New multituberculate-like teeth from the Middle Jurassic of England

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Kermack, K.A., Kermack, D.M., Lees, P.M., & Mills, J.R.E.† 1998. New multituberculate-like teeth from the Middle Jurassic of England. — *Acta Palaeontologica Polonica* **43**, 4, 581–606.

New fossil mammal teeth are described from the Middle Jurassic (Bathonian) Forest Marble of Kirtlington, Oxfordshire, England. They are referred to a new genus and species, *Eleutherodon oxfordensis*, family Eleutherodontidae nov., suborder Eleutherodontida nov., order *incertae sedis*, assigned to Allotheria Marsh, 1880. These teeth are unique, but share with multituberculates and haramiyids the longitudinal arrangement of their cusps and with the former at least the propalinal action of the jaws in chewing, and palinal movement of the dentary during the power stroke. They differ in that respect from the Greenlandic Late Triassic *Haramiyavia clemmenseni* in which an orthal movement is predominant.

Key words: Multituberculata, Haramiyidae, Bathonian, England.

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Introduction

After the discovery of two fossils horizons in the upper Bathonian (Middle Jurassic) localities at Kirtlington Old Quarry, near Oxford and at Watton Cliff in Dorset, England, by E. Freeman (Freeman 1976a, b, 1979), work by the discoverer and the University College team resulted in an abundant collection of vertebrate microfossils reviewed by Evans & Milner (1994). This collection consists of archosaurs, lepidosaurs and amphibians, plus 700 mammalian teeth along with some bones. Amongst these teeth, thirteen could be recognized as molars with allotherian affinities, and are the subject of this paper.

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† Died, January 7, 1995.

Allotheria Marsh, 1880 is one of the three subclasses of Mesozoic Mammalia currently considered (G. Hahn 1973; G. Hahn & R. Hahn 1983; Clemens & Kielan-Jaworowska 1979; Archibald 1982; Sigogneau-Russell 1989; Miao 1993; Butler & MacIntyre 1994) as composed of haramiyids and multituberculates. However Rowe (1988), Simmons (1993), and McKenna & Bell (1997) included Multituberculata but not Haramiyioidea in their Mammalia *sensu stricto*. On the other hand, Sigogneau-Russell *et al.* (1986) and G. Hahn *et al.* (1989) saw in the theroteinids a third clade of Allotheria.

Haramiyids were known until recently only by isolated teeth from the Late Triassic (Parrington 1947; Peyer 1956; Hahn 1973; Clemens 1980; Sigogneau-Russell 1989) and Early Jurassic (Pacey 1978; Butler & MacIntyre 1994) deposits of Britain, France, Switzerland and Germany. These teeth are distinguished from all contemporaneous mammals by their longitudinal arrangement of cusps, disposed in rows on each side of a central basin. Two genera were initially recognised, *Thomasia* Poche, 1908 and *Haramiya* Simpson, 1947, but Sigogneau-Russell (1989) and Butler & MacIntyre (1994) have suggested that these represent the upper (*Haramiya*) and lower (*Thomasia*) teeth of a single genus. Confirmation of this has been brought by the discovery of dentaries, a maxilla and other skeletal remains in the Late Triassic of East Greenland attributed to a haramiyid by Jenkins *et al.* (1996). The brief description of one dentary (lacking the condylar process and part of the coronoid process) with a complete dentition, and of a fragmentary maxilla and premaxilla with teeth, for which the authors created a new genus and species *Haramiyavia clemmenseni*, family Haramiyidae Simpson, 1947, also confirmed the suggestions of Sigogneau-Russell, and Butler & MacIntyre concerning the orientation of the teeth. This discovery, however, contradicts the reasonably well proved palinal movement of the jaws during mastication in this family, 'with an orthal component at the beginning of the stroke' (Butler & MacIntyre 1994: p. 433). In *Haramiyavia*, in contrast, 'the geometry (of the teeth) necessitates a 1:1 relation between upper and lower teeth, and obviates the possibility of palinal movement of a lower molariform across two upper molariforms' with a resulting 'predominantly orthal movement' (Jenkins *et al.* 1996: p. 717). Moreover, Zofia Kielan-Jaworowska (personal communication 1997) drew our attention to the fact that the masseteric fossa in *H. clemmenseni* is situated far posteriorly on the dentary, as characteristic for most mammals (Gambaryan & Kielan-Jaworowska 1995; Kielan-Jaworowska 1997) but not for rodents, small herbivorous marsupials and multituberculates: in the latter the backward power stroke resulted in a more anterior insertion of the masticatory muscles than in any other group of mammals.

In 1986, another type of longitudinally cusped teeth, *Theroteinus nikolai*, family Theroteinidae (Sigogneau-Russell *et al.* 1986) was described from the Late Triassic of France. The upper teeth lack the deep basin of haramiyids but show the distribution of cusps in three rows; in the lowers, the central basin is preserved but is closed at both ends. This taxon has been considered as the primitive sister taxon of the haramiyid-multituberculate clade (G. Hahn *et al.* 1989); but the masticatory movement has been reconstructed by these authors as predominantly orthal, this being interpreted as secondary by Butler & MacIntyre (1994).

Thus the problem arises whether *Haramiyavia clemmenseni* really belongs to the Haramiyidae, in which case propalinal movement should be questioned in that family, or whether the taxon is closer to theroteinids (as indicated also by three rows of cusps in the upper molars, against two in haramiyids).

Finally, multituberculates are widely known for their longitudinal arrangement of cusps and their palinal movement during power stroke. This was first demonstrated by Gingerich (1977), developed by Krause (1982) and subsequently established by Kielan-Jaworowska & Gambaryan (1995), who reconstructed jaw movements and masticatory musculature in Asian Late Cretaceous multituberculates. The first uncontested multituberculate mammals are known from the Kimmeridgian of Portugal and are represented by numerous partial skulls with dentitions, dentaries and isolated teeth of the family Paulchoffatiidae (G. Hahn 1969; Krause & G. Hahn 1990, and references therein). In this family, M2 is basined, and there are large buccal cusps on the lower premolars, both features resembling the haramiyid condition. The multituberculates so far described from beds older than Kimmeridgian, consist of two fragments of teeth from the Forest Marble (Bathonian) of England (Freeman 1976b, 1979) and a partial tooth dubbed *Mojo* from the Late Triassic of Belgium (G. Hahn *et al.* 1987); the multituberculate nature of these teeth cannot be unequivocally demonstrated.

This introductory presentation underlines the importance of the new teeth described below, which are mid-way in time between the haramiyids and the first certain multituberculates.

Institutional abbreviations: BDUC – Biology Department, University College, London. The catalogue numbers J.000 are of the BDUC collection. All BDUC specimens (except BDUC J.771, accidentally destroyed during examination) are now in the Natural History Museum, London, and will receive Natural History Museum catalogue numbers in the future. EF – Eric Freeman private collection (146 Haydens Road, Wimbledon, London SW19 1AE). FM is the abbreviation in Mr. Freeman's collection for Forest Marble.

Material and methods

The Kirtlington fossils were contained in bands of clays of upper Bathonian age (often called the Forest Marble by the British workers, Arkell 1931) which, in processing, yielded around 700 mammalian teeth. EF FM/K 56, BDUC J.459, J. 460, J. 461. J. 681 and J. 797 come from the 3p band of McKerrow *et al.* (1969); BDUC J. 814 from his 3u band; BDUC J. 649, J. 763 and J. 771 from his 3w (1) band; and BDUC J. 585 from his 3w(v) band. BDUC J. 183 and J. 185 come from Watton Cliff (channel fills within a thick shell detritus horizon, Freeman 1976b). Full details of the method of collection are given in Kermack *et al.* (1987).

The teeth were examined visually under a 'Zeiss Epitechniscope' binocular microscope at magnifications from × 6 to × 40; and all except EF FM/K 56 were photographed under a 'Cambridge Instruments' S-100 scanning electron microscope at magnifications from × 20 to × 1000. Both mono- and stereo-micrographs were used. The electron microscope proved of particular value in detecting wear striations.

Measurements, in millimetres, are given for the maximum length, breadth and height of each tooth. These were made on a 'Cambridge Instruments' S-100 scanning electron microscope, and are nominally accurate to three significant figures (Table 1).

Due to problems of orientation, the measurements are probably repeatable to 0.1 mm but not to 0.01 mm, the second decimal place giving, at best, an indication.

Table 1. Measurements of teeth (in mm).

Number of specimen	Type	Length	Width	Height
EF FM/K56	α	2.40	1.66	
BDUC J.185	α	2.53	1.60	1.40
BDUC J.459	α	2.14	1.88	0.80
BDUC J.460	α	2.09	1.95	1.10
BDUC J.585	α	2.72	2.28	1.44
BDUC J.681	α	2.58	1.80	1.07
BDUC J.771	α	2.47	1.66	1.40
BDUC J.814	α	2.08	1.61	0.83
BDUC J.461	β	2.56	1.63	0.81
BDUC J.649	β	1.96+...	1.57	1.17
BDUC J.183	γ	1.54	1.08	0.92
BDUC J.763	γ	1.57	1.60	0.87
BDUC J.797	ζ	1.95	1.60	0.99

Terminology

As stated above, amongst the 700 mammalian teeth, thirteen can be provisionally related to allotherian mammals. In describing these teeth, we faced the problem that has bedeviled all earlier workers on haramiyids previous to the discovery of Jenkins *et al.* (1997). Since we have no teeth *in situ* in the jaw, there was no certain method of identifying upper teeth from lower or left from right. We, however, think that we have, with reasonable probability, determined the natural orientation of the teeth in the jaw (Fig. 1).

