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## New allotherian specimens from the Middle Jurassic Woodeaton Quarry (Oxfordshire) and implications for haramiyidan diversity and phylogeny

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We report new allotherian tooth specimens from the Middle Jurassic White Limestone Formation at Woodeaton Quarry (Oxfordshire), United Kingdom. Two teeth are assigned to *Kermackodon* (= *Eleutherodon*) *oxfordensis*, a taxon whose original generic name (*Eleutherodon*) was preoccupied and is here assigned to *Kermackodon* to form a new binomial combination for the species name. *Butlerodon quadratus* gen. et sp. nov. (family Kermackodontidae), based on 13 cheek teeth and incisors, shows dental features intermediate between *K. oxfordensis* and the Late Triassic “haramiyidans” (*Haramiyavia* and *Thomasia*). *Woodeatonia parva* gen. et sp. nov. (family indeterminate), based on three teeth, is characterized by its small size. A second upper molar from a multituberculate is identified as *Hahnotherium* cf. *H. antiquum*, which possesses characters typical for multituberculates but distinctive from “haramiyidans”. The allotherian teeth from the Forest Marble Formation, previously assigned to the haramiyidans “*Eleutherodon*”, “*Millsodon*” and “*Kirtlingtonia*”, and the multituberculate *Kermackodon*, are reinterpreted as teeth from different upper or lower dental loci of the same haramiyidan species *K. oxfordensis*, which result in significant taxonomical modification of these allotherians (“haramiyidans” and multituberculates). Given that *Kermackodon* has been regarded as a transitional form between multituberculates and “haramiyidans”, these taxonomical modifications would affect interpretation of early evolution of allotherians. In a comparison of molars in known “haramiyidans”, we delve into their occlusal patterns and cusp homologies that have been controversial but pivotal for understanding evolution of allotherians. We further conduct the first phylogenetic analysis of haramiyidan species. The European Late Triassic species form the stem-ward taxa of “haramiyidans” and the Jurassic species from the United Kingdom are grouped with arboroharamiyidans from the Yanliao Biota, China, and nested in “haramiyidans”.

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**Keywords:** allotherians; haramiyidans; multituberculates; phylogeny; Middle Jurassic; Woodeaton Quarry

### Introduction

The taxon Allotheria was proposed as a mammalian order by Marsh (1880) and its content has been changing since then (Butler 2000). The most inclusive clade Allotheria supported by recent phylogenetic analyses contains Multituberculata, “Haramiyida” and Gondwanatheria (Krause *et al.* 2020), although alternative hypotheses exist (e.g. Luo *et al.* 2015). Of the three allotherian subgroups, “haramiyidans” and multituberculates are characterized by possessing a molar pattern with at least two longitudinal rows of multiple cusps. Fossils of “haramiyidans” are among the geologically oldest mammaliaforms (Clemens 1980; Sigogneau-Russell & Hahn 1994; Kielan-Jaworowska

*et al.* 2004) and documented in the earliest literature of Mesozoic mammals (Plieninger 1847; Owen 1871; Poche 1908). During the last decade there has been an impressive series of discoveries of “haramiyidans”, mainly from China, Russia and United Kingdom (see Averianov *et al.* 2019a; Mao & Meng 2019a, b and references therein), which boosted our knowledge about the morphologies of “haramiyidans”, such that we have a better understanding of differences between the molars and premolars as well as orientation and occlusal relationship of the haramiyidan teeth. In the wake of these recent discoveries there seems a resurgence of discussion on “haramiyidans” and a need to re-examine many of the European “haramiyidans” (Debuyschere 2015, 2016) given that they represent the

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earliest occurrence of the group and are critical to understanding the origin and early radiation of the group.

Here we report some new allotherian tooth specimens recovered from a terrestrial microvertebrate site at the top of the White Limestone Formation (Middle Jurassic, Bathonian) from Woodeaton Quarry (Oxfordshire), United Kingdom. The material was collected between 2013 and 2016 by a team from the Natural History Museum, London and Birkbeck College, University of London. A thorough introduction of the Woodeaton Quarry and related sites has been provided by Wills *et al.* (2019). The Woodeaton microvertebrate fauna is diverse in vertebrates and considered to be slightly older than the Forest Marble horizon that has generated most of the Middle Jurassic allotherians in the nearby Kirtlington Quarry (Freeman 1976; Kermack *et al.* 1998; Butler & Hooker 2005; Wills *et al.* 2019). The Woodeaton specimens reported here represent at least two new genera and species of Euharamiyida (Bi *et al.* 2014), one of which shows a dental morphology presumably intermediate between the Late Triassic *Thomasia* (Sigogneau-Russell 1989; Butler & MacIntyre 1994; Hahn & Hahn 2006) and the Middle Jurassic forms, such as “*Eleutherodon*” *oxfordensis* (Kermack *et al.* 1998). The new taxa add to the diversity of the Jurassic allotherians in Europe and provide new evidence about evolution of allotherians. Along with descriptions of the new specimens, we present discussions of several issues: first, in light of dentitions preserved *in situ* in the Yanliao euharamiyidans, we reconsider orientations and occlusal relationships of the teeth assigned to “*Eleutherodon*” and other taxa. Second, as noted by the late Professor P. Butler (personal communication with JJH), the generic name “*Eleutherodon*” was preoccupied and is replaced with an available existing name, *Kermackodon*. Third, we reinterpret teeth that were assigned to “*Eleutherodon*”, “*Millsodon*”, “*Kirtlingtonia*” and *Kermackodon*, respectively (Kermack *et al.* 1998; Butler & Hooker 2005) and consider them to be from different upper and lower tooth loci of the same haramiyidan species *Kermackodon oxfordensis*. Fourth, by briefly comparing the tooth morphology of the Late Triassic “haramiyidans” to those of the Jurassic ones, we discuss existing problems surrounding interpretations of tooth occlusion and homologies of tooth cusps within “haramiyidans”. Finally, we conduct the first species-level phylogeny of “haramiyidans”, constrained by the temporal and palaeogeographical distributions.

### Institutional abbreviations

**BDUC**, Biology Department, University College, London; **BMNH**, Natural History Museum, London, UK (previous

designation); **GIT**, Geologisches Institut Tübingen (now the Institut für Geowissenschaften, Eberhard Karls Universität, Tübingen); **NHMUK PV**, Natural History Museum, London, UK; **PIN**, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; **SNP**, specimens from Saint-Nicols-de Port housed in the Museum national d'Histoire naturelle, Paris.

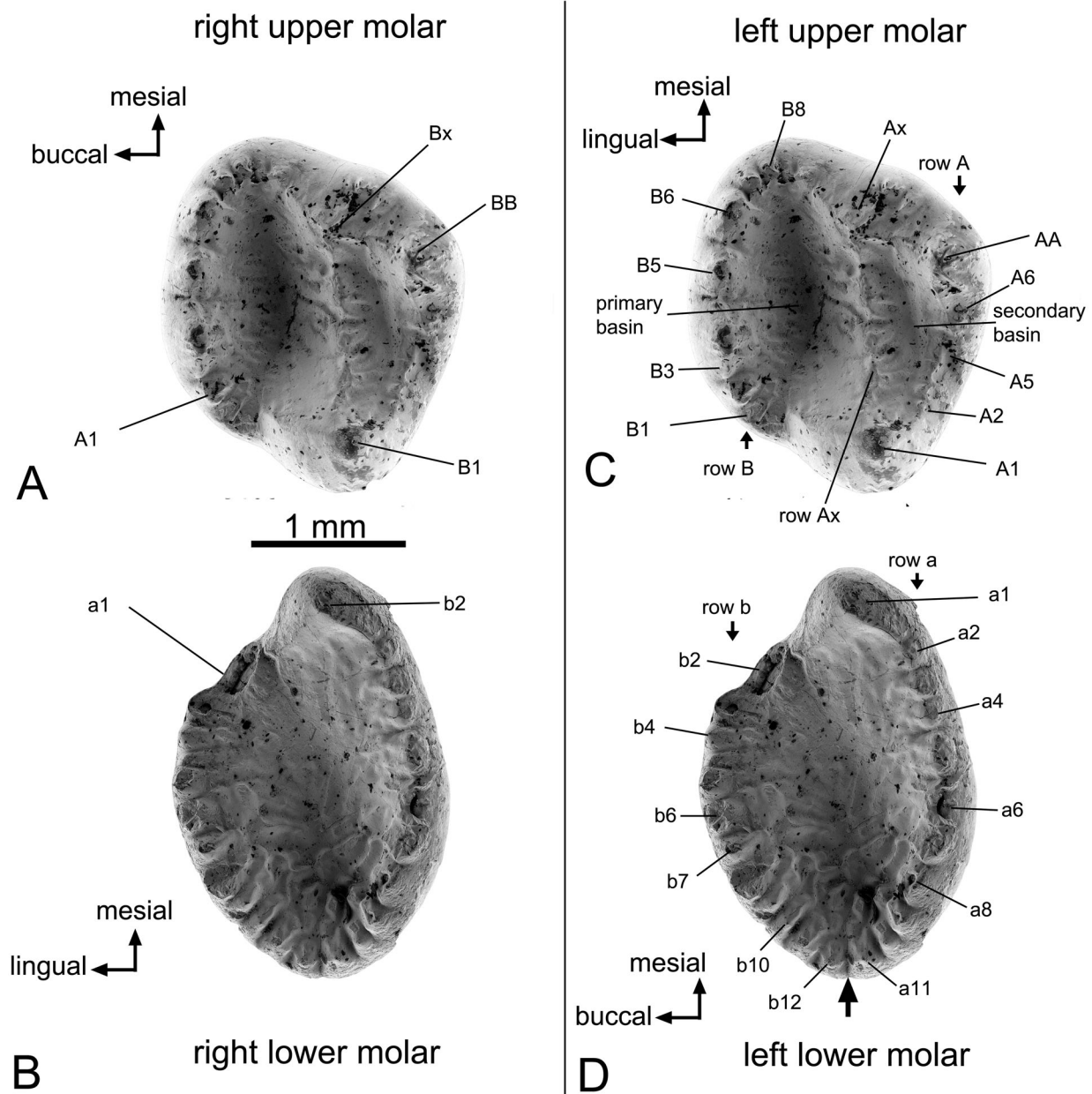
## Terminology

### Taxonomical terminology

We follow Butler & Hooker (2005) to place names of paraphyletic groups or invalid taxon names in double quotation marks, such as “haramiyidans” and “*Eleutherodon*” (this does not apply to haramiyidan used as adjective). Because “*Eleutherodon*”, “*Millsodon*”, “*Kirtlingtonia*” and *Kermackodon* are interpreted as synonyms and “*Eleutherodon*” has been preoccupied, we choose *Kermackodon* (Kermackodontidae) as the best available name to replace “*Eleutherodon*” (“Eleutherodontidae”), as we discuss below. We follow Bi *et al.* (2014) to use Euharamiyida, which is presumably a monophyletic group of Jurassic species; however, a phylogenetic reconstruction that includes key species discovered recently is needed to support this taxon.

### Tooth orientation and terminology

In the original study of *Kermackodon* (“*Eleutherodon*”) *oxfordensis*, Kermack *et al.* (1998) correctly identified the mesial-distal orientation of the molar but reversed the buccal-lingual orientation or left-right side of the molar. Butler & Hooker (2005, p. 203) pointed out: “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”. The conventional interpretation about orientation of isolated allotherian teeth was based primarily on tooth wear under the assumption that the upper molar bites laterally (buccally) to the lower molar or the buccal cusp row of the lower molar occludes with the lingual row of the upper molar in “haramiyidans” (Butler & MacIntyre 1994; Butler 2000). In light of dentitions from several euharamiyidans from the Jurassic Yanliao Biota, north-eastern China, the tooth orientation and cusp terminology have been discussed and new interpretations provided (Meng *et al.* 2014; Mao & Meng 2019b). For clarity in this study, we use Figure 1 to illustrate the differences in tooth orientation and cusp terminology used by Butler (2000) and in this study with further discussion on cusp homology provided in the Discussion.



**Figure 1.** Tooth orientation and cusp terminology of “haramiyidans”. **A, B**, conventional tooth orientation and cusp terminology of *Kermackodon* (=“*Eleutherodon*”) *oxfordensis*; **A**, upper molar (holotype, NHMUK PV M 46460) and **B**, lower molar (NHMUK PV M 46461). **C, D**, orientation and terminology used in this study (including all other figures), modified from Butler (2000) (following Meng *et al.* 2014; Luo *et al.* 2017; Mao & Meng 2019a, b).

## Material and methods

A total of 22 teeth from bed 23 (Fimbriata-Waltoni Bed), Bladon Member, the White Limestone Formation (Middle Jurassic, Bathonian) at Woodeaton Quarry (Oxfordshire), United Kingdom, are described. For comparison, we also examined and illustrated specimens of *Haramiyavia*, *Thomasia*, *Theroteinus*, *Shenshou*, *Xianshou* and *Qishou*.

SEM was performed using a FEI Quanta 450 (FEG) at Key Laboratory of Deep-Earth Dynamics of Ministry of Natural Resources, Institute of Geology, Chinese Academy of Geological Sciences and a FEI Quanta 650 at the Natural History Museum, London, with voltage of 10 kV, spot size of 3.0, beam current between 198 to 200  $\mu$ A. Both BSE and SE modes (backscattered electron and secondary electron) were applied, showing different results.



High-resolution micro-CT scanning was conducted using a GE v|tome|x s240 dual tube 240/180 kV system (General Electric, Fairfield, CT, USA) in the Microscopy and Imaging Facility of the American Museum of Natural History (AMNH) in New York. Most specimens were rescanned using the 180 kV nanofocus transmission tube, using a beam energy of 120–140 kV and 100–120  $\mu$ A with a diamond target, which allows a higher power to be run with smaller spot size. Exposure time was increased to 400–500 ms to compensate for the limited power available, dictated by spot size. In total, 1800 projections were taken for both scans. Reconstruction of the scan data was done using the Phoenix datos|x (General Electric, Wunstorf, Germany). Segmentation and rendering of the CT scanning data were processed using VGStudio Max 3.4 (Volume Graphics, Heidelberg, Germany).

A species-level phylogenetic analysis was conducted using parsimony-based methods in PAUP\* (Version 4.0a152) (Swofford 2002). The data matrix consists of 20 haramiyidan species as the ingroup and three outgroup taxa, including *Sinoconodon*, *Morganucodon* and *Megazostrodon*. We identified 74 dental characters for the analysis. Because most haramiyidan species are based on isolated teeth, we use only dental characters in this analysis. The haramiyidan taxa, character list, data matrix, search settings, and results of analyses are provided in the [Supplemental material](#).

## Systematic palaeontology

**Haramiyida** Hahn, Sigogneau-Russell & Wouters, 1989

**Euharamiyida** Bi, Wang, Guan, Sheng & Meng, 2014

**Kermackodontidae** Butler & Hooker, 2005

1998 Eleutherodontidae Kermack, Kermack, Lees & Mills: 586.

2000 Eleutherodontidae Butler: 335.

2005 Eleutherodontidae Butler & Hooker: 186.

2010 Eleutherodontidae Martin, Averianov & Pfretzschner: 297.

2011 Eleutherodontidae Averianov, Lopatin & Krasnolutskii: 103.

2017 Eleutherodontidae Luo, Meng, Grossnickle, Liu, Neander & Zhang: 326.

2017 Eleutherodontidae Meng, Grossnickle, Liu, Zhang, Neander, Ji & Luo: 291.

2021 Eleutherodontidae Wang, Wible, Guo, Shelley, Hu & Bi.

**Type genus.** *Kermackodon* Butler & Hooker, 2005.

**Included genus.** *Butlerodon* gen. nov.

**Distribution.** Oxfordshire and Dorset, England; Late Bathonian, Jurassic.

**Amended diagnosis.** Differs from other Jurassic euharamiyidans in having heart-shaped P4 and upper molars with three longitudinal rows of cusps; a secondary cusp Ax and central cusp row (row Ax) present between cusp row A and row B; a secondary basin developed between row Ax and row A; the ultimate lower premolar (p4) bearing a few uneven serrations and a small basined distal heel. Differs from Triassic “haramiyidans” in having well-developed cusps A1 and a1, small cusps between A1 and Ax, broad central basin, and development of more cusps on the basin margin. Differs from multituberculates in having molar teeth with basined crowns that bear transverse flutings with sharp edge, cusps with uneven size in which the distobuccal one is the largest on upper molars, P4 is heart-shaped, and p4 with a high crown that has a triangular profile in buccal or lingual view, a distal basined heel, a few unevenly spaced serrations, mesial end not truncated.

***Kermackodon*** Butler & Hooker, 2005

1998 *Eleutherodon* Kermack, Kermack, Lees & Mills: 586, figs 3–23.

2005 *Millsodon* Butler & Hooker: 189, figs 1, 3, 4.

2005 *Kirlingtonia* Butler & Hooker: 192, figs 1, 5.

**Type species.** *Kermackodon oxfordensis* (Kermack, Kermack, Lees & Mills, 1998).

**Diagnosis.** Differs from *Butlerodon* gen. nov. in having more cusps on upper and lower molars, a pronounced row Ax in the upper molar, lower molar spindle-shaped with broad basin, mesially extended cusp a1, and reduced cusp b1.

**Distribution.** As for the included species.

**Remarks on synonyms.** Kermack *et al.* (1998) proposed the generic name “*Eleutherodon*” for a “haramiyidan” based on tooth specimens from the Forest Marble Formation (late Bathonian) of southern England (although some or all of the ‘mammal’-bearing beds from Kirtlington Quarry are now thought to be from the White Limestone Formation based on correlations with Woodeaton Quarry [Wills *et al.* 2019]). The holotype of “*Eleutherodon*” *oxfordensis* is an upper molar with the catalogue number NHMUK PV M 46460 (BMNH M46460 in Butler & Hooker 2005 and BDUC J.460 in Kermack *et al.* 1998; Fig. 1A, C). Based on the type genus, Kermack *et al.* (1998) established the family “Eleutherodontidae” and suborder “Eleutherodontida” under order *incertae sedis* within the subclass Allotheria Marsh, 1880. However, the late Professor Percy M. Butler raised the issue (pers. comm. to JJH) that “*Eleutherodon*” was preoccupied by

*Eleutherodon heteroclitus* Mercerat, 1891, a fossil sloth from Santa Cruz province, Patagonia, Argentina that was placed in the family Megalonychidae (Mammalia, Pilosa) (Mercerat 1891, p. 24). As such, the generic name “*Eleutherodon*” Kermack *et al.* 1998 is invalid under Article 39 of the ICZN (1999) and should be replaced; so are its derivatives for higher rank taxa.

Available names to replace “*Eleutherodon*” are those proposed by Butler & Hooker (2005). In addition to description of additional specimens assigned to “*Eleutherodon*” *oxfordensis*, Butler & Hooker (2005) named three allotherian genera, including the haramiyidan “*Millsodon*” and “*Kirtlingtonia*” and the multituberculate *Kermackodon*. These taxa were based on 21 isolated teeth also from the Forest Marble Formation (late Bathonian) of Oxfordshire and Dorset, England. In light of recent discoveries of euharamiyidans (Zheng *et al.* 2013; Bi *et al.* 2014; Luo *et al.* 2017; Han *et al.* 2017; Mao & Meng 2019a) from the Jurassic Yanliao Biota that have dentitions preserved, it became obvious that the holotype specimens and most referred specimens of “*Millsodon*”, “*Kirtlingtonia*” and *Kermackodon* can be reinterpreted as teeth from different loci in the upper or lower tooth row of the same species, the haramiyidan “*Eleutherodon*” *oxfordensis*. The outcome of this interpretation deems “*Millsodon*”, “*Kirtlingtonia*” and *Kermackodon* as junior synonyms of “*Eleutherodon*”.

Among the three available junior synonyms, “*Millsodon*” was cited first in the work Butler & Hooker (2005, p. 189), whereas “*Kirtlingtonia*” and *Kermackodon* appeared on page 192 and 195, respectively. However, *Kermackodon* stands out as the best available name for the reason that it was also used at a higher taxonomical rank (e.g. Kermackodontidae) so that it has the precedence over “*Millsodon*” and “*Kirtlingtonia*” that were used only for generic rank taxa (Article 24.1, ICZN 1999). In addition, because the specimens on which *Kermackodon multicuspis* was based are better preserved and diagnosable than those on which the species of “*Millsodon*” and “*Kirtlingtonia*” were based, *Kermackodon* will best serve the stability and universality of nomenclature, following Articles 24.1 of ICZN (1999). Therefore, we use *Kermackodon* and Kermackodontidae to replace “*Eleutherodon*” and “*Eleutherodontidae*”, respectively, as the haramiyidan genus and family. In the section on tooth reinterpretation, we further discuss in detail the arguments for reassignments of the teeth reported by Butler & Hooker (2005), which justifies this nomenclature action.

***Kermackodon oxfordensis*** (Kermack, Kermack, Lees & Mills, 1998)  
(Figs 1, 2)

1998 *Eleutherodon oxfordensis* Kermack, Kermack, Lees & Mills: 586, figs 3–23.

2005 *Millsodon superstes* Butler & Hooker: 189, figs 1, 3, 4.

2005 *Kirtlingtonia catenata* Butler & Hooker: 192, figs 1, 5.

2005 *Kermackodon multicuspis* Butler & Hooker: 195, figs 6–9.

**Holotype.** A right upper molar (NHMUK PV M 46460; Fig. 1A, C).

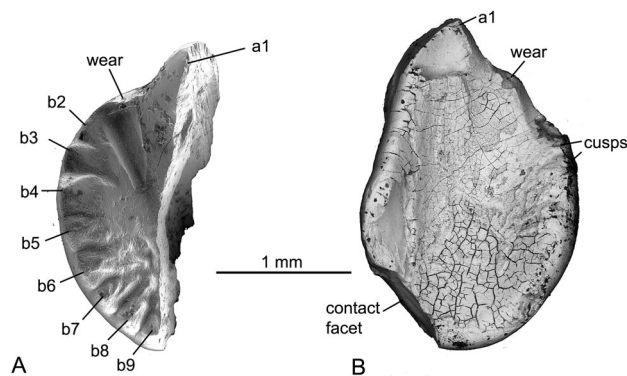
**Paratypes.** NHMUK PV M 46185, NHMUK PV M 46459, NHMUK PV M 46585, NHMUK PV M 46681, BDUC J 771, NHMUK PV M 46814, EF FM K/56 (see Kermack *et al.*, 1998 for catalogue number abbreviation), NHMUK PV M 46461, NHMUK PV M 46649. These specimens were originally described by Kermack *et al.* (1998) and listed by Butler & Hooker (2005) as paratypes, following articles 72.1.1, 72.4.5 and 73D of ICZN (1999).

