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Enamel thickness and the helicoidal wear plane in modern human mandibular molars

Gary T. Schwartz[a, b,*]

[a]*Department of Anthropology, The George Washington University, 2110 G Street, NW, Washington, DC 20052, USA*
[b]*National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA*

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Abstract

Helicoid occlusion has long been recognized as a feature characterizing the human dentition and has been viewed as an important morphological marker in the transition from *Australopithecus* to *Homo*. The hallmark of helicoidal wear is a buccal wear slope in anterior mandibular molars (and a corresponding lingual slope of wear in anterior maxillary molars) reversing to a flat or lingual-oriented one in posterior mandibular molars. If localized increases in enamel thickness are taken as evidence of an adaptation to increased wear resistance, then data on enamel thickness in unworn molars can be used to assess whether the region of greatest wear changes from anterior to posterior in such a way as to provide evidence for the helicoidal wear plane being a structural feature of the orofacial skeleton. Such a hypothesis was supported in a previous study on enamel thickness in modern human maxillary molars. As maxillary and mandibular precisely interdigitate, it is reasonable to expect that a similar pattern of enamel thickness distribution should be present in mandibular molars. To test this, data on the distribution of enamel thickness across functionally relevant regions of the crown were collected on a sample of twenty-nine completely unworn mandibular molars. Results suggest that enamel thickness increases slightly posteriorly but no evidence exists for morphological changes along the mandibular molar series of modern humans to follow a trend towards providing additional tooth material in areas under greater wear in accordance with a helicoidal wear model. This suggests that the patterning of enamel thickness must be viewed in conjunction with other features, such as the biomechanical behaviour of molars during occlusion and axial molar angulation, to ascertain the precise anatomical determinants of this unique feature of the human dentition. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Enamel thickness; Helicoid occlusion; Molar function; Mastication; Gradients

1. Introduction

The performance of dental design in the distribution of masticatory forces in modern humans is related to several morphological aspects of the dentition including the thickness of enamel and the geometry of the enamel cap. The amount of enamel and its distribution over a tooth correspond closely to the functional demands of mastication and dietary preferences. A posterior gradient in enamel thickness in maxillary molars is no doubt related to the presence of increased occlusal loading in that region of the postcanine denti-

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* Tel.: + 1(202)994-4270; fax: + 1(202)994-6097.
E-mail address: garys@gwu.edu (G.T. Schwartz).

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tion, and this has been borne out in recent studies on maxillary molars (e.g. Spears and Macho, 1995). It has also been suggested, however, that data on enamel thickness in unworn maxillary molars can be used to assess whether the region of greatest wear changes from anterior to posterior in such a way as to provide evidence for the helicoidal wear plane being a structural feature of the orofacial skeleton (Macho and Berner, 1993, 1994; Spears and Macho, 1995). The specific goal of this short study was to evaluate whether an analysis of gradient-related changes in enamel thickness of human mandibular molars supports previous claims from studies on maxillary molars; as mandibular and maxillary molars interdigitate, it is reasonable to expect that functional signals derived from studies on the maxillary dentition must hold for the mandibular dentition as well.

The distribution of enamel within a tooth is known to correspond to the functional demands of particular cusps: enamel is thickest on the lingual cusps of maxillary molars and the buccal cusps of mandibular molars. As these are "functional" cusps, thicker enamel translates into greater wear resistance and prolonged life for a tooth (Shillingburg and Grace, 1973; Molnar and Ward, 1977). Other features of molar design also affect the efficacy of redistributing masticatory stresses across teeth. For instance, functional (or supporting) cusps are rounder than non-functional (or guiding) cusps (Kraus et al., 1969; Re et al., 1983; Khera et al., 1990). Overall, the characteristically different morphology of these cusps affects the potential for abrasion and fracture under masticatory loading, especially during lateral and protrusive masticatory movements (Khera et al., 1990). Recent studies on modern humans indicate that not only is enamel distributed within a tooth in a predictable manner but that posterior molars have thicker enamel than their anterior counterparts (Macho and Berner, 1993, 1994; Spears and Macho, 1995) and that this is presumably related to a similarly oriented gradient of bite-force magnitudes (Mansour and Reynick, 1975; Molnar and Ward, 1977; Osborn and Baragar, 1985; Koolstra et al., 1988; Osborn, 1996) due, at least in part, to the anterior tilt of teeth resulting from an accentuated curve of Spee (Spee, 1890; Osborn, 1993).