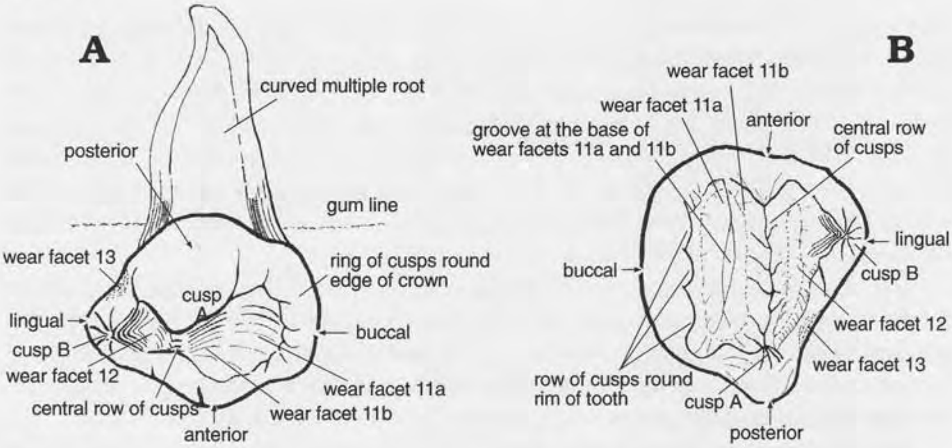

Fig. 1. **A**. Simplified diagram, based on BDUC J.460 and EF FM/K56, showing the orientation in the maxilla of an upper molar (α) of *Eleutherodon oxfordensis* gen. et sp. n. **B**. Occlusal view of the same tooth.

These molars can be separated into four groups α, β, γ, ζ. The α teeth have three longitudinal rows of cusps, and are taken to be upper molars, while the rest of the teeth belonging to the other three groups have only two rows of cusps and are taken to be lower teeth.

Capital letters are used for the cusps of the upper teeth, and lower case letters for those of the lowers. The largest cusp in each tooth will be cusp A in the uppers and cusp a in the lowers. Two digit numbers will be used to identify wear facets. The first number will be used to indicate whether the tooth is upper or lower, the second to identify the facet in order of magnitude in the tooth. Thus 11 would be the largest wear facet on an upper tooth and 21 that on a lower tooth. Wear facets can sometimes be subdivided into two parts, indicated as in facet 11, which may consist in 11a and 11b. This is illustrated in Fig. 2.

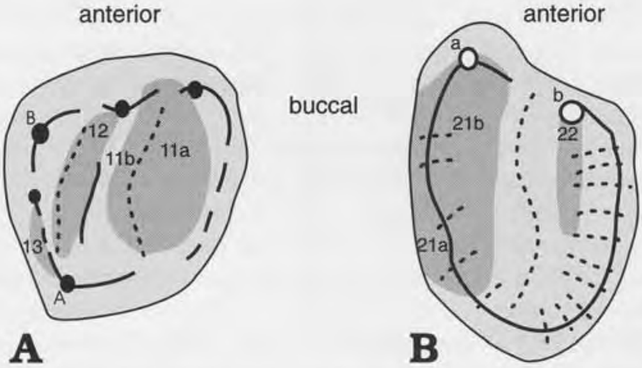

Fig. 2. 'Map' of wear facets on molars of *Eleutherodon oxfordensis* gen. et sp. n. **A**. Upper molar (α) based on BDUC J.460, drawn as though transparent and viewed apically. **B**. Lower molar (β) based on BDUC J.461. A, B, main cusps of upper molar; a, b, main cusps of lower molar. The digits refer to wear facets (see text).

As demonstrated below, it seems probable that the power stroke when the jaw closed would occur with the mandible moving posteriorly. Then the principal cusp would be distal in the upper jaw (cusp A) and mesial in the lower (cusp a). Among the teeth, EF FM/K56 is unique in having long, well preserved roots with a strong lateral curve (Figs 1 and 14). In an upper molar the roots must follow the curve of the maxilla, i.e. curve medially. In no way could they curve laterally and remain within the bone. This makes EF FM/K56 a right upper molar, and enables the rest of the teeth to be oriented, cusp A being distal and lingual.

Among the α teeth, which are the only ones identified as uppers, there is a true wear facet (13) on what was deduced from the above to be the lingual side (Figs 1 and 2A). In BDUC J. 461, a lower tooth, there is a facet (21a) on one of the lateral surfaces of the tooth (Fig. 2B): in all except highly specialized tetrapod dentitions, the upper teeth overhang the lower buccally; thus facet 21a would be on the buccal surface of the tooth and the β teeth now have been oriented, the largest cusp (cusp a) being mesial and buccal. The γ and ζ teeth also have two rows of cusps and have been assumed to be lowers; we have again taken cusp a as mesial and buccal in position although with less certainty than in the β teeth.

This orientation contradicts that of the teeth of *Haramiyavia clemmenseni*, and probably that of haramiyids, where the largest cusp is buccal on the upper molars and lingual on the lowers. However we consider that the morphological, chronological and geographical distances between the two samples may account for this discrepancy, and we estimate the above arguments as firmly established.

Systematics

Subclass Allotheria Marsh, 1880

Order *incertae sedis*

Suborder Eleutherodontida nov.

Diagnosis. — Allotheria with molar teeth having usually basined crowns, the basin being open at one end, and crossed by transverse flutings with sharp edges. Upper molars with three longitudinal rows of cusps, two of these being marginal; the row interpreted as buccal consists of a few or one cusp only. The third row is nearly central, dividing the basin into two unequal parts, deepest between the lingual and medial rows. One marginal cusp considerably larger than the others. Root either single showing incipient division, or fully divided into multiple components.

Differ from multituberculates in having cusps of different height with the distal cusp the largest, and an oval outline (rather than being roughly rectangular); differ from Jurassic and Early Cretaceous multituberculates in having three rows of cusps and the lingual row curved. Differ from haramiyid upper molars (except *Haramiyavia*) by having three rows of cusps instead of two, the latter being more numerous on the marginal rows (up to ten in the buccal row, up to 12 in the lingual row); differ from multituberculates and haramiyids by having very accentuated transverse fluting.

Lower molars with a single marginal row of cusps, continuous around the tooth except for the anterior opening into the basin. Differ from multituberculate and haramyid lower molars where the two rows of cusps are parallel and no fluting occurs.

Eleutherodontidae fam. nov.

Diagnosis. — Suborder is monotypic, erected to include the family Eleutherodontidae nov. The diagnosis is the same as for the suborder.

Remark. — The family is monotypic, erected to include *Eleutherodon* gen. nov.

One of the teeth attributed to the lower jaw, BDUC J 763, is atypical in lacking a basined crown and resembles multituberculate molars much more than do the other teeth; it is possibly not an eleutherodontidan.

Genus *Eleutherodon* nov.

Type species: *Eleutherodon oxfordensis* sp. n.

Derivation of name: Greek – *eleutheros*, a freeman, and *odous*, tooth. The name is a punning compliment to Mr. E. Freeman, who was the first worker to collect and publish mammal teeth from the Forest Marble.

Distribution. — Forest Marble (Bathonian) of Southern England.

Diagnosis (based on the holotype only). — Upper tooth, probably mammalian, with three longitudinal rows of cusps, between which are two fluted basins. One basin

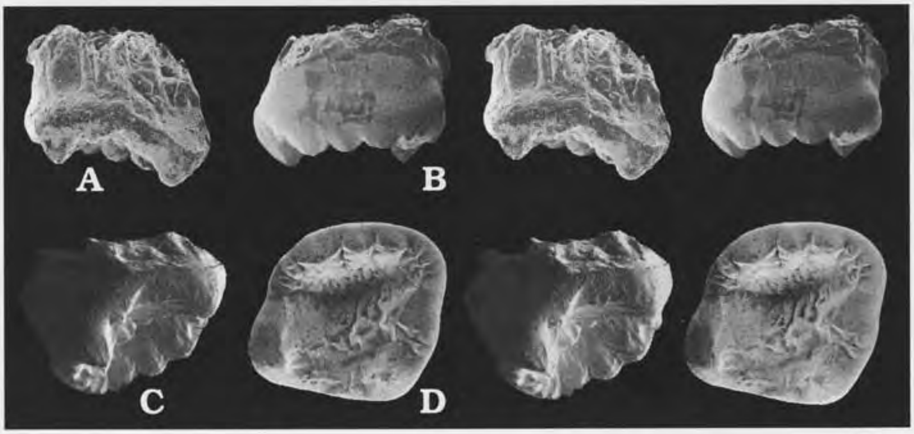

Fig. 3. *Eleutherodon oxfordensis* gen. et sp. n., upper right molar (α), holotype BDUC J.460. **A**. Lingual view. **B**. Buccal view. **C**. Occluso-lingual view. **D**. Occlusal view. In **D** anterior is to the right. SEM stereomicrographs; × about 12.

contains the largest and deepest wear facet of the tooth. This basin is open at one end, where the largest cusp of the tooth occurs at the end of the marginal row. Between the other two rows of cusps is a smaller wear facet, which passes up on to the largest cusp. A third wear facet is detectable on the lateral edge of the tooth, on the same side as the large cusp. The roots are lost in the type specimen, but some of the referred specimens show divided, or partly divided roots.

Eleutherodon oxfordensis sp. n.

Holotype: BDUC J.460, single upper molar tooth (Figs 1–4).

