Velociraptorine Dromaeosaurid Teeth from the Kimmeridgian (Late Jurassic) of Germany

Authors: Lubbe, Torsten Van Der, Richter, Ute, and Knötschke, Nils

Source: Acta Palaeontologica Polonica, 54(3) : 401-408

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2008.0007

Velociraptorine dromaeosaurid teeth from the Kimmeridgian (Late Jurassic) of Germany

TORSTEN VAN DER LUBBE, UTE RICHTER, and NILS KNÖTSCHKE

Lubbe, T. van der, Richter, U., and Knötschke, N. 2009. Velociraptorine dromaeosaurid teeth from the Kimmeridgian (Late Jurassic) of Germany. *Acta Palaeontologica Polonica* 54 (3): 401–408. DOI: 10.4202/app.2008.0007.

Six theropod teeth from a Late Jurassic (Kimmeridgian) bone bed in Langenberg Quarry of Oker (Goslar, Germany) are identified as a new dromaeosaurid taxon, here left in open nomenclature. Direct comparison reveals that the teeth are very similar to velociraptorine dromaeosaurid teeth from the Guimarota coal mine (Late Jurassic, Portugal) and to velociraptorine dromaeosaurid teeth from Uña (Barremian, Cuenca Province, Spain). Our data indicate that the teeth from the Kimmeridgian of Lower Saxony are of velociraptorine dromaeosaurid type, and therefore represent one of the oldest occurrences of the group Dromaeosauridae.

Key words: Saurischia, Theropoda, Dromaeosauridae, velociraptorine dromaeosaurid teeth, Late Jurassic, Germany.

Torsten van der Lubbe [Torsten.v.d.Lubbe@web.de] and Ute Richter [ute.richter2@gmx.net], Lower Saxony State Museum, Willy-Brandt-Allee 5, 30169 Hannover, Germany;
Nils Knötschke [palaeo_nils@hotmail.com], Dinosaurier-Freilichtmuseum Münchehagen, Alte Zollstrasse 5, 31547 Rehburg-Loccum, Germany.

Received 28 January 2008, accepted 9 December 2008, available online 20 April 2009.

Introduction

The Langenberg Quarry of Oker (Goslar) has become a world recognised Jurassic fossil locality, since the "Dinosaur Cemetery" of the dwarf sauropod dinosaur *Europasaurus holgeri* was discovered in 1998 (Laven 2001; Sander et al. 2006). The deposits at this locality have yielded a rich diversity of invertebrate, macro-, and microvertebrate fossils, derived from a palaeoenvironment comprising shallow marine lagoons and small islands (e.g., Mudroch and Thies 1996; Duffin and Thies 1997; Thies et al. 1997; Mudroch et al. 1999; Mudroch et al. 2000; Thies and Broschinski 2001; Delecat et al. 2001; Fastnacht 2005; Karl et al. 2006; Thies et al. 2007). Investigations of Pape (1970) and Fischer (1991) suggest that the calcareous sedimentary rocks exposed in Langenberg Quarry were deposited in a shallow marine inlet or in a small marginal basin of the German Late Jurassic Basin, but the nature of the palaeoenvironment in which the Kimmeridgian rocks of northwest Germany were deposited is still under dispute.

Beside the diverse invertebrate fauna including bivalves, brachiopods, gastropods, echinoderms and nautiloids, vertebrate fossils (sharks, bony fishes, crocodiles, turtles, pterosaurs) are abundant. Some layers show a greater terrestrial influence and thus bones and teeth of land vertebrates, especially of sauropods and theropods are accumulated. Thies et al. (2007) postulated an archipelago with islands of changing expansions depending on sea level.

In northern Germany, the fossil remains of theropods consist mainly of isolated teeth. Discoveries of articulated skeletons, bones or skulls are very rare. The isolated teeth of Langenberg Quarry show features hitherto only known from the Dromaeosauridae: They are strongly labiolingually compressed, strongly distally recurved and apically sharply pointed and the carinae are serrated mesially and distally, with a distinct size difference between mesial and distal denticles (Ostrom 1990).

Institutional abbreviation.—DFMMh/FV: Dinosaurier-Freilichtmuseum Münchehagen/Verein zur Förderung der Niedersächsischen Paläontologie (e.V.), Germany; CHG, NEV, SER, and VIC, collection of the University of Sciences and Technics, Languedoc, Montpellier, France (Université des Sciences et Techniques du Languedoc, Montpellier).

Other abbreviations (see also Table 1 and Fig. 3).—AL, apical length, measured from the mesialmost point at the base of the crown toward its tip; CAA, crown apical angle, calculated using the law of cosines with the values of CBL, AL, and CH; CBL, crown basal length, measured at the base of the crown from its mesialmost to its distalmost extension (excluding the carinae); CBR, crown base ratio, numerical value derived from dividing CBW through CBL (labiolingual "compression"); CBW, crown basal width, labiolingual extension of the crown at its base; CDA, crown distal angle, calculated as 180°—CMA–CAA; CH, crown height, measured from the basal-/distal-most point of the crown toward its tip; CHR, crown height ratio, numerical value derived from dividing CH through CBL (taller crowns have higher CHR values, more squat crowns have smaller CHR values);

CMA, crown mesial angle, calculated using the law of cosines with the values of CBL, AL, and CH; DA, denticles per 5 mm^1 at the most apical part of the distal carina; DAVG, average number of denticles on the distal carina of the crown^2; DB: denticles per 5 mm^1 at the most basal part of the distal carina; DC, denticles per 5 mm^1 at the centre of the distal carina; DSDI: denticle size difference index; MA, denticles per 5 mm^1 at the most apical part of the mesial carina; MAVG, average number of denticles on the mesial carina of the crown^2; MB, denticles per 5 mm^1 at the most basal part of the mesial carina; MC: denticles per 5 mm^1 at the centre of the mesial carina.

^{1} for crowns with a CBL value < 7 mm serrations were counted per 2mm, and then prorated to 5 mm.

