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Dental wear variation and implications for diet: An example from Eocene perissodactyls (Mammalia)

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ABSTRACT

Plagiolophus minor and *Palaeotherium medium* (Perissodactyla, Mammalia) co-occur in the Late Eocene site of La Débruge, France. *Plagiolophus* survived the earliest Oligocene mammalian faunal turnover, the Grande Coupure, whereas *Palaeotherium* became extinct. The diets of these two species are investigated by studying wear facet formation and the mesowear and microwear of the molar teeth. The range of variation in dietary wear is low within each species for mesowear and wear facet formation, but there is a large degree of variation within species for microwear features. Both species show high occlusal relief, approximately 50% sharp cusps and 50% round cusps, a significant proportion of early buccal phase shearing wear, polishing of the wear facets and the presence of small pits, all of which typify leaf browsers today. The general morphology of the teeth also suggests that both were browsers, sharing important characteristics with browsing rhinoceroses and hyraxes. The presence of extensive lingual phase wear, produced by grinding, suggests that a small proportion of fruit was also consumed. Coarse scratches and large pits, which may be the result of eating fruits and hard seeds, are also microwear features common to both. *Palaeotherium* exhibits less late buccal and lingual phase wear than *Plagiolophus* both of which indicate that it ate less fruit. However, the greater number of microwear features in *Palaeotherium*, may result from a diet containing more abrasive material such as seeds from fruit. The additional evidence in *Plagiolophus* of crown cementum and a shallower occlusal angle, suggests that it may have eaten tougher but less abrasive food. These dietary differences may explain the differential extinction at the Eocene–Oligocene climatic event.

1. Introduction

1.1. The Eocene–Oligocene transition and La Débruge

The Eocene–Oligocene transition was a time of major climatic change, with the Greenhouse climate of the Eocene deteriorating towards the Icehouse climate of the Oligocene (Zachos et al., 2001). A major mammalian faunal turnover, called the 'Grande Coupure' or big break (Stehlin, 1910) occurred in Europe in the earliest Oligocene. The European endemic ungulates (perissodactyls and artiodactyls) were the group most significantly affected by this event, most of which became extinct and new taxa arrived from Asia. The Grande Coupure occurred at the same time as the onset of polar glaciation in the Oligocene (Oi-1) (Hooker et al., 2004, 2007; Hooker in press).

Changes in the availability of different types of vegetation, which could result from climatic change, would have a significant and direct effect on the ungulate fauna because they are entirely dependent on plant material for nutrition. The diet of recent ungulates consists of plant material, e.g. leaves, grass, fruit, seeds, buds, nuts and sometimes bark, although some peccaries and pigs are more omnivorous and include animal material in their diet (Novak, 1999; Merceron et al., 2004). Teeth can be used to understand mammalian diet and dental wear has the potential to reveal subtle changes in diet giving a high-resolution signal. In order to exploit this potential it is necessary to understand normal variation within a population.

La Débruge is a locality in the South of France, of Late Eocene age. It belongs to Paleogene Mammalian reference level (MP) 18, and to the *Isoptychus pseudosiderolithicus–Palaeotherium muehlbergi thaleri* Mammal Biozone (Hooker, 1992). It is highly fossiliferous for a Paleogene mammal site, having yielded large numbers of specimens, especially of large mammals, to 19th century collectors (de Bonis, 1964; Hooker, 1992) and is therefore a suitable locality to assess the variation in dental wear within what is probably close to a natural population of fossil perissodactyls.

The site contains a relatively high percentage of larger mammals and, amongst the smaller mammals, a relatively high percentage of arboreal and scansorial types. Based on this ecological composition of the mammal fauna, the habitat surrounding the depositional site of La Débruge was likely to have been relatively open woodland (Hooker, 1992; JJH personal observation). The environment may not have been

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as open as it first appears, however, owing to the bias introduced by the absence of screen washing at this site (Hooker, 1992) and the consequent under-sampling of small mammals. De Bonis (1964) suggested that the depositional setting was a freshwater marsh with an herbaceous flora, owing to the presence of freshwater gastropods and lack of evidence of tree trunks in the lignitic sediments. The abundance of clastics in the deposit also suggests post-mortem transportation of the fauna.

The aim of this paper is to assess the intergeneric differences and intraspecific variability of dental wear in an assemblage of fossil perissodactyls. These data will be used to (i) determine diet and (ii) establish levels of normal variation which can in the future be applied to recognizing temporally significant variation. Such temporal variation has the potential to show whether there was dietary change across the Eocene–Oligocene transition, and could be used to discover whether palaeoenvironmental change influenced the Grande Coupure.

1.2. Teeth and dental wear

When teeth are first erupted in the mouth they display the genetically determined morphology which is a result of the evolutionary history of the organism (Fortelius and Solounias, 2000). Teeth have diverse morphologies, especially varying in cusp and crest shape and number, crown height and enamel thickness (Hilson, 2005). As the teeth are used during the lifetime of the animal, they become worn. Various processes can contribute to the dental wear, but this paper will concentrate on the wear produced by the action of tooth on tooth (attrition) (note: there is always some food between the teeth), or by food on tooth (abrasion) (Butler, 1972; Fortelius and Solounias, 2000). Dental wear can be considered at three different scales, wear facet development, mesowear and microwear (Janis, 1990; Fortelius and Solounias, 2000). Wear facets and mesowear are the wear on the tooth that is visible to the naked eye or at low magnification. Wear alters the unworn morphology of the tooth, shown by the distribution of wear facets and abraded areas, the shape of the cusps and the occlusal relief of the tooth. Microwear is the wear on the tooth that is only visible under a microscope. It commonly takes the form of pits and scratches on the enamel or exposed dentine on the surface of the tooth. It is generally studied on the occlusal surface (where the upper and lower teeth meet) although there has been some investigation of non-occlusal microwear (Ungar and Teaford, 1996).

The study of tooth wear is extremely useful for determining the diet of fossil species in the absence of direct evidence of the type of food eaten by an animal (e.g. gut content information, *in situ* coprolites etc). The wear patterns on a tooth vary according to the original morphology of the tooth, the direction of the movement of the jaw during chewing and the type of food eaten. By studying the dental wear in living organisms for which the diet is already known, either from observations of feeding or of gut content or faecal examination, comparisons with fossil wear patterns can be made. If the analogue is suitable the probable diet of the fossil species can be determined.

Various terms will be used to describe the properties of food material in this paper. Abrasive material wears away the surface of the enamel e.g. silica phytoliths in leaves, extraneous grit (quartz). Tough food is difficult to break down e.g. old leaves, woody plant tissue; toughness is a material property which measures resistance to crack growth (Lucas, 2004). Hard material is resistant to deformation under indentation e.g. silica phytoliths, grit, seed cases (Lucas, 2004). Fibrous food has a structure composed of threads e.g. leaves (Janis, 1990). Soft food yields readily to pressure e.g. fleshy fruits, fungi (Janis, 1990).

Changes in diet can result in rapid changes in the microwear produced and can vary seasonally (Walker et al., 1978; Teaford and Oyen, 1989). Microwear is considered to show the ‘last supper phenomenon’ (personal communication from Fred Grine to Janis, 1995, p. 82), recording the last few meals before the tooth was shed or the animal died. Wear facets and mesowear reflect a longer term accumulation of wear throughout the lifespan of the animal (Janis, 1990).

2. Materials

Teeth of the two species *Plagiolophus minor* (Cuvier, 1804) and *Palaeotherium medium* (Cuvier, 1804) from the locality of La Débruge, Vaucluse, France, were used for this study. The material is held in the collections of the Department of Palaeontology, Natural History Museum, London (BMNH) (Appendix Tables 1–3). Where there are multiple specimens on one registered number, the unique Bravard Catalogue number (G-prefix number) is added. The second upper

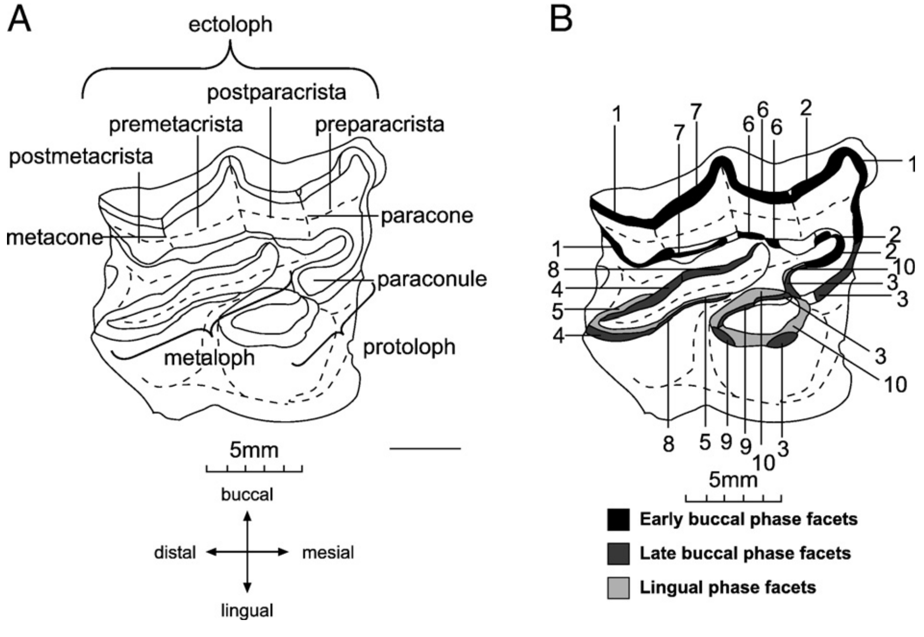

Fig. 1. An example of *Plagiolophus minor* (BMNH.28231 G240, RM^2) labelled with (A) different areas of the tooth used in this paper; (B) numbered wear facets (only enamel labelled) following Butler (1952) to show which facets are produced at different phases of the chewing cycle. Facets 1, 2, 6, and 7 correspond to early buccal wear; facets 3, 4, 8, and 9 correspond to late buccal phase wear; and facets 5 and 10 correspond to lingual phase wear.

molar (M^2) was used where available. Isolated teeth which could not be identified more specifically than either M^1 or M^2, but were of an appropriate size to be M^2, were used to increase the sample size so that it is comparable with studies of extant ungulates. Six specimens of *P. minor* and 6 specimens of *P. medium* were used to study wear facet formation (Appendix Table 1); 37 specimens of *P. minor* and 17 specimens of *P. medium* were analysed for mesowear (Appendix Table 2); and 25 specimens of *P. minor* and 19 specimens of *P. medium* were analysed for microwear (Appendix Table 3). Modern material (hyraxes, rhinoceroses, tapirs and duikers) was studied in the Department of Zoology, BMNH.

3. Methods

3.1. General morphology

Specimens of *Plagiolophus minor* and *Palaeotherium medium* were examined to document the following: jaw morphology (shape of premaxilla and mandibular symphysis, length of diastema) and tooth morphology (crown pattern, see Franzen, 1968) (Fig. 1A), crown height, enamel thickness (Remy, 1976) and presence of crown cementum. Representative examples of the teeth were photographed and drawn.

