

The first non-avian theropod from the Czech Republic

DANIEL MADZIA



Madzia, D. 2014. The first non-avian theropod from the Czech Republic. *Acta Palaeontologica Polonica* 59 (4): 855–862.

All currently known theropod specimens from the Czech Republic have been attributed to the crown clade Aves. However, an archosaur tooth in the Institute of Geological Sciences (Faculty of Science, Masaryk University), labelled as *Teleosaurus*, belongs to a non-avian theropod. The tooth comes from the Upper Jurassic (Oxfordian) carbonate rocks of Švédské šance (Brno-Slatina) and represents the first terrestrial vertebrate known from the Jurassic of the Czech Republic. The tooth is described here in detail and compared to anatomical descriptions of taxa, and comprehensive sets of quantitative and qualitative data. On the basis of the comparisons, it is concluded that the Moravian theropod was likely a basal representative of the clade Tetanurae, whose members were abundant in Europe during the Middle to Late Jurassic.

Key words: Dinosauria, Theropoda, theropod tooth, Jurassic, Oxfordian, Czech Republic.

Daniel Madzia [daniel.madzia@gmail.com], Institute of Geological Sciences, Masaryk University, 2 Kotlářská, 61137 Brno, Czech Republic; current address: Institute of Palaeobiology, Polish Academy of Sciences, ul. Twarda 51/55, 00-818 Warszawa, Poland.

Received 28 September 2012, accepted 24 January 2013, available online 4 February 2013.

Copyright © 2014 D. Madzia. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Fossil theropods from the Czech Republic have so far been restricted to members of Aves sensu Gauthier and de Queiroz (2001); e.g., Mlíkovský (1995) or Mayr and Gregorová (2012). The only material considered to be non-avian theropod is a single tridactyl footprint from whitish kaolinitic quartz sandstone in the Devět Křížů quarry near Červený Kostelec (Bohdašín Formation, Krkonoše Piedmont Basin) that was described by Zajíc (1998). However, Zajíc's (1998) interpretation is problematic for two reasons. First, the precise age of the uppermost section of the Bohdašín Formation is uncertain and ranges from the Lower to Middle Triassic depending on different criteria, such as regional geological situation within the Sudetes and ichnology (cf. Prouza et al. 1985; Zajíc 1998; Uličný 2004). Second, a tridactyl pes does not separate theropods from other dinosauiromorphs (King and Benton 1996; Brusatte et al. 2011a), so it cannot be used as the “key character” for assignment. Since the age of the Bohdašín Formation is unknown, and information on the trackmaker's foot anatomy is limited, the footprint cannot be identified as that of a theropod, but merely as an indeterminate dinosauiromorph.

A recent review of the paleontological collections of the Institute of Geological Sciences (IGS), however, revealed an archosaur tooth from a non-avian theropod dinosaur. The sample is preserved in carbonate rock with a label affixed to it, reading in German, “Teleosaurus (Zahn), Ein Meereskrokodil, Ob. Jura. Schwedenschanze” (transl. “Teleosaurus

(tooth), a marine crocodile, Upper Jurassic. Švédské šance [literally “Swedish chances”; the name of the fossil site]). This indicates that the tooth was at least for a short time deposited in the collections of the German Technical University in Brno, which was closed in 1945. I was unable to trace any information regarding the tooth in the literature.

The morphology of the tooth differs significantly from the teeth of *Teleosaurus*, as well as from other thalattosuchian crocodylomorphs. The differences are apparent especially in the morphology of the tooth crown and the serrations. When denticles are present in thalattosuchians (*Dakosaurus*, *Geosaurus*), they are either microzipodont (denticle dimensions do not exceed 300 µm; *Geosaurus*) or macrozipodont (denticle dimensions do exceed 300 µm; *Dakosaurus*). However, no macrozipodont taxon (i.e., *D. maximus*, *D. andiniensis*) shows a similar tooth morphology to the Moravian sample (cf. Young et al. 2010; Andrade et al. 2010; Young et al. 2012). On the other hand, the combination of the size, shape and proportions of the tooth crown, and the size, density and morphology of the denticles resembles lateral teeth of carnivorous theropod dinosaurs. The tooth is described here in detail and compared to the teeth of zipodont theropods.

Institutional abbreviations.—IGS, Institute of Geological Sciences, Faculty of Science, Masaryk University, Brno, Czech Republic.

Other abbreviations.—AL, apical length, the distance between the most mesial point at the base of the tooth crown and

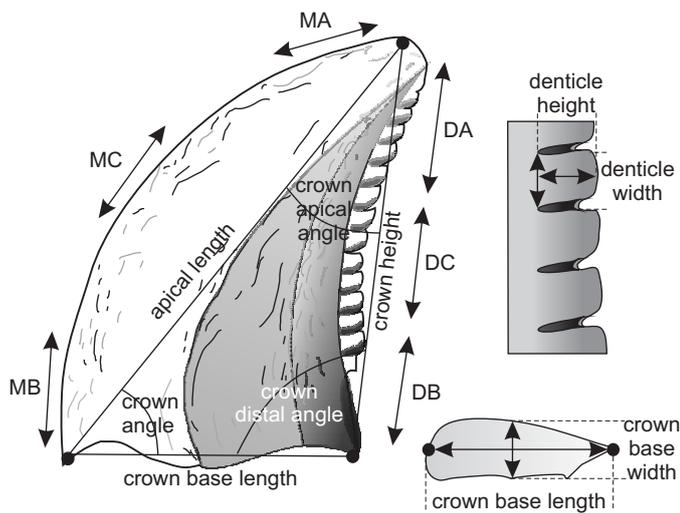


Fig. 1. Sketch of tooth crown and measurements (modified after Smith et al. 2005 and Lubbe et al. 2009). DA, number of denticles per 5 mm at the apical third of the distal carina; DB, number of denticles per 5 mm at the basal third of the distal carina; DC, number of denticles per 5 mm at the center of the distal carina; MA, number of denticles per 5 mm at the apical third of the mesial carina; MB, number of denticles per 5 mm at the basal third of the mesial carina; MC, number of denticles per 5 mm at the center of the mesial carina.

