Review of the early allotherian mammals

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Comparison of the early allotherian genera, *Haramiyavia*, *Thomasia*, *Theroteinus*, and *Eleutherodon* shows that their molariform teeth are variants of a common pattern, justifying the inclusion of these genera in a single order Haramiyida. *Haramiyavia* is made the type of a new family Haramiyaviidae. The order Haramiyida is divided into two suborders: (1) Theroteinida (only family Theroteinidae), and (2) Haramiyoidea (families Haramiyaviidae, Haramiyidae, Eleutherodontidae). Dental resemblances support the hypothesis that the Multituberculata originated within the Haramiyida, in which case the Haramiyida would be paraphyletic. Derivation of multituberculates from within the Mammaliaformes would involve a highly improbable transformation of the dentition. It is therefore postulated that allotherian (Haramiyida + Multituberculata) and non-allotherian mammaliaform clades separated before the Mammaliaformes developed a shearing dentition with unilateral occlusion and transverse jaw movements. This hypothesis implies that the two clades evolved to a large extent in parallel, to account for the apparent synapomorphies of multituberculates and therians.

Key words: Haramiyida, Multituberculata, molars, occlusion, homoplasy.

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Introduction

The term Allotheria was used originally by Marsh (1880) for an order of mammals, embracing extinct forms characterized by the possession of cheek teeth with two or more longitudinal rows of cusps. They included not only those later known as multituberculates, but also *Tritylodon* (now removed from the Mammalia) and *'Microlestes'*, now *Thomasia*. The same forms were classified by Cope (1884) in a suborder Multituberculata of the Marsupialia. Simpson (1926) treated the Multituberculata as an order. He distinguished two suborders, Tritylodontia and Plagiaulacoidea; *Thomasia* and a new genus *Microcleptes* (emended to *Haramiya*, Simpson 1947), known only by isolated teeth, were placed in a new family Microcleptidae (now

Haramiyidae), suborder *incertae sedis*. He said (Simpson 1928: p. 54): 'They show a distant resemblance to some multituberculates and may be placed in this Order, but with the understanding that there is no decisive evidence in favour of this view and that some facts oppose it'. In 1945 Simpson revived the term Allotheria for a subclass of mammals, to include the single order Multituberculata.

In 1969 G. Hahn described paulchoffatiid multituberculates from the Late Jurassic (Kimmeridgian, or possibly Oxfordian) of Portugal, older and more primitive than the plagiaulacoids hitherto known. Because of resemblances of some paulchoffatiid teeth to those of haramyids, G. Hahn (1973) included the latter in the Multituberculata as a suborder Haramiyoidea. Sigogneau-Russell *et al.* (1986) described *Theroteinus*, based on isolated teeth from the Rhaetic of France, first reported by Sigogneau-Russell in 1983. They differed from those of haramiyids in enamel structure, and their wear did not show evidence of a longitudinal (propalinal) chewing action, present in haramiyids as well as multituberculates. G. Hahn *et al.*(1989) placed *Theroteinus* in a new allotherian order, Theroteinida, and raised the Haramiyoidea to ordinal status as Haramiyida. They regarded the Theroteinida and Haramiyida as earlier branches from the stem of the Multituberculata.

Jenkins *et al.* (1983) described one tooth which might be a haramiyid from the Early Jurassic Kayenta Formation of North America.

Sigogneau-Russell (1989) described a large collection of haramiyid teeth from the Rhaetic of France, identifying incisors, premolars and molars of upper and lower dentitions; she paid particular attention to wear facets. Butler and MacIntyre (1994) revised the British Early Jurassic material in the light of Sigogneau-Russell's work. They attempted a reconstruction of the dentition, and interpreted the chewing action as a rotary movement in the sagittal plane, with a backward (palinal) power stroke. A palinal power stroke had been recognised in multituberculates by Krause (1982) and Wall & Krause (1992).

Up to this time non-multituberculate allotherians had been known only from isolated teeth. Jenkins *et al.* (1997), however, described *Haramiyavia clemmenseni* from the Late Triassic of East Greenland, based on dentaries and maxillae with teeth in place, and assigned it to Haramiyida. These authors postulated predominantly orthal movements of the dentary and on this basis concluded that haramiyids were not related to multituberculates.

Another type of allotherian, *Eleutherodon oxfordensis*, has been described by K.A. Kermack *et al.* (1998) from teeth from the Middle Jurassic (Bathonian) of England. These teeth show evidence of longitudinal, presumably palinal, chewing as in Haramiyidae, but, because of their distinctive morphology, the authors proposed for this species a new suborder Eleutherodontia, order *incertae sedis*.

Heinrich (1999) described *Staffia aenigmata* based on a tooth from the Late Jurassic of Tanzania. Because of the resemblance to teeth described as *Thomasia*, group II by Sigogneau-Russell (1989) he placed *Staffia* in the Haramiyidae, thus greatly extending the known range of the family.

Thus five genera of non-multituberculate allotherians are known: *Haramiyavia* Jenkins *et al.* (1997); *Thomasia* Poche (1908) [including *Haramiya* Simpson (1947), which was based on the upper teeth of *Thomasia*, see Butler & MacIntyre (1994)]; *Staffia* Heinrich (1999); *Theroteinus* Sigogneau-Russell (1983); and *Eleutherodon*

K.A. Kermack *et al.* (1998). These range from Late Triassic to Late Jurassic. The discovery of *Haramiyavia*, in which the teeth are preserved in place, and upper and lower dentitions are associated, provides a basis for the interpretation of the other genera that are known only by isolated teeth. In this paper the resemblances and differences between the genera are reviewed.

Abbreviations. — BDUC, Biology Department, University College, London (cited by K.A. Kermack *et al.* 1998); the specimens are now housed in the Natural History Museum, London; SNP, specimens from Saint-Nicols-de Port housed in the Museum National d'Histoire Naturelle, Paris.

Cusp nomenclature

In this paper the cusps are named in accordance with their postulated homologies with *Haramiyavia*, using the system of nomenclature of Jenkins *et al.* (1997), with minor modifications. This system was adopted from that applied to *Thomasia* and *Haramiya* by Sigogneau-Russell (1989) and Butler & MacIntyre (1994), and originally proposed by G. Hahn (1973).

On lower molars the two rows of cusps are termed a (lingual) and b (buccal) (lower case letters are used for lower teeth, capitals for upper teeth). Within the rows the cusps are numbered from mesial to distal. The mesial cusps (at the '+ end' of Butler & MacIntyre, 1994) are the largest and most constant, except that (as postulated below) b1 may be reduced or absent. The number of cusps in the rows is variable between taxa, between teeth in different serial positions, and individually; for example, in *Thomasia* additional b cusps develop at the distal end, on the 'U ridge' (Butler & MacIntyre 1994).

The pattern of upper molars is reversed: row A is buccal and row B is lingual. Row B occludes in the valley between lower rows a and b, in a similar manner to that in which lower row b occludes between upper rows A and B (Fig. 3). A similar buccal--lingual reversal of patterns occurs in many rodents: e.g., the mesoloph is buccal on upper teeth, and the mesolophid is lingual on lower teeth. A further complication arises in haramiyids in that opposing teeth are also reversed mesiodistally (Figs. 1, 2). On upper teeth the '+ end', with the largest and most constant cusps, is distal, and the mesial cusps are the most variable. Upper cusps are therefore numbered from distal to mesial. When this system was proposed it was not recognised that *Haramiya* is the upper dentition of *Thomasia*, and the same nomenclature was applied to both 'genera'; the distal end of upper teeth was conventionally taken as anterior. To renumber upper cusps from mesial to distal would not only create more confusion, but it would divorce the nomenclature from homology: for example, the enlarged distal cusp, here called B1 and considered to be homologous in different taxa and on different teeth (Fig. 2), would have to be numbered variously according to the presence or absence of minor cusps at the mesial end of the tooth.

The reversed symmetry does not occur, or has been lost, in multituberculates. G. Hahn & R. Hahn (1998) have introduced a cusp nomenclature for paulchoffatiid molars, in which, on upper as well as lower teeth, lingual (L) and buccal (B) rows are distinguished, and in each row the cusps are numbered from mesial to distal. This system provides a logical basis for description, though the authors do not discuss its implications for serial homology between adjacent teeth. There is some variation in the number of cusps, especially at the distal end of teeth of both jaws, whereas upper molars of haramiyids vary mainly at the mesial end. In allotherians the row is the functional unit, and only a few cusps are differentiated for individual functions. To apply the system of G. Hahn & R. Hahn to haramiyids, assumptions would have to be made about the homologies of their cusps to those of paulchoffatiids, but, on present knowledge, it is only possible to discuss with confidence the homologies of rows of cusps. The comparison of paulchoffatiid and haramiyid molar cusps made in this paper (p. 330) must therefore be very tentative.

Comparative descriptions

Haramiyavia* compared with *Thomasia (Figs. 1 and 2). — *Haramiyavia* has three molariform teeth in each jaw; these will be referred to as Ml–M3 (upper jaw) and ml–m3 (lower jaw). The number of molariforms in *Thomasia* is unknown, but Sigogneau-Russell (1989) distinguished in the Saint-Nicolas hypodigm three types of upper teeth, which she called *Haramiya II*, *Haramiya I*, and *Haramiya I bis*. She regarded *Haramiya II* as the last premolar. In the lower jaw *Thomasia II* was likewise regarded as a premolar. The *Thomasia I* group was not subdivided, but it exhibited a range of size and cusp number, and evidently contained more than one tooth. Butler & MacIntyre (1994) distinguished premolars, anterior molars and posterior molars in each jaw, but they thought that each group might contain more than one tooth, and in their reconstruction (fig. 13) they depicted 6 molariforms. By analogy with *Haramiyavia* it seems more probable that *Thomasia* had only three molariforms. Here the presumptive premolars, *Haramiya II* and *Thomasia II* will be compared with M1 and ml respectively of *Haramiyavia*, *Haramiya I* with M2, *Haramiya I bis* with M3, and *Thomasia I* with m2–3.