3.2. Wear facet formation

Six specimens of each species, of varying wear stage, were studied: unworn, four intermediate wear stages and highly worn (almost flat). The occlusal surfaces were examined under a stereoscopic light microscope (Nikon SMZ-10A) and the position and extent of enamel on each wear facet was recorded on a scale drawing made using a camera lucida attached to the microscope. Previous research on modern ungulates (Janis, 1990) has used a single representative tooth from each taxon, at the same relative age and stage of dental wear (lightly worn). Multiple specimens at varying wear stages were used here because teeth at comparable stages of wear may not be available in the small samples of fossil taxa (Janis, 1990), and this allows for comparison between different wear stages in different taxa.

The wear facets were numbered according to Butler (1952) (Fig. 1B). Each set of facets was produced by a different part of the chewing cycle (Janis, 1990).

(a) Facets 1, 2, 6, 7 correspond to early buccal phase wear (shearing) (= buccal phase I shearing of Janis, 1990).
(b) Facets 3, 4, 8, 9 correspond to late buccal phase wear (shearing) (= lingual phase I shearing of Janis, 1990).
(c) Facets 5, 10 correspond to lingual phase wear (grinding) (= phase II of Janis, 1990).
(d) Rounded tips of cusps correspond to tip wear (puncturing and crushing).

Shearing crush of Janis (1990) is located in the transitional zone between the two wear facets which face different directions (i.e. 1 and 7 or 2 and 6); however, this type of wear is not distinguishable from early buccal phase wear.

3.3. Mesowear analysis

Mesowear analysis is based on the method developed by Fortelius and Solounias (2000) with modifications by Rivals and Semprebon (2006). Specimens at an intermediate wear stage (not completely worn or unworn), with an intact cusp (i.e. not chipped) on the upper second molar (M^2) were selected. Specimens that showed no wear were excluded, as were specimens that were so worn that little was left of the cusp and crest morphology. The proviso suggested by Fortelius and Solounias (2000) of only using teeth where the third molar was in occlusion and the first molar was at a similar wear stage to the second could not be applied to the teeth of *Plagiolophus* and *Palaeotherium*. This is because they have a higher wear gradient than most modern ungulates, such that when M^2 is moderately worn M^3 may still be unerupted and M^1 heavily worn (see Remy, 1998). Isolated teeth were included to prevent unnecessary restriction of the sample size. The buccal profile of each tooth was drawn at 4× magnification. From this drawing the occlusal relief and occlusal shape were determined. Measurements were made (Fig. 2A) using Vernier callipers on the drawings (accuracy of the callipers is to ±0.2 mm). For each tooth row only one tooth position was used (when both the left and right upper molars from a single individual exist, both were used as different data points). The order of preference in selection of the teeth was $M^2 > M^1 > M^3$. The percentage of high occlusal relief and of each cusp shape present for each species was calculated.

Occlusal relief is the height of the cusps above the adjacent valley (Fig. 2A) and is classified as being high or low (Fig. 2B). If there is a large vertical distance between them it is high and if the vertical distance is small it is low. Fortelius and Solounias (2000) considered that occlusal relief could be judged by eye with experience, but used a quantitative index, for borderline cases between high and low occlusal relief. In this study each tooth was measured to obtain the quantitative index. The index is defined as the vertical distance between a line connecting two adjacent cusp tips and two adjacent valley bottoms (DV), divided by the length of the whole tooth (*L*) measured on the buccal profile at the top of the crown (Kaiser et al., 2000; Bernor et al., 1997; Fig. 2A). The boundaries between high and low were: selenodont forms and plagiolophodont equids = 0.1, hyracoids = 0.05 and rhinocerotids = 0.03 (Fortelius and Solounias, 2000). Cusp shape depends on the pattern of facet development and is scored as sharp, rounded or blunt (Fig. 2B).

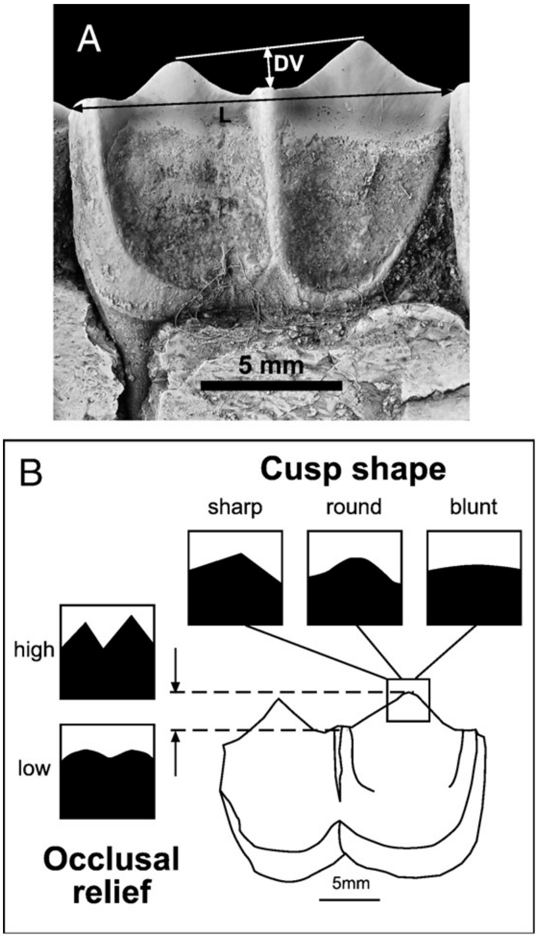

Fig. 2. (A) Position of length and height measurements taken on buccal view of *Plagiolophus minor* (BMNH.28231 G240, right M^2). *L* = length, DV = valley depth. (B) Definition of the mesowear variables, occlusal relief and cusp shape (after Kaiser and Solounias, 2003).

The hypsodonty index (HI) is a measure of relative crown height. It is used in conjunction with occlusal relief and cusp shape to interpret the mesowear data. HI = M_3 height/M_3 width. A tooth is classified as brachydont when $HI < 1.5$, mesodont when $1.5 < HI < 3$ and hypsodont when $HI > 3$ (Janis, 1990). The hypsodonty index was determined for both species from an unworn lower third molar based on the method of Janis (1988). Hypsodonty index data from Janis (1988) were used in the comparisons made by Fortelius and Solounias (2000).

3.4. Microwear analysis

A mould of the outer enamel band of the preparacrista (or the premetacrista if the preparacrista was damaged) was made using Coltène President Microsystem© light body dental moulding material. Unlike previous ungulate microwear investigations (e.g. Solounias and Semprebon, 2002; Merceron et al., 2004, 2005), the inner enamel band was not used because in palaeotheres it is thin and is worn down rapidly, particularly in *Palaeotherium*, where it is discontinuous on a large number of specimens. After removal from the tooth, the mould was surrounded by a dam of silicone rubber so that the wear facet to be studied was orientated in a horizontal plane (allowing for curvature of the facet). This mould was filled with Araldite© resin and centrifuged to remove bubbles. The finished cast was stuck to an SEM stub with Araldite© adhesive and coated with gold-palladium. Secondary electron scanning electron microscopy was used to examine the microwear on the surface of the preparacrista. The SEM used was a Hitachi S-2500 at the EMMA Unit, Natural History Museum, London. The cast was placed in the SEM chamber and the stub was tilted to an angle of 45°. Digital images were taken at magnifications of 70× and 250×. A single image at each magnification was taken from the middle of each facet if the microwear present on the facet was uniform. If, however, there was considerable variation in the microwear on the facet, a maximum of three images was taken to illustrate the variation fully. Specimens which exhibited microscopic post-mortem damage (either owing to taphonomic processes or preparation) were not used.

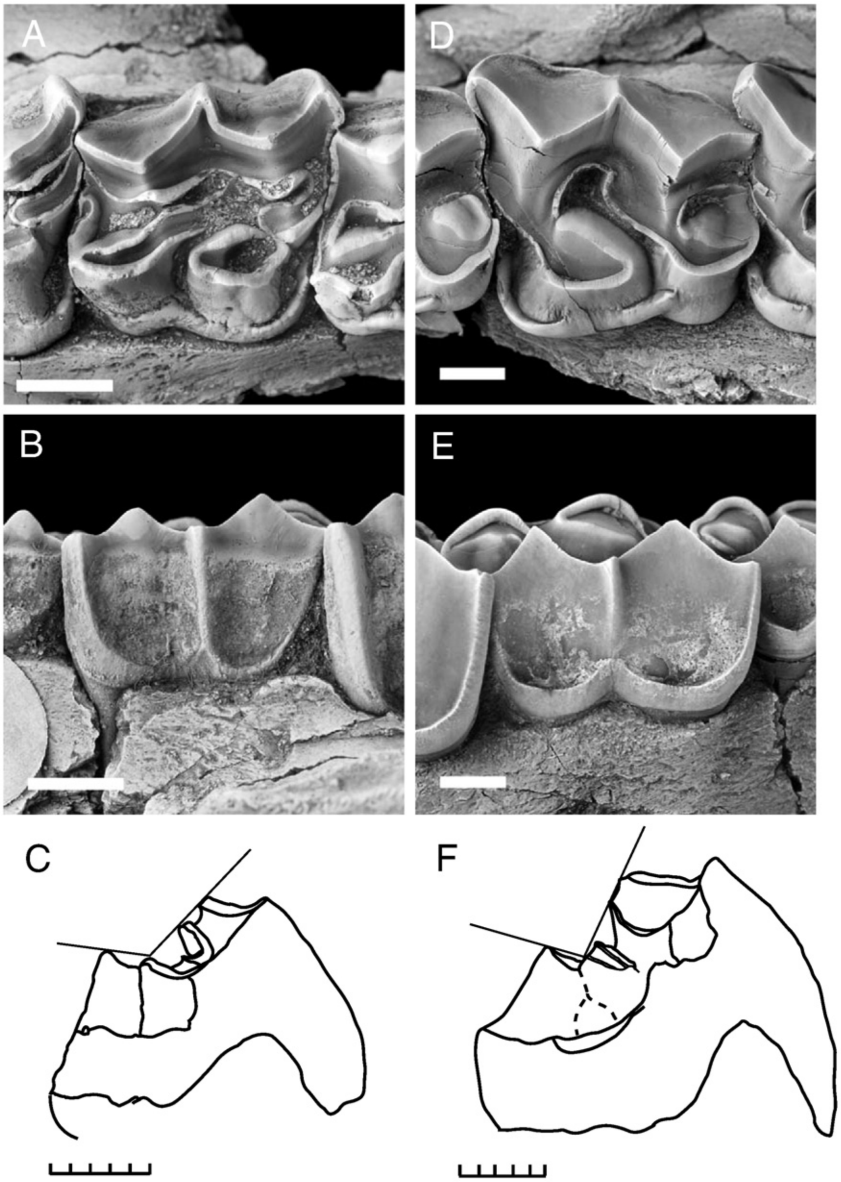

Fig. 3. General morphology of *Plagiolophus minor* (A) occlusal view, BMNH.28231 G240, right M^2; (B) buccal view, BMNH. 28231 G240, right M^2; (C) mesial view, BMNH.27182, right M^2; *Palaeotherium medium* (D) occlusal view, BMNH.27352, left M^2; (E) buccal view, BMNH. 27352, left M^2; (F) mesial view, BMNH.28236 G803, right M^2. Crown cementum is present in the central valley and buccal wall of *Plagiolophus*. The lines on (C) and (F) show the angle between the buccal and lingual phase wear facets; *Plagiolophus* has a greater angle than *Palaeotherium*. Scale bar measures 5 mm.