the crown apex; CA, crown angle, calculated using the law of cosines with the values of CBL, AL, and CH; CAA, crown apical angle, calculated using the law of cosines with the values of CBL, AL, and CH; CBL, crown base length, the distance between the most mesial and distal points at the base of the tooth crown; CBR, crown base ratio, the ratio of CBW to CBL (describes the “labiolingual compression” of the tooth crown at its base); CBW, crown base width, labiolingual extension of the tooth crown at its base; CDA, crown distal angle, calculated as $180^\circ - CA - CAA$; CH, crown height, the distance between the most distal point at the base of the tooth crown and the crown apex; CHR, crown height ratio, the ratio of CH to CBL (describes the degree of “squatness” of the tooth crown); DA, number of denticles per 5 mm¹ at the apical third of the distal carina; DAVG, average distal denticle density²; DB, number of denticles per 5 mm¹ at the basal third of the distal carina; DC, number of denticles per 5 mm¹ at the center of the distal carina; DH, height of denticle; DSDI, Denticle Size Difference Index³; DW, width of denticle; MA, number of denticles per 5 mm¹ at the apical third of the mesial carina; MAVG, average mesial denticle density²; MB, number of denticles per 5 mm¹ at the basal third of the mesial carina; MC, number of denticles per 5 mm¹ at the center of the mesial carina.

¹ serration density in the tooth crowns with a CBL value < 7 mm is counted per 2 mm; when CBL ≥ 7 mm, serrations are counted per 5 mm.

² serration counts (at the apical third, center, and basal third of the tooth crown) divided by the number of applicable positions.

³ After Lubbe et al. (2009): if MAVG or DAVG ≥ 1, then $DSDI = (MAVG + 1) / (DAVG + 1)$, else DSDI = 0.

For more information about the measurements see Smith et al. (2005) and Lubbe et al. (2009).

Geological and stratigraphical setting

The Upper Jurassic sedimentary rocks of the south-eastern margin of the Bohemian Massif are a part of Middle to Late Jurassic sedimentation cycle and represent a development of Tethyan shelf. The rocks can be divided into three facies: the basin facies formed in deeper environments (sublittoral up to bathyal zone), the carbonate platform deposited in a maximum depth of several tens of meters, and the shelf lagoon (Fig. 2). The sedimentation cycle began during the Callovian and its base is characterized by clastic sediments, which gradually pass into limestones, marlstones, and spongolites. During the Callovian and Oxfordian a regional transgression progressed deep into the Bohemian Massif from Tethys and the epicontinental sea of Western Europe at the same time, and likely produced a seaway across the Bohemian Massif. The gradual regression during the Kimmeridgian and late Tithonian terminated the sedimentation cycle (Eliáš 1981; Suk et al. 1984).

The Švédské šance fossil site is a part of the carbonate platform facies. Unfortunately, its precise age is unknown. Oppenheimer (1907) described around 130 species, but their distribution in the strata was irregular. The index fossil *Epipeltoceras bimammatum* suggests a late Oxfordian age, whereas the foraminifer fauna described by Bubík (2010) suggests a possible middle Oxfordian age. Bubík (2010), however, mentioned different stratigraphic ranges of some foraminifer species reported from different European basins. Thus, the foraminifer-based stratigraphy may be corrected in the future. Further, the borehole Slatina 1, drilled close to the Švédské šance site, corresponds lithologically and stratigraphically to the limestone of the nearby Stránská

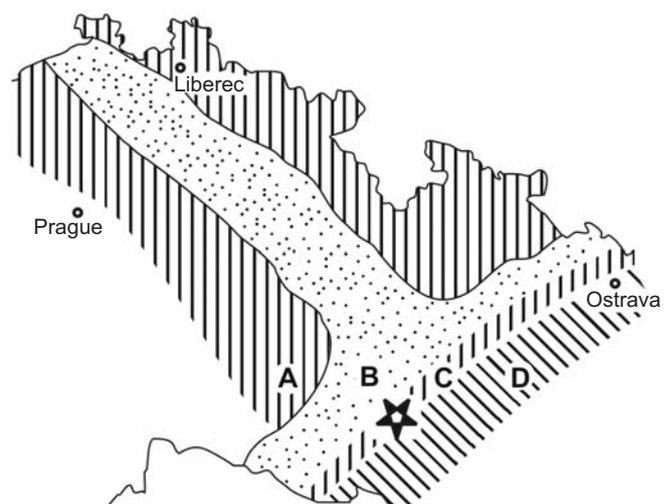


Fig. 2. Location of the discovery and paleogeography of the Czech Republic during the maximum transgression in the Late Jurassic. The depicted areas represent: the presumed extent of the landmass (A), the shelf lagoon (B), the carbonate platform (C), the basin development (D); star shows approximate position of Švédské šance (modified after Eliáš in Suk et al. 1984: 150).

skála locality, which ranges between the middle Oxfordian *Perisphinctes plicatilis* Ammonite Biozone and the lowest section of the upper Oxfordian *Epipeltoceras bimammatum* Biozone (Eliáš 1981).

Material and methods

Material.—The tooth IGS-MJ-0001 comes from the Upper Jurassic (Oxfordian) deposits at Švédské šance, Czech Republic. Photographs were taken using a standard digital camera and scanning electron microscope (SEM). Terminology follows Smith et al. (2005), supplemented by Lubbe et al. (2009); note that the absence of the basal part of the tooth crown on the distal half of the tooth means it was impossible to mark the position of point B (sensu Smith et al. 2005) accurately. Attention was paid to the height and width of denticles: although these data are normally ignored, they are mentioned here because of their potential importance for future research. Tooth measurements were made through a Leica IM 1000 with measuring module.

Tooth anatomical orientation.—The terminology of anatomical orientation follows the recommendations of Smith and Dodson (2003): apical, toward the apices of the tooth crown or the tooth base; basal, toward the cervix dentis; distal, away from the premaxillary or mandibular symphysis; labial, toward the lips; lingual, toward the tongue; mesial, toward the premaxillary or mandibular symphysis (see Fig. 3).

