FIRST JURASSIC MAMMALS OF GERMANY: MULTITUBERCULATE TEETH FROM LANGENBERG QUARRY (LOWER SAXONY)

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Two multituberculate molars from the Kimmeridgian of the Langenberg Quarry near Goslar (Lower Saxony, Germany) represent the first Jurassic mammals from Germany. An upper M1 with cusp formula 5L/4B is characterized by strongly ornamented enamel and is assigned to *Teutonodon langenbergensis* gen. et sp. n. within the plagiaulacid line. A second specimen preserving two large and one small cusp is interpreted as a lingual fragment of an eobaatarid m1. It extends the stratigraphic range of Eobaataridae from the Early Cretaceous to the Late Jurassic (Kimmeridgian) The new findings expand the geographic range of multituberculates to Central Europe.

Key words: Eobaatarid, Kimmeridgian, Multituberculata, Plagiaulacid, *Teutonodon lan-genbergensis*.

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INTRODUCTION

During Jurassic times, Germany was largely covered by epicontinental seas, and Jurassic strata of the Germanic Basin and northwest German Jurassic basin (Lower Saxon Basin) have mainly produced marine fossils. Terrestrial vertebrates such as the small juvenile theropod dinosaurs *Juravenator* Göhlich *et* Chiappe, 2006 and *Sciurumimus* Rauhut *et al.*, 2012 from the Solnhofen area in southern Germany are rare exceptions. Even in the Solnhofen area, which has yielded a reasonable number of terrestrial vertebrates during more than 200 years of extensive collecting, a mammalian specimen has never been detected. The Jurassic lagoons of the Solnhofen area were apparently too far from the coast (Ziegler 1990) for a regular input of terrestrial faunal elements. In northern Germany, the Upper Jurassic (Kimmeridgian) is developed as shallow marine to continental deposits (Pieńkowski *et al.* 2008). A relatively recently discovered locality for terrestrial vertebrates in northern Germany, the Langenberg Quarry near Goslar (Lower Saxony), has now produced the first Jurassic mammalian remains from Germany.

Institutional abbreviation.—NLMH, Niedersächsisches Landesmuseum, Hannover, Germany.

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GEOLOGIC SETTING

All described material was found in the Langenberg Quarry, a classic and well-studied outcrop exposing excellent sections of Upper Jurassic shallow marine strata (Lotze 1968; Pape 1970; Fischer 1991) near the town of Goslar, Lower Saxony, northern Germany (Fig. 1). The beds are tilted to a near vertical, slightly overturned position and the quarrying proceeds along strike, exposing the beds only in cross section and

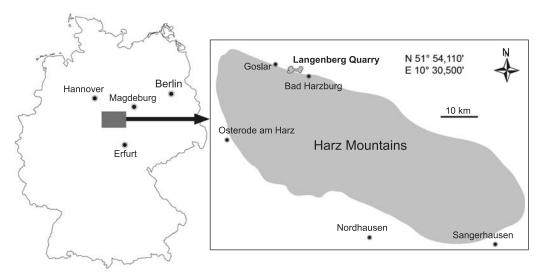


Fig. 1. Geographic position of the Langenberg Quarry at the northern rim of the Harz Mountains in Lower Saxony (Germany).

not along bedding planes. The dominant deposits are impure carbonates which grade into marls. Sediment composition and faunal content of invertebrates can vary with water depth and be influenced by water salinity, but there is no evidence of subaerial exposure (Lotze 1968; Pape 1970). The sediments in the quarry are well dated biostratigraphically and range from late Oxfordian to late Kimmeridgian in age (Lotze 1968; Pape 1970; Fischer 1991). After the stratigraphic subdivision of Fischer (1991), most of the terrestrial vertebrate remains (including the sauropod dinosaur *Europasaurus* Mateus *et al.*, 2006 in Sander *et al.* 2006 and probably the mammal teeth described herein) were found in bed 83, and not in bed 93 as incorrectly stated in recent publications (Sander *et al.* 2006; Carballido and Sander 2013; Marpmann *et al.* 2014). This bed is a light grey-greenish marly limestone. It has been assigned to the "Mittleres Kimmeridge", a northwest-German equivalent to the lower part of the upper Kimmeridgian of the international chronostratigraphic time scale (Schweigert 1999; Lallensack *et al.* 2015).

Paleogeographically, the Langenberg Quarry is located in the Lower Saxony Basin, which covered much of northern Germany in Late Jurassic and Early Cretaceous times and that was surrounded by several large palaeo-islands (Ziegler 1990), the source of the clastic components in the sediment.

