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Review of the British Haramiyidae (? Mammalia, Allotheria), their Molar Occlusion and Relationships

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Review of the British Haramiyidae (? Mammalia, Allotheria), their molar occlusion and relationships

P. M. BUTLER[1] AND G. T. MACINTYRE[2]†

[1]*Royal Holloway, University of London, Egham, Surrey TW20 0EX, U.K.*
[2]*Formerly Queens College, City University of New York, New York, U.S.A.*

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SUMMARY

Haramiyid teeth from the Rhaeto-Lias of Holwell Quarry, England, which had been previously described, were re-examined in the light of the large sample from Saint-Nicolas-de-Port. *Haramiya* and *Thomasia* are interpreted as upper and lower teeth, respectively. Differences within each 'genus' are ascribed largely to position within the dentition (anterior 'molars', posterior 'molars', 'premolars'). There is much individual variation within each of these tooth groups, but at Holwell, as well as Saint-Nicolas-de-Port, it is possible to distinguish a larger (*Thomasia moorei*) and a smaller species (*T. antiqua*, including *T. anglica*, *H. butleri*, and probably *H. fissurae*). Upper molars, but not lower molars, appear to be more advanced at Holwell than at Saint-Nicolas-de-Port.

It is inferred from tooth wear that the upper and lower molars were reversed buccolingually and anteroposteriorly, and the effective chewing stroke was longitudinal and backwards (palinal), but with an orthal component at the beginning of the stroke, giving a crushing–grinding action. The chewing movement resembled in principle that of the traversodontid *Scalaenodon*. Opposition between the teeth has probably evolved by the development of a second row of cusps from the lingual cingulum in both jaws. However, the transformation of a triconodont into a haramiyid would involve a major change from unilateral, transverse chewing to presumably bilateral, longitudinal chewing.

Possible relationships of haramiyids to multituberculates and to broad-toothed cynodonts are discussed, with their implications for early mammalian phylogeny. Support is given for ordinal separation from the Multituberculata, as Haramiyida. A new interpretation is proposed of the cusp pattern of Theroteinidae, as haramiyid relatives.

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† Deceased.

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1. INTRODUCTION

The Haramiyidae are a family of problematic relationships, known only by isolated teeth. Nearly all the material is from the Rhaeto-Lias (Triassic–Jurassic border) of Western Europe; there is a specimen from the Norian (late Triassic) of Germany (Hahn 1973), and a possible, poorly preserved tooth from the Bathonian (middle Jurassic) of England (Freeman 1976); outside Europe there is only one tooth of aberrant morphology from the Kayenta Formation (early Jurassic) of Arizona (Jenkins *et al.* 1983).

Plieninger (1847) described *Microlestes antiquus* from the Rhaetic bonebed of Degerloch, Württemberg (see Clemens 1980). The generic name was pre-occupied and was replaced by *Thomasia* Poche (1908). The type specimen was redescribed by Hennig (1922) and Simpson (1928). Owen (1871) described *Microlestes moorei* from a collection of teeth made by Moore (1867) from a fissure deposit in Holwell Quarry, Somerset, England. This species was redescribed by Simpson (1928), who selected a lectoholotype. He made it the type of a new genus *Microcleptes* (in 1947 emended to *Haramiya*), in distinction from *Thomasia*. From other teeth in the same collection, Simpson (1928) named two new species: *Microcleptes* (now *Haramiya*) *fissurae*, and *Thomasia anglica*. In 1939 Kühne made a further collection of haramiyid teeth from Holwell (Kühne 1946), and these were described by Parrington (1947). Von Huene (1933) and Hahn (1973) described additional specimens from Germany, and Peyer (1956) described 23 teeth, mostly fragmentary, from Hallau, Switzerland. The German and Swiss material was reviewed by Clemens (1980). Wouters *et al.* (1984) reported a tooth of *Haramiya* from la Gaume, Belgium. By far the largest sample of haramiyid teeth, consisting of over 200 specimens, is from Saint-Nicolas-de-Port, Lorraine, France (Sigogneau-Russell 1989). Both *Haramiya* and *Thomasia* are represented; a new species, *Haramiya butleri* Sigogneau-Russell (1990) was described.

In the absence of associated or implanted teeth, the dental organization of the Haramiyidae, and hence their relationships, are uncertain. Parrington (1947) argued that, as all known molariform teeth had a basically similar pattern, upper and lower molars must resemble each other. He fitted teeth together in occlusion so that the cusp patterns of opposing teeth were reversed, both buccolingually and anteroposteriorly. Hahn (1973) agreed with the buccolingual reversal, but not the anteroposterior one. Sigogneau-Russell (1989) considered that *Haramiya* and *Thomasia* were probably upper and lower molars, respectively, and supported Parrington's view of their relative orientation, although she was unable to explain some of the wear facets. She provisionally proposed a dental formula of two or three molars, several premolars of which the last shows the beginning of specialization, two or three upper incisors and one or two lower incisors; no canines were identified.

As to their relationships, haramiyids have generally been regarded as mammals, because of their multicuspid molars with divided roots, but these characters are present in Tritylodontidae. Support for their mammalian status is provided by their 'preprismatic' enamel structure, which resembles that of *Morganucodon* (Frank *et al.* 1984), and their small size, which suggests a high level of homeostasis (Clemens & Kielan-Jaworowska 1979). Among mammals, they have generally been associated with the Multituberculata, because of the molars with two rows of cusps that functioned in a longitudinal chewing movement, and Hahn (1973) put them within the Multituberculata as a suborder Haramiyoidea. Subsequently, Hahn *et al.* (1989) classified them with the multituberculates in the subclass Allotheria, but raised them to separate ordinal rank as Haramiyida.

Our purpose in this paper is to interpret the British specimens from Holwell, previously described by Simpson (1928) and Parrington (1947), in the light of the Saint-Nicolas-de-Port collection, paying particular attention to position in the dentition and possible specific differences. Some years ago we wrote a manuscript paper on haramiyid molar occlusion, based on the Holwell material, but desisted from publishing it in view of Sigogneau-Russell's work. It is now possible to present the paper in revised form.

2. MATERIAL

The teeth from Holwell which we have seen are as follows.

In the Bath Geological Museum, collected by Charles Moore:

- *Haramiya I* ('molars'). M 211 (lectoholotype of *H. moorei*), M 213, M 214, M 216, M 222.
- *Haramiya II* ('premolar'). M 217.
- *Thomasia I* ('molars'). M 219 (holotype of *T. anglica*), M 221.
- Five anterior teeth catalogued M 218 and M 220 cannot be matched with incisors described by Sigogneau-Russell (1989), and are probably not haramiyid.

In the Natural History Museum, London, collected by Charles Moore:

- *Haramiya I.* M 2401A (holotype of *H. fissurae*), M 2401B, M 2401C.

In the Museum of Zoology, Cambridge University, collected by W. G. Kühne:

- *Haramiya I.* H 2, H 6, H 8.
- *Haramiya II.* H 15.
- *Thomasia I.* H 4, H 5, H 7, H 12, H 17, H 19.
- Incisor. H 14. Other anterior teeth described by Parrington (1946) (H 10, H 16, H 18, H 20) are probably not haramiyid.

In the Department of Geology, Bristol University:

- *Haramiya I.* H 3.

We have not seen the two 'molars' in the Yale Peabody Museum: 13622A (*Haramiya*) and 13622B (*Thomasia*). They are described and figured by Simpson (1928).

For comparative purposes, G.T.M. examined the

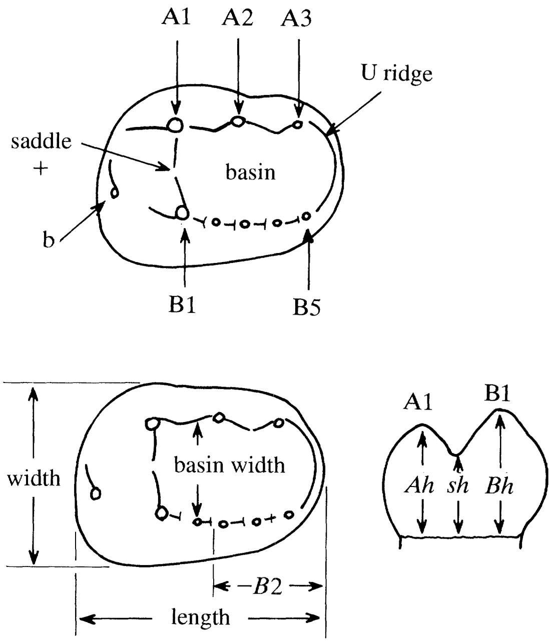


Figure 1. Cusp nomenclature and mensuration. +, positive end; −B2, length from negative end to base of cusp B2, Ah, sh, Bh, heights of A1, saddle and B1 from the lower edge of the enamel.

material in the Universities of Tübingen and Zurich, described by von Huene (1933), Peyer (1956), Hahn (1973) and Clemens (1980). P.M.B. examined the material from Saint-Nicolas-de-Port in the Institut de Paléontologie, Paris, described by Sigogneau-Russell (1989).

3. CUSP NOMENCLATURE

Haramiyid molars have two rows of cusps, which are referred to as the A row and the B row, following Hahn (1973). The A row is the 'row of 3' of Parrington (1947); the B row, with a large cusp succeeded by a number of smaller cusps of descending size, is Parrington's 'row of 5'. Between the rows is a central basin; thus each row of cusps has a basin surface and a marginal surface. The end of the tooth with the largest cusp of the B row is called the positive (+) end; the other end, where the two rows join in a U-shaped ridge, is the negative (−) end. In previous descriptions the + end has been conventionally taken as anterior, but we believe, with Sigogneau-Russell (1989: 192), that it is posterior in *Haramiya*. Cusps are numbered from the + end. *Haramiya* and *Thomasia* are distinguished by the relative sizes of cusps of the A row (Simpson 1928): in *Haramiya* the A cusps are subequal or A1 is the smallest; in *Thomasia* A1 is higher than B1 and A3 is much reduced or absent. The basin is limited towards the + end by ridges on A1 and B1 which join to form the 'saddle' of Parrington (1947, figure 3). There is frequently a ledge or cingulum at the + end of the tooth, and it may rise to a small cusp, labelled b by Sigogneau-Russell (1989), on the + side of B1.

Table 1. *Measurements of haramiyid cheek teeth from Holwell*
(All measurements are in millimetres.)

	length	width	−B2	basin width	A1 height	saddle height	B1 height
Haramiya							
M 211	2.45	1.85	1.1	1.05	0.95+	0.65	1.2
M 222	2.4	1.95	1.35	1.0	0.85	0.7	1.0
M 216	2.55	2.0	–	–	–	–	–
H 2	2.35	1.75	1.15	0.9	0.95	0.85	1.1
H 6	2.25	1.85	–	–	–	–	–
M 214	2.4	1.8	1.15	0.95	0.75+	0.55	1.1
M 213	2.05	1.5	1.05	0.75	0.85	0.55	1.0+
H 3	2.1	1.55	1.1	0.75	1.0	0.6	1.0
13622A	2.2	1.55	1.2	0.7	–	–	1.0
H 8	–	–	–	–	0.9?	–	–
M 2401A	1.95	1.55	0.7	1.0	0.45?	0.4	0.8
M 2401C	2.05	1.6	0.85	1.1	0.6?	0.35	0.8
M 2401B	–	–	0.95	1.05?	–	–	–
M 217	1.8	1.0	–	0.6	0.6	0.25	0.75
H 15	1.35	0.9	–	0.65	0.65	0.25	0.65
Thomasia							
H 7	1.7	1.25	0.45	0.7	0.8+	0.55	0.8
M 219	1.95	1.3	0.75	0.85	1.1	0.75	0.95
H 12	2.0?	1.25	0.8	0.85?	–	–	1.0?
M 221	1.8	1.0?	0.7	0.6	0.8+	–	–
13622B	1.7?	1.0?	0.75	0.55	–	–	–
H 4	–	1.05	–	–	1.15	0.9	1.0
H 17	2.2	1.5	0.85	0.9	1.35	0.85	1.05
M 212	–	1.5	0.85	0.95	–	–	–
H 5	2.45	1.6	1.0	1.0	1.35+	1.05	1.1+
H 19	2.3	1.4	0.95	0.85	1.25+	1.1	1.2+

Measurements (table 1) were made on camera lucida drawings, and checked where possible against scanning electron micrographs. Length was measured as by Sigogneau-Russell (1989); in *Haramiya*, parallel to the A row, in *Thomasia*, along the bottom of the basin. Width is perpendicular to length. Five additional measurements were made: (i) basin width, at the level of B2; (ii)–(iv) heights of A1, B1 and the saddle above the base of the enamel, seen from the + end; and (v) length – to B2, from the groove between B2 and B3 to the – end of the tooth. The last measurement was considered to be more accurate than counting the B cusps, as wear tends to remove small cusps at the – end.

4. WEAR

Wear facets were searched for by turning the tooth under a binocular microscope (magnification *ca.* ×25) with strong lateral illumination, when facets were revealed by reflection of light from the tooth surface. Facet wear indicates attrition due to tooth-on-tooth contact. It produces flat, or sometimes cylindrically concave, surfaces, generally smooth but frequently marked with parallel striations. As flat surfaces occur even on unworn parts of the tooth, the precaution was taken of comparing corresponding areas on worn and unworn teeth. The tooth surface is also subject to abrasive wear due to contact with the food and resulting in rounding and eventual removal of cusps. Also there are the effects of *post mortem* rolling and handling of the specimens. Only clearly marked facets that occurred on more than one specimen were considered as evidence for occlusal relations. The real existence of the facets was confirmed by scanning electron microscopy, which in many cases revealed striations invisible at lower magnifications.

It has not been recorded previously that in most specimens from Holwell the enamel on the cusps is black, whereas the lower parts of the crown, including the floor of the basin, are brown in colour. At the sides of the tooth a zone of brown enamel can be seen below the black (figure 2). Whether this indicates that the enamel was pigmented in life, as in shrews, or whether there was *post mortem* impregnation of the last-formed enamel is impossible to say. In a few specimens (M 212, M 214, M 221) the enamel is entirely black, and this is true of all the material from Saint-Nicolas-de-Port. When the black layer is thin, its absence from an area is a useful indicator that the surface of the enamel has been removed, whether by attrition, abrasion or erosion. Thus, on lightly worn teeth, the tips of the cusps, as well as wear facets, show up as pale patches, whereas on a completely unworn tooth (M 219) the cusp tips are black.

Interpretation of the facets was assisted by the construction of plaster or plasticine models, which upon manipulation produced areas of wear corresponding to the facets found in the fossils.

In addition to facets formed during occlusion, many

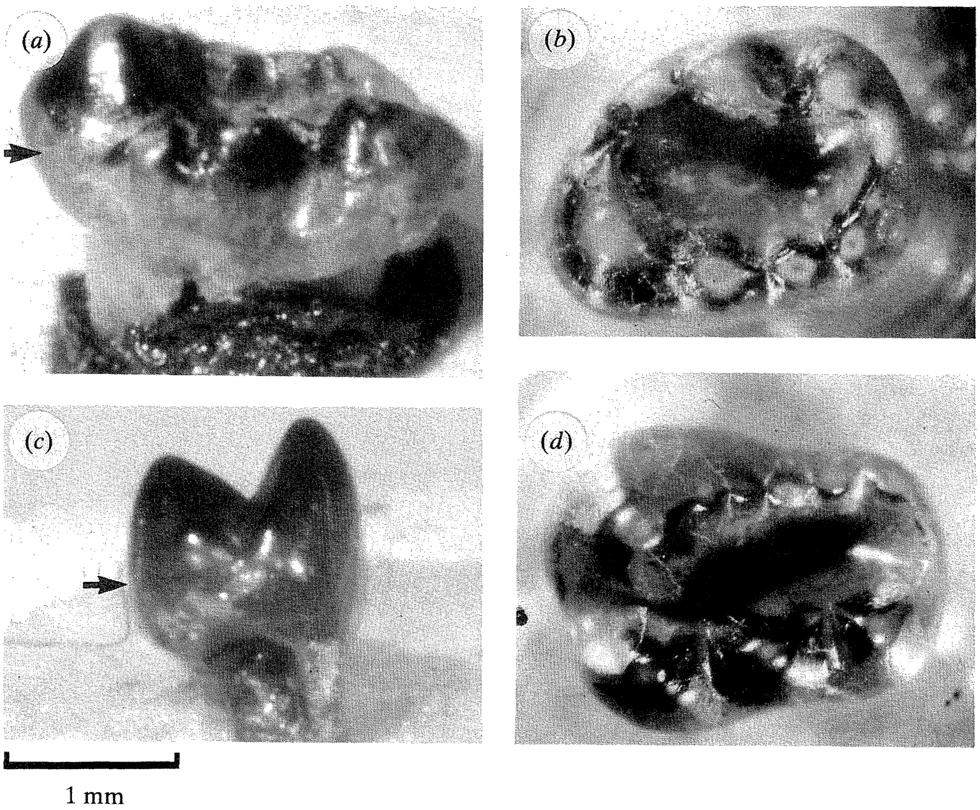


Figure 2. To illustrate black outer enamel. (*a*) M 222, A side; (*b*) M 2401A, crown view; (*c*) M 219, + end; (*d*) H 3, crown view. In (*a*) and (*c*), arrow marks lower edge of black enamel. In (*b*), black enamel is confined to cusps, from which it has been partly removed by wear. In (*d*), black enamel is retained on the marginal surface of the A cusps, but removed from the marginal surface of the B cusps.

teeth showed facets at the + or − ends due to contact with adjacent teeth in the same jaw.