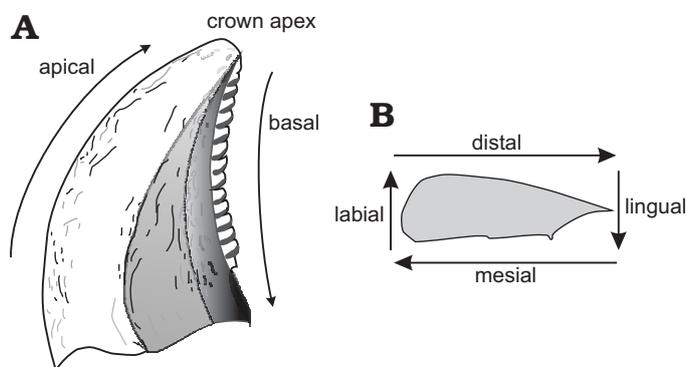


Fig. 3. Tooth orientation terminology. **A.** Theropod tooth crown in lingual view. **B.** Mid-crown cross-section of idealized theropod tooth crown. After Smith and Dodson (2003).

Theropod tooth anatomy.—Vertically, the teeth consist of the crown and the base, which are separated by the cervix dentis and terminate with the apex. Sometimes, a constriction is present between the tooth crown and the base. The apicobasally oriented enamel ridges developed on the mesial and/or distal faces of the tooth crowns in theropods with ziphodont dentition are referred to as carinae. The carinae, then, are composed of fine-to-coarse enamel bumps called denticles or serrations. In some taxa the denticles are followed by caudae (sensu Abler 1992) that are separated by interdenticular sul-

ci (sensu Smith 2007). The chambers between the adjacent denticles are referred to as cellae (sensu Abler 1992) and their marginal clefts are called diaphyses (sensu Abler 1992). Lingually and labially to the carinae the enamel occasionally forms complexes of parallel grooves and ridges called enamel wrinkles, undulations or crenulations (Brusatte et al. 2007). These structures are approximately perpendicular to the apicobasal axis of the tooth crown, and in some cases the enamel wrinkles connect across the lingual and labial sides of the tooth crown to form clearly visible bands. Sometimes the crowns also bear well developed complexes of longitudinal ridges and grooves (cf. Buffetaut 2012).

Systematic paleontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Averostra Paul, 2002

Tetanurae Gauthier, 1986

Orionides Carrano, Benson, and Sampson, 2012

Orionides indet.

Material.—Tooth (IGS-MJ-0001) from Upper Jurassic (Oxfordian), Švédské šance (Brno-Slatina), Czech Republic.

Description

The tooth (IGS-MJ-0001) is labiolingually compressed, its apical third is slightly oriented linguodistally, and carinae are located on the mesial and distal faces of the tooth crown. Thus, IGS-MJ-0001 most likely represents a lateral tooth (Fig. 4). The moderate labiolingual compression, slight tooth crown curvature, and lingually slightly displaced mesial carina might suggest that the tooth was positioned in the anterior half of the right maxilla or left dentary. The tooth is almost complete. Only a basal part of the tooth crown on the distal half of the tooth and an apical part of the tooth base are missing (Fig. 4A). The loss of part of the tooth base, however, apparently occurred after the discovery of the material because the rock with the fossil has clearly been broken off.

Denticles.—The denticles are chisel-shaped, non-inclined (Fig. 5), and present on both carinae. However, the mesial carina bears fully developed denticles only in its apical half. Approximately in the center of the mesial carina the denticles start to reduce in height. In the basal third of tooth crown, then, the denticles are completely missing. The distal carina is not wholly preserved, yet, due to the fact that the denticles do not appear to reduce their size, and the serrations on distal carinae are usually more strongly developed (D'Amore 2009), it is likely that the denticles were present along its whole length.

The density of denticulation, which was measured per 5 mm because the CBL exceeds 7 mm, is similar on both carinae. The density within the apical third of the mesial carina is 15 denticles per 5 mm. The density changes in the middle