On the lower molars of both *Haramiyavia* and *Thomasia* a1 is the highest cusp of the a row (lingual one). In *Haramiyavia*, and probably in *Thomasia*, cusp a1 on m l is the highest cusp of the lower molars. There are however four a cusps in *Haramiyavia*, 2 or 3 in *Thomasia*. In the b (buccal) row the highest cusp in *Haramiyavia* is b2, which is distal to a1. It is joined to a1 by a ridge on ml and m2, and possibly also on m3, though this cannot be seen owing to breakage. On *Thomasia* the highest b cusp is that labelled as 'b1', which in *Thomasia I* (= m2–3) is opposite a1 and joined to that cusp by a ridge (the 'saddle'). On *Thomasia II* (= ml) cusp 'b1' is distal to a1 and partly united with it, thus resembling b2 of *Haramiyavia*. On *Thomasia* m2–3 there is a small and variable cusp mesial to 'bl' (called 'b' by Sigogneau-Russell 1989), which is sometimes represented in *Thomasia II* by a cingulum at the base of a1. Cusp 'b' might be the homologue of b1 of *Haramiyavia*, in which case cusp 'b1' of *Thomasia* would be homologous with b2 of *Haramiyavia*. Distal to b2 in *Haramiyavia* there are two smaller cusps on m l and m2, and three on m3, where the last one stands more medially to close the basin. In *Thomasia*, m2 usually has 3 or 4 smaller b cusps; the last one is often on the 'U ridge' which closes the basin. In both genera m3 is smaller than m2, but in *Thomasia* it is simpler in pattern, with fewer cusps.

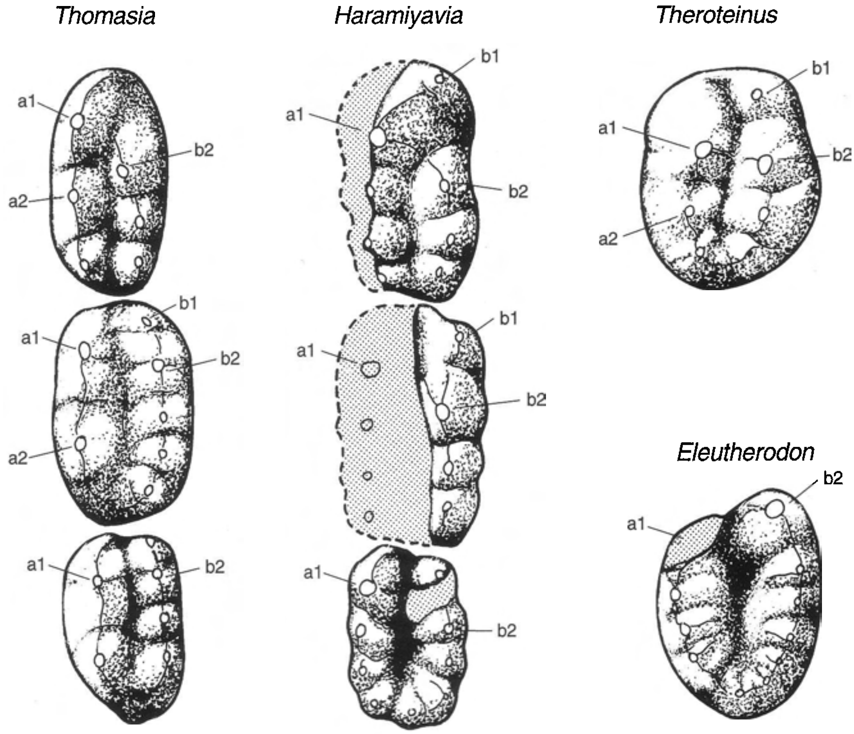

Fig. 1. Comparative crown views of right lower molariforms of allotherians, to illustrate postulated cusp homologies. Cusps are labelled in accordance with their postulated homologies with *Haramiyavia*. Not to scale. Buccal is to the right, mesial above, *Thomasia* after Sigogneau-Russell (1989); *Haramiyavia* after Jenkins *et al.* (1997); *Theroteinus* after G. Hahn *et al.* (1989); *Eleutherodon*, BDUC J.461.

On the upper molars of both genera there are three A cusps, of which A2 is the largest (Fig. 2). A 1 varies in size in *Thomasia*. *Haramiyavia* has two additional cusps, buccal to the grooves between the A cusps, and labelled by Jenkins *et al.* (1997) as Cl and C2. To avoid confusion with the lingual cusps of *Theroteinus* that were labelled C by G. Hahn *et al.* (1989), they will be referred to as AA1 and AA2. They contribute to the width of the crown, which is notably greater in *Haramiyavia*. Some specimens of *Thomasia* possess small cuspules or fragments of cingulum in the same positions (Sigogneau-Russell 1989). The B (lingual) row in *Haramiyavia* contains five cusps; this is the usual number on M2 of *Thomasia*, but it is reduced on Ml and M3. B1 is the largest B cusp in both genera. Its position in relation to A1 differs: it is more mesial than A1 in *Haramiyavia*, opposite to or more distal than A1 in *Thomasia*. The bases of A1 and B1 meet to close the basin distally, but *Haramiyavia* lacks the transverse ridge that joins the cusps in *Thomasia*. Cuspules (here called A0, B0) on the distal margin of *Haramiyavia* molars correspond to the distal cingulum, often with a ‘b’ cusp (= B0), in *Thomasia*. At the mesial end the basin is closed on M2 and M3 of *Haramiyavia* by the buccally displaced B5; in *Thomasia* the most mesial B cusps frequently stand at the end of the basin, on the ‘U-ridge’. On M1 the basin is narrowed at the mesial end, but much less so in *Haramiyavia*

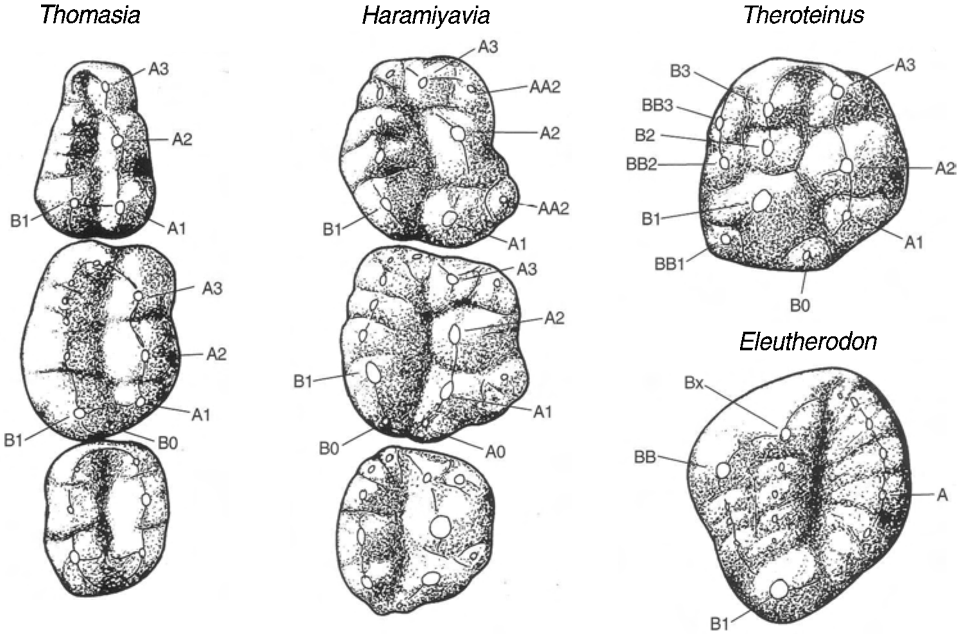

Fig. 2. Left upper molariforms of the same genera as in Fig. 1. Orientation is the same as in Fig. 1, i.e. buccal to the right, mesial above. Cusps are numbered from distal to mesial to show postulated homologies with *Haramiyavia*. In *Eleutherodon* BB and Bx are enlarged mesial cusps of the lingual (BB) and middle (B) rows, and A indicates the A row. *Thomasia* after Sigogneau-Russell (1989) ('*Haramiya I, II*'); *Haramiyavia* after Jenkins *et al.* (1997); *Theroteinus*, SNP 78 W, from a cast; *Eleutherodon*, BDUC J.460.

than in *Thomasia*, where the mesial part of the B row is reduced to a cingulum-like structure. M3 in both genera is smaller than M2, but whereas in *Haramiyavia* its cusp pattern is like that of M2, in *Thomasia* ('*Haramiya I bis*') it is simplified, especially at the mesial end.

Upper premolars of *Haramiyavia* are unknown. The last lower premolar has a single row of cusps, of which the highest seems to be serially homologous with a1 of the molars; if this is so, the b row is absent. No similar teeth have been ascribed to *Thomasia*. Simplified forms of *Thomasia II*, which might be regarded as premolars, have the b row in various degrees of reduction on the buccal side. Sigogneau-Russell (1989) described three types of upper incisor and two types of lower incisor which probably belong to *Thomasia*. In *Haramiyavia* there are four upper and four lower incisors, of which I4, i3 and i4 are small, and if present in *Thomasia* they might have been missed in the screening. I1–I3 of *Haramiyavia* are similar in size and shape, but the supposed I2 of *Thomasia* is notably different, in that it is enlarged, with a distal heel, resembling that of paulchoffatiid multituberculates.

To summarize: The molar cusp patterns of *Thomasia* can be compared in detail with those of *Haramiyavia*. There are differences in the number and relative position of cusps; for example, in *Thomasia* the molars are narrower, cusps AA are rudimentary, b1 is reduced or lost, and, except on m1, a1 is joined to b2, and A1 to B1, by transverse ridges ('saddle'). The number of molars in *Thomasia* is unknown; it is possible that the simplest teeth included in *Haramiya I bis* and *Thomasia I* are fourth molars.

