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The first non-avian theropod from the Czech Republic

DANIEL MADZIA



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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.

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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 dinosauromorphs (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 dinosauromorph.

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 microziphodont (denticle dimensions do not exceed 300 µm; *Geosaurus*) or macroziphodont (denticle dimensions do exceed 300 µm; *Dakosaurus*). However, no macroziphodont 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 ziphodont 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

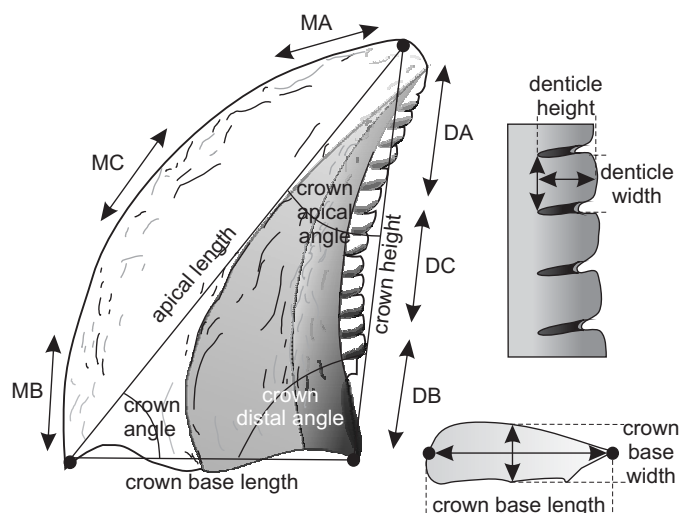


Fig. 1. Sketch of tooth crown and measurements (modified after Smith et al. 2005 and Lubbe et al. 2009). DA, number of denticles per 5 mm at the apical third of the distal carina; DB, number of denticles per 5 mm at the basal third of the distal carina; DC, number of denticles per 5 mm at the center 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 $180^\circ \text{CA} - \text{CAA}$; 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 $\text{DSDI} = (\text{MAVG} + 1) / (\text{DAVG} + 1)$, 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

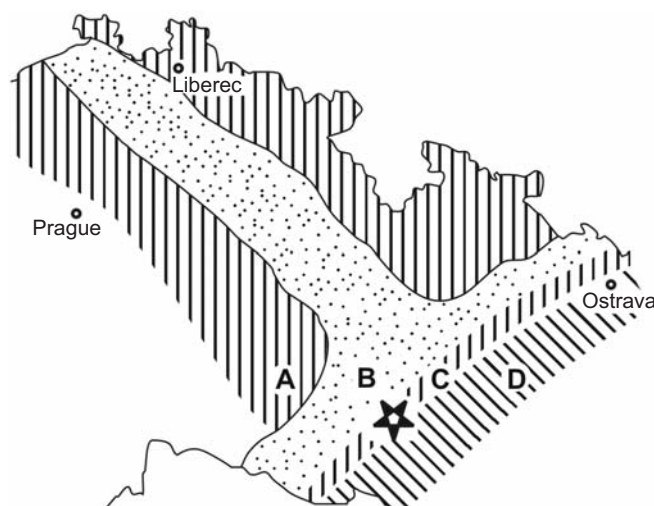


Fig. 2. Location of the discovery and paleogeography of the Czech Republic during the maximum transgression in the Late Jurassic. The depicted areas represent: the presumed extent of the landmass (A), the shelf lagoon (B), the carbonate platform (C), the basin development (D); star shows approximate 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).

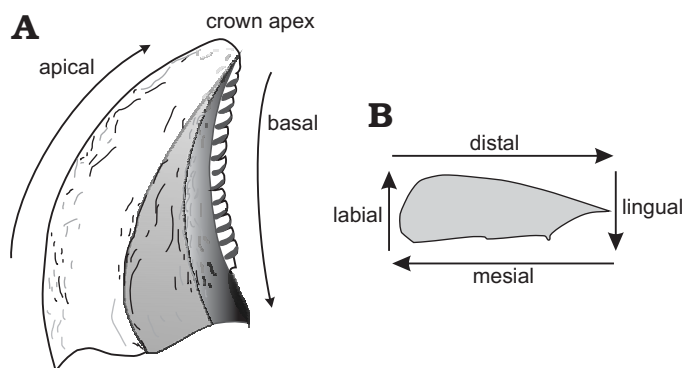


Fig. 3. Tooth orientation terminology. **A.** Theropod tooth crown in lingual view. **B.** Mid-crown cross-section of idealized theropod tooth crown. After Smith and Dodson (2003).