5. DESCRIPTION AND COMPARISONS

(*a*) **Haramiya, *group I***

Sigogneau-Russell (1989) distinguished two kinds of *Haramiya* teeth, which she put into groups I and II. In group I the B row is comparable in length to the A row, and the tooth is wide at the − end; in group II the B row is reduced towards the − end, where the tooth is narrowed. The variability of teeth of group I (length range 1.10–2.22 mm) indicated heterogeneity (figure 6). Sigogneau-Russell (1989) separated out a subgroup (*Haramiya I bis*) with only three cusps in the B row. They are on average shorter, both absolutely and relatively to width, and the distance − to B2 is smaller in proportion to tooth length. Plotting length against width for the whole assemblage shows a tendency to cluster around lengths of 1.3 mm and 1.8 mm, with most of the *bis* subgroup belonging to the lower cluster. Typical members of the higher cluster constitute the hypodigm of *H. butleri* Sigogneau-Russell (1990). There is, however, much overlap, and cases where B4 is very small or indistinct might belong to either subgroup. This would be expected if the subgroups represent adjacent teeth in the dentition of the same species. An exceptionally large specimen, SNP Ma7, with length 2.22 mm, may belong to a larger species. If this is eliminated, a wide range of size remains in both subgroups (coefficient of variation in length: *Haramiya I* 10.3, *H.I bis* 13.7), raising the possibility that more than two tooth positions are represented. For this reason the *Haramiya I* subgroup will be referred to as 'anterior molars', and the *bis* subgroup as 'posterior molars', rather than M1 and M2.

(i) *The teeth*

Fourteen teeth from Holwell conform to group I. Of these, 11 are identified as *H. moorei* and three as *H. fissurae*. Teeth of the *bis* subgroup have not been found at Holwell. The teeth referred to as *H. moorei* are rather variable in size (nine specimens, coefficient of variation (CV) length 7.2, width 10.4), and the three smallest specimens (M 213, H 3, YPM 13622A) might be second molars, if the larger teeth are first molars.

M 211 (lectoholotype of *H. moorei*) (figures 3 and 5*a*,*b*), 2.45 mm × 1.85 mm. This is widest near the + end, across A1 and B1. The + edge is somewhat oblique, receding towards the A side. The top of A1 has broken off; at its base the cusp is only a little shorter than A2. A3 is lower than A2. The A and B rows are nearly parallel, and the B row is only slightly curved. B1 is the highest cusp. B5 is distinct and similar in height to B4; it is closer to the − end of the tooth than in other specimens referred to *H. moorei*. The distance − to B2 is 45% of tooth length. At the + end there is a b cusp, joined by a cingulum to the base of A1. There is no trace of lateral cingulum on the A side, but an indistinct cingular ridge arises from B2 and extends under B3. The tooth is very lightly worn; no evidence of wear was detected in the basin or on the U-ridge. There are three separate but coplanar facets on the marginal surface of B1–B3. Some enamel has been removed from the tips of the cusps, especially B1, which has a plane of wear inclined laterally. At the + end a facet on the b cusp and adjacent cingulum is inclined in a + direction, and there seems to be a small patch of wear at the base of A1. The medial ridge of B1, forming part of the saddle, shows light horizontal wear. There are the broken bases of two probably equal roots.

M 222 (figures 2*a* and 3) is proportionately wider than M 211 (2.4 mm × 1.95 mm), and not narrowed towards the − end; the + border is more oblique and the A and B margins are parallel. The + cingulum and the top of the U-ridge have broken off. A1 is notably smaller than A2. The B row is somewhat curved, with B1 displaced medially. There are five B cusps; the distance − to B2 is about 56% of tooth length. There is no indication of a b cusp, and no lateral cingula. The tops of all cusps have been removed by wear. Wear in the − end of the basin extends as far as B2, but it is less clear on A2 and A3. The basin surface of B1 is unworn, but there is a facet on B1 on the side facing the saddle. On the marginal surface of the B row a continuous strip of wear extends from the middle of B1 to B5.

M 216 (figure 3) is similar in outline to M 222, but slightly larger (2.55 mm × 2.0 mm). It is badly fractured and heavily worn, so that few details of the cusp pattern are preserved. A2 was the largest A cusp. A bevelled area at the + margin represents the worn groove between A1 and B1.

H 2 (figures 3 and 5*i*) is narrower than M 222 (2.35 mm × 1.75 mm), which it otherwise resembles in shape. The tops of all cusps have been removed by wear. A1 is less reduced than in M 222. B1 is slightly displaced medially. The distance − to B2 is 49% of tooth length. There is no b cusp; + cingulum is weak; no lateral cingula. There is extensive wear in the basin, involving the basin slope of the U-ridge, produced by inclined movement, and of the A and B rows, produced by horizontal (longitudinal) movement. A strip of longitudinal wear on the marginal surface of the B row extends from the middle of B1 to B5. At the + end there are clear inclined facets on either side of the groove between A1 and B1, and also horizontal wear on the top of the saddle. There is a contact facet below B1 at the + end. The bases are preserved of two equal, transversely wide, grooved roots, which may have divided deeper in the jaw.

H 6 (figure 3), 2.25 mm × 1.85 mm. This is very worn; B row is completely removed by wear. The + edge is nearly transverse, giving the tooth an approximately rectangular shape. A1 is a little shorter than A2. No b or + cingulum are visible; there are no cingulum remnants on the A side. Despite the very heavy wear, black enamel persists on the marginal surface of the A cusps, as Parrington (1947) noted. There is a small area of black enamel near the − end of the basin, where the basin would reach its greatest depth. As in M 216, the + edge is bevelled by

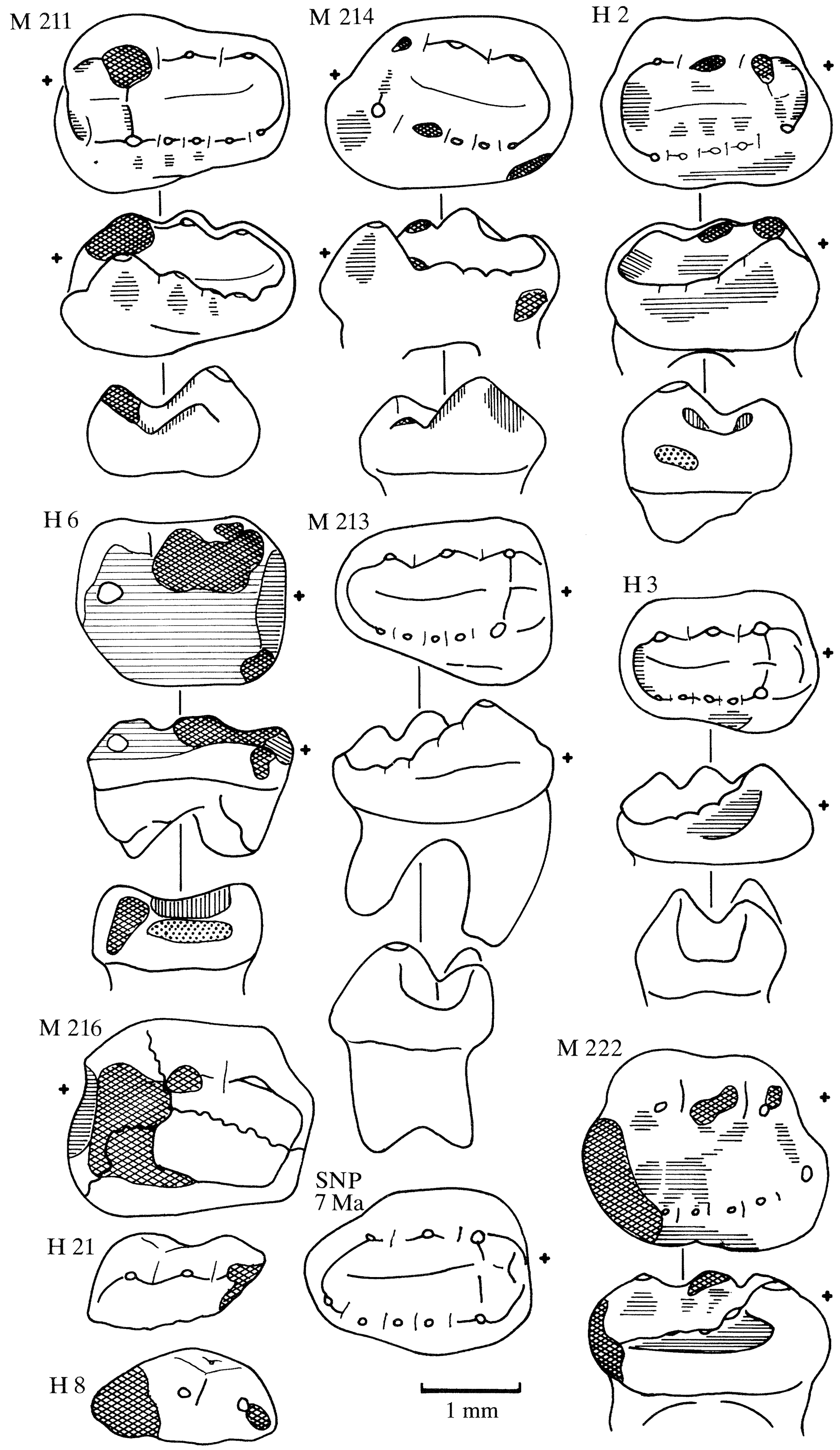


Figure 3. Camera lucida drawings of the teeth of *Haramiya moorei*, crown, B side and + end views. Parallel shading, occlusal wear; cross-hatching, broken surface; stipple, interdental wear. SNP 7 Ma is a tooth of similar size from Saint-Nicolas-de-Port.

facet wear. Contact facets are present at the + and − ends. There are two transversely widened roots as in H2.

M 214 (figures 3 and 5*d*,*e*), 2.4 mm × 1.8 mm. The + margin is markedly oblique; A and B margins parallel. A1 is much smaller than A2, and A3 is also comparatively small. B1 is displaced medially, and the B row is curved. B5 is small, but in line with B4 and B3, and not on the U-ridge; distance − to B2 is 48% of tooth length. There is no b cusp or + cingulum. A fragment of cingulum is present between A2 and A3. There is some wear near the tip of B1, on its lateral surface, and also on the medial side of B1, towards the groove separating B1 from A1. Otherwise the tooth appears to be unworn.

M 213 (figure 3). This is smaller (2.05 mm × 1.5 mm). The + edge is only slightly oblique, and the tooth is narrowed towards the – end more than in M 211. A1 is almost as large as A2. B1 is only slightly displaced medially. B5 is small but not close to the – end; distance – to B2 is 51% of tooth length. There is a + cingulum but no b cusp. A rounded cingulum is present below B1–B3. The tooth appears to be unworn. There is a contact facet at the + end. There are two roots, of which the + one is divided.

H 3 (figures 2*d*, 3 and 5*c*, *f*), 2.15 mm × 1.5 mm. This is similar to M 213: + edge is nearly transverse; greatest width is across A1 and B1; A1 is similar in size to A2; B row is nearly straight. Distance – to B2 is 52% of tooth length. There is a + cingulum but no b cusp, and no lateral cingula. Wear is light, but black enamel has been removed from the tops of all cusps. There is possible wear on the basin slope of the U-ridge, and on an area on the marginal surface of the B row, extending from the middle of B1.

YPM 13622A (after Simpson 1928), 2.2 mm ×

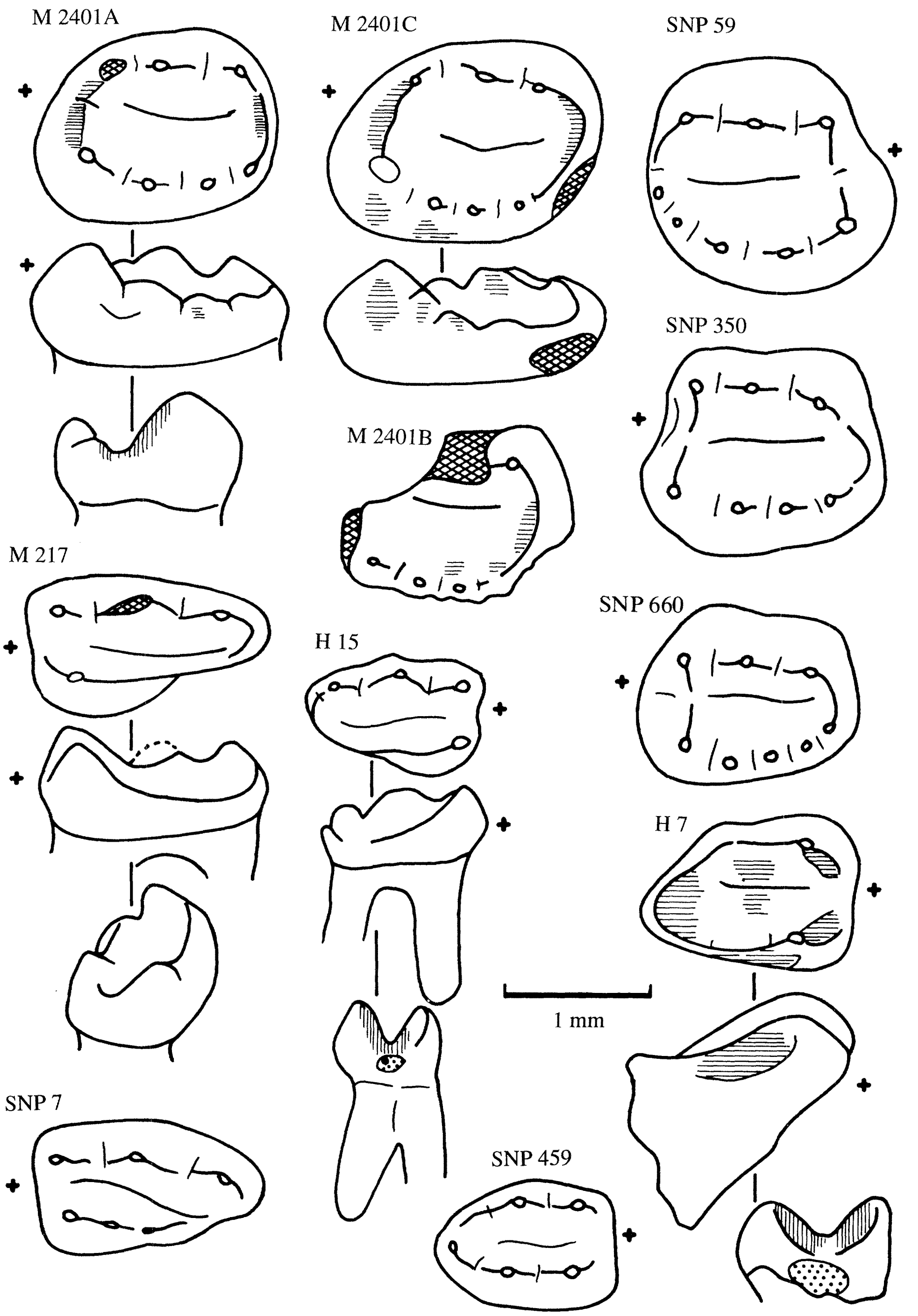


Figure 4. Camera lucida drawings. M 2401A, B and C are *H. fissurae*. M 217 and H 15 are specimens of *Haramiya II*. H 7 is a posterior molar of *Thomasia*. SNP 59, 350 and 660 are examples of *H. butleri*, for comparison with *H. fissurae*, and illustrating variation in width. SNP 7 is *Haramiya II*, and SNP 459 is a posterior molar of *Thomasia*, both from Saint-Nicolas-de-Port. Shading as in figure 3.

