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The first haramiyoid mammal from Asia

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Abstract A lower molar of a haramiyoid mammal is described from the Toutunhe Formation of Liuhuanguo near Urumqi in the southern Junggar Basin, Xinjiang, China. It is referred to *Eleutherodon* sp., otherwise exclusively known from the Upper Bathonian of England. It is the first record of the order Haramiyida from Asia and the first Mesozoic mammal described from the southern Junggar Basin. Apart from the English specimens of *Eleutherodon* and *Staffia* from the Upper Jurassic of East Africa, it is the geologically youngest haramiyoid known. It is the first vertebrate taxon from the Toutunhe Formation that is probably not endemic and lends some support to the dating of the Formation as late Middle Jurassic, probably Bathonian.

Introduction

Among the rare and enigmatic groups of Mesozoic mammals, the basal allotherians (Marsh 1880) of the order Haramiyida (systematics here follows the overview of Butler 2000) are particularly little known. Even their status as mammals is questionable, as the most inclusive recent analysis of Mesozoic mammal phylogeny (Luo et al. 2002) places them either as a sister group of tritylodontids (non-mammalian cynodonts) or the mammalian multituberculates. Until recently, only the typical, multituberculate-like teeth were recorded from several Upper Triassic and Lower Jurassic occurrences in Western and Central Europe (Hahn 1973; Hahn et al. 1989; Sigogneau-Russell 1989; Butler and MacIntyre 1994). With the recent discovery of *Haramiyavia clemmensei* in Upper Triassic rocks of Greenland (Jenkins et al. 1997), associated cranial and even post-cranial remains (Amaral

1996) have become available. The record of the Haramiyida was also considerably extended through the discoveries of *Eleutherodon oxfordensis* in the Middle Jurassic (Bathonian) of England (Kermack et al. 1998; originally not assigned to the Haramiyida, which was done by Butler 2000), and *Staffia aenigmatica*, the latest known haramiyid, from the Upper Jurassic (Kimmeridgian) of Tendaguru in East Africa (Heinrich 1999), which also represents the first record from Gondwana.

Here we report a well-preserved left lower molar from the late Middle Jurassic (Bathonian-Callovian, according to Eberth et al. 2001, but see discussion below) Toutunhe Formation of the southern Junggar Basin that is referable to *E. oxfordensis*. The specimen was discovered in a bonebed close to the top of the Toutunhe Formation (14.75 m below the overlying Qigu Formation) in the Xinjiang Uygur Autonomous Region, People's Republic of China. The bonebed yielded numerous isolated remains of osteichthyan and chondrichthyan fish, temnospondyl amphibians and reptiles, as well as several mammalian teeth, most of which are referable to a new genus and species of docodont with pseudotribosphenic molars that will be described elsewhere (Pfretzschner 2003). On top of the bonebed there is a layer rich in larger, isolated bones of fish, amphibians, and reptiles that has been termed the turtle–archosaur–amphibian assemblage by Maisch et al. (2001, 2003), from which temnospondyl amphibians (Maisch and Matzke 2004; Maisch et al. 2004), theropod dinosaurs (Maisch and Matzke 2003), rhamphoryhnchoid pterosaurs, goniopholidid crocodiles, shark remains, and, particularly, xinjiangchelyid turtles are known.

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Systematic palaeontology

Infraclass Allotheria Marsh, 1880

Order Haramiyida Hahn, Sigogneau-Russell and
Wouters, 1989

Suborder Haramiyoidea Hahn, 1973

Family Eleutherodontidae Kermack, Kermack, Lees,
and Mills, 1998

Fig. 1 Left lower molar of the eleutherodontid haramiyid *Eleutherodon* sp. from the uppermost Toutunhe Formation (late Middle Jurassic, ? Bathonian) of Liuhuanguo, SW Urumqi, Xinjiang, China, in **a** occlusal, **b** mesial and occlusal, **c** distal, **d** lingual, and **e** buccal view. The labels *a1*, *a2*, and *b2* indicate the principal cusps. Arrows labelled with *m* indicate the mesial, with *l* the lingual direction. Scale bars are 300 μm .

