the ascending

process (Rauhut et al. 2016: figs. 6-8), as it is the case in the spinosaurid *Suchomimus* (Serenio et al. 1998) and some other megalosauroids. Furthermore, as noted by Rauhut et al. (2016), the medial wall of the antorbital fossa, although damaged, seems to have been rather small in this taxon, and there is no indication of the oblique ridge seen in WMNM P80969. Although pneumatic features associated with the paranasal sinus system might be quite variable in theropods (Witmer 1997), the differences seen seem to be outside of individual variability in basal tetanuran theropods. A further difference is seen in the dentition: whereas in *Wiehenvenator*, the serrations are continuous across the tooth tip in a replacement tooth (Rauhut et al. 2016), this is not the case in WMNM P27690. Furthermore, denticle density on the teeth seems to be slightly different; whereas Rauhut et al. (2016) noted 15 denticles per 10 mm on both the mesial and distal carinae in *Wiehenvenator*, the material described here shows 12-14 on the mesial and 16 denticles per 10 mm on the distal carina. Thus, we consider it to be rather unlikely that the material described here represents the same taxon or even the same individual as the type of *Wiehenvenator albatii*.

However, despite the fragmentary nature of the remains, the preserved material allows an identification on generic level. The presence of a large maxillary fenestra, even if just developed as a depression, and of a medial pneumaticity in the base of the ascending process of the maxilla indicate that the animal represented is a tetanuran (Gauthier 1986; Rauhut 2003; Carrano et al. 2012). On the other hand, the lack of sharply defined margins of the fenestra is a character rarely seen in tetanurans, and gradually deepening rims of this opening are only known in the English Callovian afrovenatorine megalosaurid *Eustreptospondylus* (Sadleir et al. 2008) and the Late Jurassic megalosaurine *Torvosaurus* (Britt 1991; Hendrickx & Mateus 2014; Malafaia

et al. 2017a). Another conspicuous character of the maxillary fragment is the presence of an oblique ridge transversing the ventral part of the antorbital fossa and forming the ventral margin of the maxillary fenestra. Such a ridge is only present in *Torvosaurus* (Fig. 6) and represents an autapomorphy of this taxon (Britt 1991; Hendrickx & Mateus 2014). Thus, the combination of the presence of a shallow, poorly defined maxillary fossa and of the apomorphic character of the oblique ridge allows a referral of this material to the genus *Torvosaurus*.

Other characters of the material described here are consistent with this identification. One character shown by the Ornatenton material, the ventral extent of the tips of the interdental plates being considerably dorsal to the ventral extent of the lateral alveolar wall, was found to be a synapomorphy of the clade including the megalosaurines *Megalosaurus*, *Wiehenvenator* and *Torvosaurus* (Carrano et al. 2012; Rauhut et al. 2016), and thus further supports a placement of these remains among derived megalosaurines. In many megalosaurids, including *Dubreuillosaurus* (Allain 2002), *Afrovenator* (UC OBA 1; Sereno et al. 1994), *Eustreptospondylus* (OUMNH J 13558; Sadleir et al. 2008), *Duriavenator* (Benson 2008) and *Megalosaurus* (Benson 2010a), the antorbital fossa of the maxilla reaches ventrally to at least the half height of the maxillary body below the anterior end of the antorbital fenestra. In contrast, *Torvosaurus* and its closest relative, *Wiehenvenator*, have a reduced ventral extend of the maxillary antorbital fossa, which reaches one third or less of the height of the maxillary body below the anterior end of the antorbital fenestra. This is also the case in the material from the Ornatenton. Furthermore, megalosaurid theropods usually have separate interdental plates (e.g. Allain 2002; Benson 2008, 2010a; Sadleir et al. 2008), and this is also the case in *Wiehenvenator* (Rauhut et al. 2016). In contrast, the interdental plates are fused into a high medial interdental wall in *Torvosaurus* (Britt