Referred specimens: BDUC J.185, J.459, J.585, J.681, J.814, upper molars (Figs 5–13). EF FM/K56, upper molar (Fig. 14). BDUC J.183, J.461, J.649, J.763, J.797, lower molars (Figs 15–21).

Type horizon and locality: The type and referred specimens (except BDUC J.183 and J. 185) are from clay bands of the 'Kirtlington mammal bed' (Freeman 1979), Kirtlington Old Quarry, Oxfordshire (grid reference SP 494 199). BDUC J.185 and J.183 are from Watton Cliff, west of Bridport, Dorset (grid reference SY 451 908–453 907). All are of Forest Marble (Bathonian) age.

Diagnosis. — As for genus.

Description

Upper teeth. — Seven teeth are attributed to the upper jaw; they all belong to the group α, which is much the largest group. These are BDUC J.460, J.185, J.459, J.585, J.681, (J.771), J.814 and EF FM/K56.

BDUC J.460 (Figs 1–4) is a particularly well preserved tooth, from the right side of the jaw; it is taken as the typical upper tooth. It is a rough quadrilateral in outline, of greatest width at the mesial end. At the distal end is much the largest cusp (cusp A), the second largest cusp of the tooth (cusp B) lying in the linguo-mesial angle. A row of five tiny cusps and a larger cusp join cusps A and B along the lingual edge of the tooth. The gently curving buccal edge of the tooth bears a row of ten cusps. These show initially an increase in cusp

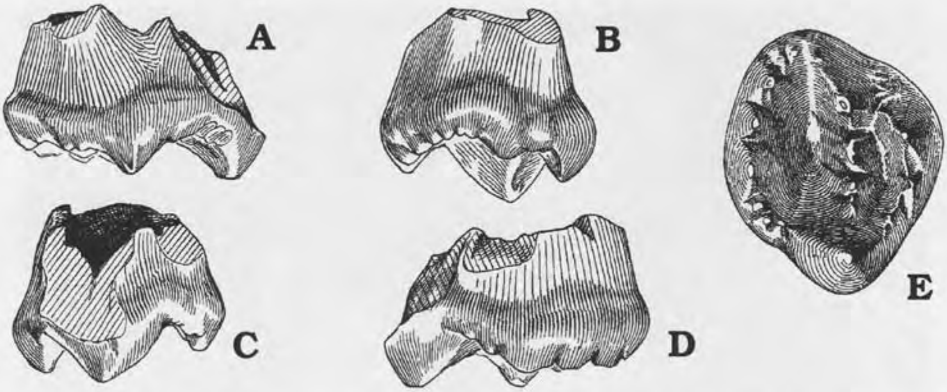

Fig. 4. *Eleutherodon oxfordensis* gen. et sp. n., upper right molar (α), holotype BDUC J.460. **A**. Lingual view. **B**. Anterior view. **C**. Posterior view. **D**. Buccal view. **E**. Occlusal view (anterior is up); × about 15.5.

size passing distally, the largest cusp in this row being the seventh from the mesial end. On the distal side of this cusp are three smaller cusps. The central row consists of four cusps, increasing in size mesially, and terminating distally in cusp A.

Between the rows of cusps are basins with wear facets against which the cusps of the lower teeth occluded. Much the largest facet is that between the buccal and central rows of cusps (facet 11). This facet is deepest in the middle and is slightly curved in the occlusal plane, the convexity facing the lingual border of the tooth. The surface of the facet shows lateral flutings, which have been worn by the main cusp (a) of the opposing lower tooth. The heaviest wear is on the lingual side of the facet. These flutings produced a series of transverse cutting edges analogous to those of a rasp. Wear striations cut across the crests of the flutes on both flanks of facet 11, indicating that motion of opposing teeth was propalinal. Facet 11 is open at the distal end, and here the wear striations show that the tip of the main cusp (a) of the opposing tooth passed between cusp A and the buccal row of cusps. At the mesial end of the tooth the rim is continuous, so that the wear facet forms a basin resembling that in the haramiyids or in some of the paulchoffatiids described by G. Hahn (1969).

The second wear facet (12) lies between the lingual row of cusps and the central row. It is smaller and shallower than facet 11, and is deepest at its mesial end. It continues up on to the main cusp (cusp A) to terminate near its tip. Facet 12 has the same transverse flutings as facet 11, but less conspicuous due to wear. The wear striations are well displayed, passing along the facet and up and on to the tip of cusp A.

Towards the distal end of the lingual side of the tooth is wear facet 13. This is restricted to the lateral surface of the tooth, but it is shown to be a true wear facet by the presence of wear striations. Like wear facet 12, facet 13 commences at cusp A, and becomes deeper as it passes mesially, eventually ending before it reaches cusp B.

The roots are missing.

Remaining α teeth (Figs 5–14). The remaining specimens of the teeth have the same general pattern as BDUC J.460, but with differences in detail, particularly in the size and number of the minor cusps. BDUC J.185, J.771, J.814 and EF FM/K56 come, like

Fig. 5. *Eleutherodon oxfordensis* gen. et sp. n. **A**. Upper right molar (α), BDUC J.185, occlusal view. **B**. Upper left molar (α), BDUC J.459, occlusal view. Anterior is to the right. SEM stereomicrographs; × about 12.

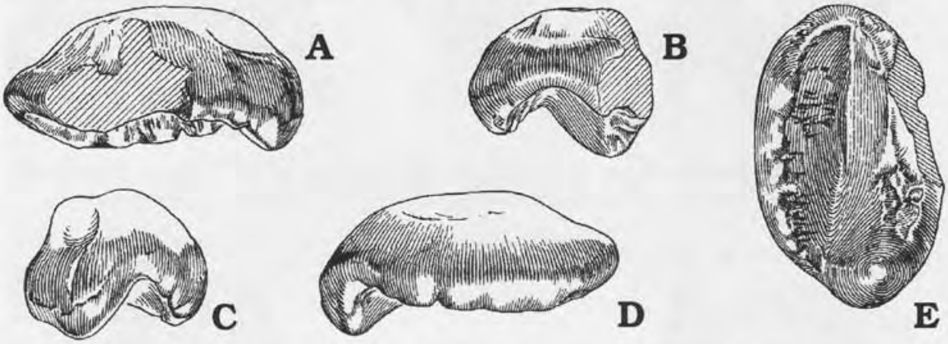

Fig. 6. *Eleutherodon oxfordensis* gen. et sp. n., upper right molar (α), BDUC J.185. **A**. Lingual view. **B**. Anterior view. **C**. Posterior view. **D**. Buccal view. **E**. Occlusal view (anterior is up); × about 15.

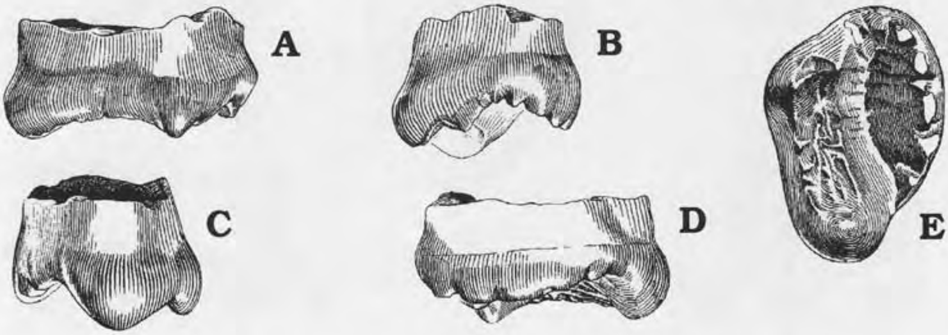

Fig. 7. *Eleutherodon oxfordensis* gen. et sp. n., upper left molar (α), BDUC J.459. **A**. Lingual view. **B**. Anterior view. **C**. Posterior view. **D**. Buccal view. **E**. Occlusal view (anterior is up); × about 14.

Fig. 8. *Eleutherodon oxfordensis* gen. et sp. n. **A**. Upper left molar (α), BDUC J.585, occlusal view. **B**. Upper left molar (α), BDUC J.681, occlusal view. Anterior is to the right. SEM stereomicrographs; × about 11.

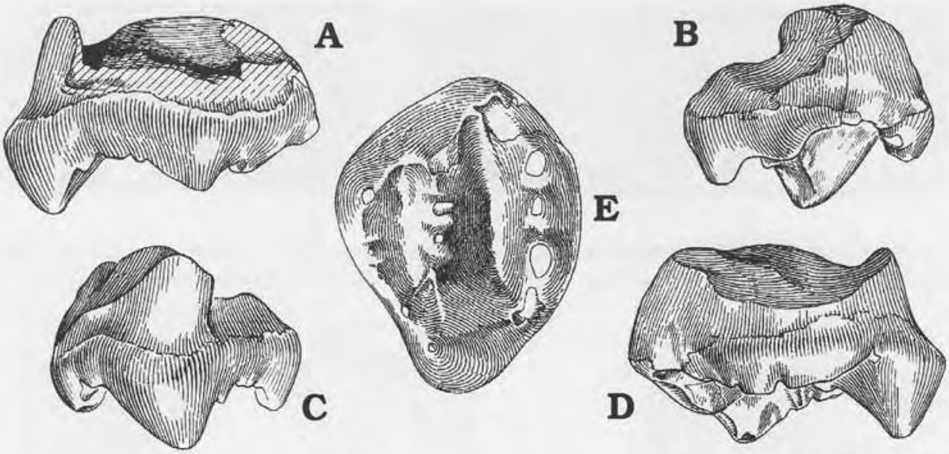

Fig. 9. *Eleutherodon oxfordensis* gen. et sp. n., upper left molar (α), BDUC J.585. **A**. Lingual view. **B**. Anterior view. **C**. Posterior view. **D**. Buccal view. **E**. Occlusal view (anterior is up); × about 15.