The first molars in both jaws are more differentiated from the second molars in *Thomasia* than in *Haramiyavia*. The upper incisors of *Thomasia* are also more differentiated. Despite these differences, there can be little doubt that the two genera are related. *Thomasia* seems to be more advanced morphologically in the direction of later multituberculates, in the reduction of the b row on m1 (if that tooth is homologous with the multituberculate p4), and in the character of I2.

In view of the morphological resemblance between the molars of *Haramiyavia* and *Thomasia*, it is unlikely that their occlusal functions were very different. Jenkins *et al.* (1997) concluded that 'the complex interlocking of the cusp rows engendered by the dentition of *H. clemmenseni* would permit only predominantly orthal movement'. While it is clear that there was no fully developed palinal movement as in multituberculates, some degree of palinal movement, at least as much as in the traversodontid *Scalenodon* (Crompton 1972; see Butler & MacIntyre 1994) does not seem impossible. Certainly the longitudinal cusp rows would prevent any significant transverse movement, such as occurred in triconodont mammals with unilateral chewing.

In support of orthal occlusion Jenkins *et al.* (1997) say: 'The crowns of upper molariform teeth are set en echelon; this step-like pattern is also reflected in the inclination of the basins of lower molariforms in which the basin floors are lower distally and higher mesially. This geometry 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.' However, the step-like pattern probably existed in *Thomasia* (see Butler & MacIntyre 1994: fig. 12). There, wear facets show that the high mesial cusps of the lower tooth first made contact with the high distal cusps of the more anterior upper tooth, and travelled upward and backward, bringing the b cusps into the basin of the following upper tooth (Fig. 3). It seems reasonable to suppose that in *Haramiyavia* the largest lower cusps bit into the notch between two upper molars, a1 occluding distolingually to the more anterior B1, and b2 distolingually to A1 (Fig. 3). As the jaws closed b2 would move back into the basin, to reach the position shown in the occlusal diagram in fig. 4 of Jenkins *et al.* (1997). This implies a distal movement of about one-third of the length of an upper molar. The amount of distal movement was probably less than in *Thomasia*, where there is evidence from wear scratches of horizontal movement in the basin. Unfortunately the single specimen of *Haramiyavia* is little worn and no wear scratches have been reported.

Heinrich (1999) based the genus *Staffia* on a single worn and eroded tooth, which because of its resemblance to *Thomasia* II he tentatively identified as the posterior lower premolar of a haramiyid. There are three lingual (a) cusps, of which a1 is much the largest, and a shorter buccal (b) row of three cusps. The basin is terminated distally by a U-ridge as in *Thomasia*. The most mesial buccal cusp (?= b2) stands more distally than a1, as in *Haramiyavia* m1 and *Thomasia II*; whether a more anterior b cusp was present cannot be seen because of wear on the buccal surface of a1. No wear facets have been preserved, but the straight groove, with apparent planing of the cusp surfaces at its sides, suggests that there was extensive propalinal occlusion as in *Thomasia* rather than in *Haramiyavia*. Further discussion of *Staffia* must be postponed till the upper molar, reported by Heinrich (1999: p. 167) has been described.

The postulated haramiyid molariform from the Early Jurassic of Arizona (Jenkins *et al.* 1983) resembles upper molariforms (M2) of *Thomasia*. It has three buccal (A)

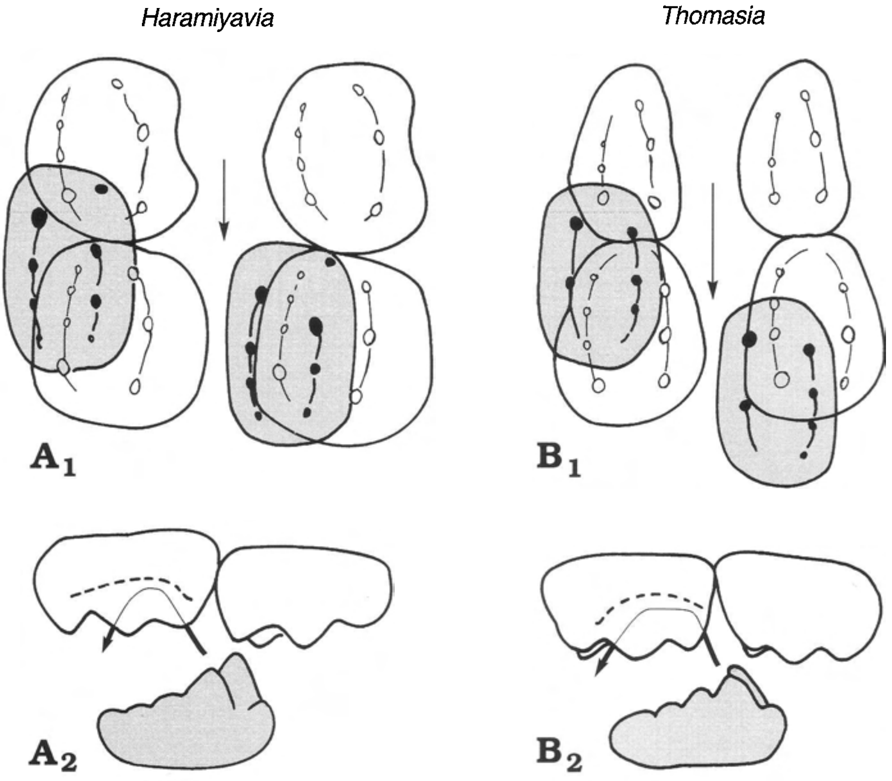

Fig. 3. Postulated molar occlusal relations of *Haramiyavia* ($\mathbf{A}_1$) and *Thomasia* ($\mathbf{B}_1$). Drawings of a lower tooth (stippled) are superimposed on those of two upper teeth to show the relative positions at the beginning and the end of the power stroke; arrows indicate postulated posterior (palinal) movement of lower teeth. Buccal to the right, mesial above. $\mathbf{A}_2$, $\mathbf{B}_2$. Right teeth seen from the buccal side, just before making contact, to show the path of cusp b2 into the basin of the upper tooth. Mesial to the right. In *Thomasia* there is a horizontal traverse of b2 along the basin, probably absent in *Haramiyavia*.

cusps, of which A2 is the largest, and on the lingual side the distal cusp (B1) is the highest. However there appears to be only one other B cusp, widely separate from B1, though smaller cusps may have been removed by wear. There is a central groove which seems to have been worn by longitudinal occlusal movement. The groove is closed mesially by a U-ridge, but unlike *Thomasia* it is open distally, as there is no ridge ('saddle') joining A1 with B1. The published figure seems to show a short lingual cingulum towards the distal end, but there are no AA cusps or buccal cingulum. This tooth resembles *Thomasia* rather than *Haramiyavia* in the more extensive palinal occlusion and the absence of AA cusps, but it differs from *Thomasia* in the absence of the saddle, and probably in the presence of only two B cusps.

Theroteinus (Figs. 1, 2, and 4). — Isolated molariform teeth of *Theroteinus* have been described by Sigogneau-Russell (1983), Sigogneau-Russell *et al.* (1986), and G. Hahn *et al.* (1989). Upper molars are proportionately short and wide, with the width somewhat greater than the length; lower molars are narrower. Variation in size is probably largely due to serial position, but the sample is too small to permit a reconstruction of

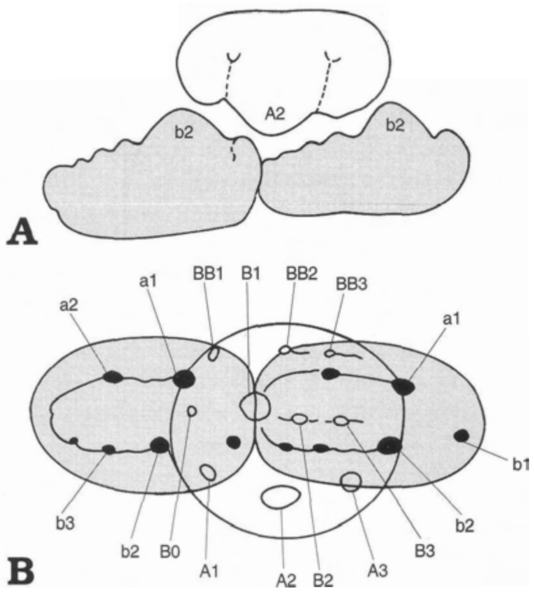

Fig. 4. Postulated occlusion of *Theroteinus*. **A**. Right teeth in buccal view, to show the relation of an upper molar to two lower molars. **B**. Superimposed drawings to show occlusal relations (lower teeth stippled). The lower buccal (b) row bites in the valley between the buccal (A) and middle (B) rows of upper cusps, and the lower lingual (a) row bites between the middle (B) and lingual (BB) rows. Mesial to the right, buccal below.

the dentition. Evidence for mesiodistal orientation is provided by contact wear. It shows that the cusps were arranged in longitudinal rows, but determination of which end was mesial depends upon comparison with *Thomasia* and *Haramiyavia*. On this basis, the highest cusps are considered to be mesial on lower teeth and distal on upper teeth. On upper molars, the lateral row of three cusps, the second one largest, was compared with the A row of *Thomasia* by Sigogneau-Russell (1983), and therefore considered to be buccal. On lower molars the highest cusp is that labelled [b1] by G. Hahn *et al.* (1989: figs. 2, 3), but it is more comparable with a1 of *Thomasia*, and it is regarded here as lingual. (In the following comparisons cuspal names used by G. Hahn *et al.* 1989, when they differ from those applied here, are in square brackets.)