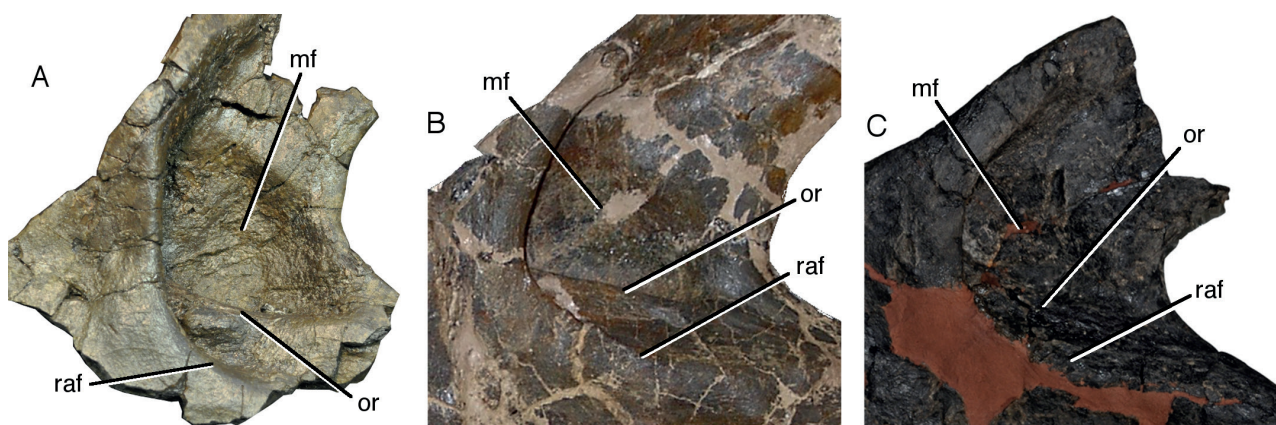


Figure 6: Comparison of the anterior end of the antorbital fossa in different specimens of *Torvosaurus*. **A**, *Torvosaurus* sp. from the Ornatenton Formation of Lutternsche Egge, North Rhine Westphalia, Germany (WMNM P80969). **B**, *Torvosaurus tanneri* from the Morrison Formation of Dry Mesa Quarry, Utah, USA (BYU VP 9122). **C**, *Torvosaurus gurneyi* from the Praia da Amoreira-Porto Novo Formation of Praia de Vermelha, Peniche, Portugal (SHN.400; right maxilla, reversed for comparison). Abbreviations: mf, maxillary fenestra; or, oblique ridge; raf, rim of antorbital fossa.

