

New teeth of allotherian mammals from the English Bathonian, including the earliest multituberculates

PERCY M. BUTLER and JERRY J. HOOKER



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Twenty one isolated multituberculate-like teeth are described from the Forest Marble (late Bathonian) of Oxfordshire and Dorset, England. Eighteen are additional to the teeth described as *Eleutherodon oxfordensis* by Kermack et al. (1998), and three of those are placed in new taxa. Six new molars of *Eleutherodon* provide further information on variation in size, proportion and root pattern. *Millsodon superstes* gen. et sp. nov. (family indeterminate), based on first and last lower molars and a referred upper molar, has resemblances to Haramiyidae and Theroteinidae. *Kirtlingtonia catenata* gen. et sp. nov. (family indeterminate), based on last upper molars and a probable upper premolar, has a slight resemblance to *Eleutherodon*, and also to M2 of some paulchoffatiid multituberculates. *Kermackodon multicuspis* gen. et sp. nov. (family Kermackodontidae nov.) and *Hahnotherium antiquum* gen. et sp. nov. (family Hahnotheriidae nov.) are based on second upper molars, recognised as multituberculate by their horizontal wear and inferred occlusal displacement with respect to m2. A lower molar referred to *H. antiquum* confirms this. A blade-like lower premolar and an upper premolar with conical cusps, referred to *Kermackodon*, are multituberculate-like, but distinctive. Divergence between the two Bathonian multituberculates indicates that the order originated much earlier, more probably from a haramiyid than from a morganucodontid source. *Mojo* is regarded as probably a haramiyid. The Hahnodontidae, which have basined wear, are removed from the Multituberculata to the “Haramiyida”.

Key words: Allotheria, “Haramiyida”, Multituberculata, dentition, occlusion, tooth cusps, Jurassic.

Percy M. Butler [percy@butler92.freerve.co.uk], Department of Biology, Royal Holloway, University of London, Egham, Surrey, TW20 0EX, United Kingdom;

Jerry J. Hooker [j.hooker@nhm.ac.uk], Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom.

Introduction

Simpson (1928) separated the order Multituberculata from other mammals in a subclass Allotheria. At that time multituberculates were unknown prior to the latest Jurassic Morrison Formation in North America and earliest Cretaceous Purbeck Limestone Formation in England. Their known range was extended back to the Kimmeridgian by Hahn's (1969) description of Paulchoffatiidae from Portugal, but the morphological gap between multituberculates and other Mesozoic mammals remained, and the origin of the order is controversial (Kielan-Jaworowska 1992, 1997; Luo et al. 2002; Kielan-Jaworowska et al. 2004). The Late Triassic–Early Jurassic Haramiyidae have been postulated as multituberculate relatives, a view formally expressed by Hahn et al. (1989), who included the orders “Haramiyida” and Theroteinida in the subclass Allotheria. However, *Haramiyavia* (Jenkins et al. 1997), from the Late Triassic of Greenland, and the only early allotherian known by more than isolated teeth, differs widely from multituberculates in jaw structure and occlusion. Butler (2000) grouped these early allotherians in the order “Haramiyida”, and pointed out some dental resemblances in support of the derivation of multituberculates from within that order.

The presence of possible multituberculates in the late Bathonian (Forest Marble) of England was first recorded by Freeman, who in 1976 described a worn upper molar from Watton Cliff, Dorset, and in 1979 a possible lower incisor from Kirtlington, Oxfordshire. A collection of thirteen multituberculate-like teeth from these localities was described by Kermack et al. (1998). They distinguished four types of molar (α , β , γ , and ζ), of which an α tooth, interpreted as an upper molar, was made the holotype of *Eleutherodon oxfordensis*. It was classified in a new suborder Eleutherodontida, order *incertae sedis*; Butler (2000) treated it as an advanced member of the “Haramiyida”. The other three types, regarded by Kermack et al. (1998) as lower molars, were referred to this species, although only the β type could be satisfactorily occluded with upper molars. It was noticed that the γ and ζ types had the closest resemblance to multituberculates. They are re-examined in the present paper, in which are described eighteen more allotherian teeth from the same localities. As well as some additional *Eleutherodon* molars, they include a number of new types of teeth, some of which are clearly multituberculate.

With the exception of four specimens from Watton Cliff, the material was collected from the Old Cement Works

Quarry, Kirtlington, Oxfordshire, by the team from University College, London, led by the late Prof. K.A. Kermack. All specimens are from the Forest Marble Formation. Stratigraphic details are given by McKerrow et al. (1969), Freeman (1979), and Dineley and Metcalf (1999), and collecting and preparation techniques are described by Freeman (1979), Ward (1984), Kermack et al. (1987) and Evans and Milner (1994). Most of the Kirtlington material came from bed 3p (in the nomenclature of McKerrow et al. 1969), but several specimens are from beds 3u, 3w(i), and 3w(iii), higher in the succession. These, plus subdivisions of bed 3p, are individually indicated in the lists of material. The exposure at Watton Cliff, Dorset, is described by Freeman (1976) and Dineley and Metcalf (1999); specimens were collected from the "Mammal Bed" (bed 8) by D.J. Ward and the University College team and also by T. and R. Batchelor.

All the surviving material is housed in the Palaeontology Department of the Natural History Museum, London (catalogued M). Most specimens were transferred from University College on Prof. Kermack's retirement, and have been re-catalogued. Specimens referred to in Kermack et al. (1998) by University College numbers (BDUC J) have been renumbered BMNH M46. A number of specimens were not received by the Museum, and appear to have been lost (including BDUC J 771, see Kermack et al. 1998: 583). The Museum, however, possesses scanning electron micrographs and drawings by A.J. Lees of these, on the basis of which we have included descriptions of three teeth that are of special interest. They are referred to by University College numbers.

In the descriptions measurements are given to the nearest 0.05 mm. The directional terms mesial, distal, buccal and lingual are used. Buccal (Latin *bucca*, cheek) is preferred to labial (Latin *labia*, lip) as applied to molariform teeth. The Latin term *crista anterobuccalis* of Hahn and Hahn (1998a) is anglicized as *anterobuccal ridge*. The names of paraphyletic groups are in quotation marks.

Institutional abbreviations.—BDUC, Biology Department, University College, London; BMNH, Natural History Museum, London; EF, Eric Freeman private collection (146 Haydens Road, Wimbledon, London SW19 1AE); FM is the abbreviation for Mr. Freeman's collection from the Forest Marble.

Systematic palaeontology

Order "Haramiyida" Hahn, Sigogneau-Russell, and Wouters, 1989

This is regarded as a paraphyletic grouping of those Allohtheria that are not multituberculates, following Butler (2000).

Family Eleutherodontidae K.A. Kermack, D.M. Kermack, Lees, and Mills, 1998

Genus *Eleutherodon* K.A. Kermack, D.M. Kermack, Lees, and Mills, 1998

Eleutherodon oxfordensis K.A. Kermack, D.M. Kermack, Lees, and Mills, 1998

Figs. 1A–C, 2.

pars *Eleutherodon oxfordensis* sp. nov.; Kermack et al. 1998: 586–595, figs. 1–14, 15A, 16, 18, 22, 23 [non figs. 15B, 17 = *Millsodon superstes* sp. nov.; non figs. 19–21 = *Hahnotherium antiquum* sp. nov.].

Holotype: BMNH M46460; right upper molar from the Old Cement Works Quarry, Kirtlington, Oxfordshire, England, bed 3p.

Paratypes (excluding those referred herein to other taxa): BMNH M46185, BMNH M46459, BMNH M46585 (bed 3w(iii)), BMNH M46681, BDUC J 771 (bed 3w(i)), BMNH M46814 (bed 3u), EF FM K/56, BMNH M46461, BMNH M46649 (bed 3w(i)).

Distribution.—Late Bathonian of England.

New material.—From Kirtlington: BMNH M46654, incomplete left lower molar; BMNH M46821, right upper molar (bed 3p(iii)); BMNH M46832, right upper molar; BMNH M46851, left lower molar, rolled (bed 3w(i)). From Watton Cliff: BMNH M34986, left upper molar; BMNH M44985, right upper molar, worn and rolled.

Comment.—The following specimens, described by Kermack et al. (1998) as *Eleutherodon oxfordensis* have been re-identified in this paper: BMNH M46183, left lower molar of *Millsodon* gen. nov.; BMNH M46763 and BMNH M46796 are multituberculate molars (*Hahnotherium* gen. nov.).

Description

Upper molars (Figs. 1A, B, 2A–D): These show the characteristic *Eleutherodon* pattern, as described by Kermack et al. (1998). The largest cusp (A of Kermack et al. 1998, B1 of Butler 2000, the terminology used herein) is at the narrow end of the tooth, presumed to be distal by analogy with *Haramiyavia* and *Thomasia*. Mesial to this there are three longitudinal rows of numerous minor cusps. The buccal row is at the top of a ridge that forms the buccal wall of the main longitudinal groove. The central row, which forms the lingual side of the groove, connects cusp B1 to a moderately high cusp Bx on the mesial border. The lingual row follows the lingual margin, from cusp B1 to an enlarged cusp BB (B of Kermack et al. 1998), at the mesiolingual corner of the crown. The groove between the central and lingual rows is much shallower than the main groove. Both grooves are richly ornamented by minor transverse ridges or flutings.

The four additional specimens illustrate the variability of the upper molars, evident from the eight examples figured by Kermack et al. (1998). BMNH M46821 (Figs. 1B, 2B) is a large tooth (3.0 × 2.2 mm), resembling BMNH M46585 in size, but longer and narrower, and with the large distal cusp B1 projecting for a greater distance beyond the end of the buccal cusp row. It is moderately worn. BMNH M46832 (Figs. 1A, 2A) is of intermediate size (2.45 × 1.8 mm), longer and proportionately narrower than the holotype. It is also moderately worn. The two specimens from Watton have lost the minor cusps on the ridges and the basin fluting by rolling. BMNH M34986 (2.3 × 1.8 mm) is a little longer and narrower than the holotype. BMNH M44985 (2.7 × 1.9 mm) is a

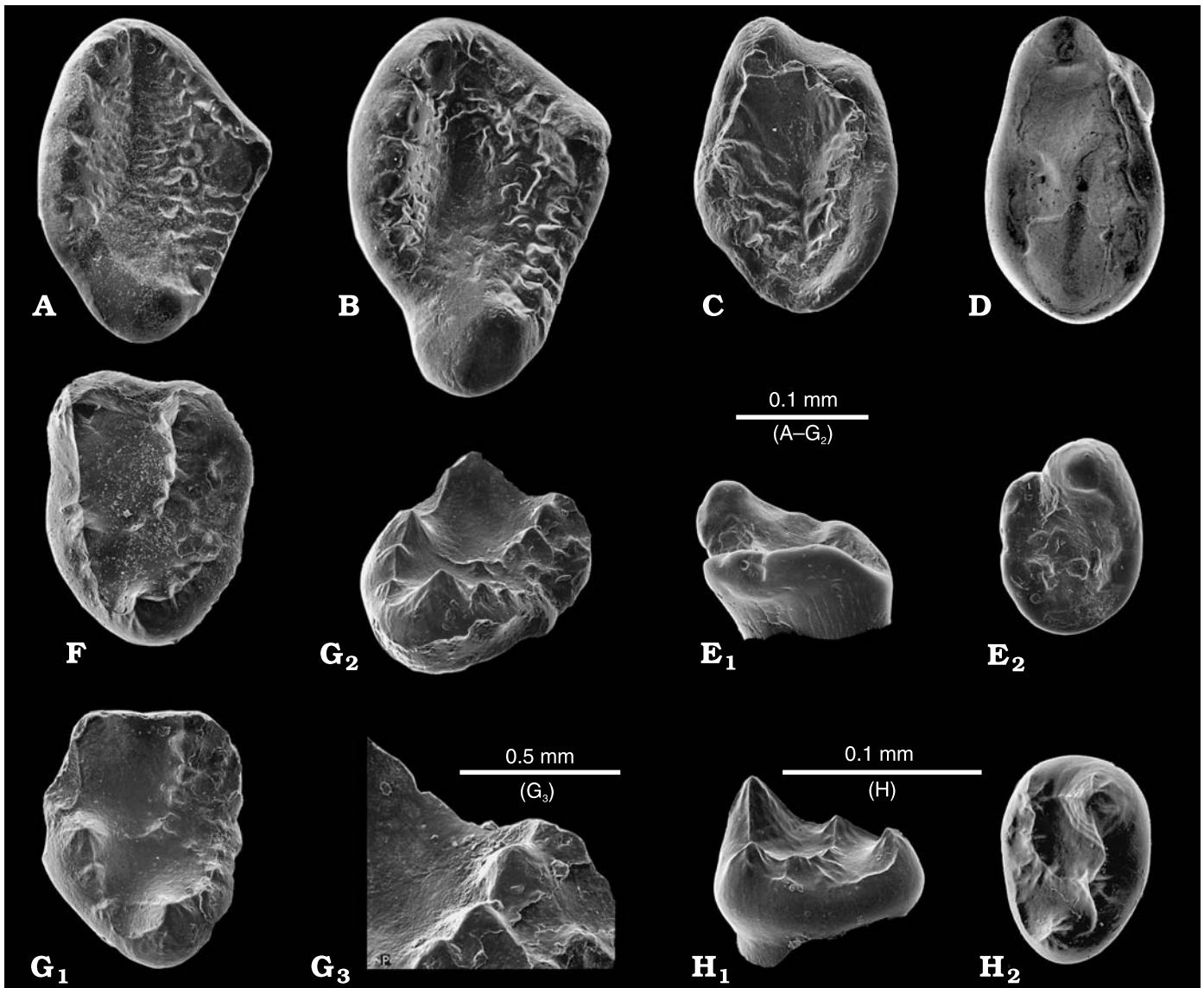


Fig. 1. Scanning electron micrographs of epoxy resin casts. All in BMNH collection. **A–C.** *Eleutherodon oxfordensis*. **A.** M46832, right upper molar. **B.** M46821, right upper molar. **C.** M46851, left lower molar. **D, E.** *Millsodon superstes* gen. et sp. nov. **D.** M46645, right lower molar (m1), holotype. **E.** M46183, left lower molar (m3), paratype in buccal (**E₁**) and occlusal (**E₂**) views. **F–H.** *Kirtlingtonia catenata* gen. et sp. nov. **F.** M46497, right upper molar, holotype. **G.** M46183, right upper molar, paratype in occlusal (**G₁**) and oblique lingual (**G₂**, **G₃**) views, higher magnification to show striations in basin. **H.** M46818, left upper premolar in lingual (**H₁**) and occlusal (**H₂**) views. Mesial end upwards in occlusal views, crown upwards in buccal and lingual views.

poorly preserved tooth in which much of the lingual cusp row, including cusp BB, has been removed.

The twelve specimens now known range in length from 2.1 to 3.0 mm (mean 2.46); the width/length ratio in eleven specimens ranges from 0.67 to 0.93. How much of this variation is due to position in the dentition is unknown. Seven teeth, ranging in length 2.4–2.9 mm and in width 1.6–2.3 mm might represent one molar, and four shorter and proportionately broader teeth (including the holotype), with length 2.1–2.25 mm and width 1.6–1.95 mm, might represent another molar. In any case, there is no indication that the difference in occlusal relations between M1 and M2 that characterises the multituberculates exists in *Eleutherodon*.