On lower molars of *Theroteinus* there are only two lingual cusps, a1 and a2 [b1, b2], of which a1 is the larger; *Haramiyavia* has four a cusps, but most specimens of *Thomasia* have two (Fig. 1). The a1 [b1] is joined by a ridge to the largest buccal cusp [a1], which is slightly more distal; this may be compared with b2 of *Haramiyavia*. It is followed by a row of up to five smaller cusps, which turns round the distal margin of the tooth to enclose the basin, as in *Thomasia* and on m3 of *Haramiyavia*. A cusp at the mesial end [c] seems to correspond to b1 of *Haramiyavia*; it stands apart from b2 and a1, from which it is separated by grooves. Lingual to b1 [c] is a small, variable marginal cusp [d] that is not represented in *Haramiyavia*.

Upper molars of *Theroteinus* differ from those of *Haramiyavia* in the presence of additional cusps on the lingual margin (Fig. 2). These were labelled C by G. Hahn *et al.* (1989), but to distinguish them from the buccal (AA) cusps of *Haramiyavia* labelled

C1 and C2 by Jenkins *et al.* (1997) they will be referred to here as BB cusps. Traces of the AA row occur in some specimens of *Theroteinus* as rudimentary cuspules at the buccal ends of the grooves between the A cusps. In both genera the A row has three cusps, of which A2 is the largest. The highest lingual cusp is B1, which is placed more distally than A2. Mesially to B1 there are two rows of cusps, a median row (B2, B3) and a lingual row (BB2, BB3). The valley between the A and B rows represents the basin of *Haramiyavia* and *Thomasia*. Cusp BB1 [C1] stands on the lingual margin distal to B1. Adjacent to it is a distal cusp [D] which might be homologous with the minor cusp B0 of *Thomasia* [b of Sigogneau-Russell 1989].

Compared with *Thomasia* and *Haramiyavia*, the molar cusps of *Theroteinus* are low, blunt and convoluted, indicative of thicker enamel. The presence of enamel tubules (Sigogneau-Russell *et al.* 1986) is another difference from *Thomasia*; the enamel structure of *Haramiyavia* is unknown. The cusp pattern of *Theroteinus* is distinctive in the presence of the BB cusps on the lingual side. Moreover, the highest upper cusps (A2, B1) are situated more mesially, and the highest lower cusps (a1, b2) more distally. If teeth are placed end to end as they would stand in the jaw, it is seen that the pairs of high cusps form ridges that cross the occlusal surface, separating concavities into which the opposing teeth bite (Fig. 4). These concavities are formed of the mesial part of one tooth and the distal part of the next. Thus upper and lower teeth alternate. The step-like arrangement would preclude horizontal longitudinal movement. Scanning electron microscopy by Sigogneau-Russell *et al.* (1986) showed no clear striations on the wear facets, but only pitting. Occlusion was therefore orthal, without any sliding contact.

Cuspal interrelations in occlusion may be envisaged by superimposing drawings of upper and lower teeth. It is seen that the lower b row opposes the valley between the upper A and B rows, with b2 biting against the mesial edge of the upper molar, at the end of the valley. The a row opposes the valley between the B and BB rows; and wears against both, whereas in *Haramiyavia* and *Thomasia* the a row is worn only on its buccal side, against the B row. Development of the BB row in *Theroteinus* extends occlusal contact to the lingual side of the a row. In relation to the lower tooth, the upper B row occludes in the valley between the a and b rows, with B1 opposing the distal margin of the tooth. B1 is also probably responsible for wear of b1 at the mesial end of the following lower tooth (see G. Hahn *et al.* 1989: text-fig. 1). Most wear seems to be on the distal part of the lower tooth and the mesial part of the upper tooth, where the contact surfaces are inclined downwards posteriorly. This suggests that occlusal pressure against the upper teeth was directed partly backwards.

That the cusp pattern of *Theroteinus* can be homologised with those of *Thomasia* and *Haramiyavia* is evidence of a phylogenetic relationship between them. The step-like arrangement of the teeth occurs in all three genera, but in *Thomasia*, and probably to a lesser extent in *Haramiyavia*, the initial contact was followed by a backward sliding movement that was absent in *Theroteinus*. Perhaps *Theroteinus* is primitive in this respect. In other characters, such as the form of the cusps and the presence of the BB row, it is clearly derived. Its molars were probably adapted for crushing hard, brittle food (Lucas 1979), contrary to G. Hahn *et al.* (1989).

Eleutherodon (Figs. 1, 2, and 5). — Based on isolated teeth from the Middle Jurassic (K.A. Kermack *et al.* 1998), *Eleutherodon* is later in date than the genera so far consid-

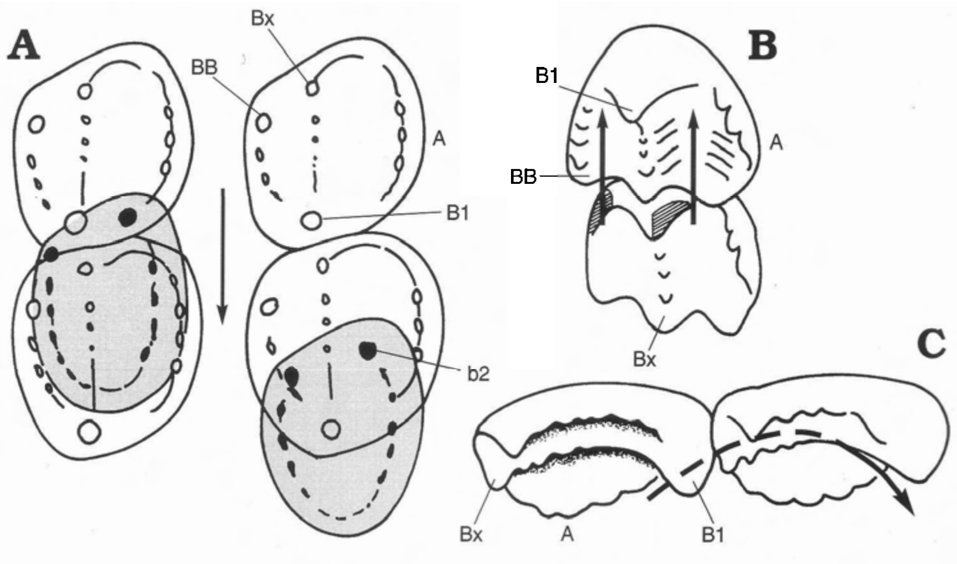

Fig. 5. Postulated occlusion of *Eleutherodon*. Lettering as on Figs. 1 and 2. **A**. Drawing of lower molar (stippled) superimposed on that of two upper molars, to show movement during the dorso-posterior power stroke; further posterior movement is partly ventral. Buccal to right, mesial above. **B**. Two adjacent right upper molars, seen from distal and partly ventral direction, to show paths (arrows) of lower cusps during the power stroke, and to explain the facets on cusp B1 (shaded). **C**. Lingual and slightly ventral view of right upper molars, to show path of lower b2 cusp along the groove.

ered, except *Staffia*, and it differs from all of them in several respects. Upper molars are rhomboidal rather than oblong or oval in shape, with oblique mesial and distal edges. The buccal-lingual orientation is indicated by the lingual curvature of the root in one of the specimens; the highest cusp is regarded as distal, by analogy with *Haramiyavia*. The eight specimens of upper molar are similar in morphology, though they vary in size and shape, and probably represent more than one tooth position. The buccal cusps, which may be considered to be homologous with the A row, are more numerous and less differentiated than in *Haramiyavia* and *Thomasia*; those in the middle of the series tend to be the highest. Lingual to the A row is a deep groove or basin, which reaches its greatest depth near the middle of its length. Its sides are ornamented by numerous transverse ridges ('fluting'). Lingual to the distal end of the basin is the highest cusp, called A by K.A. Kermack *et al.* (1998); this could be homologised with B1 of *Haramiyavia* and *Thomasia*. It stands at the end of a central row of numerous small cusps, that flanks the basin lingually, and appears to represent the B row. Unlike *Thomasia*, the more mesial B cusps increase in height, and terminate in a moderately high cusp near the middle of the mesial border of the tooth (labelled Bx in Fig. 2). It is linked by a ridge to the A row, corresponding to the U-ridge of *Thomasia*. On the lingual margin of the tooth there is a series of BB cusps, mostly small and irregular, but with a larger cusp at the mesiolingual corner of the tooth (cusp B of K.A. Kermack *et al.* 1998). A groove between the B and BB rows is shallower than that between the A and B rows.

K.A. Kermack *et al.* (1998) described a number of lower molars, identified as such because they have two rows of cusps. They differ in morphology, and only teeth of β type can be fitted with the upper molars. There are two examples of this type. BDUC J.461 has a high cusp (called a by K.A. Kermack *et al.*) which must have occluded in the basin between rows A and B of the upper tooth. Comparison with *Thomasia* indicates that this cusp is at the mesial end of the b row, on the buccal side of the tooth (Fig. 1). It has the same function as, and is probably homologous with cusp b2. The a row, on the lingual side, was interpreted as ending mesially in a large cusp (b of K.A. Kermack *et al.* 1998: fig. 2B) which has broken off. However, the broken surface seems too small, and there is an undescribed specimen (BDUC J.855) which, though rolled, shows that the first a cusp was smaller than the first b cusp. If these mesial cusps are homologous with a1 and 'b1' of *Thomasia* (= b2 of *Haramiyavia*), they differ from those in that a1 is more distal, owing to the obliquity of the mesial border of the tooth. The a and b rows are made up of numerous small cusps, and they are continuous round the distal end of the central basin, the sides of which are fluted. The second specimen described by K.A. Kermack *et al.* (1998)(BDUC J.649) is incomplete mesially. It has fewer cusps, especially in the b row where two of the cusps are enlarged.