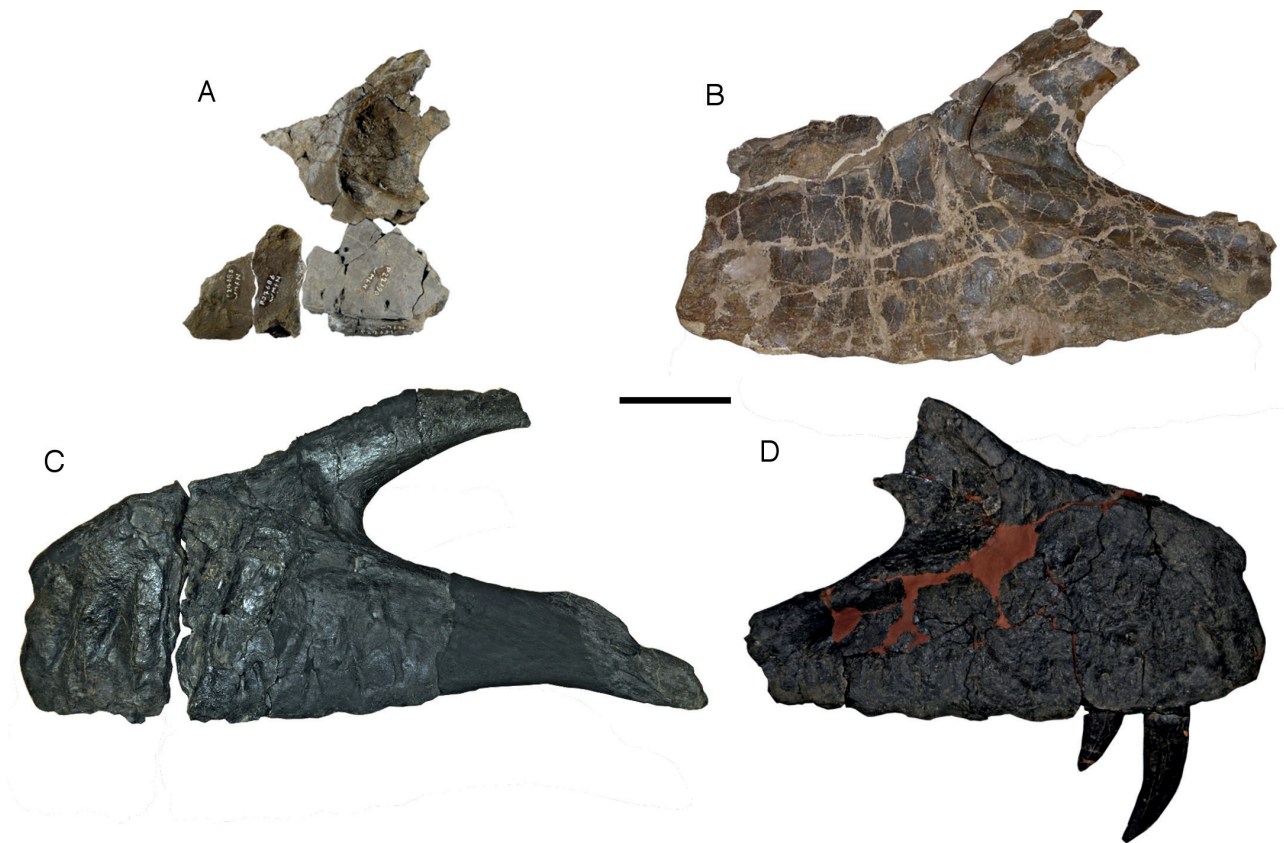


Figure 7: Comparison of maxillae of *Torvosaurus*. **A**, *Torvosaurus* sp. from the Ornatenton Formation of Lutternsche Egge, Germany. **B**, *Torvosaurus tanneri* from the Morrison Formation of Utah, USA (BYU VP 9122). **C**, *Torvosaurus gurneyi* from the Praia da Amoreira-Porto Novo Formation of Portugal, holotype left maxilla (ML 1100). **D**, *Torvosaurus gurneyi* from the Praia da Amoreira-Porto Novo Formation of Portugal, right maxilla from the same locality and probably the same individual as the holotype (SHN.400; see Malafaia et al. 2017a). Scale bar is 10 cm.

1991; Hendrickx & Mateus 2014; Malafaia et al. 2017a). Although the partial fusion of the interdental plates in the Ornatenton material might be argued to reflect the subadult and not fully mature state of the material, this seems unlikely, as fusion of the interdental plates happens very early in ontogeny in other theropods that have this feature, such as *Allosaurus* (e.g., UMNH VP 3113; see also Rauhut & Fechner 2005). The partially fused interdental plates in WMNM P27691 thus seem to represent an intermediate stage between the typical megalosaurid morphology and the derived condition in the Late Jurassic representatives of *Torvosaurus*.

Finally, the morphology of the teeth, as far as it can be compared, also agrees with the structures seen in *Torvosaurus* (Hendrickx & Mateus 2014; Hendrickx et al. 2015b, 2019; Malafaia et al. 2017a, b). As pointed out by Hendrickx et al. (2015b, 2019), megalosaurine lateral teeth have centrally placed carinae, quadrangular to rectangular denticles, and mesial denticles that are as large or even slightly larger than distal denticles, all features also shown in WMNM P27691. Furthermore, the size of the teeth, and the serration density (number of denticles per 5 mm) are within the range seen in *Torvosaurus*. Although undulations and interdenticular sulci are common in megalosaurid teeth (Hendrickx et al.

2015b, 2019), their presence is very variable, and might vary within one dentition or even between the labial and lingual side of a single tooth. Thus, the absence of these structures in the only observable tooth in the material described here is no argument against its referral to *Torvosaurus*.