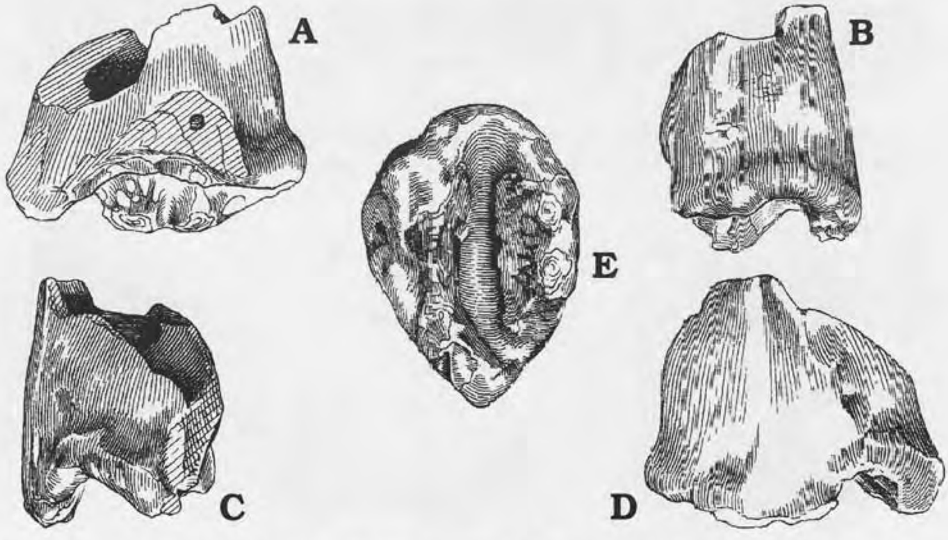

Fig. 10. *Eleutherodon oxfordensis* gen. et sp. n., upper left molar (α), BDUC J.681. **A**. Lingual view. **B**. Anterior view. **C**. Posterior view. **D**. Buccal view. **E**. Occlusal view (anterior is up); × about 15.5.

Fig 11. *Eleutherodon oxfordensis* gen. et sp. n., **A**. Upper right molar (α), BDUC J.771, occlusal view; × 12. **B**. Upper right molar (α), BDUC J.814, occlusal view; × 14. Anterior is to the right. SEM stereomicrographs.

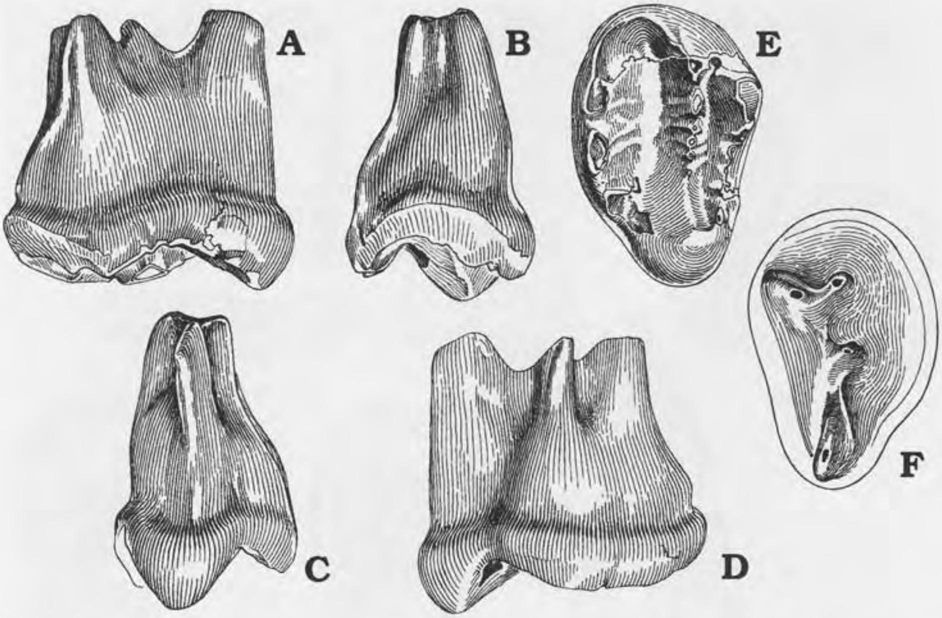

Fig. 12. *Eleutherodon oxfordensis* gen. et sp. n., upper right molar (α), BDUC J.771. **A**. Lingual view. **B**. Anterior view. **C**. Posterior view. **D**. Buccal view. **E**. Occlusal view (anterior is up). **F**. Apical view; × about 15.

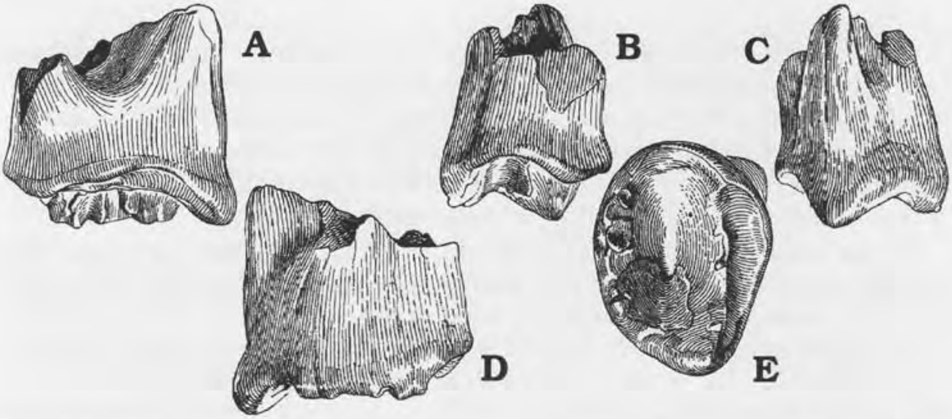

Fig. 13. *Eleutherodon oxfordensis* gen. et sp. n., upper right molar (α), BDUC J.814. **A**. Lingual view. **B**. Anterior view. **C**. Posterior view. **D**. Buccal view. **E**. Occlusal view (anterior is up); × about 15.

BDUC J.460, from the right side of the jaw: BDUC J.459, J.585 and J.681 come from the left side. Except for BDUC J.459, they have all suffered some degree of *post-mortem* damage. They all show an essentially similar pattern of wear facets to BDUC J.460. The ratio of length to width varies (Table 1), but there is no suggestion that the teeth came from two different populations.

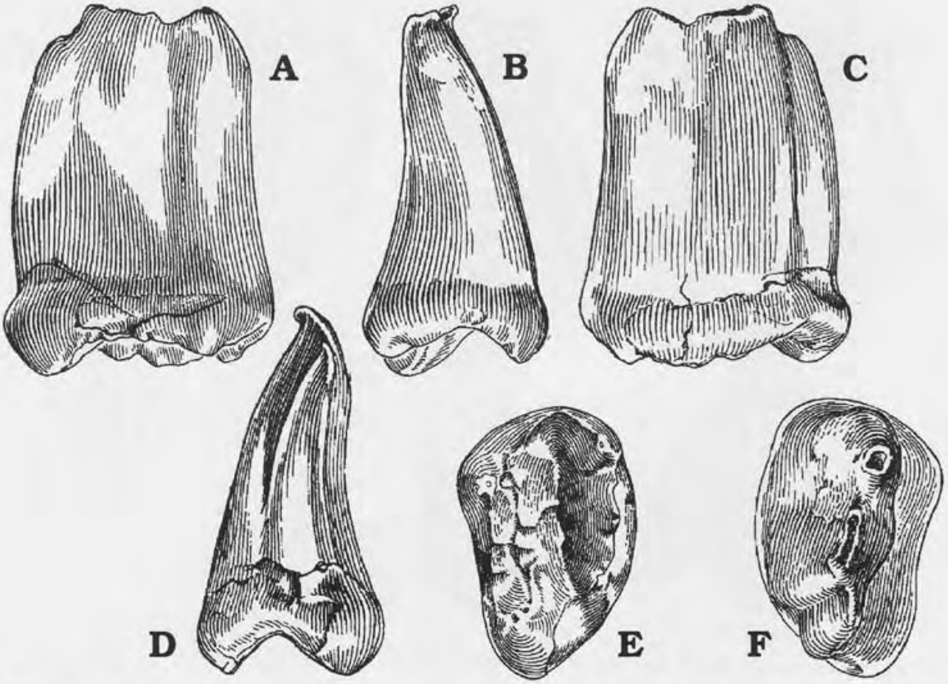

Fig. 14. *Eleutherodon oxfordensis*, gen. et sp. n., upper left molar (α), EF FM K/56. **A**. Lingual view. **B**. Anterior view. **C**. Posterior view. **D**. Buccal view. **E**. Occlusal view (anterior is up). **F**. Apical view; × about 15.

Cusp A is much the largest cusp in all the α teeth, and cusp B the second largest. Cusp B is smaller on BDUC J.459 than on the other teeth. The lingual row consists of about five cusps, while the buccal row varies between three on BDUC J.585 and ten on J.460. The central row of cusps is also variable: BDUC J.459 has a single cusp, equal in size to cusp B, at its mesial end, while, at the other extreme, BDUC J.771 had eight or nine small cusps. In BDUC J.814 the central area only consists of a low ridge.