Quantitative analysis was carried out using Microware 4.02 software (Ungar, 2002). This software was used to mark manually the position and dimensions of the microwear features on an overlay of the digital SEM image. An image taken at a magnification 250× was used and an area of 0.01377 mm^2 (640 × 480 pixels) was selected from the centre of the image. A pit is defined as having a length to breadth ratio which is less than 4:1, a scratch has a length to breadth ratio of greater than 4:1. The mean and standard deviation of the following variables were recorded automatically; feature major axis length, feature minor axis length, feature preferred orientation, feature major/minor axis ratios, feature vector length, feature tally, pit length, pit width, pit tally, scratch length, scratch breadth, scratch orientation, scratch vector length, and scratch tally. The term striation as used in Microware 4.02 software is replaced by scratch throughout text.

A qualitative assessment of the microwear was made by determining the dominant features present (small pits/large pits, fine/coarse scratches, parallel scratches/isolated scratches). The shape of the edge of the wear facet was also described (round/sharp). Although this feature is more closely related to mesowear it is described at this stage as it is seen best at the magnification used to view microwear.

4. Results

4.1. General morphology

Palaeotherium medium is a larger animal than *Plagiolophus minor*, *P. medium* is the size of a immature Brazilian tapir (*Tapirus terrestris*) and *P. minor* is the size of a roe deer (*Capreolus capreolus*). The general morphology of the teeth is illustrated in Fig. 3. The shape of the jaw is similar in both species; both have the rounded incisor row and mandibular symphysis typical of browsers (Janis, 1995); *Palaeotherium* has a shorter diastema than *Plagiolophus*. The diastema separates two functional areas: food acquisition using the anterior dentition and mastication using the cheek teeth. It also acts to lengthen the face and positions the incisors, which gather food, further from the eyes which aids in focussing on the food (Greaves, 1978; Janis, 1995).

The teeth of *Plagiolophus* and *Palaeotherium* have been described as being selenolophodont (Fig. 3A, D). Late Eocene *Palaeotherium* species have molariform premolars. The general shape of the upper molars of both genera gradually changes with increasing age. At very early wear stages the occlusal surface slopes slightly towards the lingual edge. As the tooth progresses towards an intermediate wear stage a steeply dipping buccal edge develops, which flattens slightly on the lingual edge (Fig. 3C, E). The occlusal surface is almost flat in the later wear stages. The flattening with age is more pronounced in *Plagiolophus* since this species has a smaller relative difference in height between the steep buccal cusps and flat lingual cusps than is found in *Palaeotherium*. *Palaeotherium* maintains a smaller angle between buccal and lingual phases. This is made possible by thinner enamel in the centre of the upper cheek teeth including on the small paraconule and on the lingual side of the lower cheek teeth, thereby increasing the wear in the central basin of the upper cheek teeth (Fig. 3A, C, D, F). This is a modification from the equal thickness enamel, which is the primitive palaeothere condition retained by *Plagiolophus*. Crown cementum is found in *Plagiolophus* where it fills the central valley (Fig. 3A) and covers the buccal wall (Fig. 3B). There is no crown cementum present on the teeth of *Palaeotherium* (Fig. 3D–E). Cementum strengthens teeth (Lucas, 2004) infilling the deep valleys between the enamel. Although *Plagiolophus* is lower crowned than most modern mammals with crown cementum, its shallow occlusal angle has allowed a biting surface to develop, probably with higher occlusal pressure (see Fortelius, 1982). One difference between the two genera is at the junction between the enamel and dentine on the early buccal wear facets. The enamel–dentine junction in *Palaeotherium* is relatively smooth, but in *Plagiolophus* it forms a step, with the dentine wearing away before the enamel at the same height. This can be seen clearly in the SEM images (Fig. 4) and also by direct observation of the tooth (Fig. 3A, D).

4.2. Wear facet formation

4.2.1. Variation in wear facets with successive wear stage

Plagiolophus and *Palaeotherium* both show very similar patterns of wear facet formation (Figs. 5 and 6). They have steep early buccal phase wear facets creating a shearing outer blade of enamel on the ectoloph of the upper molars. As the tooth is worn, the inner band of ectoloph enamel disappears where the dentine of the paracone and metacone merges with that of the protoloph and metaloph respectively. This occurs at an earlier wear stage in *Palaeotherium* than in *Plagiolophus*, thereby reducing the area of enamel that bears early buccal phase wear facets at each successive wear stage (Figs. 5 and 6). This reduction is enhanced in *Palaeotherium* because of their thin inner enamel.

Both species show considerable lingual phase wear. The quantity of this wear phase increases with age in both genera. This occurs because, when unworn, the lingual side of the tooth (the hypocone and protocone) takes the form of two cones. As the tooth is worn down the cone is truncated and the area of enamel exposed on the surface increases. The quantity of late buccal phase wear reaches a maximum at the intermediate wear stage where lingual phase wear takes over as the dominant wear stage on the lingual side of the tooth. This is probably related to the flattening of the occlusal surface in this area.

4.2.2. Wear facets in the intermediate wear stage and comparison with recent ungulates

The intermediate wear stage (Figs. 5C–E and 6B–E) is the stage which is used in the wear facet studies of Janis (1990) and is therefore

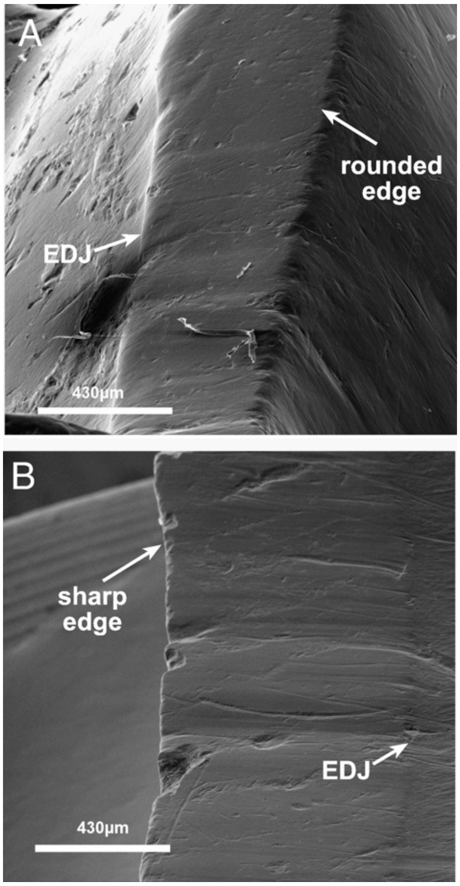

Fig. 4. SEM image (taken at 70× magnification) of the outer enamel band of the preparacrista of (A) *Plagiolophus minor* (BMNH.28232 G339, right M^2); (B) *Palaeotherium medium* (BMNH.27355, right M^2), showing the form of the enamel–dentine junction (EDJ) and buccal facet edge.

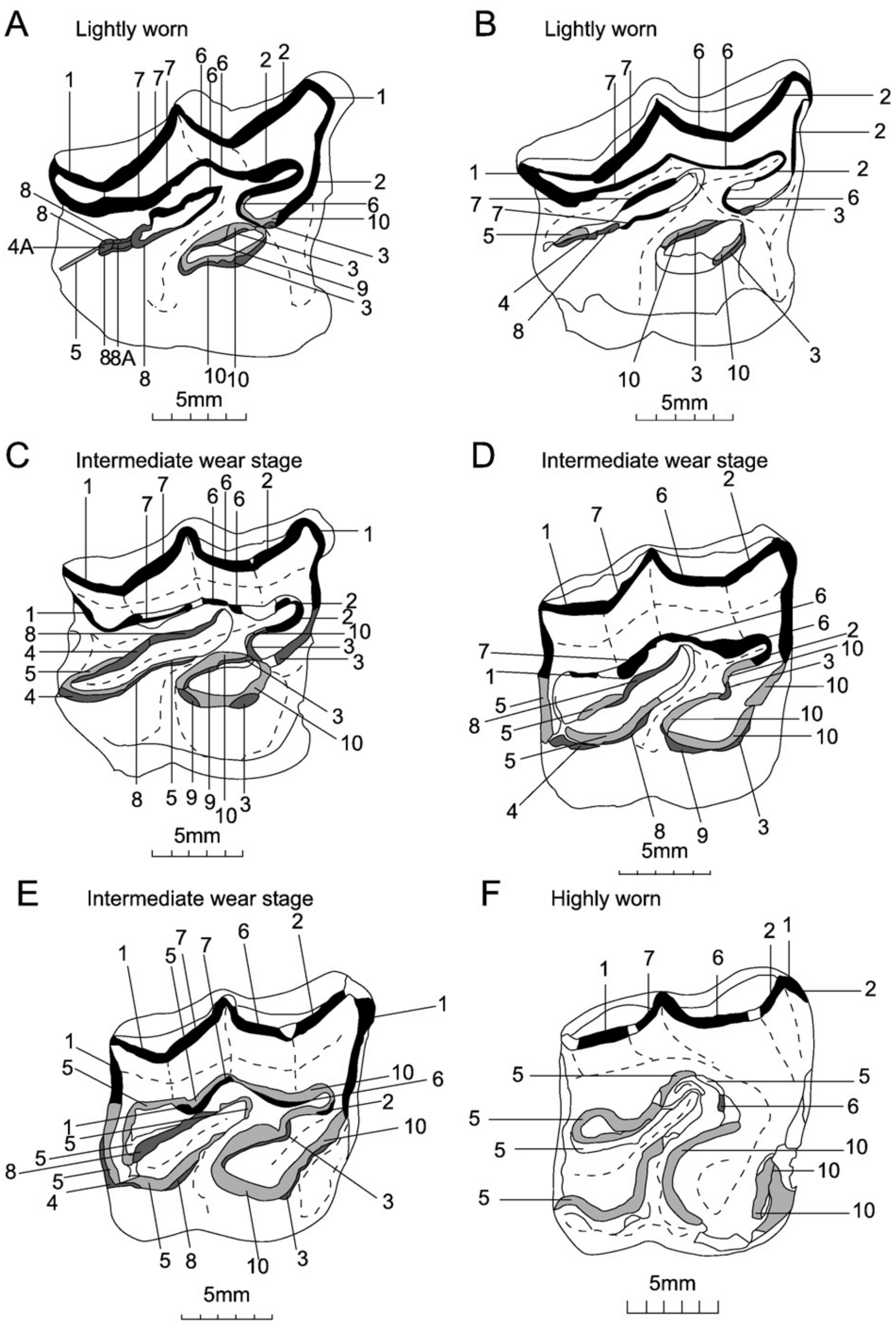

Fig. 5. Distribution of different types of wear facets (only enamel labelled) in occlusal view at different wear stages for *Plagiolophus minor* shown as right. (A) BMNH.28232 G339, left M^2 (reversed); (B) BMNH.28157, right M^2; (C) BMNH.28231 G240, right M^2; (D) BMNH.27178, left M^2 (reversed); (E) BMNH.28232 G287, left M^2 (reversed); (F) BMNH.28232 G332, left M^2 (reversed); for explanation of facets see Fig. 1B.

used here for comparisons between the two fossil species and with dietary categories based on recent ungulates with known diets. The dominant wear type in both genera is shearing, the majority of which takes place during early buccal phase. There is a high proportion of early buccal phase wear which is associated in modern ungulates with the division of tough, fibrous, flat material such as leaves (Shearing wear is necessary for cutting though the leaves to break them into small pieces.). However this is a smaller proportion than is typical of grazers, suggesting that their diet consisted of broad leaves.