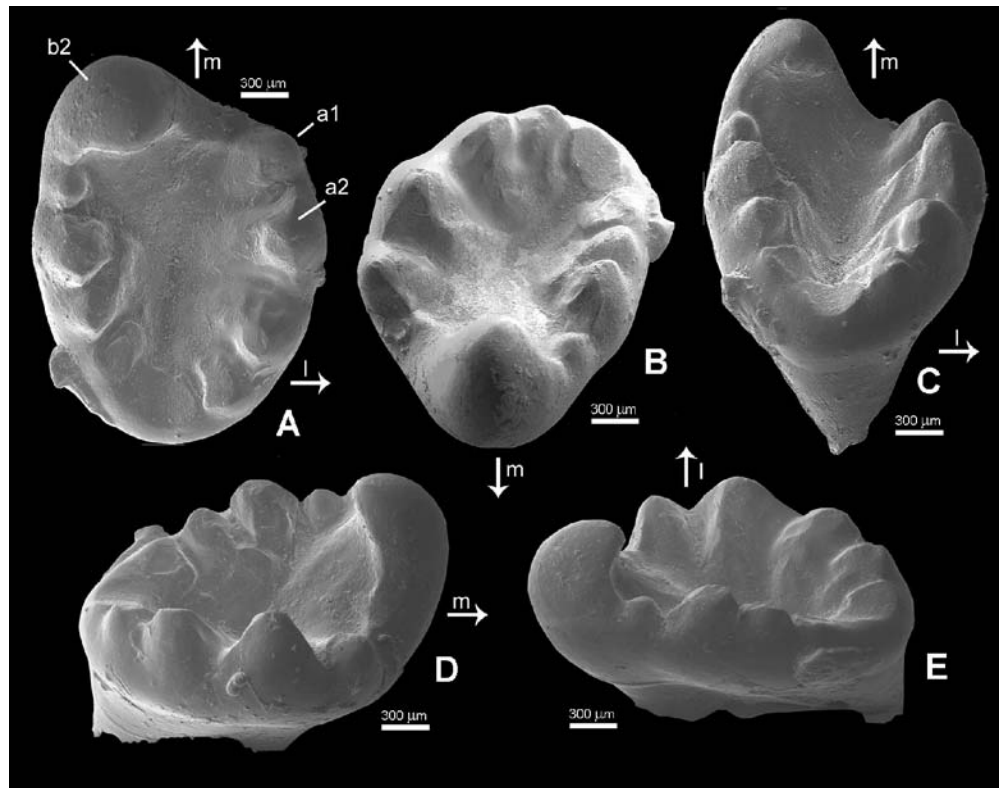
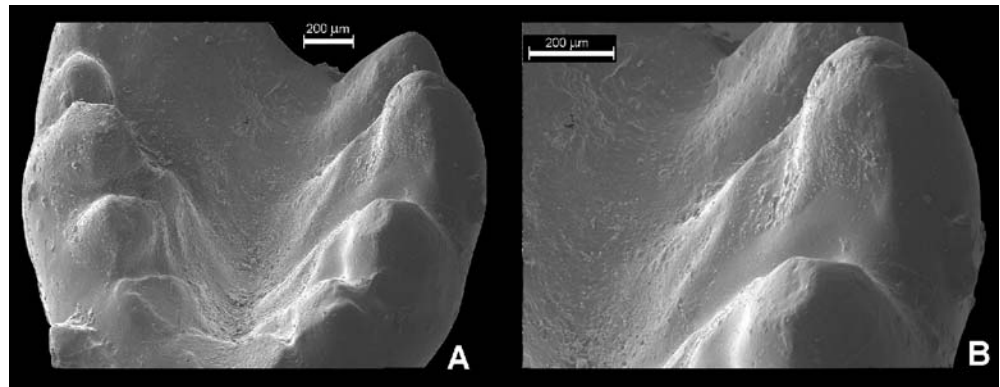


Fig 2 Details of SGP 2001/33. **a** The great occlusal basin wear facet. **b** Fluted transversal ridges on the buccal surfaces of the lingual cusps. Scale bars are 200 μm .



Genus *Eleutherodon* Kermack, Kermack, Lees and Mills, 1998

Type-species *Eleutherodon oxfordensis* Kermack, Kermack, Lees and Mills, 1998

Diagnosis: see Kermack et al. 1998 and Butler 2000 *Eleutherodon* sp.

Material: SGP¹ 2001/33 (Figs. 1, 2): an almost complete left lower molar from the uppermost Toutunhe Formation (14.75 m below the boundary to the Qigu

Formation) of Liuhuanguo, southwest Urumqi, Xinjiang (see Maisch et al. 2003 for further details).