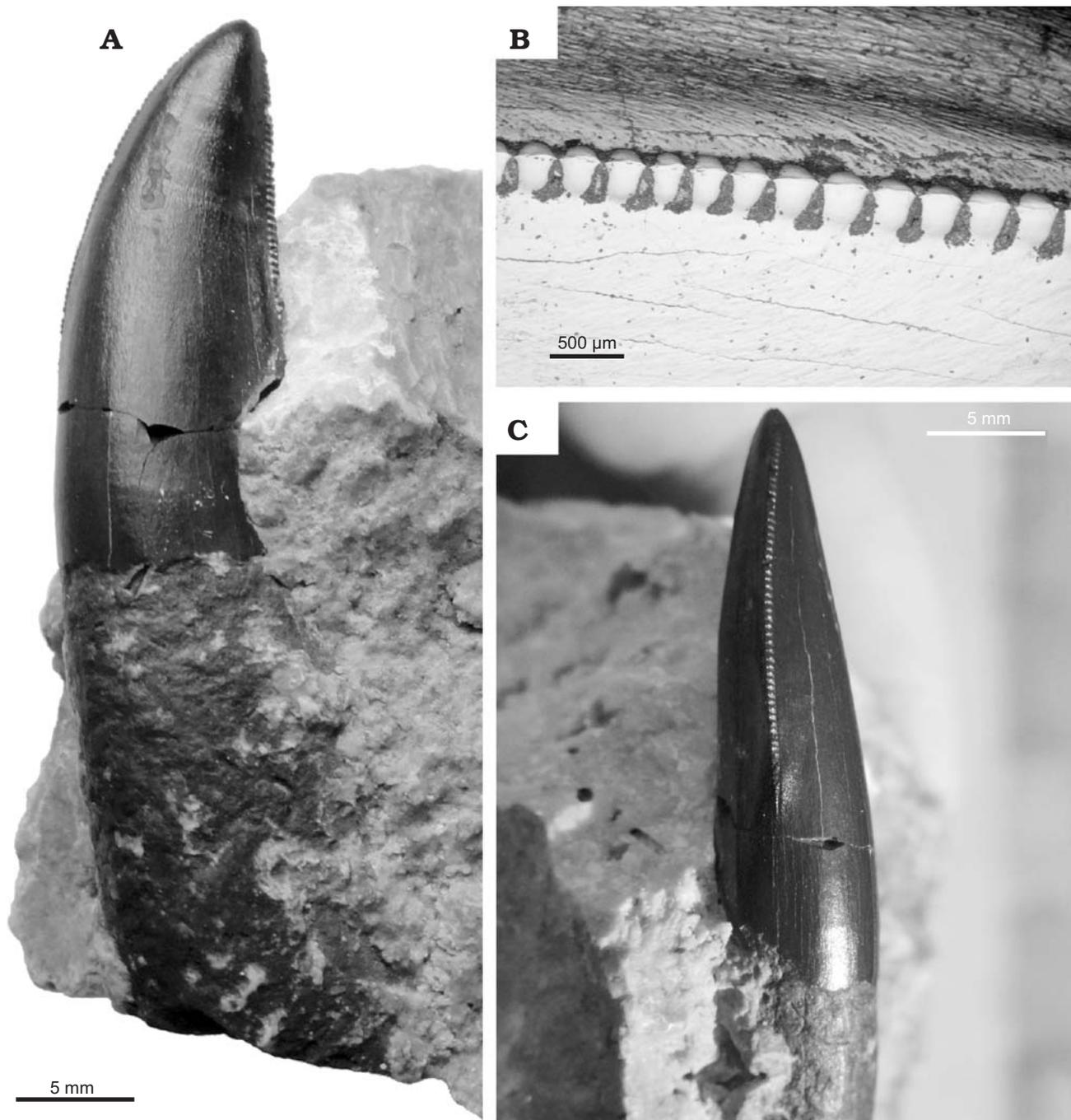


Fig. 4. Non-avian theropod tooth, IGS-MJ-0001 (*Orionides* indet.) from Upper Jurassic (Oxfordian), Švédské šance (Brno-Slatina), Czech Republic. **A.** Tooth in labial view. **B.** Detail of the serrations on the mesial carina; with the cellae filled with matrix and clear absence of the complexes of interdenticular sulci and caudae. **C.** Tooth crown from the mesial view.

section to 17 denticles per 5 mm. The basal third of the mesial carina lacks denticles. As in the mesial carina, the serration density on the distal carina was counted only on the apical third and the center (in both cases the density is equal to 15 denticles per 5 mm), as the basal third of the distal carina is not preserved. The average serration density on the mesial carina (MAVG) is 16 denticles per 5 mm, and on the distal carina (DAVG) 15 denticles per 5 mm. However, it should be noted that the serration density in the basal third of the distal carina is impossible to calculate, because this part is absent,

so it is possible that DAVG might not be accurate (the same applies for the DSDI parameter).

In addition to these parameters, attention was paid to the height and width of denticles. Normally, these measurements are not taken into account, but here they are mentioned because they could be considered in the future. This data, especially the height of denticles, could be affected by taphonomy or preservation. And, indeed, some denticles must be treated as unmeasurable. Nevertheless, the majority of denticles do not bear any traces of damage.

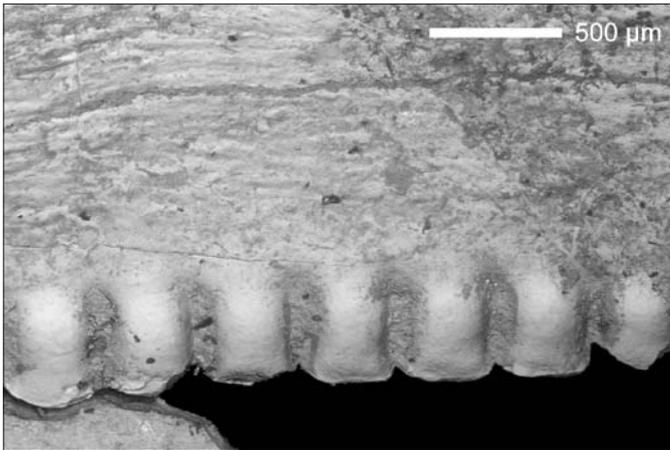


Fig. 5. Non-avian theropod tooth, IGS-MJ-0001 (*Orionides* indet.) from Upper Jurassic (Oxfordian), Švédské šance (Brno-Slatina), Czech Republic. Detail of the serrations on the distal carina from the labial view.

On the mesial and distal carinae the width of denticles is approximately the same and irregularly varies between 200 and 350 μm . This is congruent with similar serration density on both carinae. However, there are differences in denticle heights. On the mesial carina, the height of measurable denticles is 100–200 μm , whereas the denticles on the distal carina are higher (200–400 μm). These differences are consistent with the trend in Theropoda (D’Amore 2009).

Enamel structures.—No significant enamel structures, except the denticles on the carinae, are developed. Interdenticular sulci and caudae, and longitudinal ridges and grooves, are absent (Figs. 4, 5). It is possible to notice very fine mesiodistally oriented irregular “wrinkle-like strips” on the labial and lingual sides of the tooth crown, but whether these structures represent enamel wrinkles in the traditional sense remains uncertain. The tooth crown bears apparent irregularities accompanied by cracked enamel, which are interpreted as deformations. These subtle structures might be taphonomic.

Measurements.—see Table 1.

Comparisons.—In order to find the most probable phylogenetic position of the Moravian theropod, the tooth was compared to several taxa representing different theropod clades. The primary reference material consisted of a set of data published by Smith et al. (2005), which was modified on the basis of Smith and Lamanna (2006), and Ősi et al. (2010). Isolated tooth crowns from the Kimmeridgian of Germany (Lubbe et al. 2009) were also taken into account, but this material differs in several important features; particularly, the high serration density in relation to the size of the teeth is characteristic for some dromaeosaurids, to which these teeth belong. Likewise, the samples from the Cenomanian of

Morocco described by Richter et al. (2012) might be easily distinguished from IGS-MJ-0001 as well.