Within the genus *Torvosaurus*, the temporal difference from the Late Jurassic representatives of c. 10 Ma and a few morphological differences indicate that the material described here cannot be referred to any of the two known species and thus most probably represents a different species. However, we consider the material too poor to base a new taxon on it. The only partially fused interdental plates are plesiomorphic in respect to the Late Jurassic species *T. tanneri* and *T. gurneyi*, and thus indicate that this taxon is outside a sister group relationship between the latter, which is in agreement with its stratigraphic position.

Implications for the evolution and biogeography of megalosaurine megalosaurids

The Late Jurassic species of *Torvosaurus*, *T. tanneri* from the Morrison Formation of the western USA, and *T. gurneyi* from the Praia da Amoreira-Porto Novo Formation of Portugal, are among the largest theropods

known from that time (Britt 1991; Hendrickx and Mateus 2014), and both the American and the Portuguese species seem to be of closely comparable size (Fig. 7). The *Torvosaurus* maxilla from the Ornatenton Formation of Germany seems to be comparable in size with the maxilla of the sister taxon of *Torvosaurus*, *Wiehenvenator* (Rauhut et al. 2016), and is approximately 10% smaller than the maxilla of *T. tanneri* in the only comparable measure, the height of the bone at the level of the end of the antorbital fossa (Fig. 7). Thus, these derived megalosaurines were already among the largest terrestrial predators in the late Middle Jurassic, and there seems to have been only a moderate increase in body size in the genus *Torvosaurus* in the Late Jurassic. Furthermore, it is impossible to establish the ontogenetic stage of the individual represented by the remains from the Ornatenton Formation, and it thus cannot be ruled out that this genus had already reached the giant size seen in the Tithonian representatives in the Callovian.

The megalosaurid subclade Megalosaurinae includes the genera *Duriavenator*, *Megalosaurus*, *Wiehenvenator* and *Torvosaurus* (Carrano et al. 2012; Rauhut et al. 2016), with a total of five nominal species. The phylogenetic relationships between these taxa are in complete congruence with their stratigraphic occurrence, with *Duriavenator* coming from the Late Bajocian (Benson 2008), *Megalosaurus* from the Bathonian (Benson 2010a), *Wiehenvenator* from the mid-Callovian (Rauhut et al. 2016) and the two nominal species of *Torvosaurus* from the Kimmeridgian-Tithonian (Britt 1991; Hendrickx & Mateus 2014). The discovery of a Callovian species of *Torvosaurus* not only from the same levels, but even the same locality as its direct sister genus, *Wiehenvenator*, does not only increase the already remarkable diversity of Middle Jurassic megalosaurids in Europe, but also closes the temporal gap between the two genera. Together with the occurrence of the stratigraphically older consecutive sister taxa in adjacent European regions this indicates a primarily central European evolution of megalosaurines and an origin of the genus *Torvosaurus* in this area as well. Thus, the Late Jurassic occurrences of *Torvosaurus* in the Iberian peninsula and North America might be explained by dispersal from this region in the early Late Jurassic.

Soto et al. (2020) recently identified isolated teeth from the Kimmeridgian-Tithonian of the Tendaguru Formation of Tanzania and the probable Tithonian of the Tacuarembó Formation of Uruguay as *Torvosaurus* sp. However, Hendrickx et al. (2019) pointed out that isolated teeth of theropods are rarely diagnostic on genus level, and this also applies to the teeth of *Torvosaurus*. Even accounting for the unusual large size of these teeth, similarly large teeth are also found

in *Wiehenvenator* (Rauhut et al. 2016), ceratosaurids (Madsen & Welles 2000; Rauhut 2004) and carcharodontosaurids (e.g., Stromer 1931; Sereno et al. 1996). Furthermore, both in respect to morphometric data, as well as qualitative characters, the teeth of *Torvosaurus* are similar to carcharodontosaurid teeth (Hendrickx et al. 2015b, 2019; Soto et al. 2020), a group that has also been reported from the Tendaguru Formation (Rauhut 2011). Thus, although it is possible that the teeth described by Soto et al. (2020) represent a large megalosaurine megalosaurid, the identification as the genus *Torvosaurus* should be regarded as tentative at best. If megalosaurine megalosaurids were present in the Late Jurassic of the southern Hemisphere, Europe probably acted as a biogeographical turntable for this group in the Middle to early Late Jurassic (see Dunhill et al. 2016).