Roots are preserved in BMNH M46821 and BMNH M46832 (Fig. 2), which can be compared with those of BMNH M46771, BMNH M46814, and EF FM K/56, figured by Kermack et al. (1998). In all these the basal portion of the root forms an undivided root-trunk, with a height greater than that of the crown. The more apical portion is divided into a number of root elements, which remain connected to various levels, but appear as ribs on a longitudinal flange. In BMNH M46832 four elements can be distinguished: a distal root (I) below the large cusp B1, a mid-buccal (II) and a mesial buccal (III) root supporting the buccal cusp row, and a mesial lingual root (IV), below cusp BB. Root I is the first to separate; II and III remain joined for most of their length, and III

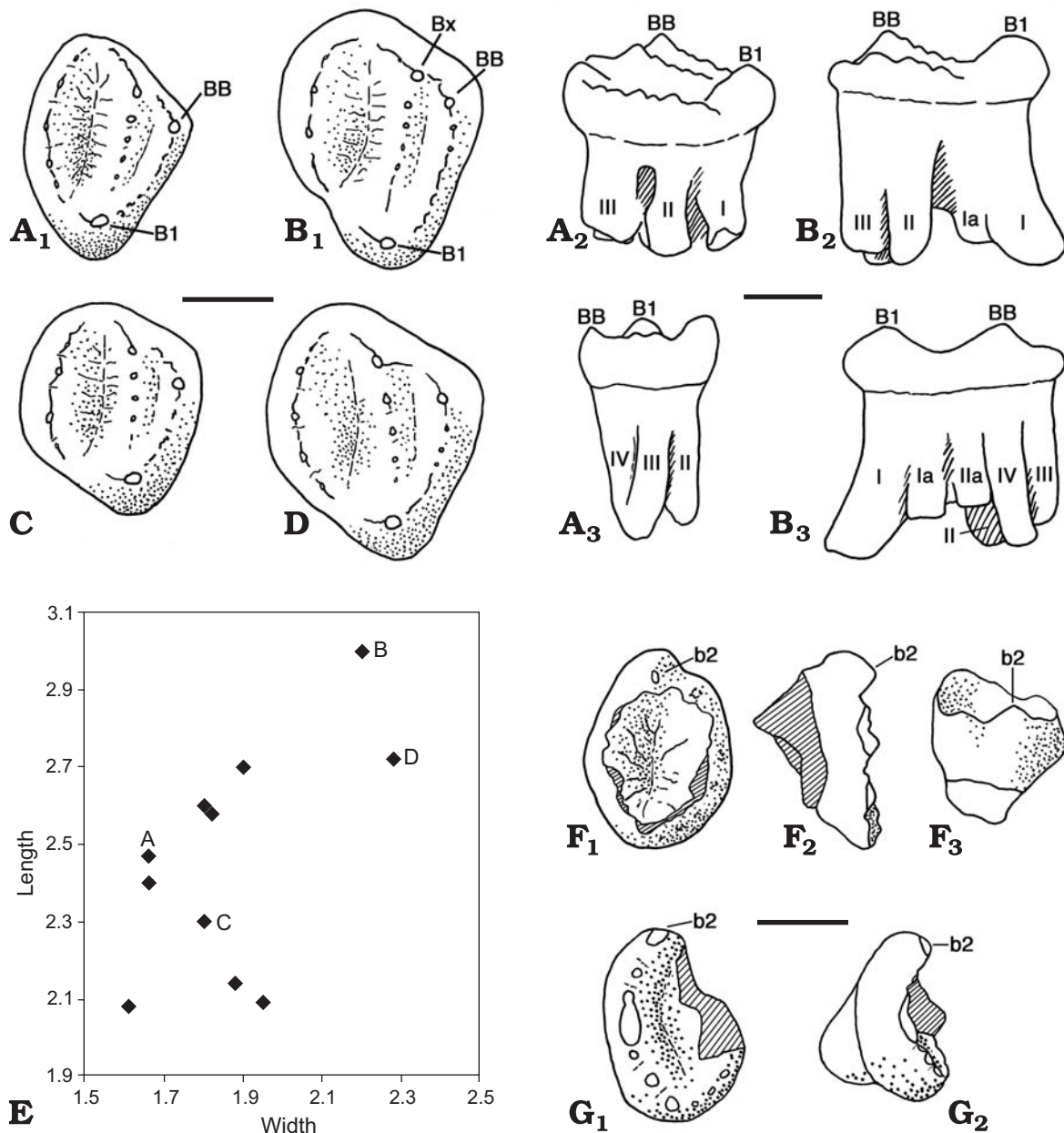


Fig. 2. *Eleutherodon oxfordensis*. All in BMNH collection. Right upper molars to illustrate variation. A. M46832. B. M46821. C. M46460 (holotype). D. M46585 (reversed). A₁, B₁, C, and D occlusal view (mesial end upwards). To show roots (crown upwards). A₂, A₃, buccal and mesial views. B₂, B₃, buccal and lingual views. E. Length plotted against width, upper molars of *Eleutherodon*. Letters refer to the specimens figured. F, G. Lower molars. F. M46851 in occlusal (F₁), buccal (F₂), and mesial (F₃) views. G. M46654 in occlusal (G₁) and buccal (G₂) views. In F₁, F₂, G₁, G₂, mesial end upwards; F₃, crown upwards. Scale bars 1 mm.

and IV are united to the tip. Corresponding root elements can be recognised in the other specimens. In BMNH M46821 the distal root (I), the largest, diverges from the rest and there is an additional root (Ia) on its mesial side. There is another additional root (IIa) on the lingual side between Ia and IV. In the remaining specimens root I is vertical and the additional roots are absent. In EF FM K/56 the roots are united for the whole of their length, and root IV appears to be absent. The root pattern of *Eleutherodon* molars differs widely from that of multituberculates, which normally have two equal and separate roots, except in some Late Cretaceous forms. It also

differs from the tooth described by Freeman (1976), which has a single root at one end and a pair of divergent roots at the other; this is interpreted in the present paper as possibly an upper molar of *Hahnotherium* new genus.

Lower molars.—BMNH M46851 and BMNH M46654 are incompletely preserved, but so far as they can be compared they agree with the β type tooth BMNH M46649 (Kermack et al. 1998: fig. 18). BMNH M46851 (Figs. 1C, 2F), a left tooth, has lost all enamel except in the basin, where the fluting is preserved, showing that the tooth was lightly worn. It is oval in outline, more convex buccally than lingually, and

with a mesial prominence towards the buccal side; it measures 2.2×1.55 mm. The highest cusp, b2 (α of Kermack et al. 1998), on the mesial prominence, is preserved only in dentine. It is followed distally by the buccal ridge, on which there appear to have been six cusps, to judge from the broken margin of the enamel. One of these, midway along the tooth, appears to have been elevated, as in BMNH M46649. The mesial lingual cusp, a1 (β of Kermack et al. 1998), which also lacks enamel, is smaller than the mesial buccal cusp, and slightly more distal. About six more lingual cusps are represented by minor elevations of the dentine. The lingual and buccal cusp rows are continuous round the distal end of the basin.

BMNH M46654 (Fig. 2G) is a left tooth that has lost the mesial half of the lingual cusp row, together with enamel on the mesial surface of cusp b2. The flutings in the basin have been completely removed by wear and the marginal cusps are represented by areas of exposed dentine. Wear seems to have been particularly heavy on the mesial half of the buccal cusp row, which declines from cusp b2 to a minimum height near the middle of its length. There is evidence of seven buccal cusps. The series is continuous round the distal end of the tooth with the lingual series, of which only the last cusps are represented. The central groove is basined, reaching its greatest depth about halfway along the tooth, and it does not cut through the distal cusp row. The tooth as preserved measures 2.25×1.4 mm.

BMNH M46461, described by Kermack et al. (1998: figs. 15A, 16), differs from the other β type teeth in that the cusps are more numerous, and those of the buccal row are more equal in size. The difference is probably due to position in the dentition.

“Haramiyida” family indeterminate

Genus *Millsodon* nov.

Type species: Millsodon superstes sp. nov.

Derivation of name: In memory of the late Professor J. R. E. Mills, whose orthodontic expertise has much aided the functional interpretation of Mesozoic mammalian teeth. Also Greek, οδους, οδοντος, tooth. Masculine.

Diagnosis.—Lower molariforms (provisionally identified as m1 and m3) differ from *Thomasia* and *Staffia* in the larger mesiolingual cusp (a1), of which the height is greater than half the length of the tooth. Mesiobuccal cusp absent on m1, rudimentary on m3. Resembles *Staffia* and differs from *Thomasia* in that cusp a1 is blunt and curved distally. Differs from *Staffia* in the absence of deep synclines between the cusps.

Referred upper molar has an enlarged distobuccal cusp, an inclined basin on its mesial side, and a third (lingual) cusp row.

Millsodon superstes sp. nov.

Figs. 1D, E, 3A, B, G, H, 4A.

pars *Eleutherodon oxfordensis* sp. nov.; Kermack et al. 1998: 593–594, figs. 15B, 17 [non figs. 1–14, 15A, 16, 18, 22, 23 = *Eleutherodon oxfordensis* K.A. Kermack, D.M. Kermack, Lees, and Mills; non figs. 19–21 = *Hahnotherium antiquum* sp. nov.].

Holotype: BMNH M46645, a first right lower molariform (m1) from Kirtlington Old Quarry, England, bed 3w(i).

Paratype: BMNH M46183, a last left lower molariform (m3), from Watton Cliff, England. Described by Kermack et al. (1998) as a right lower molar of type γ .

Referred specimen: BDUC J 3, a right upper molariform from Watton Cliff.

Derivation of name: Latin, *superstes*, a survivor.

Distribution.—Late Bathonian of England.

Diagnosis.—As for the genus, by monotypy.

Description

Holotype (Figs. 1D, 3A).—BMNH M46645 is interpreted as a right lower tooth. In crown view it is oval in outline, longer than wide (2.4×1.4 mm), rounded distally and truncate mesially. There is a slight indentation on the buccal side, near the mesial end, and a smaller indentation on the mesial border, defining a small mesiobuccal lobe of the tooth base. The crown is dominated by a high, blunt mesial cusp (a1), situated towards the lingual side; it leans slightly forward near the base, and curves backwards near the tip. Minor features of the crown have been largely removed by rolling and abrasion, but there are two longitudinal ridges separated by a median basin. The lingual ridge is continuous with the mesial cusp; it falls in height distally, and shows traces of two cuspal elevations. The buccal ridge, which is lower, curves lingually at its mesial end, where it runs up the buccal side of the mesial cusp. Buccal to the mesial cusp, on the mesiobuccal lobe, is a short ledge, rounded by wear. The top of the buccal ridge is occupied by an elongated strip of exposed dentine, probably representing a wear facet which faces somewhat buccally. The wear extends to the mesial end of the ridge, on the buccal surface of the mesial cusp. The central basin shows a longitudinal wear groove, which inclines to its greatest depth about midway along the tooth, and distally it is nearly horizontal. Enamel has been removed from the distal part by wear. The root has broken off about 0.7 mm below the crown. It is undivided at this level, but grooves on the mesial and buccal sides suggest that a mesiobuccal root, at least, separated at a deeper level.

Comparison (Fig. 3).—This tooth is similar in size to the largest lower molar of *Eleutherodon* (BMNH M46461). Both have a mesial main cusp followed by a basin between longitudinal ridges. However, the main cusp in BMNH M46461 is buccal, and a smaller lingual cusp leads the lingual ridge, while in *Millsodon* both ridges join the main lingual cusp. The main cusp is proportionately larger and more erect in *Millsodon*, occupying about 2/5 of the length of the tooth. Details of the basin and cusp rows have been removed by wear, but minor elevations indicate two cusps on the lingual ridge; there is no trace of the numerous cusps on the ridges and fluting in the basin that characterise *Eleutherodon*.

BMNH M46645 more closely resembles the supposed m1 of *Thomasia* (*Thomasia II* of Sigogneau-Russell 1989: fig. 18) (Fig. 3E). There is a large mesial cusp (a1), with a wear facet (labelled 1 by Sigogneau-Russell) and a short cingulum on the buccal side; both ridges join the main cusp; the lingual ridge is

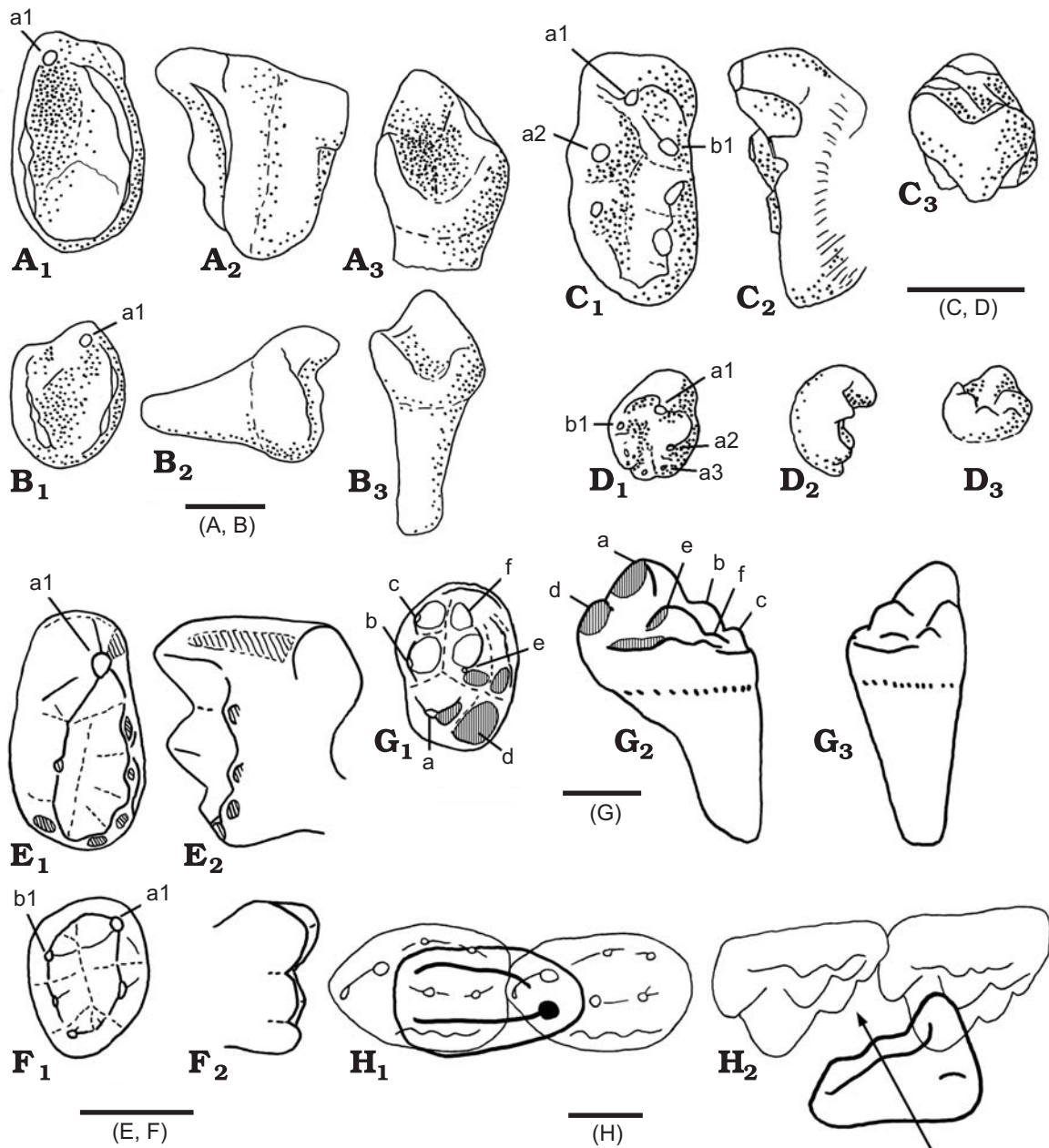


Fig. 3. "Haramiyidan" teeth. **A, B.** *Millsodon superstes* gen. et sp. nov. **A.** BMNH M46645, right m1 (holotype), in occlusal (**A₁**), buccal (**A₂**), and distal (**A₃**) views. **B.** BMNH M46183, left m3 (paratype) in occlusal (**B₁**), buccal (**B₂**), and distal (**B₃**) views. Mesial end upwards in occlusal and buccal views, crown upwards in distal view. **C, D.** *Staffia aenigmatica*. **C₁, C₂, C₃**, right m1; **D₁, D₂, D₃**, m3; redrawn after Heinrich (2002: fig. 5), corresponding views. The m3 is interpreted as a left tooth. **E, F.** *Thomasia*, redrawn after Sigogneau-Russell (1989: figs. 18, 7). **E₁, E₂**, right "*Thomasia II*" (?= m1); **F₁, F₂**, left (right reversed) small "*Thomasia I*" (?= m3). Mesial end upwards in occlusal and buccal views, crown upwards in distal views. **G.** BDUC J 3, right upper molar referred to *Millsodon superstes*, occlusal (**G₁**), lingual (**G₂**), and mesial (**G₃**) views. In **G₁** and **G₂** the wear facets, indicated by vertical hatching, are probably due to the mesial cusp of the lower molar. **G₁**, mesial end upwards; **G₂, G₃**, crown upwards. **H.** Postulated occlusal relations of upper and lower molars (shown as left in **H₂**) of *M. superstes*, based on BDUC J 3 and BMNH M46645. **H₁**, occlusal view, buccal side upwards; **H₂**, lingual view; mesial end to right in both. Scale bars 1 mm.

the higher and it has two elevations. However, in *Thomasia* the main cusp is more pointed, its mesial surface is ridged, and it is less predominant over the more distal cusps. The holotype m1 of *Staffia aenigmatica* (Heinrich 1999) (Fig. 3C) has a blunt main cusp, less high than in *Millsodon* and more curved distally. The tooth is proportionately longer and narrower, and not narrowed towards the mesial end, but it shows the mesial

and buccal slight embayments of outline seen in *Millsodon*. It differs in that the lingual cusps are separated by deep valleys (synclines), whereas in *Millsodon* and *Thomasia* they are elevations on a ridge.