Within the above-mentioned data set (SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app59-Madzia_SOM.pdf), IGS-MJ-0001 is almost indistinguishable from the teeth of basal tetanurine theropods from the Santonian of Hungary, and “*M. dunkeri*” from the Barremian of England and “*M. pannoniensis*” from the Campanian of Austria, which are also basal tetanurines (Ősi et al. 2010). The teeth are almost identical in terms of measured characters and their mutual ratios, as well as the density, shape and extent of the denticles. However, some differences can be observed in the ornamentation of the enamel. In the Hungarian tetanurines and “*M. dunkeri*” the enamel is clearly wrinkled (Ősi et al. 2010), whereas in IGS-MJ-0001 this feature is probably absent (see above). Nevertheless, the degree of enamel ornamentation in basal members of Tetanurae is relatively variable. For example, in contrast to the teeth of carcharodontosaurid allosauroids, which are characterized by very well developed enamel wrinkles that are especially prominent adjacent to the carinae (e.g., Brusatte et al. 2007), the teeth of some ziphodont megalosauroids lack the wrinkles completely (e.g., Benson 2010b). The distribution of complexes of interdenticular sulci/caudae is equally variable within clades (Benson 2010b; Benson et al. 2010), as well as in single jaws, as noted by Benson (2009) in an individual maxilla or dentary of the megalosauroid *Megalosaurus*. On the other hand, some other theropods, such as the abelisaurid *Majungasaurus*, show a more conservative pattern (see below).

There are several similarities with abelisaurid ceratosaurs, whose dental anatomy is, despite many fossils, relatively poorly studied (Smith 2007). Their teeth resemble the dentitions of some basal tetanurines in many ways; especially in the parameters of tooth crowns, such as CBL and CBW, crown shape, and denticle density (Smith 2007; Canale et al. 2009). However, it seems that in most taxa the enamel is at least partially ornamented; i.e., the denticles are usually followed by the complexes of interdenticular sulci/caudae (e.g., Benson et al. 2010). For example, although the teeth of *Majungasaurus crenatissimus* (Smith 2007) are generally similar to IGS-MJ-0001 in size, shape, and serration density, they differ in other important aspects: their mesial carinae are serrated along their whole length, and the denticles on both carinae are accompanied by the complexes of interdenticular sulci/caudae.

Comparisons to other theropod clades.—Comparisons of the tooth from Švédské šance to other theropods is problematic, because thorough descriptions of theropod teeth have been provided only for limited number of taxa (e.g., Smith

Table 1. Morphometric data of non-avian theropod tooth (IGS-MJ-0001) from Upper Jurassic (Oxfordian), Švédské šance (Brno-Slatina), Czech Republic. For explanation, see Other abbreviations.

AL	CBL	CBW	CH	CA	CDA	CAA	CBR	CHR	MA	MC	MB	DA	DC	DB	DSDI
~25	~10	~6.5	~23.4	~68	~88	~24.5	~0.65	~2.34	15	17	0	15	15	?	~1.06

2005, 2007; Dal Sasso and Maganuco 2011), and because the Moravian material is limited. Nevertheless, this tooth is confidently distinguished from basal theropods, basal ceratosaurs, and noosaurids. At the base of the tetanurine branch of *Averostra* sensu Ezcurra (2006), significant differences are evident in the case of the clades Spinosauridae and Carcharodontosauridae. Within the Coelurosauria, then, it seems unlikely that the tooth belongs to a member of Maniraptoriformes (for phylogenetic relationships among Theropoda see SOM: fig. 1).

Basal theropods, such as coelophysoids, can be distinguished from IGS-MJ-0001 on the basis of the size and shape of the tooth crowns, and higher serration density (Smith et al. 2005). The tooth crowns of basal ceratosaurs, such as *Ceratosaurus*, have also different parameters (for measurements see SOM: fig. 2). Other dissimilarities between the Moravian sample and *Ceratosaurus* include, for example, the presence of longitudinal ridges and grooves on the enamel of *Ceratosaurus* (Madsen and Welles 2000).

Assignment to Noosauridae appears to be improbable as well. If IGS-MJ-0001 was positioned in the anterior half of the jaws, as hypothesized above, it can be clearly distinguished from *Masiakasaurus knopfleri* in that it lacks the longitudinal ridges (cf. Carrano et al. 2002). Moreover, IGS-MJ-0001 has lower denticle density, its serrated mesial carina does not extend to the cervix dentis, and differs in tooth crown shape (cf. Carrano et al. 2002; Smith et al. 2005; Lindoso et al. 2012).

It is also probably not a spinosaurid because it lacks the clearly visible complexes of longitudinal ridges/grooves seen on the labial and lingual faces of the tooth crown of Cretaceous (e.g., Mateus et al. 2011) and Upper Jurassic (Buffetaut 2012) spinosaurids. Further, IGS-MJ-0001 differs from Carcharodontosauridae in the development of tooth crown ornamentation, which is characteristically wrinkled near the carinae (Brusatte et al. 2007).