All the α teeth have the same deep fluted basin (facet 11) between the buccal and central rows of cusps as BDUC J.460. The fluting is present on all except BDUC J.681 and J.814, where it is heavily worn and abraded, and is only poorly visible on BDUC J.585, another well worn tooth. Facet 12 is present in all these teeth. Facet 13 appears only in BDUC J.185, J.585 and J.681, and is lacking in BDUC J.459, which is unworn; and the facet is also lacking in BDUC J.771, J.814 and EF FM/K56 which are damaged in the relevant part of the tooth.

Other differences are probably due to differing amounts of wear. On BDUC J.185, which is a heavily worn tooth, much of the lingual flank of wear facet 11 has the fluting completely worn away leaving a flat surface, particularly towards the mesial end. So plane and polished is this surface that, when coated with the gold-palladium alloy for electron microscopy, it forms an excellent mirror. This flat surface shows the most conspicuous wear striations of any of the teeth, running parallel both with each other, and with the long axis of the tooth. Fig. 22 is an SEM micrograph of wear striations, also showing well-worn flutings. The position of the enlarged area is shown in the adjacent photograph. At the bottom of facet 11, at the level of the polished surface previously mentioned, a deep groove has been cut by the tip of the cusp of the occluding tooth. A similar groove exists in BDUC J.460 and some of the other teeth, but is much less marked. On all the α teeth facet 11 cuts through the distal margin of the tooth, but on the heavily worn EF FM/K56 it also cuts through the mesial margin, which is just nicked in BDUC J.185.

Most of the teeth have the roots missing. The exceptions are BDUC J.771 where there was a single massive root, BDUC J.814 with two roots, a simple one mesially and a compound one distally, and EF FM/K56, which has a single root made up of the fusion of three roots, one mesially and two distally. The root in this specimen is long, and curves apically in a lingual direction.

Lower teeth. — The remaining five molar teeth have only two rows of cusps. They are assumed to be lower teeth: called here β, γ, and ζ, as they show three patterns of cusp arrangement.

β **teeth** (Figs 15A, 16 and 18). There are only two teeth in category β, BDUC J.461 and J.649, of which the former is almost complete and little worn.

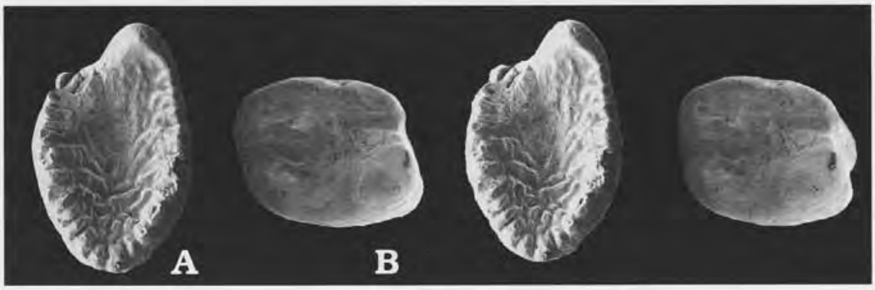

Fig. 15. *Eleutherodon oxfordensis* gen. et sp. n. **A**. Lower right molar (β), BDUC J.461, occlusal view, × about 13. **B**. Lower right molar (γ), BDUC J.183, occlusal view, × about 16. In **A** anterior is up, in **B** to the right. SEM stereomicrographs.

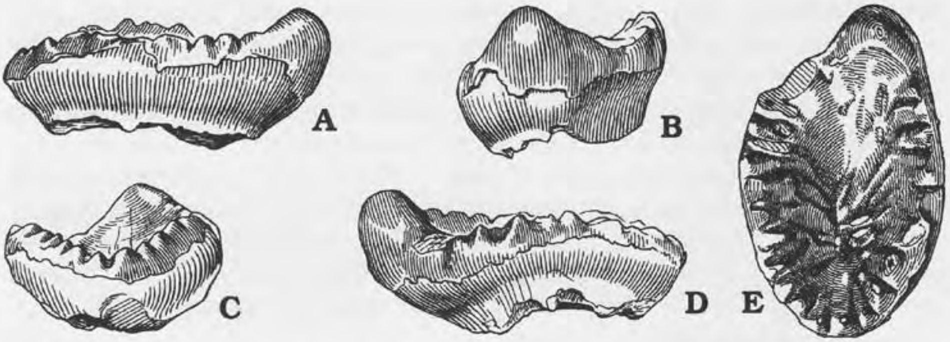

Fig. 16. *Eleutherodon oxfordensis* gen. et sp. n., lower right molar (β), BDUC J.461. **A**. Lingual view. **B**. Anterior view. **C.** Posterior view. **D**. Buccal view. **E**. Occlusal view (anterior is up); × about 17.

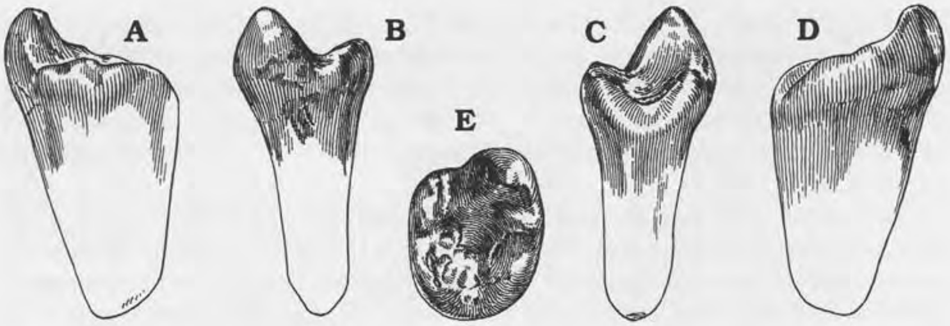

Fig. 17. *Eleutherodon oxfordensis* gen. et sp. n., lower right molar (γ), BDUC J. 183. **A**. Lingual view. **B**. Anterior view. **C**. Posterior view. **D**. Buccal view. **E**. Occlusal view (anterior is up); × about 15.5.

In **BDUC J. 461** (Figs 15, 16), the principal cusp (cusp a) is much larger than the others, and was assumed above to be mesial and buccal in the lower teeth. The lingual row of cusps terminates mesially in the largest cusp of that row (cusp b). The whole cusp has been lost, but its size is shown by its base. The twelve cusps of the lingual row form part of a continuous line of twenty one small cusps around the margin of the tooth. The remaining nine cusps form a smooth curve along the buccal margin of the tooth. Thus the clear distinction between buccal and lingual rows of cusps seen in the α teeth, is not obvious in the β teeth. There is no central row of cusps. The roots are missing.

The tooth is basined, with only one great wear facet 21 occupying the basin, and breaking through the mesial border of the rim between cusp a and the most mesial cusp of the lingual row. The facet passes up the apex of cusp a, in a similar manner to facet 12 in the α teeth. It is slightly curved and convex buccally, with conspicuous lateral flutings, which perform the same function as those in facet 11 of the type α teeth. As facet 21a, it passes onto the buccal margin of the tooth, running from the apex of cusp a to the fourth cusp of the buccal row.

Wear striations are visible, both in SEM micrographs and under a binocular microscope. As with the α teeth they run longitudinally. Fig. 22 shows an SEM micrograph of this tooth with wear striations.

BDUC J.649 (Fig. 18) is damaged and shows more wear then BDUC J.461, but is clearly of the same pattern as the latter tooth although there are some differences. It is shorter; the cusps bordering the rim are on the whole larger, and twelve in number. Cusps a and b have both been broken off, and the pulp cavity can be seen passing up into both. The tooth is basined, but the flutings have been largely worn away.

The facets are essentially similar to those of BDUC J.461, apart from the effects both of increased wear and of damage to the tooth. Facet 21 in this case nicks the distal rim, without, however, passing through it. Facet 22 is much more obvious and forms a definite notch, visible on the occlusal as well as on the buccal surface of the tooth. The main facet, incomplete due to damage, seems to have been straight.

No roots are preserved.

The complementary character of the α teeth and the β teeth leaves little doubt that they form part of the upper and lower dentition of the same species.

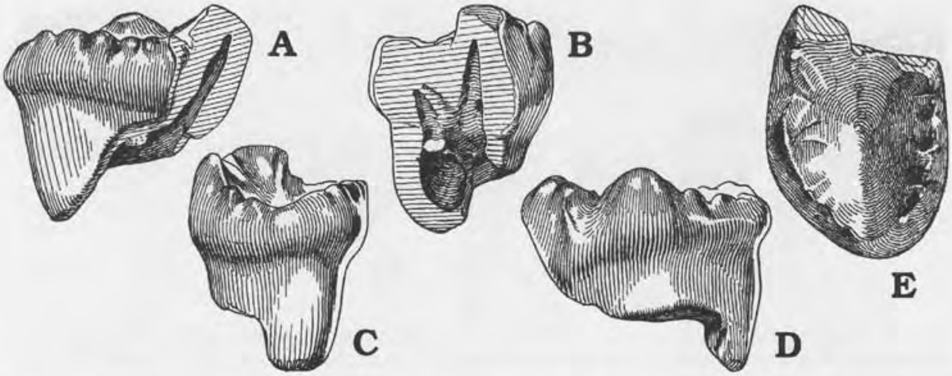

Fig. 18. *Eleutherodon oxfordensis* gen. et sp. n., lower left molar (β), BDUC J.649. **A**. Lingual view. **B**. Anterior view. **C**. Posterior view. **D**. Buccal view. **E**. Occlusal view (anterior is up); × about 16.

γ teeth (Figs 15B, 17, 19A and 20). Two teeth BDUC J.183 and J.763 fall into this group. They are very different from the other lower teeth, and may well not belong to the same genus. BDUC J.763 has the crown well preserved, but BDUC J.183, unusually for these Forest Marble teeth, has well preserved roots. They are assumed to be lowers, and to have the same orientation as the β teeth, cusp a being buccal and mesial.