K.A. Kermack *et al.* (1998) inferred from wear facets that the occlusal movement was longitudinal and backwards (palinal) (Fig. 5). The large mesial b cusp (? b2) travelled distally along the basin between the A and B rows, and at the same time B1 travelled mesially along the basin of the lower molar. The movement has an orthal component, as the lower cusp moves first upwards and then downwards, following the floor of the basin (Fig. 5C). This is similar to the occlusal movement postulated for *Thomasia* by Butler & MacIntyre (1994). The movement was probably more extensive than in *Thomasia*, as the basin extends to the full length of the tooth, whereas in *Thomasia* it is limited distally by the saddle between B1 and A1. In *Thomasia*, at the beginning of the stroke the largest b cusp is in contact with the distal cusps of the more anterior upper molar; in *Eleutherodon* there is a facet on the buccal side of B1 that could be explained in this way (Fig. 5B). In *Thomasia* the a row occludes lingually to the B row; in *Eleutherodon* the upper tooth overhangs the lower, and the BB cusps occlude lingually to the a row, which travels along the B–BB groove. The facet labelled 13 by K.A. Kermack *et al.* (1998: fig. 2) on the lingual side of B1 could be produced early in the stroke by the a1 cusp of the more posterior lower molar.

Eleutherodon resembles *Theroteinus* in the presence of BB cusps, which occlude lingually to the a row of the lower tooth. However, the simple orthal occlusion of *Theroteinus* contrasts with the markedly palinal occlusion of *Eleutherodon*, which is most similar to that of *Thomasia*. *Eleutherodon* is interpreted as a specialised derivative of a haramiyid. Besides the development of the BB cusps, the changes involved include the multiplication of cusps generally, fluting of the enamel, enlargement of the mesial cusp on the B row of the upper molar, and shortening of the a row, with reduction of its mesial cusp, in the lower molar.

The order Haramiyida. — Except *Haramiyavia*, the genera discussed here are known only by isolated teeth, and of these only *Thomasia* is represented by sufficient material to allow an attempted reconstruction of the dentition. The foregoing comparisons have therefore necessarily been based on the cusp patterns of molariform teeth. These have been interpreted as variants of a common morphotype, with the implication that the five genera, *Haramiyavia*, *Thomasia*, *Staffia*, *Theroteinus*, and *Eleuthero-*

don form a monophyletic group. I therefore include them all in the order Haramiyida. This order was proposed by G. Hahn *et al.* (1989) to include only the Haramiyidae; they separated *Theroteinus* in an order Theroteinida. Jenkins *et al.* (1997) included *Haramiyavia* in the Haramiyida. K.A. Kermack *et al.* (1998) classified *Eleutherodon* as order *incertae sedis*, but they regarded it as related to Haramiyidae and multituberculates. Before discussing their relationship to multituberculates, the resemblances and differences between the genera are summarised.

Both upper and lower molars have two main longitudinal rows of cusps, separated by a longitudinal valley or basin. The patterns of opposing teeth are to some extent reversed, bucco-lingually and mesio-distally. On upper molars the buccal row is termed A and the lingual row B; on lower molars row a is lingual and row b is buccal. In occlusion, B bites into the basin between a and b, and b bites into the basin between A and B. In *Haramiyavia* there are additional cusps buccal to row A; these are represented in some specimens of *Thomasia* and *Theroteinus* by small cuspules at the buccal ends of the grooves between the A cusps. *Theroteinus* and *Eleutherodon* have additional cusps lingual to row B, which occlude lingually to the lower a row. None of the genera has lower molar cusps lingual to row a or buccal to row b.

The upper buccal row (A) has three cusps, with the central one (A2) highest, except in *Eleutherodon* where the A cusps are more numerous and less differentiated, but here again the central part of the row is highest. In the lingual row the distal cusp (B1) is highest. Except in *Eleutherodon*, it is preceded by a series of smaller cusps which diminish mesially. In *Eleutherodon* the cusps in the middle part of the B row are small, and they become larger towards the mesial end. The distance of B1 from the distal end of the tooth is greatest in *Theroteinus* and least in *Eleutherodon*. In *Theroteinus*, *Haramiyavia*, and usually in *Thomasia* there are small cusps or a cingulum distal to B1 and A1. Mesially the B row joins the A row by a U-shaped ridge on which some small cusps can stand. This closes the basin mesially. Distally the basin is closed by meeting of the bases of A1 and B1 in *Haramiyavia*, or of A2 and B1 in *Theroteinus*, or by a transverse ridge (saddle) between A1 and B1 in *Thomasia*; it is open in *Eleutherodon*, where A1 is not differentiated.

On lower molars the highest cusp of the lingual row is mesial (a1). It is followed by one to three cusps of diminishing size, except in *Eleutherodon* where the cusps are more numerous and weakly differentiated. The highest lower buccal cusp is b2, which is connected to a1 by a ridge. Mesial to b2 is a smaller cusp (b1) at the mesial end of the tooth, best developed in *Haramiyavia* and *Theroteinus*, reduced in *Thomasia*, and absent in *Eleutherodon*. The position of b2 relatively to a1 varies. The b2 is more distal than a1 in *Haramiyavia*, especially on the first molariform, and also in the supposed equivalent tooth in *Thomasia* ('*Thomasia II*') and *Staffia*. On typical *Thomasia* molars b2 is opposite a1. No teeth of *Theroteinus* or *Eleutherodon* corresponding to *Thomasia II* have been found; in *Theroteinus* b2 is slightly distal to a1, but in *Eleutherodon* it is more mesial. Distal to b2 there are a variable number of smaller cusps, and at the distal end the b row curves round the margin of the tooth (U-ridge) to join the a row, enclosing the basin.

In *Theroteinus* upper and lower molars alternate: there is an extensive area of contact between the lower tooth and the distal part of the more anterior upper tooth. There is no evidence of a posterior sliding movement (palinal), when the teeth are in contact, and occlusion is orthal. In the other genera (if the interpretation of *Haramiyavia* is correct) the lower tooth makes only a transient contact with the distal cusps of the more anterior upper tooth. At least in *Thomasia* and *Eleutherodon* the b2 cusp moves upwards and backwards into the deepest part of the basin of the corresponding upper tooth, and then downwards and backwards at the beginning of the recovery stroke. The length of the traverse was probably small in *Haramiyavia* and greatest in *Eleutherodon.*

Comparison of Haramiyida with Multituberculata

Most authors have classified haramiyids with multituberculates because of the gross similarity of their molar teeth. These have basically two longitudinal rows of cusps, of which the buccal lower row occluded in the valley between the buccal and lingual upper rows. This type of occlusion inhibits transverse jaw movements in chewing, and some Haramiyida (*Thomasia*, *Eleutherodon*) had backward longitudinal (palinal) chewing like multituberculates. All other Jurassic mammals had transverse jaw movement, with unilateral chewing (Crompton 1995).

The resemblance to haramiyids does not however extend to multituberculate second molars. M2 is displaced lingually, so that its lingual cusps occlude lingually to the lingual row of m2 (Krause & G. Hahn 1990) (Fig. 6). Such a difference of occlusal relations between two adjacent molars is unique among mammals, and it is undoubtedly an autapomorphy of the Multituberculata. No such difference occurs in *Haramiyavia*, nor probably in *Thomasia.* Assuming that the cusp relations between M1 and m1 are more primitive, it is not easy to see how the occlusal relation between M2 and m2 originated. Perhaps the cusp rows of M2 and M 1 are not homologous, and the lingual row of M2 is a new development, like BB of *Eleutherodon*; the buccal row of M2 would then be serially homologous with the lingual (B) row of M 1, and the A row of M2 would have been reduced to the mesiobuccal corner of the tooth. Alternatively, there may have been an intermediate stage when the cusps were very low and occluded tip to tip, enabling the wear facets to migrate from the buccal to the lingual surfaces of the cusps. The lack of cusps on the buccal ridge of the paulchoffatiid m2 might be explained in this way. Another alternative, suggested by Clemens & Kielan-Jaworowska (1979), that the difference arose before the second row of cusps had evolved, would separate multituberculates widely from haramiyids.

In the case of the first molars a tentative homologisation of the cusp patterns may be made (Fig. 7). The fully horizontal chewing movement of multituberculates, which does not include an orthal element as in *Thomasia* and *Eleutherodon*, is associated with an equalisation of cuspal height; elevation of mesial lower cusps and distal upper cusps, characteristic of haramiyids, does not occur in multituberculates, except to a limited extent in paulchoffatiids. According to G. Hahn & R. Hahn (1998), on the lower molar (m1) there are plesiomorphically three buccal cusps and three lingual cusps, of which the median ones (b2, 12 in the nomenclature of G. Hahn & R. Hahn (1998), as modified by Kielan-Jaworowska & Hurum (in press) are the largest. These may be compared to b2 and a1 of haramyids. In some specimens they are connected across the longitudinal groove by a low ridge. Posteriorly to these cusps, m1 wears against M1, anteriorly it wears against P5. Of the smaller anterior cusps, b1 would cor-