**Referred specimens.** NHMUK PV M 46654; NHMUK PV M 46821; NHMUK PV M 46832; NHMUK PV M 46851; NHMUK PV M 34986; NHMUK PV M 44985 (these are specimens referred to *Eleutherodon* by Butler & Hooker 2005); BMNH M46645 (this was the holotype specimen for *Millsodon superstes*; Butler & Hooker 2005); NHMUK PV M 46497 and NHMUK PV M 46579 (these were specimens used as the holotype and paratype for *Kirtlingtonia catenata*; Butler & Hooker 2005); note that the specimen number of the paratype was M46183, perhaps a typo (Butler & Hooker 2005, fig. 1G), which differs from that in the text and fig. 5B (Butler & Hooker 2005); NHMUK PV M 46822 and NHMUK PV M 46684 (these are specimens referred to the multituberculate species *Kermackodon multicuspis* with the former selected as the holotype; Butler & Hooker 2005).

We refer two lower molars from Woodeaton Quarry to *K. oxfordensis*: NHMUK PV M 105719 (m1?) and NHMUK PV M 105712 (m1) (Fig. 2).

**Distribution.** Old Cement Works Quarry, Kirtlington, Oxfordshire, England, Late Bathonian.

**Description.** NHMUK PV M 105719 (Fig. 2A). This is a partial left lower molar (possibly m1; length = 2.27 mm) with most of lingual part broken. Cusp a1 is large and extends mesially. Between a1 and b2 there is a wear facet. Row b has eight cusps that are on the basin margin and extends with enamel ridges toward the basin centre. Cusp b4 is the largest and those distal to it gradually reduce in size distally. Wear and striations are present on the buccal side of a1, lingual side of row b, and the basin floor, which indicate primarily horizontal movement of the tooth during chewing. This partial tooth lacks b1 and has an oval outline in occlusal view, differing



**Figure 2.** Lower molars of *Kermackodon oxfordensis* from Wood Eaton Quarry. **A**, partial left lower molar (m1) (NHMUK PV M 105719) in occlusal view. **B**, a deeply worn right lower molar (m1) (NHMUK PV M 105712) in occlusal view.

from the lower molars of *Butlerodon quadratus* gen. et sp. nov. (see below); it is most similar to the lower molar of *K. oxfordensis*. Although b cusps are not so numerous as in specimens reported by Kermack *et al.* (1998, figs 15A, 16), it appears to be similar to NHMUK PV M 46851 (Butler & Hooker 2005, fig. 1C). There is no contact facet on mesial and distal ends of the tooth.

NHMUK PV M 105712 (Fig. 2B). This is a right m1 that was deeply eroded so that the tooth cusps and most ridges are erased. The length and width of the tooth are 2.42 and 1.59 mm, respectively. The tooth profile is oval with a mesially extended a1, with a wear facet lingual to a1. Several enamel ridges are discernible, extending distolingually from b cusps to the basin. Judging from these ridges, it is clear that b cusps must be at least as many as in NHMUK PV M 105719. Because of these features, plus its similar size to NHMUK PV M 105719, we identify this tooth as belonging to *K. oxfordensis*. On the distolingual end of the tooth there is a distinct contact facet that extends from the crown to the root, suggesting that this is probably m1.

**Euharamiyida** family indeterminate  
*Butlerodon* gen. nov.

**Type species.** *Butlerodon quadratus* sp. nov.

**Diagnosis.** Unique in having an enlarged b1 cusp that makes the mesial portion of m1 square-shaped. Differs from *Thomasia*, *Haramiyavia* and *Theroteinus* in having more cusps on upper and lower molars, of which A1 and a1 are distinctively large, respectively, while other cusps are proportionally small; both upper and lower molars proportionally wide and broadly basined with cusps arranged around the basin, contrasting with the blunt tooth cusps that are closely positioned on the tooth crown in the other three taxa; development of Ax cusp

on upper molar. Further differs from *Theroteinus* in having more mesiodistally elongate molars with two distinctive longitudinal rows of cusps that define a longitudinal central valley on upper and lower molars. Differs from *K. oxfordensis* in the upper and lower molars having a more rectangular outline in occlusal view, contrasting with the rhomboidal and spindle-like outline for upper and lower molars, respectively, of *K. oxfordensis*; lower molar with fewer tooth cusps, a1 not extending mesially, upper molar with weakly developed cusp row Ax, cusp AA not buccally extended and also bites into the valley of lower molar. The combination of several tooth structures, such as a distinct cusp b1, a1 not mesially extended, and initial development of row Ax on the upper molar, differentiate *Butlerodon* from other “haramiyidans”, including *Arboroharamiya*, *Shenshou*, *Xianshou*, *Vilevolodon*, *Maiopatagium*, *Sineleutherus*, *Avashishta*, *Hahnodon*, *Denisodon*, *Mojo*, *Kirtlingtonia*, *Cifelliodon* and *Sharypovoia*, among which some have only one tooth or a partial tooth preserved (see Mao & Meng 2019a and Averianov *et al.* 2019a for a review of these taxa). Differs from *Megaconus* in having basined molar with conical cusps.

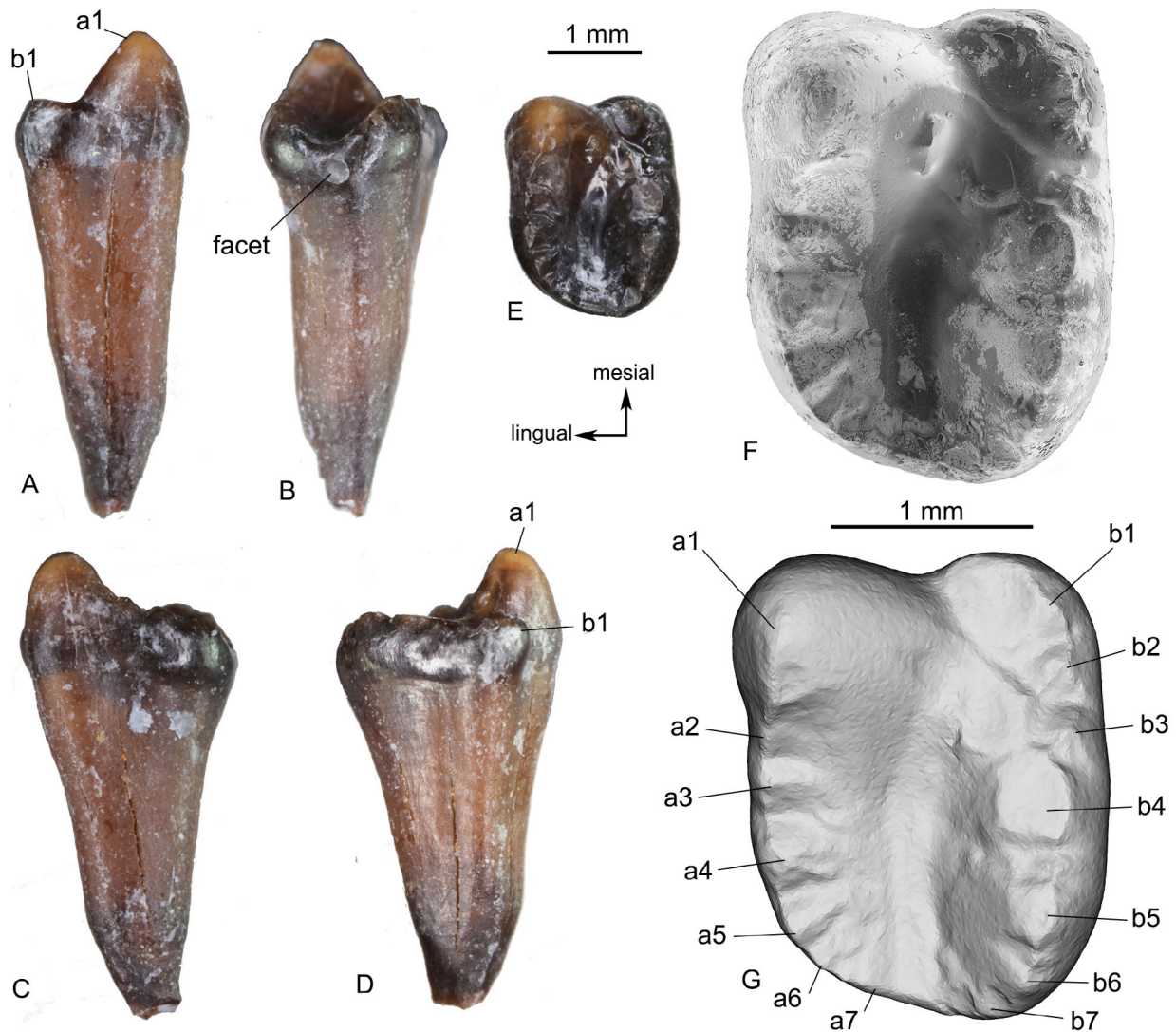
**Derivation of name.** Generic name in honour of Professor Percy M. Butler for his contribution to the study of mammals. Also in Greek, *-odon*, tooth. Masculine.

*Butlerodon quadratus* sp. nov.  
(Figs 3–8)

**Holotype.** NHMUK PV M 100089, right lower molar, probably m1.

**Paratype.** NHMUK PV M 100090, left upper molar, probably M1.





**Figure 3.** The holotype of *Butlerodon quadratus* gen. et sp. nov. from Woodeaton Quarry. **A–E**, mesial, distal, lingual, buccal and occlusal views of NHMUK PV M 100089, a right m1. **F**, SEM image of NHMUK PV M 100089 in occlusal view. **G**, CT-rendered NHMUK PV M 100089 in occlusal view. The scale above E is for A–E.

**Referred specimens.** NHMUK PV M 105709, right lower molar; NHMUK PV M 100086, eroded left lower molar; NHMUK PV M 105715, partial lower left molar; NHMUK PV M 102103, left upper premolar (P4); NHMUK PV M 105706, deeply worn upper premolar (probably a left P4); NHMUK PV M 100096, right upper premolar (P3); NHMUK PV M 100075, partial upper premolar, NHMUK PV M 105711, NHMUK PV M 100087, NHMUK PV M 105707 and NHMUK PV M 105708, all upper incisors.

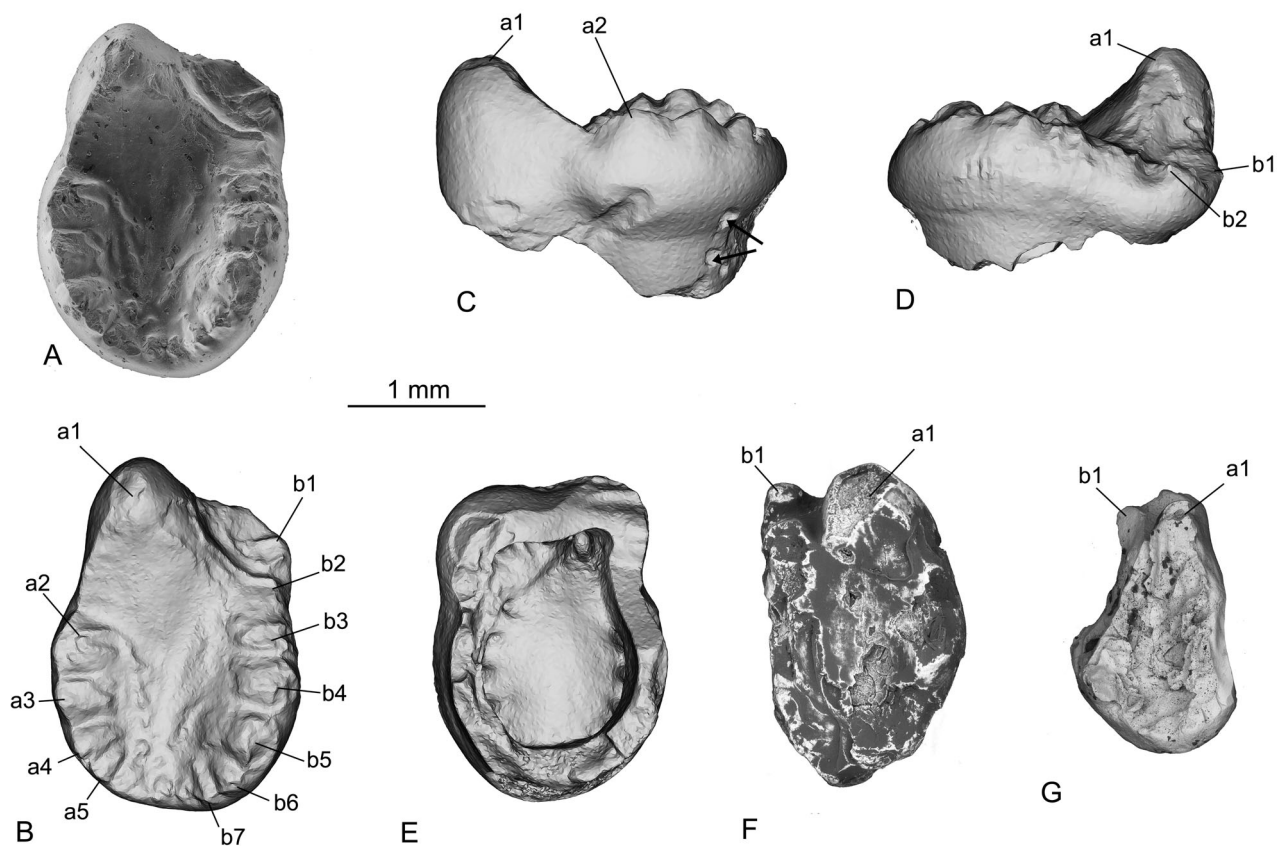
**Derivation of name.** Latin, *quadratus*, squared, referring to the square-shaped outline of mesial part of the holotype m1.

**Distribution.** Bed 23 (Fimbriata-Waltoni Bed), Bladon Member, White Limestone Formation (Middle Jurassic, late Bathonian, Great Oolite Group, Retrocostatum Zone) at Woodeaton Quarry in Oxfordshire, UK.

**Diagnosis.** Same as the genus.

**Description.** NHMUK PV M 100089 (holotype; Fig. 3). This right lower molar (length/width = 2.33/1.80 mm) is chosen as the holotype because of its completeness in crown and root conditions that provide the diagnostic features (Fig. 3). The contact facet at the distal end of the crown indicates that it is a mesial molar. Given that all other euharamiyidans (Bi *et al.* 2014) have only two upper and lower molars, respectively, this tooth should



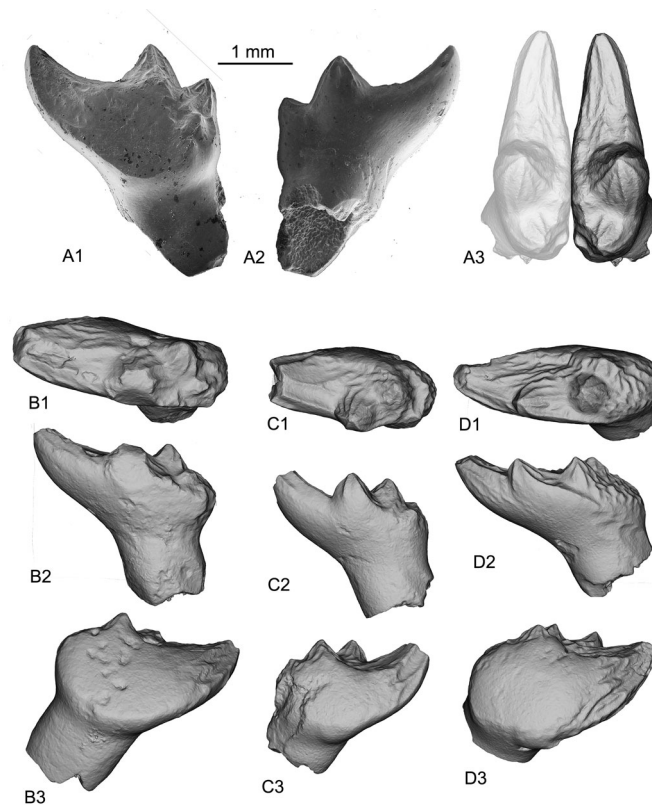


**Figure 4.** Lower molars of *Butlerodon quadratus* gen. et sp. nov. from Woodeaton Quarry. **A**, SEM image of NHMUK PV M 105709, a right lower molar in occlusal view. **B–E**, CT-scan rendered NHMUK PV M 105709 in occlusal, lingual, buccal and ventral (root broken and pulp cavity revealed) views. The arrows in **C** point to possible tooth marks. **F**, SEM image of NHMUK PV M 100086, a left lower molar in occlusal view. **G**, SEM image of NHMUK PV M 105714, a left lower molar in occlusal view.

be an m1. Typical for a lower molar of euharamiyidans, cusp a1 is the largest, followed by cusps that reduce in size distally. In addition, cusp b1 is low in position mesial to the cusp b row, which is most distinctive in the Triassic species such as *Thomasia* and *Haramiyavia*. The occlusal outline of the tooth is roughly rectangular, with a rounded distal end. Row a has seven cusps, and as in other “haramiyidans”, the mesiolingual cusp (a1) is the largest on the lower molar. Of the remaining row a cusps, a4 is the largest one. Except for a1, row a cusps are generally smaller than their opposite ones on row b. Row b also has seven cusps. A notable feature of the lower molar is the shelf-like structure at the mesiobuccal corner of the tooth crown. It is here interpreted as formed by an enlarged cusp b1. Although sizable, b1 is lower than other row b cusps and bears a concave wear facet on its tip. In this position, this wear facet is most probably created by contact with cusp AA of the opposite upper molar, consistent with the wear on cusp AA. Of the rest of the b row cusps, b4 is the largest and tallest.

Cusps b2 and b3 are small; in particular, b2 may be considered as a cuspsule. Both row a and row b cusps show wear, most notably on b4 and the lingual and buccal sides of a1. There is a wear facet on the saddle between a1 and b3. The floor of the central valley also has a grooved wear facet. The central basin is broader than those of *Haramiyavia* and *Thomasia* but narrower than that of *K. oxfordensis*. The deepest area of the central valley is between a3 and b4, similar to that of *Qishou* (Mao & Meng 2019a, b). With wear, the small distal cusps are nearly gone so that the central valley is open distally. NHMUK PV M 100089 has a single, long and robust root that tapers distally.

Cusp b1 is the most interesting structure of the tooth. It is larger than those in various lower molars of *Thomasia* (Sigogneau-Russell 1989; Butler & MacIntyre 1994; Butler 2000; Hahn & Hahn 2006; personal observations of FM and JM). A moderate b1 is present in the lower molars of *Haramiyavia* (Jenkins *et al.* 2017; Luo *et al.* 2015; personal observation by FM and JM). Although cusp b1 was identified as a small cusp at the



**Figure 5.** Upper incisors of *Butlerodon quadratus* gen. et sp. nov. from Woodeaton Quarry. **A1–2**, SEM images of a left I2 (NHMUK PV M 105711) in medial and buccal views. **A3**, CT-scan rendered tooth (NHMUK PV M 105711) in dorsal view (the semi-transparent right incisor was mirrored from the original left one). Note the orientation of the anteriorly projecting cusps of the crown and its root. **B1–3** to **D1–3**, CT-scan rendered right upper incisors in dorsal, buccal, and medial views of NHMUK PV M 100087, NHMUK PV M 105707, and NHMUK PV M 105708, respectively.

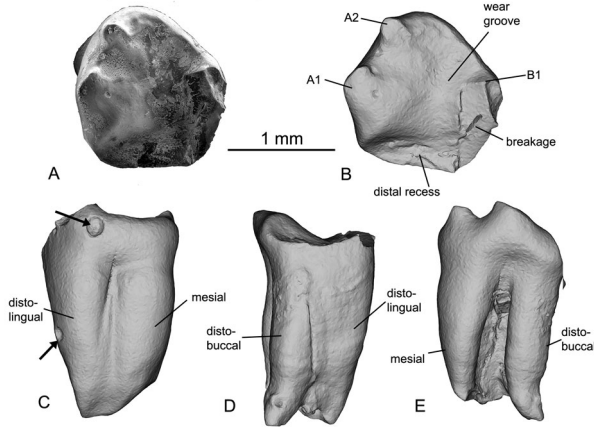
mesial end of row b in *Arboroharamiya* (Meng *et al.* 2014) and *Qishou* (Mao & Meng 2019a, b), it was interpreted as being lost in *K. oxfordensis* and other taxa, such as *Sineleutherus* (Butler 2000; Martin *et al.* 2010; Averianov *et al.* 2011). In light of the Woodeaton specimens, we think that ‘b1’ identified in *Arboroharamiya* and *Qishou* may not be homologous to b1 of NHMUK PV M 100089. The b1 of NHMUK PV M 100089 is similar to that of *Thomasia* in being lower than b2; it is more like a cingulid cusp instead of one that belongs to row b. A similar b1, although smaller, does occur in the lower molar of ‘*Sineleutherus*’ *issedonicus* from the Middle Jurassic of Siberia, Russia (Averianov *et al.* 2019a, fig. 8). We consider b1 in *Butlerodon quadratus* as a specialized feature, but this cusp was lost in other euharamiyidans except a vestigial one in ‘*Sineleutherus*’ *issedonicus* (see Discussion).

NHMUK PV M100089 has a single, long and robust root that tapers distally.

On its lingual and buccal surface, a shallow groove extends along the root for nearly its entire length; the grooves suggest that the robust root was probably

formed by fusion of two small roots. The crown and root transition is gradual but the crown is well delimited by presence of the enamel covering.

NHMUK PV M 105709 (Fig. 4A–E). This is a right lower molar with similar size (length/width= 2.56/1.80 mm) and shape to the holotype. The mesial and distal ends bear vague contact facets so that the tooth is possibly m1. The notable difference from the holotype is that in occlusal view, the mesial one-third of the tooth, at the region of a1 and b1–2, is narrower than the mid-portion of the tooth, where the lingual and buccal cusp rows bulge outward; thus the outline of the crown is more oval than rectangular. Cusp a1 is slightly more mesially extended. Cusp b1 is damaged but it is similar to that of the holotype in size and position. This tooth is less worn than the holotype so that there are some enamel ridges within the basin; the one derived from a1 and extending to the distal end of the basin is best preserved. This pattern of enamel ridge in the basin is similar to those of *Arboroharamiya* (Zheng *et al.* 2013; Meng *et al.* 2014). Given the differences, the possibility that NHMUK PV M 105709 belongs to a different species cannot be ruled out.