FOSSIL VERTEBRATES FROM THE LANGENBERG QUARRY

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

Beds 56, 73, and 83 also have produced exceptional material of non-dinosaurian vertebrates (Wings and Sander 2012). This includes the three-dimensionally preserved articulated skeleton of a small pterosaur, which has been described as the first dsungaripterid from the Kimmeridgian of Germany (Fastnacht 2005), the teeth and skeletons of a new taxon of the small non-marine atoposaurid crocodilian *Theriosuchus* Owen, 1879 (Thies *et al.* 1997; Karl *et al.* 2006), and the associated remains of a partial skeleton of a paramacellodid lizard (Richter *et al.* 2013). Diverse turtle material (including several skulls) has been found as well and comprises cf. *Thalassemys, Plesiochelys* Rütimeyer, 1873, and possibly a new taxon (Jansen and Klein 2014). In addition to abundant reptilian teeth (OW, personal observations), microvertebrate remains from the Langenberg include a diverse fish fauna represented mainly by isolated teeth of marine chondrichthyans and osteichthyans (Thies 1995; Mudroch and Thies 1996; Mudroch 2001).

TAPHONOMY

Almost all of the fossil material from terrestrial vertebrates (including both mammalian teeth described herein) was recovered after regular blasting operations in the Langenberg Quarry. Despite the large number of bones and teeth known from *Europasaurus*, the general distribution of bones and teeth in bed 83 is scarce. The skeletal remains seem to have been accumulated in certain areas, probably lenses or channels (OW, personal observations). The bone-bearing sections of bed 83 are usually 30–50 cm thick and also contain a large number of well-rounded micritic intraclasts. The combination of bone material and intraclasts is also important for recognizing blocks of this specific layer in the quarry heap after the blasting.

All herein described material was found near the coordinates: N 51°54,110', E 10°30,500' in October 2014. Because the blocks were not found in situ, it remains possible, although very unlikely, that the finds come not from bed 83, but from another bed nearby. They can, however, be certainly assigned to the lower part of the upper Kimmeridgian.

Both mammalian teeth (NLMH 105650; NLMH 105651) have been found isolated in the fine-grained marly limestone matrix, but the typical micritic intraclasts as well as isolated bones of turtles and crocodilians as well as a large number of crocodilian teeth (>100) and fish teeth were found directly associated. Most of the associated reptilian bones are very well preserved, indicating limited transport and quick



Fig. 2. NLMH 105650, holotype of the plagiaulacid-line multituberculate *Teutonodon langenbergensis* gen. et sp. n. (marked by circle) *in situ*, close to the vertebra of the crocodilian cf. *Goniopholis* during preparation (October 21, 2014).

burial. Almost all teeth are well-preserved and show no evidence of abrasion by postmortem transport. The two mammalian teeth (NLMH 105650 and NLMH 105651) were found in the same sediment block with a total diameter of approximately 30 cm. NLMH 105650 was found during preparation of a dorsal vertebra of the semiaquatic crocodilian cf. Goniopholis (Fig. 2) in the Dinosaurier-Park Münchehagen. NLMH 105651 was discovered during picking the screen-washed concentrate from the sediment matrix at the Universität Bonn. Interestingly, NLMH 105650 is almost undamaged; only one root was broken during preparation. Its two large delicate, yet fully preserved roots support the interpretation that there was very little transport before burial and suggest that the habitat was nearby.

MATERIAL AND METHODS

The present work describes two isolated mammalian teeth, NLMH 105650 and NLMH 105651, housed in the geosciences collections of the Niedersächsisches Landesmuseum in Hannover, Germany. The teeth were examined with a Zeiss Discovery V20 Stereomicroscope. Both teeth were scanned with the Micro-CT v|tome|x s 240 scanner (GE Sensing and Inspection Technologies Phoenix|x-ray) at the Steinmann-Institut of the Universität Bonn (Supplementary Online Material available at http://www.palaeontologia.pan.pl/SOM/ pp67-Martin_etal_SOM.pdf).

The SEM images of the sputter coated cast of NLMH 105650 were made using a Camscan MV 2300 (Camscan, Cambridge, UK). For molding the specimen the silicone Provil® novo Light regular (EN ISO 4823, type 3, light; Heraeus Kulzer, Hanau, Germany) was used. The cast was made using epoxy resin RenLam® M-1, hardener Ren® HY 956, and pigment Araldit® DW 0137 (Huntsman Advanced Materials, Offenbach am Main, Germany). Systematics and general nomenclature of multituberculates follow Kielan-Jaworowska *et al.* (2004). For terminology of cusps see Fig. 3.