Description

The specimen (Figs. 1, 2) represents a lower molar, as it only possesses a buccal and a lingual row of cusps. The position of the main mesiobuccal cusp allows identification as a left lower molar. In occlusal view (Fig. 1a), the crown is ellipsoidal with the mesial end wider than the distal one, which tapers slightly. The mesial edge of the crown is strongly oblique in the mesiobuccal–distolingual direction due to the strong mesial expansion of the cusp *b2*, the principal cusp of the buccal row (the homology of the cusps follows Butler 2000 rather than Kermack et al.

¹ Sino German Project collection, currently housed at the University of Tübingen, Germany. The collection remains the property of the People's Republic of China and will be transferred to a public Chinese collection after the scientific studies are finished. The final repository will be announced in an internationally accessible journal.

1998). The buccal and lingual margins of the crown are gently and evenly convex, as is the distal margin. The two rows of cusps are not parallel but converge distinctly distally.

The buccal row presents five cusps (Fig. 1a, b, e). The mesial-most is by far the largest and protrudes strongly mesially and occlusally. Its apex curves markedly distally. This cusp is here identified as b2. The following cusp is very small, less than one-fifth the size of the b2 cusp and less than one-third of the size of the following cusps. The distal three buccal cusps are again larger and decrease in size and height distally. The distal-most cusp is strongly worn or abraded at its apex. It is not clear whether there was a distal cusp connecting the buccal and lingual rows and closing the occlusal basin distally. Certainly there is no cusp remaining, but it appears as if originally one was present that was completely abraded or worn down, as particularly obvious in distal view (Fig. 1c).

The lingual row (Fig. 1a, b, d) consists of only four cusps that are subequal in size. The mesial-most, which most probably represents the cusp a1 of other haramiyids, is much smaller and lower than the cusp b2. The following cusp a2 is even slightly higher than a1. The distal-most lingual cusp is the lowest in the series.

The entire crown is traversed mesiodistally by a wide occlusal basin that extends from the mesial to the distal margin and occupies more than half the width of the crown (Figs. 1a, 2a). Transverse fluted ridges caused by wear extend from the margins of the lingual and buccal cusps towards the centre of the basin (Fig. 2a, b). They are most prominent on the lingual side of the three disto-buccal cusps and on the buccal sides of the three disto-lingual cusps (Fig. 2b). There are no clear flutings evident on the insides of cusps a1, a2, and b2. Clear wear striations have not been found during scanning electron microscope (SEM) examination of the tooth, but this may be due to preservation. The root is incomplete but appears to have had a threefold subdivision.

Comparison

The new specimen is clearly identifiable as a member of the Haramiyida by the presence of two rows of lower cusps of which the mesiobuccal one is the largest and which are of unequal height. It can be identified as a member of the suborder Haramiyoidea, as the occlusal basin occupies most of the length of the molar (in contrast to *Theroteinus*, where it is considerably shorter, Hahn et al. 1989; Butler 2000). Among haramiyoids, the Chinese specimen is indistinguishable from the material described by Kermack et al. (1998) as *Eleutherodon oxfordensis*. Kermack et al. (1998) distinguish three types among the lower molars that they refer to this taxon (types β , γ , and ζ). They admit that the γ teeth probably belong to a different taxon, a view with which we agree.

The other lower molars agree with the Chinese specimen in the following features that are diagnostic of *Eleutherodon* (cf. Kermack et al. 1998; Butler 2000):

there are two rows of cusps that are not parallel but converge distally; the mesial margin of the lower molars is oblique, due to the strong development of the buccal cusp b2; the lower occlusal basin extends for the entire length of the tooth without an intervening saddle; there is a strong fluting of the margins of the lower occlusal groove or basin.

The only apparent difference to the British material lies in the fact that the Chinese specimen has only five buccal, and four (or five if the worn distal cusp is counted into this series) lingual cusps. In the British specimens the number of cusps is usually larger. However, the ζ lower molar described by Kermack et al. (1998) also has only four to five buccal and seven lingual cusps. The β teeth have 21 and 12 cusps, respectively, so that there appears to be an enormous variation of cusp number in the material attributed to *E. oxfordensis*. As otherwise the teeth agree perfectly in morphology, the fact that the Chinese specimen has two cusps less than any of the British specimens does not merit taxonomic distinction. The enormous variation in the number of cusps in *Eleutherodon* might be attributed to different positions of the lower molars in the jaws. It could also be caused by ontogeny. With the little material presently at hand, this is impossible to decide. If with a larger sample available the Chinese form should turn out to constantly display fewer cusps in the lower molars than the British *Eleutherodon*, a taxonomic distinction might be warranted. At the moment, considering the apparent, although small differences to the British specimens, we consider it best to refer the specimen to *Eleutherodon* sp.