BDUC J. 763 (Figs 19A and 20) is a left molar, and differs from all the specimens so far described in not being basined, the main area of wear cutting completely through the tooth at both mesial and distal ends. BDUC J.763 is also broader relative to its length than are the preceding teeth. The buccal margin of the tooth is straight, with three large cusps, which increase in size passing mesially, the largest cusp of the tooth (cusp a) being at its mesio-buccal angle. Although this cusp is the largest cusp in the tooth, it does not have the preponderance in size over the other cusps that it has in the α and β teeth. In this respect BDUC J.763 resembles J.797 (Fig. 21), a ζ type tooth.

Fig. 19. *Eleutherodon oxfordensis* gen. et sp. n. **A**. Lower left molar (γ), BDUC J.763, occlusal view, × 13. **B**. Lower left molar (ζ), BDUC J.797, occlusal view, × 12. Anterior is to the right. SEM stereomicrographs.

The lingual border of the tooth is curved, and bears four small cusps. These small cusps seem to have remained separate to the bottom of the wear groove, while the large buccal cusps arise well above the lowest point of the groove. In other words, the tooth is asymmetric in cross section, the buccal rim standing higher than the lingual rim.

The main area of wear, lying between the two rows of cusps, is divided into two separate wear facets by an inclined longitudinal ridge. The larger wear-facet is on the

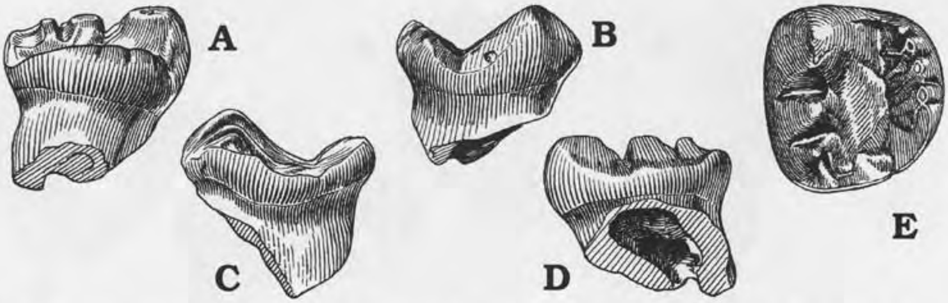

Fig. 20. *Eleutherodon oxfordensis* gen. et sp. n., lower left molar (γ), BDUC J.763. **A**. Lingual view. **B**. Anterior view. **C**. Posterior view. **D.** Buccal view **E**. Occlusal view (anterior is up); × about 16.

buccal side of the ridge, and is broadest at its distal end. The other facet is on the lingual side of the longitudinal ridge, and the facet is broadest at its mesial end. Both facets lack the fluting seen in the other teeth. The wear striations, seen with both the light and electron microscopes, show that the relative movement of this tooth was entirely propalinal. In this it differs from the β and ζ teeth. This may perhaps be explained by the γ teeth being the last lower molars, so that movement of the cusp A of the upper molar only corresponds to the first half of the movement on the other lower teeth. Alternatively, as has been said, the γ teeth may be from another species. There is another wear facet running along the outer (buccal) face of the buccal row of cusps. This is not so easily visible in the occlusal view, but can be seen in the appropriate lateral view. These wear facets are not easily equated to those of the other teeth.

There is a single broken root.

BDUC J.183 (Fig. 15B) is similar to J.763 in structure, although the proportions of the two teeth are rather different, BDUC J.183 being like all the teeth except BDUC J.763, longer than wide. BDUC J.183 is from the other side (right) of the jaw to BDUC J.763, and heavily worn and abraded; how much of this wear occurred during life cannot be determined, but a considerable amount must have been *post mortem*. All fine detail in the tooth has consequently been lost. The lingual row of cusps has been almost completely obliterated, but the buccal row shows the remains of the three large cusps. The lateral wear facet seen in BDUC J.763 is not visible.

There is a single long massive root. Owing to its preservation the natural orientation of this tooth is quite unequivocal – the buccal row of cusps stood much higher in the jaw than the lingual row. These γ teeth show the greatest resemblance to the molars of multituberculates of any of the Forest Marble teeth.

ζ tooth BDUC J.797 (Figs 19B and 21). The only tooth in this category is assumed to be a lower one. It is well preserved, except that after death, and before fossilization, it attracted the attention of some organism which bored tiny holes in it.

Due to the damage it is uncertain whether there was a single large cusp at the mesial end of the buccal row (cusp a), which has been cut in half by the boring organism, or two cusps. On the first assumption, which is the more probable, another boring has cut into the distal side of the same cusp. The difference in size between cusp a and the other cusps of the tooth is less in this specimen than in the α and β teeth. The next cusp on

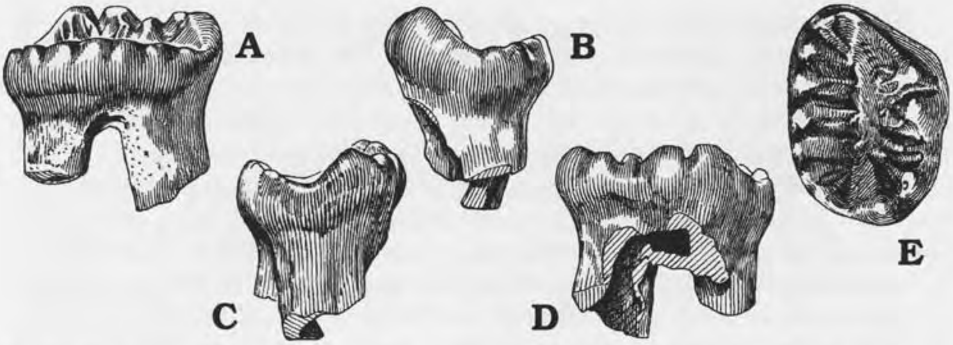

Fig. 21. *Eleutherodon oxfordensis* gen. et sp. n., lower left molar (ζ), BDUC J.797. **A**. Lingual view. **B**. Anterior view. **C**. Posterior view. **D**. Buccal view. **E**. Occlusal view (anterior is up); × about 14.5.

the distal side has been almost completely eroded away on its mesial side by the same borer that damaged the distal side of cusp a, and on its distal side by another. There then follows a small, undamaged cusp, followed by another which extends to the mid-line of the tooth. On the assumption that there is a single large cusp at the mesial end of the row, there are four cusps in the buccal row, otherwise there are five. The lingual row of cusps is undamaged; there are seven cusps, the largest being in the middle of the row.

There seems to be only a single large basined wear facet, probably representing 21b in the β teeth, but in this specimen the wear facet seems, by the evidence of the wear striations, to break through the rim distally as well as mesially. The facet has the usual lateral flutes passing down its side, with wear heaviest on the buccal side of the facet, causing the flutes to be worn down.

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.

If BDUC J.797 be oriented in the jaw on the assumption that its roots are vertical, then the rim bearing the large buccal cusps stands well above the rim bearing the smaller lingual cusps. This helps to give the tooth the appearance of a multituberculate molar.

Occlusion and chewing

From the analysis of the wear facets and associated striations it is possible to work out the occlusion of the teeth and the chewing mechanism.

Wear facets (Figs 2 and 22). — On recent therian teeth, the position of the wear facets follows closely the pre-existing surfaces of the teeth. This is not so with the teeth described in this paper: a well-marked facet in the therian sense is only visible after considerable wear has occurred. The position of these wear facets is shown in Figs 2 and 22 and has been mentioned above for each tooth described. We shall briefly summarize them.

Between the buccal row of cusps and the central row of an upper molar, lies the largest and deepest wear facet of the tooth, facet 11. The latter is deepest in the middle and slightly curved, with the convexity facing its lingual border. Its surface is fluted and worn particularly on its lingual side by the action of the opposing cusp. The flutings produce a series of transverse cutting edges analogous to those of a rasp.

The second wear facet in the upper molar, facet 12, lies between the lingual row of cusps and the central row. This is a smaller and shallower facet, being deepest at its mesial end. The fluting, which is so striking in facet 11, is absent in facet 12. This facet 12 is formed by cusp b of the lower tooth shearing along the groove between the lingual and central row of upper cusps, to a point near the tip of cusp A. The third wear facet, 13, lying on the lingual side of the upper tooth, begins at cusp A and becomes deeper as it passes mesially and eventually ends before the level of cusp B.

The complete pattern of faceting is found only in BDUC J.460 and J.459 (Figs 3 and 5B), which are undamaged. In the remaining teeth only parts of the pattern are visible, due to *post-mortem* damage. There are other differences between the teeth, which are most probably due to differing amounts of wear, and to the different position of the teeth in the jaw. BDUC J.459 shows little sign of wear and facet 13 is therefore completely missing. On BDUC J.185 (Fig. 5A), which is a heavily worn tooth, a deep groove has been cut at the bottom of facet 11 by the opposing cusp a. A similar groove exists on other teeth but is much less marked. On all the other teeth facet 11 cuts through the distal margin of the tooth, but on the heavily worn EF FM/K56 (Fig. 14) it cuts through the mesial margin as well, which is also nicked on the worn BDUC J.185.