Paratype (Figs. 1E, 3B).—BMNH M46183 is a small and proportionately shorter tooth of similar type (1.6 × 1.15 mm).

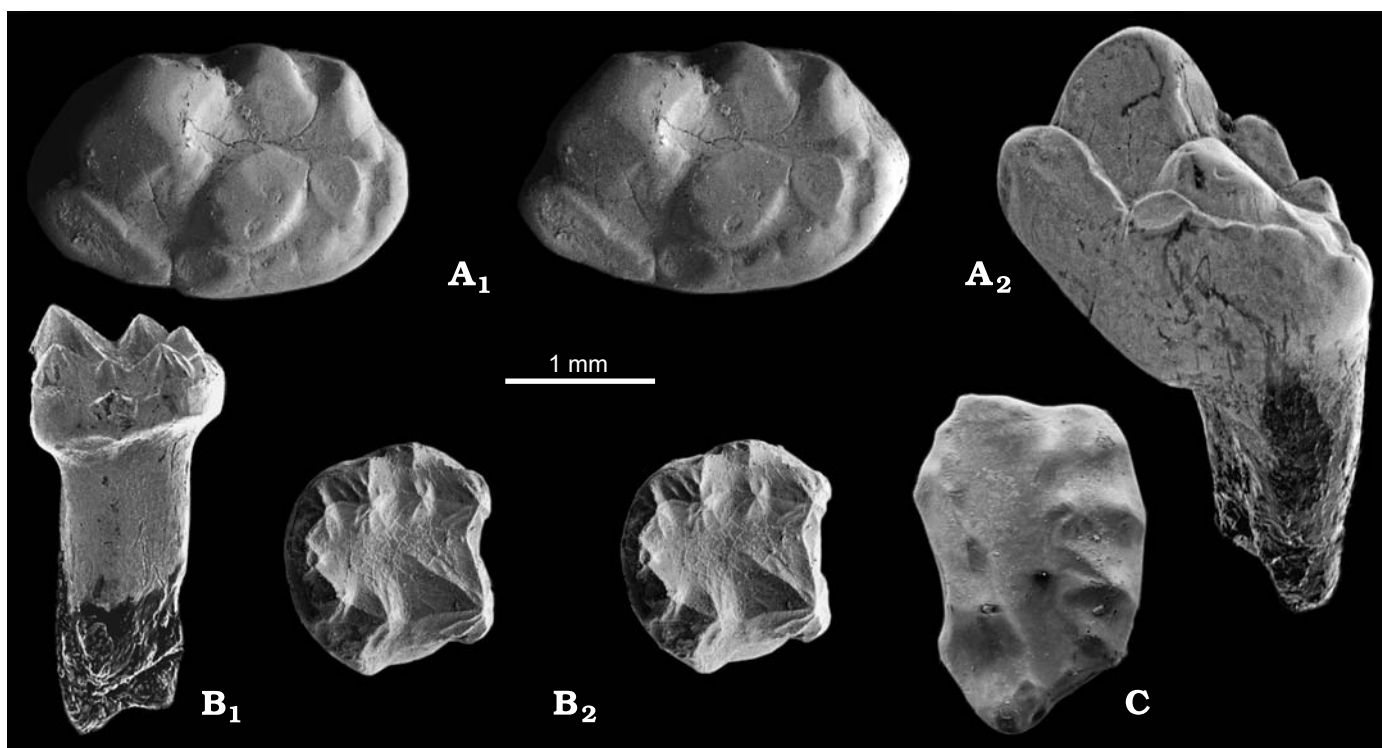


Fig. 4. Scanning electron micrographs of specimens now missing. **A.** BDUC J 3, left upper molar referred to *Millsodon superstes* gen. et sp. nov. in occlusal view (stereo) (A_1) and lingual view (A_2). **B.** BDUC J 562, undetermined haramiyid molar in lingual view (B_1) and occlusal view (stereo) (B_2). **C.** BDUC J 682, left upper premolar referred to *Hahnotherium antiquum* gen. et sp. nov. in occlusal view. Mesial end to the right in A_1 and B_2 , upwards in C, crown upwards in lingual views.

Kermack et al. (1998) interpreted it as a right lower molar of type γ , but it is regarded here as a left lower molar. It is heavily worn and abraded. The outline is rounded distally and obliquely transverse mesially; with a small mesial embayment. The large mesiolingual cusp is similar in shape to that of the holotype. It is continuous with the lingual ridge, which has two elevations. The buccal ridge is lower and worn on the top, and the number of buccal cusps is uncertain. There was evidently no large mesiobuccal cusp as in *Thomasia* (compare Figs. 3B and 3F). Unlike in the holotype, the buccal ridge extends to the mesial border and is separated from the main lingual cusp by a valley; a trace of the connection may be represented by a faint ridge on the distobuccal slope of the main cusp, pointing towards the buccal ridge. There is a single root, flattened buccolingually.

Comparison.—The resemblances and differences between BMNH M46183 and BMNH M46645 are consistent with their occupying different dental positions in the same species. BMNH M46183 has a superficial resemblance to the smaller type of *Eleutherodon* lower molar such as BMNH M46851, but the larger mesial cusp is lingual, not buccal as in *Eleutherodon*, there are fewer cusps, no indications of fluting, and the main mesial cusp is larger. On the more distal molars of *Haramiyavia* and *Thomasia* the buccal row extends forward past a1 to the mesial end of the tooth. This feature is represented by a ridge in BMNH M46183, which because of its small size and undivided root is probably a last

molar. However, the normally large cusp (b2), buccal to a1, is not developed (Fig. 1E₁).

A posterior lower molar of *Staffia* has recently been described by Heinrich (2001) and it may be compared with BMNH M46183 (Fig. 3B, D). In *Staffia* the last molar is much smaller in comparison to m1 than in *Millsodon*. Heinrich interpreted the tooth as from the right side, but comparison with the English specimen indicates that it is a left tooth: the cusps labelled b1 and b2 by Heinrich are lingual and should be called a2 and a3 (Fig. 3D₁). If this orientation is accepted, the following differences may be noted: *Staffia* is shorter relatively to width; the mesial margin is more oblique and lacks the indentation; the mesial cusp (a1) is lower and more convex in lateral profile; it is widely separated from a2 (“b1”) by a valley; a3 (“b2”) is much smaller. Most of these differences may be ascribed to the greater reduction of the *Staffia* tooth, but the separation of a2 from a1 occurs also on m1. In *Staffia* the buccal row contains two distinct cusps; it is connected to the buccal side of a1 by a ridge that follows the mesial margin and forms the mesial edge of the basin. This is not present in BMNH M46183. It might be compared with a ridge in the buccal side of a1 on the first molariform of *Staffia*.

Referred specimen BDUC J 3 (Figs. 3G, 4A).—This tooth from Watton Cliff is now missing, and it is described on the basis of scanning electron micrographs and camera lucida drawings. It is included in this paper because of a possible identity with *Millsodon*.

BDUC J 3 is interpreted as a right upper molariform (?M1), on the assumption that the highest cusp is distal as in other "haramiyidans". The presence of a third row of cusps indicates an upper tooth, and wear facets show that the additional row is lingual. The tooth measures 2.55×1.7 mm, comparable in length with upper molars of *Eleutherodon* and m1 of *Millsodon*. The cusps are blunt, rounded and separated by sulci; there are no enamel ridges on their slopes. The highest cusp (*a*) is distobuccal; it is followed mesially by a buccal cusp *b*, about half its height, and a still smaller cusp *c* near the mesial end of the tooth. A distolingual cusp *d*, is about half as high as *a*, beyond which it projects distally. Mesial to and slightly more lingual than *a* is cusp *e*, similar in height to *d* and *b*; it is preceded by a lower cusp *f*, now worn off. The groove between *b* and *c* buccally and *e* and *f* lingually represents the basin of other "haramiyidans". On the lingual margin, mesially to *d*, is a row of low rounded cuspules, forming a cingulum. The distal root has completely broken off; the mesial root is about 1.7 mm long. If the root is considered to be vertical, the crown basin would be inclined at about 30 degrees to the horizontal, facing forwards.

The tooth is only moderately worn and exhibits clear wear facets (Fig. 4A). Two principal groups of these are distinguishable (Fig. 3G): facets on *b*, *c*, *e*, and *f*, sloping into the basin, are presumably due to contact with buccal cusps on the lower molar; lingually inclined facets on *a* and *d* imply occlusion against the buccal side of a large lingual cusp of the more posterior lower molar. By superposition of drawings it was possible to fit m1 of *Millsodon* with two adjacent copies of BDUC J 3 (Fig. 3H). The lower tooth moved backwards and upwards, its mesial main cusp passing lingually to the upper cusps *a* and *d*. At the end of the movement the ridges on the distal part of the lower tooth would come into contact with the ridges on the mesial part of the following upper tooth: the buccal lower ridge would bite in the basin of the upper tooth, and the lingual lower ridge would pass to the lingual side of cusps *e* and *f*; the tip of upper cusp *a* would meet the distal end of the basin of the lower tooth. The effect would be a crushing action, directed backward and upward, together with some shear between the main cusps. There is no indication of the horizontal sliding action found in *Thomasia*, but some resemblance to that postulated for *Theroteinus* (Butler 2000), except that in that case the highest cusps are more centrally placed and the movement was probably vertical.

Compared with *Theroteinus* (see Butler 2000: fig. 4), the high cusp *a* appears to correspond to A2, with *d*, *a*, *b*, *c* representing the buccal (A) row. The B row however is short, with only two cusps, *e* and *f*. B1, which in *Theroteinus* stands lingually to A2, is missing, thus providing space for the large lower cusp a1.

Because BDUC J 3 can be fitted occlusally with BMNH M46645 we refer it to *Millsodon superstes* as a probable upper molar. It represents a hitherto unknown type of "haramiyidan": possibly it is a derivative of the Theroteinidae, or a specialised relative of the Haramiyidae. Until better material

is found we prefer to classify it as "Haramiyida" *incertae sedis*.

Genus *Kirtlingtonia* nov.

Type species: Kirtlingtonia catenata sp. nov.

Derivation of name: From Kirtlington, Oxfordshire, from which the material was obtained. Feminine.

Diagnosis.—Upper molar with a central basin, flanked buccally by a crest on which stand an anterior and a median pointed cusp, with minor elevations more distally. The basin is shallow, without fluting. Lingually to the basin is a central row consisting of a moderately high mesial cusp followed by a chain of about 6 cusps of diminishing size; the chain curves buccally at its end, where it crosses the basin towards the median buccal cusp. There is an enlarged cusp at the distal end of the tooth (?= cusp B1 of *Eleutherodon*). On the mesiolingual side of this is a diminishing series of 3 or more smaller cusps. Lingual to the central row are numerous minor cusps, irregularly arranged. Differs from *Eleutherodon* in the pointed cusps, the small number of buccal cusps, the absence of fluting in the groove, failure of the central row to unite with cusp B1, and the absence of the lingual groove and cusp BB.

Upper premolar semi-molariform.

Kirtlingtonia catenata sp. nov.

Figs. 1F, G, 5A–C.

Holotype: BMNH M46497, the crown of a right upper molar, probably unerupted.

Paratype: BMNH M46579, right upper molar with root.

Referred specimen: BMNH M46818, left upper premolar (bed 3p(iii)). All are from the Kirtlington Mammal Bed, Oxfordshire.

Derivation of name: Latin, *catena*, a chain, referring to the chains of minor cusps.

Distribution.—Late Bathonian, England.

Diagnosis.—As for the genus, by monotypy.

Description.—BMNH M46497, the holotype (Figs. 1F, 5A) is an unerupted tooth crown without roots, with the pulp cavity fully exposed basally. It measures 2.2×1.7 mm. The paratype (Figs. 1G, 5B) is a functioning tooth with a root, similar in size and crown pattern to the holotype. Comparison with *Eleutherodon* indicates that these are right upper molars, and because the root of the paratype is undivided they are regarded as last molars.

The holotype tooth is longer than wide, transverse mesially and convex distally. The highest cusp (here called *a*) stands at what is assumed to be the mesiobuccal corner of the crown; it is prismatic, pointed at the tip, with ridges on its slopes. It stands at the end of a buccal crest, which rises at mid-length to a cusp (*b*), followed by two minor elevations. At the distal end the crest turns lingually to join a distal cusp (*c*). Lingual to cusp *a* is a prismatic mesial cusp (*d*), which stands at the end of a central row of minor cusps of diminishing size. The central row curves at its distal end towards the buccal cusp *b*. The area between the buccal crest and the central row forms a basin,