However, despite the conspicuous cluster of megalosaurine megalosaurids in the Middle Jurassic of Europe, the biogeographic conclusions presented above should be seen as tentative, due to the very poor Middle Jurassic theropod record from most other continents. With the identification of a Late Jurassic age for the Shaximiao Formation of China (Wang et al. 2018), and given the stratigraphic uncertainty of the Tiouraren Formation of Niger (Sereno et al. 1994; Rauhut & López-Arbarello, 2009), Europe is the only continent that has yielded a notable Middle Jurassic theropod fauna, with the exception of the Cañadón Asfalto Formation of Argentina (Bonaparte 1979, 1986; Rauhut 2005; Pol & Rauhut 2012; Rauhut & Pol 2019). However, the latter fauna is probably earliest Middle Jurassic in age (Cúneo et al. 2013) and might thus be too old to provide information on the evolution of megalosaurines. Therefore, the interpretations presented here need to be tested in the light of discoveries from other continents.

Acknowledgements

We thank Friedrich Albat, who found the specimen. Furthermore, we thank the geoscientific preparators of the LWL-Westfälisches Museum für Naturkunde, especially Michael Ludorf and Manfred Schlösser, who carried out the excavation and prepared the finds. We furthermore thank Brooks Britt for access to *Torvosaurus tanneri*, and Alexandra Fernandes, Elisabete Malafaia, Octávio Mateus, Simão Mateus, and B. Silva for access to various specimens of *Torvosaurus gurneyi*. Critical comments by the handling editor Rico Schellhorn and two anonymous reviewers helped to improve the manuscript.

References

Allain, R. 2001: Redescription de *Streptospondylus altdorfensis*, le dinosaure théropode de Cuvier, du Jurassique de Normandie. – *Geodiversitas* 23(3): 349-367.