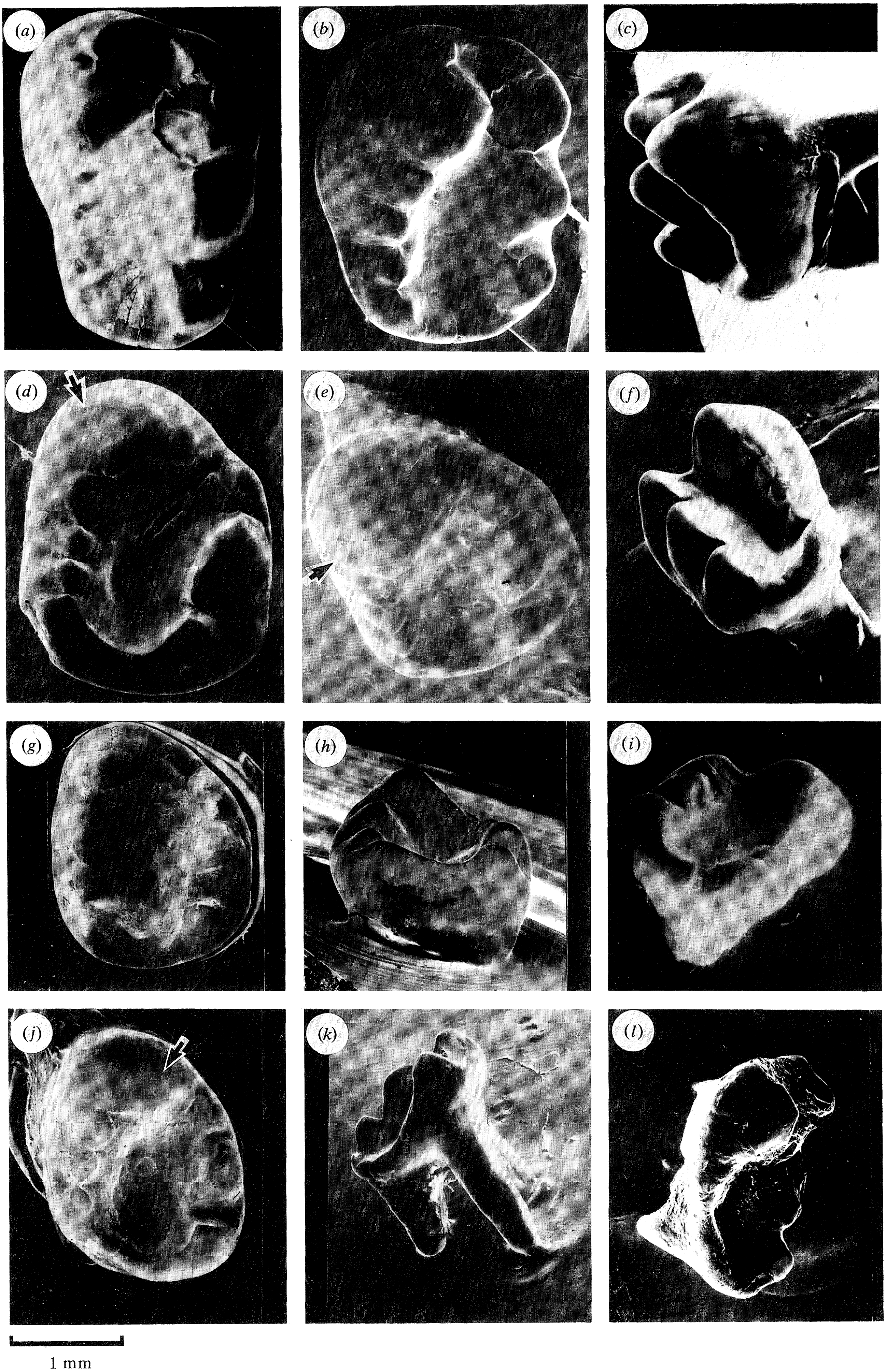


Figure 5. For description see opposite.

1.55 mm. This is narrowed at the − end as in H 3, but the + margin is more oblique and A1 (broken at the top) is smaller. There is a sixth B cusp at the end of the U-ridge; distance − to B2 is 55% of tooth length. A + cingulum is present but no b cusp; no lateral cingula.

H 8 (figure 3) is a fragment with B1 and B2. B1 was displaced medially as in M 222 and M 214, and there is a weak cingulum on the B side as in M 213.

H 21 (figure 3) is a fragment showing A2, A3 and part of A1. It is similar in size to H 2. There is a cingulum on the A margin, now damaged by flaking.

M 2401A (holotype of *H. fissurae*) (figures 2*b*, 4 and 5*g*,*h*), 1.95 mm × 1.55 mm. The + margin is very oblique, forming a continuous curve with the A margin. A1, which is broken at the tip, is very small. B1 is displaced medially, and the B row is markedly curved. There are only four distinct B cusps; the distance − to B2 is 36% of tooth length. The + cingulum, b cusp and lateral cingula are absent. Wear is light, shown by loss of black enamel from the tips of the cusps, and from small areas at the edge of the U-ridge and at the + end, below B1.

M 2401C (figures 4 and 5*j*), 1.95 mm × 1.7 mm. Similar to M 2401A except that B4 is less close to the − end; distance − to B2 is 41% of tooth length. There is a rounded cingulum on the B margin. It is somewhat more worn: wear is present on the U-ridge, on the marginal side below B2–B4, and at the + end on both sides of the groove between A1 and B1, but mainly on B1. There is also possible wear on the marginal surface of B1, and a possible contact facet at the − end.

M 2401B (figure 4). This is an incomplete tooth with A3 and four B cusps. The first three B cusps resemble B2–B4 of M 2401C; the last B cusp (supposedly B5) is merely an elevation, displaced medially on the U-ridge. The tooth was similar in size to M 2401A and C. Wear is present on the basin slope of the U-ridge and B4.

(ii) *Comparisons*

The two complete specimens of *H. fissurae* approach in length the smallest specimens referred to *H. moorei* (M 213, H 3, YPM 13622A), but they differ from these in shape, being broader, with a very oblique + margin, giving the tooth a broadly oval shape. A1 is much reduced, and B1 is displaced to a median position, giving a marked curvature to the B row. These characters are approached by M 214, which Parrington (1947) identified as *H. fissurae*. However, M 214 is larger and proportionately narrower, and its B5 is distinct and in line with the other B cusps, as in other specimens of *H. moorei*. In *H. fissurae* B5 is absent or a rudimentary elevation on the U-ridge; the distance of B2 from the − end in two specimens is 36% and 41% of tooth length, compared with 45–56% (mean 50.9%) in seven specimens of *H. moorei*.

SNP Ma7 (figure 3), the largest tooth from Saint-Nicolas-de-Port (2.22 mm × 1.78 mm) is within the size range of *H. moorei*. It is narrowed towards the − end, the + margin is nearly transverse, A1 is subequal to A2, and there is a + cingulum. B1–B4 are in line, but the small B5 is on the U-ridge, a situation that does not occur in *H. moorei* from Holwell. The distance − to B2 is 47% of tooth length.

SNP 59 (figure 4; Sigogneau-Russell 1989, figure 24) is proportionately wide (1.92 mm × 1.88 mm), with an oblique + edge and curved B row. It differs from *H. fissurae* in that A1 is less reduced, B1 is less displaced medially, and B5 is present on the U-ridge. A3 is relatively small.

The remaining specimens of *Haramiya I* from Saint-Nicolas-de-Port (excluding *I bis*) comprise the hypodigm of *H. butleri*. They are on average smaller than *H. moorei*; the largest specimens are about equal in length to *H. fissurae*. They vary in the same ways as *H. moorei*: the tooth may narrow towards the − end, or the A and B margins may be parallel; the + margin varies in obliquity; A1 varies in size in comparison with A2, the + cingulum and b cusp may be present or absent; cingulum cuspules (*tubercules accessories* of Sigogneau-Russell (1989)) may occur between the A cusps. A trace of cingulum on the B side, noted in M 211 and M 213, occurs in one specimen (Sigogneau-Russell 1989: 159). *H. butleri* differs from *H. moorei* in the development of the − end of the B row: the distance − to B2 ranges from 33% to 44% (mean 40%); B5 is often absent, or, when present, it is displaced medially, to stand on the U-ridge.

The tooth from la Gaume, Belgium, described by Wouters *et al.* (1984), is very small (1.3 mm × 1.0 mm), with a length in the range of *Haramiya I bis* from France, but it has four B cusps. For this reason the authors identified it as *H. fissurae*, and it approaches that species in the obliquity of the + margin and curvature of the B row. However, it is only two thirds the size and probably specifically distinct.

The tooth from Hallau (AIII-309 + 314) described by Clemens (1980) is similar in size (2.23 mm × 1.83 mm) to SNP Ma7. Referred to *H. moorei* by Clemens, it differs from Holwell specimens in the absence of B5: the distance − to B2 is 44% of tooth length (measured from the figure). There is a small fragment of cingulum between the bases of A1 and A2, and another between B3 and B4. AIII-372, a fragment with B1–B3, classified as *Thomasia* by Clemens, seems to be similar. AIII-307 contains a row of three A cusps, of which A1 can be identified by the saddle ridge. As A1 is not higher than A2, the specimen is one of *Haramiya*. The length as preserved is 1.3 mm; the tooth would be a little longer than this, but it was clearly much smaller than the Holwell

Figure 5. Scanning electron micrographs. (*a*) M 211 (holotype of *Haramiya moorei*), crown view; (*b*) the same, obliquely from B side; (*c*) H 3, from B side; (*d*) M 214, crown view; (*e*) the same, + end view; (*f*) H 3, obliquely from − end; (*g*) M 2401A (holotype of *H. fissurae*), crown view; (*h*) the same, from − end; (*i*) H 2, obliquely from − end; (*j*) M 2401C, crown view; (*k*) H 15, from B side; (*l*) M 217, from B side. Arrows on (*d*), (*e*) and (*j*) show the lateral facet on B1.

specimens. Either it represents a smaller species, perhaps the same as the la Gaume specimen, or it is an example of *Haramiya I bis*.

1430/2, from Olgahain, described by Hahn (1973) as *Thomasia* sp.2, is a *Haramiya* in which A3 is rather small (as in M 214), as was pointed out by Sigogneau-Russell (1989). Only the − part of the tooth is preserved. It shows a cingulum below the B cusps. The width was less than that of the corresponding part of AIII-309 + 314.

(*b*) **Haramiya, *group II***

Sigogneau-Russell (1989) included in this group teeth in which the B row is abbreviated; it is reduced below A3 to a low ridge, and the tooth is narrowed at the − end. She regarded these teeth as premolars of the species of which group I were the molars. (The terms 'premolar' and 'molar' are used in a morphological sense only, and do not imply a mammalian mode of replacement). There is a considerable range of size (length 1.4–2.26 mm; cv 13.0), indicating that more than one type of tooth is represented. Five small specimens, with mean length 1.51 mm, may represent a more anterior premolar; if these are excluded, the mean length of the remaining 18 is 1.99 mm, with a cv of 8.7. Comparison of means of this subgroup with *Haramiya I*, exclusive of *bis*, shows that the premolars are longer (ratio 1.14) and narrower (ratio 0.90) than the molars.

(i) *The teeth*

Two teeth from Holwell belong to group II.

M 217 (figures 4 and 5*l*), 1.8 mm × 1.0 mm. This is much narrowed towards the − end; the + margin recedes slightly towards the B side. The tooth appears to be little worn, but somewhat rolled. There are three distinctly separated A cusps, of which A2 is broken. A3 is somewhat lower than A1, and shorter at the base than A2. A3 is placed slightly more medially than A1 and A2. B1 is about equal in height to A1; the remaining B cusps have been removed by rolling. The B row is continued as a cingulum-like ridge below A3, joining the − ridge of A3 at the end of the tooth. There is no b cusp; the + cingulum may have been removed by rolling. The flattened tip of B1 may be due to wear, and there is a possible facet on the basin surface of A3. Remnants indicate a divided + root and a transversely narrower − root.

H 15 (figures 4 and 5*k*). This is much smaller (1.35 mm × 0.9 mm) than M 217, and proportionately shorter due to the relatively smaller A3. A1 is somewhat shorter but more acute than A2; A3 is slightly displaced medially. B1 is similar to A1 in height. The rest of the B row consists of a ridge that declines and becomes narrower till opposite the middle of A3. It is smooth in profile, perhaps due to wear, as minor grooves on the marginal surface indicate the remnants of three cusps. The ridge continues as a cingulum (equivalent to the U-ridge) to join the − ridge of A3. A minute cusp stands on the

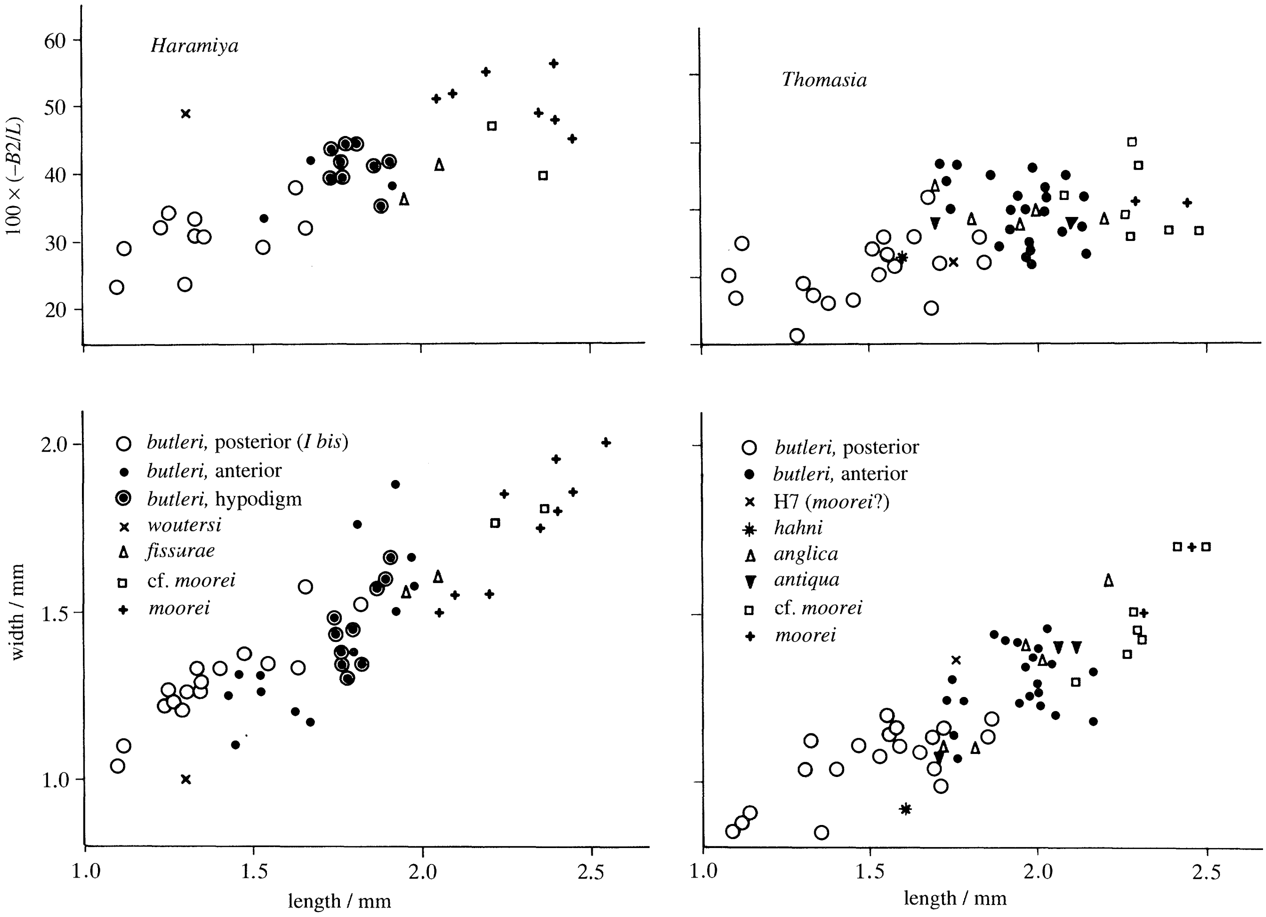


Figure 6. Haramiyid molars. Width and proportionate length of −B2 plotted against length.

ridge close to A3. There is no b cusp at the + end, and the + cingulum is hardly indicated. The tooth is worn at the tips of the cusps and on the surfaces of A1 and B1 (mainly A1) facing the saddle. A contact facet is present at the + end. There are two roots at the + end and one at the − end.

(ii) *Comparisons*

If the proportionate sizes of premolars and molars are the same as in *H. butleri*, the molar corresponding to M 217 would measure 1.75 mm × 1.22 mm. This is too small for *H. moorei* and narrower than in *H. fissurae*. It falls within the range of *H. butleri* from Saint-Nicolas-de-Port, although it is longer in proportion to width than most of those specimens.

H 15 is within the range of the smallest specimens from Saint-Nicolas-de-Port, regarded as penultimate premolars of *H. butleri*.

(*c*) **Thomasia**, ***group I***

Thomasia is distinguished from *Haramiya* by the organization of the A row: A1 is higher than B1, and A3 is very small or absent. As in *Haramiya*, *Thomasia* teeth fall into two groups. Compared with *Haramiya I* teeth of the same length, those of *Thomasia I* are narrower, especially towards the − end. The broadening of the + half of the crown that frequently occurs in *Haramiya* is absent; the A and B margins are nearly parallel or converge smoothly in a − direction. The + margin is transverse or recedes towards the B side, not towards the A side as in *Haramiya*. The basin is narrower. B1 is not displaced medially as in some specimens of *Haramiya*, so that curvature of the B row is slight or absent. In two-rooted teeth of *Haramiya I* both roots are transversely wide in cross-section; in *Thomasia* only the + root is transverse, and the − root is extended longitudinally. Teeth in *Thomasia* group II ('premolars') are narrow at the + end, where B1 is absent, perhaps united with A1.

The sample of *Thomasia I* from Saint-Nicolas-de-Port is heterogeneous: tooth length ranges from 1.09 mm to 2.49 mm, with a CV of 18.8 (figure 6). Increase of length is associated with the addition of cusps at the − end. A3 occurs only on the larger teeth. B cusps appear first on the U-ridge in a more or less median position, and as they develop they become aligned with the B row. In the smallest specimens B3 is still on the U-ridge; in large specimens four B cusps are in alignment and B5 is displaced medianly. The distance − to B2 ranges from 26% to 47% of the tooth length. The height of A1 increases in proportion to length (ratio about 0.6), but the saddle is weak in small specimens and becomes higher in large specimens. In small specimens the root is undivided. Such differences may reasonably be attributed to position in the dentition, the smaller and simpler teeth standing posteriorly to the larger teeth. Owing to the continuous nature of the variation, distinguishing subgroups is necessarily somewhat arbitrary, but using the number of B cusps in alignment (ignoring cusps on the U-ridge) it was possible to pick out 15 teeth with two or three B cusps. This subgroup would roughly correspond to *Haramiya I bis*. Twenty-eight teeth with four aligned cusps may be taken as anterior molars.