It is unlikely that IGS-MJ-0001 belongs to Coelurosauria, but there is a few ziphodont clades that could be considered. Although early tyrannosauroids were present in Europe during the Late Jurassic (e.g., Rauhut 2003; Benson 2008; Rauhut et al. 2010; Brusatte and Benson 2013), knowledge of their dental anatomy is limited (e.g., Zinke 1998; Rauhut et al. 2010). Among early tyrannosauroids, IGS-MJ-0001 can be compared to proceratosaurids. It clearly differs from the teeth of *Proceratosaurus bradleyi* in its larger size, less inclined apical third of the tooth crown and considerably lower denticle count per 5 mm on both carinae (cf. Rauhut et al. 2010). It is similar to *Kileskus aristotocus* in terms of CBL, CBR, and CBW (cf. Averianov et al. 2010), but the denticle count of the latter is unavailable. The serration density of IGS-MJ-0001 resembles teeth of the Early Cretaceous proceratosaurid *Sinotyrannus kazuoensis*, but these are larger (cf. Ji et al. 2009). For now, treating IGS-MJ-0001 as a possible early tyrannosauroid would be unsupported. Although many similarities to more derived tyrannosauroids (e.g., Smith et al. 2005; Smith 2007; Brusatte et al. 2011b,

2012) may be noted, such as similar size, shape and serration density, the tooth crowns in all of the better known advanced tyrannosauroids have relatively well developed ornamentation. These include the enamel wrinkles and distinctive complexes of interdenticular sulci/caudae. Late Jurassic compsognathids have generally smaller teeth that possess higher density of denticulation and this is restricted to the distal carinae (Dal Sasso and Maganuco 2011).

Basal Alvarezsauridae can be excluded too based on comparisons to the earliest known alvarezsaurid, *Haplocheirus sollers*, which has very small teeth that are serrated only distally (Choiniere et al. 2010; Han et al. 2011). Teeth of advanced alvarezsaurids (the Alvarezsauridae) are minute and simplified (e.g., Longrich and Currie 2009).

Among ziphodont maniraptoriforms, IGS-MJ-0001 can be safely distinguished from Paraves in terms of tooth crown morphology, size, and serration density. For example, the teeth of paravian coelurosaurids are often smaller than IGS-MJ-0001 and more strongly inclined (e.g., Hwang et al. 2002; Smith et al. 2005; Norell et al. 2009; Lü et al. 2010; Turner et al. 2012). The denticle density is usually higher (Smith et al. 2005; Lubbe et al. 2009; Ősi et al. 2010) and in some paravians (Troodontidae), the tooth crowns are separated from the bases by distinctive constrictions (e.g., Holtz et al. 1998; Lü et al. 2010), a feature that is absent in IGS-MJ-0001.

Discussion and conclusions

The ziphodont archosaur tooth described here (IGS-MJ-0001) is evidently from a non-avian theropod and, thus, the first Jurassic terrestrial vertebrate from the Czech Republic. The size, morphology, extent and density of the denticles, and outer appearance of the enamel of IGS-MJ-0001 support its affiliation with the base of Orionides, the least inclusive tetanurine clade containing megalosauroids and avetheropods (Carrano et al. 2012). Although IGS-MJ-0001 shares some similarities with the teeth of abelisaurid ceratosaurs, the size, tooth crown morphology, and the extent and density of the denticulation are almost identical to the anatomy of the tetanurine teeth described by Ősi et al. (2010).

The tetanurine origin of the Moravian theropod is also in accordance with paleobiogeographical knowledge, as early tetanurines with similar tooth anatomy were abundant in Europe during the Middle to Late Jurassic (e.g., Weishampel et al. 2004; Mateus et al. 2006; Benson 2010a, b). Specifically, attention should be paid to the megalosaurid megalosauroids and sinraptorid (= metriacanthosaurid sensu Carrano et al. 2012) allosauroids (Benson 2010a). To a lesser extent, Allosauridae were present as well (Mateus et al. 2006). A more precise resolution of the phylogenetic affinities of the Moravian theropod requires additional, and more complete, comparative material.

Acknowledgements

I thank Nela Doláková (IGS) for access to the specimen. Obtaining measurements and SEM photographs was possible thanks to the kindness of Martin Ivanov and Jindřich Štelcl (both IGS). I also express my gratitude to Jakub Březina, Rostislav Brzobohatý (both IGS), Miroslav Bubík (Czech Geological Survey, Brno, Czech Republic), and Andrea Cau (Biological, Geological and Environmental Department, University of Bologna, Italy), with whom I have had helpful discussions. Roger Benson (Department of Earth Sciences, University of Oxford, UK), Steve Brusatte (School of GeoSciences, University of Edinburgh, UK), and Mark Young (School of Biological Sciences, University of Edinburgh, UK) provided valuable reviews that improved the manuscript. Jakub Březina and Michal Matějka (Borohrádek, Czech Republic) informed me about the specimen. Magdalena Łukowiak (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland) kindly helped with the preparation of the Figs. 1–3 and Kyle Freeman (Warsaw, Poland) checked the language of the manuscript.