**Figure 6.** Right upper premolar (P3) (NHMUK PV M 100096) of *Butlerodon quadratus* gen. et sp. nov. from Woodeaton Quarry. **A**, SEM image of the tooth in occlusal view. **B–E**, CT-scan rendered tooth in occlusal, lingual, distal, and buccal views. Arrow in **C** points to possible tooth mark.

NHMUK PV M 100086 (Fig. 4F). This is a left lower molar (length/width= 2.35/1.49 mm) and has been deeply weathered so that it has been covered with glue in preparation. Nonetheless, its general morphology is still discernible. In particular, the tooth has a large a1 and a distinct b1, characteristic for the lower molar of *Butlerodon*. The bulging lingual surface suggests that it is more similar to NHMUK PV M 105709 than to the holotype. The gap between a1 and b1 may be created by erosion. As in the holotype, it has one root that tapers distally. There is a possible contact facet on its mesial end, suggesting this is m1.

NHMUK PV M 105715 (Fig. 4G). A partial left lower molar (length/width= 1.93/? mm). It has cusp a1 and the base of b1 so that it is assigned to *Butlerodon*.

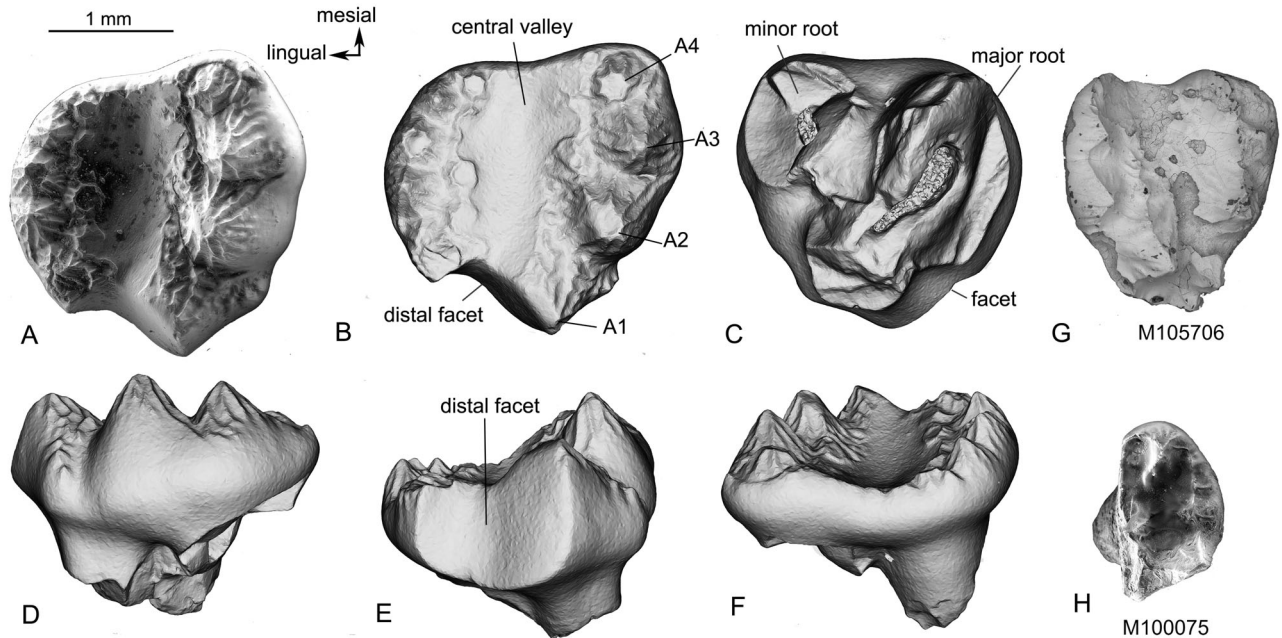
Upper incisors (Fig. 5). There are five upper incisors in the collection from Woodeaton. Of the five, we assign four to *Butlerodon quadratus*, including NHMUK PV M 105711 (length/width= 3.12/1.07 mm), NHMUK PV M 100087 (2.96/1.10 mm), NHMUK PV M 105707 (\*2.32/1.17 mm, tip broken and the asterisk indicates estimated length), and NHMUK PV M 105708 (2.86/1.11 mm). It is difficult to be certain about the precise location of these isolated upper incisors, but it has been noted that the upper incisors of *Thomasia* were very similar to the second upper incisor of the Paulchoffatiidae (Hahn & Hahn 2006). In addition, these teeth are similar to the upper incisor interpreted as I2 in the euharamiyidans from the Yanliao Biota, such as *Xianshou* (Bi *et al.* 2014) and *Qishou* (Mao & Meng 2019a). Thus, we consider these upper incisors as I2. These upper incisors are assigned to *B. quadratus* because of their relatively large size. In contrast, the

much smaller one (NHMUK PV M 105718) is assigned to *Woodeatonia parva* gen. and sp. nov. (Figs 9 and 10). These upper incisors are proportionally large relative to the molars assigned to *B. quadratus*; this is similar to those of *Xianshou linglong* (Bi *et al.* 2014) and a new specimen from the Yanliao Biota (unpublished data, personal observation by FM and JM) where the upper dentitions are preserved. By relative tooth size it is also possible that some of the upper incisors may belong to *Kermackodon oxfordensis*, but there seems no criterion to differentiate them so we tentatively assigned all these to *Butlerodon*. However, we assign the two upper incisors (NHMUK PV M 46234 and NHMUK PV M 46056) reported from the Kirtlington Formation by Butler & Hooker (2005; BMNH M46234 and BMNH M46056 in this paper) to *K. oxfordensis* (see below).

For each I2, the medial side of the tooth crown bears a flat facet, which is interpreted as the contact facet for the opposite incisor. A similar facet exists on the I2, assigned to *Allotheria incertae sedis* (NHMUK PV M 46234; BMNH M46234 in Butler & Hooker 2005), that was interpreted as a ‘wear facet’, as in *Sineleutherus uyguricus* (Martin *et al.* 2010). However, there are no striations on this rather extensive facet. Moreover, it requires a vertical shearing counterpart, in a shape of a flat surface, on the buccal side of the lower incisor to create such a flat wear facet on I2 from tooth contact. The morphology of the lower incisor from the Yanliao euharamiyidans, such as *Qishou* (Mao & Meng 2019a), does not support the interpretation as a wear facet; instead, this facet is best interpreted as the contact facet (Fig. 5, A3). Presence of this contact facet indicates that there was only one pair of upper incisors in *Butlerodon quadratus* and I1 was lost.

These upper incisors are more complex in morphology than those of *Thomasia* (Sigogneau-Russell 1989; Hahn & Hahn 2006), *Shenshou* (Bi *et al.* 2014) and *Qishou* (Mao & Meng 2019a). Although variation exists, these teeth are similar in having a tripartite crown in lateral or medial view, consisting of three main cusps that decrease in size distally. The cusps bear fine enamel flutings. The upper incisor crown of *Thomasia* (group 3 of Hahn & Hahn 2006) is roughly equivalent (perhaps homologous) to the mesial two cusps of the incisor reported here. In relation to the long axis of the single, well-developed root of the upper incisor, the mesial and most robust cusp is more mesially extended in *B. quadratus*. As in *Qishou* (Mao & Meng 2019a), there is a bending between the incisor crown and root that allows the roots of the two teeth be implanted separately in the premaxillary bones while their crowns could meet in the medial line. Along with the conical lower incisors, the





**Figure 7.** Upper premolars (P4) of *Butlerodon quadratus* gen. et sp. nov. from Woodeaton Quarry. **A**, SEM image of NHMUK PV M 102103 (a left P4) in occlusal view. **B–F**, CT-scan rendered NHMUK PV M 102103 in occlusal, ventral (root, flipped horizontally), buccal, mesial, and distal views. **G**, SEM image of NHMUK PV M 105706 (a left P4) in occlusal view. **H**, SEM image of a partial P4 (NHMUK PV M 100075).

upper incisor pair with multiple cusps forms a complex “holding” device for food picking.

NHMUK PV M 100096 (Fig. 6). This specimen is identified as a right P3 owing to its small size (length/width = 1.53/1.41 mm) and simple crown morphology. The tooth was worn but its general morphology is discernible. There is no contact facet at the mesial end and the orientation is partly determined by the wear groove, which is longitudinal and there is a broad central valley with the distal end being worn deepest to form a distal recess. There are two buccal cusps, of which A1 is significantly larger than A2. Cusp B1 is partly preserved but distal to it, the lingual side of the tooth was broken. The root of NHMUK PV M 100096 shows some subdivision, or fusion of three smaller roots: a mesial, a distolingual and a distobuccal one. On the buccal side, the mesial and distal roots are still separated, and in the lingual and distal views the roots are fused but a vertical groove suggests fusion of two roots. The root condition of NHMUK PV M 100096 is more complex than that of molars in which the roots have fused into one that tapers distally.

Identification of the tooth locus for these isolated teeth is challenging. In the collection from the Woodeaton Quarry, NHMUK PV M 102103 is more likely P4 or the ultimate upper premolar (see below). If NHMUK PV M 100096 and NHMUK PV M 102103 belong to the same species, as we assume here, the former has to be P3. Our

identification of NHMUK PV M 100096 as a P3 is also based on the current knowledge of euharamiyidans from China in which there are only two upper premolars. In general, P4 is notably wider than the molar and is more complicated in morphology than all other cheek teeth, whereas P3 is small and simple in crown features. However, there is evidence that three upper premolars exist in the euharamiyidans (unpublished data; personal observation by FM and JM); thus, the possibility that NHMUK PV M 100096 is P2 cannot be ruled out.

NHMUK PV M 100096 is similar to the tooth identified as P4 (PIN 5087/101) of *Sharypovoia arimasporum* from the Middle Jurassic (Bathonian) of Western Siberia, Russia (Averianov *et al.* 2019a, fig. 2). The size, general outline of the crown, distributions of cusp A1, A2 and B1, and the deeper distal end of the crown are largely comparable between the two specimens. PIN 5087/101 has a central cusp, which is absent in NHMUK PV M 100096 probably because of deep wear in the latter. A main difference between the two is that NHMUK PV M 100096 shows sign of multiple roots that have not fully fused, whereas PIN 5087/101 has a single and robust root that tapers distally.

NHMUK PV M 102103 (Fig. 7A–F). This tooth was tentatively assigned to the then multituberculate *Kermackodon* (Wills *et al.* 2019, fig. 10J) because of its similarity to NHMUK PV M 46822, the holotype of



“*Kermackodon multicuspis*” that has a heart-shaped crown in occlusal profile (Butler & Hooker 2005, fig. 6A). As discussed below, we have reinterpreted NHMUK PV M 46822 as a P4 of the euharamiyidan *Kermackodon oxfordensis*. Similarly, we interpret NHMUK PV M 102103 as P4 based on its morphology and relative size (length/width= 2.50/2.39 mm) to the molars. As in *Arboroharamiya*, *Velivolodon* and *Xianshou* where the upper dentitions are preserved, P4 is wider than the upper molars and broadly basined; it bears many conical cusps with numerous enamel flutings. Moreover, the basined floor commonly shows a longitudinal wear or a groove that was created by palinal grinding against cusp a1 of p4.

Although NHMUK PV M 102103 has a similar shape to NHMUK PV M 46822, its pointed end was notched or incurved. This notch does not seem to be due to breakage; it may be interpreted as the recess that lodged the mesial end of the following tooth in an interlocking relationship. In the description of NHMUK PV M 46822, the pointed end of NHMUK PV M 46822 was described to be distal, and this orientation is supported by a large contact facet on the distolingual flank of the tooth (Butler & Hooker 2005); thus, NHMUK PV M 46822 would be a left P4. The distal recess of NHMUK PV M 102103 is at the same position as the contact facet on NHMUK PV M 46822. In reported euharamiyidans, P4 has the distal end concave and the mesial end convex (Meng *et al.* 2014; Meng *et al.* 2017; Luo *et al.* 2017), but a new specimen (unpublished data; personal observation by FM and JM) shows an opposite orientation of P4, indicating that the morphology of P4 in “haramiyidans” may be diverse. We consider the notched end of NHMUK PV M 102103 to be distal and the tooth as an upper left P4.

As in other P4s of euharamiyidans, the buccal cusps (A) of NHMUK PV M 102103 are generally larger than the lingual ones (B). Of the four buccal cusps, A2 and A3 are subequal and A4 is small. The full size of A1 is unknown because its distal portion was notched. Preserved row B cusps are arranged in two nearly parallel rows in a curved course. The lingual row consists of larger B cusps in which those in the middle are larger than others on the mesial and distal ends of the row. The lingual row, or chain, consists of minute cusps that had been deeply worn. It may be inferred that more small cusps were in the basin centre of the crown but were erased by wear. All main cusps bear fine enamel ridges that radiate from the cusp tip in all directions.

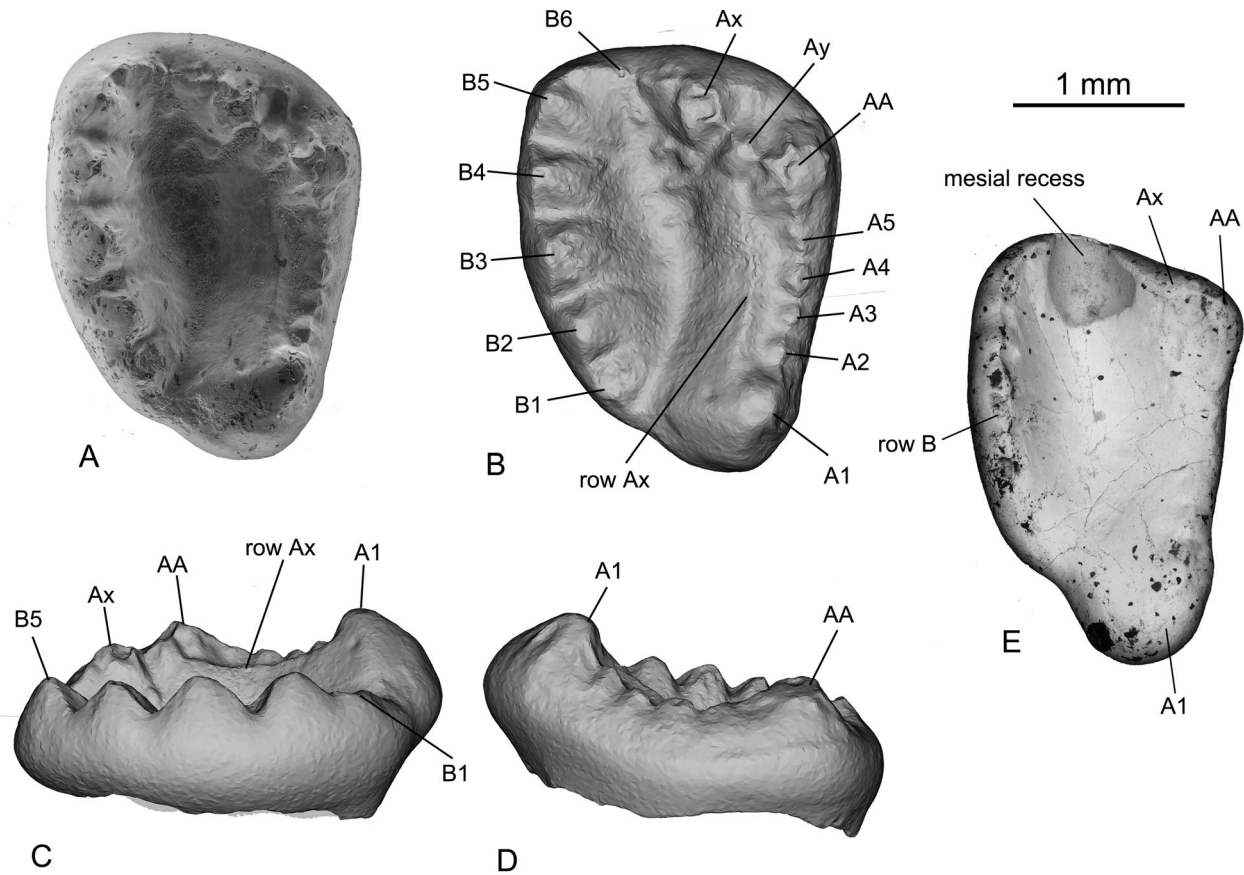
The tooth has two roots, as shown by their broken bases (Fig. 7C). The minor root is on the mesiobuccal corner of the crown and supports cusps A3–4. The major root is mesiodistally long and has an

asymmetrical dumbbell-shaped cross-section, which suggests that the root was formed by fusion of two small roots. The major portion of the root supports the lingual side of the crown, while the minor one supports the distal end of the tooth, mainly cusp A1.

The central basin of NHMUK PV M 102103 is a broad longitudinal trough with a smooth wear surface; this indicates palinal grinding of p4 against cusp a1. In addition, small wear facets are also present on the tips of some A and B cusps. In NHMUK PV M 46822 there is a central groove created by wear; it is narrow and straight. As mentioned above, this wear groove has been used as evidence for identification of the tooth as from a multituberculate (Averianov *et al.* 2021). The wear is light in NHMUK PV M 46822 but it still shows that the anterior portion of the wear groove is wider and deeper than the posterior portion. This is echoed by the deeper wear in NHMUK PV M 46822. The wear valley is also wider anteriorly and narrow posteriorly; it is concave with the deepest area lingual to cusp A3. This unequivocally shows that the wear is mesiodistally straight but not horizontal, displaying a “haramiyidan” rather than a multituberculate wear pattern.

NHMUK PV M 105706 (Fig. 7G). This is a deeply worn tooth with much of the enamel gone, particularly on the presumably buccal side where the larger cusps are located. The lingual cusps are well preserved and show sharp cusps with enamel ridges. Partly because the enamel on the buccal side was peeled off, NHMUK PV M 105706 (length/width=2.10/1.84 mm) is smaller than NHMUK PV M 102103; nonetheless, this tooth would still be smaller if it were complete, judging from the well-preserved lingual side. The tooth has a heart-shaped profile with cusps bearing enamel flutings, similar to NHMUK PV M 102103, which secured its identification as a left P4. Because of its smaller size, whether it belongs to *Butlerodon* is uncertain. If it does, this could be from an individual smaller and probably younger than the one to which NHMUK PV M 102103 belongs. Because size is a crucial parameter in tooth identification and association, we use Figure 9 to visualize relative sizes of some key specimens. It is clear that the size of NHMUK PV M 105706 is smaller than NHMUK PV M 102103 but still proportionally too large to match the small teeth assigned to *Woodeatonia parva* gen. and sp. nov. (see below). Thus, we tentatively keep this tooth in *Butlerodon quadratus*.

NHMUK PV M 100075 (Fig. 7H). This tooth fragment bears small cusps with enamel flutings, typical for an upper premolar; it is likely a lingual portion of a premolar. By its estimated size, we regard it as a tooth fragment of *Butlerodon quadratus*.



**Figure 8.** Upper molars of *Butlerodon quadratus* gen. and sp. nov. from Woodeaton Quarry. **A**, SEM image of the left M1 (paratype, NHMUK PV M 100090) in occlusal view. **B–D**, CT-scan rendered NHMUK PV M 100090 in occlusal, lingual and buccal views. **E**, SEM image of a left M2 (NHMUK PV M 102102) in occlusal view.

NHMUK PV M 100090 (paratype; Fig. 8A–D). NHMUK PV M 100090 is a left M1 (this appears to be the tooth figured in Wills *et al.* [2019, fig. 10I], but that tooth was numbered as M 102102, which is the number for the tooth described below). The crown is low and the root has been broken. There is no contact facet on either end, but based on size of A1 (not so greatly extended distally) we consider it an M1. The tooth is wide mesially and gradually narrows distally (length/width=2.45/1.82 mm). As in other euharamiyidans, cusp A1 is the largest cusp of the upper molar and also distally extended. In contrast, this configuration is not as obvious in *Theroteinus* and *Haramiyavia*. Wear facets on its lingual and buccal sides indicate that A1 is the primary cusp that bit into the valley of the lower molar. Mesial to A1 are four small cusps that are subequal in size and denoted as A2–5. Cusp AA at the mesial end of row A is the second largest cusp of the tooth. Cusp AA bears distinct wear facets on its tip and buccal side (see Tooth wear and occlusion below). Another main

cusp at the middle position on the mesial border of the tooth is denoted as Ax, similar to that in *Kermackodon oxfordensis* (Fig. 1A, C). A small cusp lies between cusp AA and Ax, which is absent in *K. oxfordensis*. A ridge runs between A1 and Ax. By position, we consider this ridge as representing the initial development of row Ax; it is well developed as a central cusp row in *K. oxfordensis*, which differs from the condition in NHMUK PV M 100090. Between the ridge and row A there is a narrow secondary basin. In *K. oxfordensis* this basin is broader and cusp AA is more buccally projected so that the upper molar of *K. oxfordensis* has a rhomboidal outline. Row B in NHMUK PV M 100090 has six cusps with B3 being the largest. All B cusps bear wear facets on their basin side. The central (primary) basin is broad with its deepest region buccal to cusp B3. The central basin valley has a curved course and opens narrowly between A1 and B1.

NHMUK PV M 102102 (Fig. 8E). This is a worn tooth but the wear is even for the entire tooth (length/

width= 2.44/1.57 mm). Although worn, it can be identified as a left upper molar of a euharamiyidan. The tooth crown is narrow, differing from that of *Kermackodon*, and cusp A1 is distinct and distally extended. It is also discernible that cusp AA is large and a weak cusp Ax with a distal extension as a weak ridge is present on the lingual side of AA. Row B appears to have 5 or 6 small cusps. The central basin is broad and structureless. There is a concavity at the mesial end of the occlusal plane; it does not look like a breakage; instead, it was possibly created by contact with cusp a1 of the lower molar during chewing. Another possibility is that this is a dental caries. There is no contact facet on either end of the crown. Based on its extended A1, presence of a weak row Ax, and matching size, we identify NHMUK PV M 102102 as M2 of *Butlerodon quadratus*.