(i) *The teeth*

At Holwell, one tooth (H 7) belongs to the posterior molar subgroup, and nine are identified as anterior molars. There are no examples of group II.

H 7 (figures 4 and 9*h*,*i*), 1.75 mm × 1.25 mm. The outline is trapezoidal, + edge transverse, − edge oblique owing to the A row being much shorter than the B row. The tooth is worn, with A1 and B1 rounded and other cusps worn off, so that the A and B rows are smooth in profile. There appear to have been two A cusps and three B cusps. The distance − to B2 is about 26% of tooth length. The saddle is low. There is no b cusp. Traces of black enamel remain on the marginal surface of A1. The U-ridge has been worn away, the area of wear inclined downwards into the basin. There is a large area of wear on the marginal surface of the B row. Inclined facets are present on the + surfaces of A1 and B1. There is a contact facet at the + end, and also a smaller one at the − end, near the end of the A row. The root, of which only a fragment remains, was probably not divided.

M 219 (holotype of *T. anglica*) (figures 2, 7 and 9*a*,*b*), 1.95 mm × 1.3 mm. The A and B sides are parallel, the + margin transverse, and the − end broadly rounded. A1 is the highest cusp; a small A3 is present. There are five B cusps, of which B5 is placed medially, on the U-ridge; it is higher than B4 and B3. The distance − to B2 is 38% of tooth length. The saddle is fairly high (saddle height/tooth length = 0.38). A small b cusp is present. The tooth is unworn; tips of the cusps are sharp.

H 12 (figure 7). This is a poorly preserved tooth with the surface much cracked and eroded, probably similar in size to M 219 (estimated 2.0 mm × 1.25 mm). The + end is broken but the tip of B1 is preserved, with the rest of the B row. B5 is absent. B4 is slightly more median than the other B cusps. Nothing can be seen of the A row. There were two roots, of which the − one is preserved.

M 221 (figure 7), 1.8 mm × 1.0? mm. The width cannot be accurately measured as the tooth is mounted on its B side; it seems to be narrower than M 219. Rolling has removed the prominent parts: a continuous area of dentine represents A1, B1 and the connecting saddle, and also A2; the top of B3 has been removed, and enamel has flaked off over a large area on the marginal side of A1. A3 appears to have been present, although now worn off. B4 is near the − end of the tooth, but in line with the rest of the B row. B5 is absent; there are no cusps on the U-ridge. At the + end there is no indication of a cingulum or b cusp. There are two roots.

YPM 13622B (Simpson 1928, figure 18; plate 2, figure 4). This is incomplete at the + end, where the whole of A1 and part of B1 are missing. The length as preserved is 1.55 mm, and the original length would be about 1.7 mm. The width is about 1.0 mm. Thus the tooth was smaller than M 219. There is a small A3 as in M 219. B3 is the lowest B cusp, B4 is in line, and B5 is more median, on the U-ridge. Between B5 and

A3 there are two 'very minute cusp-like apices' on the U-ridge.

H4 (figure 7). This is the + end of a tooth, with the root. Width is 1.05 mm. The + margin is transverse. Heights of A1 and B1 resemble M 219, but the saddle is higher and the tooth is much narrower, in agreement with M 221 and YPM 13622B. There is a + cingulum below B1. A1 and B1 show inclined areas of wear on either side of the groove, the facet on A1 being the larger; there is a very small area of wear on the cingulum below B1. The top of the saddle shows horizontal wear. In addition there is some wear at the tip of B1, on the − part of its marginal surface, and on the basin slopes of A1 and B1. The root is grooved but not divided.

H 17 (figure 7). This is larger than M 219 (2.2 mm × 1.5 mm), which it resembles in general shape. A3 is a little larger than in M 219. Four B cusps are in line; B5 is not differentiated from the U-ridge. The distance − to B2 is 39% of tooth length. There is no + cingulum or b cusp. Saddle height is 39% of tooth length. Enamel has been removed from the tips of the cusps. Wear on the basin slope of the U-ridge continues, with longitudinal striations, on the A and B cusps; there is also longitudinal wear on the top of the saddle. A continuous area of wear extends along the marginal surface of B2–B4. On the + side of A1 there is a steeply inclined facet. B1 also shows wear on its + surface, and high on B1 there is another facet, facing somewhat laterally, parallel to the facet on A1. A contact facet is present below B1 at the + end. There are two roots; the + root is grooved but not divided.

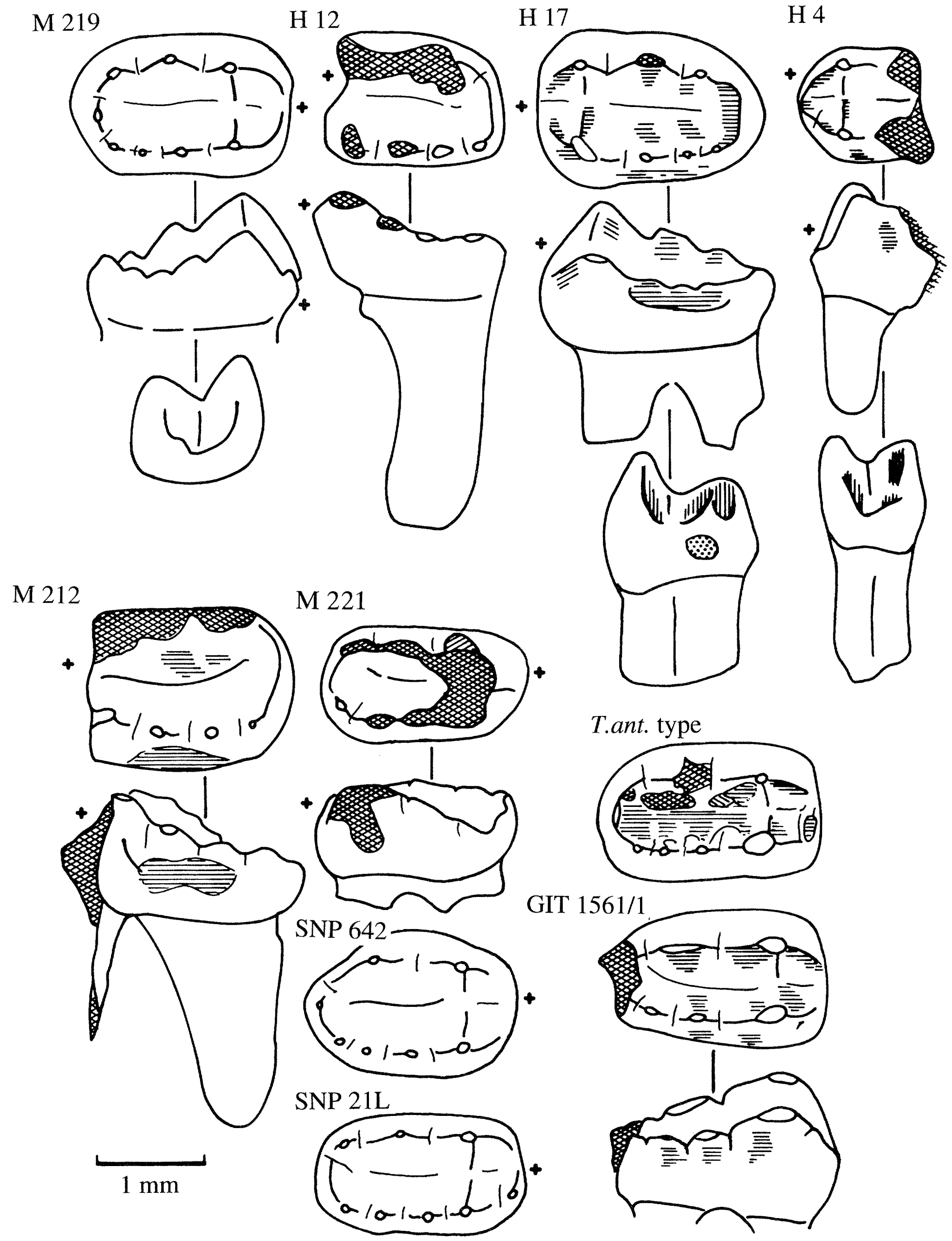


Figure 7. Camera lucida drawings of molars of *Thomasia anglica*, crown, B side and + end views. For comparison, two lower molars referred to *H. butleri* (SNP 642, SNP 21L) and two teeth of *T. antiqua* (the type, and GIT 1561/1). Shading as in figure 3.

M 212 (figure 7). Width is 1.5 mm. This is an incomplete specimen in which the + end has broken off, the break passing across the tips of A1 and B1. The A row is badly flaked, but A3 was probably present. There are four B cusps, and no elevations on the U-ridge. This tooth seems to have resembled H 17. The only clear evidence of wear is a facet on the marginal surface of B2 and B3.

H5 (figures 8 and 9*c*,*e*,*f*), 2.45 mm × 1.6 mm, the largest *Thomasia* tooth from Holwell. It is proportionately longer than M 219, with which it agrees in the transverse + margin and broadly rounded − end. It is rather heavily worn: B1, the saddle, A1 and A2 are occupied by a continuous area of exposed dentine. A3 was probably larger than in M 219, but has now worn off. The B row is worn to a ridge, on which lunules of dentine show that B4 was in line and B5 was medially displaced but on the B side of the midline. The saddle was high; its height as preserved is 43% of tooth length. There is no + cingulum or b cusp. Wear has removed enamel from the basin slope of the U-ridge, extending to involve the whole of what can be seen of the basin, with the exception of a small area where enamel persists. This is the 'pit' of Parrington (1947). It is not, as he supposed, the point of contact with an opposing B1 cusp, but an area at the lowest point of the basin that escaped wear as the opposing B1 travelled longitudinally. Marginal to the B row there is a strip of wear extending from the middle of B1 to B4. At the + end, facets on A1 and B1 flank the groove, and there is an additional facet high on the external surface of B1, parallel to the facet on A1. A contact facet is present at the + end. An inclined facet on the − surface of the U-ridge could have been produced by contact with the following tooth. There are two roots.

H 19 (figures 8 and 9*d*,*g*), 2.3 mm × 1.4 mm. This tooth has the appearance of being compressed towards the + end, with a very high saddle so that A1 and B1 appear to be connate. Parrington (1947) suggested that it might be a stage towards the formation of a shearing tooth like P/4 of multituberculates. However, a large area of dentine is exposed on A1, and it is probable that much of that cusp has been flaked off. Saddle height is 48% of tooth length, perhaps not much greater than in H 5, where the very worn saddle height is 43%. In supposed premolars from Saint-Nicolas-de-Port (*Thomasia II*) there is a single large cusp at the + end that could represent A1 + B1 fused together, and H 19 might possibly be at an intermediate stage in the process of fusion. Rolling has removed the tops of the cusps. A3 was present. Four B cusps are in line; whether B5 was present on the U-ridge cannot be seen owing to breakage. A cingulum is present at the + end. An area in the deepest part of the basin seems to be unworn. Marginal wear facets are present below B2 and B4. There are two roots.

(ii) *Comparisons*

Among teeth from Saint-Nicolas-de-Port referred to the posterior molar subgroup, H 7 resembles most closely in shape SNP 459 (1.38 mm × 0.93 mm), in which B4 is represented by a median elevation of the U-ridge (figure 4). However, H 7 is larger; it is of similar length to, and greater width than, the largest specimen in the subgroup (SNP 90: 1.71 mm × 1.05 mm).

M 219, the type of *T. anglica*, is similar in length

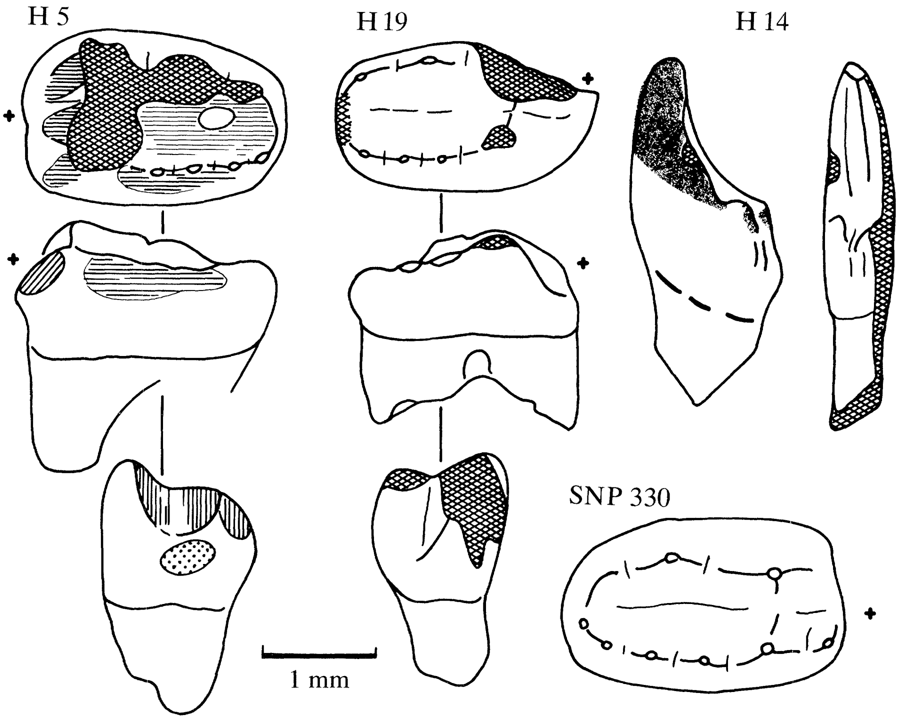


Figure 8. Camera lucida drawings. H 5, H 19, referred to *H. moorei*; crown, B side and + end views; shading as in figure 3. SNP 330, from Saint-Nicolas-de-Port. H 14, upper second incisor, medial and posterior views, extent of black enamel indicated by shading.

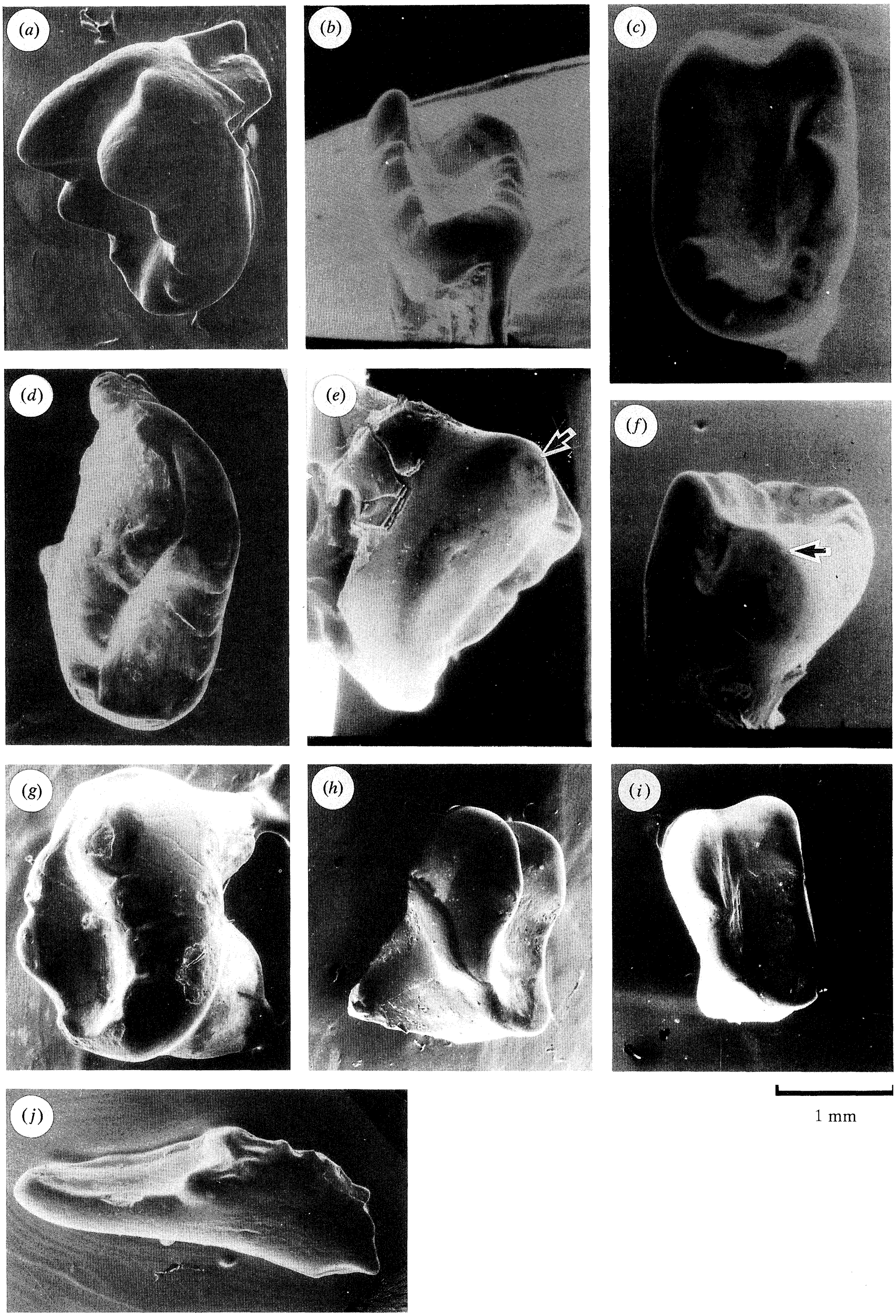


Figure 9. Scanning electron micrographs. (*a*) M 219 (holotype of *Thomasia anglica*), obliquely from B side; (*b*) the same, obliquely from − end (approximately in the direction of relative occlusal movement); (*c*) H 5, crown view; (*d*) H 19, crown view; (*e*) H 5, from B side; (*f*) H 5, from + end; (*g*) H 19, obliquely from B side; (*h*) H 7, from B side; (i) H 7, crown view; (*j*) H 14, medial view. Arrows on (*e*) and (*f*) indicate the lateral facet on B1.

and width to several specimens from Saint-Nicolas-de-Port: SNP 9, 431, 642 (figure 7), 434, 663, 11, 150 (length 1.86–2.03 mm, width 1.25–1.36 mm). These vary in the distinctness of A3, in the development of B5 on the U-ridge, and in the development of cusp b. Taking this variation into account, it is impossible to separate these specimens from *T. anglica*, as Sigogneau-Russell (1989) noted. Six further specimens in the same length range are narrower (the minimum width is 1.09 mm in SNP 50L), and it appears that width varies independently of length as in *Haramiya I.* Shorter teeth, in the length range 1.75–1.85 mm, comparable with M 221, range in width from 0.96–1.14 mm. M 221 is closest to SNP 490 (1.75 mm × 0.96 mm). The incomplete specimen YPM 13622B appears to resemble SNP 4 (1.75 mm × 0.96 mm).