SYSTEMATIC PALAEONTOLOGY

Mammalia Linnaeus, 1758 Multituberculata Cope, 1884 Plagiaulacid line

Family indet.

Genus Teutonodon gen. n.

LSID urn:lsid:zoobank.org:pub:AAB91665-4045-403F-BA29-B9EE46D87EFD

Etymology: After Teutones, Germanic tribe of antiquity. In the Middle Ages, Teutonia was the common name for the geographical area of Germany.

Diagnosis. — As for the type and only species.

Distribution. — As for the type and only species.

Teutonodon langenbergensis sp. n.

(Figs 3, 4A–H)

Etymology: After the Langenberg, the hill between Goslar and Bad Harzburg, where the Langenberg Quarry is located. Holotype: NLMH 105650, upper right M1 (Figs 3, 4A–H).

Type locality and horizon: Langenberg Quarry near the town of Goslar, Lower Saxony, northern Germany. N $51^{\circ}54,110^{\circ}$, E $10^{\circ}30,500^{\circ}$. Bed 83 (after Fischer 1991), a light grey-greenish marly limestone within the Sünteln-Formation. Based on ostracodes and rare finds of ammonites, it has been assigned to the "Mittleres Kimmeridge", a northwest-German equivalent to the lower part of the upper Kimmeridgian of the international chronostratigraphic time scale (Schweigert 1999; Lallensack *et al.* 2015).

Differential diagnosis. — M1 cusp formula 5L/4B. Enamel strongly ornamented with pits and grooves. Cusp bases coalescent, increasing in size from front to back on the lingual side. Lingual cusp row strongly worn. Differs from the allodontid line by coalescent cusps and ornamented enamel. Differs from paulchoffatiid line by the presence of an incipient posterolingual ridge (strongly worn). Differs from M1 of Ptilodontidae and Taeniolabidae by the presence of only two rows of cusps. Differs from M1 of Plagiaulacidae, Eobaataridae, and *Janumys* Eaton *et* Cifelli, 2001 by a higher number of cusps. Differs from M1 of Albiobaataridae by a larger size and lower number of cusps.

Description. — The shape of the tooth crown of NLMH 105650 (Figs 3, 4A-D) is rectangular with the lingual side longer and more strongly worn than the buccal side. The lingual side comprises five cusps which are all strongly worn with the dentine exposed (except for the anteriormost cusp). The cusps increase in size from front to back, but the remaining base of cusp L4 appears slightly larger than that of cusp L5. Besides the apical wear of the cusps, the entire lingual flank of M1 is worn flat with an elongated field of dentine exposed at the base of cusp L4/5 in the vicinity of the poorly developed posterolingual ridge. The buccal flanks of the lingual cusps are also strongly worn with longitudinal striations. There are four buccal cusps of which the anteriormost (cusp B1) and posteriormost (cusp B4) are smaller than cusps B2 and B3. The buccal cusps are worn only on their lingual side within the longitudinal valley of the crown. Otherwise they are unworn and show a typical plagiaulacid pattern of enamel crests extending from their apices. The cusps of both sides are sitting close together with confluent bases. The longitudinal valley of the crown is V-shaped and is oriented in antero-lingual direction.

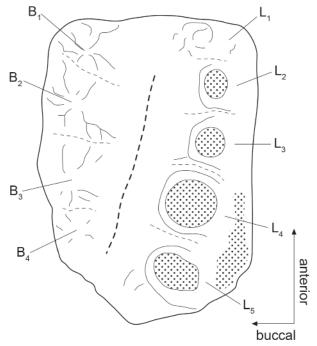


Fig. 3. Schematic drawing of the occlusal surface of NLMH 105650 with terminology of cusps. Dotted pattern illustrates exposed dentine.

The anterior side of M1 is flat with a slight indentation at the buccal side for accommodation of the preceding premolar. The distal side is rounded with the buccal flank angled at about 45° and the lingual flank at 25°, giving the posterior end of the tooth crown a somewhat asymmetric appearance. The buccal flank is slightly damaged.

The M1 has two large roots that are slightly curved in lingual direction and a small root between the two larger roots at the labial side.

Measurements. — Length = 2.51 mm, width = 1.73 mm.