References

- Abler, W.L. 1992. The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals. *Paleobiology* 18: 161–183.
- Andrade, M.B., Young, M.T., Desojo, J.B., and Brusatte, S.L. 2010. The evolution of extreme hypercarnivory in Metriorhynchidae (Mesoeucrocodylia: Thalattosuchia) based on evidence from microscopic denticle morphology. *Journal of Vertebrate Paleontology* 30: 1451–1465.
- Averianov, A.O., Krasnolutski, S.A., and Ivantsov, S.V. 2010. A new basal coelurosaur (Dinosauria: Theropoda) from the Middle Jurassic of Siberia. *Proceedings of the Zoological Institute RAS* 314: 42–57.
- Benson, R.B.J. 2008. New information on *Stokesosaurus*, a tyrannosaurid (Dinosauria: Theropoda) from North America and the United Kingdom. *Journal of Vertebrate Paleontology* 28: 732–750.
- Benson, R.B.J. 2009. An assessment of variability in theropod dinosaur remains from the Bathonian (Middle Jurassic) of Stonesfield and New Park Quarry, UK and taxonomic implications for *Megalosaurus bucklandii* and *Iliosuchus incognitus*. *Palaeontology* 52: 857–877.
- Benson, R.B.J. 2010a. A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and 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 tetanurines. *Journal of Systematic Palaeontology* 8: 131–146.
- Benson, R.B.J., Carrano, M.T., and Brusatte, S.L. 2010. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidae) that survived to the latest Mesozoic. *Naturwissenschaften* 97: 71–78.
- Brusatte, S.L. and Benson, R.B.J. 2013. The systematics of Late Jurassic tyrannosauroids (Dinosauria: Theropoda) from Europe and North America. *Acta Palaeontologica Polonica* 58: 47–54.
- Brusatte, S.L., Benson, R.B.J., Carr, T.D., Williamson, T.E., and Sereno, P.C. 2007. The systematic utility of theropod enamel wrinkles. *Journal of Vertebrate Paleontology* 27: 1052–1056.
- Brusatte, S.L., Benson, R.B.J., and Norell, M.A. 2011b. The anatomy of *Dryptosaurus aquilunguis* (Dinosauria: Theropoda) and a review of its tyrannosauroid affinities. *American Museum Novitates* 3717: 1–53.
- Brusatte, S.L., Carr, T.D., and Norell, M.A. 2012. The osteology of *Alioramus*, a gracile and long-snouted tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. *Bulletin of the American Museum of Natural History* 366: 1–197.
- Brusatte, S.L., Niedzwiedzki, G., and Butler, R.J. 2011a. Footprints pull origin and diversification of dinosaur stem lineage deep into Early Triassic. *Proceedings of the Royal Society B* 278: 1107–1113.
- Bubík, M. 2010. Foraminiferová fauna oxfordských vápenců na Švédských šancích u Brna. *Geologické výzkumy na Moravě a ve Slezsku* 17: 112–116.
- Buffetaut, E. 2012. An early spinosaurid dinosaur from the Late Jurassic of Tendaguru (Tanzania) and the evolution of the spinosaurid dentition. *Oryctos* 10: 1–8.
- Canale, J.L., Scaferla, C.A., Agnolin, F.L., and Novas, F.E. 2009. New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften* 96: 409–414.
- Carrano, M.T., Benson, R.B.J., and Sampson, S.D. 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 10: 211–300.
- Carrano, M.T., Sampson, S.D., and Forster, C.A. 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 22: 510–534.
- Choiniere, J.N., Xu, X., Clark, J.M., Forster, C.A., Guo, Y., and Han, F. 2010. A basal alvarezsaurid theropod from the Early Late Jurassic of Xinjiang, China. *Science* 327: 571–574.
- D'Amore, D.C. 2009. A functional explanation for denticulation in theropod dinosaur teeth. *The Anatomical Record* 292: 1297–1314.
- Dal Sasso, C. and Maganuco, S. 2011. *Scipionyx samniticus* (Theropoda: Dinosauria: Scipionidae) from the Lower Cretaceous of Italy—osteology, ontogenetic assessment, phylogeny, soft tissue anatomy, taphonomy and palaeobiology. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 37: 1–281.
- Eliáš, M. 1981. Facies and paleogeography of the Jurassic of the Bohemian Massif. *Sborník geologických věd. Geologie* 35: 75–144.
- Ezcurra, M.D. 2006. A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan & Lucas, 1999 from the Upper Triassic of New Mexico, USA. *Geodiversitas* 28: 649–684.
- Gauthier, J. 1986. Saurischian monophyly and the origin of birds. In: Padian, K. (ed.), *The Origin of Birds and the Evolution of Flight. Memoirs of the California Academy of Sciences* 8: 1–55.
- Gauthier, J. and de Queiroz, K. 2001. Feathered dinosaurs, flying dinosaurs, crown dinosaurs, and the name “Aves”. In: J. Gauthier and L.F. Gall (eds.), *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom*, 7–41. Peabody Museum of Natural History, Yale University, New Haven.
- Han, F., Clark, J.M., Xu, X., Sullivan, C., Choiniere, J., and Hone, D.W.E. 2011. Theropod teeth from the Middle–Upper Jurassic Shishugou Formation of northwest Xinjiang, China. *Journal of Vertebrate Paleontology* 31: 111–126.
- Holtz, T.R., Jr., Brinkman, D.L., and Chandler, C.L. 1998. Denticle morphometrics and a possibly omnivorous feeding habit for the theropod dinosaur *Troodon*. *Gaia* 15: 159–166.
- Hwang, S.H., Norell, M.A., Ji, Q., and Gao, K. 2002. New Specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from Northeastern China. *American Museum Novitates* 3381: 1–44.
- Ji, Q., Ji, S.-A., and Zhang, L.-J. 2009. First large tyrannosauroid theropod from the Early Cretaceous Jehol Biota in northeastern China. *Geological Bulletin of China* 28: 1369–1374.
- King, M.J. and Benton, M.J. 1996. Dinosaurs in the Early and Mid Triassic?—the footprint evidence from Britain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 122: 213–225.
- Lindoso, R.M., Medeiros, M.A., Carvalho, I. de S., and Marinho, T. da S. 2012. *Masiakasaurus*-like theropod teeth from the Alcântara Formation, São Luís Basin (Cenomanian), northeastern Brazil. *Cretaceous Research* 36: 119–124.
- Longrich, N.R. and Currie, P.J. 2009. *Albertonykus borealis*, a new alvarezsaur (Dinosauria: Theropoda) from the Early Maastrichtian of Alberta, Canada: implications for the systematics and ecology of the Alvarezsauridae. *Cretaceous Research* 30: 239–252.
- Lubbe, T. van der, Richter, U., and Knötschke, N. 2009. Velociraptorine dromaeosaurid teeth from the Kimmeridgian (Late Jurassic) of Germany. *Acta Palaeontologica Polonica* 54: 401–408.