**Remarks.** *Butlerodon* is similar to *Kermackodon* in having a heart-shaped P4 with similar pattern of cusp distribution and a cusp Ax in the upper molar. However, although variations exist in the upper molars of *Kermackodon* (Kermack *et al.* 1998), cusp Ax and row Ax in the genus are better developed than in *Butlerodon*, with cusp AA being more buccally projected and the secondary basin bearing wear facet 12 being broader than that of *Butlerodon*. The lower molars, however, show greater differences between the two taxa. The lower molar of *Kermackodon* is spindle-shaped in occlusal outline; it has a broad basin and bears many cusps and the basin floor is filled with convoluted enamel ridges that are derived from the cusps. Cusp a1 of *Kermackodon* extends mesially and cusp b1 was lost. The similarities in the upper molars and differences in the lower molars presents an interesting contrast. These features show that the lower molar of *Kermackodon* is more derived than that of *Butlerodon*; the latter is more similar, primitively, to those of *Thomasia* (Sigogneau-Russell 1989; Butler & MacIntyre 1994; Butler 2000).

*Woodeatonia* gen. nov.

**Type species.** *Woodeatonia parva* sp. nov.

**Included species.** The type species only.

**Derivation of name.** After the type locality Woodeaton Quarry, Oxfordshire, United Kingdom. Feminine.

**Diagnosis.** A small euharamiyidan that differs from other “haramiyidans”, except for *Arboroharamiya jenkinsi* and *Vilevolodon diplomylos*, in being spindle-shaped in occlusal profile; a1 of m1 inflated and positioned near the longitudinal axis (middle line) of the tooth; b1 of m1 small; M1 two-rooted and having row

A cusps decreasing in size mesially so that the mesio-buccal cusp (A4 or AA) is small.

*Woodeatonia parva* sp. nov.

(Fig. 10)

**Holotype.** NHMUK PV M 105714, right lower molar (m1).

**Paratype.** NHMUK PV M 100088, right upper molar.

**Referred specimens.** NHMUK PV M105718, right upper incisor. Specimens from Forest Marble Formation: NHMUK PV M 46183 (paratype of “*Millsodon superstes*” [Butler & Hooker 2005]; see Discussion); NHMUK PV M 46818 (a referred specimen of “*Kirtlingtonia catenata*” [Butler & Hooker 2005]); NHMUK PV M 46562 (an undetermined haramiyid [Butler & Hooker 2005]). See discussion for reinterpretation of the Forest Marble specimens.

**Derivation of name.** *parva*, Latin, feminine singular of *parvus*, small, referring to the small size of the referred teeth.

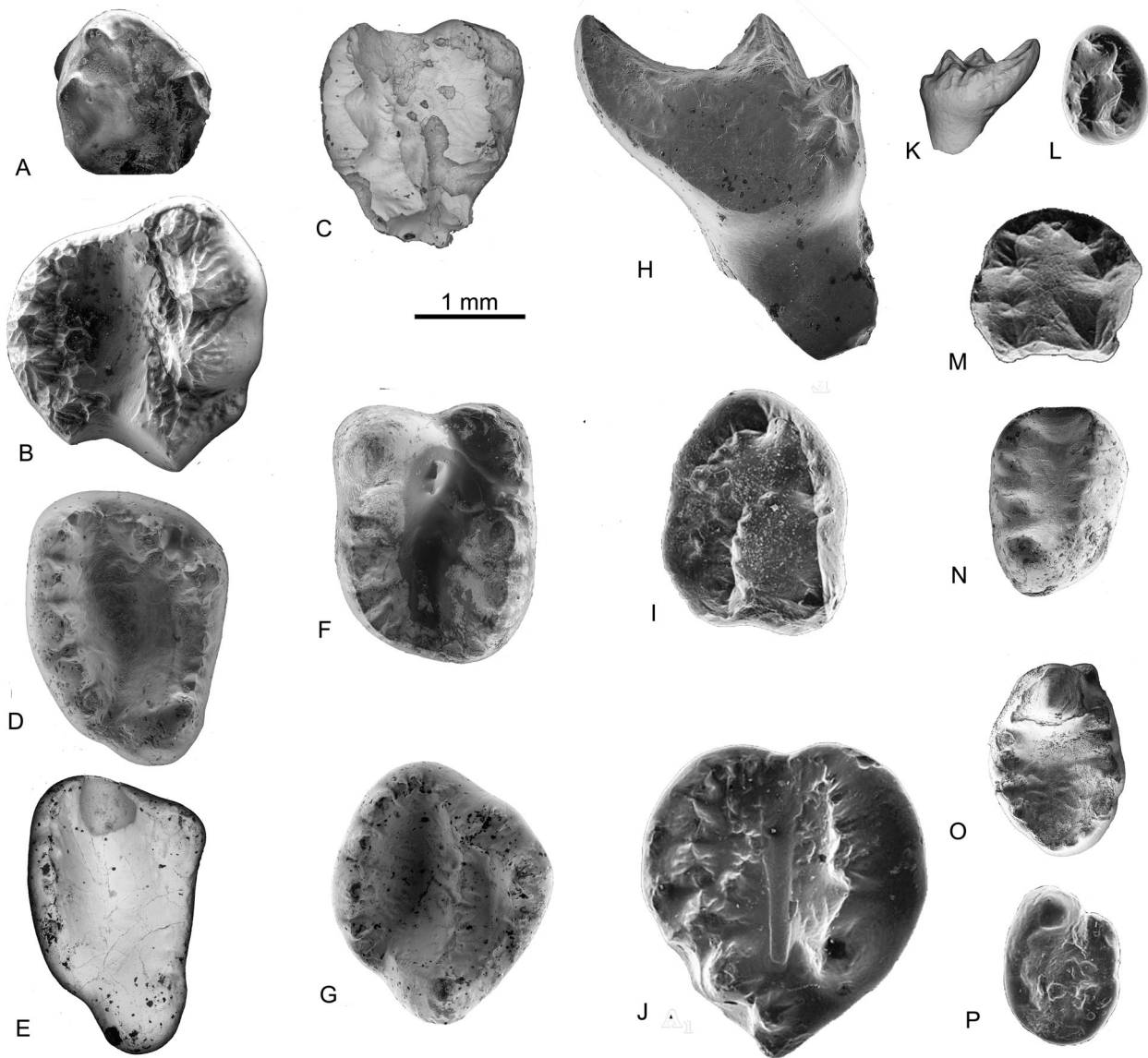
**Distribution.** Bed 23 (Fimbriata-Waltoni Bed), Bladon Member, White Limestone Formation (Middle Jurassic, late Bathonian, Great Oolite Group, Retrocostatum Zone) at Woodeaton Quarry in Oxfordshire, UK, as for *Butlerodon quadratus*.

**Diagnosis.** Same as for the genus.

**Description.** NHMUK PV M 105714 (holotype; Fig. 10A–D). This is a right m1 (length/width= 1.77/1.25 mm) with the crown base poorly preserved. Although the enamel layer around the side of the crown and on cusp a1 has been worn or partly peeled off, the general morphology of NHMUK PV M 105714 is clear. It is considerably smaller than those of *Butlerodon quadratus* and *Kermackodon oxfordensis*. The tooth crown has a spindle-shaped profile and a predominant a1 that is positioned on the longitudinal axis of the tooth and accounts for nearly one-third of the crown length. By the tooth shape, we think it is most likely a m1. It has a small b1 at the buccal base of a1. There are seven row b cusps, of which b4 is the largest; other b cusps decrease in size away from b4. Enamel ridges are present, extending from cusps to the basin centre.

NHMUK PV M 100088 (paratype; Fig. 10E–H). The size of the tooth (length/width= 1.71/1.23 mm) is comparable to that of NHMUK PV M 105714. We identify this tooth as the right upper molar, probably M1. There is no contact facet on either end of the crown. The tooth is wide mesially and gradually narrows distally. There are four A cusps and three (possibly four) B



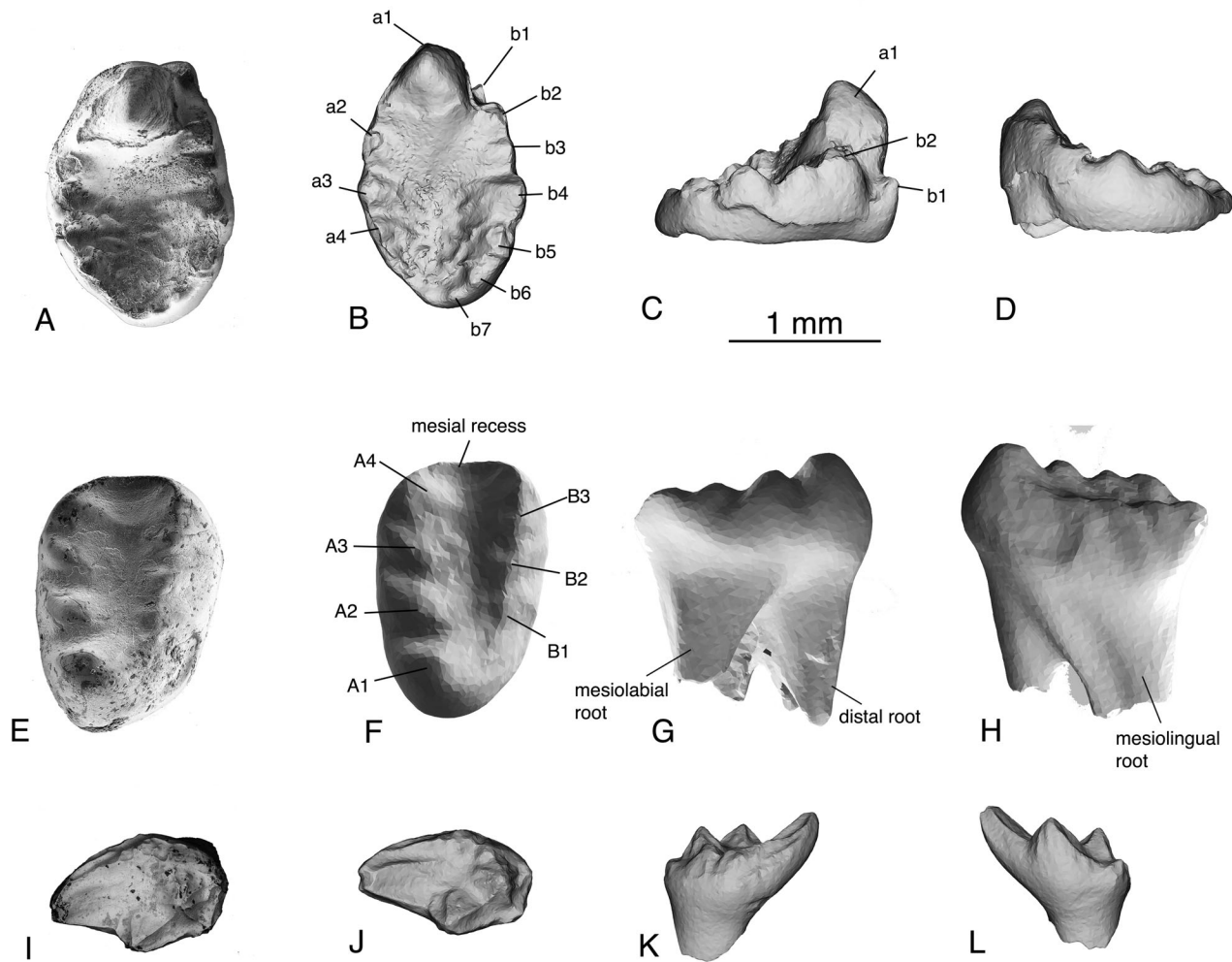


**Figure 9.** Tooth size comparison among selected specimens of the Middle Jurassic euharamiyidans of England. **A**, right P3 (NHMUK PV M 100096) of *Butlerodon quadratus*; **B**, left P4 of *B. quadratus* (NHMUK PV M 102103); **C**, left P4 (NHMUK PV M 105706), possibly of *B. quadratus*; **D**, left M1 (paratype, NHMUK PV M 100090) of *B. quadratus*; **E**, left M2 (NHMUK PV M 102102) of *B. quadratus*; **F**, right m1 (NHMUK PV M 100089, holotype) of *B. quadratus*; **G**, left M1 (holotype, NHMUK PV M 46460) of *Kermackodon oxfordensis*; **H**, left I2 (NHMUK PV M 105711) of *B. quadratus*; **I**, right P3 (NHMUK PV M 46497) of *K. oxfordensis* (this is the holotype of “*Kirtlingtonia catenata*”, originally identified as a right upper molar [Butler & Hooker 2005]; see Discussion); **J**, left P4 (NHMUK PV M 46822) of *K. oxfordensis* (this is the holotype of “*Kermackodon multicuspis*”, originally identified as a left M2 [Butler & Hooker 2005]); **K**, right I2 (NHMUK PV M 105718) of *Woodeatonia parva* gen. et sp. nov.; **L**, left P3 (NHMUK PV M 46818) of *W. parva* (this upper premolar was assigned to “*Kirtlingtonia catenata*” [Butler & Hooker 2005]); **M**, right P4 (NHMUK PV M 46562) of *W. parva* (originally identified as an undetermined haramiyidan molar [Butler & Hooker 2005]); **N**, right M1 (NHMUK PV M 100088, paratype) of *W. parva*; **O**, right m1 (NHMUK PV M 105714, holotype) of *W. parva*; **P**, left m2 (photographically reversed horizontally; NHMUK PV M 46183) of *W. parva* (originally identified as a right lower molar [Kermack *et al.* 1998]) but later re-identified as a lower left m3 and assigned to “*Millsodon superstes*” [Butler & Hooker 2005]). All teeth are on the same scale. See Discussion for tooth reinterpretation and association.

cusps. A1 is the largest cusp and forms the distal portion of the crown; other A cusps gradually reduce in size mesially. B cusps are small and subequal in size.

The central basin is shallow and does not have a distal notch. There is a recess at the mesial end of the crown, which is probably created by contact with cusp a1 of





**Figure 10.** Teeth of *Woodeatonia parva* gen. et sp. nov. from Woodeaton Quarry. **A**, SEM image of NHMUK PV M 105714 (holotype) in occlusal view. **B–D**, CT-scan rendered images in occlusal, buccal, and lingual views of NHMUK PV M 105714. **E**, SEM image of NHMUK PV M 100088 (paratype) in occlusal view in contrast to the paratype of *Butlerodon quadratus* (NHMUK PV M 100089), showing the difference of size and shape (on the same scale). **F–H**, CT-scan rendered images in occlusal, buccal, and lingual views of NHMUK PV M 100088. **I**, SEM image of the right upper incisor (NHMUK PV M 105718) in occlusal view. **J–L**, CT-scan rendered images in occlusal, lingual, and buccal views of NHMUK PV M 105718.

the lower molar that is likely positioned near the longitudinal axis; this seems consistent with the a1 condition of NHMUK PV M 105714. The tooth has two separate roots instead of a fused and robust one. The distal root supporting A1 is small while the mesial one is large and consists of two portions: a major lingual part (mesiolingual root) and a minor buccal part (mesiolabial root) (Fig. 10G, H).

NHMUK PV M 105718 (Fig. 10I–L). This is a right upper incisor. Although its crown morphology is generally similar to those assigned to *Butlerodon* (Fig. 5), it is the smallest upper incisor (length/width = 1.177/0.807 mm) in the collection, in sharp contrast to those of *Butlerodon* (Fig. 9). Similar to the upper

incisors of *Butlerodon*, NHMUK PV M 105718 has a main procumbent cusp that is followed by two sizeable distal cusps and several minor cusps. The main cusps bear enamel ridges. This incisor also differs from those of *Butlerodon* in lacking the medial contact facet; in this regard it is similar to that of *Xianshou linglong* (Bi *et al.* 2014) in which there is a small I1 so that the enlarged I2s did not contact each other on the midline. Whether I1 was present in *Woodeatonia parva* is unknown. Without the contact facet on the medial side of the tooth, the tooth is identified as a right incisor because the second cusp is at the lateral side of the crown, as in those of *Butlerodon* (Fig. 5).

**Remarks.** Compared to *Butlerodon quadratus* and *Kermackodon oxfordensis*, *Woodeatonia parva* is small (Fig. 9). It is distinctive in having a predominant a1 positioned on the longitudinal axis of m1. Unlike many other euharamiyidans, the degree of a1 enlargement and the general profile of the tooth are similar to those of *Arboroharamiya jenkinsi* (Zheng *et al.* 2013; Meng *et al.* 2014), but the latter is much larger in absolute size, lacks cusp b1, and has strong a and b cusps (Zheng *et al.* 2013; Meng *et al.* 2014). Presence of a small b1 contrasts it with *B. quadratus* which has an enlarged one; it also differs from taxa that lack b1, such as *K. oxfordensis*. The upper molar (NHMUK PV M 100088) is unique among known “haramiyidans” in having a large A1 but weak B cusps and the central basin does not have a distal notch or saddle. It further differs from the Triassic forms in having A1, instead of A2, as the largest A cusp; it differentiates from the Jurassic forms in having A cusps gradually reducing in size mesially. In other Jurassic species, A1 and AA are large and separated by a series of small cusps or a ridge. The identification of NHMUK PV M 100088 remains to be tested with new discoveries.

**Haramiyida incertae sedis**  
(Fig. 11)

**Description.** NHMUK PV M 105710 (Fig. 11A). This tooth is identified as a left upper molar (length/width=2.15/1.92 mm). It is low-crowned with cusp A1 being proportionally small and slightly distobuccally extended so that the tooth crown is wide distally, unlike other upper molars examined in this study. As in other upper molars, such as NHMUK PV M 100090, the cusp in the middle of row B is the largest (highest). However, the B cusps are proportionally small, compared to specimens that can be identified to species. There are additional small cusps and enamel ridges buccal to row B so that the lingual side of the basin forms a rough surface. There is no enlarged cusp AA, which is similar to the upper molar of *Woodeatonia parva* (Fig. 10E) but differs from other “haramiyidans”. These differences suggest that NHMUK PV M 105710 may belong to a new taxon. Given the limited material, we tentatively treat this molar as “Haramiyida” *incertae sedis*.

NHMUK PV M 100094 (Fig. 11B–D). This is a damaged tooth and covered with thick glue, so only its CT images are presented. Much of the tooth crown is broken. Weak enamel ridges exist in the tooth basin. Its single root is strong but simple, and tapers distally, suggesting a molar.

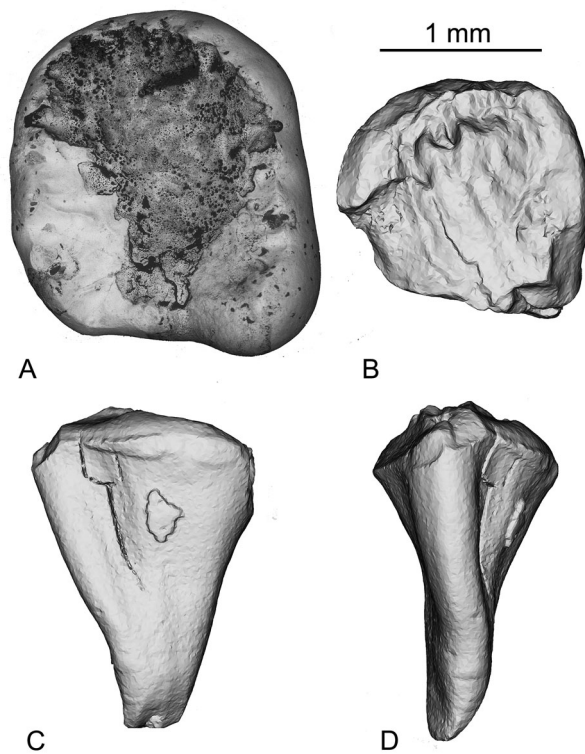
**Multituberculata** Cope, 1884  
**Hahnotheriidae** Butler & Hooker, 2005

**Hahnotherium cf. H. antiquum** Butler & Hooker, 2005  
(Fig. 12A, B)

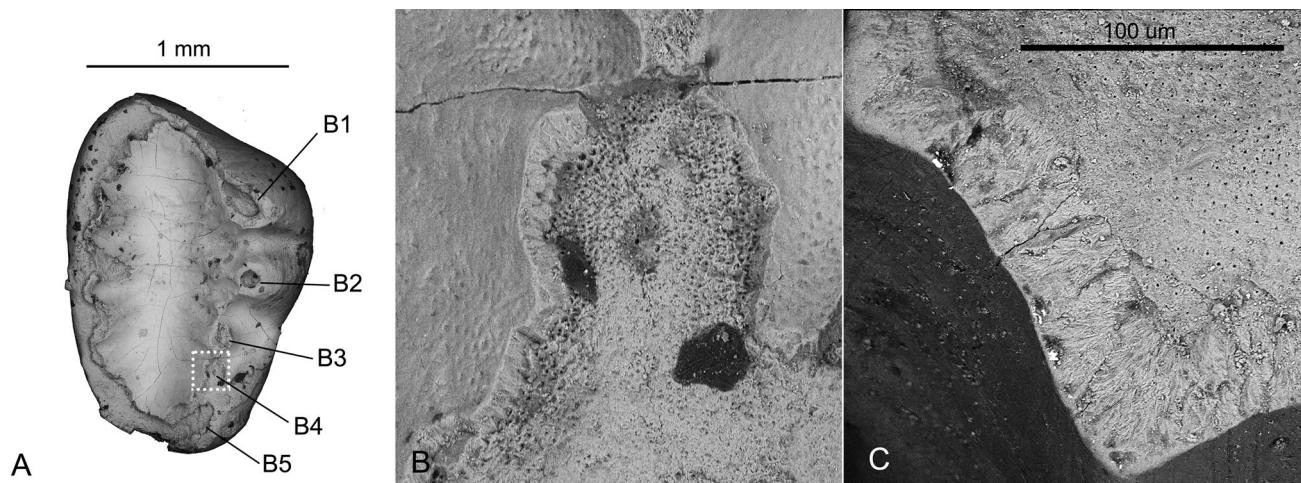
**Referred specimen.** A left M2 (NHMUK PV M 102104; Fig. 12A) (length/width= 1.78/1.22 mm).