^{2} apical + centre + basal (if applicable) serration counts divided by the number of applicable positions.

Locality, geological and stratigraphical setting

The Langenberg Quarry, a working quarry of the "Rohstoffbetriebe Oker GmbH and Co." for cement and road gravel, is located on the southern slope of the Langenberg, 5 km east of Goslar near the Harz Mountains, Lower Saxony, northern Germany (Fig. 1).

The Mesozoic sediments of Langenberg Quarry are part of the southern flank of the Subhercynian Syncline. Due to the strong uplift of the Harz Mountains during Late Cretaceous times, the sedimentary sequence was completely inverted, and now dips to the south at an angle of about 70°. Thus the extensive bedding planes, which are widely visible from the south, are the sub-surface of the beds. The more durable beds of the sequence, which are resistant to erosion, form a narrow but distinct ridge in the landscape, which runs parallel to the main fault of the northern slope of the Harz Mountains ("Harz-Nordrand-Störung").

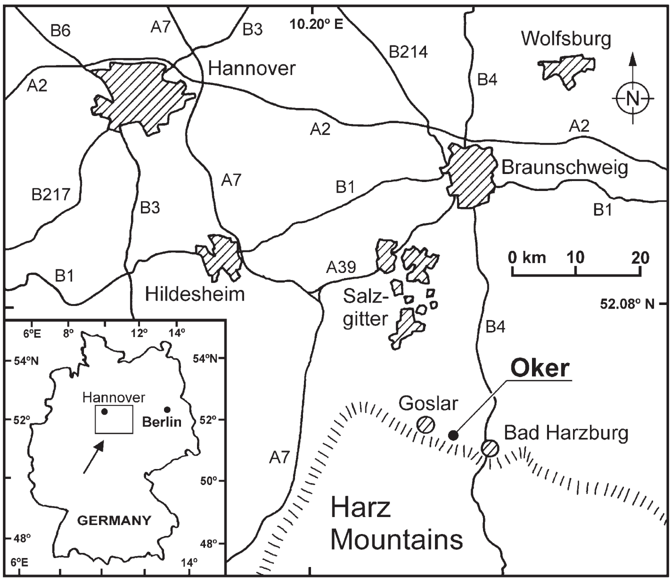

Fig. 1. Geographic location of Langenberg quarry ("Rohstoffbetriebe Oker") east of Oker (Goslar), Harz Mountains, Germany (from Mudroch and Thies 1996).

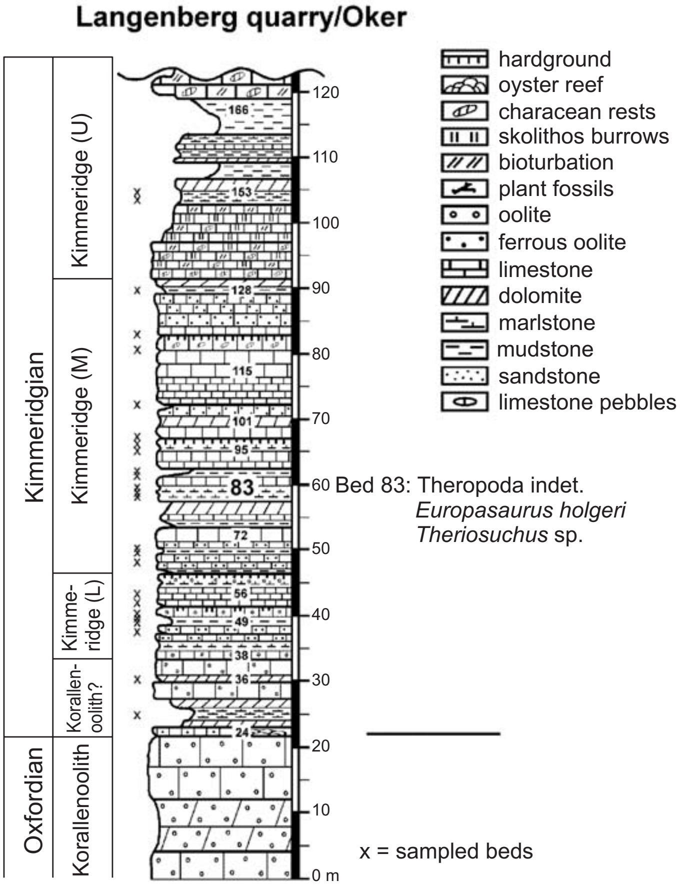

Fig. 2. The lithostratigraphic log of the Kimmeridgian of the Langenberg quarry near Oker, Harz Mountains, Germany. The examined theropod teeth were found in bed 83 together with skeletal remains of *Europasaurus holgeri* (modified after Thies et al. 2007).

The sedimentary environment belongs to the North German Late Jurassic Basin, in which a shallow epeiric sea connected to the Tethys Ocean during the Kimmeridgian. The stratigraphic section at Langenberg Quarry exposes and shows the most complete succession of Kimmeridgian rocks in northwestern Germany. The nearly 200 m thick and largely calcareous to marly Upper Jurassic sequence reaches from the Lower Coral Rag ("Unteren Korallenoolith", upper Oxfordian) up to the Kimmeridge marls (lower Kimmeridgian). An exact correlation with the subboreal standard zonation based on ammonoids is not possible, because ammonoids are extremely rare at Langenberg Quarry (Thies et al. 2007). The upper Oxfordian sediments ("Unterer to Mittlerer Korallenoolith") reveal fully marine conditions. During the Kimmeridgian the environment became more and more brackish because of increasing freshwater influx (Gramann et al. 1997; Mudroch et al. 1999).

The "Kimmeridge-Marls" of the Langenberg area were probably deposited in a shallow water basin in a lagoonal or bay-like environment. The fine stratigraphy is based on microfossils (Pape 1970; Zihrul 1990; Thies et al. 2007). Fischer (1991) gave an overview of this succession, discussing stratigraphy, lithology, and facies variation.