The lower or β teeth are basined; each with a single large wear facet 21 occupying the basin and breaking through the rim in BDUC J.461 (Fig. 15A) between cusp a and the most mesial cusp in the lingual row, but only nicking the rim in the much more worn BDUC J.649. The facet passes up the apex of cusp a and in BDUC J.461 is slightly curved and convex buccally, with conspicuous lateral flutings, which perform the same function as those on facet 11 of the upper teeth. Fig 2B shows how facet 21 can be divided into 21a and 21b. Due to wear and damage this main facet is incomplete in BDUC J.649 but it was probably straight, unlike that in BDUC J.461. There is an indication of another wear facet (21a) in BDUC J.461 on the buccal margin of the tooth running from the apex of cusp a to about the level of the fourth cusp in the buccal row. In BDUC J.649 this facet is much more obvious forming a definite notch, visible on the occlusal and the buccal surfaces of the tooth.

The rest of the teeth are all believed to have come from lower jaws and do not seem to be complementary to the upper or α teeth as are the β teeth. The wear-facet pattern on the γ tooth BDUC J.763 differs from that in previous α and β groups, since the tooth is not basined (Fig. 19A). The main area of wear lies between the two main cusps and is divided into two separate wear facets by an inclined longitudinal ridge. The larger facet is on the buccal side of the ridge and is broadest at its mesial end. The other facet is on the lingual side of the ridge and also broadest at its mesial end. The fluting seen in the α and β teeth is absent. There is a third facet running along the outer (buccal) face of the buccal row of cusps.

In teeth other than these γ teeth, the opposing main cusp (A or a) commences on the margin of the opposing basin, moves distally and down into the bottom of the basin,

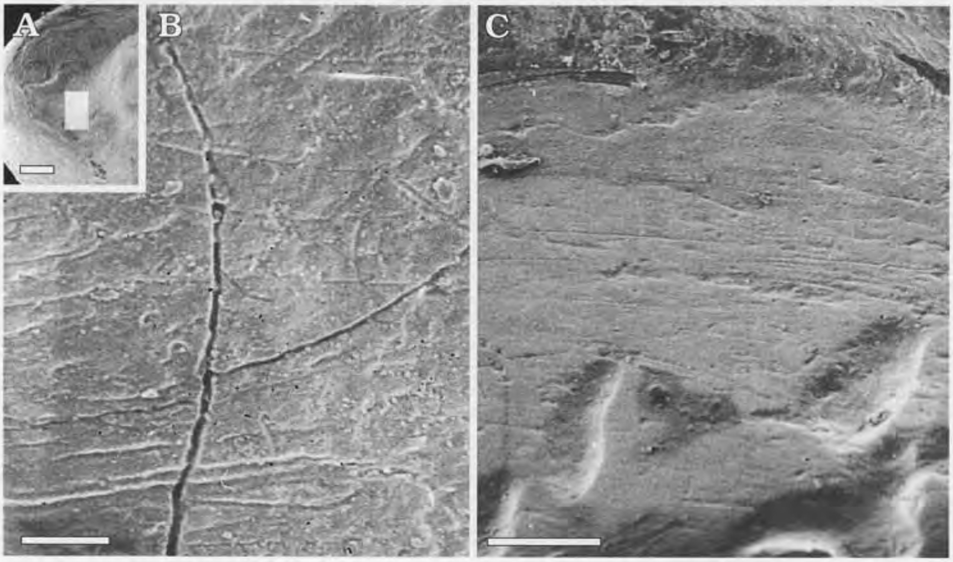

Fig. 22. *Eleutherodon oxfordensis* gen. et sp. n., longitudinal wear striations **A**. Lower left molar (β), BDUC J.461, left part of cusp a (scale bar 100 μ) showing area enlarged in **B** (scale bar 10 μ). **C**. Upper right molar (α), BDUC J.185 (scale bar 100 μ). SEM micrographs.

and then rises up to the distal margin. In the γ teeth the movement is entirely in one plane. It is difficult to visualize how this difference could occur in two teeth in the same jaw, and, taken with other factors we conclude that these γ teeth probably came from a different species to the α and β teeth.

The main slightly curved facet of the ζ tooth BDUC J.797 is basined and breaks through the margins of the tooth at both mesial and distal ends (Fig. 19B). Wear seems to be greater on the buccal side of the fluted basin. There are then sufficient similarities to the β teeth for us to conclude that this tooth belongs to the same animal, probably at a different position in the dental series.

Wear striations (Fig. 22). — Simpson (1926) comments that the molar teeth of every multituberculate genus that he has examined showed fine striations due to wear, and that the direction of these striations enabled him to determine the relative movement of the teeth in mastication. Mills (1955, 1966) developed this method and showed that these striations are of general occurrence in mammalian teeth. The direction of the striations indicate the exact direction of jaw movement during occlusion and mastication.

The wear striations are minute and not always easy to see. Krause (1982) and Sigogneau-Russell (1989) made use of a scanning electron microscope to examine and photograph the striations. We adopted this technique with success, confirming the presence of striations by viewing the teeth under a binocular microscope at × 40 after examining the SEM micrographs.

Krause (1982) comments on the absence of wear striations in some specimens of the Palaeocene multituberculate *Ptilodus mediaevus* from Swain Quarry in Wyoming. He suggests that this may be due to a difference in diet, the difference perhaps being seasonal. The striations are not always present in our Forest Marble material, since in comparing two similar specimens one may show wear striations and another not. Despite this, enough of our specimens show wear striations for definite conclusions to be reached. In our Forest Marble teeth all the wear striations run parallel or nearly so, with their long axes (Fig. 22 shows wear striations on SEM micrographs of BDUC J.185 and J.461). This indicates that the movement of the opposing tooth was propalinal.

As previously indicated, the facets on BDUC J.460, although essentially propalinal, are slightly curved. Facet 11 is slightly curved in BDUC J.459, J.771, J.814 and EF FM/K56, although curvature is less marked in BDUC J.585 and in J.681 it is almost straight and quite straight in BDUC J.185. Facet 12 is straight in BDUC J.459 and J.771 although in these teeth facet 11 shows slight curvature.

This curvature of the facets in some, but not all teeth, requires explanation. Jaw movement was essentially propalinal (probably palinal in the chewing phase), with both mandibular condyles moving posteriorly. Towards the end of the shearing action there is a small amount of ectal (buccal) movement. This could be produced if the contralateral condyle moved faster, and therefore further, than the ipsilateral condyle. Alternatively, as suggested to us by Percy M. Butler, since the occlusal surfaces of the teeth are inclined lingually, it might be due to the lower jaw beginning to move downward in opening.

Action of the teeth. — During the chewing cycle the lower molar teeth move across their opposing teeth as illustrated diagrammatically in the five parts of Fig. 23. This figure shows an upper molar or α tooth, based on BDUC J.460, in thick outline, drawn as though it is transparent and viewed apically in superimposition on a lower molar or β tooth. The latter is shown in thin outline and is based on a slightly reconstructed BDUC J.461. There is of course, no guarantee that these teeth came from the same individual. The outlines do not superimpose exactly and the figure is purely diagrammatic.

The principal chewing action consists of cusp a of the lower molar shearing along the lingual basin of the upper tooth producing facet 11a. This is somewhat analogous to the way in which the hypoconid of a typical tribosphenic molar shears into the trigon of the upper molar. The difference is that in the Forest Marble teeth the motion is propalinal, while in the therians it is essentially buccal. Cusp a of the lower tooth passes out of facet 11a through the groove between cusp A and the buccal row of cusps in the distal margin of the upper tooth, often causing wear striations along the facet and onto cusp A, as illustrated in Fig. 22. Since the mesial margin is nicked only in heavily worn teeth (BDUC J.185 and more definitely in EF FM/K56) the mesial end of a more distal upper tooth may have been positioned at a more dorsal level than its neighbour, so that it lay above the distal margin of the latter. However, the power stroke takes place as the jaw is closing so this would give the appearance of the mesial end of the upper tooth being at a higher level than the distal end. Cusp b of the lower tooth is more distally placed than cusp a, and therefore contacts the upper molar more distally, producing the facet 12 on the buccal side of the smaller basin of the upper tooth. The wear facet 12 finally passes up onto the mesial side of cusp A, suggesting that the jaw starts to open again before its backward movement is completed.