Family Eobaataridae Kielan-Jaworowska et al., 1987

Gen. et sp. indet.

(Fig. 4I-N)

Included specimen: NLMH 105651, lingual fragment of right lower m1.

Locality: Langenberg Quarry near the town of Goslar, Lower Saxony, northern Germany. N 51° 54,110', E 10° 30,500'.

Description. — NLMH 105651 is interpreted as a lingual fragment of a right lower eobaatarid cheek tooth, most probably a m1, with three cusps in a row. The two anterior coalescent cusps are large and of

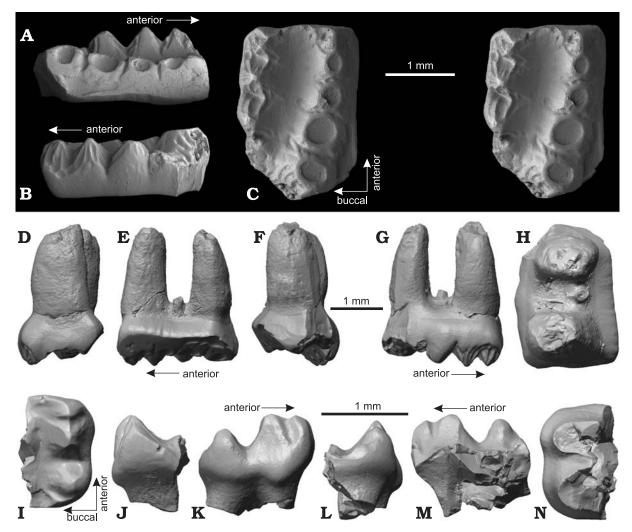


Fig. 4. SEM images (A–C) and digital models (D–N) of right upper M1 of *Teutonodon langenbergensis* and indeterminate eobaatarid right lower m1 from Langenberg quarry. A–H. *Teutonodon langenbergensis* (NLMH 105650, holotype), in lingual (A), labial (B), and occlusal (C, stereo-pair) views of tooth crown and anterior (D), lingual (E), posterior (F), labial (G), and cervical (H) views of entire tooth. I–N. Indeterminate eobaatarid m1 (NLMH 105651), in occlusal (I), anterior (J), labial (K), posterior (L), and cervical (N) views, and lingual view of broken side (M).

similar height, the posterior cusps is much lower and separated by a deep notch. The anteriormost cusp is recurved posteriorly and separated from the following cusps by two shallow grooves on the lingual and buccal side. The tooth originally had two rows of cusps with a deep V-shaped longitudinal valley in between. The preserved cusps are worn on the buccal side, particularly the middle cusp, and their lingual aspect is unworn. The V-shaped longitudinal valley is anteriorly and posteriorly open. The tooth has two roots of similar size and the crown is bulging somewhat lingually.

Measurements. — Length = 1.38 mm, preserved width = 0.93 mm, width of preserved cusp row (buccal edge of crown to midline of the V-shaped longitudinal valley) = 0.62 mm.

DISCUSSION AND COMPARISONS

Following Kielan-Jaworowska and Hurum (2001) "Plagiaulacida" are grouped into three lineages, the allodontid line, the paulchoffatiid line, and the plagiaulacid line. "Plagiaulacida" represent a paraphyletic array of more plesiomorphic multituberculates than Cimolodonta and occur in Europe from the ?Middle Jurassic (Bathonian) or Late Jurassic (Kimmeridgian) to Early Cretaceous (Barremian). In North America, they are recorded from the Late Jurassic to the Early–Late Cretaceous boundary, in Asia from the Late

Jurassic (Oxfordian) to the Early Cretaceous, and in northern Africa from the Early Cretaceous (?Berriasian) of Morocco (Kielan-Jaworowska *et al.* 2004 and references therein).

NLMH 105650. — An affiliation of *Teutonodon langenbergensis* gen. et sp. n. (NLMH 105650) with the allodontid line can be ruled out because allodontids lack enamel ornamentation and have well separated molar cusps. So far, allodontid-line taxa have been recorded only from the Late Jurassic Morrison Formation (see Kielan-Jaworowska *et al.* 2004) and earliest Cretaceous Lakota Formation (Cifelli *et al.* 2014) in the western USA.