The theropod teeth were found in bed 83 (see Fig. 2), a layer which also contains bones and teeth of the dwarf sauropod *Europasaurus holgeri* (see Sander et al. 2006). Bed 83 consists of grey mudstones and limestones and represents sedimentation with mixed salinities under seasonal monsoon-like weather conditions with a wet season, characterised by humidity and low salinity and a dry season, characterised by aridity and high salinity (Thies et al. 2007).

Material and methods

Tooth nomenclature.—We follow the topological definitions of Smith et al. (2005), as follows: apical, toward the tip of the crown; basal, toward the base of the crown; distal, away from the body axis; labial, toward the lips; lingual, toward the tongue; mesial, toward the body axis.

During preparation of the huge blocks with bones, skulls and teeth of *Europasaurus holgeri*, seven theropod teeth were discovered. All figured specimens are housed in the collection of the Dinosaurier-Freilichtmuseum Münchehagen (DFMMh), Lower Saxony, Germany under catalogue numbers FV 382, 383, 530, 658, 707.1, 705, and 790.5.

Photography of small specimens was done using a scanning electron microscope (SEM) and of larger teeth with standard digital cameras.

Measurements were taken with standard callipers and from SEM and digital photographs, following protocol described by Smith et al. (2005; Table 1, Fig. 3).

In order to assess the affinities of the teeth from Langenberg Quarry we followed the methods described by Farlow et al. (1991), Fiorillo and Currie (1994), Baszio (1997), Holtz et al. (1998), Park et al. (2000), Rauhut (2002), Sankey et al. (2002), Perea et al. (2003), and Sweetman (2004). In order to allow easier comparison of the new specimens to others already described, DFMMh/FV 530 and DFMMh/FV 383 were also measured according to methods given in Sankey et al. (2002) and obtained values, and photos of specimens then used for comparison.

We also used the morphometric data published by Smith et al. (2005) and Smith and Lamanna (2006) for comparison with the Langenberg specimens. Since it represents the most complete set of data for theropod teeth published to date we will refer to it further on as “the standard”.

In addition to the characters used by Smith et al. (2005) and Smith and Lamanna (2006), we calculated three additional numerical values in order to achieve a more detailed description of tooth morphology. The first two values, CDA (crown distal angle) and CAA (crown apical angle), were calculated using the law of cosines. Whereas CDA is a character describing how strongly a crown is recurved distally, CAA describes how sharply the crown is pointed apically.

Table 1. Morphometric data of five specimens from Langenberg quarry of Oker.

Specimen	DFMMh/ FV 383	DFMMh/ FV 530	DFMMh/ FV 382	DFMMh/ FV 658	DFMMh/ FV 790.5
Side	N.A.	N.A.	N.A.	N.A.	N.A.
Position	isolated	isolated	isolated	isolated	isolated
CBL	6.94	5.71	5.81	8.8	1.87
CBW	3.11	2.68	3.40	4.80	1.30
CH	9.72	7.15	9.66	24.50	2.81
AL	13.74	10.74	11.17	26.60	3.49
CBR	0.45	0.47	0.59	0.55	0.70
CHR	1.40	1.25	1.66	2.78	1.50
CMA	41.66	37.86	59.84	66.76	53.41
CAA	28.34	29.35	31.33	19.27	32.30
CDA	110.00	112.78	88.82	93.97	94.30
MA	29.00	32.50	31.80	29.00	16.66
MC	27.00	32.50	22.50	23.00	12.66
MB	0.00	0.00	0.00	0.00	0.00
DA	25.00	27.50	30.00	25.00	13.33
DC	24.00	26.50	27.50	28.00	12.66
DB	26.00	31.30	35.00	32.00	13.33
MAVG	28.00	32.50	27.15	26.00	14.66
DAVG	25.33	28.43	30.83	28.33	13.11
DSDI	1.10	1.14	0.88	0.92	1.11

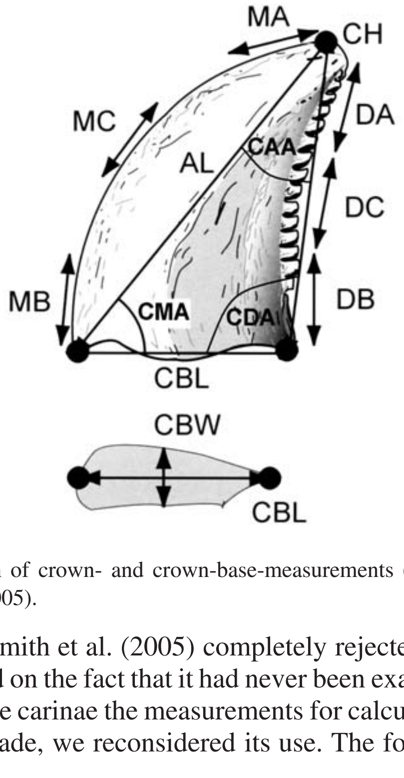

Fig. 3. Sketch of crown- and crown-base-measurements (modified after Smith et al. 2005).

While Smith et al. (2005) completely rejected the use of DSDI based on the fact that it had never been exactly defined where on the carinae the measurements for calculating DSDI are to be made, we reconsidered its use. The following formula:

If MAVG OR DAVG ≥ 1

then $\mathrm{DSDI} = \mathrm{MAVG} + 1/\mathrm{DAVG} + 1$ else $\mathrm{DSDI} = 0$

permits calculation of the DSDI value without the need to define exact areas of measurement because those are already defined for MA, MC, MB, DA, DC, DB (Fig. 3).

DOI: 10.4202/app.2008.0007

Systematic palaeontology

Dinosauria Owen, 1842
Theropoda Marsh, 1881
Maniraptora Gauthier, 1986
Dromaeosauridae Matthew and Brown, 1922
gen. et sp. indet.