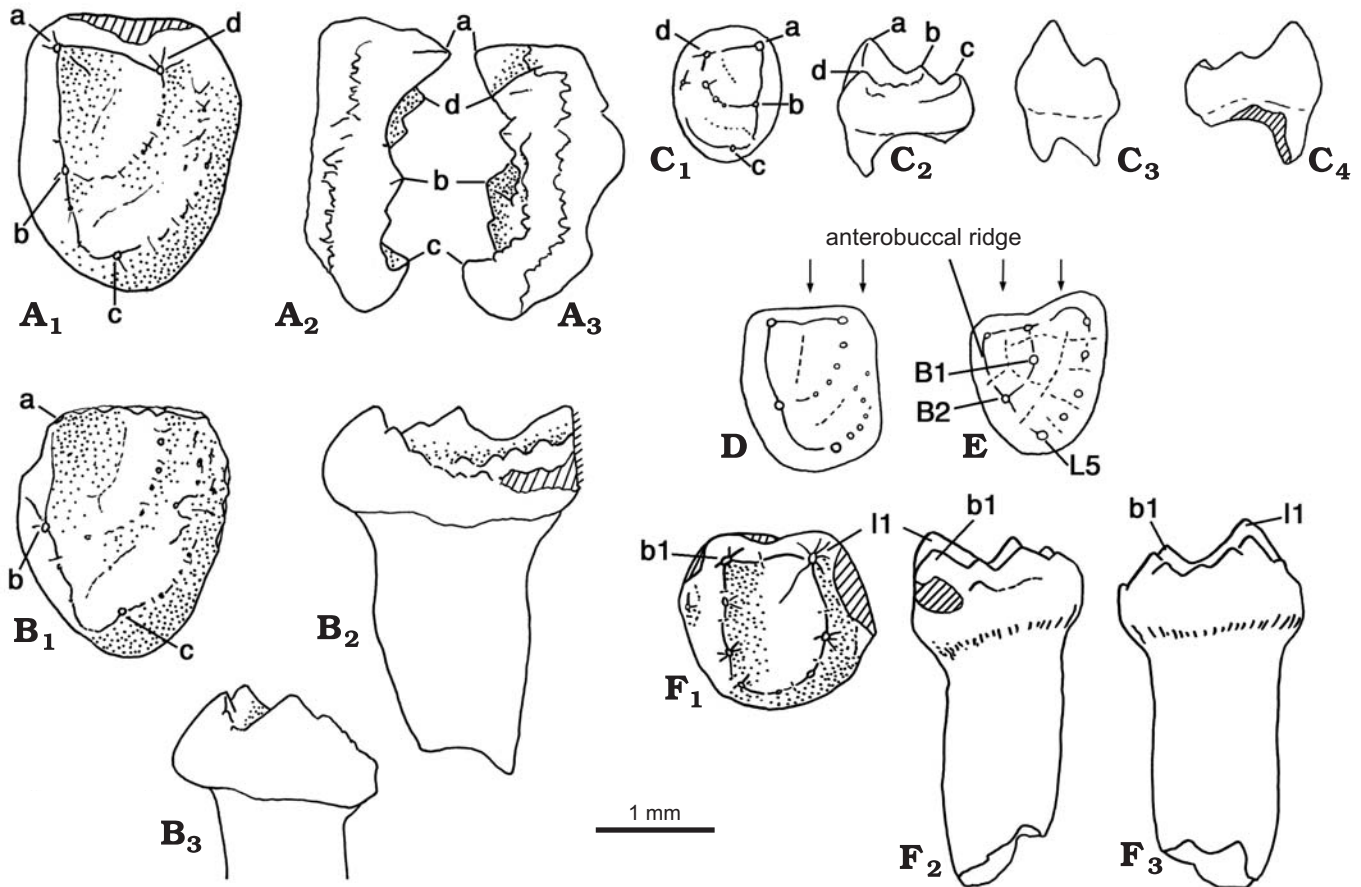


Fig. 5. A–D. *Kirtlingtonia catenata* gen. et sp. nov. A. BMNH M46497, right last upper molar (holotype) in occlusal (A₁), buccal (A₂), and lingual (A₃) views. B. BMNH M46579, right last upper molar (paratype) in occlusal (B₁), lingual (B₂), and distal (B₃) views. C. BMNH M46818, left upper premolar (referred) in occlusal (C₁), lingual (C₂), mesial (C₃), and buccal (C₄) views. D, E. Comparison of *Kirtlingtonia* (D) with M2 of a paulchoffatiid, genus B (after Hahn and Hahn 1998a) (E). Arrows represent postulated position of buccal and lingual cusp rows of m2. Not to scale. F. BDUC J 562, undetermined haramiyid, interpreted as a left lower molar, in occlusal (F₁), lingual (F₂), and distal (F₃) views. Mesial end upwards in A₁, A₂, A₃, B₁, C₁, D, E, F₁; crown upwards in B₂, B₃, C₂, C₃, C₄, F₂, F₃.

shallower than in *Eleutherodon* and without the fluting characteristic of that genus. On the lingual margin of the tooth, a series of small cusps of diminishing size runs mesiolingually from cusp *c*, and the area lingual to the central row is occupied by about 6 minor cusps or wrinkles, irregularly arranged.

BMNH M46579, the paratype, is incomplete mesially, where the edge of the crown has broken away, including much of cusps *a* and *d* and the mesial part of the buccal and lingual margins. As preserved, it measures 2.05 × 1.7 mm. The only wear observed is in the basin, where longitudinal striations indicate the passage of an opposing cusp as far back as the ridge that connects cusp *b* to the central row. Wear buccal to the buccal row or lingual to the central row cannot be determined owing to breakage.

The root is 2.4 mm long. It measures in cross-section 1.2 mm mesiodistally and 0.9 mm in width. Its cross-sectional area is thus much smaller than the area of the crown, which overhangs the root especially on the buccal side.

Comparison.—The row of minor cusps lingual to the basin suggests a comparison with the middle row on *Eleutherodon* upper molars. In that case cusp *d* would be homologous with

the enlarged cusp (Bx) at the mesial end of the middle row of *Eleutherodon* (Fig. 2B₁). The enlarged distal cusp *c* might be compared with cusp B1 of *Eleutherodon*. However, in *Kirtlingtonia* the cusp row is diverted buccally towards cusp *b*, but in *Eleutherodon* it connects with cusp B1, though in one specimen (BMNH M46459; Kermack et al. 1998: fig. 7) it ends to the buccal side of cusp B1. There are many other differences: in *Eleutherodon* the cusps are less sharply pointed; the buccal cusps are more numerous, and the mesial one is not enlarged; the basin is deeper and its sides are fluted; there is a lingual groove and an enlarged lingual cusp BB.

The multituberculate M2 has been modified in adaptation to its lingual position in relation to M1, resulting in a different occlusal relation to m2. Whereas the buccal cusps of M1 occlude laterally to m1, those of M2 occlude in the median valley of m2. It appears as if the buccal cusps of M2 had jumped across the buccal cusps of m2. A more likely hypothesis is that the cusp rows of M2 are not serially homologous with those of M1; when M2 shifted lingually, the buccal cusp row was reduced, to become the anterobuccal ridge (Hahn and Hahn 1998a). The lingual row now became the buccal

row, and a new row was added on the lingual side. With this in mind, M2 of Paulchoffatiidae (Hahn and Hahn 1998a) may be compared with the *Kirtlingtonia* tooth (Fig. 5D, E). The anterobuccal ridge is confined to the mesial half of the tooth. It is followed distally by a large cusp (B2 in the nomenclature of Hahn and Hahn 1998a) that is frequently connected by a ridge to the more mesial part of the buccal row (B1, B0). B2 could be homologous with cusp *b* of *Kirtlingtonia*, the anterobuccal ridge with the mesial part of the buccal crest (with cusp *a*), and B1–B0 with the central cusp row arising from cusp *d*. Most paulchoffatiids have a distal cusp (usually termed L5) corresponding to cusp *c*. The series of lingual cusps is not represented in *Kirtlingtonia*, but it may be foreshadowed by the series of small cusps on the mesial side of *c*. If the M2/m2 occlusion is a diagnostic character of the order, *Kirtlingtonia* is not a multituberculate, but it illustrates the type of tooth from which the multituberculate M2 could have been derived.

Upper premolar (Figs. 1H, 5C).—BMNH M46818 has only about half the linear dimensions of *Kirtlingtonia* molars (1.1 × 0.85 mm) but the similarity of pattern indicates that either it represents a smaller species or it occupies a different position in the dentition. It is considered to be from the left side. The highest cusp (*a*), assumed to be mesiobuccal, is proportionately higher than cusp *a* of the holotype: its height is about 70% of the tooth length, compared with about 45% in the holotype. It is conical and sharply pointed. It is connected by a crest to a lower cusp (*b*) midway along the tooth. This is joined to a still lower distal cusp (*c*). Lingual to *a* is a mesiolingual cusp (*d*), which gives rise to a lingual ridge, made up of a row of minor cusps, that turns buccally towards the buccal cusp *b*. The disto-lingual part of the crown is occupied by a ledge that extends from the tip of cusp *c*. The root is broken; from the fragment that survives, it appears to be vertical, and overhung by the crown buccally and lingually. If this tooth belongs to *K. catenata*, the elevation of cusp *a* makes it unlikely to be a posterior molar; it is provisionally identified as a semi-molariform premolar.

“Haramiyidan” molar BDUC J 562

Figs. 4B, 5F.

This tooth was collected from the Kirtlington Mammal Bed, Old Cement Works Quarry, Kirtlington, but is now missing. The following description is based on scanning electron micrographs and drawings.

Description.—BDUC J 562 is a relatively small molariform tooth, approximately square in outline (length 1.4 mm, width 1.5 mm). The single root indicates that it is a last molar, but whether upper or lower is uncertain. It is described here as a left lower molar, with a rounded distal margin and the highest cusps mesial. However, the presence of an additional marginal cusp might represent the rudiment of a third row, and the tooth might be upper. In that case, the highest cusps might be distal, as in other “haramiyidans”. For descriptive pur-

poses the buccal and lingual cusps are referred to as b1... and l1... respectively, without implications of homology.

The tooth is unworn, but it has lost enamel from the mesial margin and part of the lingual margin. The cusps are sharply pointed, with apical angles of about 90 degrees. They are connected by crests and have radial ridges on their slopes. The highest cusp, considered to be mesiolingual (l1) is connected by a transverse crest to the first buccal cusp (b1), and it also has an oblique ridge running into the basin. There are four lingual cusps of diminishing size; at the distal end the series curves buccally to meet the end of the buccal row, closing the basin. The lingual margin next to l1 has broken off, but a small prominence lingual to l2 suggests that a cingulum may have been present there. Of the four buccal cusps, b1 and b3 are lower than l1 and similar in height to l2; b2 and b4 are small. An additional small cusp stands on the buccal margin next to b2. The basin, bounded mesially by the ridge from b1 to l1 and distally by the terminal part of the lingual cusp row, is free of ornament except for the ridges on the cusps. It is shallowly concave, deepest between l2 and b3. The root is 2 mm long, and slightly curved mesially. Transversely it measures 1.0 × 1.15 mm, thus much less than the crown.

Comparison.—This tooth shows some resemblance to *Thomasia*, especially the shorter posterior upper molars called *Haramiya I bis* by Sigogneau-Russell (1989): the distal cusps connected by a transverse ridge (“saddle”), and closure of the basin by union of the cusp rows (“U-ridge”). However, the cusps of *Thomasia* are more rounded, and they do not have radial ridges. There is more resemblance in this respect to *Kirtlingtonia*, with which BDUC J 562 also agrees in the relatively small cross-sectional area of the root. It is somewhat narrower than M2 of *Kirtlingtonia* but much shorter, and occlusion between the teeth seems unlikely. Interpretation of J 562 must await the discovery of further material; at present it can only be classified *incertae sedis*.

Order Multituberculata Cope, 1884

Distinguished from “Haramiyida” by fully horizontal chewing, by the lingual displacement of M2 relatively to m2, and by blade-like specialisation of lower premolars.

Suborder *incertae sedis*

The two families described here lie outside the morphological range of the “Plagiaulacida” as described by Hahn and Hahn (2004), and are regarded as earlier offshoots from the multituberculate stem.

Family Kermackodontidae nov.

Type genus: *Kermackodon* gen. nov. by monotypy.

Diagnosis.—Second upper molar wide mesially and narrowed distally. Cusps pointed when unworn, of unequal height; cusps of each row connected by a longitudinal crest. Lingual row markedly convex, the last cusp closing the central valley distally. Seven lingual cusps, the most mesial ones smallest. Five buccal cusps, of which the last two are large, and the first

three are elevations on the mesial crest of the fourth. Antero-buccal ridge possibly represented by a rounded cingular shelf. Differs from “*Plagiaulacida*” (except possibly *Albionbaataridae* of which M2 is unknown) in the more numerous, pointed cusps, joined by longitudinal crests (as opposed to blunt cusps separated by transverse grooves). Resembles most *Paulchoffatiidae* and differs from other “*Plagiaulacida*” in the pointed distal end of the tooth, curvature of the lingual row, and closure of the central valley by a distal cusp.

Referred posterior lower premolar (p4) differs from other multituberculates in being triangular in side view, the blade rising to a central peak; and falling to cingulum level at the mesial and distal ends; there are four denticulations, three close together near the peak; buccal cusp row semicircular, confined to the distal end of the tooth and in continuity with the distal end of the blade.

Genus *Kermackodon* nov.

Type species: Kermackodon multicuspis sp. nov.

Derivation of name: Named in memory of the late Professor Kenneth A. Kermack, in recognition of his important contributions to knowledge of Mesozoic mammals. Also from Greek, οδους, οδοντος, tooth. Masculine.

Diagnosis.—As for family, by monotypy.

Kermackodon multicuspis sp. nov.

Figs. 6A–C, 7A, 8A, 9.

Holotype: BMNH M46822, a left upper molar (M2) from the Old Cement Works Quarry, Kirtlington, bed 3p(iii).

Referred specimens: (a) BMNH M46684, a left lower last premolar (p4), from the Old Cement Works Quarry, Kirtlington. (b) BMNH M46640, an incomplete right upper premolar, not the last (P3 or P4); from the Old Cement Works Quarry, Kirtlington, bed 3w(i).

Derivation of name: From Latin *multus*, many and *cuspis*, sharp point.

Distribution.—Late Bathonian of England.

Diagnosis.—As for the genus.

Description of upper molar (Figs. 6A, 7A).—BMNH M46822 is heart-shaped in crown view, almost as wide as long (2.85 × 2.6 mm), buccally and lingually convex, mesially transverse with a slight embayment, and pointed distally. The distal point is probably artificially sharpened by breakage of the distal end of the lingual margin. There are buccal and lingual rows of cusps on either side of a longitudinal valley. The cusp rows are somewhat curved, especially the lingual row, and they converge towards the distal end. The cusps are pointed, with enamel ridges on their slopes, and those of each row are joined by a longitudinal crest.

There are five buccal cusps, of which the most distal (B5) is the highest as preserved, B4 is somewhat lower but worn or damaged at the tip, and B3–B1 are smaller elevations on the mesial crest of B4. B5 is pyramidal, with a mesial ridge to B4 and a strong mesiolingual ridge running obliquely into the valley. Buccally to B4–B1 the margin of the crown is swollen to form a smoothly rounded shelf at cingulum level without enamel ornamentation.

There are seven lingual cusps, forming a series that follows the curvature of the lingual margin. They diminish in size mesially from a maximum at L6. L6 is less high than B5. L7 is smaller than L6 and placed nearer to the midline, on the distal prominence of the outline and partly blocking the central valley. At its mesial end the lingual row is continuous with a transverse marginal ridge, which joins the end of the buccal row. Each lingual cusp bears, in addition to the longitudinal connecting ridge, a ridge on its buccal (valley) side, best developed on L6. A mesiobuccal ridge on L5 descends obliquely down the buccal surface of L4 and L3, where it gives rise to a series of three small cusps. Both sides of the mesial part of the central valley are ornamented by numerous enamel cuspules, irregularly arranged. On the lingual margin below L3–L5 is a series of three small cingulum cusps, of which the first and third are connected by ridges to L3 and L4 respectively. Below L6 and L7 the lingual margin is broken. This may have happened in life as the exposed enamel is smoothed.

A striking feature of the central valley is the longitudinal wear groove, which runs horizontally along most of the length of the tooth, but does not cross the margins. It begins mesially in a shallowly basined area distal to the transverse ridge, and ends at the mesial side of L7. The groove is narrow and clearly marked, as if produced by the tip of a sharp cusp. On the lingual side of the valley there is wear on the buccal ridges of L5 and L6, and on the supplementary cusps below L3 and L4. No wear could be detected on the lingual side of the lingual cusps. On the buccal side of the valley, there is some wear on the mesiolingual crest of B5, and small facets near the tips of B4, B3 and B2, inclined lingually. The tips of the highest cusps, L6, L5, B5, and B4, have been removed, perhaps by abrasion. The buccal surface of the buccal cusps, and the buccal shelf, appear to be unworn. If the occlusal relation between the second molars was that typical of multituberculates, the opposing m2 must have had a high lingual cusp row, but the buccal row was probably poorly developed.

The roots have been broken off close to the crown, and the pulp cavity is fully exposed. A bay in the mesial margin of the root base indicates that the mesial root was grooved and perhaps divided.

Comparison.—The *Kermackodon* molar is in the length range of upper molars of *Eleutherodon* and much larger than the molars of the Late Jurassic and Early Cretaceous multituberculates classified by Kielan-Jaworowska and Hurum (2001) in the paraphyletic suborder “*Plagiaulacida*”. It differs from *Eleutherodon* and resembles multituberculates in the horizontal, rather than basined longitudinal wear groove, and in the absence of the third (lingual) row of cusps (unless the lingual cingulum cusps represent this). The approximately triangular shape of the tooth, wide mesially with an embayment and pointed distally, approaches M2 of some paulchoffatiids, e.g., genus A (Hahn and Hahn 1998a: figs. 19, 20) and genus D sp. 1 (Hahn and Hahn 1998a: fig. 23). In these the lingual row is curved so that the last lingual cusp is near the distal buccal cusp, closing the central valley (Fig.