**Description.** This tooth has been tentatively identified as belonging to *Hahnotherium antiquum* (Wills *et al.* 2019). It is partly eroded and the enamel layer on the lingual side has been peeled off. However, the general profile of the tooth crown, the cusp size and shape, and the straight longitudinal central valley indicate a multituberculate. This tooth is similar to the holotype of *Hahnotherium antiquum* (NHMUK PV M 46797) (Butler & Hooker 2005, fig. 6; note that in the caption the specimen number was NHMUK PV M 46717). NHMUK PV M 46797 was originally identified as a left lower molar of “*Eleutherodon*” *oxfordensis* (Kermack *et al.* 1998), but Butler & Hooker (2005) considered it a left second upper molar of a multituberculate. As in NHMUK PV M 46797, NHMUK PV M 102104 is wide mesially and gradually narrows distally. The lingual side of the crown is more mesially extended. The buccal row has five cusps with B1 being the largest, which is followed by a sizable B2; these two cusps are separated by a transverse groove, a feature that does not appear in the molars of “haramiyidans”. Cusps B3 and B4 are conical and significantly smaller than B1 and B2, whereas B5 appears large and crescentic at the distobuccal corner of the tooth. There are enamel ridges that extend transversely from each cusp to the basin floor. These ridges are so fine that in the SEM image the basin floor appears smooth. These fine transverse ridges in a broad and straight central valley are also character that differs from the molar of “haramiyidans”. On the mesial end of the tooth, there is a large contact facet, most of which is on the root. This facet indicates an M1 with a relatively wide and flat distal end and is another feature that differs from the M2 of “haramiyidans”. The wear facets on B cusps are similar to those on NHMUK PV M 46797 in that the buccal parts of the facets incline to face ventrobuccally, indicating the typical M2 occlusion of multituberculates in which the buccal cusp row of M2 bites in the valley of m2. This MM2 occlusal mode was considered as a shared feature of multituberculates and euharamiyidans (Meng *et al.* 2014; Mao & Meng 2019b).

The tooth has three roots: two mesial roots and one distal one, as indicated by the bases of the broken roots. Of the two mesial roots the lingual one is larger while the distal root is the largest of the three. The mesial and roots are separated by a considerable space. The root condition appears different from that of NHMUK PV M 46797 (BDUC J.797), as described by Kermack *et al.*



**Figure 11.** Teeth of “Haramiyida” *incertae sedis* from Woodeaton Quarry. **A**, occlusal view of left upper molar (NHMUK PV M 105710); **B–E**, occlusal, lateral, and distal views of a partial lower molar? (NHMUK PV M 100094).



**Figure 12.** The second upper molar of *Hahnotherium* cf. *H. antiquum* (NHMUK PV M 102104) from Woodeaton Quarry. **A**, occlusal view of the M2; **B**, close-up view of the boxed area in **A**, showing the sign of enamel prisms; **C**, natural fractural section at the tip of the upper incisor of *Butlerodon* (NHMUK PV M 105707), showing the prismless and columnar divergent enamel.

(1998, p. 597): “There are three roots arranged in a triangle: two lingually and one buccally. Stumps of the lingual roots remain; the buccal root has been completely broken away”. However, Butler & Hooker (2005, p. 200) wrote instead: “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”. Because the mesiobuccal root is the smallest of the three in NHMUK PV M 102104 and the same area was broken in NHMUK PV



M 46797, it is not conclusive that the root condition is so different in the two teeth; we would predict that they are similar. In either case, however, the multi-root condition is another possible feature in which multituberculates differ from euharamiyidans.

Moreover, as revealed by SEM imaging (Fig. 12B) the enamel shows sign of the prisms in the naturally fractural section and in the worn surface of the tooth. The prism density varies at different depths within the enamel layer and when the enamel was slightly worn they will show as circular pits on the enamel surface (Mao *et al.* 2015). These features are visible in NHMUK PV M 46797, which is another piece of evidence supporting its identification as a multituberculate. In contrast, the enamel of the euharamiyidans is basically prismless and consists of columnar divergence units of crystallites so that on the enamel surface or tangential section, there is no circular structure (Mao *et al.* 2017). Similar enamel microstructure is present in the naturally fractured section of the upper incisor of *Butlerodon* (Fig. 12C). On worn surfaces of other teeth assigned to euharamiyidans, there is no sign of the prisms.

**Remarks.** Averianov *et al.* (2021) provided the most recent summary about the earliest known multituberculates. The authors recognized that M2 of the Middle Jurassic multituberculates differs from those of advanced multituberculates by having a larger number of cusps and a ridge-like lingual cusp row; they also considered that *Hahnotherium* is more primitive in having five buccal cusps, compared to other Jurassic forms in which the buccal cusps of M2 range from two to four (Yuan *et al.* 2013; Martin *et al.* 2021). Butler & Hooker (2005) considered *Hahnotherium antiquum* as one of the earliest multituberculates. The age range of the genus would be slightly extended by NHMUK PV M 102104, given the lower stratigraphical position of the mammal-bearing bed in Woodeaton Quarry (Wills *et al.* 2019). NHMUK PV M 102104 shows again that the chronologically older multituberculate has five buccal cusps on M2 and that the tooth is proportionally long with relatively simple structures.

Although the general shape and buccal cusp number of NHMUK PV M 102104 are similar to the holotype of *Hahnotherium antiquum*, differences do exist. The central valley of NHMUK PV M 102104 is gently broad and is even in width. Because of the fine ridges from the cusps, the basin floor appears smooth. In NHMUK PV M 46797, the enamel ridges leading from the cusps to the central valley are more pronounced and make the basin floor rugged. Cusps b3 and b4 are conical and b4 is distal to b3 in NHMUK PV M 102104. In NHMUK PV M 46797, b3 is transversely extended and b4 is more buccally positioned at the margin of the tooth.

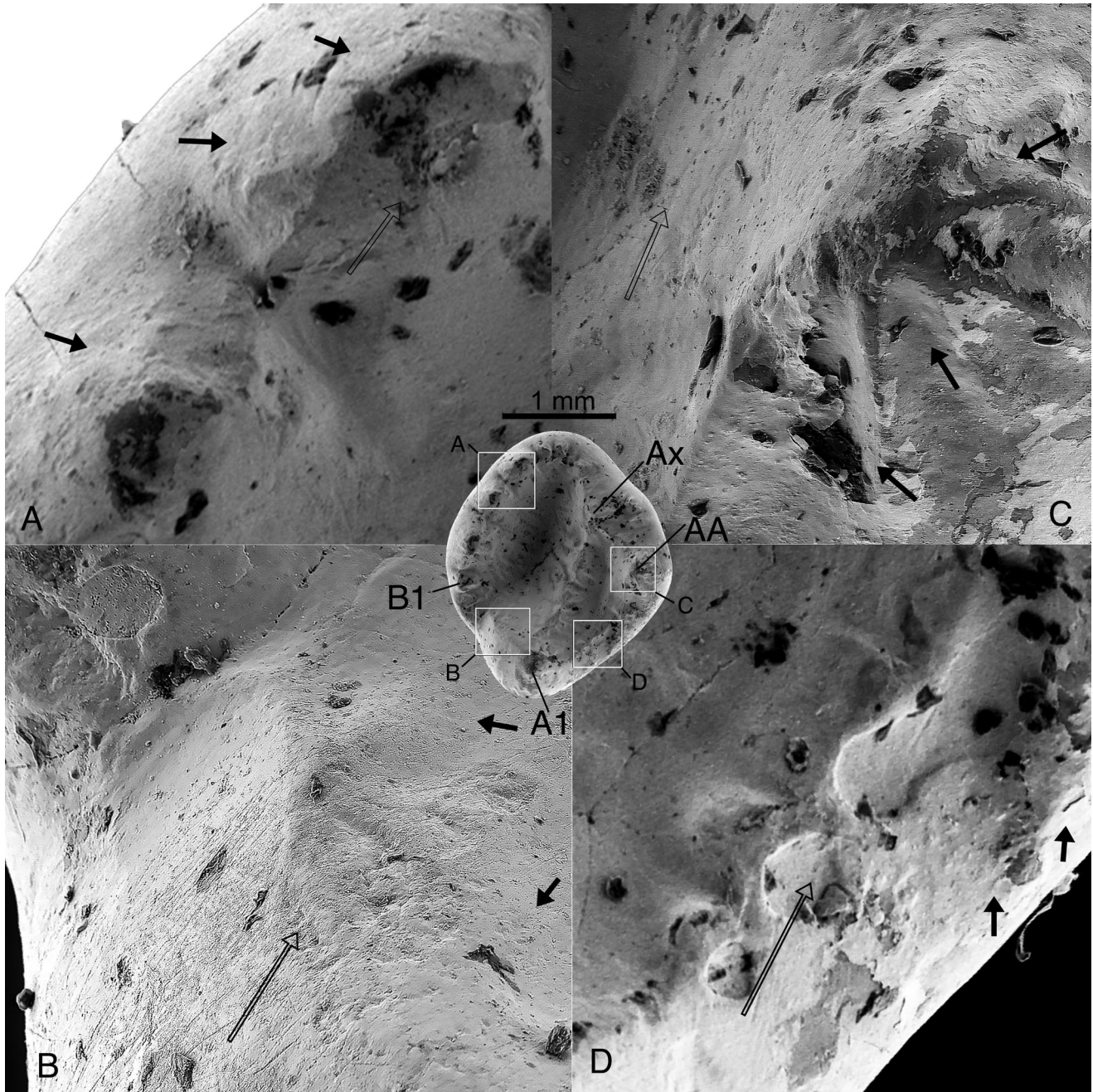
Because of these differences, we assign this tooth as *Hahnotherium* cf. *H. antiquum*. NHMUK PV M 102104 is similar in general shape to M2 of *Tagaria antiqua*, a multituberculate from the Middle Jurassic (Bathonian) Itat Formation, Western Siberia, Russia (Averianov *et al.* 2021). However, there are also differences between the two specimens. M2 of *T. antiqua* has three buccal (B) cusps that are more robust and has many enamel ridges derived from the cusps, which fill the tooth basin; the latter feature is more similar to NHMUK PV M 46797. As in other Jurassic multituberculates, the cusp size of NHMUK PV M 46797 changes gradually, with the mesiobuccal cusp the largest in M2. In Jurassic euharamiyidans, A1 (distobuccal) is the largest cusp that commonly extends distally and cusps between cusp A1 and AA are considerably small or absent. The configuration of the central valley in NHMUK PV M 102104 and other M2s assigned to multituberculates is distinctive from the basined tooth floor of euharamiyidans and suggests a relatively horizontal movement of chewing, as already noted for *Hahnotherium* by Butler & Hooker (2005). It is clear that the upper molars of the Middle Jurassic multituberculates and euharamiyidans are different in cusp shape, cusp size variation, basin shape, M1–M2 contact relation, tooth root, and enamel microstructures.

## Discussion

### Tooth wear and occlusion

Kermack *et al.* (1998) and Butler & Hooker (2005) have discussed the tooth wear of haramiyidan specimens from the Kirtlington Quarry. Kermack *et al.* (1998, figs 2, 22) provided SEM figures showing longitudinal wear striations on lower and upper molars as well as a ‘map’ of wear facets on molars. Here we provide more detailed SEM photographs supplementing wear details of the holotype specimen (NHMUK PV M 46460) of *Kermackodon oxfordensis* (Fig. 13) in comparison to those of *Butlerodon quadratus* (Fig. 14). The wear facets of *Kermackodon oxfordensis* we recognized largely match what had been mapped by Kermack *et al.* (1998), but those authors did not show the wear on the lingual side of cusp A1 (Fig. 13B). The wear facets on the lingual and buccal sides of A1 are distinct, indicating that A1 is the primary functional cusp that bit in the central valley of the lower molar in occlusion. The wear on the sides of A1 have the features of an attritional facet, which is commonly planar with marginal separation from the surrounding enamel and shows clearly the main direction of striations. These features are produced by tooth–tooth contacts during the power stroke



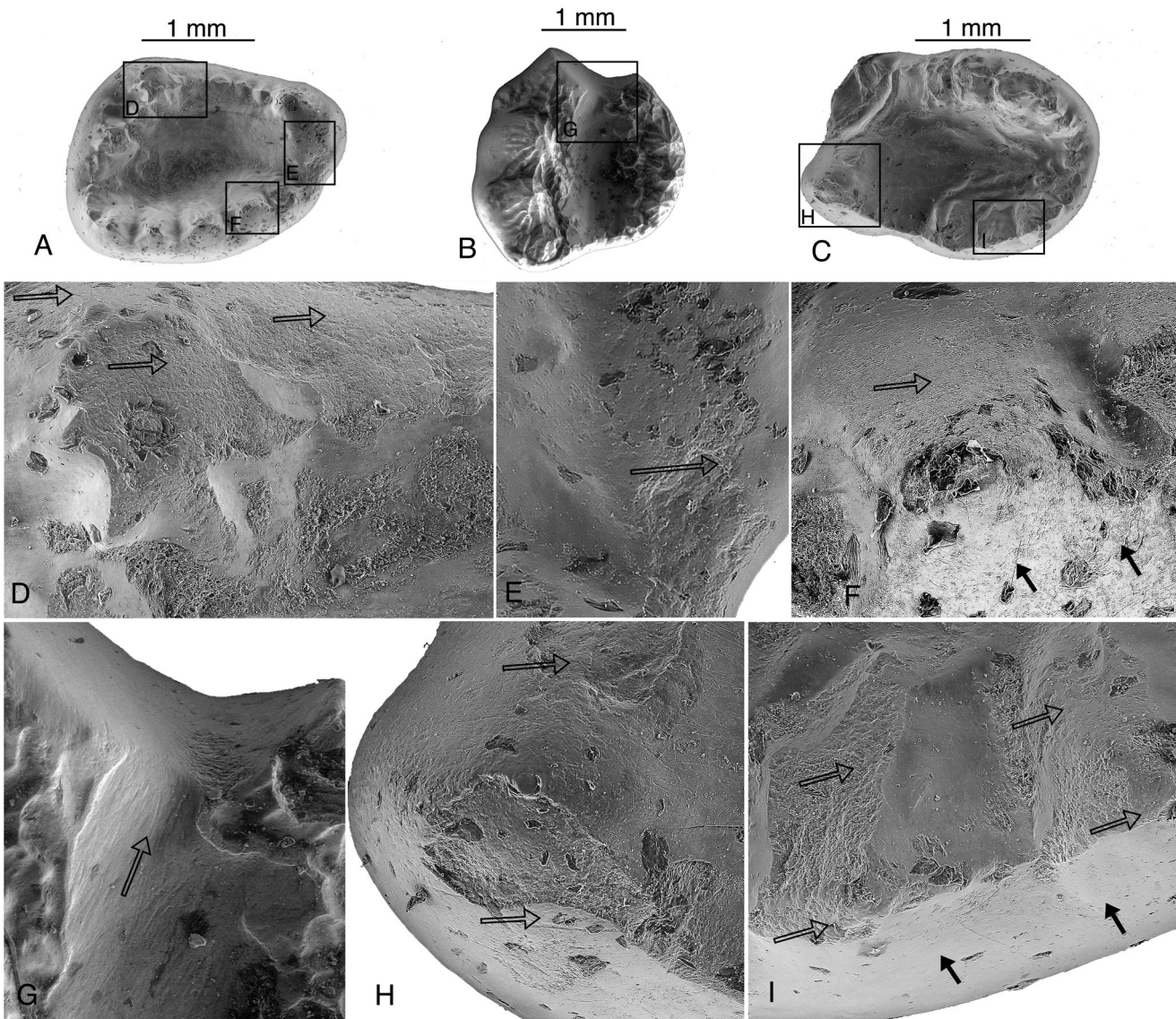


**Figure 13.** Wear pattern of the holotype (NHMUK PV M 46460) of *Kermackodon oxfordensis* from Kirtlington. **A–D**, close-up views corresponding to the boxed areas on the tooth in the centre of the plate. Hollow arrow on wear facet indicates the wear area and direction of striations, which reflect the movement direction of the lower molar. Solid arrow points to unworn area of the tooth.

(Koenigswald *et al.* 2013). The linear striations must be produced by palinal movement of the lower molar against the upper. However, from the uneven topology of the tooth surface it can be inferred that the chewing movement cannot be horizontal, as recognized by Butler & MacIntyre (1994). Wear facets and striations are present only on the lingual side of cusp AA; this is the evidence that cusp AA did not bite into the central basin of

the lower molar but did buccally to row b of the lower molar. Echoing the AA wear, there is notable apical wear on small cusps between A1 and AA (Fig. 13D). These small cusps are much lower than cusps A1 and AA; they must be created by contact with cusp tips of row b of the lower molar and the latter had to move between A1 and AA during mastication. On row B, wear facets are distributed on buccal sides of B cusps, indicating that the





**Figure 14.** Tooth microwear of *Butlerodon quadratus* gen. et sp. nov. **A–C**, SEM images of M1 (NHMUK PV M 100090), P4 (NHMUK PV M 102103) and m1 (NHMUK PV M 105709) in occlusal views. **D–I**, close-up views of wear facets and striations corresponding to the boxed areas in **A–C**. Hollow arrows on wear facets indicate the direction of striations and solid ones point to unworn area of the tooth.

lingual side of row B did not engage in tooth contact when chewing. The above features, along with the extra cusp Ax and row Ax, characterize the “*Eleutherodon*”-occlusal pattern (Mao & Meng 2019b).

In *Butlerodon quadratus* (Fig. 14), wear can be seen on M1, P4 and m1. Fig. 14D–F shows wear of M1 on the buccal side of A cusps, lingual side of A1, and buccal side of B cusps, respectively. The wear patterns on cusp AA and the small cusps between A1 and AA differ from that in *Kermackodon oxfordensis* and show that row A had to bite in the central basin of the lower molar so that the wear can be produced on their buccal

sides instead of on the lingual side of cusp AA and on cusp tips of the small cusps. Wear in row B is present on the buccal sides of the cusps. Corresponding to the wear of the upper molar, m1 wear is on the lingual and buccal sides of a1 and on row a cusps. Because the distal a cusps are much lower than a1, wear is distributed more on the buccal sides than the lingual sides of the cusps. The wear distributions show that the lingual cusps of the lower molar occlude in the central basin of the upper molar.

The most distinct attritional wear is on P4, where the floor of the central basin has been fully worn to form a

longitudinal valley of the tooth length. There is no wear on either the lingual or buccal surface of the tooth. This wear pattern indicates that a main cusp, a1 of p4, has occluded in the basin and moved palinally. However, the course of the movement is not horizontal but curved dorsoventrally, as evidenced by the shape of the valley that is deeper in the centre and shallower on the two ends. The mesiodistal orientation of the valley and the striations on the wear facet clearly show the direction of the chewing movement of p4 or jaw movement during occlusion and mastication in life, as already recognized by Kermack *et al.* (1998).

The lower molar (NHMUK PV M 100089, holotype) and upper molar (NHMUK PV M 100090, paratype) of *Butlerodon quadratus* match well in size. Their occlusal relationship can be reconstructed based on tooth wear (Fig. 15A, B). We infer that the tooth occlusal pattern of *B. quadratus* is similar to multituberculate M2/m2 occlusion, termed the MM2 mode (Mao & Meng 2019b), in which the lingual row of the lower molar bites in the central basin of the upper molar and the buccal cusp row of the upper molar bites in the basin of the lower molar. In particular, cusp AA of the upper molar bites in the central basin or lingual to the buccal row of the lower molar. This occlusal pattern is present in *Shenshou* and *Qishou* from the Yanliao Biota and euharamiyidans from the Siberian Jurassic (Averianov *et al.* 2019a); it is different from, and probably more primitive than, the “*Eleutherodon*”-mode in *Kermackodon oxfordensis* in which cusp AA is buccal to, row b of the lower molar (Mao & Meng 2019b). The length of the central valley of P4, created by contact with a1 of p4, likely reflects the minimum distance of the palinal movement of the lower jaw.

Because of the poor preservation, wear facets are not clear in *Woodeatonia parva*. However, its cusp size and shape show that cusps a1 and A1 are the primary functional cusps, as in other euharamiyidans, and the tooth occlusal relationship can be reconstructed as in Figure 15C, D. It is clear that the occlusal patterns of *Kermackodon*, *Butlerodon* and *Woodeatonia* differ, but they share a common feature: as in other euharamiyidans, with the exception of *Maiopatagium furculiferum*, the lingual cusp row of the lower molar bites in the central basin of the upper molar. This is an important configuration that affects recognition of the primary cusp row and cusp homology and interpretation of the evolution of “haramiyidans”.

### Reinterpretation of teeth

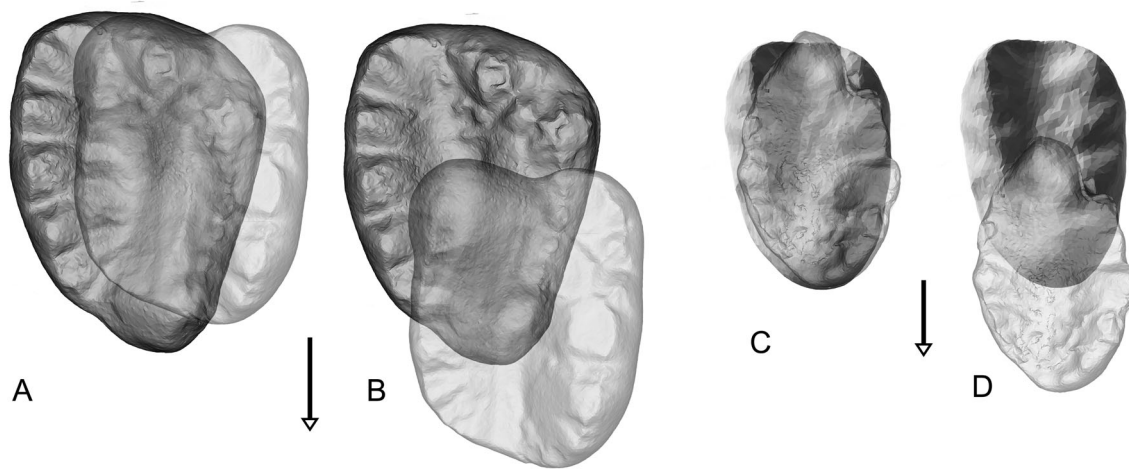
Here we present our reinterpretation for the teeth previously assigned to “*Millsodon*”, “*Kirtlingtonia*” and “*Kermackodon multicuspis*” (Butler & Hooker 2005),

which justifies the nomenclatural action in replacing the preoccupied generic name “*Eleutherodon*” with *Kermackodon*. These teeth are from the Forest Marble Formation of Oxfordshire and Dorset and have been described in detail by Kermack *et al.* (1998) and Butler & Hooker (2005). We reinterpret that most of these teeth are from different upper or lower tooth loci of the same haramiyidan species, *Kermackodon oxfordensis*.