Description

No significant portion of the root is preserved in any of the specimens and there are no visible signs of resorption, which, together with tooth tip- and denticle-wear, indicates that all specimens represent shed teeth. Whether shedding occurred pre- or post-mortem cannot be determined. Except for DFMMh/FV 658 and DFMMh/FV 707.1 (Fig. 4C, E), the specimens described here are small (CH < 10 mm). The height of the crowns (from the apex to the base of the crown) ranges from 2.81 to 24.5 mm, with a CBL ranging from 1.87 to 8.8 mm. All specimens are strongly labiolingually compressed (average CBR < 0.5) and strongly distally recurved, so that the tooth apex extends behind the level of the base of the crown, except for DFMMh/FV 382 (Fig. 4D) and DFMMh/FV 790.5, which are less strongly recurved and less labiolingually compressed. Denticles are present on the entire distal carina of all specimens. Mesially, the serration does not reach beyond the apical half of the carina in any specimens except for DFMMh/FV 658 in which the apical 70% of the mesial carina is serrated. The cross sectional shape of all specimens is a flat oval with the exception of DFMMh/FV 790.5 where it is oval. The carinae run gradually along the midline of the teeth in most specimens except for DFMMh/FV 382, where the mesial carina is offset about 5° towards the lingual side relative to perpendicular at the base of the crown and the distal carina twists slightly toward the lingual side of the crown at its centre but approaches the perpendicular line again near the crown base. In all specimens the denticles on the mesial carina are smaller than those on the distal carina. The denticles on all specimens are of subrectangular shape in lateral view and slightly inclined apically. Wear on the tooth tip is present in all specimens except for DFMMh/FV 707.1 (Fig. 4C) in which the apical part is missing, and for DFMMh/FV 790.5. Given the very small size of the latter crown it is likely that specimen DFMMh/FV 790.5 belongs to a hatchling or juvenile. Denticle wear is visible on both the mesial and distal apical serrations of all specimens.

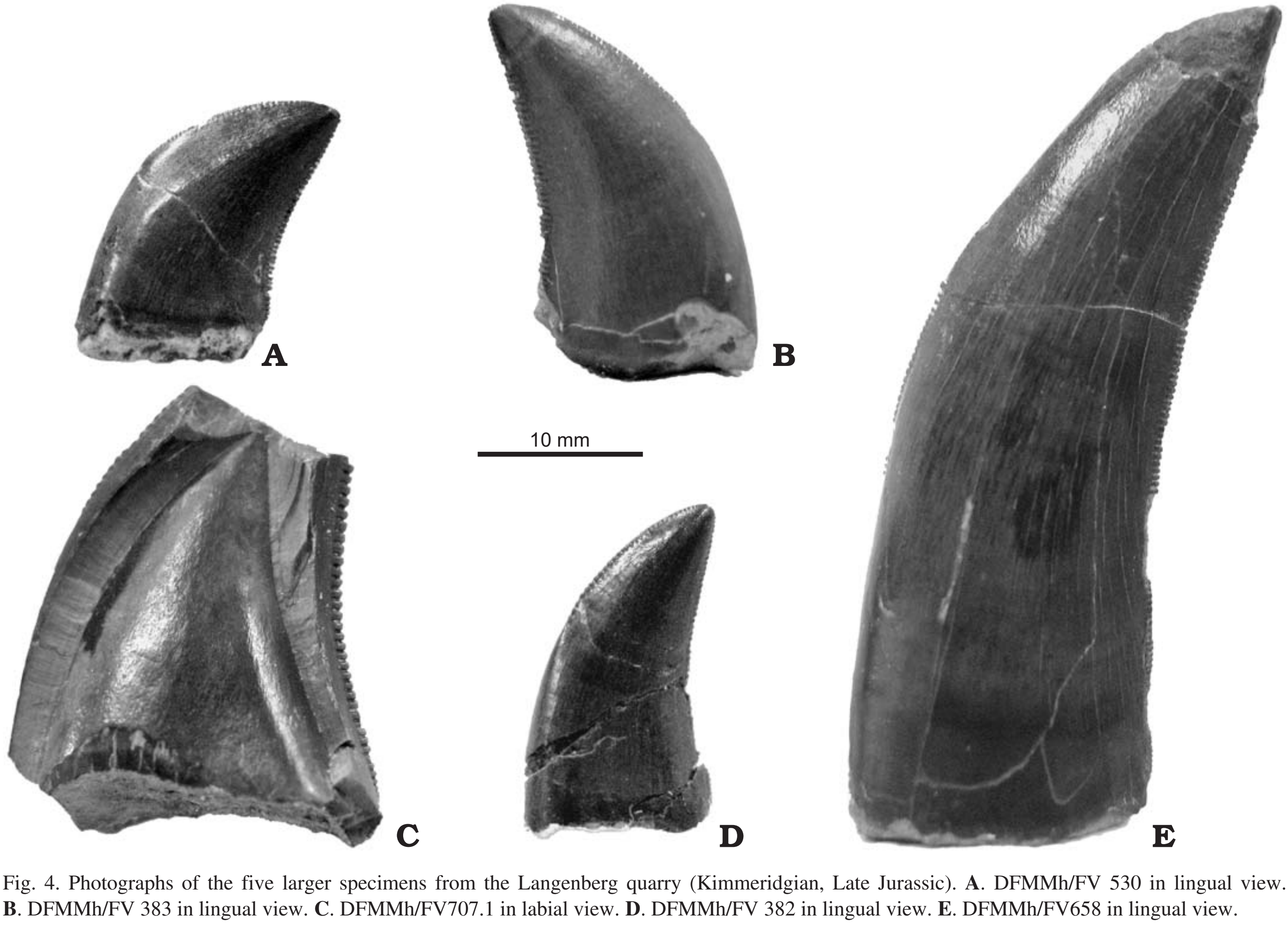

Fig. 4. Photographs of the five larger specimens from the Langenberg quarry (Kimmeridgian, Late Jurassic). **A**. DFMMh/FV 530 in lingual view. **B**. DFMMh/FV 383 in lingual view. **C**. DFMMh/FV707.1 in labial view. **D**. DFMMh/FV 382 in lingual view. **E**. DFMMh/FV658 in lingual view.