Both genera show very little late buccal phase wear, created on the lingual side of the tooth, although there is more of this wear stage in *Plagiolophus* than in *Palaeotherium*. This phase is reduced when the diet consists of fibrous foods (e.g. broad leaves, grass blades), in which case early buccal phase wear becomes dominant (Janis, 1990). Therefore a high proportion of late buccal phase wear is associated with eating soft foods such as fleshy fruit or fungi. Very little late buccal phase wear suggests that there were a significant proportion of leaves in the diet of both species. The higher proportion of early than late buccal phase in *Palaeotherium* suggests a slightly more fibrous diet than *Plagiolophus*.

Both genera also exhibit a substantial lingual phase wear. *Plagiolophus* has more than *Palaeotherium*, but the proportions vary within this wear stage. Lingual phase wear is produced by a grinding action (as the teeth move out of occlusion) and is prominent when the diet includes fruit and is reduced when the diet consists solely of leaves (Janis, 1990). The lingual phase wear facets are less clearly defined than those produced by buccal phase wear, suggesting that more abrasion occurred in lingual phase than in buccal phase where

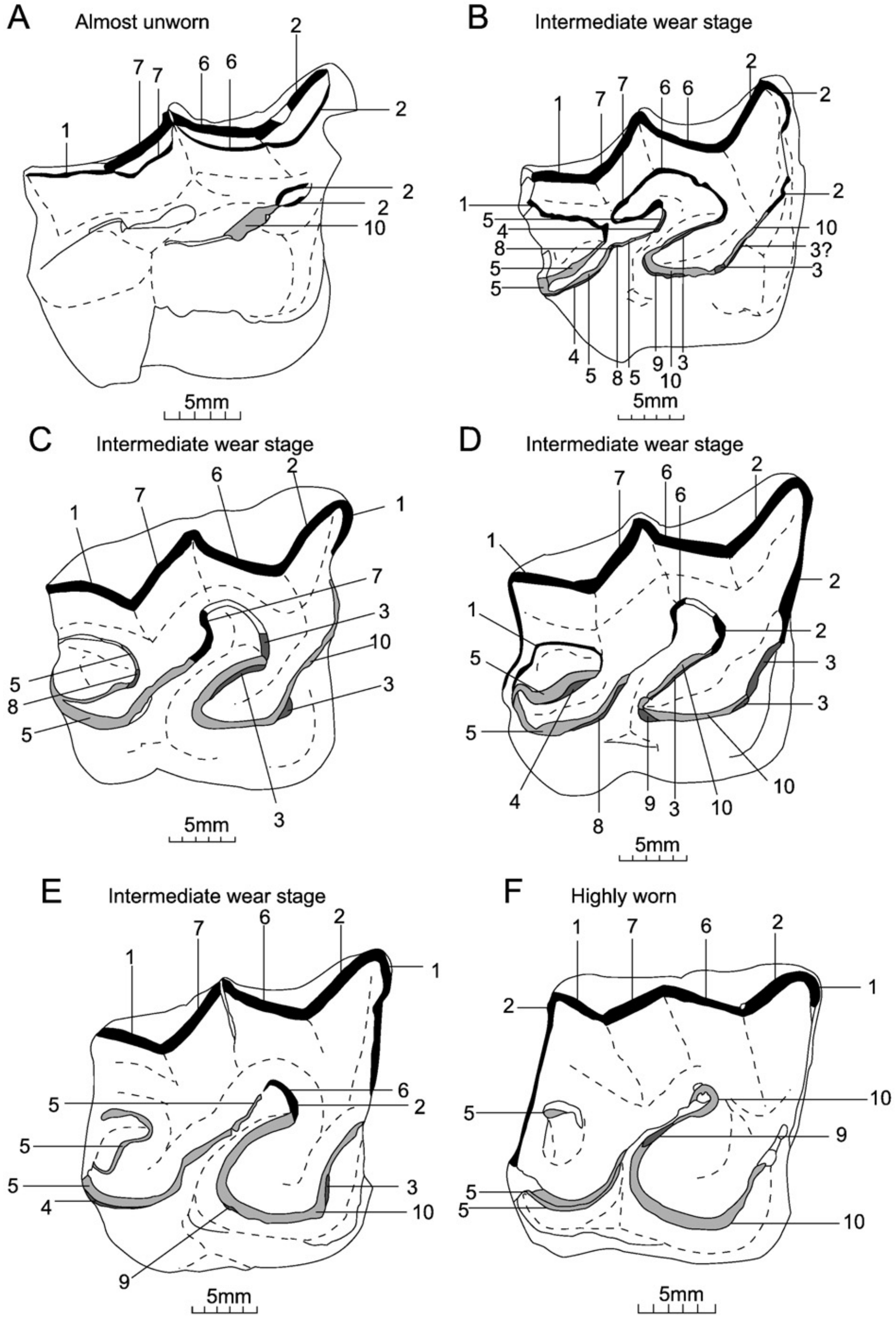

Fig. 6. Distribution of different types of wear facets (only enamel labelled) in occlusal view at different wear stages for *Palaeotherium medium* shown as right. (A) BMNH.27360, right M^2; (B) BMNH.28237 G1000, right M^2; (C) BMNH.27352, left M^2 (reversed); (D) BMNH.28354, right M^2; (E) BMNH.28236e G798, right M^2; (F) BMNH.28237 G927, right M^1; for explanation of facets see Fig. 1B.

attrition dominated. According to Janis (1990) grazers and regular browsers have a very small proportion of lingual phase wear and there is a greater proportion in high-level browsers (e.g. okapi, giraffe, tapirs), mixed feeders and frugivores. The lingual phase wear suggests that some fruit was included in the diet of both species, but that it was more important in the diet of *Plagiolophus*.

Rhinoceroses have a fairly similar tooth morphology to the palaeotheres, although the π-shaped pattern of lophs lacks the w-shape of the ectolophs. The wear facets occur in similar positions (Butler, 1952), with the sloping early buccal phase facets on the ectoloph and the small areas of late buccal phase and lingual phase wear extending across the protoloph and metaloph. This pattern occurs in the browsing rhinoceroses but not in the short-grass grazer, *Ceratotherium simum* (white rhinoceros). Hyraxes have a loph pattern very similar to that of palaeotheres and the browser *Dendrohyrax* and the mixed feeder *Heterohyrax* also show similar distributions of facets (Janis, 1979, 1990). The grazer *Procavia* has very little lingual or late buccal phase wear which is unlike *Plagiolophus* or *Palaeotherium*.

Very little tip wear is found on the teeth of *Plagiolophus* and *Palaeotherium* (too little to be marked in figures). Tip wear is caused when soft food is pulped or hard, brittle food is shattered, e.g. fruits, buds, seeds and nuts (Janis, 1990).

4.3. Mesowear analysis

Occlusal relief and cusp shape data for *Plagiolophus* and *Palaeotherium* (Appendix Table 2) are summarized in Table 1. Both genera show high relief and sharp to rounded cusps. On the few

Table 1
Statistical tests applied to mesowear data

Species	*N*	Occlusal relief (mean quantitative index (DV/*L*))	Occlusal relief (SD of quantitative index (DV/*L*))	Cusp relief (% high-% low)	Cusp shape (% sharp-round-blunt)
Plagiolophus minor	37	0.13	0.03	88.2–11.8	58.8–41.2–0
Palaeotherium medium	17	0.12	0.02	91.9–8.1	45.9–54.1–0
Statistical test		Student's *t* test $t=0.673$ $p=0.504$ $DF=52$		Chi^2 test Chi^2=3.389 $p=0.0656$ $DF=1$	Chi^2 test Chi^2=0.889 $p=0.346$ $DF=1$

occasions that the relief is classified as low according to the quantitative index, it is found to be very close to the border between high and low relief. If a different cut off for low occlusal index (e.g. 0.05) were used there would be no significant change in the results. Neither species shows any incidence of blunt cusps (Fig. 7). This indicates that the diet does not include any highly abrasive material (e.g. phytolith rich grass). The high occlusal relief also suggests that the diet was not very abrasive. The Student's *t* test and the chi squared test were applied to test the significance of these distributions. There is no statistically significant difference in occlusal relief index, percentage cusp relief or cusp shape between the two species (Table 1). This suggests that both genera had diets consisting of material with very similar properties. Both genera fit into the range of browsers (leaf or fruit diet) or mixed feeders (consume a mixture of browse and graze) established by Fortelius and Solounias (2000) based on extant ungulates.

None of the rhinoceroses show similar patterns of mesowear to *Plagiolophus* (88.2% high, 58.8% sharp, 42.2% round) and *Palaeotherium* (91.9% high, 45.8% sharp, 54.1% round). Data from Fortelius and Solounias (2000) show that the browsing rhinoceroses have 100% high cusps, 80–100% sharp cusps and 0–20% round cusps, whilst *Ceratotherium simum* (grazing white rhino) has 100% low cusps, 72% round and 28% blunt cusps. The browsing hyrax *Dendrohyrax* has the most similar mesowear signature with 75–100% high cusps and approximately 50% sharp and 50% round (Fortelius and Solounias, 2000; SCJ personal observation).

The hypsodonty index for *Palaeotherium medium* is 1.33 and for *Plagiolophus minor* is 1.50 (Appendix Table 4). Both genera are brachydont. When the hypsodonty index is plotted against percentage of high cusp relief, and percentage of sharp, round and blunt cusps (see Table 1) respectively, *Plagiolophus* and *Palaeotherium* fall neatly within the range of browsers based on the classifications for recent ungulates (Fortelius and Solounias, 2000, figs. 6 and 7). Although the range for mixed feeders overlaps with browsers, *Plagiolophus* and *Palaeotherium* consistently plot just outside the overlap. Rivals and Semprebon (2006, fig. 3) introduced a separate classification for fruit browsers based on mesowear scores and hypsodonty index but again *Plagiolophus* and *Palaeotherium* fit into the browser range and do not to have a high enough proportion of rounded cusps to be considered fruit browsers.