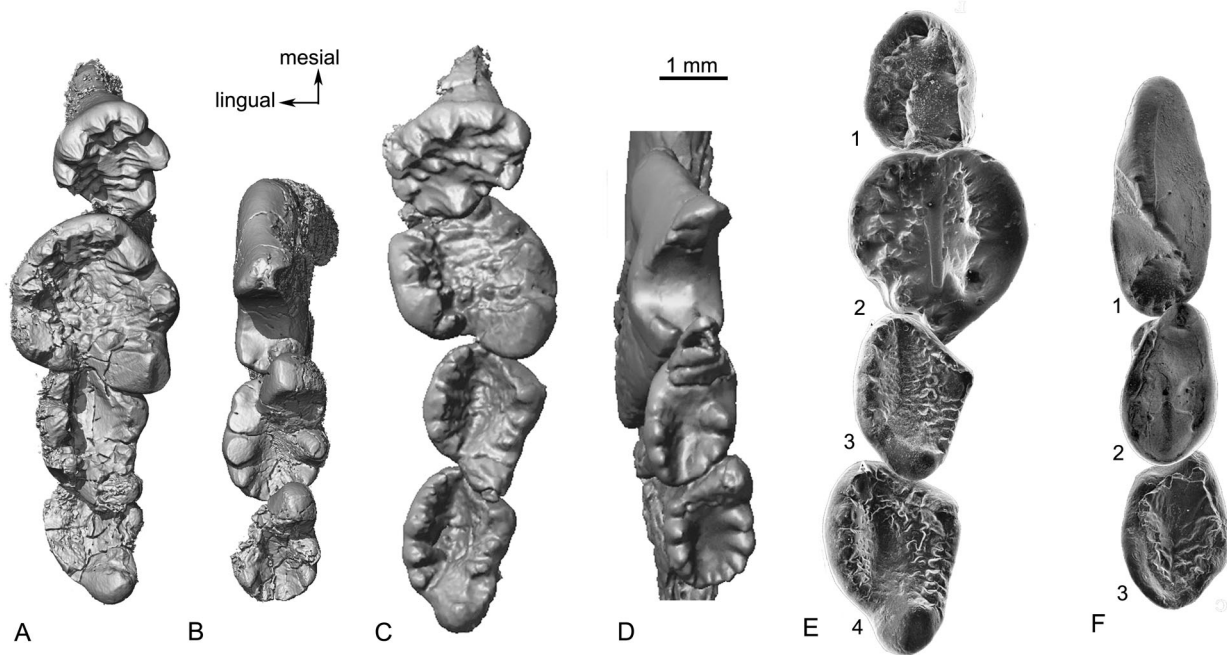
“*Millsodon*”. The type species of the genus is “*Millsodon superstes*”, which was based on three specimens: NHMUK PV M 46645 (holotype), NHMUK PV M 46183 (paratype), and BDUC J 3 (referred specimen). The holotype of “*M. superstes*” was provisionally identified as an m1 (Butler & Hooker 2005, fig. 1D), which we support here. This tooth was heavily worn so that its size was likely altered (reduced, particularly narrowed) and cusps were erased except for cusp a1. However, its fusiform shape with a1 near the longitudinal axis of the tooth is clear. As noted by Butler & Hooker (2005), this tooth is similar in size and shape to the lower molar (NHMUK PV M 46461) reported by Kermack *et al.* (1998), except that its a1 is lingual (originally identified as buccal) near the longitudinal axis of the crown. As shown in *Arboroharamiya* (Zheng *et al.* 2013; Meng *et al.* 2014) and *Vilevolodon* (Luo *et al.* 2017), cusp a1 on m1 is proportionally larger and positioned near the longitudinal axis, whereas a1 of m2 is relatively smaller and more buccally positioned. As noted by Butler & Hooker (2005), NHMUK PV M 46645 is also similar to the holotype of *Allostaffia aenigmatica* (Heinrich 1999, 2001) that has a1 on the middle line of the lower tooth and may have a different type of tooth occlusion (Mao & Meng 2019b). For the teeth from the same localities that have similar size and morphology, it appears better to interpret them as from different tooth loci rather than from different genera and species. We reinterpret NHMUK PV M 46645 as m1 and NHMUK PV M 46851 (Kermack *et al.* 1998, fig. 15A) and NHMUK PV M 46461 as m2 of *Kermackodon oxfordensis* (Fig. 16F).

NHMUK PV M 46183 was originally identified as a right lower molar by Kermack *et al.* (1998) but later re-identified as a lower left m3 and used as the paratype of “*Millsodon superstes*” (Butler & Hooker 2005, fig. 1E). This tooth is indeed most likely an ultimate lower molar and based on the fact that all Jurassic euharamiyidans from Yanliao Biota have two molars in each jaw quadrant, we reinterpret this tooth as a left m2. The tooth is small (length/width = 1.6/1.15 mm); it does not match the size of m1 (NHMUK PV M 46645) and the holotype upper molar of *K. oxfordensis* (Fig. 9) but fits well in shape and size to the teeth of *Woodeatonia parva* gen. and sp. nov. (Fig. 9P); thus, we assign this tooth to





**Figure 15.** Inferred molar occlusal relationship in *Butlerodon quadratus* (A, C) and *Woodeatonia parva* (B, D). A, C, at the occlusal position. B, D, at the end of the chewing stage. The lower teeth are photographically rendered to be semi-transparent. The upper molar of C, D is horizontally flipped. Each pair of teeth is at the same scale, but not to scale between the pairs.



**Figure 16.** Tooth association of *Kermackodon oxfordensis* in comparison with dentitions of *Xianshou* and *Vilevolodon*. A, B, occlusal views of upper and lower dentitions of *Xianshou linglong*. C, D, occlusal views of upper and lower dentitions of *Vilevolodon diplomylos* (modified from Luo *et al.* 2017 with permission from *Nature*). E, F, occlusal views of reconstructed upper and lower dentitions of *K. oxfordensis*. E1, P3 (NHMUK PV M 46497), holotype of “*Kirtlingtonia catenata*”; E2, P4 (NHMUK PV M 46822), holotype of “*Kermackodon multicuspis*”; E3–4, M1–M2 (NHMUK PV M 46821 and NHMUK PV M 46832); F1, p4 (NHMUK PV M 46684), referred to “*Kermackodon multicuspis*”; F2, m1 (NHMUK PV M46645), holotype of “*Millsodon superstes*”; F3, m2 (NHMUK PV M 46851), referred to “*Eleutherodon*” *oxfordensis*. Images of E and F are modified from Butler & Hooker (2005). For comparison some teeth have been photographically reversed to make all consistently as left teeth. All teeth are on the same scale.



*W. parva* (included in the referred specimens of the species).

BDUC J 3 was identified as a possible left upper molar (Butler & Hooker 2005, fig. 4A). This tooth is peculiar in its cusp morphology, arrangement, and wear. Butler & Hooker (2005) considered it as representing a hitherto unknown type of “haramiyidan”, possibly a derivative of Theroteinidae, or a specialized relative of “haramiyids”. Hahn & Hahn (2006) thought that this tooth has the same basic structure of the upper molar of *Theroteinus*, whereas Debuyschere (2016) argued that it can be compared with the lower molars of *Theroteinus*. All these interpretations, however, converge on theroteinids, and if so, it represents a temporal extension of *Theroteinus* from the Late Triassic to the Middle Jurassic. Given the peculiarity of this tooth and the uncertainty of its being an upper or lower molar, we would not assign it to any species but echo that it is a hitherto unknown type of “haramiyidan”.

“*Kirtlingtonia*”. “*Kirtlingtonia catenata*” was based on three teeth: NHMUK PV M 46497 (holotype, originally identified as a right upper molar), NHMUK PV M 46579 (paratype, a right upper molar; note the number ‘M46183’ in Butler & Hooker 2005, fig. 1G appears to be a typo) and NHMUK PV M 46818 (a referred left upper premolar); all are from the Kirtlington Mammal Bed, Oxfordshire. The two teeth identified as right upper molars are highly similar in morphology despite the partial breakage of NHMUK PV M 46579. Based on the undivided root in NHMUK PV M 46579, the two teeth were regarded as ultimate upper molars (Butler & Hooker 2005). However, Butler & Hooker (also in Hahn & Hahn 2006) noted many differences these teeth have from the upper molars of *Kermackodon oxfordensis*.

We reinterpret NHMUK PV M 46497 and NHMUK PV M 46579 as the penultimate upper premolars (P3) of *Kermackodon oxfordensis*, which can be associated with the molars and P4 of the species (Fig. 16E). These teeth differ from the molar pattern in other “haramiyidans” in cusp shape and arrangement so that the cusps were denoted differently (Butler & Hooker 2005); instead, they have some upper premolar features, such as there are only a few main cusps that are conical and relatively small and uneven, the cusp bears a pointed tip from which fine enamel ridges (flutings) radiate on cusp slopes in all directions, and there is an internal line of minute cusps that curves towards the large cusp that is about midway down one side, which is not present in any known upper molar of euharamiyidans. These structures, along with tooth size and cusp number, are similar to those of the penultimate premolar of some euharamiyidans, such as *Xianshou* and *Vilevolodon* (Fig. 16).

The tooth crowns of NHMUK PV M 46497 and NHMUK PV M 46579 are longer than wide, consistent with the dimensions of P3 in Yanliao euharamiyidans. In contrast, P4 is commonly wider than long. With the new interpretation, the orientation of the tooth has been changed: the largest cusp, originally denoted as cusp ‘a’ that is at the mesiobuccal corner of the crown (Butler & Hooker 2005), is now regarded as being at the distobuccal end of the crown (Fig. 16E).

NHMUK PV M 46818 is a very small upper premolar and Butler & Hooker (2005) considered it either coming from a smaller species or occupying a different locus in the dentition. Given our re-interpretation of NHMUK PV M 46497 and NHMUK PV M 46579 as P3s of *K. oxfordensis* and the small size of NHMUK PV M 46818, the latter can only be interpreted as P2. This implies that *K. oxfordensis* has at least three upper premolars. The upper premolars were unknown in *Haramiyavia*, but based on its lower dentition that has four premolars, it is possible that the upper dentition has more than two premolars. As a general pattern in allotherians, the upper premolars could be as few as, but never fewer than, the lower ones. In most cases, there are more upper premolars than lower ones, which forms the physical basis for palinal chewing. In all published euharamiyidan specimens from the Yanliao Biota, there are two upper premolars and one lower premolar. However, a new specimen of an unnamed euharamiyidan (unpublished data) possesses three upper premolars, including a large P4 and two smaller and subequal mesial premolars (P3 and P2). Although it is probable that *K. oxfordensis* could have three upper premolars, NHMUK PV M 46818 appears to be still too small to be P2 of *K. oxfordensis*. Another possibility is that NHMUK PV M 46818 belongs to a different species, which is what we advocate in this study. Based on its small size, the only referable species is *Woodeatonia parva* in which the tooth may be interpreted as P3 (Fig. 9). We have assigned this tooth to *W. parva* as a referred specimen.

**Kermackodon.** The type species is “*Kermackodon multicuspis*” and the genus was placed in the monotypic family Kermackodontidae under Suborder *incertae sedis* within Multituberculata. The species was based on three isolated teeth, of which the holotype was identified as a left upper molar (M2) (NHMUK PV M 46822; Butler & Hooker 2005, fig. 6A; note that in the figure caption the tooth was denoted as a ‘right M2’). The referred specimens are NHMUK PV M 46684 (a left p4) and NHMUK PV M 46640 (a partial upper premolar). Butler & Hooker (2005) noted the differences of NHMUK PV M 46822 from upper molars of multituberculates and “haramiyidans” when they reported these

teeth. At the time, there was no unequivocal evidence of the ultimate upper premolar of “haramiyidans”, so the multituberculate M2 became the best possible interpretation.

NHMUK PV M 46684 was identified as a left p4 of a multituberculate mainly because of its longitudinal serrated blade with oblique ridges, and the distobuccal series of small cusps (Butler & Hooker 2005). As noted by Butler & Hooker (2005), however, there are many differences between this tooth and a typical multituberculate p4, such as the triangular profile of the main cusp (blade), large size compared to p4 of Jurassic paulchofatiids, serrations unequally spaced, and lack of the concavity at the mesial end for receiving p3. At the time, possible ultimate lower premolars of “haramiyidans” for comparison were those from the Triassic *Thomasia* (Sigogneau-Russell 1989) and *Haramiyavia* (Jenkins *et al.* 1997), which differ considerably from NHMUK PV M 46684.

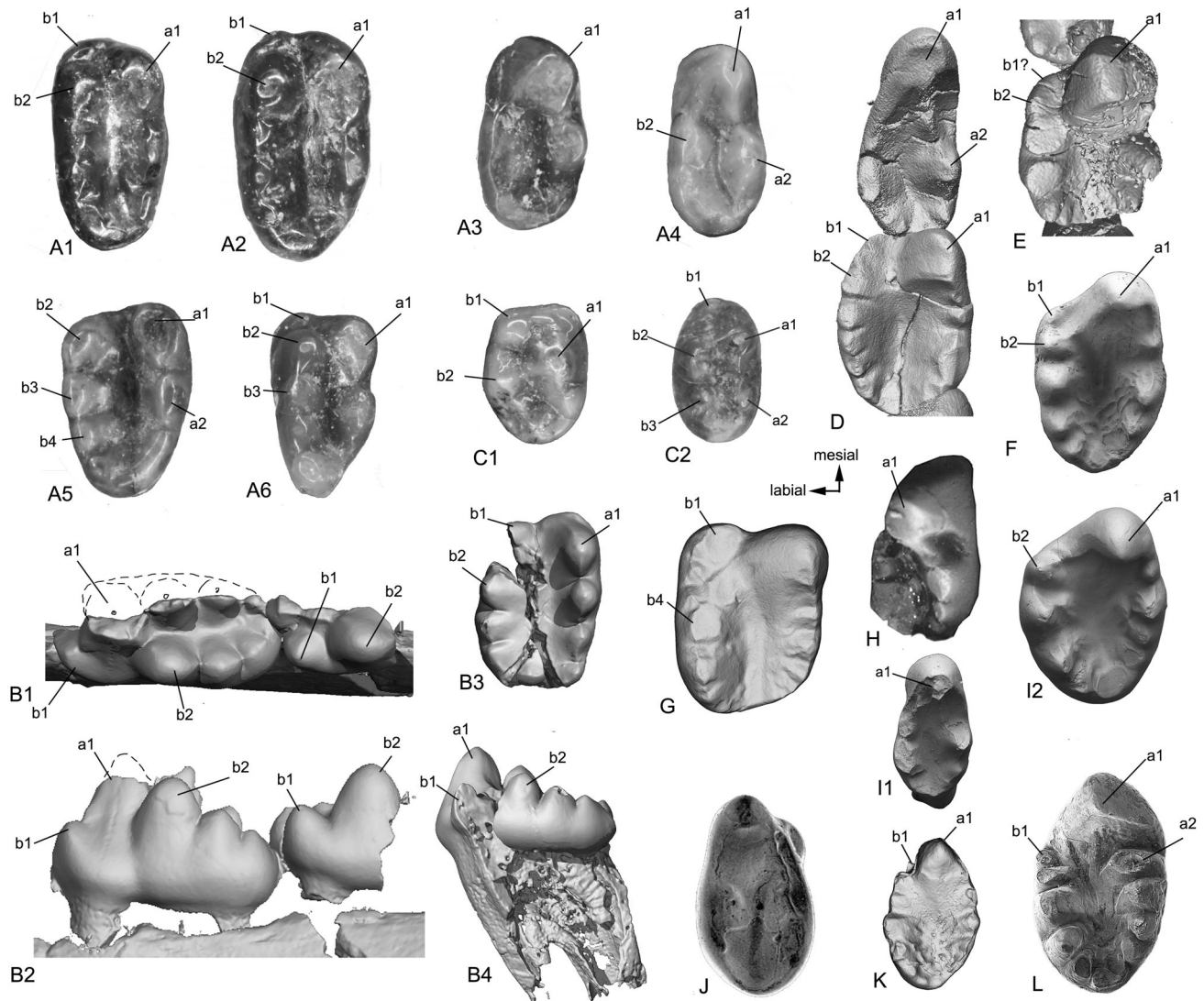
With more discoveries of Jurassic multituberculates and “haramiyidans” during the last two decades, particularly those from the Jurassic Yanliao Biota, it becomes obvious that the holotype of “*K. multicuspis*” is better interpreted as an ultimate left upper premolar (P4) of a euharamiyidan (Fig. 16E). The morphology of the Jurassic multituberculate M2 (Yuan *et al.* 2013; Averianov *et al.* 2021; this study) is characterized by features that are highly different from that of NHMUK PV M 46822. The latter has a heart-shaped profile in occlusal view and is relatively wide and basined with cusps on the buccal and lingual sides; its sharp cusps with radial enamel flutings are connected by longitudinal crests. These features are typical of P4 in euharamiyidans. In the Jurassic euharamiyidans, the p4 in some species, such as *Arboroharamiya*, *Xianshou* and *Vilevolodon*, is highly specialized, having a hypertrophic al and reduced distal portion of the crown so that the tooth crown is triangular in lateral view, closely similar to NHMUK PV M 46684.

Averianov *et al.* (2021) still considered *Kermackodon* a multituberculate because of the horizontal rather than basined wear on the surface of NHMUK PV M 46822 and the presence of serrations on the p4; they further inferred that morphologically the teeth of *Kermackodon* and *Megaconus* (see Meng *et al.* 2014 for a discussion of this taxon) are transitional between euharamiyidans and the Middle Jurassic multituberculates. The wear on the tooth (NHMUK PV M 46822) is a narrow groove that gradually narrows distally and ends mesial to the distal end of the crown (Fig. 9J). This wear pattern does not look like any in a multituberculate M2; it is most likely created by a pointed cusp of the lower tooth, such as a1 of NHMUK PV M 46684, that furrows through

the crown surface of NHMUK PV M 46822. The Woodeaton specimen (NHMUK PV M 102103), interpreted as P4, shows that the wear groove is not horizontal when the tooth is deeply worn. More importantly, both NHMUK PV M 46822 and NHMUK PV M 102103 do not have any wear on the buccal side of the buccal cusp row. Presence of such wear is the most diagnostic feature of the multituberculate M2 because the buccal row occludes in the central valley of m2 in all multituberculates. This is particularly evident in NHMUK PV M 102103 where the central valley has been deeply worn but the lingual and buccal sides of the crown show no sign of wear. The uneven and few serrations on the p4 (NHMUK PV M 46684) are quite different from those of multituberculates, such as the holotype p4 of the multituberculate *Tashytkia* from the Middle Jurassic (Bathonian) Itat Formation from the Berezovsk coal mine in Krasnoyarsk Territory, Western Siberia, Russia, which has many and evenly sized and spaced serrations (Averianov *et al.* 2021, fig. 6), in addition to many other differences already noted by Butler & Hooker (2005). Moreover, new evidence from a Jurassic euharamiyidan (unpublished data; personal observation by FM and JM) shows presence of a few serrations on p4 of euharamiyidans. With all the evidence, it is better to interpret NHMUK PV M 46822 and NHMUK PV M 46684 as P4 and p4, respectively, of the euharamiyidan *Kermackodon oxfordensis*. They are not from a multituberculate.

The referred right upper premolar (NHMUK PV M 46640) is incomplete, not comparable to any tooth of euharamiyidans, so that its identification remained uncertain. Averianov *et al.* (2021) suggested it as a possible deciduous premolar of a multituberculate, but Butler & Hooker (2005) noted that its large size and robust roots make it unlikely to be a deciduous tooth. We tentatively assign it to Multituberculata *incertae sedis*; the possibility that it belongs to *Hahnotherium antiquum* (Butler & Hooker 2005) cannot be ruled out.

**NHMUK PV M 46562 (BDUC J 562).** This tooth was originally identified as an “undetermined haramiyid molar” (Butler & Hooker 2005, p. 194). The authors noted: “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”. Meng *et al.* (2014) regarded this tooth as an upper premolar that is somewhat similar to those assigned to *Sineleutherus issedonicus* (Averianov *et al.* 2011, fig. 1). With NHMUK PV M 46822 being reinterpreted as P4 and NHMUK PV M 46497 and NHMUK PV M 46579 as



**Figure 17.** Comparison of lower cheek teeth from selected taxa of “haramiyidans”. Teeth are in occlusal view except for B2 and B4. **A**, lower teeth of *Thomasia*. **A1**, mesial molar (m1?, SNP 664); **A2**, molar (SNP 338W), **A3**, premolar (p4, SNP 144L); **A4**, lower molar (p4, SNP 66W) (**A3**, **A4** are group *Thomasia* II teeth of Sigogneau-Russell 1989; see also Debuyschere 2015); **A5**, molar (m2, SNP 106W; note absence of b1); **A6**, molar (m2, SNP 490W); **B**, molars of *Haramiyavia* (see also Luo *et al.* 2015). **B1–2**, occlusal and buccal views of the left m1–2; **B3–4**, occlusal and buccal views of left m3. **C**, lower molars of *Theroteinus*. **C1**, molar (m1?, SNP 309W, *Theroteinus rosieriensis*); **C2**, molar (m1?, SNP 61 W, *Theroteinus nikolai*; see also Debuyschere 2016); **D**, cheek teeth (p4–m1) of *Qishou* (modified from Mao & Meng 2019a); **E**, molar (m1) of *Xianshou linglong*; **F**, molar of ‘*Sineleutherus issedonicus*’ (Averianov *et al.* 2019a); **G**, molar (m1) of *Butlerodon quadratus* (NHMUK PV M 100089, holotype); **H**, premolar (p4) of *Shenshou lui*; **I1**, premolar (p4) of *Sharypovia arimasporum* (Averianov *et al.* 2019a); **I2**, molar of *Sineleutherus uyguricus* (Martin *et al.* 2010; Averianov *et al.* 2019a); **J**, molar (m1) of *Kermackodon oxfordensis* (NHMUK PV M46645, holotype of “*Millsodon superstes*”); **K**, molar (m1) of *Woodeatonia parva* (NHMUK PV M 105714, holotype); **L**, molar (m1) of *Arboroharamiya jenkinsi* (Zheng *et al.* 2013; Meng *et al.* 2014). To facilitate comparison some tooth images were photographically reversed (flipped) so that all teeth in crown view are in the same orientation as left teeth. Cusp labelling is from original studies. Teeth are not to scale. Images in F and I are courtesy of A. Averianov.