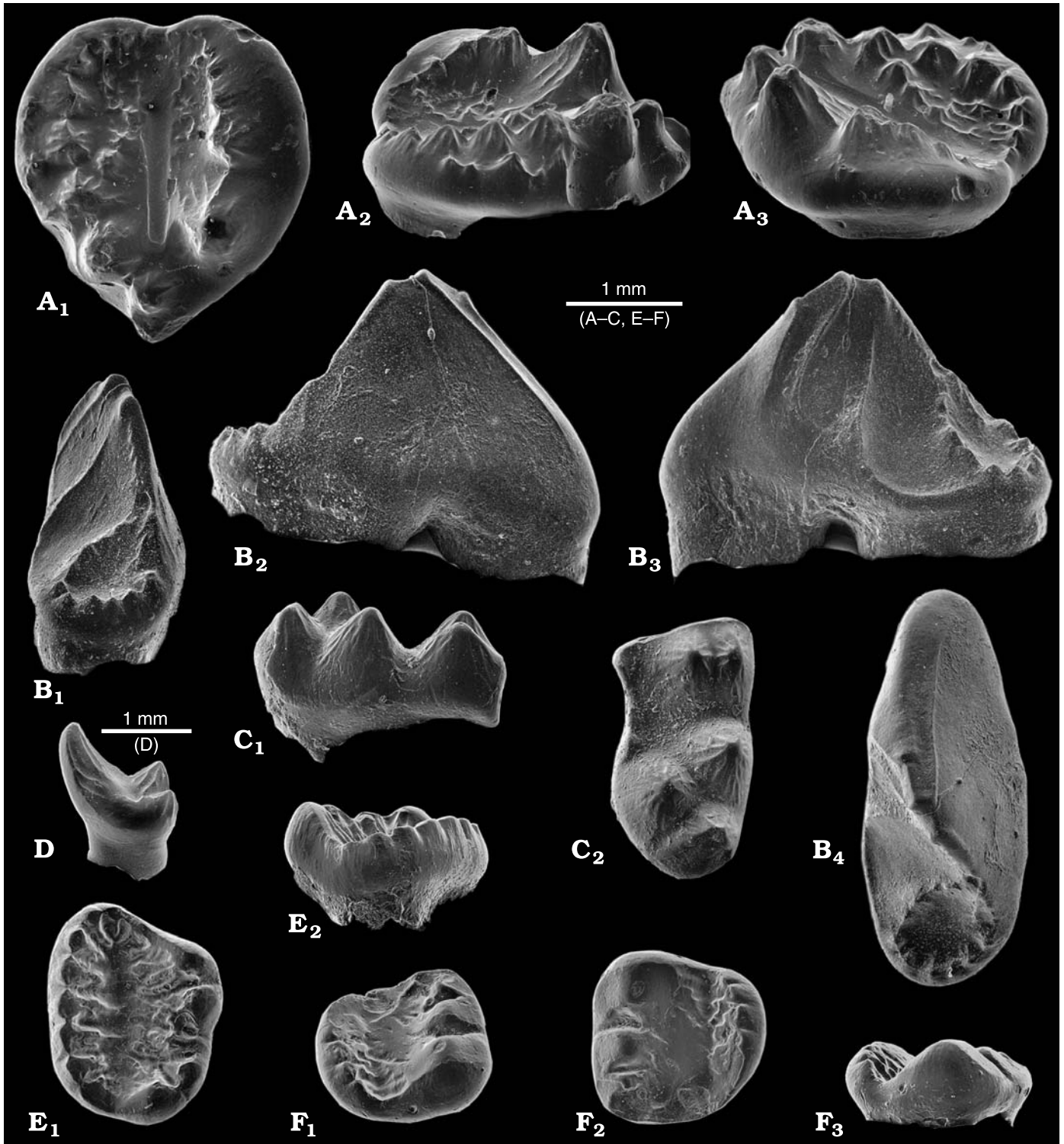


Fig. 6. Scanning electron micrographs of epoxy resin casts. **A–C.** *Kermackodon multicuspis* gen. et sp. nov. **A.** BMNH M46822, right M2 (holotype) in occlusal (A₁), oblique lingual (A₂), and oblique buccal (A₃) views. **B.** BMNH M46684, right p4 (referred) in distal (B₁), lingual (B₂), buccal (B₃), and occlusal (B₄) views. **C.** BMNH M46640, right upper premolar (referred) in lingual (C₁) and occlusal (C₂) views. **D.** *Allotheria incertae sedis*, BMNH M46234, left I2, lingual view. **E, F.** *Hahnotherium antiquum* gen. et sp. nov. **E.** BMNH M46717, left M2 (holotype) in occlusal (E₁) and mesio-lingual (E₂) views. **F.** BMNH M46773, right m2 (referred) in mesio-occlusal (F₁), occlusal (F₂), and mesio-lingual (F₃) views. Mesial end upwards in A₁, B₄, C₂, E₁, F₂, crown upwards in A₂, A₃, B₁, B₂, B₃, C₁, D, E₂, F₃.

7B). The number of lingual cusps in paulchoffatiids (3 to 6, most frequently 4 or 5) is smaller than in *Kermackodon* (7).

In the buccal row the two large cusps, B4 and B5, correspond to B1 and B2 of paulchoffatiids. Mesially three small cusps

develop from the crest of B4, but in paulchoffatiids a cusp B0 may develop from the marginal crest. The mesiobuccal rounded ledge may represent the anterobuccal ridge, which varies in Paulchoffatiidae and is absent in genus A; however, the absence of a wear facet and of wrinkling makes this identification uncertain.

Kermackodon differs from Paulchoffatiidae in the form of the molar cusps. These are pointed, with well developed radial ridges, and they are connected by longitudinal crests; in paulchoffatiids and in nearly all later multituberculates they are blunt and separated by transverse grooves. Possibly the difference is due to greater thickness of enamel which results in swelling of the cusps. Pointed cusps resembling those of *Kermackodon* occur in M1 of *Proalbionbaatar* (Hahn and Hahn 1998b), the only albionbaatarid upper molar known. In this all the cusps are ornamented with radial enamel ridges, and the lingual cusps, 6 or 7 in number, are joined by a longitudinal crest. The narrowness of the wear groove on the *Kermackodon* M2 indicates that the lingual cusps of m2 were also pointed.

In M2 of other "Plagiaulacida" the number of lingual cusps is reduced to 3 (the tooth identified as *Parendotherium* or *Eobaatar* by Hahn and Hahn (1992) is exceptional in having 4). The lingual row is straight and the distal end of the tooth is broadened so that the outline becomes trapezoidal rather than triangular. The central valley is open distally, the distal lingual cusp being more widely separated from the distal buccal cusp. Development of a cusp (B0) at the mesial end of the buccal row varies. It is best developed in *Eobaatar*, where it differentiates from the marginal ridge. The anterobuccal ridge is most frequently a cingulum-like structure (Fig. 7C), whose wear continues that of the central valley of M1, due to the buccal cusps of m1, as in *Bolodon* (see Kielan-Jaworowska and Ensom 1992: pl. 3). It is more strongly developed in *Glirodon*, where it forms two cusps (Kielan-Jaworowska and Hurum 2001: pl. 1). It seems to be absent in *Ctenacodon*, but: the type of *C. laticeps* figured by Kielan-Jaworowska et al. (1987) shows a wear facet on the buccal surface of B1. Lingual cingular cusps are developed only in the pinheirodontid *Iberodon* (Hahn and Hahn 1999).

M2 of *Kermackodon* shows some resemblance to Paulchoffatiidae among multituberculates, but differs particularly in the more numerous cusps, which are pointed, with sharp ridges. We classify *Kermackodon* in a new family Kermackodontidae. A relationship with Albionbaataridae is possible, but M2 of that family is unknown. The multituberculate-like premolars described below, because of their large size and aberrant character, are provisionally included in the Kermackodontidae and referred to *Kermackodon multicuspis*.

Description of referred lower premolar (Figs. 6B, 8A).—BMNH M46684 is a mesiodistally elongated tooth, much longer than wide (3.5 × 1.5 mm), and similar in size to p4 of *Plagiaulax becklesii*. It is narrower mesially than distally. The crown is dominated by a longitudinal crest ("blade"), which is triangular in profile, with the highest point slightly mesial to the middle. In crown view the blade is seen to be

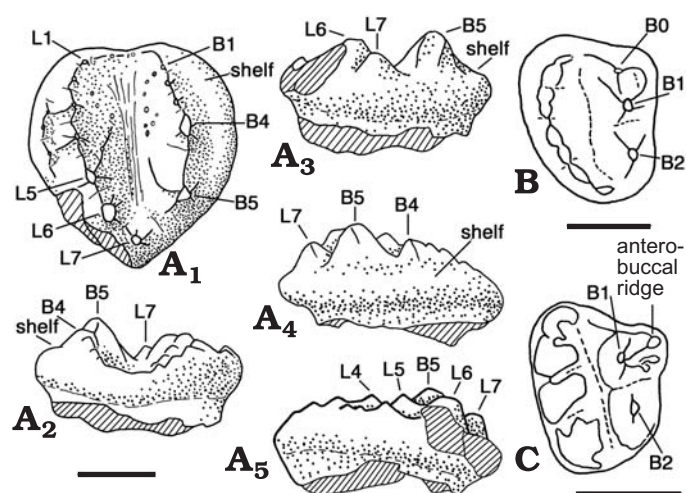


Fig. 7. A. *Kermackodon multicuspis* gen. et sp. nov., BMNH M46822, left M2 (holotype) in occlusal (A₁), mesial (A₂), distal (A₃), buccal (A₄), and lingual (A₅) views. B. Paulchoffatiid M2 (re-drawn and simplified after Hahn 1969: fig 80). C. *Bolodon osborni* M2 (re-drawn from Kielan-Jaworowska and Ensom 1992: pl. 3: 8)). Mesial end upwards in A₁, B, C, crown upwards in the rest. Scale bars 1 mm.

somewhat oblique to the long axis of the tooth, being more lingual distally. At the distal end the edge of the blade is continuous with a series of cusps which extends onto the buccal side for about one-quarter of the length of the crown. In buccal view the maximum height of the blade measures 2.2 mm from the base of the enamel. There are three small elevations (serrations) near the highest part of the blade; the second is the highest, the first is on the anterior slope, and the third is closely behind the second. From the first two serrations arise low ridges that run halfway down the buccal surface with an obliquely forward inclination. They resemble the "Kannelierungen" (Hahn 1969) that are associated with the serrations on lower premolars of other multituberculates. A ridge from the third serration has a different character: it is vertical, longer, reaching cingulum level, and it takes the form of a slight angulation of the tooth surface; more distally the buccal surface is shallowly concave. The distal slope of the edge of the blade has been blunted by wear, but halfway down there is an indication of a fourth serration. That this is not an artefact due to wear is shown by the presence of a short ridge on the lingual surface. A series of six small cusps forms an arc from the end of the blade, at cingulum level, along the distal margin and the distal end of the buccal margin. The series is continued as a ridge, weakly differentiated into three cusps, that runs up the buccal surface in the direction of the fourth serration. Mesial to the series of cusps, the buccal cingulum is represented by a horizontal convexity that meets the vertical ridge from the third serration. On the lingual surface a ridge arises from the second serration and runs obliquely forward, closely parallel to the mesial edge of the blade. There are two slight swellings at cingulum level above the root bifurcation, and from these faint vertical ridges arise. Near the distal end a short vertical ridge runs from the fourth

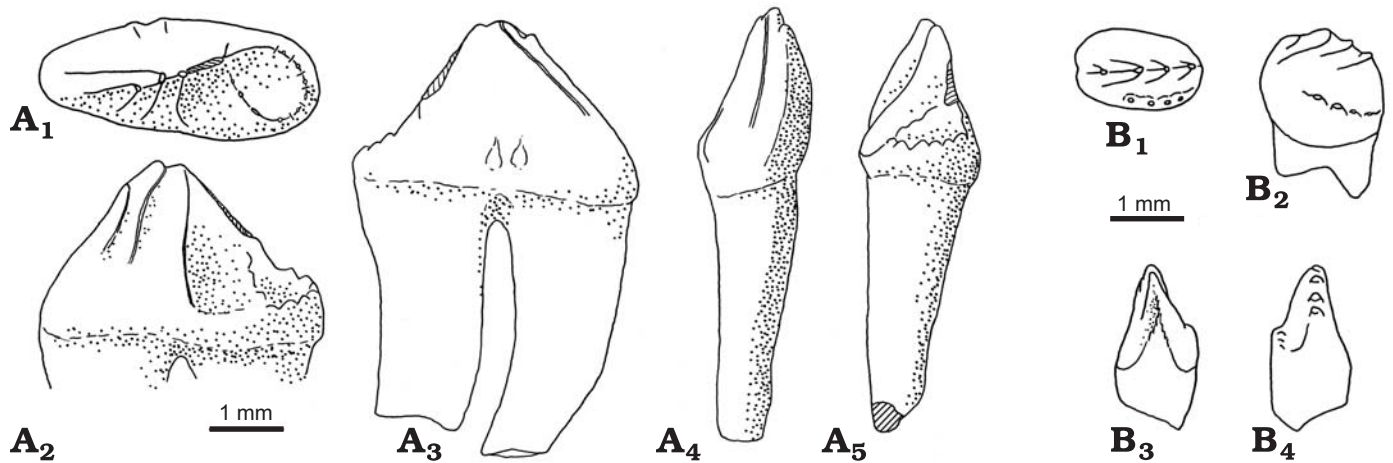


Fig. 8. A. BMNH M46684, left p4, referred to *Kermackodon multicuspis* gen. et sp. nov. in occlusal (A₁), buccal (A₂), lingual (A₃), mesial (A₄), and distal (A₅) views. B. Paulchoffatiid p4 (redrawn and simplified after Hahn 1969: fig. 29) in occlusal (B₁), buccal (B₂), mesial (B₃), and distal (B₄) views. Lingual side upwards in A₁, B₁, crown upwards in the rest.

denticulation. The enamel reaches a somewhat lower level above the anterior root than above the posterior root. There is no groove in the anterior surface, such as exists in paulchoffatiids for reception of the more anterior tooth. The roots are slightly distally curved towards the tips and slightly flattened buccolingually; the posterior root is the larger.

The only evidence of wear is on the edge of the posterior part of the blade, between denticulations 3 and 4. It is inclined distally at an angle of 60 degrees to the long axis of the tooth.

Comparison.—The longitudinal serrated blade with oblique ridges, and the distobuccal series of small cusps, are characters of multituberculate lower premolars. Because of its elongated form and comparatively large size BMNH M46684 is identified as a last premolar (p4). The triangular profile of the blade, however, differs from that of other multituberculates, in which the top of the blade is arched or horizontal; exceptional is the reduced p4 of taeniolabidoids such as *Catopsalis*. BMNH M46684 is larger than p4 of paulchoffatiids (Fig. 8B), and longer in proportion to width and height. It is narrower mesially, and the mesial end is not truncate as in paulchoffatiids and plagiaulacids. With only four serrations, M46684 agrees with paulchoffatiids, but the serrations are unequally spaced, and oblique ridges are confined to the mesial part of the tooth. A trace of a triangular profile survives in paulchoffatiids, in which the height of the blade declines from a maximum at serration 2. However, the blade remains high at its mesial and distal ends, whereas in BMNH M46684 it falls to cingulum level. Thus at the mesial end there is in paulchoffatiids a concavity below the blade for reception of p3, but this does not exist in BMNH M46684, in which the premolars would not form an integrated unit as they do in paulchoffatiids. Distally the blade is continuous with the buccal cusp row in BMNH M46684, but in paulchoffatiids it ends well above the buccal cusps, and is linked to them by a vertical ridge. The buccal cusp row in paulchoffatiids extends farther forward along the tooth, to the level of serration 2, but there is a resemblance to BMNH

M46684 in that the series curves upward at its mesial end. Kielan-Jaworowska and Ensom (1994: pl. 2: 6, 7) described a p4 from the Purbeck Limestone, which they suggested might belong to *Albionbaatar*. It has a short, arcuate buccal row, which rises distally to join the end of the blade.