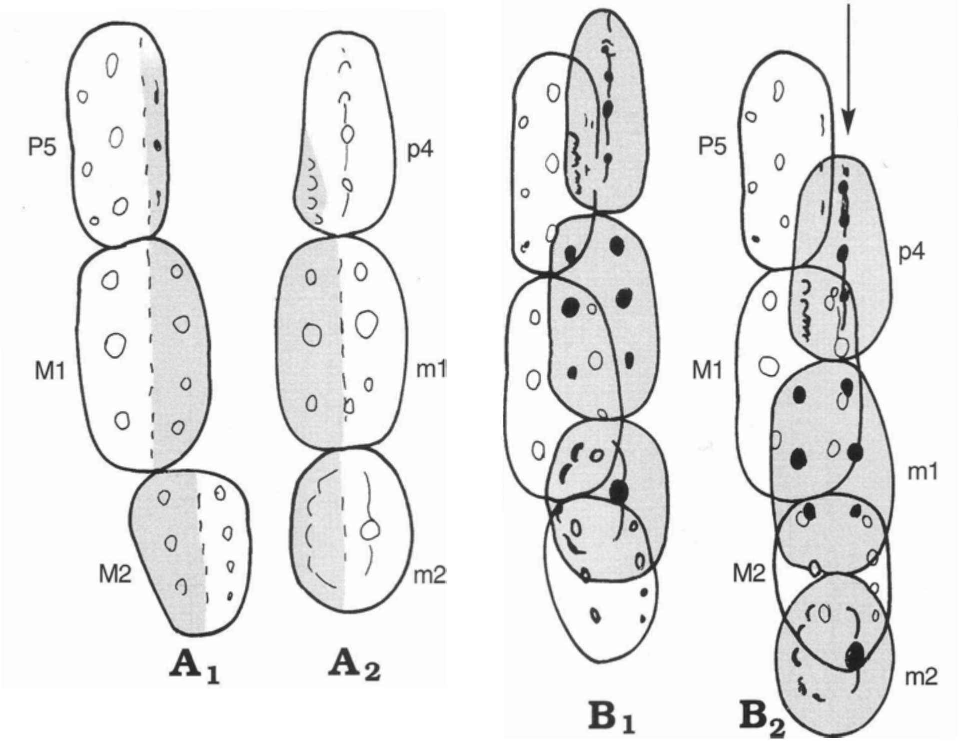

Fig. 6. Schematic diagram to show relation of cusp rows in a generalised paulchoffatiid. P5–M2 (A_1) and p4–m2 (A_2) in crown view. Shaded are the rows believed to be homologous with rows B (upper) and b (lower) of haramiyids. **B**. Occlusal relations when the lower teeth at the beginning (B_1) and the end (B_2) of the stroke. Arrows indicate suggested length of traverse of lower teeth. Lower teeth in **B** are darker shaded. Buccal to the left, mesial above.

respond to the haramiyid b1, but 11 is not represented in haramyids, unless it is equivalent to the mesial cusp labelled d in *Theroteinus* by G. Hahn *et al.* (1989).

G. Hahn & R. Hahn (1998) consider that the upper molar (M1) primitively had three buccal cusps and four lingual cusps; these must correspond to the A and B rows of haramiyids. The distal buccal cusp (B3), which is frequently missing, would be the homologue of A1 of *Thomasia*, which tends to be reduced. The distal lingual cusp (usually the 4th) is displaced centrally, and it seems more likely that the penultimate lingual cusp (L3 in most cases) is the equivalent of the haramiyid B1. Several of the drawings in G. Hahn & R. Hahn's paper (1998: figs. 3, 6, 8, 10b) show a slight ridge connecting B2 with the penultimate lingual cusp. Possibly this marks the posterior limit of the wear due to m1, but it is not homologous with the 'saddle' of *Thomasia*, which connects B1 to A1 (?= L3 to B3 of paulchoffattids). At the mesial end of the tooth the 'crista anterior' of G. Hahn & R. Hahn (1998) represents the 'U-ridge' of *Thomasia*.

The blade-like (sectorial) p4 is one of the most obvious multituberculate apomorphies, but it may be foreshadowed by '*Thomasia II*' and m1 of *Haramiyavia*, in which the buccal row is reduced and confined to the distal part of the tooth. If *Thomasia II* is homologous with m 1 of *Haramiyavia*, as suggested in this paper, the

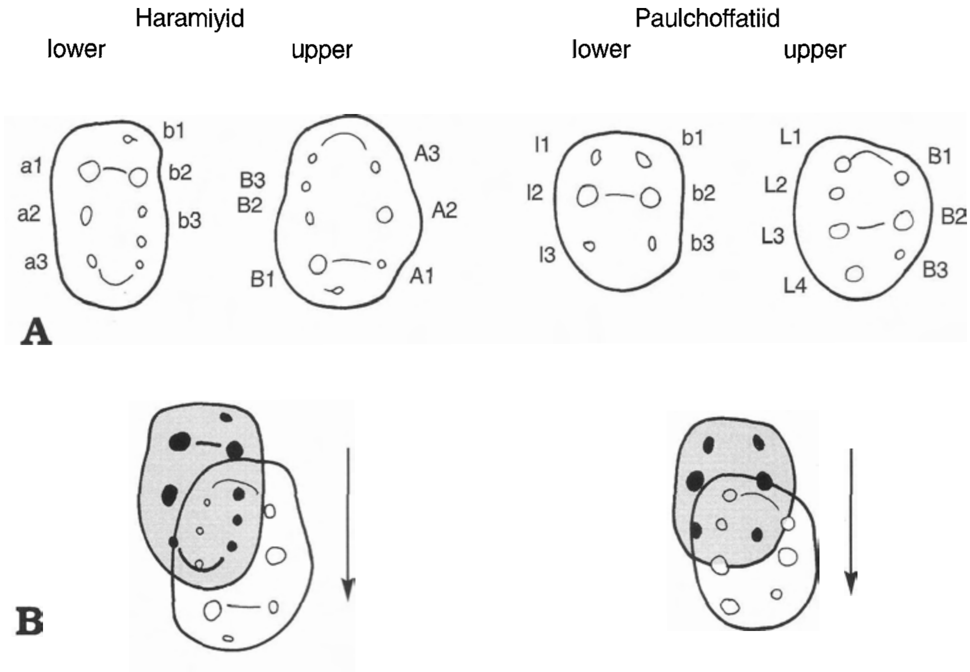

Fig. 7. **A.** Tentative comparison of molar cusp patterns of a haramiyid (*Thomasia*) and a generalised paulchoffatiid. Paulchoffatiid cusps are labelled following G. Hahn & R. Hahn (1998). Buccal to the right, mesial above. **B.** Postulated occlusal relations at the beginning of the stroke; lower molars stippled; arrows indicate suggested traverse. It is suggested that on lower molars haramiyid a1 = paulchoffatiid I2, and haramiyid b2 = paulchoffatiid b2; on upper molars haramiyid B1 = paulchoffatiid L3, and haramiyid A2 = paulchoffatiid B2.

three molars of that genus could represent p4 to m2 of multituberculates. (It should be noted that the nomenclature of *Haramiyavia* is morphological, without implications of replacement). The last upper premolar (P5) is molariform in *Kuehneodon*, with two rows of cusps, but in other multituberculates the lingual row (= B of haramiyids) of the premolars is reduced or lost, and additional cusps, buccal to the A row, form a crushing platform that does not occlude with the lower teeth; the blade of p4 shears against the lingual side of the A row. In '*Haramiya II*' (?= upper premolars of *Thomasia*) the B row is reduced.

The series *Haramiyavia–Thomasia–Eleutherodon* indicates how the palinal occlusion of the Multituberculata could have evolved. In *Haramiyavia*, and also in *Theroteinus*, owing to the step-like arrangement of the teeth, the surfaces that meet at the end of the power stroke are tilted, to face forward on upper molars and backward on lower molars, so that the force exerted by lower teeth on upper teeth has a backward component. A backward force is primitive in synapsids (Barghusen 1968; Bramble 1973; Kemp 1982: p. 229), and palinal occlusion evolved in herbivorous cynodonts (Traversodontidae, Tritylodontidae) independently of Allotheria (Crompton 1972). There is evidence of a backward component in *Docodon* (Gingerich 1973; Butler 1988), but generally in non-allotherian mammals the transverse chewing movement is slightly forward, probably owing to the action of the external masseter and pterygoid muscles.

The forward tendency reaches its highest development in rodents, where the masseter musculature is most specialised. Gambaryan & Kielan-Jaworowska (1995) reconstructed the jaw musculature of some multituberculates and found a striking convergence with rodents, despite the diametrically opposite chewing movements. They attributed the backward movement of multituberculates to the anterior insertion of the masseter, which is farther forward than in other mammals. It seems not impossible that specialisation of the masseter had some relation to the evolution of the sectorial premolars. The only known haramiyid dentary is that of *Haramiyavia* (Jenkins *et al.* 1997), which resembles that of other primitive mammals such as *Morganucodon* and *Kuehneotherium*: the masseteric fossa does not extend beyond the posterior part of the last molar, and the condyle is above the level of the teeth. If multituberculates were derived from haramiyids, much transformation ot the mandible must have taken place. Unfortunately the jaws of *Thomasia* and *Eleutherodon*, which might be expected to throw light on the mulituberculate condition, are unknown.

The Multituberculata are clearly a monophyletic group, with many derived characters in common to all of them. The Haramiyida are not multituberculates, but there are a number of suggestive resemblances that seem to indicate that they are earlier offshoots from the multituberculate stem, as G. Hahn *et al.* (1989) postulated. Haramiyida and Multituberculata would constitute an allotherian clade, with a separate history going back to the Triassic. The Haramiyida would be a paraphyletic group, containing those allotherians that did not reach the multituberculate level.

Classification of the Allotheria

On the basis of the above hypothesis, I propose the following classification. Pending the full description of the skeleton of *Haramiyavia* (Jenkins *et al.* 1997) it is necessarily based on the dentition. The order Haramiyida is considered to contain four families: Haramiyidae, Theroteinidae, Eleutherodontidae, and a new family Haramiyaviidae, proposed for *Haramiyavia*. The Theroteinidae differ from the other three families in the relative positions of upper and lower teeth. In Theroteinidae the opposing teeth alternate, and occlusion is completely orthal. In Haramiyaviidae, Haramiyidae and Eleutherodontidae upper and lower teeth are nearly opposite, and each lower tooth makes only transient contact with the more anterior upper tooth. These three families show different stages in the evolution of palinal chewing. I group them in a suborder Haramiyoidea, as opposed to the suborder Theroteinida that includes only the Theroteinidae. I regard this family as an early side-branch from the stem of the Haramiyoidea. The Eleutherodontidae, although they differ from other Haramiyida in many autapomorphies, resemble Haramiyidae in occlusion, and they are regarded as specialised members of the Haramiyoidea clade. Possibly the Multituberculata also arose within the Haramiyoidea. The classification may be expressed formally as follows.