The two largest specimens from Saint-Nicolas-de-Port resemble H 5: SNP 34 (2.4 mm × 1.6 mm) and SNP 330 (2.49 mm × 1.6 mm; figure 8). Another six specimens have lengths about 2.3 mm and widths 1.3–1.4 mm, similar to H 19. All these teeth agree with H 5 in the presence of B5, which is situated laterally to the midline, towards the B side. The saddle is high, 45–48% of tooth length in the least-worn specimens. Cusp b is variable: it is large in SNP 330, absent in SNP 34. A3 is present in three cases, and represented by a ridge in five. SNP 392, although somewhat smaller (2.09 mm × 1.22 mm) resembles these in the lateral position of B5 and the high saddle.

H 17 (2.2 mm × 1.5 mm) cannot be matched with any specimen from Saint-Nicolas-de-Port. It differs from the large specimens just mentioned by the absence of B5. In proportions it agrees with M 219, and it may be regarded as a large example of the *T. anglica* group.

Simpson (1929) distinguished *T. antiqua* from *T. anglica* by the stronger development of A3 and the presence of a b cusp. However, Sigogneau-Russell (1989) showed these characters to be variable in the Saint-Nicolas-de-Port population. The type of *T. antiqua* (figure 7) measures 2.1 mm × 1.3 mm, a little longer and proportionately narrower than M 219. The outline of the − end is less symmetrical, receding towards the A side. In both, B5 is an elevation of the middle of the U-ridge, the distance − to B2 is about 40% of tooth length, and saddle height is about 40% of tooth length. In *T. antiqua* cusp b is larger, and it carries a wear facet that lies in the same steeply inclined plane as a facet on the medial surface of B1. There is a small contact facet below cusp b. A1 is less high and less sharply pointed than in M 219, but it resembles many worn specimens from Saint-Nicolas-de-Port.

GIT 1430/1 (Hahn 1973) is smaller (1.7 mm × 1.0 mm). It resembles the type of *T. antiqua* in morphology, except that A1 is higher and more pointed. In this respect it resembles M 219 and other lightly worn specimens from Saint-Nicolas-de-Port. Hahn says that GIT 1430/1 is more worn than the type, but its facets are limited in area, whereas in the type wear in the basin extends from the U-ridge as far as B1 and A1.

GIT 1561/1 (figures 7 and 10), from the Rhaetic bonebed of Olgahain, is one of a number of specimens in Tübingen found after the publication of Clemens's (1980) paper. These will be the subject of a paper in preparation by W. A. Clemens and W.-E. Reif, and GIT 1561/1 is described here with their agreement. The tooth is broken at the − end beyond A2 and B3. Its length as preserved is 2.05 mm; the original length is estimated at 2.15 mm. The width is 1.3 mm, reduced towards the − end. The top of A2 has broken off, and the other cusps are rounded by wear; as preserved, A1 is only a little higher than B1. Unlike the type of *T. antiqua* there is no b cusp. Ridges on the + surfaces of A1 and B1 meet in a fragment of cingulum. The intervening groove, that slopes down from the saddle, shows a wear facet on each side, that on A1 being the larger. A1 and A2 are separated by a notch, but there is no indication of A3. B2 and B3 are preserved, and there is a fragment of B4 near the broken end. There is a continuous area of wear along the bottom of the basin, extending onto the basin surface of each cusp. This wear is consistent with a horizontal movement of the opposing cusp, except at the + end of the basin where wear on B1 implies a more upward (or downward) movement. The marginal surface of each B cusp shows wear polish. The roots are not preserved. Despite the absence of cusp b, this tooth is probably conspecific with *T. antiqua*.

Two fragmentary specimens from Hallau resemble *T. antiqua* in size. A III-377 shows A1 and B1–B3. Its width is about 1.3 mm. The + cingulum and a small b cusp were present. A III-370 is half a tooth with the B row, length 1.98 mm (Clemens 1980, figure 4). There are four B cusps, and none visible on the U-ridge; a b cusp was present.

A III-295 (Peyer 1956, figure XLI) is the + half of a larger tooth, width 1.7 mm, thus wider than H 5. The cusps are sharp and the tooth was therefore unworn, but A1 is relatively lower and less acute than in GIT 1430/1. There is a + cingulum but no b cusp. A3 and the B row beyond B2 are not preserved.

A III-323 (Peyer 1956, figure LXIX) is the − half of a still larger tooth, with width about 2.1 mm. A1 is missing and A2 has broken off. A ridge − to A2 terminates in a small cusp at the end of the U-ridge. Four B cusps are preserved, presumed to be B2–B5; unlike H 5 and large specimens from Saint-Nicolas-de-Port, B5 is in line with the other B cusps. The possibility that this is a *Haramiya* cannot be excluded.

The middle Keuper specimen (Hahn 1973, figure 2) is small (1.6 mm × 0.8 mm). It has lost all enamel except on the upper part of A1, but that cusp is high and sharp, and the tooth must have been unworn. There are only three B cusps, but B3 is at some distance from the − end, and additional small cusps might have been present in the enamel. The narrowness of the tooth may also be partly due to the absence of enamel. A3 is well developed.

(*d*) *Incisors*

(i) *The teeth*

Of five simple teeth described by Parrington (1947), and five more in the Moore Collection (M 218, M 220), only one (H 14) may be safely identified as haramiyid. It closely resembles teeth identified as I2/ by Sigogneau-Russell (1989). H 16 has some resemblance to a haramiyid lower incisor, but it is much larger (length 4.2 mm, 1.8 times as long as the largest specimen from Saint-Nicolas-de-Port), and Parrington was probably correct in identifying it as tritylodontid. H 20 may be another example of the same type.

H 14 (figures 8 and 9*j*) is the probably medial half of a tooth that has been split longitudinally. The medial surface is flat. It is divided from the concave posterior surface of the main cusp by a strong ridge that ends in a small basal cusp. A small indentation on the ridge appears to be due to the loss of a flake of enamel. A weak median ridge can be seen on the concave surface. A second basal cusp, more lateral and somewhat more posterior than the first, has been partly removed by the break. A groove separates the two basal cusps, and below them is a rounded cingulum. Some wrinkling of the enamel occurs between the cingulum and the cusps. Only part of the root is preserved, but it can be seen that the crown somewhat overhung the root anteriorly. The inclination of the enamel margin, at about 45° to the long axis, shows that the tooth was procumbent. The lower part of the enamel is brown, but above 0.5 mm it is black, including the basal cusps, except for a small area of wear on the medial basal cusp. Measured by the method of Sigogneau-Russell (1989, figure 1*g*), the length (crown height) is 2.1 mm, the thickness (anteroposterior) is 1.3 mm.

(ii) *Comparisons*

Nine specimens of I2/ from Saint-Nicolas-de-Port cluster around a thickness of 1.05 mm (range 0.90–1.22 mm), but two are larger (1.53 mm and 1.59 mm) and are believed to belong to a larger species. If it is assumed that the nine specimens belong to *H. butleri*, the ratio, mean thickness of I2/: mean length of M1/, is about 0.6. On this basis H 14 would correspond to a molar length of about 2.15 mm, at the low end of the range of *H. moorei*.

A III-260 from Hallau (Peyer 1956, figure VI) is much smaller than H 14 (length 1.6 mm, thickness 0.75 mm), and at the low end of the range of Saint-Nicolas-de-Port specimens of I2/, which it resembles in form (Sigogneau-Russell 1989: 182).

6. TAXONOMY

Haramiya and *Thomasia* occur together in the local faunas of Holwell, Saint-Nicolas-de-Port and Hallau. Until recently only *Thomasia* had been reported from the Tübingen-Stuttgart area, but identification of GIT 1430/2 as *Haramiya* by Sigogneau-Russell (1989) showed that both genera were there too. In the largest sample, from Saint-Nicolas-de-Port, *Thomasia* and *Haramiya* postcanines have been found in approximately equal numbers (85 *Thomasia*, 81 *Haramiya*). Within each 'genus' most variation can be ascribed to differences of serial position (premolars, anterior molars, posterior molars), and no variation attributable to upper–lower differences has been detected (figure 6). Further, in the incisors, where upper and lower teeth are distinct, it is not possible to distinguish *Thomasia* from *Haramiya*. We therefore support the hypothesis of Sigogneau-Russell (1989) that *Thomasia* and *Haramiya* are opposing dentitions of the same genus. *Haramiya* Simpson 1947 then falls into synonymy with *Thomasia* Poche 1908.

Contact facets at the + and − ends of the molars show that the teeth were placed in the jaw with their rows of cusps longitudinal (Hahn 1973). *Haramiya* teeth are therefore on average wider than *Thomasia* teeth of the same length. In cynodonts, tritylodonts, triconodonts and therian mammals the upper molariform teeth are nearly always as wide as or wider than the lower ones, and the greater width of *Haramiya* molars suggests that they belong to the upper jaw. It is true that lower molars of multituberculates are in many cases wider than corresponding upper molars (Sigogneau-Russell 1989: 189), but this may be a consequence of their more specialized dentition. We postulate that the Haramiyidae are more primitive in this respect, and that *Haramiya* represents upper teeth, *Thomasia* lower teeth.

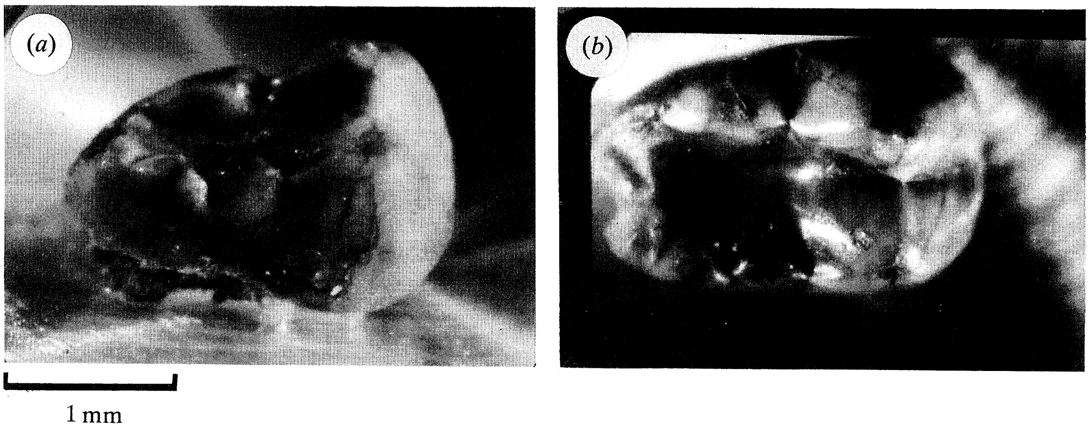


Figure 10. GIT 1561/1, obliquely from B side, and crown view.

(*a*) *Specific distinctions*

Most morphological differences that have been observed in haramiyid teeth appear to be associated with position in the dentition. However, there are differences within each tooth type in characters such as size, proportions, the presence of cusp b, and the development of cusps at the – end, that cannot be explained in this way, but must be due to individual or interspecific variation. Using size as a criterion, most of the material from Saint-Nicolas-de-Port can be referred to a single species, of which anterior upper molars (*Haramiya I*) were named *H. butleri* by Sigogneau-Russell (1990), but a few teeth within each category seem to represent a larger species, of the size of *H. moorei* from Holwell. These include upper molars (SNP Ma7), lower molars (SNP 330, 34), upper premolars (SNP Ma6, 460, 201, 440), lower premolars (SNP 2Ph, 432), upper incisors (SNP 128, 363) and lower incisors (SNP 317, 123).

Larger and smaller species can also be distinguished at Holwell. Upper molars of the larger species (*H. moorei*) are clearly different from *H. butleri*, not only in size but also in the longer – end of the B row, where B5 stands in line with B2–B4 and in most specimens is removed from the end of the tooth. SNP Ma7, from Saint-Nicolas-de-Port, although of the size of *H. moorei*, is less advanced in that B5 is in a more medial position, on the U-ridge. On the basis of size, the anterior lower molars H 5 and H 19, the posterior lower molar H 7, and the upper incisor H 14, can be referred to *H. moorei*. The anterior lower molars have a high saddle, and, at least in H 5, B5 is situated laterally, instead of occupying a median position on the U-ridge. Large lower molars from Saint-Nicolas-de-Port are indistinguishable from H 5 in these characters.

Smaller teeth from Holwell are within or slightly above the range of *H. butleri*. They include upper molars (*H. fissurae*), lower molars (*T. anglica*), and upper premolars. The upper molars differ from those of *H. butleri* in the greatly reduced A1 and greater curvature of the B row, but the lower molars cannot be separated from those referred to *H. butleri*. If it is postulated that *T. anglica* is the lower teeth of *H. fissurae*, we would have two species at Holwell corresponding to the larger and smaller species at Saint-Nicolas-de-Port, but distinguishable in the upper molars and not in the lower molars. The upper molars of the Holwell forms seem to be more advanced, suggestive of a later date, perhaps Liassic as opposed to Rhaetian; the problem of the relative ages of the Rhaeto-Liassic mammal-bearing deposits was reviewed by Clemens (1980).

Size differences suggest that more than one species of haramiyid was present in the Rhaetic of Germany and Switzerland. *Thomasia antiqua*, in which we include GIT 1430/1 and 1561/1, is based on lower molars. Their size range is similar to *H. butleri* from Saint-Nicolas-de-Port and *T. anglica* from Holwell, and, taking likely variation into account, these species cannot be distinguished from *T. antiqua*. Only one incomplete upper molar is referable to *T. antiqua* (1430/2); it is unusual in its small A3, which may be an individual variation. There is a larger species, of the size of *H. moorei*, represented by a complete upper molar (A III-309 + 314), and an incomplete lower molar (A III-295). The upper molar differs from *H. moorei* in the absence of B5; it might be related to SNP Ma7 from Saint-Nicolas-de-Port. A III-323, an incomplete tooth, may represent a species larger than *H. moorei*.

The small upper molar from la Gaume (Wouters *et al.* 1984) and the lower molar from Halberstadt (Hahn 1973) represent two additional species.

(*b*) *Classification*

The use of size as a primary criterion results in the following provisional classification.

Family Haramiyidae Simpson 1947
  Syn. Microlestidae Murray 1866 pro parte. (This family included all the then known Mesozoic mammals.)
    Thomasiidae Poche 1908
    Microcleptidae Simpson 1928
Sole genus, *Thomasia* Poche 1908. Type species, *T. antiqua*
    Includes *Microcleptes* Simpson 1928 = *Haramiya* Simpson 1947

T. antiqua (Plieninger 1847)
  Syn. *Microlestes antiquus*, Plieninger 1847
    Thomasia anglica, Simpson 1928
    (?) *Microcleptes fissurae*, Simpson 1928
    Haramiya butleri, Sigogneau-Russell 1990
  Holotype: a lower molar from Degerloch, Baden-Württemberg (see Clemens 1980)
  Hypodigm (revised by Hahn 1973), the type and GIT 1430/1
  Anterior lower molars: length 1.7–2.2 mm; four B cusps in line; B5 absent or in a median position on the U-ridge; distance – to B2 35–41% of tooth length. Variable in width/length ratio, and in development of cusp b and A3
  Anterior upper molars adequately known only at Saint-Nicolas-de-Port. Length 1.7–2.05 mm; four B cusps in line; B5 if present displaced medially; distance – to B2 is 35–45% of tooth length. Variable in width/length ratio and cusp b; cusp A3 reduced in the only specimen from Baden-Württemberg. Advanced(?) specimens from Holwell (*M. fissurae* Simpson) have greatly reduced A1 and greater curvature of the B row.