- Lü, J.-C., Xu, L., Liu, Y.-Q., Zhang, X.-L., Jia, S.H., and Ji, Q. 2010. A new troodontid theropod from the Late Cretaceous of central China, and the radiation of Asian troodontids. *Acta Palaeontologica Polonica* 55: 381–388.
- Madsen, J.H. Jr. and Welles, S.P. 2000. *Ceratosaurus* (Dinosauria, Theropoda): a revised osteology. Utah Geological Survey *Miscellaneous Publication* 00-2: 1–80.
- Marsh, O.C. 1881. Principal characters of American Jurassic dinosaurs, Part V. *American Journal of Science* 21: 417–423.
- Mateus, O., Araújo, R., Natário, C., and Castanhinha, R. 2011. A new specimen of the theropod dinosaur *Baryonyx* from the early Cretaceous of Portugal and taxonomic validity of *Suchosaurus*. *Zootaxa* 2827: 54–68.
- Mateus, O., Walen, A., and Antunes, M.T. 2006. The large theropod fauna of the Lourinhã Formation (Portugal) and its similarity to that of the Morrison Formation, with a description of a new species of *Allosaurus*. In: J.R. Foster and S.G. Lucas (eds.), *Paleontology and Geology of the Upper Jurassic Morrison Formation. New Mexico Museum of Natural History and Science Bulletin* 36: 123–129.
- Mayr, G. and Gregorová, R. 2012. A tiny stem group representative of Pici (Aves, Piciformes) from the early Oligocene of the Czech Republic. *Paläontologische Zeitschrift* 86: 333–343.
- Mlíkovský, J. 1995. Tertiary avian localities of the Czech Republic. In: Mlíkovský, J. (ed.), *Tertiary avian localities of Europe. Acta Universitatis Carolinae, Geologica* 39: 551–557.
- Norell, M.A., Makovicky, P.J., Bever, G.S., Balanoff, A.M., Clark, J.M., Barsbold, R., and Rowe, T. 2009. A review of the Mongolian Cretaceous dinosaur *Saurornithoides* (Troodontidae: Theropoda). *American Museum Novitates* 3654: 1–63.
- Oppenheimer, J. 1907. Der Malm der Schwedenschanze bei Brünn. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns* 20: 221–271.
- Ősi, A., Apesteguía, S., and Kowalewski, M. 2010. Non-avian theropod dinosaurs from the early Late Cretaceous of central Europe. *Cretaceous Research* 31: 304–320.
- Owen, R. 1842. Report on British fossil reptiles. *Report of the British Association for the Advancement of Sciences* 9: 60–204.
- Paul, G.S. 2002. *Dinosaurs of the Air: The Evolution and Loss of Flight in Dinosaurs and Birds*. 472 pp. The John Hopkins University Press, Baltimore.
- Prouza, V., Táslel, R., Valín, F., and Holub, V. 1985. Gravelly to sandy braidplain deposition in the Buntsandstein-facies Bohdašín Formation in Northeastern Bohemia (Czechoslovakia). In: D. Mader (ed.), *Aspects of Fluvial Sedimentation in the Lower Triassic Buntsandstein of Europe. Lecture Notes in Earth Sciences* 4: 397–410.
- Rauhut, O.W.M. 2003. A tyrannosauroid dinosaur from the Late Jurassic of Portugal. *Palaeontology* 46: 903–910.
- Rauhut, O.W.M., Milner, A.C., and Moore-Fay, S. 2010. Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society* 158: 155–195.
- Richter, U., Mudroch, A., and Buckley, L.G. 2012. Isolated theropod teeth from the Kem Kem Beds (Early Cenomanian) near Taouz, Morocco. *Paläontologische Zeitschrift* published online.
- Smith, J.B. 2005. Heterodonty in *Tyrannosaurus rex*: implications for the taxonomic and systematic utility of theropod dentitions. *Journal of Vertebrate Paleontology* 25: 865–887.
- Smith, J.B. 2007. Dental morphology and variation in *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. In: S.D. Sampson and D.W. Krause (eds.), *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoir* 8: 103–126.
- Smith, J.B. and Dodson, P. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology* 23: 1–12.
- Smith, J.B. and Lamanna, M.C. 2006. An abelisaurid from the Late Cretaceous of Egypt: implications for theropod biogeography. *Naturwissenschaften* 93: 242–245.
- Smith, J.B., Vann, D.R., and Dodson, P. 2005. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. *The Anatomical Record Part A* 285: 699–736.
- Suk, M., Bližkovský, M., Buday, T., Chlupáč, I., Cicha, I., Dudek, A., Dvořák, J., Eliáš, M., Holub, V., Ibrmajer, J., Kodým, O., Kukul, Z., Malkovský, M., Menčík, E., Müller, V., Tyráček, J., Vejnar, Z., and Zeman, A. 1984. *Geological History of the Territory of the Czech Socialist Republic*. 396 pp. Geological Survey, Praha.
- Turner, A.H., Makovicky, P.J., and Norell, M.A. 2012. A review of dromaeosaurid systematics and paravian phylogeny. *Bulletin of the American Museum of Natural History* 371: 1–206.
- Uličný, D. 2004. A drying-upward aeolian system of the Bohdašín Formation (Early Triassic), Sudetes of NE Czech Republic: record of seasonality and long-term palaeoclimate change. *Sedimentary Geology* 167: 17–39.
- Weishampel, D.B., Barrett, P.M., Coria, R.A., Le Loeuff, J., Xu, X., Zhao, X., Sahní, A., Goman, E.M.P., and Noto, C.R. 2004. Dinosaur distribution. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, Second Edition, 517–606. University of California Press, Berkeley.
- Young, M.T., Brusatte, S.L., de Andrade, M.B., Desojo, J.B., Beatty, B.L., Steel, L., Fernández, M.S., Sakamoto, M., Ruiz-Omeñaca, J.I., and Schoch, R.R. 2012. The Cranial Osteology and feeding ecology of the metriorhynchid crocodylomorph genera *Dakosaurus* and *Plesiosuchus* from the Late Jurassic of Europe. *PLoS ONE* 7: e44985.
- Young, M.T., Brusatte, S.L., Ruta, M., and Andrade, M.B. 2010. The evolution of Metriorhynchoidea (Mesoeucrocodylia, Thalattosuchia): an integrated approach using geometric morphometrics, analysis of disparity, and biomechanics. *Zoological Journal of the Linnean Society* 158: 801–859.
- Zajíc, J. 1998. The first find of the dinosaurian footprint in the Czech Republic (the Krkonoše Piedmont Basin) and its stratigraphic significance. *Journal of the Czech Geological Society* 43: 273–275.
- Zinke, J. 1998. Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal). *Paläontologische Zeitschrift* 72: 179–189.