Subclass Allotheria Marsh, 1880

Diagnosis. — Mammals in which the upper and lower molariform teeth have basically two longitudinal rows of cusps, which relate so that the buccal lower row bites into the valley between the upper rows (additional rows may develop on upper teeth). Occlusion is bilateral; the movement is vertical (orthal) or posterior (palinal), or a combination of these, but not significantly transverse. In primitive non-allotherian Mammaliaformes molariform teeth have one row of cusps, that functioned in unilateral occlusion in which the buccal surfaces of lower cusps sheared against the lingual surfaces of upper cusps, involving a transverse jaw movement.

Included orders: Haramiyida G. Hahn *et al.*, 1989; Multituberculata Cope, 1884.

Occurrence. — Late Triassic–Late Eocene of the world except Australian region and Antarctica.

Order Haramiyida G. Hahn, Sigogneau-Russell, & Wouters, 1989

Diagnosis. — Allotherians which differ from multituberculates in presence of postdentary-trough (known only in *Haramiyavia*), and differ from multituberculates (except Paulchoffatiidae) in that the cusps of molariform teeth are of unequal height. On upper teeth the buccal row has three cusps, the middle one highest, except in Eleutherodontidae where there may be as many as ten cusps, highest near the middle of the series. The number of lingual upper cusps and of buccal and lingual lower cusps varies; the highest cusp is towards the distal end in the upper lingual row and towards the mesial end in the lower rows. Molar occlusion ranges from orthal to palinal, but there is always an orthal component that is lacking in multituberculates. A high distal lingual upper cusp occludes in the longitudinal valley of the lower molar, and a high mesial buccal lower cusp occludes in the valley of the upper molar. As far as known (*Haramiyavia*, *Thomasia*) the last upper molar is not displaced lingually as in multituberculates.

Included suborders: Theroteinida G. Hahn *et al.,* 1989; Haramiyoidea G. Hahn, 1973.

Occurrence. — Late Triassic–Middle Jurassic (Bathonian) of Europe; Late Triassic of Greenland; Early Jurassic of North America; Late Jurassic of Africa.

Suborder Theroteinida G. Hahn, Sigogneau-Russell, & Wouters, 1989, new rank

Diagnosis. — Haramiyids with fully orthal occlusion, in which upper and lower molars alternate, so that each lower molar bites against two upper molars. The highest cusps are more centrally placed on the teeth than in Haramiyoidea, and the longitudinal valleys are short.

Sole family: Theroteinidae Sigogneau-Russell *et al.*, 1986.

Occurrence. — Late Triassic of Europe.

Family Theroteinidae Sigogneau-Russell, Frank, & Hemmerlé, 1986

Diagnosis. — Upper molars short and wide, with an additional lingual row of cusps. Cusps low and obtuse.

Resembles Haramiyaviidae in subcircular outline of the upper molars, which have three rows of cusps, but the additional cusps in Haramiyaviidae are buccal. Eleutherodontidae have a third row on the lingual side, but they differ from Theroteinidae in tooth shape, cusp form and number, and occlusion. Theroteinidae differ from Haramiyidae (*Thomasia*) in the presence of tubules in the enamel.

Sole genus: *Theroteinus* Sigogneau-Russell, Frank, & Hemmerlé, 1986.

Occurrence. — As for the suborder.

Suborder Haramiyoidea G. Hahn, 1973

Diagnosis. — Haramiyids in which the lower molars are nearly opposite the upper molars, so that there is only transient contact with the more anterior upper molar. The median valley is longer than in Theroteinida, occupying most of the length of the tooth, except on anterior lower molariforms (unknown in Eleutherodontidae), where it is confined to the distal part of the tooth. Palinal occlusal movement developed to various extents; it is incipient in Haramiyaviidae and most extensive in Eleutherodontidae.

Included families: Haramiyaviidae nov.; Haramiyidae Simpson, 1947; Eleutherodontidae K.A. Kermack *et al.*, 1998.

Occurrence. — Late Triassic–Middle Jurassic (Bathonian) of Europe; Early Jurassic of North America; Late Jurassic of Africa.

Family Haramiyaviidae nov.

Diagnosis. — Upper molariforms wide (subcircular), with additional cusps on the buccal side. (In Theroteinidae and Eleutherodontidae the additional cusps are lingual). On lower molariforms the highest buccal cusp is the second; it is placed more distally than the highest (first) lingual cusp. First upper molariform resembles the second, except that it is narrower mesially; on first lower molariform the longitudinal valley is confined to the distal part of the tooth. Palinal occlusal movement was probably short. Lower premolariforms with a single row of cusps (upper premolariforms unknown). Incisors unspecialised: I1–3 equal in size. The dentary (unknown in other Haramiyida) possesses a trough for postdentary bones; masseteric fossa does not extend forward below the molars as in multituberculates.

Sole genus: *Haramiyavia* Jenkins, Gatesy, Shubin, & Amaral, 1998.

Occurrence. — Late Triassic of Greenland.

Family Haramiyidae Simpson, 1947

Diagnosis. — Differing from Haramiyaviidae as follows: Upper molariforms longer than wide, with two rows of cusps, the supplementary buccal cusps absent or represented by a cingulum. The basin is closed distally by a ridge ('saddle') between the buccal and lingual cusps. On lower molars the first buccal cusp is rudimentary or absent. Except on the anterior molariform, the highest (second) buccal cusp is directly opposite the first lingual cusp and joined to it by a saddle, that closes the basin mesially. Palinal chewing, in which cusps moved longitudinally in the basin of the opposing tooth, was well developed. Anterior upper molariform more narrowed mesially, with lingual cusps confined to the distal part of the tooth. Referred upper incisors differentiated: I2 enlarged, with distal basal heel. The mandible is unknown.

Included genera: *Thomasia* Poche, 1908 (including *Haramiya* Simpson, 1947), and ?*Staffia* Heinrich, 1999.

Occurrence. — Late Triassic–Early Jurassic of Europe; Late Jurassic of East Africa.

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

Diagnosis. — Haramiyoidea with upper molars wide, rhomboidal in outline and possessing three rows of cusps. The additional row is lingual and occludes lingually to the lower molar (a character shared with Theroteinidae, probably by convergence). Lower molars oval, with two rows of cusps that are continuous round the distal end. The largest cusps are at the distal end of the middle row on upper molars, and at the mesial end of the buccal row on lower molars; also the mesial upper lingual cusp is enlarged. Minor cusps are numerous and variable. The longitudinal groove of upper molars, between the buccal and middle cusp rows, extends the whole length of the tooth; it is not interrupted by a saddle as in Haramiyidae. Palinal occlusion was extensive, but retained an orthal component as in Haramiyidae. Upper molar has a shorter and shallower groove, between the middle and lingual cusp rows, for occlusion with lower lingual cusps. The sides of the occlusal grooves of upper and lower teeth are covered with numerous minor transverse ridges ('fluting'). Eleutherodontidae differ from all other Haramiyida in: the more numerous cusps (e.g. there are up to ten upper buccal cusps); the anterior position of the large lower buccal cusp, which projects mesially beyond the lingual row; and the fluting.

Sole genus: *Eleutherodon* K.A. Kermack, D.M. Kermack, Lees, & Mills, 1998.

Occurrence. — Middle Jurassic (Bathonian) of England.

Haramiyoidea *incertae sedis*

(1) The 'haramiyid' from the Lower Jurassic of Arizona, described by Jenkins *et al.* (1983). See p. 323.

(2) The allotherian tooth described by Freeman (1976) from the Middle Jurassic (Bathonian) of England. The crown is poorly preserved, but the possession of three roots, due to subdivision of the (?)posterior root, occurs in some specimens of *Thomasia*, and it has not been observed in Jurassic multituberculates.

Order Multituberculata Cope, 1884

Diagnosis. — Allotherians which differ from Haramyida in that the molar occlusal movement is fully palinal; longitudinal wear grooves are horizontal, not basined as in Haramiyidae and Eleutherodontidae. There are plesiomorphically two rows of cusps. Within each row the cusps are equal in height (except in Paulchoffatiidae, where some inequality survives as a plesiomorphy). The last (second) upper molar is displaced lingually in relation to the last lower molar. Premolars are clearly differentiated from the molars. On lower premolars the lingual row is elevated and the buccal row is reduced or lost; on upper premolars the lingual row is reduced. A possible early stage in the transformation may be seen in the anterior molariforms of Haramiyidae.

Included suborders and families: see Kielan-Jaworowska and Hurum (in press).

Occurrence. — Middle Jurassic–Late Eocene of the world except Australian region and Antarctica.

Multituberculates coexisted with *Eleutherodon* in the Middle Jurassic (Bathonian) of England. Teeth described by K.A. Kermack *et al.* (1998: figs. 20, 21) as *Eleutherodon* types γ and ζ differ from *Eleutherodon* and resemble multituberculates in showing fully horizontal wear in the central groove. The tooth of ζ type (BDUC J.797) may be a multituberculate upper molar. Additional multituberculate teeth from the Forest Marble, including premolars, are currently under study by the author. *Mojo*, known only by an incomplete, worn tooth from the Rhaetic of Belgium (G. Hahn, Lepage, & Wouters 1987) was tentatively interpreted as an upper premolar of a multituberculate. G. Hahn *et al.* (1989) compared it with the lower molar of *Theroteinus*, but rejected relationship because of the horizontal wear. They retained *Mojo* in the Multituberculata, but because evidence for this position is so scanty, and in view of the early date, *Mojo* is best classified as ?Haramiyida *incertae sedis.*

Relation of Allotheria to other mammals

Cladistic studies of the relationship of the multituberculates to other early mammals have led to a variety of conclusions (summarised by Kielan-Jaworowska 1997). Thus Rowe (1988) placed the multituberculates as the sister-group of the Theria (marsupials + placentals), Wible (1991) reanalysed Rowe's data and made the multituberculates the sister-group of all modern mammals, including monotremes, but more advanced than morganucodontids. Wible & Hopson (1993), from basicranial characters, found evidence for a sister-group relation to monotremes. Miao (1993), on the other hand, regarded the multituberculates as the sister-group of all the other mammals combined, including morganucodontids; this was in agreement with the earlier view of McKenna (1987). Lillegraven & G. Hahn (1994), using additional information on the paulchoffatiid periotic, confirmed the result of Wible (1991); however, in the light of the study of *Haldanodon* by Lillegraven & Krusat (1991), which indicated that homoplasy was probably important in Mesozoic mammals, they concluded that 'a very early divergence of multituberculates from other mammals remains a distinct possibility'. Kielan-Jaworowska & Gambaryan (1994), from a study of the postcranial skeleton, supported this view.