T. moorei (Owen 1871)
  Syn. *Microlestes moorei*, Owen 1871
    Microcleptes moorei Simpson 1928
    Haramiya moorei Simpson 1947
  Lectoholotype (Simpson 1928): an upper molar from Holwell (M 211)
  Hypodigm (upper molars), M 211, M 212, M 213, M 214, M 222, H 2, H 3; (lower molar), H5
  Anterior lower molars (inadequately known from type locality): length 2.3–2.45 mm; B5 displaced onto U-ridge, but less medial than in *T. antiqua*; saddle height > 40% of tooth length

Anterior upper molars: length 2.05–2.55 mm; five B cusps in line; distance − to B2 is 45–56% of tooth length. Variable in size of A1 and obliquity of + border. In more primitive(?) specimens B5 is absent (Hallau) or displaced medially (Saint-Nicolas-de-Port)

T. woutersi, new species

Holotype, the upper molar from la Gaume described and figured by Wouters *et al.* (1984)

Distinguished by small size. Length 1.3 mm; B5 absent; + margin oblique; B row curved as in '*H. fissurae*'

T. hahni, new species

Holotype, the lower molar from the Middle Keuper of Halberstadt, Germany, described and figured by Hahn (1973)

Length 1.6 mm; tooth relatively narrow; B4 not present (at least in dentine); distance − to B2 is about 33% of tooth length; A3 comparatively large. Owing to loss of enamel, some details of the crown, such as the possible presence of minor cusps at the − end, are unknown.

7. OCCLUSION

If *Haramiya* and *Thomasia* are from opposing jaws, the problem arises of how they functioned together. Their similarity of pattern and mode of wear finds an analogy in many rodents, where the patterns of upper and lower molars resemble each other but are reversed buccolingually and anteroposteriorly. In rodents this relation is associated with propalinal (longitudinal) chewing, and one would expect that in haramiyids, where chewing was again propalinal, the same type of upper/lower symmetry would occur. It should be noted, however, that in multituberculates resemblances between upper and lower teeth are less close.

As Parrington (1947) noted, the marginal surface of the A row never shows wear, whereas the B row is worn from both sides (figure 2*d*). This is true both of *Haramiya* and *Thomasia*. The A row therefore occluded outside the opposing B row, either buccally or lingually, while the B row occluded in the basin between the A and B rows of the opposing tooth. In nearly all vertebrates, upper teeth bite laterally (buccally) to lower teeth, and it would be expected that the A row was buccal in *Haramiya*, lingual in *Thomasia*.

However, multituberculates are exceptional in that, whereas the first molars relate in the way just described, the relation between the second molars is reversed, M2/ biting more lingually than M/2. First and second molars therefore wear in different ways. If we are correct in interpreting *Haramiya I bis* as posterior upper molars, their occlusal relations are essentially the same as those of anterior molars, the A row being worn only on the basin side. The possibility that the A row is buccal on anterior molars and lingual on posterior molars is precluded by the continuous transition between *Haramiya I* and *I bis*. Similar considerations apply to *Thomasia*. It is concluded that the difference in occlusal relations characteristic of multituberculates was not present in haramiyids.

Parrington (1947) postulated that the upper and lower patterns were reversed longitudinally as well as transversely. He rejected the alternative, that the teeth faced the same way in both jaws, because that would imply that the B row bit across the U-ridge of the opposing tooth. Hahn (1973) correctly noted that the U-ridge does wear, and he rejected Parrington's hypothesis, supposing that the + end was anterior in both jaws. Longitudinal wear scratches, demonstrated by Sigogneau-Russell (1989) and confirmed by us, show that the chewing movement was propalinal, and the occlusal relations cannot be understood by merely fitting upper and lower teeth together.

Sigogneau-Russell (1989) recorded the wear facets in detail. There is much variation, largely due to differences of individual age, but partly due to inexactness of fit; haramiyid facets do not have the high regularity that characterizes the teeth of therian mammals. The pattern of wear is common to *Haramiya* and *Thomasia*, and in the following summary they are considered together.

Wear at the tops of the cusps ranges from removal of the outer enamel to exposure of dentine. This is termed abrasion by Sigogneau-Russell.

In the basin, wear seems to start at the edge of the U-ridge (H 3, M 2401A, M 2401C) (facet 5 of Sigogneau-Russell), and spreads to involve the A and B rows (M 222, H 2, H 17, H 5, H 19) (facets 3 and 4). Wear scratches are horizontal in the middle part of the basin, but inclined near the U-ridge and on the basin surfaces of A1 and B1. An area at the deepest part of the basin (the 'pit' of Parrington) may escape wear for a time (H 5, H 6, H 19). Some teeth (M 222, H 2, M 211, H 4, H 17) show wear on the top of the saddle or on adjacent slopes of A1 and B1, produced by horizontal movement.

On the marginal surface of the B row, wear appears at an early stage. In a lightly worn specimen (M 211) there are three areas on different cusps, but in most cases they have merged to form a continuous strip, from below the − half of B1 to B4. Striations are longitudinal (facet 6).

At the + end of the tooth there are facets that cannot be produced by horizontal movement, but require an inclined movement at about 40° to the base of the enamel. They are usually situated on the faces of A1 and B1 on either side of the groove that runs from the saddle, but they can occur on ridges on the + sides of the cusps, and on cusp b or the cingulum. As Sigogneau-Russell (1989) noted, in *Thomasia* the facet on A1 is larger than that on B1, and in *Haramiya* the reverse is the case. These facets appear at an early stage of wear, and persist even when all the cusps have been worn away (H 6, M 216). An additional, more lateral facet is present high on B1 in H 17, H 5, M 214, and possibly M 2401C. It is parallel to the facet on A1 (figures 5*d*,*e*,*j* and 9*e*,*f*). It was observed certainly in only one case from Saint-Nicolas-de-Port (Sigogneau-Russell 1989: 194).

If two teeth are placed end to end, as the contact facets indicate, the U-ridge of one tooth would be close to the elevated + end of the following tooth. This would complete a basin, between the saddle of one tooth and the saddle of the next, in which the opposing tooth would function. Striations show that the B row of cusps moved along this basin. The inclination of the wear facets on the + side of A1 and B1 is similar to that of the basin surface of the U-ridge (figures 5*f*, *i* and 9*b*), so that an opposing B1 could slide down the + surface of one tooth, and across the U-ridge into the basin of the next tooth. Reaching the + end of the basin, the opposing cusp would rise up the surfaces of A1 and B1 as the teeth begin to separate at the end of the stroke. There would thus be a rotary chewing movement in the sagittal plane (Sigogneau-Russell 1989: 193) (figure 11).

The fact that wear takes a similar form in upper (*Haramiya*) and lower (*Thomasia*) molars suggests that the patterns are reversed anteroposteriorly. If upper and lower teeth faced the same way, e.g. with their + ends anterior, they would wear in different ways, for if (say) the B cusps of *Thomasia* approached the *Haramiya* basin from the − end, the B cusps of *Haramiya* would approach the *Thomasia* basin from the + end. But, in *Haramiya* as well as in *Thomasia*, the facets on the + side of A1 and B1 are clearer and more constant than those on the − side of those cusps, consistent with their formation during jaw closure rather than during jaw opening. Also, it is less easy to conceive of the + facets of *Haramiya* being produced by contact with the basin surface of Al and B1 of *Thomasia*.

If the patterns are reversed, the smaller B cusps would precede B1 as it travelled along the basin; they would pass between the opposing A1 and B1, causing wear of the top of the saddle and adjacent surfaces of those cusps. The length of the traverse during a chewing cycle would be approximately equal to the length of the basin on the larger (anterior) molars. It would therefore be greater than the basin length of the shorter, posterior molars, where B1 presumably passed between the opposing A1 and B1 (figure 12). The saddle of posterior molars is low, so the basin is open at the + end, allowing B1 to pass freely (Sigogneau-Russell 1989: 193).

Sigogneau-Russell (1989, figure 69) pointed out a difficulty in the interpretation of facets 1 (on A1) and 2 (on B1) at the + end. Both facets must be due to the opposing B1 as it passed down the groove between A1 and B1, but, although facet 2 (B1–B1) was normally present, she was unable to find a facet on B1 due to contact with A1. Such a facet does occur in a few cases from Holwell (H 17, H 5, M 214, perhaps M 2401C), situated high on B1 and facing partly laterally, parallel to the facet on A1. In most cases it can only be supposed that the contact was near the top of B1, where the facet would be obscured by abrasion. This would imply that the upper molar was tilted, relative to the lower, so that its cusps pointed more lingually (figure 12). Sigogneau-Russell noted that the abraded tops of the B cusps are inclined laterally in *Thomasia I* and sometimes in *Haramiya I*.

Support for anteroposterior reversal of the patterns is provided by the supposed premolars, *Haramiya II* and *Thomasia II* (Sigogneau-Russell 1989: 191–192). *Haramiya II* is narrowed towards the − end, and *Thomasia II* is narrowed towards the + end where a single cusp seems to be the equivalent of A1 + B1. It seems reasonable to suppose that the narrow ends of both teeth point anteriorly. On the assumption that the orientation of the premolars is the same as that of the molars, it follows that the + end is anterior in *Thomasia* and posterior in *Haramiya*. The large cusp of *Thomasia II* would occlude lingually to the − end of *Haramiya II*, its lateral facet (labelled 1 by Sigogneau-Russell) produced by wear against A2 and A3. Facet 7, on the lingual surface of A1 + B1, would presumably be due to contact with B1 of a more anterior upper premolar (figure 12).

If the + end of the upper teeth is posterior, and the lower teeth move in a + direction along the upper teeth, it follows that the effective chewing stroke was backwards (palinal), the converse of that of rodents, in which chewing involves a forward (proal) movement of the lower jaw. Moreover, in rodents it is usually more or less oblique, with a lingual component (Butler 1985); the molars wear flat, and grinding takes place between crossing enamel ridges (Rensberger 1973). In haramiyids the movement was restricted to a longitudinal direction by the structure of the teeth, rows of cusps travelling along grooves; transverse movement would be possible only when the teeth were not in occlusion. Sigogneau-Russell (1989: 194) noted that abrasion of the tops of the A and B cusps can be inclined marginally, thus in opposite directions, which seemed to imply a transverse component of jaw movement. Such abrasion could occur when the teeth are separated by bulky food objects. Abrasion of the B cusps would also be produced by contact with food in the basin during chewing. Haramiyid molars would be effective for dealing with soft food such as plant material. Food could be cut between the serrated edges of the A and B rows and further reduced by a pounding–grinding action in the basin by the B1 cusp.

8. RELATIONSHIPS

(*a*) *Multituberculates*

The large sample from Saint-Nicolas-de-Port has made possible a more distinct conception of the organization of the haramiyid dentition (figure 13). Although the dental formula remains uncertain, it is clear that the molars and posterior premolars were arranged with their rows of cusps longitudinal, and that they functioned in a propalinal chewing action in which the effective stroke was probably in a backward direction. The largest cheek teeth were the first molars and last premolars. The number of molars in each jaw may have been as few as two, but it is possible that the groups that we have categorized as anterior and posterior molars contained more than one tooth. There is evidence of a smaller penultimate premolar in each jaw, and this may have been preceded by some small, simplified teeth, included in the category 'dents de morphologie particulière' by Sigogneau-Russell (1989). There is no evidence of differentiated

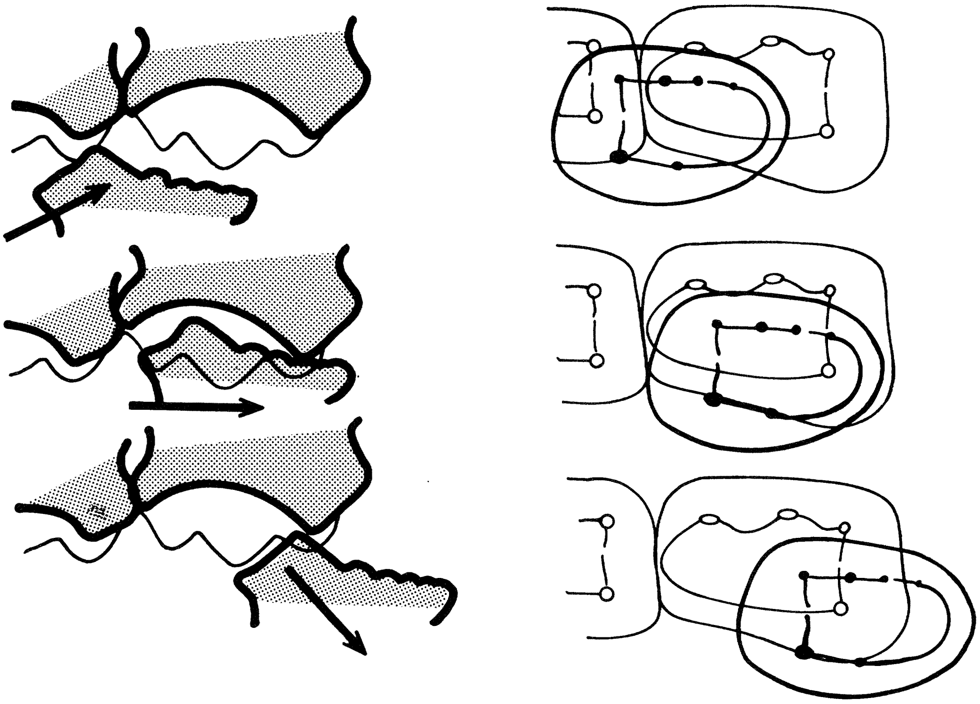


Figure 11. Right: three successive positions during the occlusal movement of a lower (*Thomasia*) molar in relation to two adjacent upper (*Haramiya*) molars; posterior to the right. Left: The teeth represented in longitudinal section, along the B row of *Thomasia* and the basin of *Haramiya*. The lower molar moves posteriorly along the upper molar, from − to +; the reciprocal anterior movement of the upper molar along the lower molar is again from − to +.

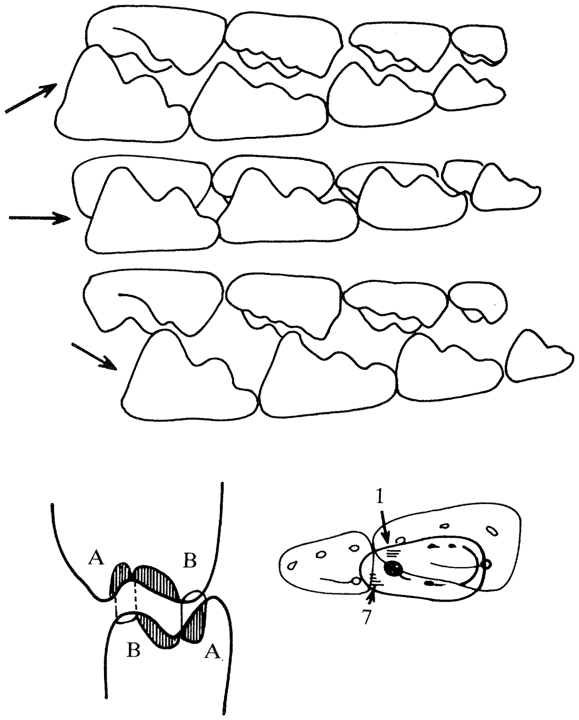


Figure 12. Reconstruction of the posterior part of the dentition, in lingual view, at three stages of the chewing cycle. Posterior to the right. A posterior premolar and three molars are represented, but the number of teeth may have been greater. Below, left: explanation of facets on the + surfaces. Below, right: last lower premolar (*Thomasia*) in occlusion with two upper premolars (*Haramiya*), to explain facets 1 and 7 of Sigogneau-Russell (1989).

canines. Three upper incisors were present, the second one enlarged, and there was an enlarged procumbent lower incisor.

This arrangement is obviously similar to that of multituberculates. In both groups the cheek teeth possessed two rows of cusps, of which (except for the second molars of multituberculates) the buccal lower row occluded in the longitudinal valley between the upper rows (Hahn 1969, 1973). This remains true despite the fact that the comparisons made by Hahn (1973) between individual haramiyid teeth and those of paulchoffatiids are not supported by us. Thus Hahn (1973, figures 11–13) compared the left M/2 of a paulchoffatiid with H 7, which in our opinion is a right posterior molar; the lingual cusp of the paulchoffatiid molar corresponds to A1, not B1. Again (figures 7–10), he compared a left molar of *Thomasia antiqua* with left upper P5/ and M1/ of *Kuehneodon*. The resemblance of *Thomasia II* to posterior lower premolars of multituberculates (Sigogneau-Russell 1989: 156) may be significant. In both cases the buccal row of cusps is confined to the posterior part of the tooth, and the cutting blade of multituberculates seems to be an exaggeration of the A row.