4.4. Microwear

The quantitative microwear data for *Plagiolophus* and *Palaeotherium* are listed in Appendix Tables 3A and B. *Palaeotherium* has a greater mean number of microwear features than *Plagiolophus* (Table 2); *Palaeotherium* also has a greater mean number of pits and scratches than *Plagiolophus*. There is a statistically significant difference (Table 2) between the mean number of pits for *Plagiolophus* and *Palaeotherium* (Student's *t* test, $t=3.087$, $DF=41$, $p=0.00361$) as well as between the mean number of scratches (Student's *t* test, $t=3.529$, $DF=41$, $p=0.00105$).

Fig. 8 shows the number of pits plotted against the number of scratches for both species. The ranges for the two species overlap and the specimens are fairly evenly distributed within their groups. The exceptions are two specimens of *Palaeotherium medium* which have particularly high pit numbers (BMNH.28236 G805 and BMNH.28236 G815 both with 126 pits). The specimens of *Palaeotherium* show greater numbers of microwear features than *Plagiolophus*. With a single exception (BMNH.27355, 11 scratches and 18 pits) specimens of *Palaeotherium* have 40 to 246 scratches and 32 to 126 pits. Specimens of *Plagiolophus* have 1 to 157 scratches and 1 to 87 pits. This indicates that *Palaeotherium* included a type of food in its diet which is more likely to cause microwear features than the food eaten by *Plagiolophus*. The overlap in the range suggests an overlap in the properties of the material that they ate and consequently that they shared at least part of the same diet. The presence of a large number of microwear features, particularly scratches, in *Plagiolophus* and *Palaeotherium* is an indicator of the consumption of a large amount of abrasive material.

None of the other microwear variables measured show statistically significant differences in the means. This indicates that the average microwear textures (shapes and sizes of scratches and pits) and the orientations of the microwear are similar for the two species at this scale. The high values for the standard deviations of many of the variables indicate the large degree of variation in microwear within the sample.

The frequency of the number of scratches for each individual was plotted in a histogram (Fig. 9). The distribution for each taxon does not plot into the two completely separate bimodal peaks which are characteristic of a seasonal regional mixed feeder (mixed feeder which varies its diet between the seasons) (see raw scratch distributions in Solounias and Semprebon, 2002; Semprebon et al., 2004). This does not, however, remove the possibility that *Plagiolophus* and *Palaeotherium* are meal by meal mixed feeders (vary diet on a meal by meal basis) (Solounias and Semprebon, 2002).

There is considerable variation in the microwear of both species, with each species showing a range of microwear patterns (Fig. 10). In general the microwear of the two species is very similar (as can be seen in the absence of significant differences between the two taxa for quantitative measurement of the texture). Both species show coarse to fine unidirectional scratches (Figs. 4 and 10A–B, D–E). The scratches are orientated approximately perpendicular to the buccal edge of the enamel band in a bucco-lingual direction. There are many small pits (<10 μm) and a few larger pits. Enamel prisms are visible in both

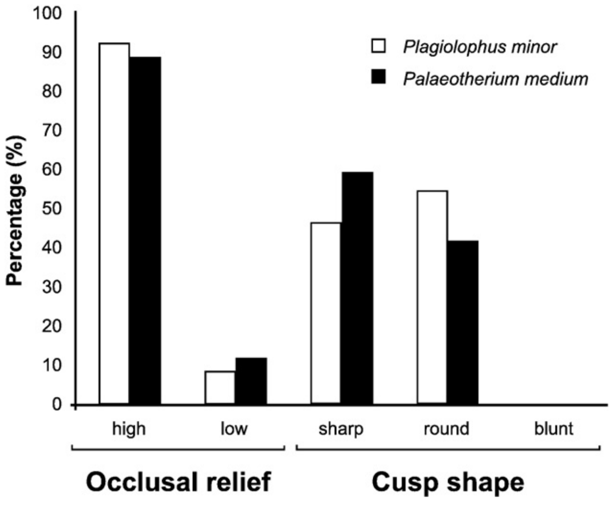

Fig. 7. Histograms showing the percentage of high and low occlusal relief and of each type of cusp shape for *Plagiolophus minor* and *Palaeotherium medium*. Both species show similar percentages of each variable in the range typical of browsers.

Table 2
Microwear results summary

Species	*N*	No. of features		No. of pits		Range of pits	No. of scratches		Range of scratches	Percentage pits
		Mean	SD	Mean	SD		Mean	SD		
Palaeotherium medium	19	180.16	71.31	60.84	28.19	11–246	119.32	61.33	18–126	36.8%
Plagiolophus minor	24	100.75	55.31	35.71	25.12	1–87	65.04	39.10	1–157	37.3%
Student's *t* test		*t*=4.115 *p*=0.00018 *DF*=41		*t*=3.087 *p*=0.00361 *DF*=41			*t*=3.529 *p*=0.00105 *DF*=41			

species showing evidence that the surface was polished, a feature of attritional wear. Although the wear facets are considerably scratched, the polished surface is a result of attrition (Walker et al., 1978). This is characteristic of leaf browsers and is produced as the teeth are in contact with small amounts of flat food between the shearing planes. This action also produces tiny pits because of prism plucking (Walker, 1984; Schubert et al., 2006). *Plagiolophus* shows more polishing than *Palaeotherium* (compare Fig. 10C and F). The wear facets of *Palaeotherium* (Fig. 4B) are more uniformly covered in microwear features than those of *Plagiolophus* (Fig. 4A). In *Plagiolophus* the edges of the facets are often rounded and slightly chipped (Fig. 4A) whereas in *Palaeotherium* the facet edges are sharper and heavily chipped (Fig. 4B).

5. Discussion

5.1. Variation within species

The different types of dental wear studied within the fossil species *Plagiolophus minor* and *Palaeotherium medium* exhibit different ranges of variation. The variation in wear facet formation (Figs. 5 and 6) is a product of varying wear stages. For specimens of approximately the same age the pattern of wear facet formation is stable and facets form to the same degree in the same places. The two mesowear variables show different degrees of variation. There is little variation in cusp height within each species (Fig. 7; Table 1) with approximately 90% high cusps in both species; however, cusp shape varies between sharp to round in a continuous spectrum and no individuals have blunt cusps. There is considerable variation in the microwear, from specimens with barely any features (Fig. 10C, F) to very highly scarred surfaces (Fig. 10A–B, D–E). The relative proportion of pits to scratches also varies (pit percentage) and most of the facet surfaces have very different appearances.

These results are not surprising given the timescale of formation of each of the scales of wear. Wear facets and mesowear are formed over the lifetime of the animal and are cumulative. Therefore they reflect a long period of wear and will average out the effect of different types of food eaten (assuming that there is some variation in the diet). Microwear on the other hand is formed on a short timescale and reflects the diet of an animal immediately before it died. This will be different for different animals and hence there is a large degree of variation between individuals of comparable age. Therefore microwear studies require a larger sample size to assess the pattern of the microwear of any species than is necessary for a mesowear or wear facet proportion study. The assessment of variation has therefore demonstrated that the variation in wear facets and mesowear is minimal and any differences between fossil assemblages have dietary significance. For microwear, substantial assemblages are needed to account for individual variation and to infer a dietary distinction.

5.2. Dietary classification of Plagiolophus and Palaeotherium

The data gathered from each category of dental wear are used to assess the diet of *Plagiolophus* and *Palaeotherium*. This is accomplished either by determining the probable food type which caused the wear or by comparing what is observed in the fossil species with the signatures of wear from living ungulates with known diets.

The proportions of each type of wear facet are similar in both *Plagiolophus* and *Palaeotherium*. Early buccal phase dominates, followed by lingual phase, with a very small proportion of late buccal phase and little or no crushing tip wear. However, neither fit closely into any one of the previously defined dietary categories (Janis, 1990). Despite this, there are similarities with various types of browsers and mixed feeders. High level browsers, defined by Janis (1990) as those that take leaves from above the ground e.g. *Okapia johnstoni* (okapi) and *Giraffa camelopardalis* (giraffe), display little or no late buccal

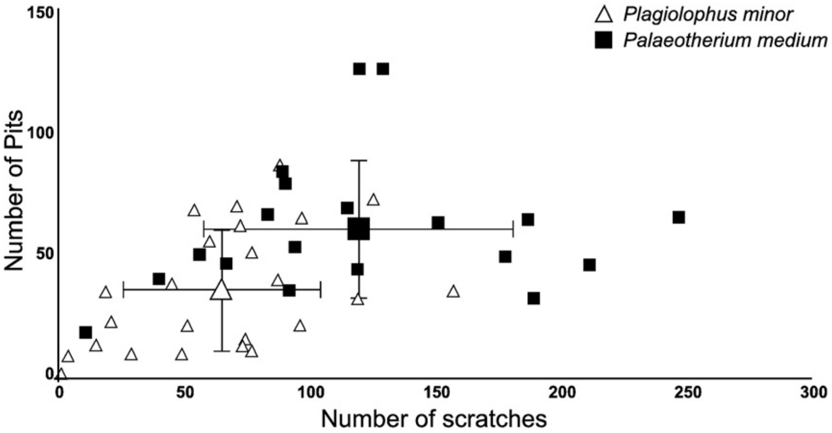

Fig. 8. Graph of number of pits against number of scratches for *Plagiolophus minor* (white triangles) and *Palaeotherium medium* (black squares). Large symbols show mean values with error bars. *Palaeotherium* shows a tendency towards more scratches and more pits than *Plagiolophus*.