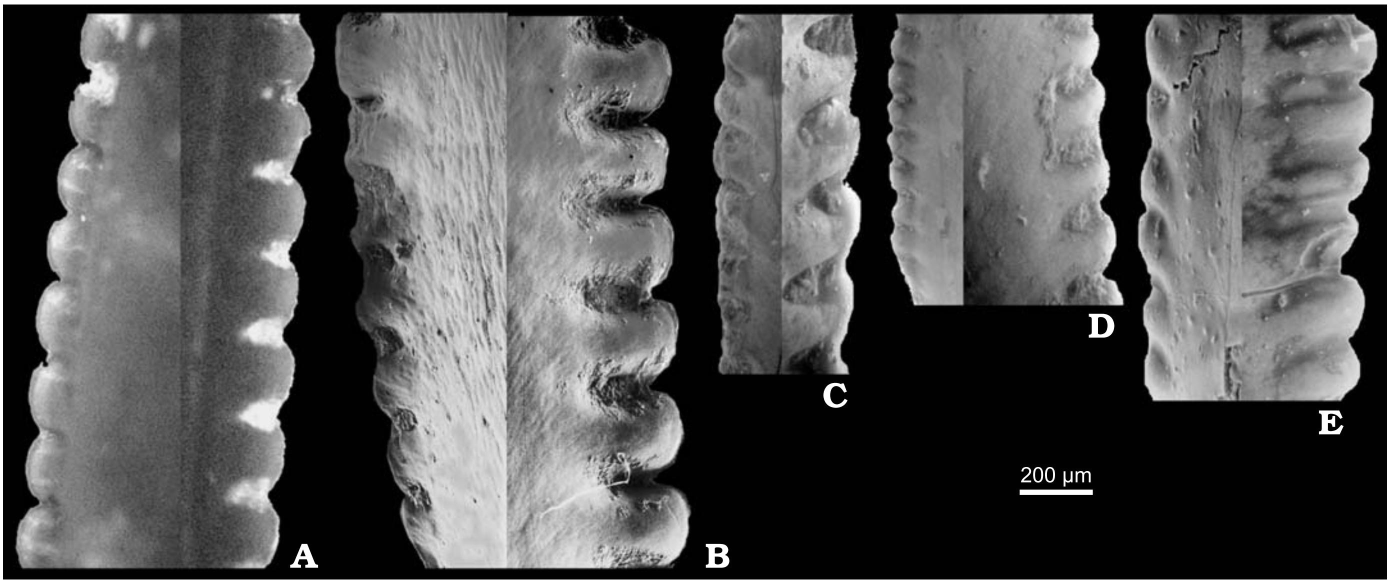

Fig. 5. Digital (**A**) and scanning electron microscope (**B**–**E**) photographies of the five larger specimens from the Langenberg quarry (Kimmeridgian, Late Jurassic): DFMMh/ FV658 (**A**), DFMMh/ FV707.1 (**B**), DFMMh/ FV383 (**C**), DFMMh/ FV 530 (**D**), and DFMMh/ FV 382 (**E**).

Apart from DFMMh/FV 382, which shows multiple cracks in the enamel, and DFMMh/FV 707.1, in which the apical part is missing, all specimens are excellently preserved. In DFMMh/FV 707.1 the labial side of the crown the enamel and part of the dentine have broken off. The resorbtion facet of a partially erupted (about 50%) replacement tooth (apparently lost with the shedding of the crown) is visible on the labial side. The enamel on the lingual side is well preserved and shows three minor cracks, which run almost perpendicular toward the base. Their almost perpendicular orientation might indicate that they were caused by pressures exerted on the crown by the erupting replacement tooth.

The enamel is smooth in all specimens and ridges are generally lacking or very faint, nor are colour banding or wrinkles visible, which might indicate growth lines (compare Sweetman 2004).

Comparisons

We found no or only very few similarities to the teeth from Langenberg/Oker in the literature based on the following taxa: *Archaeopteryx* sp. (Weigert 1995); *Compsognathus longipes* (Stromer 1934); *Juravenator starki* (Göhlich and Chiappe 2006); *Carcharodontosauridae* gen. et sp. indet. (Veralli and Calvo 2004); *Allosauridae* gen. et sp. indet. (Park et al. 2000); *Theropoda* gen. et sp. indet. (Perea et al. 2003).

For the following comparison of the Langenberg tooth specimens with other theropod teeth we chose publications with regard to a good availability of morphometric data, photos/drawings, detailed descriptions of the tooth specimens and a determination of the teeth to the family Dromaeosauridae and Troodontidae.

Comparisons with teeth of Dromaeosauridae.—The Langenberg teeth are similar to tooth IWCMS.2002.2 described by Sweetman (2004). However, it remains unclear whether the apical part of the mesial carina of this specimen is serrated or not and, moreover this tooth is slightly more recurved than any of the Langenberg teeth.

There is only a superficial resemblance between the Langenberg teeth and those of *Microraptor zhaoianus* (Hwang et al. 2002). Similar in general form and appearance, the Langenberg teeth are serrated on both their mesial and distal carina whereas they are not in *M. zhaoianus*. Those teeth are constricted between crown and root and are more strongly recurved distally than the Langenberg specimens. Moreover, the denticles of *M. zhaoianus* are proportionally much larger than those of the Langenberg teeth.

Teeth of *Graciliraptor lujiatunensis* (Xu and Wang 2004) are similar to the Langenberg teeth because they show a size difference of denticles between mesial and distal serration but they differ in being less distally recurved and less sharply tapered apically. Moreover, the carinae of the rostral maxillary teeth of *Graciliraptor lujiatunensis* are smooth.