If multituberculates were derived from haramiyids at least some of the characters that they share with therians would be homoplasies. Among these is freeing of the ear ossicles from the dentary. In *Haramiyavia* a sulcus in the dentary shows that the postdentary bones were still attached (Jenkins *et al.* 1997), but the ear ossicles of multituberculates resemble those of modern mammals (Rougier, Wible, & Novacek 1996). The sulcus is retained in *Kuehneotherium*, but lost not only in later therians but also in triconodontans; either the triangular cusp pattern of *Kuehneotherium* evolved independently, as suggested by Rougier, Wible, & Hopson (1996), or detachment of the ear ossicles occurred several times, as Allin & Hopson (1992) proposed. Mobility of the pectoral girdle, by reduction of the coracoid and the development of a pivotal clavicle-interclavicle joint, occurred in a triconodont (*Jeholodens*) convergently with multituberculates and therians (Ji *et al.* 1999). In general, it seems reasonable to suppose that similar animals, exposed to a similar environment, would tend to evolve in the same direction. This is especially so in the case of complex structures such as the ear, where modification is constrained by the necessity to maintain function throughout the evolutionary change. One would therefore expect homoplasy to be a common phenomenon. Computer programs based on parsimony and designed to construct trees of minimum length would tend to underestimate the importance of parallel evolution, by confusing homoplasies with synapomorphies.

Teeth evolve as part of a feeding system that includes the jaws and jaw muscles. At the morganucodontid level and above (Mammaliaformes of Rowe 1988) the molars function in unilateral chewing with lateral excursion of the mandible (Crompton 1989, 1995). The teeth are primitively triconodont, and occlusion consists of a shear between the lingual surfaces of upper cusps and buccal surfaces of lower cusps. Each cusp has precise occlusal relations with opposing cusps, though these relations differ in different groups (Mills 1971; Crompton 1974; Crompton & Luo 1993), indicating that occlusal precision evolved more than once. In multituberculates chewing is bilateral, with longitudinal movements of the mandible; there are essentially two rows of cusps, which occlude in longitudinal grooves, and there are no individual intercuspal relations. If multituberculates are mammaliaforms a very considerable transformation would have to be assumed, not only of the teeth but of the chewing mechanism. In monotremes there are two rows of cusps, but chewing is transverse, and the cusps interdigitate in a precise manner (Kielan-Jaworowska *et al.* 1987; Archer *et al.* 1992). Meng & Wyss (1995) pointed to a resemblance of multituberculate molars to those of the pteropodid bat *Harpionycteris*, but this is very superficial: pteropodids have an interlocking dentition, clearly of tribosphenic origin, in which pairs of mesial upper cusps (paracone, protocone) alternate with pairs of mesial lower cusps (protoconid, metaconid). Derivation of multituberculates from a mammaliaform stock seems improbable.

The triconodont molar pattern of early mammaliaforms, with a principal cusp flanked mesially and distally by smaller cusps, can be traced back to the basal Triassic, e.g. the cynodont *Thrinaxodon* (Crompton & Jenkins 1968). Primitively the lower teeth passed up lingually to the upper teeth but did not occlude with them; the teeth functioned to hold and tear the food (Crompton 1972; Kemp 1979). Occlusal contact between the buccal surface of lower teeth and the lingual surface of upper teeth, resulting in vertical shear, developed in some cynodonts such as *Cynognathus*, and in trithelodontids (Crompton 1995). At the mammaliaform level transverse movement of the jaw was involved in unilateral shearing, with definitive functional interrelations of individual cusps. The allotherians do not fit into this sequence. Shear in *Thomasia*, *Eleutherodon* and multituberculates is horizontal and palinal, rather than transverse, and it seems to have evolved from an orthal, crushing type of occlusion in which cusps bit into longitudinal valleys on opposing teeth. Occlusion was bilateral, and it did not involve transverse jaw movements. To derive such teeth from those of a primitive cynodont it must be supposed that occlusal contact developed by broadening of the teeth, which functioned by opposition rather than by shearing. This implies that divergence between allotherians and other mammals took place prior to the Mammaliaformes stage, as postulated by McKenna (1987), Miao (1993), and Kielan-Jaworowska & Gambaryan (1994), and that the apomorphies shared by multituberculates and non-allotherian mammaliaforms are parallelisms.

If allotherian molars were derived from triconodont molars, the second row of cusps was presumably developed from a cingulum, either buccal or lingual. Possible modes of transformation were discussed by Butler & MacIntyre (1994). They postulated that on the upper molar the buccal (A) row represents the original triconodont series, and the B row developed from the lingual cingulum. A2 would then be homologous with the largest cusp of the triconodont molar (cusp A in the nomenclature of Crompton & Jenkins 1968). Upper premolars are unknown in *Haramiyavia*, but in reduced specimens of '*Haramiya II*', which are probably upper premolars of *Thomasia*, it is the lingual (B) row that is reduced. If it can be assumed that premolars are undeveloped molars, it follows that on the upper teeth the primary row is buccal, and the lingual row is secondary.

Lower premolars of *Haramiyavia* have a single row of cusps that appears to be serially homologous with the lingual (a) row of the molars; a reduced buccal (b) row is present in *Thomasia II*, especially in the smallest specimens (see Sigogneau-Russell 1989: figs. 20, 21). Thus the primary cusps of lower haramiyid molars appear to be lingual, and the buccal cusps to be secondary. This is unexpected, in that lower teeth of cynodonts and early mammals usually have a cingulum only on the lingual side. However, as was noted by Sigogneau-Russell (1989), there is a buccal cingulum in the trithelodontid *Pachygenelus*, in which the highest cusp is mesial as in the a row of *Thomasia*. Butler & MacIntyre (1994: p. 454) rejected the solution in which the b row was the new development, because this would mean that the b row was inserted between the shearing upper A and lower a rows, resulting in a dysfunctional intermediate stage. If haramiyids acquired the b and B rows of cusps prior to the evolution of shearing, this difficulty would not arise.

It should be noted that in the broad-toothed cynodonts, Diademodontidae and Traversodontidae, simplified anterior and posterior teeth show that the highest cusps are buccal in both jaws. In developing teeth of *Ornithorhynchus* the primary cusps are lingual in the upper jaw and buccal in the lower jaw (Green 1937), i.e. the opposite of that postulated for allotherians.

Because of their evolutionary plasticity, teeth are often thought to be of secondary value in higher-rank phylogeny. Yet the changes that they undergo are not arbitrary, but are controlled by functional necessities; the teeth must continue to function throughout the evolutionary transformations of the body as a whole, and phylogenetic reconstructions must be consistent with dental evolution. Teeth are subject to homoplasy (parallelism and convergence) as much as other organs, and dental resemblances, when unsupported by other evidence, can be misleading. Likewise, phylogenies based on cranial and skeletal characters must be suspect if they imply improbable dental transformations. Two hypotheses about the origin of multituberculates have been considered here: either they were specialised haramiyid derivatives, or they were highly aberrant mammaliaforms. The first seems possible, though it implies much parallelism to other mammals; the second involves a highly improbable transformation of the dentition and chewing mechanism. The evidence from the teeth indicates that the first hypothesis is the more likely to be correct. It implies that an allotherian clade separated from a non-allotherian mammaliaform clade, probably in the Middle Triassic, before the evolution of unilateral shearing occlusion, and that the two clades evolved to a large extent in parallel.

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Przegląd wczesnych ssaków z podgromady Allotheria

PERCY M. BUTLER

Streszczenie

Praca przedstawia rewizję wczesnych przedstawicieli ssaków z podgromady Allotheria. Wykazano, że rodzaje *Haramiyavia, Thomasia, Theroteinus* i *Eleutherodon* mają podobny typ budowy zębów, co pozwala na ich zaliczenie do wspólnego rzędu Haramiyida. Dla *Haramiyavia* zaproponowano utworzenie nowej rodziny Haramiyaviidae. Rząd Haramyida został podzielony na dwa podrzędy: (1) Theroteinidea, do którego zaliczono tylko jedną rodzinę Theroteinidae, i (2) Haramiyoidea, obejmującą rodziny Haramiyaviidae, Haramiyidae i Eleutherodontidae.

Podobieństwo budowy zębów w tych grupach do zębów wieloguzkowców (Multituberculata) wskazuje, że wieloguzkowce wyodrębniły się spośród Haramyioidea. Jeżeli tak, to Haramiyida byłyby grupą parafiletyczną.

Alternatywna możliwość, sugerowana przez innych badaczy, że wieloguzkowce wyodrębniły się spośród Mammaliaformes, pociągałaby za sobą przyjęcie nieprawdopodobnych przekształceń budowy zębów podczas powstawania wieloguzkowców. Dlatego autor postuluje, że Allotheria (do których należą Haramiyida i Multituberculata) oddzieliły się od pozostałych grup ssaków, zaliczanych do Mammaliaformes, zanim u tych ostatnich pojawiło się uzębienie tnące oraz jednostronna okluzja (to jest żucie raz lewą, raz prawą połową szczęk), wraz z poprzecznym ruchem szczęk podczas żucia. Hipoteza ta przyjmuje, że dwa klady: Allotheria i Mammaliaformes (z których usunięto wieloguzkowce) rozwijały się równolegle. Wówczas dopiero pojawiły się rzekome wspólne apomorfie wieloguzkowców i ssaków właściwych, na podstawie których wielu autorów uznaje wieloguzkowce za grupę siostrzaną ssaków właściwych.