Owing to its almost unworn condition, BMNH M46684 provides little evidence bearing on function. In paulchoffatiids the top of the blade wears against the lingual cusp row of P5 in a longitudinal grinding action, but the Bathonian tooth clearly did not function in this way. Wear on the distal edge of the blade is steeply inclined, in contrast to the horizontal wear of the M2 holotype. In the Paleocene neoplagiaulacid *Xanclomys* (Rigby 1980), in which p4 is triangular in profile, it is tilted so that the distal slope of the edge is horizontal. Though curvature of the roots suggests that BMNH M46684 may have been tilted forward to some extent, this would not be enough to correct the inclination of the wear surface. Perhaps the wear was not due to contact with an opposing tooth but with food, as in the orthal slicing-crushing action of *Ptilodus* (Krause 1982).

Sigogneau-Russell (1989) compared the haramiyid tooth "*Thomasia II*" with p4 of multituberculates (Fig. 3E). It is longer than wide, and narrower mesially than distally as in BMNH M46684. There is a lingual row of three cusps connected by a ridge, which would correspond to the blade, but the cusps are larger and more individualised than the serrations of multituberculates, and the highest cusp is mesial rather than central in position. A buccal row of lower, smaller cusps occupies the distal two-thirds of the tooth, merging mesially into the slope of the largest lingual cusp. In comparison the buccal cusps of BMNH M46684 are smaller and restricted to near the distal end, but they are more extended in paulchoffatiids, which might be more primitive in this respect. *Thomasia* resembles BMNH M46684 and differs from paulchoffatiids in that the lingual and buccal rows are continuous at the distal end of the tooth; the connection forms the "U-ridge" of haramiyids.

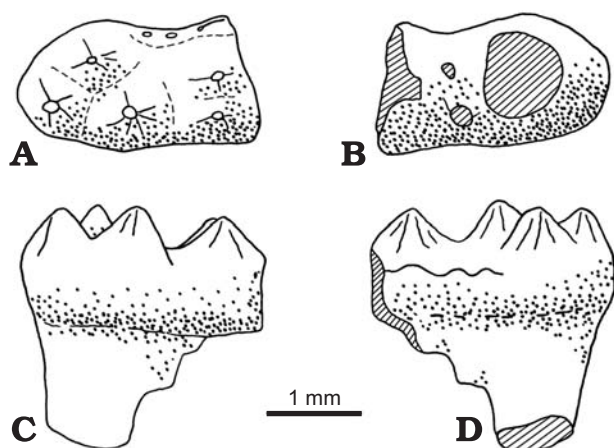


Fig. 9. BMNH M46640, right P3/4, referred to *Kermackodon multicuspis* gen. et sp. nov. **A.** Occlusal view, mesial to right. **B.** Basal view, mesial to left. **C.** Lingual view. **D.** Buccal view, crown upwards in C and D.

Description of referred upper premolar (Fig. 9).—BMNH M46640 is an incomplete tooth, interpreted as from the right side. The mesial end, with most of the anterior root, is missing. As preserved, the tooth measures 2.3 mm in length and 1.2 mm in width; assuming that the roots were equal the original length is estimated at about 2.6 mm. It is thus much longer than upper premolars of paulchoffatiids and other early multituberculates: e.g. length of P5 of *Kuehneodon simpsoni* is 1.7 mm (Hahn 1969) and that of P4 of *Psalodon potens* is 2.2 mm (Simpson 1929). In crown view the lingual margin is straight, the distal end is rounded and more prominent towards the lingual side, and the buccal margin has a shallow bay, above the bifurcation of the roots. Anterior to the bay the tooth is slightly wider than towards the distal end. These features can be seen again for example in P4 of *Kielanodon hopsoni*, *Bolodon elongatus*, and *Psalodon potens*. There are three lingual and two buccal cusps, but one or two additional cusps were probably present on the missing mesial portion. The cusps are conical, subequal in height, and with radial ridges on their slopes as in other multituberculates. The two distal lingual cusps and the distal buccal cusp form an equilateral triangle, and the mesial buccal and lingual cusps stand close together and are connate at the base. There is a buccal cingulum on the anterior part of the tooth, with three low elevations. The lingual ledge that occurs on posterior premolars of paulchoffatiids is absent, and there is no evidence of shearing wear on the lingual surface of the tooth. The posterior root is approximately circular in section at mid-length, where it has broken. There are two small accessory roots (now broken off) between the main roots; the buccal one is midway between the main roots, and the lingual one is joined by a flange to the distal root.

Comparison.—Paulchoffatiid upper premolars are differentiated into an anterior group, of mesiodistally short teeth, usually with two buccal and two lingual cusps, and a posterior group of longer, more complex teeth that are involved in shearing against the lower premolars. P1–P3 are in the first

group, except in *Kielanodon*, where P3 is elongated like P4. P4 is in the posterior group with P5, except in *Meketichoffatia* and one species of *Kuehneodon* (*K. dryas*), where P4 is short like P3 (Hahn 1977). In teeth of the posterior group there is a middle row of four cusps, and usually a lingual row of reduced cusps that may be represented only by a shelf, in most cases worn off against p4. BMNH M46640 does not fall clearly into either group. Its elongated form suggests comparison with the posterior group, but it has no lingual ledge, and there is no evidence of shear (though this might be due to lack of wear). P3 of *Kielanodon hopsoni* (Hahn 1987) is an elongated tooth with four lingual cusps and two buccal cusps; possibly BMNH M46640 had a fourth lingual cusp at the anterior end that has not been preserved. In P3 of *Pseudobolodon krebsi* there is a triangle of two lingual cusps and a buccal cusp on the posterior part of the crown, and a pair of cusps anteriorly (Hahn and Hahn 1994), as in BMNH M46640, but the tooth is short. A possible dP4 of *Kuehneodon* figured by Hahn (1969: fig. 66) resembles BMNH M46640 in being elongated, wider mesially, and having a triangular arrangement of cusps on the distal half, but there is an additional distobuccal cusp. However, the large size of BMNH M46640 and its robust roots make it unlikely to be a deciduous tooth. If it is a P4 the absence of the lingual ledge might be plesiomorphic.

Family Hahnotheriidae nov.

Type genus: *Hahnotherium* gen. nov.

Diagnosis.—Second upper molar longer lingually than buccally, only slightly narrowed distally. There are five buccal cusps, separated by transverse valleys, and seven lingual cusps on a ridge. Anterobuccal ridge absent. Central valley horizontal, rather than basined, open distally, its sides ornamented by regular series of ridges arising from the cusps. There are probably three roots, due to division of the mesial root.

Second lower molar short, with three lingual cusps, the first highest; buccal row shorter than lingual row, with several small cusps on a ridge.

Genus *Hahnotherium* nov.

Type species: *Hahnotherium antiquum* sp. nov.

Derivation of name: Named in honour of Professor Gerhard Hahn, whose work laid the foundation for our knowledge of early multituberculates. Also from $\theta\epsilon\pi\tau\omicron\nu$ (Greek), wild beast. Neuter.

Diagnosis.—With the characters of the family, by monotypy.

Comment.—This genus is proposed for the two most multituberculate-like molars described by Kermack et al. (1998). They identified M46797 as a left lower molar (group ζ); it is interpreted here as a left second upper molar, and made the holotype of a new genus and species. The second specimen, M46763, also previously regarded as a left lower molar (group γ), is interpreted here as a right second lower molar, and tentatively referred to the same species. M46183, also included in group γ , has been interpreted in this paper as a posterior lower molar of *Millsodon superstes*.

Hahnotherium antiquum sp. nov.

Figs. 4C, 10, 11A, 12.

pars *Eleutherodon oxfordensis* sp. nov.; Kermack et al. 1998: 595–597, figs. 19–21 [non figs. 1–14, 15A, 16, 18, 22, 23 = *Eleutherodon oxfordensis* KA. Kermack, D.M. Kermack, Lees, and Mills; non figs. 15B, 17 = *Millsodon superstes* sp. nov.].

Holotype: BMNH M46797, a left second upper molar, from the Old Cement Works Quarry, Kirtlington, bed 3p. Described by Kermack et al. 1998: 596, figs. 19B, 21 as *Eleutherodon oxfordensis*, group ζ.

Referred specimens: (a) BMNH M46763, a right second lower molar. Figured by Kermack et al. 1998: 595, figs. 19A, 20 as *Eleutherodon oxfordensis*, group γ; (b) BDUC J 782, left upper premolar (now missing). Both are from Kirtlington, bed 3w(i).

Derivation of name: *antiquum* (Latin), ancient. This is one of the earliest multituberculates.

Distribution.—Late Bathonian of England.

Diagnosis.—As for the genus, by monotypy.

Description of upper molar (Figs. 6E, 10).—BMNH M46797 is identified as multituberculate because of its horizontal, as opposed to basined, longitudinal wear groove between buccal and lingual cusp rows. It was described by Kermack et al. (1998) as a left lower molar, but it has more resemblance to a paulchoffatiid left upper molar. The mesial end is oblique, the lingual cusp row projecting beyond the buccal row, as is usually the case in paulchoffatiid upper molars. The tooth measures 1.9 mm in length and 1.55 mm in breadth, giving a L/B index of 1.23; this is below the range of later paulchoffatiid M1 (1.36–1.82) but within the range of M2 (1.0–1.5) (data from Hahn and Hahn, 1998a). However, there is no antero-buccal ridge, and the tooth is less narrowed distally than is usual in multituberculate M2. Identification as M2 rather than M1 is supported by the absence of wear on the lingual surface of the lingual cusps, by the presence of facets on the buccal side of the buccal cusps, and by a contact facet on the mesial surface but not at the distal end.

There are five buccal cusps, but Kermack et al. (1998) suggested that there may have been only four, the mesial cusp having been cut in two post-mortem by a boring organism. There appear to be three “borings” into the buccal row; the two more distal ones are in line with grooves in the buccal slope of the central basin and they are clearly intercuspals. Careful cleaning of the region showed that there are no borings: the cusps are separated by steep-sided grooves in which the enamel is intact. The grooves are bordered by crests emanating from the mesial and distal sides of the adjacent cusps. Buccally they are terminated by meeting of the mesial and distal crests to form a rim; lingually they extend more shallowly into the central basin where bifurcating crests trend mesiolingually and distolingually from the cusps. The buccal cusps are not connected by a longitudinal crest as in *Kermackodon*. The two most mesial buccal cusps (B1, B2) are higher than the rest; B3, the smallest, is displaced lingually; B5 is distolingual to B4, on the distal margin of the tooth. In Paulchoffatiidae the buccal cusps distal to B2 are reduced or absent, except in *Meketichoffatia*. The antero-buccal ridge is

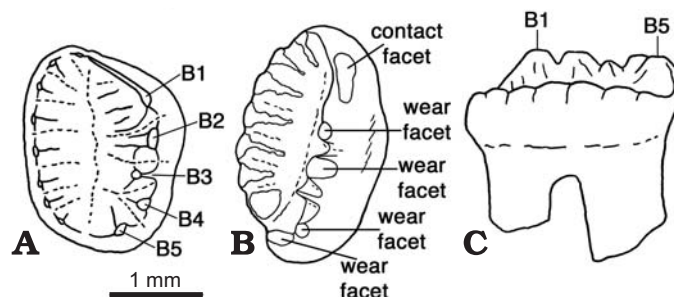


Fig. 10. *Hahnotherium antiquum* gen. et sp. nov., BMNH M46797, left M2 (holotype). A. Occlusal view, mesial end upwards. B. Oblique mesio-buccal view; to show buccally facing facets on buccal cusps; and contact facet at mesial end. C. Lingual view, crown upwards.

absent, unless it is represented by a swelling at cingulum level below B1–B2.

The seven lingual cusps have the appearance of low elevations on a ridge, but their tips have been removed by wear. They form a graded series that diminishes mesially and distally from a maximum at L3–L5. Adjacent cusps are separated by shallow grooves, crossed by a fragment of the longitudinal crest. Each cusp gives rise to a ridge on the lingual slope of the central valley. There are no ridges on the lingual surface of the lingual cusps. L1 is connected to B1 by a ridge that follows the mesial margin of the tooth; it shows two low elevations. The central valley is open distally between B5 and L7. Its sides are richly ornamented with enamel ridges from the cusps, similar to the fluting of *Eleutherodon*.

Wear is evident on both sides of the central valley, due to the lingual cusps of m2. The lingual surface of the lingual cusps is unworn. The buccal cusps, except B3, are worn at the tip and high on their buccal sides, due to wear in the valley of m2 (Fig. 10B). This pattern of wear shows that the tooth was displaced lingually in relation to m2 as in other multituberculates.

The tooth probably had three roots, though only two (mesiolingual and distal) are preserved; a large area of the tooth base having broken off on the buccal side. The probable presence of a third root suggests comparison with the very worn tooth from Watton Cliff described by Freeman (1976). This is not very different in size and proportions (2.0 × 1.5 mm; L/B 1.33). It has two roots at one end, which is presumably mesial.

Comparison.—*Eleutherodon* upper molars resemble *Hahnotherium* in the fluting of the central valley, but differ in many other respects, for example the third row of cusps, basining of the central valley, and the large distal cusp. *Kermackodon* agrees with *Hahnotherium* in lacking the antero-buccal ridge and in having 5 buccal and 7 lingual cusps, but there are many differences: the largest buccal cusps are distal in *Kermackodon*, mesial in *Hahnotherium*; in *Kermackodon* the tooth is narrowed distally, and the central valley is blocked by the distal lingual cusp; the cusps are sharper, with stronger ridges; the buccal cusps are connected by a longitudinal crest; ornamentation of the central valley is very different.

In Paulchoffatiidae B1 and B2 are enlarged, and the more distal buccal cusps are reduced or lost; the number of lingual cusps is also reduced, most frequently to 4 or 5. The tooth is narrow distally, and the central valley is usually closed by the last lingual cusp. In other “Plagiaulacida” the central valley is open distally as in *Hahnotherium*, but buccal cusps distal to B2 are absent and there are only three lingual cusps. The lingual cusps of *Hahnotherium*, which are low elevations on a ridge, differ from those of other multituberculates, which are broader, rounded, and separated by transverse grooves. Though folding of the enamel in the central valley is usual, it does not have the regular pattern shown by *Hahnotherium*. Absence of the anterobuccal ridge is a character shared only with paulchoffatiid species A and with *Ctenacodon*, among “plagiaulacidans”.

These differences exclude *Hahnotherium* from existing families of the “Plagiaulacida”, and a new family Hahnotheriidae is proposed for it.

Description of referred lower molar (Figs. 6F, 11A).—BMNH M46763 was interpreted by Kermack et al. (1998) as a left lower molar (group γ) of *Eleutherodon*, but it has more resemblance to a multituberculate right second lower molar. There is a row of three discrete cusps, which must be lingual, and a buccal row in which the cusps are minor elevations on a ridge. The tooth is equal in length and width (1.6 × 1.6 mm), and thus proportionately shorter than the holotype upper molar. It is moderately worn, and a small area at the distal end is broken. The buccal margin is convex and somewhat shorter than the lingual margin. The lingual cusp row occupies two thirds of the width of the tooth. The lingual cusps are blunt and pyramidal, and separated by deep transverse grooves. They diminish in size from L1 to L3. Their lingual surfaces are worn flat, presumably against the lingual cusps of M2. Ridges on their buccal surface have been largely removed by wear against the buccal cusps of M2. A stronger buccal ridge on L1 runs in an obliquely distal direction across the central valley towards B3. Wear on the main buccal ridge increases towards the distal end. Four buccal cusps are visible on its mesial half; more distal cusps have probably been removed by wear. Each cusp gives rise to a ridge on the buccal side of the central valley, producing a similar ornamentation to that on the lingual side of the valley of the holotype.