The chewing cycle of multituberculates was palinal, in the sagittal plane with the power stroke directed backwards (Krause 1982; Wall & Krause 1992), as we have postulated for haramiyids. The molars, however, are not basined, lacking the saddle, and the chewing movement is purely horizontal; the orthal component operates only in the cutting action of the premolars. The cheek teeth of multituberculates are more differentiated than in haramiyids, both within each jaw and between upper and lower dentitions, although the differentiation is less marked in paulchoffatiids. In particular, the difference of occlusal relations between first and second molars does not occur in haramiyids. While haramiyids would be expected to be more primitive in view of their early date, the degree of reversed symmetry of opposing molars is equalled only among advanced rodents, and it is unlikely to be a primitive character. Evidence of reversed symmetry in multituberculates is scanty. In late Cretaceous forms with complex molars, such as *Meniscoessus* and *Cimolomys*, the least developed cusps are anterior on upper molars, posterior on lower molars. In Jurassic multituberculates, comparison of adjacent teeth suggests that anterior cusps are added in the upper premolar region (see Hahn 1969:70ff; the tooth named P1/ is now considered to be the premolariform canine, following Hahn (1977)). To a basic pair of buccal and lingual cusps are added an anterolingual and then an anterobuccal cusp; a fifth, anterolingual cusp can appear on P3/. However, on P4/ and P5/ there are additional posterior cusps that seem to have developed from the posterior cingulum; they might be compared with cusp b of haramiyids.

Unfortunately, discussion of haramiyid relationships must depend entirely on evidence from the dentition, and it is well known that phylogenetic analyses based on single-organ systems give inconsistent results (Kielan-Jaworowska 1992). Thus the commonly held view of the relationship of docodonts to morganucodontids, based largely on teeth, was revised by Lillegraven & Krusat (1991) as a result of their study of the skull of *Haldanodon*; they considered 19 of the resemblances to *Morganucodon* to be homoplastic.

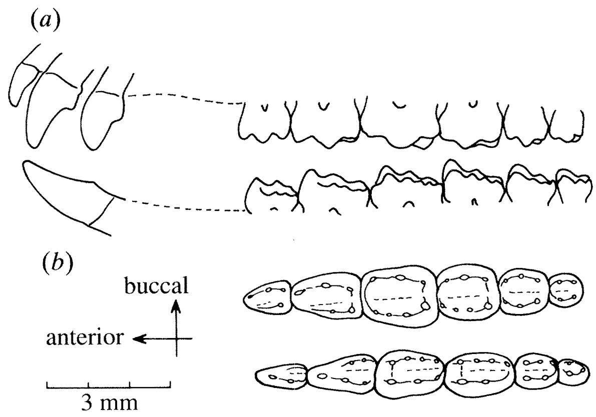


Figure 13. Reconstruction of the dentition of *Thomasia antiqua* from Saint-Nicolas-de-Port (= *Haramiya butleri*). The number of cheek teeth is unknown; here 2 premolars, 2 anterior molars and 2 posterior molars are posited. Additional teeth may have been present in the diastema. (*a*) Left upper and lower dentition seen in lateral (buccal) view; (*b*) Left upper and right lower cheek teeth in crown view.

Multituberculates have advanced beyond *Morganucodon* and share many derived characters with modern mammals. Cladistic analyses give different results, depending on the characters used (Kielan-Jaworowska 1992). Rowe (1988) grouped them with tribosphenic mammals, largely on characters of the limbs and girdles, which are more advanced than those of monotremes. Wible (1991), on cranial characters, placed them below the monotremes, but found 13 characters in which they are more derived than *Morganucodon*. If multituberculates are related to haramiyids they would have already separated from morganucodontids in the Rhaetic, and a considerable amount of homoplasy between multituberculates and therians must be postulated (Miao 1993). One example of undoubted parallelism is provided by enamel structure, which is pre-prismatic in Jurassic plagiaulacoids (as in haramiyids) but prismatic in Cretaceous multituberculates (Frank *et al.* 1984; Fosse *et al.* 1985; Krause & Carlson 1987). The alternative view, that the shared derived characters of multituberculates and therians indicate relationship, would seem to imply that the resemblances of haramiyids to multituberculates are due to parallelism or convergence (Rowe 1993).

(*b*) *Triconodonts*

A triconodont molar pattern, with a central cusp flanked by anterior and posterior cusps, is common to all Rhaetic and early Jurassic mammals, except haramiyids, and it is considered to be an ancestral mammalian character, derivable from the cheek tooth pattern of cynodonts such as *Thrinaxodon* (Crompton & Jenkins 1968; Parrington 1971; Crompton & Sun 1985). The lower teeth closed lingually to the upper teeth, and occlusal shear developed between the lingual surface of upper cusps and the buccal surface of lower cusps. To derive the molars of haramiyids

Table 2. *Comparison of multituberculate and haramiyid dentitions*

Similarities	
3 upper incisors, I 2/ largest; enlarged lower incisor	
Canines reduced or absent	
Palinal chewing, without transverse component; cusps work in longitudinal grooves	
Cheek teeth with two rows of cusps (additional rows added secondarily on some multituberculate teeth)	
Premolars differentiated from molars; lower premolars with B row incomplete anteriorly	
Differences	
M: Occlusal relations different between anterior and posterior molars	H: Occlusion of all molars similar
Two molars in each jaw	Probably more than two molars
Molar chewing fully longitudinal; no saddle	An orthal component; basin formed by saddle
Little sign of reversed upper/lower symmetry	Reversed symmetry of molars

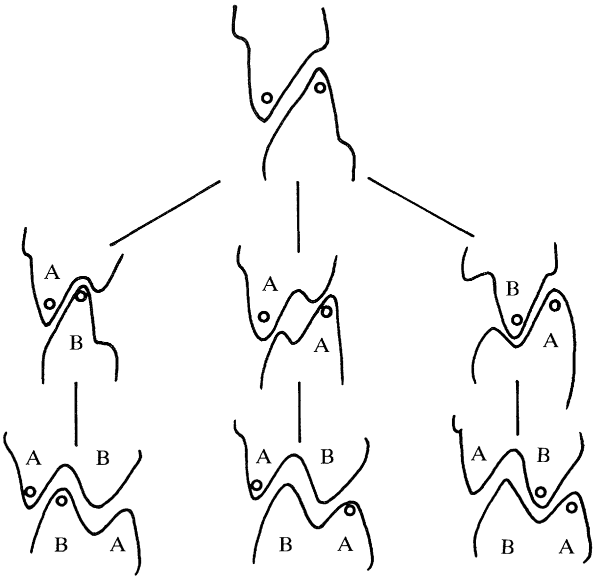
and multituberculates from such a system implies the development of additional cusp rows from cingula. In the case of upper teeth, the A row would represent the original triconodont series, and the B row would be developed from the lingual cingulum (figure 14*a*). Crompton (1974) compared the A row of *Haramiya* with the main cusp row of upper molars of *Megazostrodon*, but he thought that the B row was buccal, derived from the buccal cingulum. *Helvetiodon*, interpreted by Clemens (1980) as upper molars with cusps on the lingual cingulum, would make a better comparison. On lower molars, however, if the A row is primary and the B row has developed from a buccal cingulum, there would be a loss of functional continuity as the B row was intercalated between the lower and upper A rows (figure 14*b*). Only in the case of multituberculate second molars does A (upper)–A (lower) occlusion occur. In the lower jaw, on first molars of multituberculates, and in haramiyids, the B row must be primary and the A row a development of the lingual cingulum. The problem of the homology of triconodont and multituberculate cusp rows was discussed by Bohlin (1945). His solution (figure 14*c*) was similar to ours but reversed buccolingually; the primary cusp rows are B above and A below, and upper A and lower B are developed from buccal cingula. The disadvantage of this hypothesis is that, whereas lingual cingula are commonly present on triconodont molars of both jaws, buccal cingula are rare on lower molars: *Hallautherium* (Clemens 1980) is exceptional.

Relating multituberculate to triconodont teeth is not merely a question of cusp homology, but one of transformation of function. Morganucodontids, triconodontids, amphilestids and kueneotheriids have purely shearing teeth, with no opposition between upper and lower molars. Opposition developed later, in tribosphenic therians and independently in docodonts (Butler 1988). The chewing cycle was transverse, with lingual movement guided by contact between the lingual surfaces of upper cusps and the buccal surfaces of lower cusps. Chewing was therefore unilateral (Crompton & Sun 1985). However, in haramiyids and multituberculates upper and lower molars were opposed, and they operated in a longitudinal chewing cycle in which the direction of posterior movement was controlled by rows of cusps. Transition between these two types of occlusion is difficult to envisage. It is true that in elephants and rodents forward longitudinal (proal) chewing evolved from transverse chewing, but at least in rodents some transverse movement remains, and the homology of cusps and wear facets can be traced (Butler 1985). No intermediate stage in the evolution of the multituberculate dentition has been found. Although Hopson & Crompton (1969) found evidence in a juvenile *Ornithorhynchus* of posterior jaw movement, in the adult 'the jaws work laterally like those of a cow when chewing its cud' (Burrell 1927: 156). Transverse chewing was fully developed in the fossil monotremes *Steropodon* (Kielan-Jaworovska *et al.* 1987) and *Obdurodon* (Archer *et al.* 1993). Only the haramiyids show a significant similarity to multituberculates, but their differences from morganucodontids imply a long period of separate evolution in the Trias.

(*c*) *Traversodontids*

Commonly in reptiles lower teeth bite lingually to upper teeth, but broadening of the teeth to result in opposition has evolved several times, for example in procolophonids and therocephalians, supposedly in adaptation to herbivory (Gow 1978). In broad-toothed ('gomphodont') cynodonts, additional cusps develop lingually in both jaws, as may be seen in *Diademodon* where the lingual region is absent on the posterior ('sectorial') teeth. In traversodontids (Crompton 1972) (figure 15) the lower molars have a high lingual cusp which is joined by a transverse ridge to the highest buccal cusp; these might be compared with A1, B1 and the connecting saddle of haramiyids. Posteriorly there is a basin, bounded buccally by a cuspidate longitudinal ridge (cf. B row), but open lingually. On upper teeth the transverse ridge bears three cusps, buccal (cf. A1), central and lingual. The lingual cusp bites lingually to the lower tooth and is therefore not represented in haramiyids; the central cusp might represent B1, but there is no B row. The basin on upper molars is anterior to the transverse ridge, and it is bounded buccally by a longitudinal ridge, representing the A row.

The chewing action, deduced by Crompton (1972) from wear facets in *Scalaenodon*, was essentially similar to that posited for haramiyids, except that the teeth are shorter and the amount of posterior movement is less (figure 15). The main lower cusps ('A1,B1') passed up the posterior slope of the transverse ridge of the upper tooth and into the basin of the following



(*a*) (*b*) (*c*)

Figure 14. Three hypothetical methods of deriving a haramiyid molar from a triconodont molar. Teeth in cross-section; lingual to the right. Additional cusp row developed from (*a*) lingual cingulum in both jaws, (*b*) lingual cingulum above, buccal cingulum below, and (*c*) buccal cingulum in both jaws.

tooth. Crompton found some additional facets which he ascribed to a forward chewing stroke, but it seems more probable that they were produced, like similar facets in haramiyids, during the return stroke. Thus there would be a cyclic movement in the sagittal plane. In haramiyids the teeth are longer and the backward movement was more extensive; the basins are bounded lingually by additional cusp rows (B above, A below), and the upper tooth does not project lingually beyond the lower tooth, the lingual cusp of the upper transverse ridge being absent. These differences do not seem to us to prohibit a relationship of haramiyids to traversodontids, but in the complete absence of osteological data it is impossible to say whether the resemblances are due to parallel evolution.

(*d*) *Tritylodontids*

These resemble haramiyids in the organization of the incisors, the absence of canines, and the palinal chewing action of the cheek teeth. Loss of the canine may be adaptive to propalinal jaw movement, as in rodents; the canine precludes such movement in *Diademodon* (Grine 1977). Within dentitions, the more complex teeth, as compared with the less complex, have additional cusps anteriorly in the upper jaw, posteriorly in the lower jaw, as in haramiyids. Unlike haramiyids, tritylodontid postcanines are not differentiated into ‘premolars’ and ‘molars’. The chewing stroke was fully horizontal; the teeth are not basined, but possess longitudinal rows of crescentic cusps.

Tritylodontids differ from haramiyids in having three rows of upper cusps, of which the lingual row occluded lingually to the lower molar, as in traversodontids. Crompton (1972) regarded tritylodontids as derived from traversodontids, but Kemp (1983) disputed this, because of their greater resemblance to *Morganucodon* in many osteological details. However, the considerable difference in the dentition requires explanation (cf. Sues 1985).

(*e*) *Trithelodontids*

Sigogneau-Russell (1989: 195) suggested a relationship of haramiyids with Trithelodontidae. In *Pachygenelus* the lower postcanines have a longitudinal series of cusps diminishing in size posteriorly (Gow 1980), which might be compared with the B row of *Thomasia*, and a lingual cingulum, which could give rise to the A row. The upper teeth of *Pachygenelus* have a buccal cingulum but no lingual cingulum, although in *Trithelodon* the lingual cingulum is present and develops some minor cusps that could represent the B row. However, occlusion was unilateral, of a purely shearing type, and the teeth were replaced alternately (Shubin *et al.* 1991).

(*f*) *Theroteinids*

Hahn *et al.* (1989) included the Theroteinidae in the Allotheria, as a new order Theroteinida. Only isolated teeth are known. They differ from those of haramiyids in having very low, rounded cusps, which wear at the top and function in an orthal chewing action (Sigogneau-Russell *et al.* 1986). Such teeth would be most effective for breaking hard, brittle food (Lucas 1979), such as seeds, and not soft fruits as Hahn *et al.* (1989) suppose. Taking the difference of cusp form into account, it is not difficult to homologize the lower molar pattern with that of haramiyids (figure 16). The cusps labelled b1 and b2

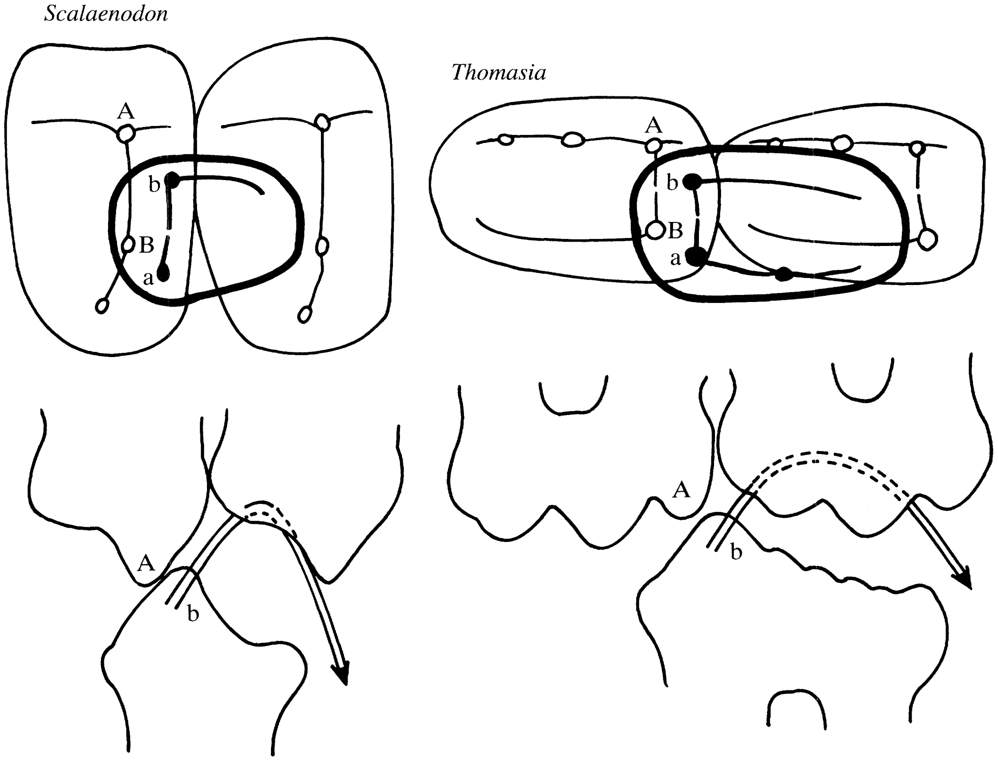


Figure 15. Occlusion in a traversodontid compared with that in a haramiyid.

are A1 and A2; the a cusps form a series like the B row and U-ridge of haramiyids; the ridge connecting a1 and b1 represents the saddle; c is a development of the anterior cingulum, like cusp b of haramiyids. The upper molar is less easy to interpret. A1–A3 and B1 are most likely to be homologous with their namesakes in *Haramiya*; D and C1 are developed from the + (posterior) cingulum. Anterior to B1, however, there are two rows of cusps, a median series B2 and B3, and a lingual series C2 and C3. Hahn *et al.* (1989) appear to equate the C series of cusps with the small cusps that frequently develop in *Haramiya* on the lateral surface of the A row, but those are buccal, whereas on our interpretation the C cusps are lingual. Moreover, C2 and C3, unlike C1, do not have the appearance of having been formed from a cingulum, but they stand partly anterior to B1, so that B1, C2 and C3 form a curved series like the B row in broad examples of *Haramiya* (e.g. *H. fissurae*). The median series, B2 and B3, would in that case be new developments in the basin. On this interpretation, the theroteinids are relatives of haramiyids with a specialized crushing dentition, in which the propalinal chewing movements have presumably been lost.