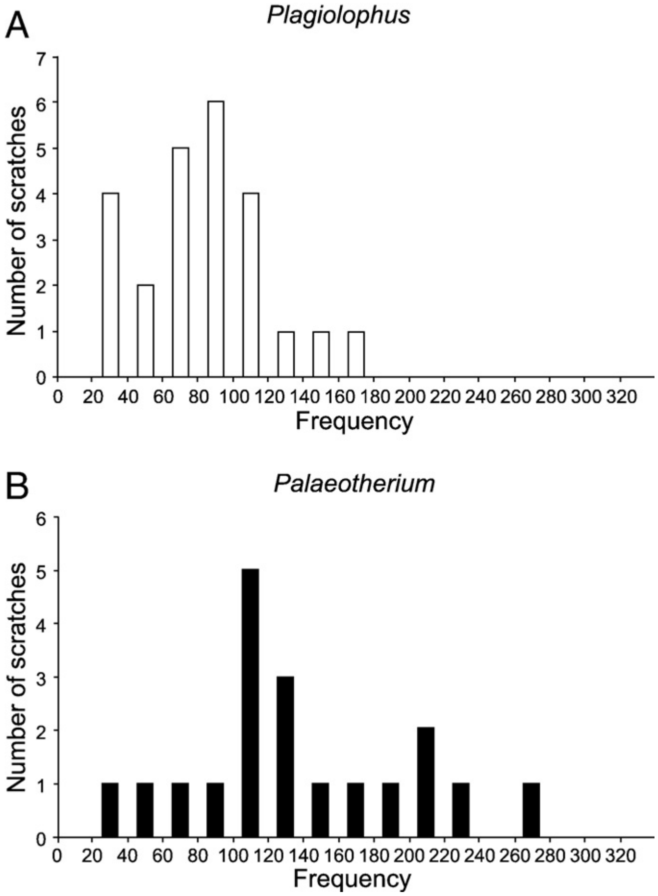

Fig. 9. Histograms showing the frequency distribution of the number of scratches per individual for (A) *Plagiolophus minor* and (B) *Palaeotherium medium*. Both show a unimodal distribution, indicating that neither species is a seasonal regional mixed feeder (Solounias and Semprebon, 2002).

phase wear. In contrast, other high browsers, such as tapirs (*Tapirus* spp.), have very different bilophodont teeth with substantial late buccal phase (Butler, 1952, fig. 14). Mixed feeders show some late buccal phase, whilst grazers show none. Most regular leaf browsers show a much smaller proportion of lingual phase wear than the palaeotheres. However, browsing rhinoceroses, the hyraxes *Dendrohyrax* (a browser) and *Heterohyrax* (a mixed feeder) show similar patterns of wear to *Plagiolophus* and *Palaeotherium*. These modern taxa are also the mammals whose molar gross morphology is closest to palaeotheres. The percentage of lingual phase in *Plagiolophus* and *Palaeotherium* is also similar to that in many fruit browsers, but in the latter it is accompanied by a large quantity of tip wear (Janis, 1990). Tip wear is almost entirely absent in *Plagiolophus* and *Palaeotherium*. This suggests that although lingual phase wear is an indication of fruit eating, it may also be significant when other food types such as broad leaves dominate the diet. This is particularly true of *Dendrohyrax*, which is a leaf browser, with less than 10% intake of fruit (Janis, 1990). The proportions of the different wear phases therefore categorise *Plagiolophus* and *Palaeotherium* as leaf browsers, which ate a small proportion of fruit.

The mesowear, including hypsodonty data, places *Plagiolophus* and *Palaeotherium* within the range of leaf browsers, which suggests that fruit was not a major component of their diet. It is possible that the small proportion of fruit suggested by the wear facet evidence is not registered by the mesowear analysis because this method only takes account of the buccal cusps. Nevertheless, the minimal amount of tip wear associated with rounded cusps in some individuals could be evidence of minor frugivory.

Interpreting the microwear is more complex. The polishing of the wear facets and the presence of small pits are characteristic of leaf browsers and it is possible that the coarse scratches and large pits are the result of eating hard fruits and seeds. There are various abrasives in the diet of ungulates, which are capable of causing microwear features. Silica phytoliths, which constitute one such abrasive (Walker et al., 1978), are found in the leaves of most plants, but are most abundant in grasses. Soil or grit particles, which stick to the food and are then consumed, can be abundant in food sourced from the ground and are a significant component of the diet of low level grazers (Mainland, 2003) or suids which root in the ground (Solounias and Semprebon, 2002). Grit is also found in large proportions in diets of animals from open, arid environments where it causes intensive pitting of the enamel (Merceron et al., 2005). Hard vegetable matter, e.g. seeds and nuts, which are eaten as part of a frugivorous diet, or bark or twigs, which are eaten by

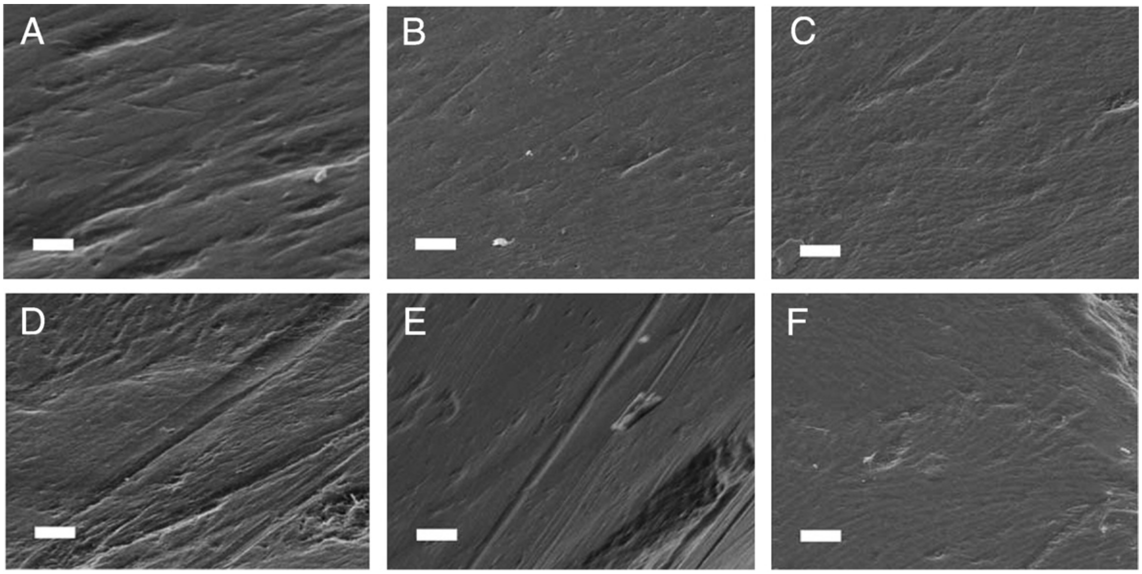

Fig. 10. SEM images (taken at 250× magnification) showing the variety of microwear seen in *Plagiolophus minor* (A) BMNH.G278, left M^2; (B) BMNH.28231 G240, right M^2; (C) BMNH.28232 G339, right M^2; and *Palaeotherium medium* (D) BMNH.28236 G810, right M^2; (E) BMNH.27352, left M^2; (F) BMNH.27360, right M^2. Scale bar 12 μm.

elephants (Solounias and Semprebon, 2002), are also potential abrasives.

Grit is more likely to be ingested when the plant source is closer to the ground (Mainland, 2003), for example during short-grass grazing or eating fallen fruit. *Plagiolophus* and *Palaeotherium* have fairly long necks, which led Franzen (1989) to interpret them as high browsers. The environment of La Débruge was woodland and therefore not open or arid (Hooker, 1992). Therefore grit is unlikely to be have been a significant factor in the production of microwear features in the study taxa.

The mode of comminution of the abrasive material is responsible for the form that the microwear takes. Grazers which shear grass with a transverse motion show many scratches as a result of the abrasive silica phytoliths consumed, (e.g. *Bison bison* (American bison) Solounias and Moelleken, 1992; Solounias and Semprebon, 2002). The number of scratches in *Plagiolophus* and *Palaeotherium* is not high enough for either to be a grazer. However, coarse scratches are not usually found in taxa eating almost entirely leaves. The microwear might therefore be interpreted to represent a mixed feeding diet with a component of graze and browse to explain the high scratch numbers and high numbers of small pits. However, a mixed feeding diet is not consistent with the wear facet or mesowear evidence.

Comparing the data from this study with microwear images from other studies, taken at comparable magnifications (Solounias et al., 2000; Rivals and Deniaux, 2003), fruit browsers (browsers which include a significant proportion of fruit in their diet) have either approximately equal numbers of pits and scratches or more scratches than pits. In *Plagiolophus* and *Palaeotherium* there are more scratches than pits, suggesting that they are fruit browsers. However, fruit browsers show a higher number of large pits because they process hard, brittle food such as nuts and seeds by crushing (e.g. *Tapirus bairdii* (Baird's Tapir), *Cephalophus* spp. (duiker), Solounias and Moelleken, 1992; Solounias and Semprebon, 2002). They also have more scratches than pure leaf browsers. If the scratches in *Plagiolophus* and *Palaeotherium* are produced by seeds within the fruit, frugivory could nevertheless be a minor component of a diet consisting predominantly of leaves.

Taken together, the evidence from wear facet proportions, mesowear and microwear argues for a leaf browsing diet with a small proportion of frugivory for *Plagiolophus* and *Palaeotherium*.

5.3. Dietary differences between Plagiolophus and Palaeotherium

There are a few gross dental differences between *Plagiolophus* and *Palaeotherium*. The smaller angle between buccal and lingual phases in *Palaeotherium* (Fig. 3F) resembles that of browsing rhinos (Fortelius, 1982, p. 169–172). Crown cementum, as seen in *Plagiolophus*, is found in the short-grass grazing white rhinoceros, *Ceratotherium simum*, and is absent in all the browsing rhinoceroses. The browsing black rhino *Diceros bicornis* and the Sumatran rhino *Dicerorhinus sumatrensis* have a flat enamel–dentine junction like *Palaeotherium* whereas the grazing *C. simum* has a stepped, rounded enamel–dentine junction like *Plagiolophus.* These ‘grazer-like’ characteristics of *Plagiolophus* suggest not that it was necessarily a grazer, but that there was higher occlusal pressure in *Plagiolophus* than in *Palaeotherium* (see above, Section 4.1; Fortelius, 1982).

Palaeotherium has less late buccal phase wear than *Plagiolophus*, suggesting that it ate less fruit and more fibrous material such as leaves. *Plagiolophus* on the other hand has more lingual phase wear than *Palaeotherium*, which indicates that it ate more fruit.

The mesowear of both *Plagiolophus* and *Palaeotherium* shows a similar overall pattern indicating similar diets. The mesowear differences between the two species are not statistically significant and therefore show no dietary differentiation. This lack of distinction is consistent with the recognition that mesowear records a more generalized view of the diet than do other parameters.

Microwear shows considerable variation within each species, but although their ranges of microwear variation overlap, the mean values for the numbers of microwear features are significantly different. The larger numbers of pits and scratches found in *Palaeotherium* indicate that the average diet contains more abrasive material than *Plagiolophus*. The source of this abrasive material is uncertain because comparative modern data are not yet available for this particular microwear method. The difference could either be because (i) *Palaeotherium* was living in a more open microhabitat (more grit) than *Plagiolophus*; (ii) was grazing as part of a mixed feeding diet (more phytoliths and grit, feeding closer to the ground); (iii) was consuming a greater proportion of hard seeds; or (iv) was consuming plant material, other than grass, with a silica phytolith component. The lack of low, rounded to blunt cusps and the rounded incisor arcade, however, indicates that the abrasion is minor and is unlikely to be due to grazing or mixed feeding. Grit has been eliminated as a significant abrasive agent on habitat grounds (see above Section 5.2).

The wear facet analysis suggests that *Plagiolophus* ate a greater proportion of fruit than *Palaeotherium.* This counters the idea that, if the abrasion which produced the microwear features is due only to fruits and seeds, *Palaeotherium* ate more of the same type of fruits and seeds to produce the higher number of microwear features. The evidence from general morphology of a higher occlusal pressure in *Plagiolophus* and of the more abrasive microwear in *Palaeotherium* may be a result of slightly different properties of food. Thus, *Plagiolophus* ate more tough food (e.g. mature leaves, tough fruit) which required higher occlusal pressure, but the food was also less abrasive (contained fewer hard particles). *Palaeotherium*, on the other hand ate less tough food (fresh leaves, fleshy fruit), but which must also have been more abrasive (hard seeds within the fruit). However, for both *Palaeotherium* and *Plagiolophus*, leaves were the most important part of the diet.