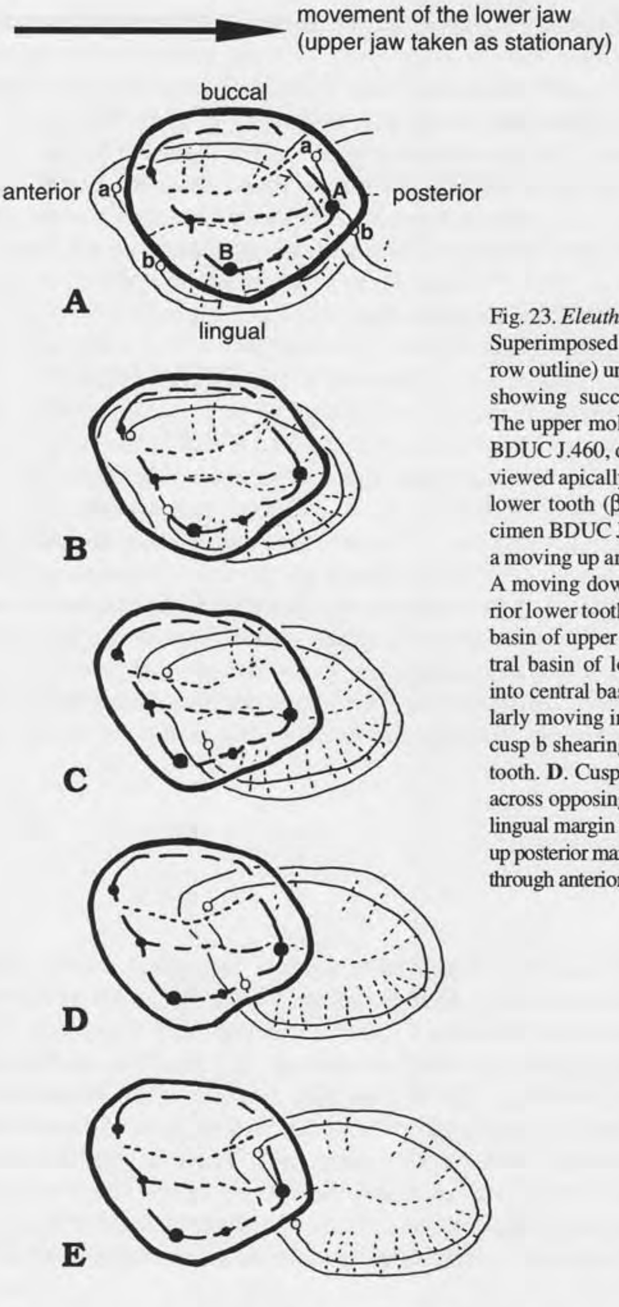

Fig. 23. *Eleutherodon oxfordensis* gen. et sp. n. Superimposed diagrams of lower molar (narrow outline) under upper molar (thick outline), showing successive phases of mastication. The upper molar (α) is based on the holotype BDUC J.460, drawn as though transparent and viewed apically, to allow superimposition. The lower tooth (β) is based on the referred specimen BDUC J.461, slightly restored. **A**. Cusp a moving up anterior edge of upper tooth; cusp A moving down anterior edge of more posterior lower tooth. **B**. Cusp a moving into central basin of upper tooth; cusp A moving into central basin of lower tooth. **C**. Cusp a moving into central basin of upper tooth; cusp A similarly moving into central basin of lower tooth; cusp b shearing down lingual groove of upper tooth. **D**. Cusps a and A similarly progressing across opposing basins; cusp b moving through lingual margin of upper tooth. **E**. Cusp a moving up posterior margin of upper basin; cusp A cutting through anterior margin of lower tooth.

It is not easy to see how facet 13 on the lingual side of some of the upper molars (e.g., BDUC J.460) was produced. This problem would be solved and the difficulties of occlusion simplified if the teeth were offset to some extent laterally in the jaw. This is true of Jurassic multituberculates, where the two upper molars have a considerable offset from each other.

The wear on the basined area of the upper teeth is generally not heavy, although the crests of the flutes are almost always worn away to some extent, indicating they functioned as the teeth of a self-sharpening rasp. In BDUC J.185 the flutes on the mesio-lingual surface of the basin are completely worn away to a smooth plane.

In the lower molar, cusp A of the occluding upper molar, preceded by the central row of cusps and cusp B, at the mesial end of the row, shears along the central basin, as indicated in Fig. 23 and moves along facet 21 of the lower molar. Since the upper molar overhangs the lower buccally, facet 11a shears against facet 21a and facet 11b similarly shears against facet 21b. The buccal row of cusps of the upper tooth works against the buccal surface of the buccal row of the lower tooth to produce facet 22. This is indicated by the lower heavy broken line on the buccal side of the tooth in Fig. 23.

In the upper molars, the small cusps of the buccal, lingual and central rows vary in number between specimens. It should be appreciated that the function of these small cusps differs from that of the principal cusps A and B and indeed from that of similar cusps in the teeth of therian mammals. In the latter, each cusp shears buccally along an opposing groove and cannot change its position without changes in the opposing tooth. This makes for stability in the structure and form of the teeth. The small cusps in the Forest Marble teeth shear almost propalinally, and nothing shears across any tooth bucco-lingually between the cusps. Variation in the number of cusps is therefore possible with no interference in function. These cusps could serve to cut the fibrous vegetable food, whilst the principal cusps in their opposing grooves crush it against the cutting edges of the transverse flutes. Alternatively, these small cusps may prevent the food from slipping during mastication. It is also possible that both functions apply.

Relationships

Thus the jaw movement must have been almost entirely propalinal, with a minute buccal component. This observation is of importance in determining the affinities of the animals which bore the teeth. Simpson (1926) commented that the motion in the lower molars of multituberculates was always propalinal. This has been confirmed by Krause (1982). Butler & MacIntyre (1994) state that amongst early mammals and therapsids propalinal chewing movements only occur in four groups: traversodont cynodonts, tritylodonts, haramiyids and multituberculates. These new teeth from the Forest Marble constitute a fifth group in which the motion of the lower molars is entirely propalinal. These teeth show no resemblance to those of traversodonts and tritylodonts, but they do show other similarities to the teeth of haramiyids and multituberculates. These are:

(1) the arrangement of the cusps in mesio-distally running rows: two in haramiyids (the Greenlandic form excluded), three in theroteinids, two (Late-Jurassic/Early Cretaceous) or three (Late Cretaceous/Early Tertiary) in multituberculates: the third lingual row of cusps on M1/ makes its appearance in an incipient form referred to as a postero-lingual wing or ridge (Kielan–Jaworowska *et al.* 1987; Kielan-Jaworowska & Ensom 1992) in the Late Jurassic Plagiaulacidae; the plagiau-

lacid M2/ keeps two rows of cusps; so do the upper molars of the Jurassic Paulchoffatiidae, where M2 is basined;

(2) the almost exclusive propalinal movement of the molars in chewing (again, the Greenlandic form excluded). In haramiyids, this character has been substantiated by the study of wear facets and SEM observation of longitudinal striations (Sigogneau-Russell 1989; Butler & MacIntyre 1994).

The teeth from the Forest Marble described in this paper display both these attributes with an apparently backward power stroke. With the exception of the teeth BDUC J. 183 and J.763, the molars have the main wear facet forming a basin, open at one end and closed at the other. This is a character they share with generalized haramiyids and M/2 of paulchoffatiid multituberculates. Longitudinal striations have similarly been observed on wear facets.

In the Greenlandic form, the masticatory movement has been deduced as orthal; but neither wear facets nor striations have been mentioned, so that conclusive comparison with it and haramiyids remains incomplete. Thus, in the present state of knowledge, we consider that the two apomorphies enumerated above link the Forest Marble teeth with haramiyids and multituberculates in the subclass Allotheria Marsh, 1880, of which they form a fourth branch, Eleutherodontida nov. (the third being possibly the theroteinids). They appear, however, too specialized to be near the ancestry of Late Jurassic multituberculates.

Finally, assembling the teeth into a dentition is almost impossible with the very limited sample at our disposal. The supposed presence of three patterns of lower molars and only one of uppers is not helpful. It should also be emphasized that the ensemble of teeth studied above is very small compared to the total number of mammalian teeth collected; there is no doubt that these teeth were transported a considerable distance to be deposited where they were fossilized and eventually found. Sorting, abrasion and loss by stranding undoubtedly occurred on the journey.

Conclusion

Eleutherodon oxfordensis was a small shrew-like mammal living in a diverse and rich environment of plants and small vertebrates. The assemblage is dominated by aquatic elements (salamanders, turtles, crocodiles, choristoderes), but there was also a strong terrestrial component, including lizards and many small mammals. It can be said that the vertebrate faunas of the time were 'in a highly experimental phase of evolution', in an effort to take advantage of the rapidly evolving supply of plants and invertebrates.

The discovery of *Eleutherodon oxfordensis* gen. et sp. n. shows that our simplistic ideas on the evolution and interrelationships of Jurassic mammals in general and Allotheria in particular are very inadequate. The broad generalisations of the past no longer apply. More information is needed and this can only be acquired from the examination of new exposures in order to discover assemblages similar to those found in Kirtlington Quarry. When the latter and hopefully new material has been thoroughly examined and described, then the evolution of Jurassic mammals should be better and more fully understood.

Acknowledgments

We thank all the people who made this work possible and in particular: Mr. Eric Freeman, Mr. D. Ward, Dr. Bill Wimbledon, Mrs Frances Mussett, Dr. Susan Evans and Professor Avrion Mitchison. Eric Freeman, David Ward and Bill Wimbledon gave unstinted help to the University College London team in the collection of the fossiliferous material. Mr. Freeman most generously encouraged and helped our own work at the site, and lent us for description material from his own collection. Drs. S.E. Evans and D. Sigogneau-Russell provided considerable help in the editing of the manuscript. Mrs J. Pendjyky played a key role in the preparation of figures for publication.

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Nowe zęby ssaków ze środkowej jury Anglii

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Streszczenie

W pracy opisano kolekcję pojedynczych zębów ssaków ze środkowej jury (batonu) Anglii. Kolekcja pochodzi z osadów znanych jako Forest Marble, występujących w Kirtlington, w Oxfordshire. Wszystkie zęby zaliczono do nowego gatunku i rodzaju *Eleutherodon oxfordensis*, dla którego utworzono nową rodzinę Eleutherodontidae i nowy podrząd Eleutherodontida. Podrząd ten, zaliczony do rzędu *incertae sedis* umieszczono w podgromadzie Allotheria, do której zalicza się też wieloguzkowce (Multituberculata). Nowe zęby mają unikalną budowę, ale łączy je z wieloguzkowcami i haramiyidami ułożenie guzków w podłużne rzędy, a z wieloguzkowcami ponadto ruch żuchwy ku tyłowi podczas żucia (palinalny). Pod tym względem różnią się one od triasowej *Haramiyavia clemmenseni* (zaliczonej do haramiyidów) z Grenlandii, u której zrekonstruowano pionowe ruchy żuchwy podczas żucia.