(*g*) *Conclusion*

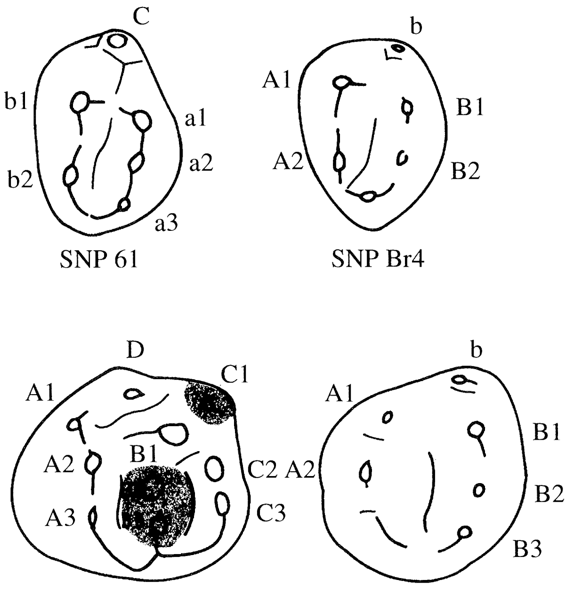
Are the haramiyids mammals? Whether they had acquired the dentary-squamosal jaw articulation is unknown, but they have reached the mammalian level in some characters of the dentition. The mode of occlusion would seem to preclude alternate tooth replacement; sequential replacement was already present in broad-toothed cynodonts (Crompton 1972; Osborn 1974). Division of molar roots is a consequence of the extended length of the tooth; it does not occur on the short posterior molars. Root division is present in tritylodontids, although their root pattern is different from that of haramiyids (Hopson, cited by Wible 1991). Differentiation of the postcanine dentition into 'premolars' and 'molars' does not occur in tritylodontids; in mammals, including multituberculates (Greenwald 1988) but not *Gobiconodon* (Jenkins & Schaff 1988), replacement is confined to the premolar region, but whether this was true of haramiyids is unknown. Haramiyid enamel is pre-prismatic, resembling that of morganucodontids and kuehneotheriids (Frank *et al.* 1984; Sigogneau-Russell *et al.* 1986), but prisms have been reported in the tritylodontid *Oligokyphus* (Dauphin & Jaeger 1987) and in trithelodontids (Grine & Vrba 1980).

Haramiyids show resemblances in the dentition to multituberculates and to broad-toothed cynodonts. Three different hypotheses of their relationships are possible (Fig. 17).

1. Haramiyids are advanced cynodonts with mammal-like characters, like tritylodontids and trithelodontids. They were derived from traversodontids, and their resemblances to multituberculates are homoplastic.
2. Haramiyids are a primitive sister-group of the multituberculates, to be included in the Mammalia, subclass Allotheria. Resemblances in the teeth to traversodontid cynodonts are homoplastic.
3. Traversodontids, tritylodontids, haramiyids and multituberculates form a herbivorous clade which crossed the reptile–mammal boundary independently of the insectivorous–carnivorous triconodont-like mammals; this implies that the class Mammalia is diphyletic.

Hypothesis 1 fits best with the numerous skeletal characters in which multituberculates are more advanced than triconodonts (*Morganucodon*) in the direction of therian mammals. It involves the difficulty of deriving the multituberculate dentition, with its palinal chewing, from that of a triconodont. Hypothesis 2 also involves this difficulty. Moreover, as a haramiyid was present in the Keuper, it implies a very early separation of the haramiyid–multituberculate clade, and therefore increases the probability that most multituberculate–therian resemblances are homoplastic. Hypothesis 3 accounts for the origin of palinal chewing, but it implies an even greater degree of parallel evolution, as the mammalian characters of multituberculates would be acquired independently from other mammals. On the basis of parsimony, hypothesis 1 is to be preferred, but the problem will be solved only when more information is available, particularly from the early Jurassic. Data bearing on the origin of the multituberculate dentition is especially desirable.

In the present state of knowledge a definitive higher order classification of the Haramiyidae is probably impossible. If hypothesis 1 is adopted, the Haramiyidae would have to be removed from the Allotheria, and indeed from the Mammalia. If they are provisionally left in the Allotheria, they differ in a number of ways from the Jurassic and later multituberculates, notably: (i) the basined molars which functioned by a partly orthal occlusal movement; (ii)



SNP 61 SNP Br4

RAS 801 SNP 461 (rev.)

Figure 16. Comparison of theroteinid teeth (SNP 61, RAS 801) with 'posterior' molars of haramiyids (SNP Br4, SNP 461).

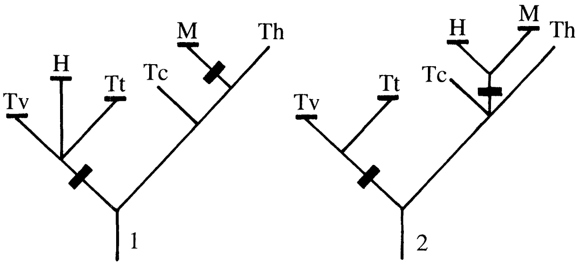


Figure 17. Three hypothetical phylograms. Abbreviations: Tv, traversodontids; Tt, tritylodontids; H, haramiyids; M, multituberculates; Tc, triconodonts (morganucodontids); Th, therians. Acquisition of propalinal chewing indicated by a bar.

the reversed symmetry of upper and lower molars; and (iii) the similar occlusal relations of anterior and posterior molars. These differences seem sufficient to justify separation of the Haramiyidae from the order Multituberculata, and we follow Hahn *et al.* (1989, text-figure 12), who gave them the status of a separate order, Haramiyida.

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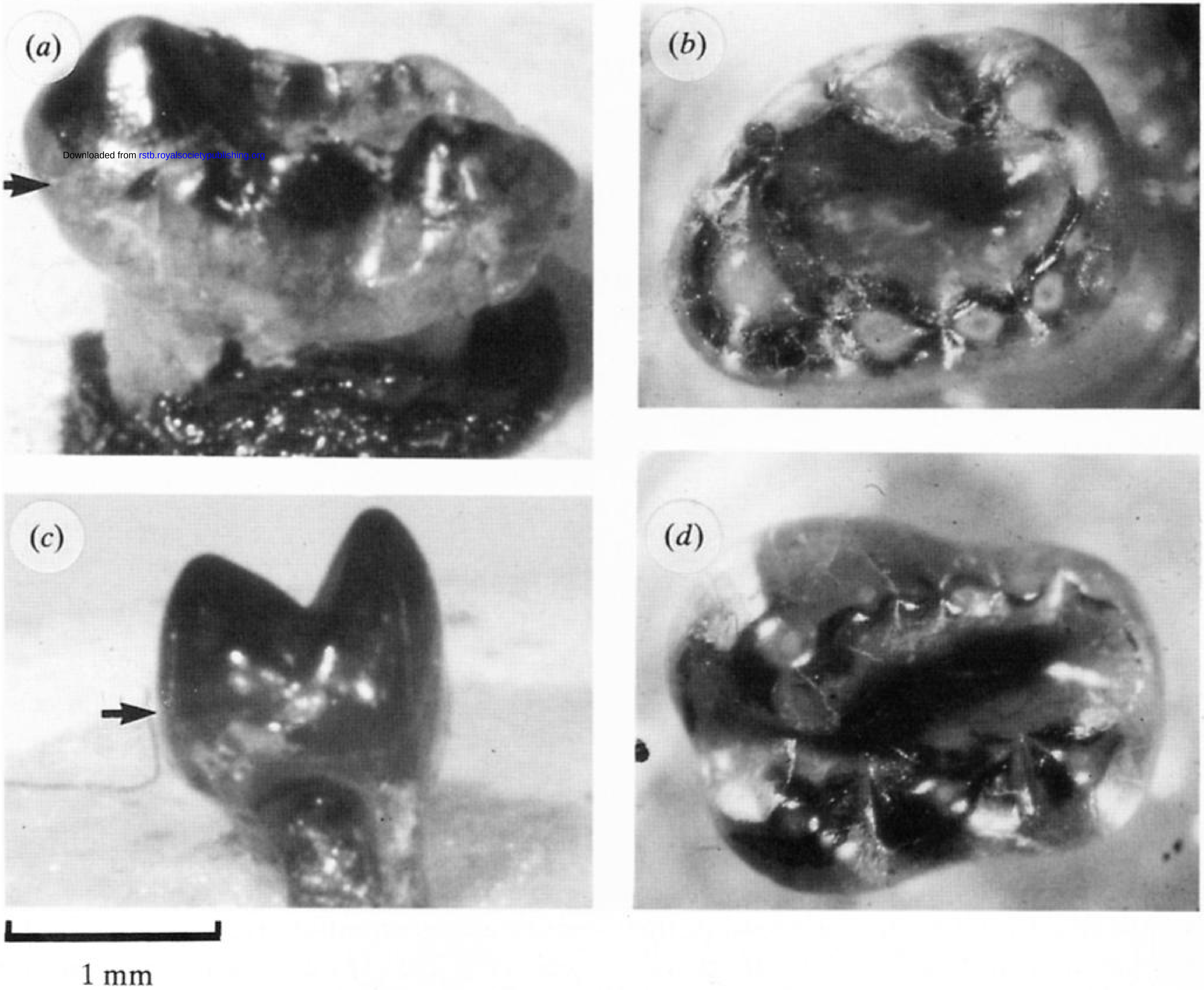

igure 2. To illustrate black outer enamel. (*a*) M 222, A side; (*b*) M 2401A, crown view; (*c*) M 219, + end; (*d*) I 3, crown view. In (*a*) and (*c*), arrow marks lower edge of black enamel. In (*b*), black enamel is confined to usps, from which it has been partly removed by wear. In (*d*), black enamel is retained on the marginal surface f the A cusps, but removed from the marginal surface of the B cusps.

Figure 5. For description see opposite.

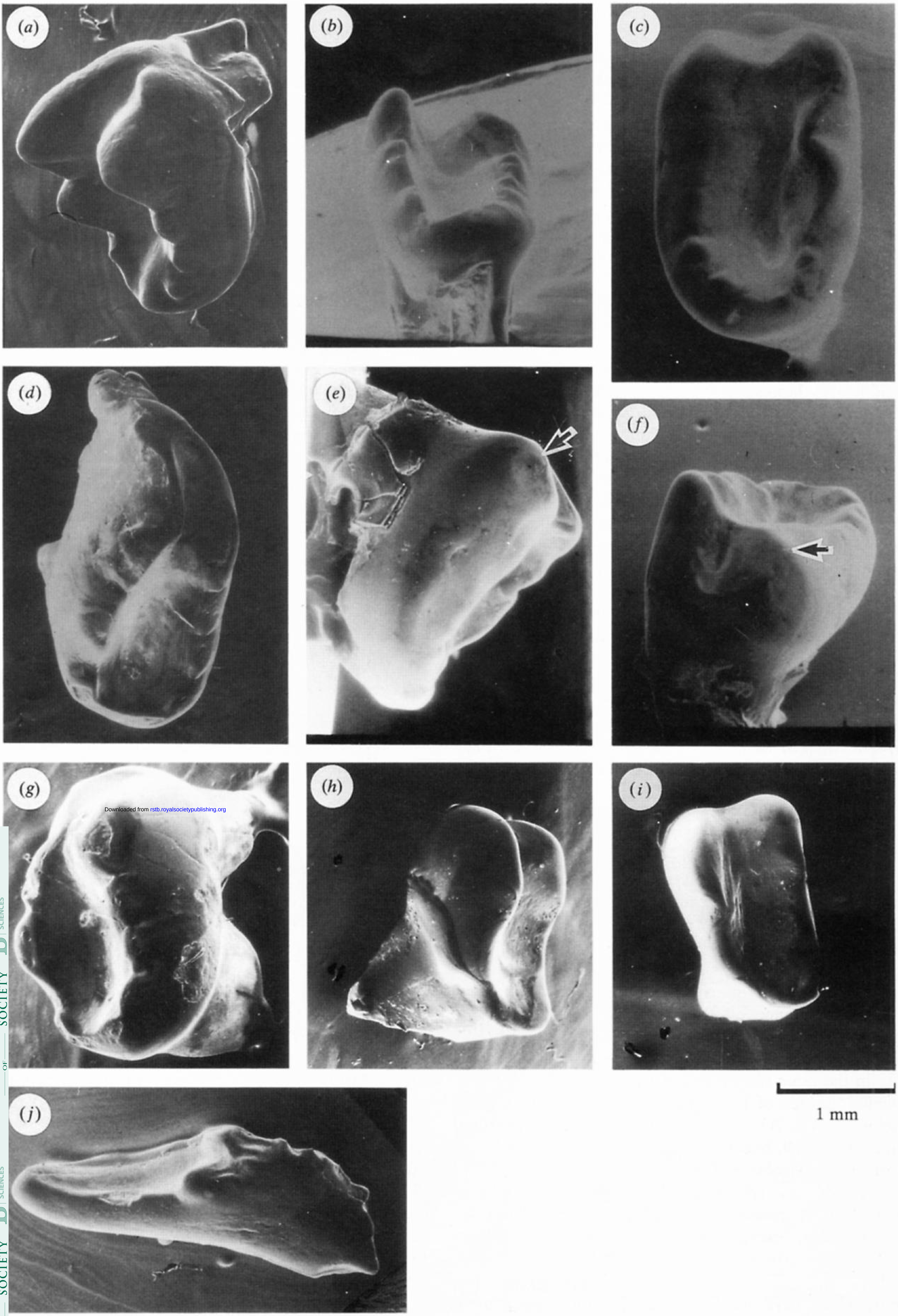

Figure 9. Scanning electron micrographs. (*a*) M 219 (holotype of *Thomasia anglica*), obliquely from B side; (*b*) the same, obliquely from − end (approximately in the direction of relative occlusal movement); (*c*) H 5, crown view; (*d*) H 19, crown view; (*e*) H 5, from B side; (*f*) H 5, from + end; (*g*) H 19, obliquely from B side; (*h*) H 7, from B side; (i) H 7, crown view; (*j*) H 14, medial view. Arrows on (*e*) and (*f*) indicate the lateral facet on B1.

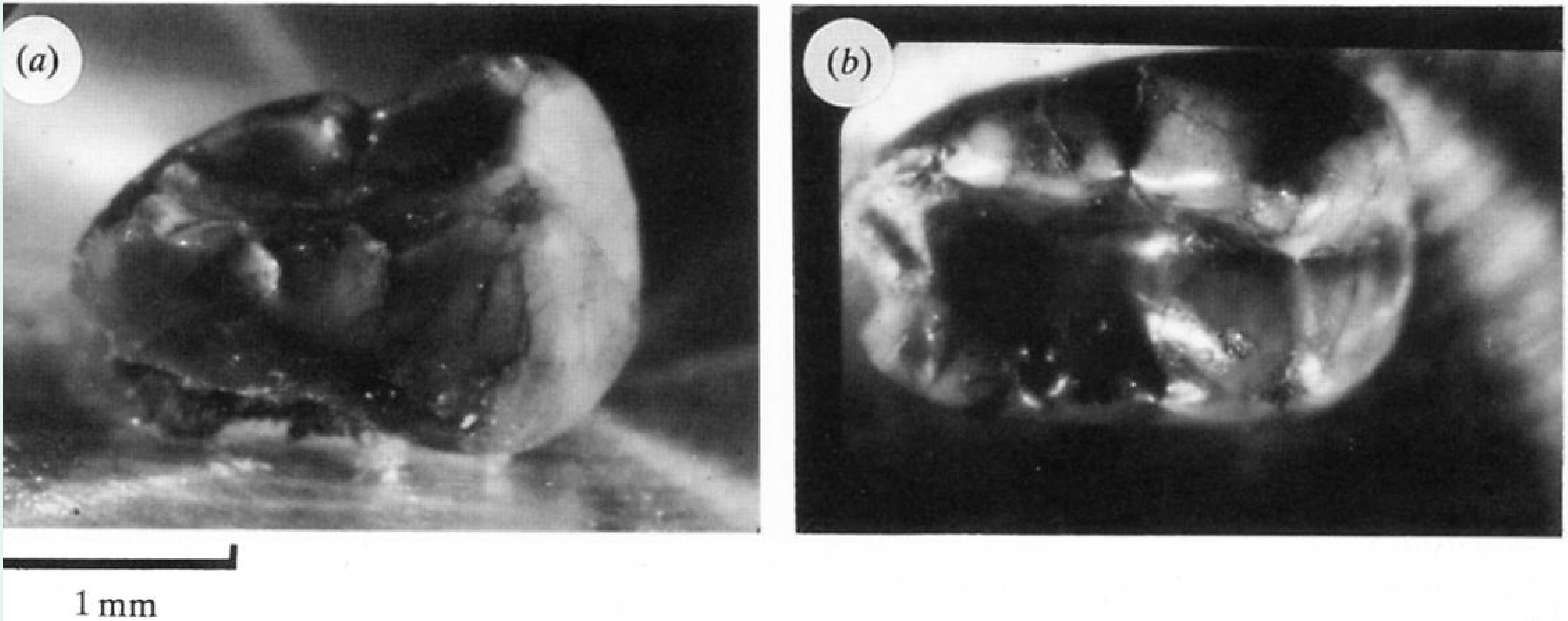

Figure 10. GIT 1561/1, obliquely from B side, and crown view.