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

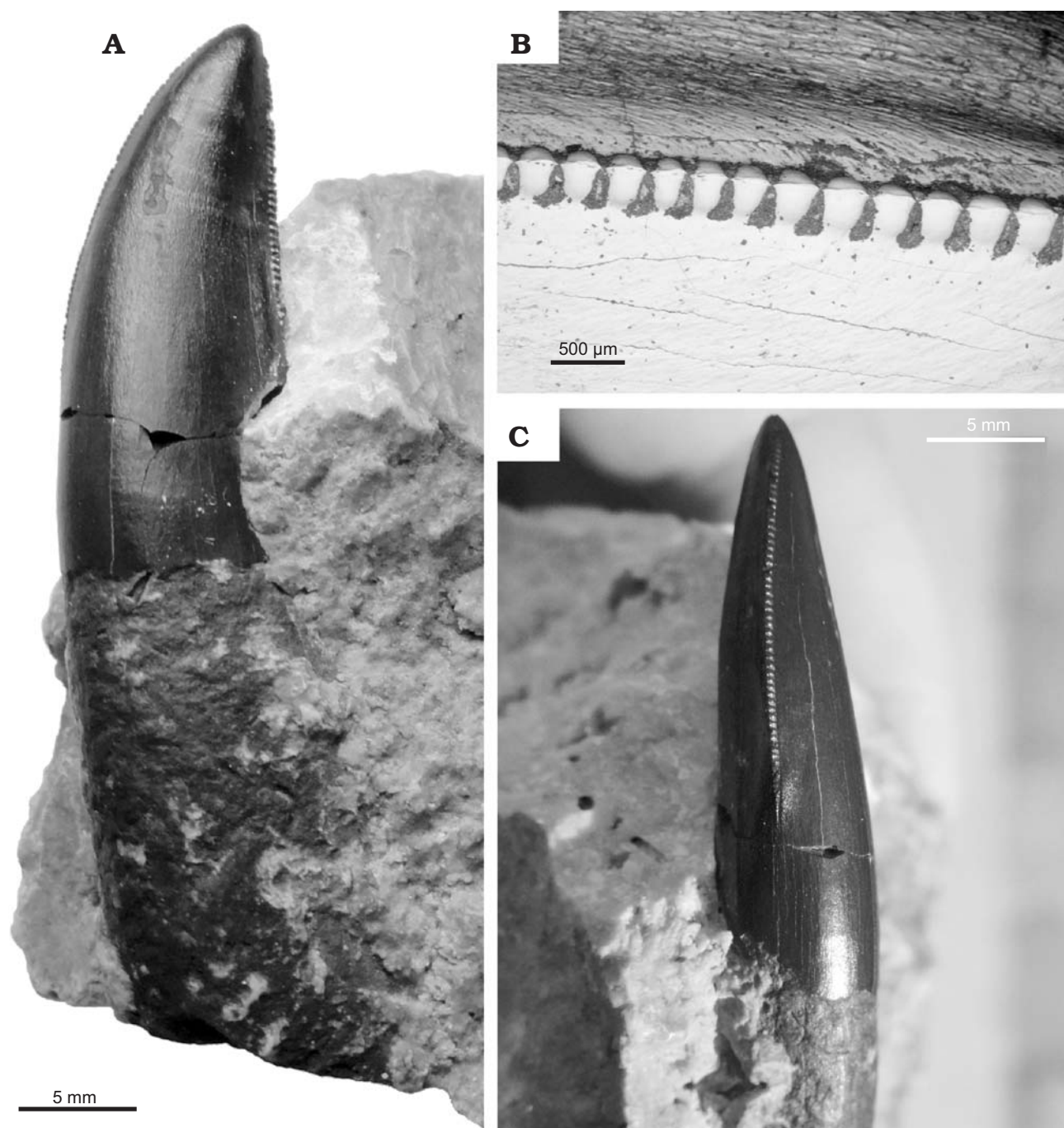


Fig. 4. Non-avian theropod tooth, IGS-MJ-0001 (*Orionides* indet.) from Upper Jurassic (Oxfordian), Švédské šance (Brno-Slatina), Czech Republic. **A.** Tooth in labial view. **B.** Detail of the serrations on the mesial carina; with the cellae filled with matrix and clear absence of the complexes of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

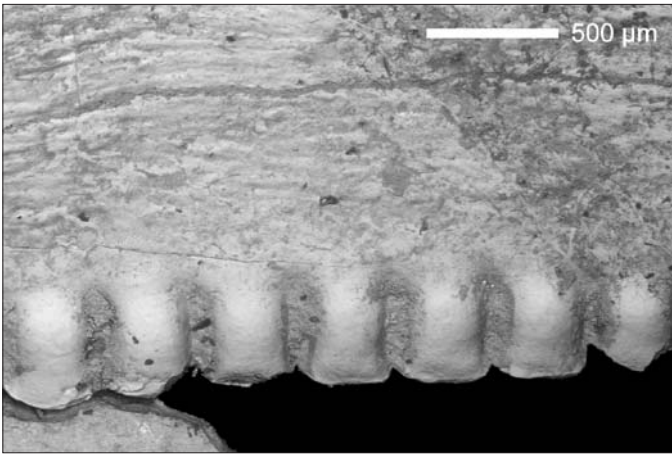


Fig. 5. Non-avian theropod tooth, IGS-MJ-0001 (*Orionides* indet.) from Upper Jurassic (Oxfordian), Švédské šance (Brno-Slatina), Czech Republic. Detail of the serrations on the distal carina from the labial view.

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 noasaurids. 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 Noasauridae 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 coelurosaurs 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.

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