The Langenberg teeth are similar to those of *Sinornithosaurus millenii* described by Xu and Wu (2001) with respect to size difference of the denticles between mesial and distal serrations, subrectangular shape of denticles, strongly distally recurved crown and apically pointed crown, which is labiolingually compressed. The latter character is not mentioned by Xu and Wu (2001), but it is seen on their fig. 5B–I. The teeth of *S. millenii* differ from those of Langenberg quarry in having a groove anterior to the distal carina, and some of the premaxillary teeth have smooth carinae. Moreover, the Langenberg teeth are on average larger than those of *S. millenii*.

DOI: 10.4202/app.2008.0007

Dromaeosaurid teeth from the Late Cretaceous at four localities of southern France (Buffetaut et al. 1986) resemble those from Langenberg in possessing distally recurved crowns, which are labiolingually compressed, but the Langenberg teeth are on average larger than those from France. There is also a distinct size difference of the denticles between the mesial and distal serrations in one specimen (SER 03, Buffetaut et al. 1986: fig. d) from France. The mesial carina of specimen NEV 12 (Buffetaut et al. 1986: fig. a), VIC 17 (Buffetaut et al. 1986: fig. b, c) and CHG 48 (Buffetaut et al. 1986: fig. e) is smooth in contrast to the Langenberg specimens with the central and apical part of the mesial carinae being serrated. The teeth from southern France show proportionally finer serration than that of the teeth from Langenberg quarry.

A theropod tooth from the Wadi-Milk Formation, northern Sudan (Rauhut and Werner 1995) resembles the Langenberg teeth in that it is strongly labiolingually compressed, and strongly distally recurved. There is also a distinctive size difference of denticles between mesial and distal serrations. In contrast the Wadi-Milk specimen shows denticles that are more strongly apically inclined.

Three teeth from the Kem-Kem-beds of the Tafilalt region, southern Morocco (Amiot et al. 2004: pl. 1: 4–6) classified as velociraptorine dromaeosaurid resemble those from Langenberg in CH and CBL size range. They are similar with respect to size difference between mesial and distal serrations, subrectangular shape of denticles, being strongly distally recurved and possessing an apically pointed crown, which is labiolingually compressed. But there are some differences, in general form of the teeth from Morocco and in the distribution of the mesial serration over the carinae, from those of the Langenberg teeth. The denticles of the mesial carina are absent in specimen M-CH-009 whereas in specimens M-ZA-014 and M-JQ-012 the mesial carina is serrated over almost its entire length. The latter character is not mentioned in the text but it is seen on the figures (Amiot et al. 2004: figs. 4 and 6, pl. 1).

Theropod teeth from Uña in Spain (Rauhut 2002) classified as velociraptorine dromaeosaurid are almost indistinguishable from those from Langenberg. Especially one specimen (Rauhut 2002: fig. 2G) resembles specimen DFMMh/FV 530 in all aspects, except that the size difference between mesial and distal denticles is slightly more developed in the Spanish specimen.

The detailed description of the teeth of *Deinonychus antirrhopus* (Ostrom 1969) and morphometric data published by Smith et al. (2005) and Smith and Lamanna (2006) allow a thorough comparison with the Langenberg teeth. The former are similar in size and overall dimensions but the largest crown of one Langenberg tooth is still larger than the largest *D. antirrhopus* tooth in the standard. The values calculated for CMA for the Langenberg teeth fall within the margin of tooth crowns of *D. antirrhopus* in the standard, except for specimen DFMMh/FV 658, which is slightly less recurved. Similar values for CBR indicate that the *D. antirrhopus* teeth and those from Langenberg are about equally labiolingually compressed. The main differences between the two taxa are that *D. antirrhopus* teeth possess proportionally finer serrations, and the mesial carina is serrated over almost its entire length (Ostrom 1969).

The Langenberg teeth are very similar to those of *Velociraptor mongoliensis* in being labiolingually compressed, distally recurved, showing a distinctive size difference between mesial and distal denticles, and a mesial carina, which is serrated only in its central and apical part. General form, size, and distribution of the mesial and distal serrations over the carinae of DFMMh/FV 530 match those of the tooth depicted in Barsbold and Osmólska (1999: fig. 2C). The detailed morphometric data given for the *V. mongoliensis* teeth by Smith et al. (2005) and Smith and Lamanna (2006) indicate that the main differences between the teeth lie in their size, with the Langenberg teeth being on average larger and showing proportionally higher values for CBL than those of *V. mongoliensis*.

The velociraptorine dromaeosaurid teeth from the coal mine of Guimarota (Late Jurassic, Portugal) depicted in Rauhut (2000: fig. 11.11) appear to be very similar to those from Langenberg. Denticle size difference, orientation, and shape match very nicely. Specimen GUI D 67 shows strong similarities to the Langenberg teeth and supports our hypothesis that the specimens from Langenberg quarry and those from Guimarota may belong to the same taxon.

Comparisons with teeth of Troodontidae.—Although specimen DFMMh/FV790.5 shows some similarity to teeth of *Troodon formosus* (see Holtz et al. 1998) in being of small size and in possession of coarser serration than any other teeth from Langenberg quarry of Oker; it also differs from the dentition of *T. formosus* in other aspects. The denticles of DFMMh/FV 790.5 show different proportions to those of *T. formosus* teeth and are only slightly inclined towards the crown apex if at all instead of being "apically hooked". Moreover, specimen DFMMh/FV 790.5 lacks the constriction between crown and root that is typical of *T. formosus* teeth.

Discussion

Comparison with other theropod teeth indicates that those from Langenberg are more similar to velociraptorine dromaeosaurid teeth than to any other dentition known within Theropoda. The teeth of *Velociraptor mongoliensis* represented in the standard are most similar to the specimens from Langenberg. However, the Langenberg teeth belong to a species not represented in the standard. The morphology of the Langenberg teeth fits significantly better with that of the Dromaeosauridae than with that of any other group represented in the standard.

The most compelling pieces of evidence for dromaeosaurid affinities of the teeth from Langenberg quarry of Oker are the distinctive size difference between mesial and distal denticles (see Fig. 5), and the strong labio-lingual compression of the crowns.