Teutonodon differs from Portuguese paulchoffatiids and from Chinese *Rugosodon* Yuan *et al.*, 2013 in possessing molar cusps of similar height and by a posterolingual ridge on M1 (Hahn and Hahn 2000; Yuan *et al.* 2013). This ridge is present, albeit strongly worn, on NLMH 105650. In NLMH 105650, the bases of the cusps vary in diameter, but the heights of the cusps are almost equal as evident from the unworn buccal cusp row. Paulchoffatiids have been recorded from the Kimmeridgian Guimarota beds and the Early Cretaceous (Barremian) Lourinhã-Formation of Portugal (Hahn and Hahn 2000).

Plagiaulacids are characterized by a tendency of molar cusps to coalesce, as well as ornamented enamel with grooves and pits. Within the Late Jurassic to Early Cretaceous Plagiaulacida, an upper M1 is only known for *Bolodon osborni* Simpson, 1928 which has a cusp formula of 3:4 (Hahn and Hahn 2004). The molars of Plagiaulacidae and Early Cretaceous Eobaataridae generally have a lower number of cusps than seen in NLMH 105650 (Hahn and Hahn 2004). The albionbaatarids *Proalbionbaatar plagiocyrus* Hahn *et* Hahn, 1998 from the Late Jurassic and *Albionbaatar denisae* Kielan-Jaworowska *et* Ensom, 1994 from the Early Cretaceous have much smaller M1s with a higher number of cusps. The Late Cretaceous *Janumys erebos* Eaton *et* Cifelli, 2001 was interpreted as related to the plagiaulacid line, based on P4, M1, m1, and m2, which are all smaller than NLMH 105650. M1 of *Janumys erebos* is more elongated than NLMH 105650 and its cusp formula is 3-4:4.

The *Paracimexomys*-group represents the most plesiomorphic (informal) group of Cimolodonta. Although it comprises taxa with ornamented enamel, the ornamentation is much weaker than in NLMH 105650. Stratigraphically, the *Paracimexomys*-group has been recorded from the Aptian–Albian to Maastrichtian of North America and the Late Cretaceous (?Maastrichtian) of Europe (Rădulescu and Samson 1986; Eaton and Nelson 1991; Cifelli 1997). Given the differences in enamel ornamentation and the lower stratigraphic occurrence, an affiliation of NLMH 105650 with the *Paracimexomys*-group is unlikely.

NLMH 105651. — The tooth fragment most closely resembles the lingual portion of right m1 of *Eobaatar magnus* Kielan-Jaworowska *et al.*, 1987 (pl. 2: 2) from the Early Cretaceous (Aptian or Albian) of Mongolia, but is 20% smaller. Eobaataridae have been reported from the Valanginian of southeastern England (Wadhurst Formation, Cliff End), the early Barremian of Spain (Camarilla Formation, Galve; Pié Pajarón; Uña), the Barremian of China (Yixian Formation, Liaoning Province), and the Aptian or Albian of Mongolia (Höövör Beds, Gobi Desert) (Woodward 1911; Simpson 1928; Crusafont-Pairó and Adrover 1966; Kielan-Jaworowska *et al.* 1987; Hahn and Hahn 2001; Hu and Wang 2002). Eobaataridae are characterized by ornamented enamel and coalescing cusps at the lower molars (Kielan-Jaworowska *et al.* 2004, p. 316). NLMH 105651 shows coalescence of the two anterior cusps, but enamel ornamentation is not evident. However, in *Eobaatar* Kielan-Jaworowska *et al.* 1978 enamel ornamentation is mainly present at the labial portion of the lower molars (Kielan-Jaworowska *et al.* 1987, pl. 2: 1, 2), whereas the lingual portion is smooth.

CONCLUSIONS

The presence of multituberculate teeth at the Langenberg Quarry extends the occurrence of plagiaulacid-line taxa to the Late Jurassic of northern Germany. One specimen serves as the holotype for a new taxon, *Teutonodon langenbergensis*. The presence of this taxon in the Late Jurassic of northern Germany is not surprising, as members of the plagiaulacid line have been hitherto known from the Late Jurassic to Early Cretaceous of North America (Morrison and Lakota formations), Europe (southern England, Portugal, Spain), and Asia (China, Mongolia) (Kielan-Jaworowska *et al.* 2004; Cifelli *et al.* 2014). A second, fragmentary specimen compares most favorably with Eobaataridae (*e.g., Eobaatar magnus*) known otherwise from the Early Cretaceous of Europe and Asia. The record of the first Jurassic mammals from Germany demonstrates the potential of the Langenberg Quarry for further discoveries of terrestrial vertebrates, including the exciting possibility of a major stratigraphical range expansion for eobaatarid multituberculates.

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