P3s of *Kermackodon oxfordensis*, the identity of NHMUK PV M 46562 as an upper premolar remains dubious. There exist at least two possibilities: it is a P2 of *K. oxfordensis* or it belongs to a different species. The first possibility means that there must be three upper premolars in *K. oxfordensis*. In all known euharamiyidans from the Yanliao Biota, there are only two premolars in the upper dentitions, denoted as P3 and P4. Nonetheless, an unpublished specimen representing a new species from the Yanliao Biota does possess three upper premolars. Thus, it is possible that *K. oxfordensis* has three upper premolars. However, the crowns of all known P3 and the P2 (in the unpublished specimen) of the Yanliao euharamiyidans are longer than wide, whereas NHMUK PV M 46822 is slightly wider than long, which is typical of P4. Also because of its relatively small size, we tentatively interpret this tooth as a right P4 of *Woodeatonia parva* (Fig. 9M).

**NHMUK PV M 46234 and 46056.** These are two upper incisors, identified as left I2, and assigned to *Allotheria incertae sedis* (Butler & Hooker 2005). These teeth have been compared to I2 of paulchoffatiid *Kuehneodon* and *Henkelodon* as well as those of *Thomasia* (Hahn 1969, 1973), but they were more complex than the other forms. A key feature the two incisors have is the ‘wear’ facet on the medial surface of each tooth. This flat and smooth facet can be better interpreted as the contact facet for the opposite incisor, similar to those in the upper incisors of *Butlerodon quadratus* (Fig. 5) and euharamiyidans from the Jurassic Yanliao Biota, such as *Qishou* (Mao & Meng 2019a). In paulchoffatiid multituberculates, such a contact facet is absent on the upper incisor; this is also true in the upper incisor (I2) of the Middle Jurassic multituberculate *Tashtykia primaeva* (Averianov *et al.* 2021, fig. 2) that has a different and simple crown morphology. Thus, NHMUK PV M 46234 and M 46056 are more likely to belong to a euharamiyidan. We assign these two upper incisors to *K. oxfordensis*.

### Tooth association

Euharamiyidans from the Chinese Jurassic Yanliao Biota show that their dentitions have been highly specialized and display distinctive morphologies. The upper cheek teeth consist of three distinct types: the mesial premolar(s), the ultimate premolar, and the two molars, whereas their lower cheek teeth have two types: the sole premolar and two lower molars. These teeth form different functional units. Except for the peculiar BDUC J 3 and the fragmentary NHMUK PV M 46640, teeth referred to “*Millsodon superstes*”, “*Kirtlingtonia catenata*” and “*Kermackodon multicuspis*” in Butler &

Hooker (2005) can be reinterpreted as from different loci of the upper or lower tooth rows of *Kermackodon oxfordensis* (Fig. 16E, F). The reconstructed upper and lower cheek tooth rows of *Kermackodon oxfordensis* are shown in Figure 16. Using the dentitions of the Yanliao euharamiyidans, such as *Vilevolodon* and *Xianshou*, as a template, we assume that *K. oxfordensis* had one lower premolar (p4) and two upper premolars (p3–4) in each lower and upper jaw and two molars in each jaw quadrant. In general, M2 differs from M1 in having the distally projecting lobe with a large A1 cusp, and m1 differs m2 in having a larger a1 that is more buccally positioned.

It must be noted that because these isolated teeth are most likely from different individual animals, their association as a dentition is only interpretive, illustrating our view about the tooth loci and orientations. For instance, M2 (NHMUK PV M 46821) is larger than M1 (NHMUK PV M 46832) and P4 is not in a perfect alignment with M1; these are probably unnatural owing to the fact that these teeth came from different individual animals. With that in mind, we would consider this association to be largely analogous to those of *Xianshou* and *Vilevolodon* (Fig. 16) that best interpret the identities of these teeth that were previously assigned to different genera and species.

### Tooth occlusion of “haramiyidans”

Tooth occlusal patterns of “haramiyidans” appear to be complicated and controversial, as summarized by Mao & Meng (2019b). There exist at least two views about tooth occlusal pattern in the Triassic species. The conventional view is that the Triassic species have the multituberculate M1/m1 occlusal pattern (Jenkins *et al.* 1997; Butler 2000; Debuyschere 2015; Luo *et al.* 2015), whereas the alternative view advocates the multituberculate M2/m2 occlusal pattern (Meng 2014; Meng *et al.* 2014; Mao & Meng 2019b); these two patterns were termed as MM1 and MM2 mode, respectively (Mao & Meng 2019b). The MM1 tooth occlusal mode for the Triassic species is primarily based on the assumption that in allotherians, with the exception of multituberculate M2/m2, the buccal cusp row of the lower molar occludes in the longitudinal valley between the two rows of the upper molar. The MM2 mode was mainly based on the tooth occlusion present in the Yanliao euharamiyidans, except for *Maiopatagium furculiferum* (Meng *et al.* 2017), in which row a of the lower molar bites between rows A and B of the upper molar. Thus, if the Triassic species had the MM1 mode, there must be a chewing function ‘jump’ from MM1 to MM2 during the evolution of “haramiyidans” (Mao & Meng 2019b).

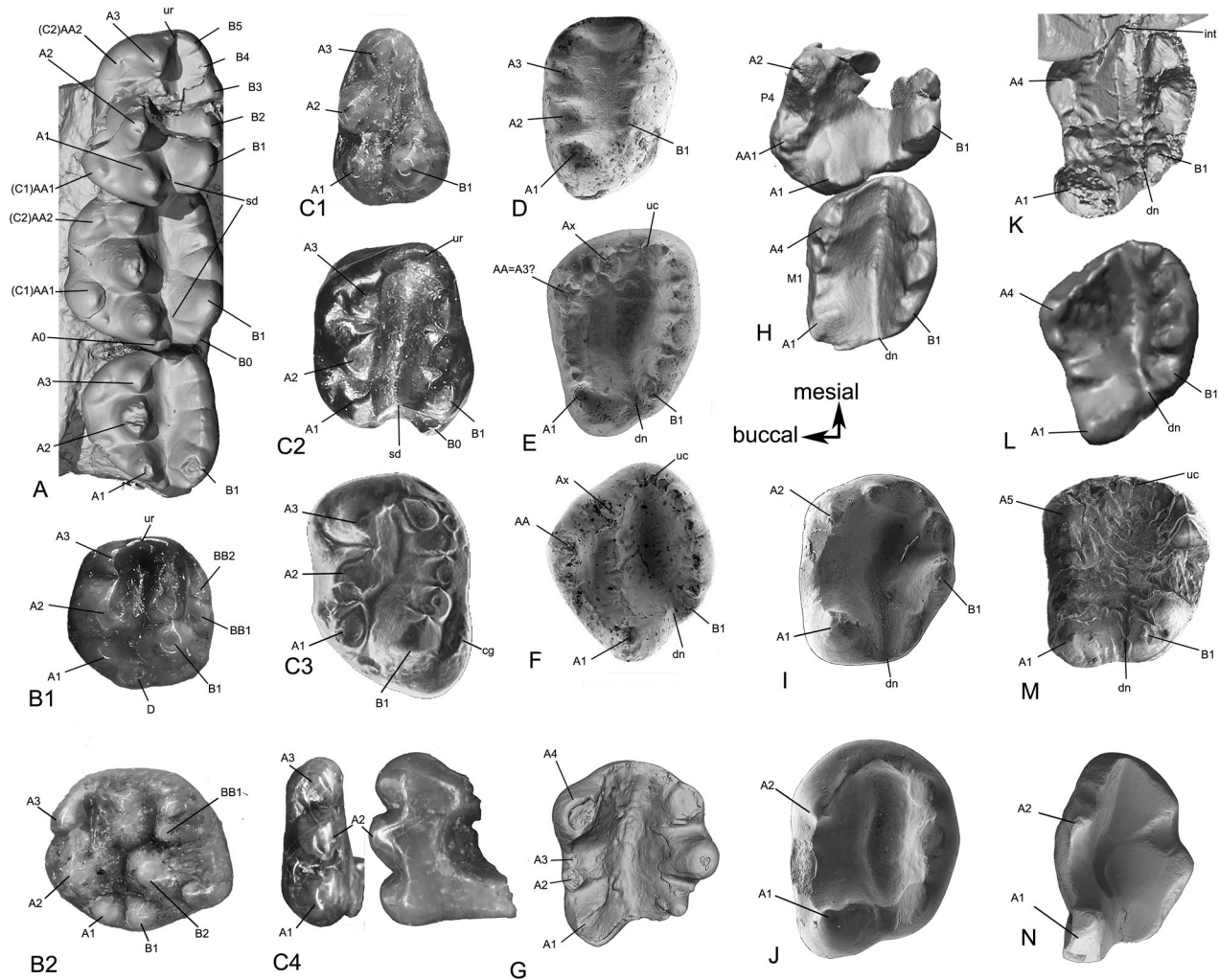
The main reason that the occlusal pattern remains unsettled in the Triassic species is because there are no associated upper and lower dentitions from the same individual animal and with unambiguous wear on isolated teeth (Meng *et al.* 2014; Mao & Meng 2019b). Even for *Haramiyavia*, the upper and lower dentitions are not from the same individual and its occlusal relationship was interpreted by scaling down the upper molars by 17% to match the lower ones (Jenkins *et al.* 1997; Luo *et al.* 2015). For *Thomasia*, which was represented by numerous teeth, the specimens display a considerable variation in morphology. Among these specimens, a few show tooth wear (Sigogneau-Russell 1989) but most of them do not (Debuysschere 2015; personal observation by FM and JM). Here we present images of some lower molars that bear clear wear facets (Figs 17A). In these molars, apical wear appears on both row a and row b cusps, but a1 is clearly the deepest worn cusp, which is inconsistent with the view that row b is the primary functional cusp row. We also present two p4s of *Thomasia* to show a different degree of wear (Fig. 17A3, A4). This type of tooth was classified as group “*Thomasia* II” by Sigogneau-Russell (1989) and was subsequently considered as either m1 (Butler 2000) or lower premolar (Debuysschere 2015). Because of their similarity to p4 of euharamiyidans, such as *Shenshou* and *Qishou* (Bi *et al.* 2014; Mao & Meng 2019a; Fig. 17D, H), these teeth can now be confidently identified as p4. The wear of these teeth is similar to that of p4 of *Shenshou* and *Qishou* in which a1 is the most worn cusp. This indicates that a1 of p4 of *Thomasia* is the main functional cusp that occluded in the basin of P4. In *Qishou* (Fig. 17D), a1 as the main functional cusp of p4 aligns with the functional row a of the molars. Then, it would be difficult to interpret why the main functional cusp row switched to row b in molars of *Thomasia*, if the MM1 mode for *Thomasia* holds.

It should be noted, however, that molars of the Triassic species differ from those of the Jurassic ones in having a narrow, often not straight, central valley. In *Theroteinus*, there is no central valley (Sigogneau-Russell *et al.* 1986; Debuysschere 2015, 2016). In general, A1/a1 are not enlarged and tooth cusps are few but proportionally large and blunt, compared to the Jurassic species. These features indicate that the tooth occlusion is primarily cusp-to-cusp, not cusp-to-valley; this is true even for the Early Jurassic *Thomasia* cf. *moorei* from Pant Quarry, south Wales, where the tooth wear was reported to be apical (Clemens 2007). In fact, the apical wear is on both row a and row b cusps (Fig. 18C3). Perhaps it may not be appropriate to describe the occlusion of the Triassic “haramiyidans” as either the buccal

or lingual cusp row of the lower molar occluding in the longitudinal valley between the two rows of the upper molar; their blunt cusps cannot be accommodated by the narrow central valley, if there is any. The cusp-to-cusp occlusion allows the power stroke of chewing to be either orthal, as in *Theroteinus* (Sigogneau-Russell *et al.* 1986; Butler 2000), predominantly orthal, as in *Haramiyavia* (Jenkins *et al.* 1997), or considerably palinal, as in *Thomasia* (Butler & MacIntyre 1994; Butler 2000).

The molars of Jurassic species have a broad basin and, except for the enlarged cusps A1 and a1, cusps are proportionally small and marginally positioned (Figs 17, 18), which makes it possible for pestle-and-mortar (Butler & Hooker 2005) or cusp-to-valley occlusion. The Jurassic euharamiyidans, except for *Maiopatagium furculiferum* (Meng *et al.* 2017), have the MM2 occlusal mode or its derivative (Zheng *et al.* 2013; Bi *et al.* 2014; Meng *et al.* 2014; Luo *et al.* 2017; Mao & Meng 2019a, b). *Kermackodon* was considered as having a derivative pattern of MM2 mode (the “*Eleutherodon*”-mode, see Mao & Meng 2019b); it is unique in having the buccally projected cusp AA and development of row Ax and the secondary basin between row AA and Ax (Fig. 1). In occlusion, row b of the lower molar crosses row A between cusp A1 and AA. This occlusal pattern raised the issue of whether cusp AA or Ax of *Kermackodon* is the primary cusp. As discussed above, *Butlerodon quadratus* has a MM2 occlusal mode; its initial development of row Ax provides evidence favouring cusp AA as the primary cusp in *Kermackodon* (see below).

*Maiopatagium furculiferum* represents a unique case among Jurassic euharamiyidans in which “the lingual-most cusp row of lower molars occluded lingual (medial) to the upper molars, and the buccal cusp row of upper molars occludes outside the lower molars” (Meng *et al.* 2017; Supplemental material). This implies the MM1 (multituberculate M1/m1 occlusion) occlusal mode, as noted by Mao & Meng (2019b). Lower molars of *M. furculiferum* are unknown and the occlusal relationship of this species was based on the wear pattern interpreted for the upper molars. In a recent study, Averianov *et al.* (2019a, fig. 6) reported three new euharamiyidan species, *Sharypovoia arimasporum*, *S. magna* and *Maiopatagium sibiricum*. The wear facets of the upper molars of these species show a clear MM2 occlusal mode, similar to the Yanliao euharamiyidans except for *M. furculiferum*. As noted by Averianov *et al.* (2019a), the wear pattern of *M. sibiricum* is not consistent with the wear pattern proposed in the type species. It is difficult to imagine that two species of the same genus with similar tooth morphologies display



**Figure 18.** Comparison of upper cheek teeth in occlusal view from selected taxa of “haramiyidans”. **A**, M1–3 of *Haramiyavia clemmenseni*; **B1**, molar of *Theroteinus nikolai* (SNP 78W, holotype; Debuyschere 2016); **B2**, molar of *Theroteinus rosieriensis* (SNP 2 Ma, holotype; Debuyschere 2016); **C1**, molar of *Thomasia* (a *Haramiyavia* II tooth of Sigogneau-Russell 1989, SNP 3PH; see also Debuyschere 2015); **C2**, molar of *Thomasia* (M1?, SNP 209W); **C3**, molar of *Thomasia* cf. *moorei* (NHMUK PV M 45421; modified from Clemens 2007, fig. 3E). **C4**, occlusal and buccal views of upper tooth of ?haramiyid (SNP 176 W) (Sigogneau-Russell 1989); **D**, M1 of *Woodeatonia parva* (NHMUK PV M 100088, paratype); **E**, molar of *Butlerodon quadratus* (NHMUK PV M 100090); **F**, molar of *Kermackodon oxfordensis* (NHMUK PV M 46460, holotype); **G**, molar of *Cryoharamiyavia tarda* (modified from Averianov *et al.* 2019b); **H**, P4–M1 of *Qishou* (modified from Mao & Meng 2019a); **I**, molar of *Sharypovoia arimasporum* (modified from Averianov *et al.* 2019a); **J**, right M1 of *Sharypovoia magna* (modified from Averianov *et al.* 2019a); **K**, molar (M1) of *Xianshou linglong*; **L**, molar of *Vilevolodon diplomylos* (modified from Luo *et al.* 2017 with permission from *Nature*); **M**, molar (M1) of *Arboroharamiyavia jenkinsi* (Zheng *et al.* 2013; Meng *et al.* 2014); **N**, M1 of *Maiopatagium sibiricum* (Averianov *et al.* 2019a). To facilitate comparison some tooth images have been photographically reversed (flipped) so that all teeth are in the same orientation as the right teeth. **Abbreviations:** **cg**, cingulum; **dn**, distal notch; **int**, interlocking contact; **sd**, saddle; **uc**, ‘U’-shaped cusp chain; **ur**, U-ridge. Cusp labelling is from original studies. Teeth are not to scale. Images in I, J, and N are courtesy of A. Averianov.

such fundamentally different occlusal patterns. It seems that either the taxonomical assignment is inappropriate or the interpretations of tooth occlusion of the two species were incorrect. Nonetheless, the new evidence from Western Siberia, Russia, United Kingdom and China shows that the MM2 mode is the general occlusal pattern in Jurassic euharamiyidans.

### Cusp homology

For cusp homology of haramiyidan teeth, there are two basic issues to be investigated: first, the homology of tooth cusps between the primitive “haramiyidans”, mainly the Triassic *Haramiyavia*, *Thomasia* and *Theroteinus*, and other non-mammalian cynodonts. This issue bears on what could be the precursor that gave



rise to the “haramiyidan” tooth pattern. Second, the homology of tooth cusps within “haramiyavians”, concerning what is the ancestral dental pattern of the group and how it gave rise to those in more advanced forms so that homologous traits among “haramiyidans” may be traced. For the first issue, the possibility that the haramiyidan molars were derived from triconodont molars by development of a second row of cusps from the cingulum, either buccal or lingual, has been postulated (Butler & MacIntyre 1994; Butler 2000); these authors also pointed out the difficulty of transferring a triconodont tooth pattern to a haramiyidan one because this involves a major change from unilateral, transverse chewing to presumably bilateral, palinal chewing. Similar consideration was given by others (Clemens & Kielan-Jaworowska 1979; Clemens 1980; Meng 2014). If multituberculates were derived from “haramiyidans” (Butler 2000; Butler & Hooker 2005; Hahn & Hahn 2006), then a related issue is how the multituberculate tooth pattern was derived from that of primitive “haramiyidans”. In this study, we focus our discussion on cusp homology within “haramiyavians”, which would be the premise for understanding evolution and phylogeny of the group. Our discussion builds on Butler’s (2000) interpretation of tooth homologies for “haramiyidans” and extends to include key taxa known today.

For isolated teeth that show a wide variation, identifying a tooth and inferring homologies of tooth cusps are not easy. This is particularly so when a specimen has an unusual morphology that may be interpreted differently. For instance, a recent study reported three haramiyidan teeth from the Late Triassic Rhaetian bedded sequence at Holwell, Somerset, UK (Whiteside & Duffin 2021). Of the three, one tooth (NHMUK PV M 106297) was identified as a right lower molar that was used as the holotype for *Theroteinus jenkinsi*. The second tooth (NHMUK PV M 106295) was identified as a left m2, assigned to *Thomasia antiqua*; the third one (NHMUK PV M 106296) was a left M2 assigned to *T. moorei*. However, NHMUK PV M 106297 may be interpreted as an upper premolar of *Thomasia*, similar to some teeth reported from Saint-Nicolas-de-Port, France, that have been assigned to *Thomasia*. These teeth are small and double-rooted and have a rounded and simple crown (Sigogneau-Russell 1989; personal observation by FM and JM). Similarly, NHMUK PV M 106295 may be interpreted as an upper molar and NHMUK PV M 106296 as a lower molar. While additional evidence is needed to test these interpretations, it is cautioned that there exist exceptions to the interpreted homologous structures.

**Lower teeth.** Among the Triassic “haramiyidans”, namely *Theroteinus*, *Haramiyavia* and *Thomasia*, the lower molar is transversely narrow with a narrow central valley; cusp a1 is the largest cusp but not inflated, nor is it mesially extended, compared to the Jurassic forms (Fig. 17). A feature common to the Triassic species is presence of b1 in the lower molars, which is a cingulid-like cusp that is positioned lower than other cusps. In occlusal view, b1 usually aligns evenly with a1 or projects slightly more mesially than a1. However, b1 is absent in some teeth referred as lower molars of *Thomasia antiqua*, such as NHMUK PV M 106295 (Whiteside & Duffin 2021) and GIT 1561/1 and GIT 1561/17 (Clemens & Martin 2014). In the Saint-Nicolas-de-Port specimens, there is at least one lower tooth that does not have cusp b1 (Fig. 17A5), as noted by Debuyschere (2015). If identifications of these teeth are correct, cusp b1 may be interpreted as having been lost in those specimens. In *Haramiyavia* (Fig. 17B), b1 is mesial to a1 on m1 but reduces in size and retracts distally in m2 and m3. In these Triassic species b2 is consistently the largest cusp on row b and the central basin is narrow in *Haramiyavia* and *Thomasia* and nearly absent in *Theroteinus*. *Haramiyavia* shows that a1 is the largest cusp at the mesiolingual corner of the lower molar and this cusp orientation can be assumed for *Thomasia* and *Theroteinus*; it is consistent with the cusp orientation in the Jurassic species (Fig. 17). Given the relative cusp size, shape and position, cusps a1, b1 and b2 in the Triassic species could be reasonably homologized.

Among the Jurassic forms, the cusp homology has been proposed by Butler (2000, figs 1, 2) based on the molar orientation known at the time, in which the lingual and buccal cusp rows were reversed and the largest cusp of the lower molar was considered as b2, as shown in Figure 1B. In the light of the Yanliao euharamiyidan dentitions it is clear that the largest cusp of the lower molar is a1, so the discrepancy in the molar cusps between Triassic and Jurassic “haramiyidans” has been removed. In lower molars, a1 is the largest cusp at the mesiolingual corner of the crown in “haramiyidans”. Cusp a1 in Jurassic “haramiyidans” becomes further enlarged or hypertrophied; it is mesially extended and in some with the tip distally hooked. Despite variations in shape and size, the homology of a1 may be established within “haramiyidans”. Under this assumption, an unresolved issue is the switch of the functional cusp row from row b in Triassic species to row a in Jurassic forms, if the interpretation of tooth occlusion for the Triassic species holds (Jenkins *et al.* 1997; Debuyschere 2015; Luo *et al.* 2015).

In contrast to cusp a1, other cusps display a higher degree of variation. Cusp b1 is present in *Butlerodon* and *Woodeatonia* and enlarged in the former, as we reported above. In both genera, however, b1 is positioned low and retains its cingulid-like shape. Reduction or loss of b1 appears to be common in Jurassic species (Fig. 17) and may be interpreted as a derived feature. In contrast, the enlarged b1 in *Butlerodon* probably represents an autapomorphic feature. In most Jurassic species the mesial end of row b is notably distal to a1 due to the mesial extension of the latter and loss of b1. It must be pointed out that in some species, such as *Arboroharamiya jenkinsi*, the mesial cusp on row b was denoted as b1, but its homology was not intended (Meng *et al.* 2014; Fig. 17L); such a cusp is small but is not cingulid-like.