- Allain, R. 2002: Discovery of megalosaur (Dinosauria, Theropoda) in the Middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. – *Journal of Vertebrate Paleontology* 22(3): 548-563.
- Antunes, M. T. & Mateus, O. 2003: Dinosaurs of Portugal. – *Comptes Rendus Palevol* 2: 77-95.
- Benson, R. B. J. 2008: A redescription of '*Megalosaurus hesperis* (Dinosauria, Theropoda) from the Inferior Oolite (Bajocian, Middle Jurassic) of Dorset, United Kingdom. – *Zootaxa* 1931: 57-67.
- Benson, R. B. J. 2010a: A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. – *Zoological Journal of the Linnean Society* 158: 882-935.
- Benson, R. B. J. 2010b: The osteology of *Magnosaurus nethercombensis* (Dinosauria, Theropoda) from the Bajocian (Middle Jurassic) of the United Kingdom and a re-examination of the oldest records of tetanurans. – *Journal of Systematic Palaeontology* 8(1): 131-146.
- Benson, R. B. J. & Barrett, P. M. 2009: Dinosaurs of Dorset: Part I, the carnivorous dinosaurs (Saurischia, Theropoda). – *Proceedings of the Dorset Natural History and Archaeological Society* 130: 133-147.
- Bonaparte, J. F. 1979: Dinosaurs: a Jurassic assemblage from Patagonia. – *Science* 205: 1377-1379.
- Bonaparte, J.F. 1986: Les Dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique moyen de Cerro Cóndor (Chubut, Argentine). – *Annales de Paléontologie* 72: 247-289, 326-386.
- Britt, B. B. 1991: Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. – *BYU Geology Studies* 37: 1-72.
- Carrano, M. T., Benson, R. B. J. & Sampson, S. D. 2012: The phylogeny of Tetanurae (Dinosauria: Theropoda). – *Journal of Systematic Palaeontology* 10(2): 211-300.
- Cúneo, R., Ramezani, J., Scasso, R. A., Pol, D., Escapa, I. H., Zavattieri, A. M. & Bowring, S. A. 2013: High-precision U–Pb geochronology and a new chronostratigraphy for the Cañadón Asfalto Basin, Chubut, central Patagonia: Implications for terrestrial faunal and floral evolution in Jurassic. – *Gondwana Research* 24: 1267-1275.
- Currie, P. J. & Zhao, X.-J. 1993: A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. – *Canadian Journal of Earth Sciences* 30: 2037-2081.
- Dunhill, A. M., Bestwick, J., Narey, H. & Sciberras, J. 2016: Dinosaur biogeographical structure and Mesozoic continental fragmentation: a network-based approach. – *Journal of Biogeography* 43(9): 1691-1704.
- Escaso, F., Ortega, F., Dantas, P., Malafaia, E., Pimentel, N., Pereda-Suberbiola, X., Sanz, J., Kullberg, J., Kullberg, M. & Barriga, F. 2007: New evidence of shared dinosaur across Upper Jurassic Proto-North Atlantic: *Stegosaurius* from Portugal. – *Naturwissenschaften* 94(5): 367-374.
- Fitzinger, L. 1843: *Systema Reptilium. Fasciculus Primus. Amblyglossae*. Apud Braumüller and Seidel Bibliopolas, Vienna. (In Latin)
- Foster, J. R. 2007: *Jurassic West. The dinosaurs of the Morrison Formation and their world*. Bloomington and Indianapolis: Indiana University Press.
- Galton, P. M. & Jensen, J. A. 1979: A new large theropod dinosaur from the Upper Jurassic of Colorado. – *BYU Geology Studies* 26(2): 1-12.