Comparison (Fig. 11).—With a length/breadth ratio of 1.0, this tooth agrees with m2 of *Parachoffatia staphylos* (Hahn and Hahn 1998a), but it is proportionately shorter than m2 of other multituberculates. It is also distinctive in the proportionately short and narrow buccal cusp row, which is longer than the lingual row in other multituberculates.

In Paulchoffatiidae there is a large lingual cusp, labelled L2 or L1+2 by Hahn and Hahn (1998a) because a more mesial cusp occurs in *Kuehneodon* and *Guimarotodon*. Except in *Paulchoffatia*, a ridge arising from L2 crosses the central valley. This ridge might be compared with the more oblique ridge that arises from L1 in BMNH M46763, in which case L1 of *Hahnotherium* might be homologous with

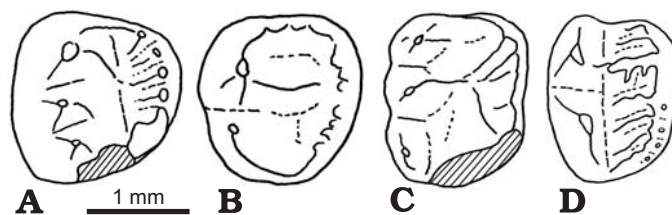


Fig. 11. Right second lower molars. A. BMNH M46763, referred to *Hahnotherium antiquum* gen. et sp. nov. B. *Kuehneodon* sp. (based on Hahn 1969: fig. 36). C. *Pinheirodon vastus* (based on Hahn and Hahn 1999: fig. 4b). D. *Bolodon osborni* (based on Kielan-Jaworowska and Ensom 1992: pl. 3: 5). Mesial end upwards.

L2 of paulchoffatiids. Distal to L2 there are two small cusps in *Paulchoffatia*, one in *Meketibolodon* and *Kuehneodon*. In Pinheirodontidae (Hahn and Hahn 1999) there are three lingual cusps that diminish in size from L1 to L3. A ridge from L2 crosses the valley, but it is inclined mesially, instead of being transverse as in Paulchoffatiidae or inclined distally as in BMNH M46763. In *Ctenacodon* and *Glirodon* there are three lingual cusps of equal size. *Bolodon* and *Eobaatar* have two equal lingual cusps, which is the usual condition of later multituberculates.

In Paulchoffatiidae and Pinheirodontidae the buccal row is reduced to a ridge, on which numerous minute cusps can be seen on unworn teeth (e.g., *Parachoffatia*, Hahn and Hahn 1998a: fig. 41). The valley is ornamented by numerous ridges that arise from the cusps. In *Bolodon* and *Eobaatar* the buccal row again forms a ridge, from which cusps are rapidly removed by wear. To judge by the number of transverse ridges on the buccal side of the valley, the number of buccal cusps was probably more than three, perhaps six or more. In *Ctenacodon* and *Glirodon* the buccal cusps are reduced to three; they are more distinct, but still united by a longitudinal ridge, whereas the lingual cusps are separated by deep grooves.

Wear on the lingual surface shows that the lingual shift in occlusal relations between the last molars had taken place. BMNH M46763 resembles BMNH M46797 in width, cusp form and enamel ornamentation, and it is possible that they represent m2 and M2 of the same species. However, BMNH M46763 is much shorter mesiodistally, whereas in those later multituberculates in which upper and lower molars of the same species are known m2 is somewhat longer than M2. Reference of BMNH M46763 to *Hahnotherium antiquum* must be considered provisional.

Note on Hahnodontidae.—*Hahnodon taqueti* is known by a single tooth from the Early Cretaceous of Morocco, interpreted as m2 by Sigogneau-Russell (1991) because of resemblances to the basined m2 of paulchoffatiids. It has three cusps: a mesial cusp on one side of the central valley, and two cusps on the other side, of which the distal one is the larger. Sigogneau-Russell was uncertain of the orientation: she hesitantly interpreted the single cusp as buccal, and the tooth as from the left side. However, this makes the buccal cusp higher than the lingual cusps, a character otherwise unknown in multituberculate m2. Alternatively, if the tooth is from the

right side, the single cusp, from which a ridge obliquely crosses the valley, might be compared with the large lingual cusp (L2) of paulchoffatiids and L1 of *Hahnotherium*.

Hahn and Hahn (2003) have described as *Denisodon moroccensis* another molar from the same locality. They followed Sigogneau-Russell's (1991) orientation, regarding the highest cusp as mesiobuccal (b1). This tooth differs from *Hahnodon* in that the mesial lingual cusp (l1) is larger and joined at the base to b1. The distal lingual cusp (which they call l3) is smaller, and there is a small distal buccal cusp (b2). l3, b2 and a small distal elevation stand at the edge of the basin that occupies the distal part of the crown. It seems not impossible that *Denisodon* is the first molar of *Hahnodon*. Neither tooth shows evidence of horizontal chewing, but wear occurs on the inclined surfaces of cusps around the basin, implying a large orthal component of chewing. The action seems to have been one of pestle-and-mortar crushing rather than of the horizontal grinding that is characteristic of multituberculates. Moreover, there is no evidence of wear on the lateral surface that would indicate a lingual shift in the relative position of M2. These characters in our view remove the Hahnodontidae from the order Multituberculata, and we classify them in the paraphyletic order "Haramiyida" *sensu* Butler (2000).

Description of referred left upper premolar (Figs. 4C, 12).—This specimen is now missing. The following description is based on scanning electron micrographs and drawings.

BDUC J 782 is the crown of a tooth, lacking roots, and with the pulp cavity exposed in basal view. It measures (from the scaled photograph) 1.8 mm long and 1.2 mm wide. The mesial margin and most of the lingual margin have broken off, but the tooth was probably wider mesially than distally. The buccal margin is convex, and the distal end is oblique and most prominent lingually. The tooth resembles P4 and P5 of paulchoffatiids. A longitudinal groove separates a lingual row of four cusps from a middle row, also of four cusps,

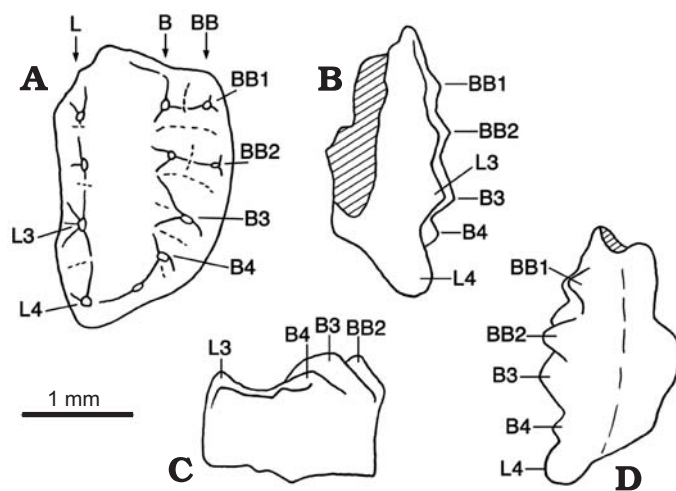


Fig. 12. BDUC J 782, left upper premolar, referred to *Hahnotherium antiquum* gen. et sp. nov. in occlusal (A), lingual (B), distal (C), and buccal (D) views. The three rows of cusps are labelled L, B, BB. Crown upwards in C, mesial end upwards in the rest.

and there are two additional cusps on the mesial part of the buccal margin. Wear is light except at the mesial end of the lingual row. The cusps are low, but pointed at the tips, with apical angles of about 100°.

The lingual cusps increase in height from L1 to L3; L1 has been almost removed by wear, but L3 has lost only the extreme tip. L4, of similar height to L3, stands on the distolingual prominence of the outline. It is connected to L3 by a low longitudinal crest. The central valley is flat longitudinally and shallowly concave transversely. Its buccal margin is formed by the middle (B) row of cusps, of which the highest is B3. A mesiolingual ridge on B3 joins a distolingual ridge on B2, and a distolingual ridge on B3 joins a mesiolingual ridge on B4. A small elevation on the distal margin partly closes the central valley. The cusps of the third row (BB1, BB2) are joined by rounded ridges with B1 and B2 respectively; BB2 is equal to B2 in height and BB1 is lower. A transverse valley separates B1+BB1 from B2+BB2, and similar valleys demarcate B2+BB2 from B3, and B3 from B4.

Comparison.—Typically in multituberculates the posterior premolars (P4, P5) differ from M1 in the reduction or eventual loss of the lingual row, and the development of additional (BB) cusps on the buccal side. As a result the original buccal row is displaced lingually to a median, or in advanced forms a lingual position. *Kuehneodon* is exceptional in that the lingual cusps are large and the buccal cusps stand on the buccal half of the crown. BDUC J 782 agrees with *Kuehneodon* in this respect, but it possesses two BB cusps on the mesial part of the buccal margin. These two cusps are a widespread feature of "plagiaulacidan" upper premolars, and their absence in *Kuehneodon* may be secondary.

The low crown of BDUC J 782, its pointed cusps, and the rounded, rather than furrowed valleys, may be primitive features resulting from a smaller thickness of enamel. Alternatively, the absence of roots may indicate that it is a milk tooth that has been shed. BDUC J 782 is comparable in size to *Hahnotherium antiquum*, and it might belong to that species. It cannot occlude with the lower premolar referred to *Kermackodon*. Also, it is unlikely to be adjacent to the upper premolar BMNH M46640, which completely lacks the lingual cusp row.

Allotheria incertae sedis

Material.—Upper second incisors. BMNH M46234, left I2 from the Kirtlington Mammal Bed; BMNH M46056, left I2, worn, from Watton Cliff. Both are of late Bathonian age.

Description (Figs. 6D, 13).—BMNH M46234 is a single-rooted tooth with a procumbent main mesial cusp and two lower distal cusps. It resembles I2 of "plagiaulacidan" multituberculates and incisors referred to *Thomasia* by Sigogneau-Russell (1989). The main cusp is tilted forward in relation to the root. Its tip, which is unworn, is backwardly curved, with distobuccal and mesiolingual ridges. The buccal surface is convex, the lingual surface flatter with a weak median ridge. The conical distobuccal cusp is about half as high as the main

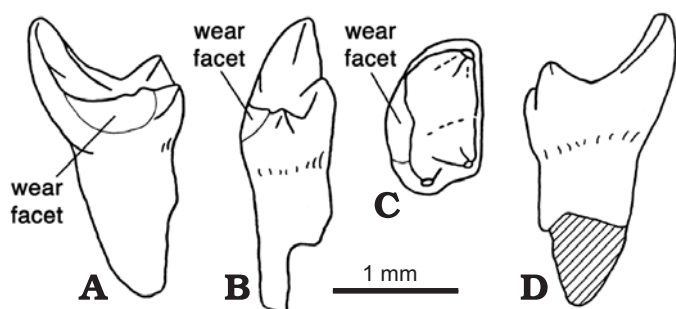


Fig. 13. *Allotheria incertae sedis*, BMNH M46234, left I2 in lingual (A), distal (B), occlusal (C), and buccal (D) views. Mesial end upwards in C, crown upwards in the rest.

cusps, from which it is separated by a V-shaped valley. The distolingual cusp, which is also conical, is lower than the distobuccal cusp and placed somewhat more distally. The two distal cusps are separated by a valley, and a number of enamel ridges run down their slopes. The mesiolingual ridge curves distally towards the base, where it has been removed by wear. The wear facet extends along the lingual margin of the tooth as far as the base of the distolingual cusp. It faces lingually (i.e. medially), indicating that the lower incisor closed medially to the upper.

The tooth measures 1.1 mm in length (perpendicularly to the root) and 0.65 mm in width; the height of the main cusp, from the buccal enamel border is 1.2 mm. Only the basal part of the root is preserved. This measures 0.75 mm mesiodistally and 0.6 mm buccolingually.

BMNH M46056 is probably a second example of the same tooth. It is somewhat larger: length 1.3 mm, width 0.7 mm, height of cusp 1.4 mm. It is heavily worn, especially from the lingual side where the distolingual crest has disappeared, but the remains of the two distal cusps can be recognised.

Comparison.—In Paulchoffatiidae (Hahn 1969) the main cusp is stouter and more prismatic, with a stronger median lingual ridge. Some specimens have two or more distal cusps, but these are smaller in proportion to the main cusp than on the Kirtlington tooth. Wear involves first the tip of the main cusp and spreads down its lingual surface, whereas the Kirtlington tooth wears at the lingual margin. A strong median lingual ridge is present again in the eobaatarid *Loxaulax* (Clemens and Lees 1971; Butler and Ford 1977), and in the allodontid *Psalodon*. These have a single distal cusp, proportionately smaller than the distobuccal cusp of BMNH M46234.

Upper incisors referred to *Thomasia* (Sigogneau-Russell 1989) agree with the Kirtlington tooth in the weak development of the median lingual ridge. Some specimens have two distal cusps, though they are proportionately smaller than in BMNH M46234. Wear appears to be from the lingual side: a specimen (SNP 363) shows a large facet involving the base of the mesiolingual ridge and extending to the distolingual cusp, as in BMNH M46234.

In Paulchoffatiidae I2 is large, comparable in length with the molars: the length ratio I2/ M1 in *Kuehneodon simpsoni*

is 0.95, in *K. dryas* 0.97, and in *Henkelodon naias* 1.03 (Hahn 1969, 1977). Based on teeth from different individuals, I2/ M2 is about 0.85 in the plagiaulacid *Bolodon osborni* (Kielan-Jaworowska and Ensom 1992) and in *Loxaulax valdensis* (Clemens and Lees 1971). BMNH M46234 is smaller in proportion to upper molars from Kirtlington: the ratio of lengths is in *Eleutherodon* (mean) 0.45, in *Kirtlingtonia* 0.50, in *Kermackodon* 0.39, and in *Hahnotherium* 0.54. The ratios for the larger incisor BMNH M46056 range from 0.45 to 0.63. Thus the Bathonian incisors are proportionately smaller than in later multituberculates. In *Thomasia* from Saint-Nicolas-de-Port, Butler and MacIntyre (1994) estimated that the ratio I2/ M was about 0.6. The Bathonian incisors may therefore be “haramiyidan”. Possibly they belong to *Eleutherodon oxfordensis*, which is the species most frequently represented by molars.

Discussion

The origin of Multituberculata is a major unsolved problem of Mesozoic mammalian phylogeny (for detailed discussion see Luo et al. 2002, Kielan-Jaworowska et al. 2004, and references therein). Very pertinent is the question of the relation of multituberculates to the haramiyids, with which they share the character of allotherian molar teeth (Butler 2000). These have longitudinal rows of cusps, which functioned in grooves between opposing cusp-rows, with a backwardly directed power stroke. Other mammals had a transverse power stroke, and chewing was unilateral, interdigitating cusps having individual relations. The allotherian teeth from the Bathonian are of interest in that they are intermediate in age between the haramiyids of the Rhaetian–Early Jurassic and the paulchoffatiid multituberculates of the Kimmeridgian. They include multituberculates with presumably plesiomorphous characters, together with non-multituberculates classified as “Haramiyida” (*sensu* Butler 2000).

As all the teeth are isolated, problems of orientation (buccal-lingual, mesial-distal) have arisen, and the association of the teeth into dentitions must necessarily be a matter of judgement. Five species are distinguished, based on molars. In addition to *Eleutherodon oxfordensis*, described by Kermack et al. (1998), we recognise two species of “haramiyidans”, *Millsodon superstes*, and *Kirtlingtonia catenata*, and two multituberculates, *Kermackodon multicuspis* and *Hahnotherium antiquum*. The molar BDUC J 562 may represent another “haramiyidan”. *Eleutherodon oxfordensis* is represented by several upper molars and four lower molars; and it is possible that the specimens of I2, classified as *Allotheria incertae sedis*, belong here. The other species are represented by only two or three specimens. *Millsodon superstes* is known only by worn first and third lower molariforms and a referred upper molar. *Kirtlingtonia catenata* is represented by two last upper molars and an upper premolar. *Kermackodon multicuspis*, interpreted as an aberrant multituberculata, is known by M2 and referred up-

per and lower premolars. A second multituberculate, *Hahnotherium antiquum*, is represented by M2 and referred m2 and posterior upper premolar.