The Woodeaton specimens also raise the issue on the homology of cusp b2 in “haramiyidans”. As noted above, b2 is the largest cusp on row b in the Triassic forms. In the Jurassic forms, however, the largest b cusp is usually in the middle position of row b (Fig. 17). In the holotype of *Butlerodon quadratus* (NHMUK PV M 100089), for instance, the cusps denoted as b2 and b3 are small and cuspule-like, whereas b4 is the largest. By its position and size, it cannot be ruled out that cusp b4 in NHMUK PV M 100089 is actually homologous to b2 in the Triassic forms and cusps b2 and b3 in NHMUK PV M 100089 may be secondary cuspules. Similarly, a2 is the second largest cusp in the Triassic species but it is commonly small in the Jurassic species; a cusp denoted as a3 or a4 is the second largest one in row a. Whether the cusp denoted as a2 in different species is homologous remains dubious. Thus, the cusp numbers denote the relative positions of cusps in the row but not necessarily their homology. Cusp a1 is the only homologous cusp that can be established on the lower molar among “haramiyidans”.

**Upper teeth.** The upper molars of “haramiyidans” display a higher degree of disparity than the lower molars (Fig. 18). Of the three Triassic taxa (*Haramiyavia*, *Thomasia* and *Theroteinus*), the upper molar of *Haramiyavia* has extra cusps (AA) on the buccal side of row A, whereas in *Theroteinus* extra cusps (BB) were on the lingual side of row B. Development of the cingulum in the Early Jurassic *Thomasia cf. moorei* (Clemens 2007; Fig. 18C3) appears to be a unique feature that may warrant a different species. Despite these differences, the upper molars of the Triassic “haramiyidans” show a consistent cusp morphology in having three A cusps that have comparable size, shape and number (Fig. 18). Of the three A cusps, the middle one (A2) is the largest, similar to the triconodont tooth. These cusps are larger than B cusps except for B1, and well

separated by a transverse notch; each cusp is flat lingually and convex buccally. In some teeth, a small cusp distal to A1 is denoted as A0 (Butler 2000; Hahn & Hahn 2006). Butler & Macintyre (1994) considered row A cusps as primary in “haramiyidans” that are potentially homologous to the main cusps of the triconodont molar and row B cusps to be developed from the lingual cingulum. Crompton (1974) also compared the A cusps of the teeth (assigned to “*Haramiya*”) with the main cusps of the upper molar of *Megazostrodon*, but he identified the B cusps as being buccal, derived from the buccal cingulum (Butler & Macintyre 1994). The interpretation of Butler & Macintyre (1994) gains support from the fact that some teeth assigned to group “*Haramiya II*” (Sigogneau-Russell 1989) have a sizable B1 but the other B cusps reduce in size mesially or assume a ridge-like form (Fig. 18C1). An extreme condition is shown in SNP 176 (Saint-Nicolas-de-Port, Upper Triassic, France), that has only three cusps, which by their shape and relative sizes are most likely A cusps (Fig. 18C4). This and another similar tooth were identified as possible “haramiyidan” teeth (Sigogneau-Russell 1989) but whether these teeth are premolars or molars remains unclear (Debuyschere 2015). Nonetheless, these morphological variations suggest that row A is unlikely the primary cusp row. Following Butler (2000), we consider that cusp A1, A2 and A3 are homologous within the Triassic “haramiyidans” and potentially homologous to the main cusps, corresponding to cusp C, A, and B, respectively, in triconodont molars.

For teeth that have a fully developed row B in the Triassic species, there are more than three cusps in which B1 is the largest and the remaining B cusps gradually reduce in size mesially and show a trend of coalescence. A small cuspule distal to B1 is present in some molars, which was denoted as cusp ‘b’ (Butler & Macintyre 1994) or B0 (Butler 2000; Hahn & Hahn 2006; Clemens & Martin 2014) but Debuyschere (2015) considered the small cuspule as B1 and the largest cusp as B2. Because this cuspule is not a stable feature, we follow Butler (2000) to consider it B0 (Fig. 18). Following Butler (2000), we assume B1, but not other B cusps, as homologous in the Triassic species.

In the Jurassic species, the upper molars differ considerably from those of the Triassic forms (Fig. 18). The most prominent feature is an enlarged A1 that is commonly extended distally. By its position at the distobuccal corner, it can be homologized with A1 in the Triassic species (note that A1 was identified as B1 in “*Eleutherodon*” [Butler 2000]). However, there is no cusp that can be readily homologized to A2. *Woodeatonia parva* (NHMUK PV M 100088) has a

distinct A2 that is smaller than A1, contrasting to the condition in the Triassic species. In other Jurassic forms, a ridge or a series of small cusps variable in number is commonly mesial to A1 (Fig. 18). Thus, A2 is either reduced in size or lost, which may have been associated with changes of the occlusal patterns (Mao & Meng 2019b). At the mesiobuccal corner of the upper molar is a main cusp that has been denoted differently because of the variable small cusps between it and A1. For instance, it is A2 in *Sharypovoia* (Averianov *et al.* 2019a), A4 in *Qishou* (Mao & Meng 2019a), and A5 in *Arboroharamiya* (Meng *et al.* 2014); it could be A6 in *Butlerodon* and A7 or A8 in *Kermackodon oxfordensis*. Because there exist variable small cusps in various species, this cusp numbering obscures the homology and divorces the nomenclature from homology, as pointed out by Butler (2000). For instance, A2 in *Sharypovoia* is certainly not homologous to A2 in *Arboroharamiya jenkinsi*; similarly, both may not be homologous to A2 in *Thomasia*.

By its position at the mesiobuccal corner of the tooth crown, it is possible to homologize this main cusp in all Jurassic species, except for *Woodeatonina parva*. To reflect the possible homology, we follow Butler (2000) to denote the large cusp at the mesiobuccal corner of the upper molar as cusp AA instead of numbering it (Figs 1, 18). By its position, cusp AA may be homologized to A3 in the Triassic species, but this is less certain than that of A1. It should be noted that cusp AA as a main cusp is different from the secondary cusps denoted as cusp C (Jenkins *et al.* 1997) or AA1-2 for *Haramiyavia* (Butler 2000).

Cusp Ax (originally Bx in Butler 2000) and row Ax in *Kermackodon oxfordensis* and *Butlerodon quadratus* are not present in the Triassic species, nor are they in other Jurassic euharamiyidans. It could be questioned whether AA or Ax is the primary cusp that is potentially homologous to A3 in the Triassic species. Butler (2000) compared cusp AA (BB as a lingual cusp at the time) to the lingual BB cusps of *Theroteinus*, implying that this cusp is a secondary one. We would argue that cusp AA is the primary one and Ax is a secondary structure for at least two reasons. First, cusp AA in *Kermackodon oxfordensis* is buccally projected and occludes buccal to the buccal row of the lower molar, as in *Arboroharamiya* and *Vilevolodon* (Mao & Meng 2019b). This occlusal relationship is further confirmed by the wear pattern (Fig. 13). By position and function, the mesiobuccal main cusp in *Arboroharamiya* and *Vilevolodon* should be made equivalent to cusp AA of *K. oxfordensis*, whereas there is no additional cusp (Ax) lingual to AA in the former. If cusp AA is secondary, it would be difficult to interpret how it evolved at the

expense of Ax. Second, row Ax in *Butlerodon quadratus* represents an initial stage of this cusp row and cusp AA has not extended buccally but retains the primitive occlusal relationship in that it bites lingual to the buccal row of the lower molar, similar to that of *Shenshou* and *Qishou* as shown above. Thus, both the initial row Ax and AA position of *B. quadratus* suggest that AA is primary and Ax secondary. In this regard, the molar morphology of *B. quadratus* may be considered as being intermediate between those of *Thomasia* and *Kermackodon oxfordensis*. By its position, we postulate cusp Ax in *Kermackodon oxfordensis* and *Butlerodon quadratus* to be homologous and represent a synapomorphy of the two genera. Because of their great variability, it is not practical to homologize other A cusps in the Jurassic species.

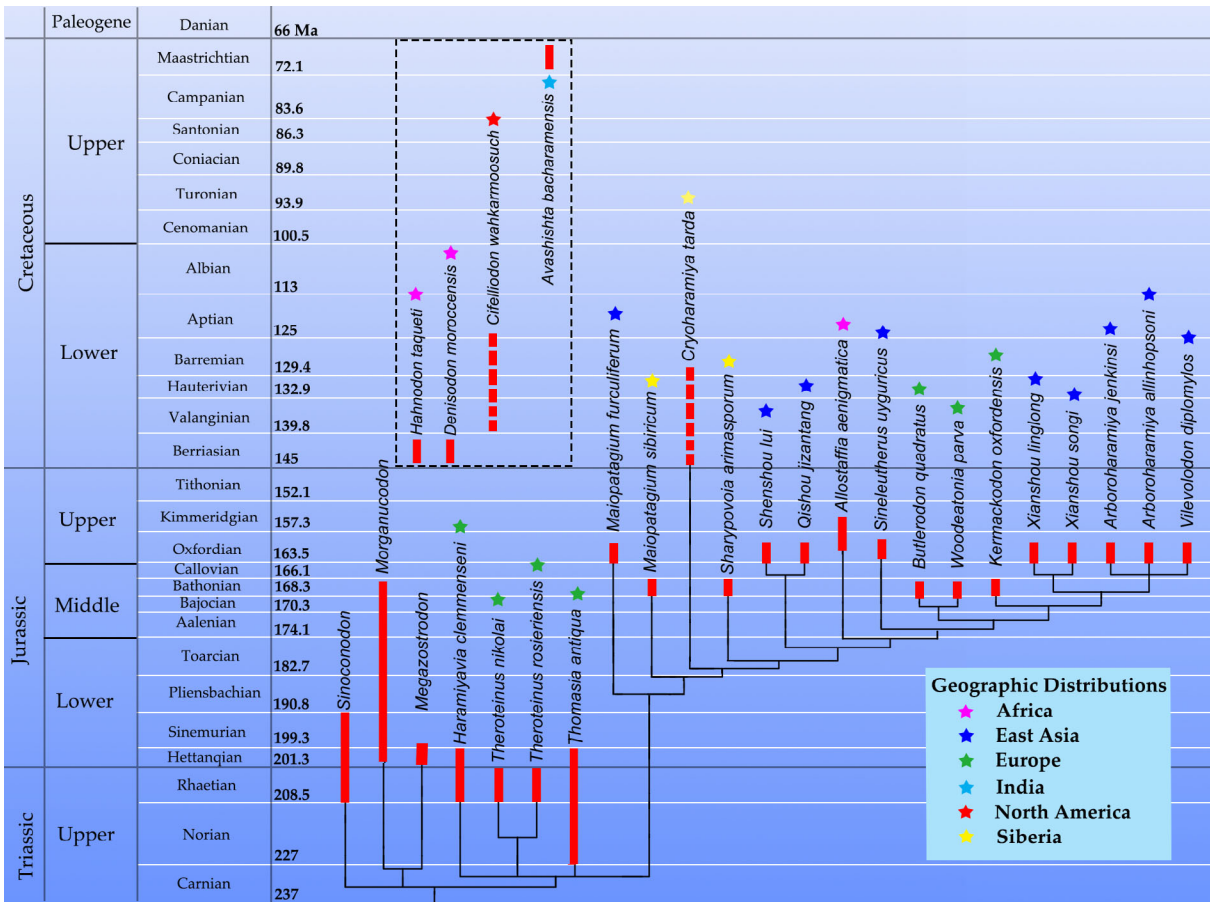
In the Jurassic species, B cusps vary in number and are arranged in a curved line. Contrasting to the Triassic species, the cusp denoted as B1 by its position is universally small and more mesially positioned than distally extended A1 (Fig. 18). The largest B cusp is commonly in the middle position of row B. Whether the cusp denoted as B1 is homologous to that of the Triassic species remains unclear. Thus, it may be practical to consider row B, instead of any individual cusp, as a homologous feature for the Jurassic euharamiyidans. Because of the reduction of B1, the saddle between A1 and B1, a common feature in the Triassic species, is lost in the Jurassic ones so that the distal end of the central basin opens as a distal notch (Fig. 18). Because of the variable B cusp number, it is difficult to speculate on any homology for individual B cusps, as noted by Butler (2000).

## Phylogenetic analysis

With the discussion on dental morphologies of “haramiyidans”, we conduct the first phylogenetic analysis of haramiyidan species. Figure 19 illustrates the time calibrated strict consensus result of 10 equally most parsimonious trees, with palaeogeographical distributions labelled for each species.

As expected, species of *Thomasia*, *Theroteinus* and *Haramiyavia* are stem taxa for “haramiyidans”. The relationship of the three genera remains unresolved, which may be attributed to their possession of primarily plesiomorphic characters. The rest of the selected species are all from the Jurassic and form a clade that may be viewed as Euharamiyida (Bi *et al.* 2014) with an expanded membership. This grouping is also supported by some recent phylogenetic analyses that include major clades of mammaliaforms (Krause *et al.* 2020; Mao *et al.* 2021). For the Jurassic species, *Maiopatagium*





**Figure 19.** Time calibrated phylogeny of “haramiyidans”. The cladogram represents the strict consensus of 10 equally most parsimonious trees (tree length = 137; consistency index = 0.7518; homoplasy index = 0.2482; retention index = 0.8682). Red bars indicate the temporal occurrences of the selected species. The dashed red bar represents uncertain age ranges for *Cifelliodon wahkarmoosuch* (Early Cretaceous; 139–124 Ma; Huttenlocker *et al.* 2018) and *Cryoharamiya tarda* (Early Cretaceous; Berriasian–Barremian; Averianov *et al.* 2019b). The four species in the dashed box are not included in the phylogenetic analysis but displayed here to show the temporal and geographical distributions that they represent. See [Supplemental material](#) for details of phylogenetic analysis.

*furculiferum* is most closely positioned to the stem. Although this species is known only from the upper dentition, its dental morphology is generally primitive compared to other Jurassic species. As we noted above, the unusual tooth occlusal pattern of *M. furculiferum*, as interpreted by Meng *et al.* (2017), is similar to that interpreted for *Haramiyavia* (Luo *et al.* 2015). The other species of the genus, *Maiopatagium sibiricum* (Averianov *et al.* 2019a), has a different occlusal pattern and is separated from *M. furculiferum* in the phylogeny, which echoes our view that either one of the interpretations for the occlusal pattern of the two species is incorrect or *M. sibiricum* should be placed in a different genus. *Sharypovoia arimasporum* (Averianov *et al.* 2019a) and *Cryoharamiya tarda* (Averianov *et al.* 2019b), along with *M. sibiricum*, are also from Siberia. The three species form a polytomy, partly because they are represented by limited tooth specimens.

*Cryoharamiya tarda*, for instance, is based on one upper molar, whereas *M. sibiricum* is based on a P4 and an M1. *Qishou jizantan* and *Shenshou lui* form a sister group that corresponds to Shenshouidae, as originally defined (Mao & Meng 2019a). *Sharypovoia* was also placed in Shenshouidae (Averianov *et al.* 2019a), but this is not supported here. The European Jurassic species are closely clustered with the more derived euharamiyidans from the Yanliao Biota, including species of *Xianshou*, *Arboroharamiya* and *Vilevolodon* that may be included in the family Arboroharamiyidae (Zheng *et al.* 2013); these species have highly specialized upper incisors, ultimate premolars, and molars within “haramiyidans”.

The temporal occurrences of the Late Triassic species are consistent with their basal positions in the phylogeny and roughly coeval with the basal mammaliaforms, such as *Sinoconodon* and morganucodontids. These earliest

“haramiyidans” are currently known only in Europe. A temporal hiatus among known “haramiyidans” exists in the Early Jurassic, separating the Late Triassic “haramiyidans” from the Middle Jurassic species. This hiatus may result from a low diversity of “haramiyidans”, or from poor preservation, or both. The Middle–Late Jurassic witnessed a diversification of euharamiyidans, both in diversity and disparity, which may be viewed as part of the mid-Jurassic major adaptive radiation of mammaliaforms (Luo 2007; Meng 2014; Close *et al.* 2015). For the Middle Jurassic euharamiyidans, Averianov *et al.* (2021) thought that the oldest record is from the Middle Jurassic (Bathonian) Itat Formation in West Siberia. Our analysis, however, shows that the European species are at least coeval with the Siberian species, if not any earlier, and are also nested within euharamiyidans. Species from both Europe and Siberia appear older than those from the Yanliao Biota in north-eastern China. As summarized by Mao *et al.* (2021), the Yanliao euharamiyidans are from the Linglongta phase, younger than the Daohugou phase, of the biota; it ranges from 164 to 159 Ma. For the Siberian euharamiyidans, *Cryoharamiya tarda* represents a species that persisted into the Early Cretaceous as “the youngest representative of Euharamiyida” and the northernmost occurrence of “haramiyidans” in terms of the palaeolatitude (Averianov *et al.* 2020). In contrast, the diverse Yanliao euharamiyidans did not persist into the Early Cretaceous Jehol Biota, as reflected by the current fossil record. Given that ancient forms, such as the fossorial tritylodontid *Fossiomanus sinensis* (Mao *et al.* 2021), survived into the Early Cretaceous Jehol Biota and that the taphonomical conditions that preserved both biotas are similar, lack of euharamiyidan fossils in the Jehol Biota may be due to other factors. These primarily arboreal animals may be impacted by the change from gymnosperm-dominant forests in the Jurassic to an ecosystem in which angiosperms flourished in the Cretaceous, as speculated by Han *et al.* (2017). The species from India, Morocco and United States, presumably “haramiyidans”, are from the Cretaceous, representing the latest records of the group (Fig. 19).

Euharamiyidans and earliest unequivocal multituberculates co-existed in the Middle Jurassic in Eurasia (Butler & Hooker 2005; Yuan *et al.* 2013; Averianov *et al.* 2020; this study), but a Bayesian phylogenetic tip-dating analysis showed that the origin of euharamiyidans predated that of multituberculates (Mao *et al.* 2021). The chronological data are consistent with the hypothesis that multituberculates were probably derived from “haramiyidans” (Butler 2000; Butler & Hooker 2005; Hahn & Hahn 2006; Bi *et al.* 2014; Mao *et al.* 2021).

Based on the original interpretations of the teeth assigned to the multituberculate “*Kermackodon multicuspis*” and *Hahnotherium antiquum*, Butler & Hooker (2005) postulated that multituberculates originated much earlier, more probably from a haramiyid than from a morganucodontid source. Averianov *et al.* (2021) also considered the tooth morphology of “*K. multicuspis*” as transitional between euharamiyidans and multituberculates. Our reinterpretation of the “*K. multicuspis*” teeth as from a euharamiyidan has changed the taxonomical placement but the morphological similarity and dissimilarity of these teeth to euharamiyidans and multituberculates remain.

## Conclusions

Tooth specimens from the White Limestone Formation (Middle Jurassic, Bathonian) at Woodeaton Quarry (Oxfordshire), United Kingdom, document at least four species of allotherian: the haramiyidan *Kermackodon oxfordensis* (= “*Eleutherodon*” *oxfordensis*), *Butlerodon quadratus* gen. et sp. nov., *Woodeatonia parva* gen. et sp. nov., and the multituberculate *Hahnotherium* cf. *H. antiquum*. The Woodeaton species add to the allotherian diversity in Europe. They are different, in morphology and thus diversity, from those of the Forest Marble Formation. Whether these differences are of evolutionary significance within the time interval between the two assemblages is unclear. With many discoveries of “haramiyidans” made in Europe and Asia in the last decade, this poorly known group has now become much better understood in their tooth orientation, dentition, variation of tooth morphology at different loci, and tooth occlusion. It is clear now that the incisors, penultimate and ultimate premolars, and molars of the Jurassic euharamiyidans have differentiated into modules with unique and distinctive morphologies that probably functioned as units in food processing. The accumulated knowledge further allows reinterpretation of isolated teeth previously assigned to various genera as teeth from different tooth loci of the same species; this improves our understanding of the morphology, biology, and taxonomy of “haramiyidans”.

There is increasing evidence that the Jurassic euharamiyidan species have the multituberculate M2/m2 occlusal pattern, whereas the occlusal pattern of the Triassic species remains uncertain. The major hurdle remains in interpreting the evolutionary change from the MM1 occlusal mode in the Triassic species to the MM2 mode in Jurassic ones, if the interpretation of MM1 mode for the former holds. Given that “the teeth must continue to function throughout the evolutionary transformations of

the body as a whole” (Butler 2000, p. 339), this abrupt change appears unusual and remains to be tested with new evidence. Perhaps the cusp-to-cusp occlusion, neither MM1 nor MM2 mode, better portrays the occlusal pattern of the Triassic species.

It is also clear that there are considerable differences in tooth morphologies between the Triassic and Jurassic “haramiyidans”. A general trend is P4/p4 specialization that increases the functional role of this pair of teeth for food processing in the Jurassic species. For molars, the Jurassic species differ from the Triassic ones in having enlarged cusps A1 and a1 on molars, cusp A2 of upper molars replaced by low ridge or a chain of small cusps, B1 reduced with the cusp at the mid-position of row B becoming the largest, the central basin of molars expanded. Tooth cusp homologies among “haramiyidans” were obscured or lost due to these changes. Nonetheless, it is still feasible to postulate homologies for several main tooth cusps, which is critical in understanding evolution and phylogeny of “haramiyidans”.

The Woodeaton allotherian assemblage is slightly older than the one from the Forest Marble Formation (late Bathonian) of Oxfordshire and Dorset; they are similar in having both “haramiyidans” and multituberculates in which haramiyidan specimens are predominant in abundance over multituberculates. This composition is similar to that of the Jurassic allotherian assemblages in Asia (Meng 2014; Averianov *et al.* 2019a, 2021), and it shows again that, in addition to other contemporary taxa, such as eutriconodontans (Wills *et al.* 2019), the oldest multituberculates co-existed with “haramiyidans”. Although *Kermackodon* was removed from multituberculates and placed in “haramiyidans”, the tooth morphologies that were considered to be transitional between multituberculates and “haramiyidans” (Averianov *et al.* 2021) remain; thus, that “haramiyidans” and multituberculates are most closely related and that multituberculates evolved from “haramiyidans” still appear to be the best working hypotheses (Butler 2000; Butler & Hooker 2005; Hahn & Hahn 2006; Bi *et al.* 2014; Mao *et al.* 2021).

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## Supplemental material

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