- Gauthier, J. 1986: Saurischian monophyly and the origin of birds. – *Memoirs of the Californian Academy of Science* 8: 1-55.
- Hanson, M. & Makovicky, P. 2014: A new specimen of *Torvosaurus tanneri* originally collected by Elmer Riggs. – *Historical Biology* 26(6): 775-784.
- Hendrickx, C. & Mateus, O. 2014: *Torvosaurus gurneyi* n. sp., the largest terrestrial predator from Europe, and a proposed terminology of the maxilla anatomy in nonavian theropods. – *PLoS ONE* 9(3): e88905.
- Hendrickx, C., Mateus, O. & Araújo, R. 2015a: A proposed terminology of theropod teeth (Dinosauria, Saurischia). – *Journal of Vertebrate Paleontology* 35(5): e982797.
- Hendrickx, C., Mateus, O. & Araújo, R. 2015b: The dentition of megalosaurid theropods. – *Acta Palaeontologica Polonica* 60(3): 627-642.
- Hendrickx, C., Mateus, O., Araújo, R. & Choiniere, J. N. 2019: The distribution of dental features in non-avian theropod dinosaurs: Taxonomic potential, degree of homoplasy, and major evolutionary trends. – *Palaeontologia Electronica* 22(3): 1-110.
- Li, F., Peng, G., Ye, Y., Jiang, S. & Huang, D. 2009: [A new carnosaur from the Late Jurassic of Qianwei, Sichuan, China]. – *Acta Geologica Sinica* 83(9): 1203-1213. (in Chinese)
- Liston, J. 2010: The occurrence of the Middle Jurassic pachycormid fish *Leedsichthys*. – *Oryctos* 9: 1-36.
- Madsen, J. H. 1976: *Allosaurus fragilis*: a revised osteology. – *Utah Geological and Mineralogical Survey Bulletin* 109: 3-163.
- Madsen, J. H. J. & Welles, S. P. 2000: *Ceratosaurus* (Dinosauria, Theropoda). A revised osteology. – *Miscellaneous Publication, Utah Geological Survey* 00-2: 1-80.
- Malafaia, E., Dantas, P., Ortego, F. & Escaso, F. 2007: Nuevos restos de *Allosaurus fragilis* (Theropoda: Carnosauria) del yacimiento de Andrés (Jurásico Superior; Centro-Oeste de Portugal). In: Cambra-Moo, O., Martínez-Pérez, C., Chamero, B., Escaso, F., de Esteban Trivigno, S. & Marugán-Lobón, J. (eds), *Cantera Paleontológica*, 255-271. Cuenca: Diputación Provincial de Cuenca.
- Malafaia, E., Escaso, F., Mocho, P., Serrano-Martinez, A., Torices, A., Cachao, M. & Ortega, F. 2017b: Analysis of diversity, stratigraphic and geographical distribution of isolated theropod teeth from the Upper Jurassic of the Lusitanian Basin, Portugal. – *Journal of Iberian Geology* 43(2): 257-291.
- Malafaia, E., Mocho, P., Escaso, F., Dantas, P. & Ortega, F. 2019: Carcharodontosaurian remains (Dinosauria, Theropoda) from the Upper Jurassic of Portugal. – *Journal of Paleontology* 93(1): 157-172.
- Malafaia, E., Mocho, P., Escaso, F. & Ortega, F. 2017a: New data on the anatomy of *Torvosaurus* and other remains of megalosauroid (Dinosauria, Theropoda) from the Upper Jurassic of Portugal. – *Journal of Iberian Geology* 43(1): 33-59.
- Malafaia, E., Ortega, F., Escaso, F. & Silva, B. 2015: New evidence of *Ceratosaurus* (Dinosauria: Theropoda) from the Late Jurassic of the Lusitanian Basin, Portugal. – *Historical Biology* 27(7): 938-946.
- Malafaia, E., Ortega, F., Silva, B. & Escaso, F. 2008: Fragmento de un maxilar de terópodo de Praia da Corva (Jurásico Superior. Torres Vedras, Portugal). – *Palaeontologica Nova* 8: 273-279.