Eleutherodon resembles *Thomasia* in the presence of basined wear-grooves on the molars. An enlarged mesial buccal cusp on the lower molar travelled distally along the upper molar basin, while an enlarged distal cusp on the upper molar travelled mesially along the lower molar basin. Basing of the wear grooves shows that some orthal (vertical) movement was involved; in multituberculates the wear is horizontal.

Eleutherodon differs from *Thomasia* and primitive multituberculates in the presence on upper molars of a third (lingual) row and a second wear groove, which occluded with the lingual cusp row of the lower molar. It is also specialised in the presence of numerous small cusps, and in the complex root pattern of upper molars. Variation in proportions suggests that there may be two molars, as in multituberculates and also as postulated in *Thomasia* (*Haramiya I* and *I bis* of Sigogneau-Russell, 1989), but the difference in occlusal relations between M1 and M2 of multituberculates did not occur. The multicusp I2, which might belong to *Eleutherodon*, resembles *Thomasia* as well as “plagiaulacidans”, but it bites laterally to the lower incisor as in *Thomasia*. *Eleutherodon* appears to be a specialised haramiyid derivative, but there is no evidence for a special relationship to the multituberculates.

Millsodon differs from other “haramiyidans” in the enlargement of the mesiolingual cusp (a1 of Butler 2000) on the lower molariforms. The mesio-buccal cusp is absent on m1 as in Haramiyidae, but it has been lost on m3, and also probably on m2, which is unknown. If the upper molar BDUC J 3 is correctly referred, the occlusion involved a crushing action produced by the upward and backward movement of the lower teeth, rather than the grinding action postulated for *Thomasia* and *Eleutherodon*. BDUC J 3 has a third, lingual row of cusps like *Theroteinus*, and a relationship with the Theroteinidae seems possible.

Kirtlingtonia is known only by the last upper molar (M2?) and an upper premolar. The molar shows some resemblance to *Eleutherodon*, but it differs in the shallowness of the basin, which lacks the transverse fluting. It also lacks the lingual groove and lingual cusp row, the corresponding part of the tooth being occupied by numerous irregular cuspules. A resemblance to M2 of paulchoffatiids was noted, if the antero-buccal ridge is homologised with the buccal row of *Kirtlingtonia*, but evidence for occlusion is lacking. The premolar has a high mesial cusp, absent in multituberculates.

Kermackodon and *Hahnotherium* are recognised as multituberculates by the horizontal wear groove on the molars, which is basined in “Haramiyida”. Both are known by second upper molars, but the differences between these are great enough to justify separation at the family level: the new families Kermackodontidae and Hahnotheriidae are proposed. An m2 and a P5? are referred to *Hahnotherium*, and a p4 and a P3/4, of larger size, to *Kermackodon*.

On M2 of *Hahnotherium* the wear groove reaches the distal margin of the crown, but in *Kermackodon* it is blocked distally by the distal lingual cusp, as in most paulchoffatiids. Both have five buccal cusps, but these are differently organised in the two genera. In *Kermackodon* the largest buccal cusps are distal (B4, B5), but in *Hahnotherium* they are mesial (B1, B2) as in paulchoffatiids. There are seven lingual cusps in both genera; in *Kermackodon* they diminish in size mesially, as in paulchoffatiids, but in *Hahnotherium* they are largest in the middle of the series.

The cusps of *Kermackodon* are sharp, with strong ridges, and they are joined by longitudinal crests. In *Hahnotherium* the cusps are blunt, and the buccal row has no longitudinal crest, but the cusps are separated by transverse valleys that resemble the sulci of later multituberculates.

A diagnostic character of Multituberculata is the difference in molar occlusion between the first and the second molars. M2 is displaced lingually with respect to M1 so that, whereas the central groove of M1 is worn by the buccal cusp row of m1, the central groove of M2 is worn by the lingual cusp row of m2. The lingual row of M2 wears on its buccal surface against the lingual row of m2, but its lingual surface has no occlusal contact. Absence of wear on the lingual side of the tooth identifies the holotypes of *Kermackodon* and *Hahnotherium* as second molars. Small facets on the buccal side of the *Hahnotherium* molar would be produced by contact with the buccal row of m2. Corresponding facets were not seen in *Kermackodon*, perhaps due to light wear, or to reduction of the buccal cusps of m2.

The antero-buccal ridge of later multituberculates (Hahn and Hahn 1998a) functions as a distal continuation of the wear groove of M1, and it wears against the buccal row of m1 at the end of the stroke. According to Hahn (1969: fig. 81) the crest originated as a mesio-buccal ridge on cusp B1, connecting that cusp to the mesial marginal ridge (crista anterior of Hahn and Hahn 1998a). Absence of the antero-buccal ridge in some paulchoffatiids and probably in *Ctenacodon* would be plesiomorphic. On the other hand, comparison with *Kirtlingtonia* (Fig. 5D, E) suggests that the antero-buccal ridge may be the remnant of a buccal cusp row, lost when M2 shifted lingually in relation to m2. In that case its absence would be derived. That a definitive antero-buccal ridge is not developed in *Kermackodon* and *Hahnotherium* might support Hahn's theory, but the problem remains of how the shift of M2 took place.

The lower molar referred to *Hahnotherium* is identified as m2 by its occlusal relations, shown by wear on both sides of the lingual cusp row. The pattern of three separated lingual cusps and a buccal row with numerous minor cusps on a ridge could be ancestral to those of later multituberculates. The Hahnodontidae however are exceptional; because of their basined wear they should be removed from the Multituberculata to the “Haramiyida”.

The lower premolar, referred to *Kermackodon*, shares with other multituberculates the reduction of the lingual cusps to serrations on a blade, with oblique ridges descend-

ing from the first two serrations, and a series of minor buccal cusps near the distal end. It differs from p4 of paulchoffatiids, and may be primitive, in the triangular shape of the blade, its distal continuity with the buccal cusp row, and the absence of a mesial groove for contact with p3. The lower premolars were not integrated into a functional unit as in other multituberculates. The only wear on the specimen indicates a semi-orthal jaw movement, difficult to reconcile with the horizontal movement inferred from the wear of M2.

The incomplete upper premolar referred to *Kermackodon* is recognised as multituberculate by the conical cusps with radiating ridges on their slopes. It is possibly a penultimate premolar (P4), but it completely lacks the lingual shelf or reduced lingual cusps that are normally present on P4–P5. The P5 or P4 referred to *Hahnotherium* has three rows of cusps, with a formula 4:4:2, probably plesiomorphic for multituberculates.

The Hahnotheriidae seem to be more closely related to later multituberculates than the Kermackodontidae, but both families possess some autapomorphic dental characters that separate them from other allotherians. The origin of the order must be sought further back, perhaps in the Early Jurassic, or even earlier. The Bathonian specimens do not provide evidence of triconodont or morganucodont relationships, but the shared allotherian tooth pattern, with longitudinal rows of cusps and evidence of palinal chewing, supports “haramiyidan” affinity. The narrow, two-rooted p4 of *Kermackodon* has a superficial resemblance to morganucodont molars, but the minor cusps develop from the buccal side of the principal cusp-row, instead of from a lingual cingulum as in morganucodonts. On lower premolars of *Haramiyavia* the single row of cusps resembles the lingual row of the molars (Jenkins et al. 1997: fig. 1), and on supposed lower premolars of *Thomasia* the buccal cusps are reduced (Sigogneau-Russell 1989: figs. 20, 21). *Hallautherium* (Clemens 1980), which has a buccal cingulum, may be a haramiyid relative.

Mojo, known only by an incomplete and worn tooth from the Rhaetic of Belgium, was interpreted as a multituberculate because of a resemblance to upper premolars of paulchoffatiids (Hahn et al. 1987). These teeth wear on the top, not by occlusion but probably against large food objects held between the upper and lower premolars. It seems unlikely that such a specialised function had developed as early as the Rhaetic. Moreover, the *Mojo* tooth has two areas of wear: a large distal, somewhat concave area is separated by a ridge from a smaller mesial area that slopes mesially. This implies contact with two opposing teeth, as would occur on a molar. Hahn et al. (1987) noted a resemblance to a lower molar of *Thomasia antiqua*, and Hahn et al. (1989) compared *Mojo* with the upper molar of *Theroteinus*. Worn examples of these have a similar arrangement of two areas of wear, which occurs also in *Thomasia moorei* (Butler and MacIntyre 1994: fig. 3, H6). If the *Mojo* tooth is a molar, the lack of longitudinal wear striations would exclude it from the Multituberculata. Butler (2000) classified it as *Haramiyida incertae sedis*.

Implications for basal mammalian phylogeny

Multituberculates are unique among Mesozoic mammals in many characters, not only in the dentition but also in the skull and postcranial skeleton (Gambaryan and Kielan-Jaworowska 1995, 1997; see also Kielan-Jaworowska et al. 2004 for review). Simpson (1945: 168) stated: “The multituberculate structure was so radically distinctive throughout their history that it seems hardly possible that they are related to other mammals except by a common origin at, or even before, the appearance of the class as such, a conclusion that necessitates placing them in a separate subclass as well as order”. Many subsequent authors have postulated a later separation, noting that multituberculates share various derived non-dental characters with more advanced mammals, particularly eutriconodontans, monotremes and primitive trechnotherians such as *Zhangheotherium*. Luo et al. (2002), in a critical review, say (p. 32): “Each of the hypotheses for multituberculate relationships requires an enormous number of convergences among well-established characters or character complexes”. Their most parsimonious cladogram puts the multituberculates in the Mammalia crown-group, as the sister-group to *Zhangheotherium*, but the “Haramiyida”, represented by *Haramiyavia*, are excluded from the mammals as the sister-group of Tritylodontida. However, an alternative tree (Luo et al. 2002, modified by Kielan-Jaworowska et al. 2004: fig. 15.2), in which *Haramiyavia* and the multituberculates are sister-groups, is not significantly longer, by a non-parametric test. Even this solution, however, places allotherians crownward of morganucodontans, *Kuehneotherium*, docodontans and *Hadrocodium*.

If multituberculates are related to “haramiyidans” their lineage, independent from other mammals, would go very far back, as “haramiyidans” coexisted with morganucodontans in the Rhaetic and there is a “haramiyidan” tooth from the Norian (Hahn 1973). This would support the views of Simpson (1945), McKenna (1987), Miao (1993) and Butler (2000) that the multituberculates are the sister-group of all other mammals. *Thomasia*, for long an isolated and problematic genus, has now been associated with *Haramiyavia* and *Theroteinus* from the Late Triassic (Butler 2000) and three genera from the Middle Jurassic, described in this paper, and the “Haramiyida” survived in Africa with *Staffia* in the Late Jurassic and (if our interpretation is correct) Hahnodontidae in the Early Cretaceous. Unfortunately, with the exception of *Haramiyavia*, of which the dentary and part of the maxilla have been described, the “Haramiyida” are known only by isolated teeth. The dentary of *Haramiyavia* has primitive characters shared with morganucodontans, notably the trough for accommodation of postdentary bones (Jenkins et al. 1997), and it shows none of the special features of multituberculates, which must be presumed to have evolved during the long interval between the Late Triassic and the Late Jurassic.

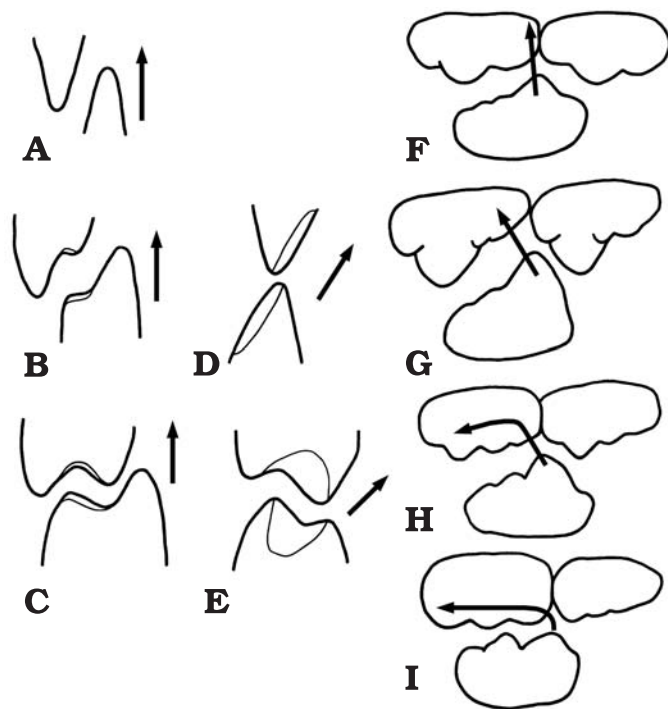


Fig. 14. Diagrams to illustrate postulated evolution of occlusion. A–E. Divergence between Allotheria and Mammaliaformes. The teeth are seen mesiodistally, buccal to the left. Arrows indicate direction of the power stroke. A. Plesiomorphic condition, e.g., *Sinoconodon*, with no occlusal contact. B, C. Opposition develops by formation of supplementary cusps in Allotheria; B is a hypothetical transitional stage. D. Unilateral transverse shearing in morganucodonts. E. Rearrangement (triangulation) of cusps, as in symmetrodonts, resulting in mesially and distally facing wear facets. F–I. Allotherians illustrating stages in the evolution of palinal occlusion. Teeth seen in side view, distal to the left. F. Vertical crushing in *Theroteinus*. G. Distally oblique crushing in *Millsodon*. H. Basin grinding with palinal movement in *Thomasia*. I. Horizontal palinal grinding in multituberculates.

A major obstacle to the derivation of the Multituberculata within the mammalian crown group is the dentition. Apart from multituberculates, crown-group mammals (eutricodontans, “symmetrodontans”, australosphenidans) have dentitions which operate by a unilateral transverse shearing action, in which individual cusps occlude in definite ways; it is very difficult to imagine how such a dentition could have given rise to the multituberculate type, with a bilateral longitudinal grinding action involving rows of cusps. On the other hand, a series of allotherians, *Theroteinus*–*Millsodon*–*Thomasia*–multituberculate, illustrates how palinal grinding could have evolved from orthal crushing (Fig. 14). The common ancestor of *Theroteinus* and the Morganucodontidae could be envisaged as having an orthal chewing movement with little occlusal contact, as in *Sinoconodon* (Crompton and Sun 1985: 112). In *Theroteinus* the orthal chewing was retained, and an additional series of cusps developed, lingually on upper teeth, buccally on lower teeth, resulting in a crushing occlusion. In Morganucodontidae lateral movement and rotation of the jaw resulted in shearing between the lingual surface of upper teeth

and the buccal surface of lower teeth on one side of the mouth. The difference might be adaptive to diet, more granivorous in the case of *Theroteinus*, more insectivorous in Morganucodontidae, and perhaps foreshadowing the difference between the supposedly plant-eating multituberculates and the other, mostly insectivorous mammals later in the Mesozoic. This would imply an early separation of the mammals into two clades, Allotheria and Mammaliaformes, which evolved in parallel. However, by the Late Jurassic onwards the multituberculates had advanced beyond the morganucodontan level in numerous skeletal characters that they shared with mammals of the crown group. Although it might seem improbable that so many resemblances could be due to convergent evolution, many multituberculate skeletal elements are highly distinctive and recognizable as belonging to the order even when found isolated. It remains to be seen whether this distinctiveness is purely autapomorphic or is evidence of such convergence. As long as we only have teeth of the critical taxa, we feel it necessary to adopt the Allotheria concept as a working hypothesis; no doubt the discovery of mammalian skeletal material in the Jurassic will throw new light on the problem. Whatever the final outcome, the teeth described herein give the first glimpse of an unexpected diversity of allotherians in the Middle Jurassic.

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