The other haramiyoid genera differ considerably from *Eleutherodon*, and thus from the Chinese specimen. All the other genera of the suborder Haramiyoidea (*Thomasia*, *Haramiyavia*, and *Staffia*) lack the diagnostic features of *Eleutherodon* enumerated above (Butler and MacIntyre 1994; Jenkins et al. 1997; Heinrich 1999; Butler 2000). *Thomasia* and the only representative of the Theroteinoidea, *Theroteinus*, furthermore differ by having only two lingual cusps. It is therefore clear that the specimen does not have any close relationship to any of the other nominal haramiyid genera.

Discussion

The discovery of a specimen of *Eleutherodon* sp. in the Toutunhe Formation is of particular importance for a number of reasons. First, it is the first record of the order Haramiyida from Asia. Second, it is the first Mesozoic mammal from the southern Junggar basin and, of course, the first mammal from the Toutunhe Formation. Third, together with the English *Eleutherodon* specimens it is the geologically youngest representative of the group, except *Staffia aenigmatica* from the Tendaguru Formation (Kimmeridgian) of East Africa. The fossil record of Middle Jurassic mammals is generally extremely sparse, with the findings almost completely restricted to England (particularly the Bathonian, where most finds occur in the

“Stonesfield Slate” and the Kirtlington mammal bed, Freeman 1979) and a few localities in East and Central Asia. The genera *Ambondro* from Madagascar (Flynn et al. 1999) and, possibly, *Asfaltomylos* (Rauhut et al. 2002) from Argentina are the only Middle Jurassic mammals from Gondwana known to date.

The Middle Jurassic record of Asian mammals has been so far restricted to the dubious *Liaotherium* from presumably Middle Jurassic strata of Liaoning (Zhou et al. 1991), a single, probably docodont upper molar (Nessov et al. 1994) and a well-preserved lower molar of the docodont *Tashkumyrodon desideratus* (Martin and Averianov 2004), both from the late Middle Jurassic Balabansai Formation of the Fergana Basin in Kyrgyzstan.

As there are correspondences in the Jurassic mammalian faunas of England and Asia, the mammals are of particular importance for biostratigraphy, because most other Middle and Late Jurassic tetrapods from Central and East Asia are endemic, due to the isolation of much of the Asian continent from the Middle Jurassic to the Lower Cretaceous (Russell 1993). It is conceivable that the small mammals were able to disperse to the Asian continent by “island hopping” or on natural rafts, a possibility that was not open to larger terrestrial tetrapods and freshwater forms.

The most important genera for stratigraphic correlation at the moment are *Shuotherium* and *Eleutherodon*. The enigmatic genus *Shuotherium* was originally identified from Eastern Asia (the Upper Shaximiao Formation of Sichuan, Chow and Rich 1982; Wang et al. 1998) with the species *S. dongi* (Chow and Rich 1982, based on a partial lower jaw) and *S. shilongi* (Wang et al. 1998, based on an isolated upper molar). The Upper Shaximiao Formation is usually considered as Middle or Upper Jurassic in age. Recently, Sigogneau-Russell (1998) described *Shuotherium* from the Upper Bathonian Forest Marble of Kirtlington, Oxfordshire, England, including the new species *S. kermackii*. This important find shows that there is a link between the later Jurassic mammalian faunas of Western Europe and Central Asia. The fact that *S. kermackii* is from the same locality and horizon as the type material of *E. oxfordensis*, and that the Chinese species of *Eleutherodon* is now also known from the Upper Toutunhe Formation, provides some evidence that both the Toutunhe and the Upper Shaximiao formations might be considered as late Middle Jurassic, possibly Bathonian, in age. As the correspondence between the Toutunhe haramiyid and *E. oxfordensis* is only on the generic, but not on the specific level, it is tempting to assume, but by no means certain, that the Toutunhe Formation is very probably not younger than Bathonian in age. If this is true, at least the lower part of the Qigu Formation, which conformably overlies the Toutunhe Formation and has also yielded fossil vertebrates, although no mammals (Maisch et al. 2001, 2003; Maisch and Matzke 2004) might belong to the Middle Jurassic (Callovian), not to the Upper Jurassic as generally assumed (contra Eberth et al. 2001). This hypothesis was first put forward by Maisch

et al. (2001) and is to some extent corroborated by the finding of the Bathonian mammal *Eleutherodon* close to the top of the Toutunhe Formation. However, before these biostratigraphic correlation problems can be settled, additional fossil vertebrate material, particularly additional mammalian specimens, are needed.

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