Average tooth size (excluding DFMMh/FV 790.5) suggests that the animals from the Langenberg quarry were within the size range of larger dromaeosaurid taxa such as *Deinonychus*. Especially, the relatively large size of specimen DFMMh/FV 658 implies that the "Langenberg dromaeosaurid" might have been a bit larger than the North American taxon.

At least specimen DFMMh/FV 790.5 represents a juvenile specimen. This is indicated by the very small size of the crown itself, and the size of the denticles in relation to the size of the whole crown. The other teeth probably originate from adult or subadult specimens, although all are relatively small.

We interpret velociraptorine dromaeosaurid teeth reported from the Late Jurassic of Portugal by Zinke (1998) and the Langenberg teeth as evidence suggesting that the Dromaeosauridae were ubiquitous across the region of the European Archipelago at that time. Morphological similarity between the German and Portuguese specimens suggests that they might belong to a single, possibly widespread taxon. However, here we refrain from erecting a new binomen for the taxon because more material will undoubtedly be found in the Langenberg quarry bone-bearing rocks, which are still awaiting preparation.

Conclusions

According to morphometric data and their analysis, the theropod teeth from Langenberg quarry of Oker represent some of the earliest known dromaeosaurid specimens. As such they are of importance for our understanding of the stratigraphic extent and the possible geographic origin of the Dromaeosauridae. The presence of a dromaeosaurid contemporaneous with *Archaeopteryx* indicates that the two groups Avialae (sensu Gauthier 1986) and Dromaeosauridae (sensu Sereno 2005) were already distinct in Late Jurassic time.

Acknowledgements

We thank Mike Reich and Till Heinrichs (Geowissenschaftliches Zentrum der Universität Göttingen, Göttingen, Germany) for doing the SEM photography. Our special thanks goes to Detlev Thies, Alexander Mudroch, Hannover, Germany) and Tony Thulborn (Monash University, Brisbane, Australia) for correcting the manuscript and for their helpful comments, and to Susan Turner (Monash Geosciences,Brisbane, Australia) for improving the English of the manuscript. We also thank Nick Snels (Arendonk, Belgium) for providing additional help in the very early stages of this study, and Denver Fowler (Museum of the Rockies, Montana, USA) for his helpful comments. We are grateful for the support of the quarry owner Fabian von Pupka.

References

Amiot, R., Buffetaut, E., Tong, H., Boudad, L., and Kabiri, L. 2004. Isolated theropod teeth from the Cenomanian of Morocco and their palaeobiogeographical significance. *Revue de Paleobiologie Vol. spec.* 9: 143–149.

Barsbold, R. and Osmólska, H. 1999. The skull of *Velociraptor* (Theropoda) from the Late Cretaceous of Mongolia. *Acta Palaeontologica Polonica* 44 (2): 189–219.

Baszio, S. 1997. Systematic palaeontology of isolated dinosaur teeth from the latest Cretaceous of south Alberta, Canada. *Courier Forschungs-institut Senckenberg* 196: 33–77.

Buffetaut, E., Marandat, B., and Sigé, B. 1986. Découverte de dents de Deinonychosaures (Saurischia, Theropoda) dans le Crétacé supérieur du Sud de la France. *Comptes Rendus de l'Academie des Sciences de Paris* 303 (II): 1393–1396.

Carpenter, K. 1982. Baby dinosaurs from the Late Cretaceous Lance and Hell Creek formations and description of a new species of theropod. *Contributions to Geology*, *University of Wyoming* 20 (2): 123–134.

Delecat, S., Peckmann, J., and Reitner, J. 2001. Non-rigid cryptic sponges in oyster patch reefs (Lower Kimmeridgian, Langenberg/Oker, Germany). *Facies* 45: 231–254.

Duffin, C.J. and Thies, D. 1997. Hybodont shark teeth from the Kimmeridgian (Late Jurassic) of northwest Germany. *Geologica et Palaeontologica* 31: 235–256.

Farlow, J.O., Brinkman, D.L., Abler, W.L., and Currie, P.J. 1991. Size, shape and serration density of theropod dinosaur lateral teeth. *Modern Geology* 16: 161–198.

Fastnacht, M. 2005. The first dsungaripterid pterosaur from the Kimmeridgian of Germany and the biomechanics of pterosaur long bones. *Acta Palaeontologica Polonica* 50 (2): 273–288.

Fiorillo, A.R. and Currie, P.J. 1994. Theropod teeth from the Judith River Formation (Upper Cretaceous) of South-central Montana. *Journal of Vertebrate Palaeontology* 14 (1): 74–80.

Fischer, R. 1991. Die Oberjura-Schichtenfolge vom Langenberg bei Oker. *Arbeitskreis für Paläontologie Hannover – Zeitschrift für Amateur-Paläontologie* 19 (2): 21–36.

Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. *In*: K. Padian (ed.), The Origin of Birds and the Evolution of Flight. *Memoirs of the California Academy of Sciences* 8: 1–55.

Göhlich, U.B. and Chiappe, L.M. 2006. A new carnivorous dinosaur from the Late Jurassic Solnhofen archipelago. *Nature* 440: 329–332.

Gramann, F., Heunisch, C., Klassen, H., Kockel, F., Dulce, G., Harms, F.-J., Katschorek, T., Mönnig, E., Schudack, M., Schudack, U., Thies, D., and Weiss, M. 1997. Das Niedersächsische Oberjura-Becken – Ergebnisse interdisziplinärer Zusammenarbeit. *Zeitschrift der Deutschen Geologischen Gesellschaft* 148 (2): 165–236.

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., Qiang, J., and Geqin, G. 2002. New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from northeastern China. *American Museum Novitates* 3381: 1–44.

Karl, H.-V., Gröning, E., Brauckmann, C., Schwarz, D., and Knötschke, N. 2006. The Late Jurassic crocodiles of the Langenberg near Oker, Lower Saxony (Germany), and description of related materials (with remarks on the history of quarrying the "Langenberg Limestone" and "Obernkirchen Sandstone"). *Clausthaler Geowissenschaften* 5: 59–77.