6. Conclusions

The range of variation in wear facet formation, occlusal relief and cusp shape is low within each species. Therefore smaller sample sizes that may be found in other fossil assemblages could be used for dietary interpretation using mesowear. The large degree of variation within species for microwear data means that sample size needs to be large enough to account for it.

Both *Plagiolophus* and *Palaeotherium* were leaf browsers, which consumed a large proportion of broad leaves and a small proportion of fruit. This is based on: rounded incisor arcade; near-equal proportions of sharp and rounded cusps; high occlusal relief; brachydonty; microwear showing coarse to fine scratches, small pits and attritional polishing; and substantial lingual phase wear.

The stepped ectoloph enamel edges, the large angle between buccal and lingual phase wear directions, the presence of crown cementum and the fewer microwear features for *Plagiolophus* indicate a tougher but less abrasive diet. *Plagiolophus* exhibits more grinding (lingual phase) wear (associated with frugivory) than *Palaeotherium*, which shows more shearing (early buccal phase) wear. Both taxa consumed only a small proportion of fruit, *Plagiolophus* ate more than *Palaeotherium* and the fruit eaten by the latter caused more abrasive wear e.g. from hard seeds.

The results show that *Plagiolophus* and *Palaeotherium* have different diets, which indicates that there may have been a dietary component in the extinction of *Palaeotherium* and the survival of *Plagiolophus* at the Grande Coupure. *Plagiolophus* had the ability to include tougher mature leaves and tougher fruits in its diet. Therefore, *Plagiolophus* might have been better able to adapt to the climatic changes across the Grande Coupure. Our continuing work on species of *Plagiolophus* and *Palaeotherium* (where present) from immediately pre- and post-Grande Coupure sites, will investigate the hypothesis that changing food availability was an important factor in mammalian extinctions across the Eocene–Oligocene transition.

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Appendix

Table 1
Specimens used for wear facet analysis (all specimens held in BMNH)

Species	Specimen number	Tooth
Plagiolophus minor	28232 G339	LM^2
Plagiolophus minor	28157	RM^2
Plagiolophus minor	28231 G240	RM^2
Plagiolophus minor	27178	LM^2
Plagiolophus minor	28232 G287	LM^2
Plagiolophus minor	28232 G332	LM^2
Palaeotherium medium	27360	RM^2
Palaeotherium medium	28237 G1000	RM^2
Palaeotherium medium	27352	LM^2
Palaeotherium medium	28354	RM^2
Palaeotherium medium	28236e G798	RM^2
Palaeotherium medium	28237 G927	RM^1

Table 2
Mesowear analysis data

Species	Specimen number	Tooth	Cusp shape	Vertical cusp height (DV) (mm)	Length of tooth (*L*) (mm)	Quantitative index (DV/*L*)	Occlusal relief
Plagiolophus minor	27142	LM^2	Sharp	7.6	62.0	0.12	High
Plagiolophus minor	27142	RM^1	Sharp	4.6	54.4	0.08	Low
Plagiolophus minor	27143	RM^2	Round	8.0	58.8	0.14	High
Plagiolophus minor	27143	RM^2	Sharp	9.6	62.1	0.15	High
Plagiolophus minor	27149	LM^2	Round	5.9	56.9	0.10	High
Plagiolophus minor	27150	LM^2	Round	7.4	58.3	0.13	High
Plagiolophus minor	27151	LM^2	Round	9.6	63.0	0.15	High
Plagiolophus minor	27154	LM^2	Round	10.3	52.0	0.20	High
Plagiolophus minor	28157	RM^2	Round	8.4	64.7	0.13	High
Plagiolophus minor	27165	LM^2	Round	6.7	50.0	0.13	High
Plagiolophus minor	27167	RM^2	Round	5.9	52.0	0.11	High
Plagiolophus minor	27172	LM^2	Sharp	6.4	59.6	0.11	High
Plagiolophus minor	27178	LM^2	Sharp	9.0	57.7	0.16	High
Plagiolophus minor	27182	LM^3	Sharp	9.4	68.7	0.14	High
Plagiolophus minor	27182	LM^3	Sharp	5.5	58.1	0.09	Low
Plagiolophus minor	27182	RM^2	Round	6.5	65.3	0.10	High
Plagiolophus minor	28232	RM^2	Round	7.3	55.6	0.13	High
Plagiolophus minor	28232	LM^2	Sharp	5.7	57.3	0.10	High
Plagiolophus minor	27232 G349	LM^2	Sharp	7.1	61.4	0.12	High
Plagiolophus minor	28231 G240	RM^2	Sharp	7.0	57.8	0.12	High
Plagiolophus minor	28232 G258	RM^2	Sharp	6.3	60.8	0.10	High
Plagiolophus minor	28232 G284	RM^2	Round	8.8	59.5	0.15	High
Plagiolophus minor	28232 G285	LM^1	Round	7.4	53.0	0.14	High
Plagiolophus minor	28232 G287	LM^2	Round	7.5	62.8	0.12	High
Plagiolophus minor	28232 G294	LM^2	Sharp	10.3	60.5	0.17	High
Plagiolophus minor	28232 G295	RM^2	Round	7.0	52.4	0.13	High
Plagiolophus minor	28232 G317	LM^2	Round	6.0	57.0	0.11	High
Plagiolophus minor	28232 G325	RM^2	Sharp	7.5	51.8	0.14	High
Plagiolophus minor	28232 G327	RM^2	Round	4.4	61.8	0.07	Low
Plagiolophus minor	28232 G335	RM^2	Sharp	6.7	58.4	0.11	High
Plagiolophus minor	28232 G339	RM^2	Sharp	6.8	67.8	0.10	High
Plagiolophus minor	28232 G342	RM^2	Round	8.0	53.3	0.15	High
Plagiolophus minor	28232 G343	RM^2	Sharp	9.2	60.0	0.15	High
Plagiolophus minor	28232 G344	RM^2	Sharp	7.0	57.6	0.12	High
Plagiolophus minor	28232 G354	RM^2	Round	6.9	66.7	0.10	High
Plagiolophus minor	28232B G281	RM^2	Round	12.5	51.2	0.24	High
Plagiolophus minor	28233 G631	RM^1	Round	6.7	55.2	0.12	High
Palaeotherium medium	27351	RM^2	Sharp	9.0	88.9	0.10	High
Palaeotherium medium	27352	LM^2	Sharp	12.2	93.3	0.13	High
Palaeotherium medium	27353	LM^2	Sharp	11.6	83.4	0.14	High
Palaeotherium medium	27354	RM^2	Round	8.1	87.8	0.09	Low
Palaeotherium medium	27355	RM^2	Sharp	11.0	80.6	0.14	High
Palaeotherium medium	27360	RM^1	Round	10.9	86.4	0.13	High
Palaeotherium medium	27361	LM^3	Round	11.3	90.4	0.13	High
Palaeotherium medium	27379	LM^2	Sharp	10.3	84.1	0.12	High
Palaeotherium medium	28236	LM^3	Sharp	14.8	99.3	0.15	High
Palaeotherium medium	28236 G796	LM^1	Sharp	12.5	84.2	0.15	High
Palaeotherium medium	28236 G802	LM^1	Round	9.5	79.0	0.12	High
Palaeotherium medium	28236 G803	RM^2	Sharp	10.2	86.9	0.12	High
Palaeotherium medium	28236 G805	RM^2	Sharp	9.2	83.4	0.11	High
Palaeotherium medium	28236 G810	RM^2	Round	10.3	87.8	0.12	High
Palaeotherium medium	28236 G815	RM^2	Round	11.4	90.2	0.13	High
Palaeotherium medium	28236e G788	RM^2	Sharp	14.6	102.2	0.14	High
Palaeotherium medium	28237 G1000	RM^2	Round	7.4	84.2	0.09	Low

Table 3A
Microwear data for *Plagiolophus minor*

Specimen number	27143	27145	27150	27175	28232 G287	28232 G293	28232 G318	28232 G331	28232 G342	28232 G384	28232b G281	G278	27172
Feature major axis length mean	16.78	8.58	9.63	9.52	15.76	12.78	16.53	13.81	27.69	11.95	27.35	12.81	7.66
Feature major axis length standard deviation	9.78	6.04	10.81	6.78	28.68	9.85	29.32	16.22	36.38	11.40	34.34	11.73	5.10
Feature minor axis length	2.19	2.49	1.90	2.18	1.12	1.26	3.01	1.62	2.11	2.26	4.25	2.57	1.64
Feature minor axis standard deviation	1.60	1.65	1.63	1.62	0.88	1.29	3.80	1.29	1.30	2.20	3.62	1.88	0.93
Feature preferred orientation	1.55	31.50	28.28	161.05	11.03	17.68	49.16	175.19	8.10	23.62	178.81	16.60	3.20
Feature preferred orientation standard deviation	8.61	13.52	19.56	16.73	9.44	10.26	18.08	8.04	23.23	15.71	21.81	13.81	15.82
Feature major/minor axis ratios	10.33	4.41	7.34	5.54	13.80	15.88	6.56	10.18	14.69	9.28	11.02	6.36	5.42
Feature major/minor axis ratios standard deviation	8.23	3.94	9.37	5.01	18.70	15.77	6.34	7.10	14.13	10.79	19.80	7.18	4.10
Feature vector length	0.96	0.89	0.79	0.84	0.95	0.94	0.82	0.96	0.72	0.86	0.75	0.89	0.86
Feature tally	59.00	54.00	141.00	123.00	127.00	192.00	44.00	117.00	38.00	162.00	28.00	134.00	83.00
Pit tally	10.00	35.00	70.00	69.00	40.00	35.00	23.00	21.00	9.00	65.00	13.00	62.00	38.00
Pit length mean	8.43	6.06	5.17	6.56	3.79	7.28	8.45	6.06	8.28	8.07	13.38	8.19	5.10
Pit length standard deviation	5.60	3.36	2.94	4.88	2.04	5.45	7.81	3.28	3.05	4.97	7.86	5.97	2.86
Pit width mean	3.08	2.79	2.31	2.61	1.31	2.69	3.91	2.14	3.32	3.64	4.84	3.13	1.93
Pit width standard deviation	2.15	1.78	1.60	1.97	0.80	2.27	4.51	1.00	1.65	2.72	2.09	2.03	1.06
Striation tally	49.00	19.00	71.00	54.00	87.00	157.00	21.00	96.00	29.00	97.00	15.00	72.00	45.00
Striation length mean	18.49	13.21	14.03	13.30	21.27	14.01	25.38	15.51	33.71	14.55	39.46	16.78	9.82
Striation length standard deviation	9.60	7.15	13.62	7.02	33.26	10.20	40.30	17.40	39.85	13.58	43.39	13.87	5.58
Striation breadth mean	2.01	1.93	1.50	1.62	1.03	0.94	2.03	1.51	1.73	1.34	3.75	2.09	1.40
Striation breadth standard deviation	1.43	1.22	1.58	0.70	0.91	0.59	2.60	1.32	0.92	1.01	4.57	1.60	0.74
Striation orientation mean	1.77	30.96	27.35	161.98	10.87	16.54	52.15	175.20	5.71	23.18	0.82	16.24	4.61
Striation orientation standard deviation	8.43	7.32	18.21	11.97	7.77	9.08	14.75	7.88	25.27	14.16	23.62	9.44	12.99
Striation vector length	0.96	0.97	0.82	0.92	0.96	0.95	0.88	0.96	0.68	0.88	0.71	0.95	0.90