- Marsh, O.C. 1881: Principal characters of American Jurassic dinosaurs. – Part V. American Journal of Science (Series 3) 21: 417-423.
- Mateus, O. 2006: Late Jurassic dinosaurs from the Morrison Formation (USA), the Lourinha and Alcobaca Formations (Portugal), and the Tendaguru Beds (Tanzania): A comparison. – New Mexico Museum of Natural History and Science Bulletin 36: 1-9.
- Mateus, O., Walen, A. & Antunes, M. T. 2006: The large theropod fauna of the Lourinha Formation (Portugal) and its similarity to that of the Morrison Formation, with a description of new species of *Allosaurus*. – New Mexico Museum of Natural History and Science Bulletin 36: 123-129.
- Michelis, I., Sander, P. M., Metzendorf, R. & Breitzkreuz, H. 1996: Die Vertebratenfauna des Calloviums (Mittlerer Jura) aus dem Steinbruch Störmer (Wallücke, Wiehengebirge). – Geologie und Paläontologie in Westfalen 44: 5-66.
- Mönning, E. 1993: Die Ornatenton-Formation in NW Deutschland. – Newsletter in Stratigraphy 28(2/3): 131-150.
- Owen, R. 1842: Report on British fossil reptiles, part II. – Reports of the British Association for the Advancement of Science, 11: 60-204.
- Pérez-Moreno, B. P., Chure, D. J., Pires, C., Marques da Silva, C., Dos Santos, V., Dantas, P., Póvoas, L., Cachão, M., Sanz, J. L. & Galopim de Carvalho, A. M. 1999: On the presence of *Allosaurus fragilis* (Theropoda: Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. – Journal of the Geological Society 156: 449-452.
- Pol, D. & Rauhut, O. W. M. 2012: A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. – Proceedings of the Royal Society London B 279(1741): 3170-3175.
- Rauhut, O. W. M. 2003: The interrelationships and evolution of basal theropod dinosaurs. – Special Papers in Palaeontology 69: 1-213.
- Rauhut, O. W. M. 2004: Provenance and anatomy of *Genyodectes serus*, a large-toothed ceratosaur (Dinosauria: Theropoda) from Patagonia. – Journal of Vertebrate Paleontology 24(4): 894-902.
- Rauhut, O. W. M. 2005: Osteology and relationships of a new theropod dinosaur from the Middle Jurassic of Patagonia. – Palaeontology 48(1): 87-110.
- Rauhut, O. W. M. 2011: Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). – Special Papers in Palaeontology 86: 195-239.
- Rauhut, O. W. M. & Fechner, R. 2005: Early development of the facial region in a non-avian theropod dinosaur. – Proceedings of the Royal Society London B 272: 1179-1183.
- Rauhut, O. W. M., Foth, C., Tischlinger, H. & Norell, M. A. 2012: Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the Late Jurassic of Germany. – Proceedings of the National Academy of Sciences 109(29): 11746-11751.
- Rauhut, O. W. M., Hübner, T. R. & Lanser, K.-P. 2016: A new megalosaurid theropod dinosaur from the late Middle Jurassic (Callovian) of north-western Germany: implications for theropod evolution and faunal turnover in the Jurassic. – Palaeontologia Electronica 19(2.26A): 1-65.
- Rauhut, O. W. M. & López-Arbarello, A. 2008: Archosaur evolution during the Jurassic: a southern perspective. – Revista de la Asociación Geológica Argentina 63(4): 557-585.
- Rauhut, O. W. M. & López-Arbarello, A. 2009: Considerations on the age of the Tiouaren Formation (Iullemeden Basin, Niger, Africa): Implications for Gondwanan Mesozoic terrestrial vertebrate faunas. – Palaeogeography, Palaeoclimatology, Palaeoecology 271: 259-267.
- Rauhut, O. W. M., Piñuela, L., Castanera, D., García-Ramos, J.-C. & Sánchez Cela, I. 2018: The largest European theropod dinosaurs: Remains of a gigantic megalosaurid and giant theropod tracks from the Kimmeridgian of Asturias, Spain. – PeerJ 6: e4963.
- Rauhut, O. W. M. & Pol, D. 2019: Probable basal allosauroid from the early Middle Jurassic Cañadón Asfalto Formation of Argentina highlights phylogenetic uncertainty in tetanuran theropod dinosaurs. – Scientific Reports 9: 18826.
- Rieggraf, W. v. 1994: Der Ornatenton in Deutschland und seine Äquivalente. In: Martill, D.M. & Hudson, J. D. (eds), Fossilien aus Ornatenton und Oxford Clay, 7-72. Korb: Goldschneck-Verlag.
- Sadleir, R., Barrett, P. M. & Powell, H. P. 2008: The anatomy and systematics of *Eustreptospondylus oxoniensis*, a theropod dinosaur from the Middle Jurassic of Oxfordshire, England. – Monograph of the Palaeontographical Society 160: 1-82.
- Sereno P. C., Beck A. L., Dutheil D. B., Gado B., Larsson H. C. E., Lyon G. H., Marcot J. D., Rauhut O. W. M., Sadleir R. W., Sidor C. A., Varricchio D. J., Wilson G. P. & Wilson J. A. 1998: A long-snouted predatory dinosaur from Africa and the evolution of the spinosaurids. – Science 282: 1298-1302.
- Sereno, P. C., Dutheil, D. B., Iarochene, M., Larsson, H. C. E., Lyon, G. H., Magwene, P. M., Sidor, C. A., Varricchio, D. J. & Wilson, J. A. 1996: Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. – Science 272: 986-991.
- Sereno, P. C., Wilson, J. A., Larsson, H. C. E., Dutheil, D. B. & Sues, H.-D. 1994: Early Cretaceous dinosaurs from the Sahara. – Science 266: 267-271.
- Soto, M., Toriño, P. & Perea, D. 2020: A large sized megalosaurid (Theropoda, Tetanurae) from the Late Jurassic of Uruguay and Tanzania. – Journal of South American Earth Sciences 98: 102458.
- Stromer, E. 1931: Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. – Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung, Neue Folge 9: 1-23.
- Wang, J., Ye, Y., Pei, R., Tian, Y., Feng, C., Zheng, D. & Chang, S.-C. 2018: Age of Jurassic basal sauropods in Sichuan, China: A reappraisal of basal sauropod evolution. – GSA Bulletin 130(9-10): 1493-1500.
- Waskow, K., Grzegorzczak, D. & Sander, P. M. 2018: The first record of *Tyrannoneustes* (Thalattosuchia: Metriorhynchidae): a complete skull from the Callovian (late Middle Jurassic) of Germany. – PalZ 92: 457-480.
- Witmer, L.M., 1997: The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. – Society of Vertebrate Paleontology, Memoir 3: 1-73.