Laven, T.A. 2001. *Kraniale Osteologie eines Sauropoden (Reptilia, Saurischia) aus dem Oberjura Norddeutschlands und dessen phylogenetische Stellung*. 127 pp. Unpublished M.Sc. thesis, Johannes-Gutenberg-Universität, Mainz.

Mudroch, A. and Thies D. 1996. Knochenfischzähne (Osteichthyes, Actinopterygii) aus dem Oberjura (Kimmeridgium) des Langenberges bei Oker (Norddeutschland). *Geologica et Palaeontologica* 30: 239–265.

Mudroch, A. Thies, D., and Baumann, A. 1999. ^{87}Sr/^{86}Sr Analysis on Late

DOI: 10.4202/app.2008.0007

Jurassic fish teeth. Implications for paleosalinity of fossil habitats. *In*: G. Arratia (ed.), Mesozoic Fishes—Systematics and the Fossil Record. *Proceedings of the 2nd International Meeting, Buckow 1997*, 595–604. Verlag Dr. Friedrich Pfeil, München.

Ostrom, J.H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Peabody Museum of Natural History, Bulletin* 30: 1–165.

Ostrom, J.H. 1990. Dromaeosauridae. *In*: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 269–279. University of California Press, Berkley.

Pape, H.-G. 1970. Die Malmschichtenfolge vom Langenberg bei Oker (nördl. Harzvorland). *Mitteilungen des Geologischen Institutes der TU Hannover* 9: 41–134.

Park, E.-J., Yang, S.-Y., and Currie, P.J. 2000. Early Cretaceous dinosaur teeth of Korea. *Palaeontological Society Korea, Special Publications* 4: 58–98.

Perea, D., Ubilla, M., and Rojas, A. 2003. First report of theropods from the Tacuarembó Formation (Late Jurassic–Early Cretaceous), Uruguay. *Alcheringa* 27: 79–83.

Perea, D., Ubilla, M., and Rojas, A. 2003. First report of theropods from the Tacuarembó Formation (Late Jurassic–Early Cretaceous), Uruguay. *Alcheringa* 27: 79–83.

Rauhut, O.W.M. 2000. The dinosaur fauna from the Guimarota mine. *In*: T. Martin and B. Krebs (eds.), *Guimarota—A Jurassic Ecosystem*, 75–82. Verlag Dr. Friedrich Pfeil, München.

Rauhut, O.W.M. 2002. Dinosaur teeth from the Barremian of Uña, Province of Cuenca, Spain. *Cretaceous Research* 23: 255–263.

Rauhut, O.W.M. and Werner, C. 1995. First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). *Paläontologische Zeitschrift* 69: 475–489.

Sander, M., Mateus, O., Laven, T., and Knötschke, N. 2006. Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur. *Nature* 441: 739–741.

Sankey, J.T., Brinkman, D.B., Guenther, M., and Currie, P.J. 2002. Small theropod and bird teeth from the Late Cretaceous (late Campanian) Judith River Group, Alberta. *Journal of Paleontology* 76 (4): 751–763.

Sereno, P.C. 2005. The logical basis of phylogenetic taxonomy. *Systematic Biology* 54 (4): 595–619.

Smith, J.B. and Lamanna, M.C. 2006. An abelisaurid from the Late Cretaceous of Egypt: implications for theropod biogeography. *Naturwissenschaften*, Short Communication DOI 10.1007/s00114-006-0092-3.

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.

Stromer, E. 1934. Die Zähne des *Compsognathus* und Bemerkungen über das Gebiss der Theropoda. *Centralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B* 4: 74–85.

Sweetman, S.C. 2004. The first record of velociraptorine dinosaurs (Saurischia, Theropoda) from the Wealden (Early Cretaceous, Barremian) of southern England. *Cretaceous Research* 25: 353–364.

Thies, D. and Broschinski, A. 2001. Teeth of a small durophagus crocodile from the Late Jurassic (Kimmeridgian) of north Germany. *Geologische Beiträge Hannover* 2: 65–70.

Thies, D., Mudroch, A., and Turner, S. 2007. Jurassic marine-nonmarine correlation of the Kimmeridium, Oker, Germany. *Progress in Natural Science* 17 (5): 79–87.

Thies, D., Windolf, R., and Mudroch, A. 1997. First record of Atoposauridae (Crocodylia: Metamesosuchia) in the Upper Jurassic (Kimmeridgian) of Northwest Germany. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 205 (3): 393–411.

Veralli, C. and Calvo, J.O. 2004. Dientes de terópodos carcharodontosáuridos del Turoniano superior-Coniaciano inferior del Neuquén, Patagonia, Argentina. *Ameghiniana* 41 (4): 1–4.

Weigert, A. 1995. Isolated teeth of cf. *Archaeopteryx* sp. from the Upper Jurassic of the coal mine Guimarota (Portugal). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte H* 9: 562–576.

Xu, X. and Wang, X.-L. 2004. A new dromaeosaur (Dinosauria: Theropoda) from the Early Cretaceous Yixian Formation of Western Liaoning. *Vertebrata PalAsiatica* 4: 111–119.

Xu, X. and Wu, X.-C. 2001. Cranial morphology of *Sinornithosaurus millenii* Xu et al. 1999 (Dinosauria: Theropoda: Dromaeosauridae) from the Yixian Formation of Liaoning, China. *Canadian Journal of Earth Sciences* 38: 1739–1752.

Zihrul, B. 1990. Mikrobiostratigraphie, Palökologie und Mikropaläontologie in Gesteinen des Unteren und Mittleren Malm am Langenberg bei Goslar/Oker. *Clausthaler Geowissenschaftliche Dissertationen* 38: 1–220.

Zinke, J. 1998. Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal). *Paläontologische Zeitschrift* 72 (1/2): 179–189.