Specimen number	28232 G327	27142	27149	27161	28232 G301	28232 G339	28232 G344	28232 G353	27178	28231 G240	28157	Mean	SD
Feature major axis length mean	29.54	8.70	13.03	19.31	10.51	9.96	11.37	19.21	8.55	7.76	13.23	14.68	6.41
Feature major axis length standard deviation	4.35	8.06	11.41	24.10	13.07	7.52	7.45	23.05	4.45	11.82	18.46	16.65	11.29
Feature minor axis length	8.33	1.86	1.68	1.64	1.73	1.57	1.87	1.92	2.82	1.20	1.58	2.20	0.81
Feature minor axis standard deviation	3.10	1.29	1.85	1.55	1.44	1.20	1.30	1.73	0.95	0.73	1.75	1.82	0.91
Feature preferred orientation	41.99	168.09	21.26	12.04	133.05	30.02	140.74	18.76	10.87	32.95	17.80	54.29	68.22
Feature preferred orientation standard deviation	23.76	20.54	11.38	10.54	10.70	16.62	13.28	12.65	20.84	12.21	7.85	14.97	4.96
Feature major/minor axis ratios	3.70	5.79	12.55	14.93	7.38	10.27	7.08	12.85	3.43	8.52	10.48	9.29	3.77
Feature major/minor axis ratios standard deviation	0.86	5.96	15.30	18.64	8.42	13.75	4.19	10.32	2.47	15.15	10.41	10.03	5.42
Feature vector length	0.71	0.77	0.92	0.93	0.93	0.85	0.90	0.91	0.77	0.91	0.96	0.86	0.08
Feature tally	2.00	115.00	72.00	86.00	198.00	128.00	151.00	88.00	12.00	175.00	89.00	100.15	52.39
Pit tally	1.00	55.00	21.00	13.00	73.00	51.00	32.00	11.00	8.00	87.00	15.00	37.69	22.50
Pit length mean	32.61	5.60	6.27	6.41	5.44	6.39	7.28	9.42	6.39	3.52	10.23	7.29	2.37
Pit length standard deviation	n/a	3.87	4.01	2.84	4.38	4.06	3.47	5.14	1.85	1.94	10.80	4.62	1.89
Pit width mean	10.52	2.21	2.33	2.39	1.97	2.36	2.62	3.97	3.14	1.45	3.19	2.90	0.92
Pit width standard deviation	n/a	1.30	2.35	1.15	1.27	1.34	1.48	2.59	1.00	0.79	2.97	1.97	0.94
Striation tally	1.00	60.00	51.00	73.00	125.00	77.00	119.00	77.00	4.00	88.00	74.00	62.46	40.37
Striation length mean	104.21	11.54	15.81	21.61	13.48	12.33	12.47	20.61	12.86	11.95	13.84	19.19	8.74
Striation length standard deviation	n/a	9.73	12.30	25.47	15.36	8.33	7.85	24.27	5.23	15.48	19.65	19.60	14.14
Striation breadth mean	24.18	1.55	1.41	1.51	1.60	1.05	1.67	1.63	2.18	0.96	1.25	1.76	0.70
Striation breadth standard deviation	n/a	1.20	1.55	1.58	1.52	0.75	1.17	1.36	0.38	0.59	1.16	1.47	1.07
Striation orientation mean	64.41	169.79	21.17	11.51	133.02	29.45	140.57	17.46	6.82	31.15	17.44	40.57	58.61
Striation orientation standard deviation	n/a	18.97	10.62	10.11	9.30	15.38	12.91	11.62	19.12	10.57	7.49	13.15	5.99
Striation vector length	n/a	0.80	0.93	0.94	0.95	0.87	0.90	0.92	0.80	0.93	0.97	0.89	0.10

Table 3B
Microwear data for *Palaeotherium medium*

Specimen number	27353	27355	27360	28236 G785	28236 G790	28236 G802	28236 G805	28236 G810	28236a	28236e G798	28237 G1000
Feature major axis length mean	14.40	23.98	9.87	11.67	14.78	8.38	7.66	12.61	11.54	11.19	16.39
Feature major axis length standard deviation	13.49	35.45	12.70	8.97	20.46	7.56	6.62	13.48	15.65	13.38	20.27
Feature minor axis length	2.14	4.39	1.99	2.27	2.07	1.69	1.70	1.61	2.07	2.03	1.54
Feature minor axis standard deviation	2.46	3.51	4.04	2.52	1.81	1.31	1.33	1.78	1.30	2.45	3.24
Feature preferred orientation	29.95	12.01	176.60	9.30	6.35	25.65	4.95	24.93	0.02	163.88	2.20
Feature preferred orientation standard deviation	15.16	20.10	28.06	19.30	17.55	12.56	13.80	11.76	15.51	17.08	12.14
Feature major/minor axis ratios	10.59	6.99	9.67	8.03	10.68	8.47	5.83	10.56	7.12	7.55	18.76

Table 3B (***continued***)

Specimen number	27353	27355	27360	28236 G785	28236 G790	28236 G802	28236 G805	28236 G810	28236a	28236e G798	28237 G1000
Feature major/minor axis ratios standard deviation	11.09	10.51	19.06	10.75	19.53	17.59	6.57	10.04	9.37	9.05	30.05
Feature vector length	0.87	0.78	0.62	0.80	0.83	0.91	0.89	0.92	0.86	0.84	0.91
Feature tally	127.00	29.00	113.00	184.00	147.00	169.00	255.00	251.00	149.00	106.00	163.00
Pit tally	35.00	18.00	46.00	69.00	53.00	79.00	126.00	64.00	66.00	50.00	44.00
Pit length mean	7.53	10.10	7.12	9.22	7.37	5.89	6.22	6.96	7.55	7.01	6.49
Pit length standard deviation	4.73	4.94	12.02	8.91	5.17	3.01	4.35	6.10	4.64	8.93	7.96
Pit width mean	3.27	4.54	3.23	3.69	2.92	2.32	2.23	2.52	2.78	2.63	2.81
Pit width standard deviation	2.89	2.29	6.05	3.54	1.99	1.22	1.46	2.76	1.43	3.10	5.91
Striation tally	92.00	11.00	67.00	115.00	94.00	90.00	129.00	187.00	83.00	56.00	119.00
Striation length mean	17.02	46.67	11.75	13.13	18.95	10.56	9.06	14.55	14.72	14.92	20.05
Striation length standard deviation	14.78	50.65	12.90	8.72	24.35	9.47	8.03	14.72	20.05	15.52	22.16
Striation breadth mean	1.71	4.14	1.15	1.42	1.60	1.14	1.19	1.30	1.51	1.49	1.07
Striation breadth standard deviation	2.14	5.05	1.00	0.86	1.51	1.14	0.96	1.14	0.83	1.51	0.92
Striation orientation mean	29.95	3.97	175.25	8.43	5.52	25.15	3.77	24.57	1.89	162.41	2.91
Striation orientation standard deviation	12.87	16.78	21.77	19.58	17.24	11.65	12.46	11.46	12.82	14.74	11.09
Striation vector length	0.90	0.84	0.75	0.79	0.83	0.92	0.91	0.92	0.90	0.88	0.93

Specimen number	28237 G927	27351	27352	27354	28237	28236 G796	28236 G808	28236 G815	Mean	SD
Feature major axis length mean	9.58	13.19	11.79	14.23	9.30	11.91	12.17	8.26	12.95	4.52
Feature major axis length standard deviation	7.21	8.96	14.97	12.78	9.80	14.90	10.07	7.43	15.28	8.06
Feature minor axis length	2.03	1.72	1.21	1.36	1.93	1.56	1.42	1.84	2.14	0.78
Feature minor axis standard deviation	1.73	1.27	1.57	0.88	1.53	1.26	0.95	1.16	2.34	0.94
Feature preferred orientation	23.54	15.50	48.21	162.07	21.65	5.99	178.22	13.21	41.44	64.52
Feature preferred orientation standard deviation	18.55	8.48	8.49	9.75	15.86	19.06	8.96	16.66	16.64	4.72
Feature major/minor axis ratios	8.56	10.93	15.38	12.17	7.15	10.49	12.12	5.32	9.48	3.49
Feature major/minor axis ratios standard deviation	12.10	11.24	25.49	10.15	8.38	11.77	14.49	4.81	13.96	6.89
Feature vector length	0.81	0.96	0.96	0.94	0.86	0.80	0.95	0.84	0.84	0.09
Feature tally	80.00	257.00	227.00	221.00	173.00	214.00	312.00	246.00	153.91	64.21
Pit tally	40.00	46.00	49.00	32.00	84.00	63.00	66.00	126.00	59.09	27.98
Pit length mean	6.47	8.01	6.61	6.39	6.43	5.89	6.38	5.90	7.41	1.25
Pit length standard deviation	4.66	5.02	7.49	3.43	4.34	3.13	3.83	3.58	6.43	2.68
Pit width mean	2.90	2.84	2.30	2.04	2.72	2.24	2.16	2.19	2.99	0.67
Pit width standard deviation	2.00	1.60	2.89	1.01	1.72	1.44	1.26	1.13	2.97	1.66
Striation tally	40.00	211.00	178.00	189.00	89.00	151.00	246.00	120.00	94.82	44.87
Striation length mean	12.68	14.32	13.21	15.56	12.01	14.43	13.73	10.73	17.40	10.27
Striation length standard deviation	7.98	9.23	16.17	13.31	12.43	17.01	10.65	9.39	18.31	11.99
Striation breadth mean	1.16	1.48	0.91	1.25	1.19	1.28	1.22	1.47	1.61	0.86
Striation breadth standard deviation	0.74	1.04	0.69	0.80	0.78	1.06	0.73	1.08	1.55	1.22
Striation orientation mean	21.25	14.89	48.13	161.87	21.36	7.08	177.24	12.08	40.35	64.39
Striation orientation standard deviation	16.49	7.27	6.75	7.64	10.93	17.72	7.64	14.67	14.77	3.59
Striation vector length	0.85	0.97	0.97	0.97	0.93	0.83	0.97	0.88	0.87	0.06

Table 4
Hypsodonty index calculations

Species	Specimen Number	Tooth	Height (mm)	Width (mm)	Hypsodonty Index	Hypsodonty classification
Palaeotherium medium	28236 G829	Lower LM3	13	9.8	1.33	Brachyodont
Plagiolophus minor	No number	Lower LM3	11.4	7.6	1.50	Brachyodont

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