Gradient-related changes in enamel thickness along the maxillary molar series of modern humans have also been interpreted as evidence for a disparity in masticatory loads between 'functional' (or supporting) and 'non-functional' (or guiding) cusps (Spears and Macho, 1995). A tendency towards increased 'symmetry' in enamel thickness overlying corresponding functional and non-functional portions of the crown can be interpreted as an indication of more equivalent occlusal forces exerted over the cusps. Conversely, increasing 'asymmetry' in enamel thickness between corresponding functional and non-functional regions of the molar may indicate a more strict reliance on either shearing or crushing/grinding as the predominant form of masticatory stress. The finding of increasing 'symmetry' in modern human maxillary molars led Spears and Macho (1995) to the conclusion that masticatory loads exerted over the protocone and paracone become more equal in the posterior molars: 'the distinction between functional and non-functional cusps [in the posterior molars] is less clear than it is in first maxillary molars where the protocone is clearly more prominent' (p. 395). This suggested to them the presence of a functional gradient in modern humans

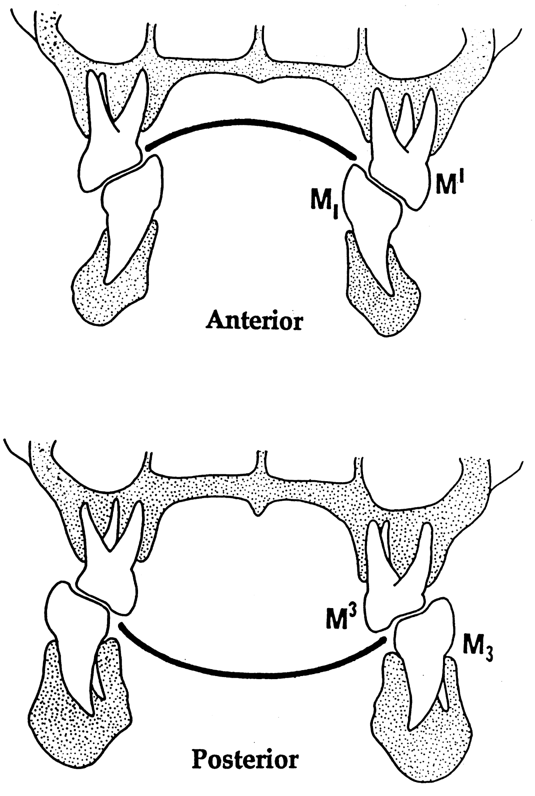

Fig. 1. Changes in the relation of the maxillary and mandibular arches from anterior to posterior such that maxillary arches are wider in the anterior molar region while mandibular arches are wider in the posterior molar region. This arrangement would cause the region of greatest wear to shift along the molar row and has been referred to as the 'arcadal hypothesis' (Campbell, 1925). This spiralling of the wear plane from anterior to posterior characterizes the helicoidal plane of occlusal and can be illustrated by examining the change in an imaginary curve, referred to as the curve of Monson (shown in black), aligned along the left and right dentition in the anterior and posterior molar regions. Adapted from Tobias (1980).

whereby anterior molars perform more shearing and posterior molars perform more crushing and grinding.

It is also likely that the modern human patterning of enamel thickness distribution reflects a more global pattern of wear and occlusion, and that the presence of complicated gradients of enamel thickness both within and among molars predisposes molars to wear in a helicoidal fashion. Although a suite of morphological features is responsible for creating and maintaining helicoid occlusion, data on enamel thickness have been used to provide strong evidence for the predisposition of molars to wear in a helicoidal fashion. Morphological changes along the maxillary molar series of modern humans 'follows a trend towards providing additional tooth material in areas under greater functional demands resulting in a lingual slope of wear anteriorly and a flat or even buccal one posteriorly' (with a corresponding buccal wear slope in anterior mandibular molars reversing to a flat or lingual-oriented one in posterior mandibular molars) providing evidence for the proposal that modern human teeth are adapted to a helicoidal plane of occlusion (Macho and Berner, 1994, p. 327) (Fig. 1). If localized increases in enamel thickness are taken as evidence of an adaptation to increased wear resistance, then data on enamel thickness in unworn molars can be used to assess whether the region of greatest wear changes from anterior to posterior in such a way as to provide evidence for the helicoidal wear plane being a structural feature of the orofacial skeleton; i.e. proportionally thicker enamel over the buccal occlusal slope of mandibular first molars and lingual occlusal slopes of mandibular third molars would therefore suggest a differential reorganization of the enamel cap to accommodate a helicoidal wear plane.

The goals here then were to use data on the distribution of enamel thickness at corresponding functional regions of mandibular molar crowns to: (1) determine if posterior mandibular molars possess thicker enamel at most regions of the tooth crown, as occlusal loads in this region are higher; (2) test if modern human mandibular molars are adapted to accommodate a functional gradient from anterior to posterior, i.e. posterior mandibular molars should possess more equivalent amounts of enamel over corresponding functional areas of the crown than do anterior molars; and (3) evaluate whether the patterning of enamel thickness distribution indicates a predisposition of mandibular molars to wear in a helicoidal manner.

2. Material and methods

The total sample consisted of twenty-nine permanent mandibular molars (M_{1-3}), all of which were from different individuals, derived from the collections of the Department of Oral Biology at the Dental School, Newcastle, UK. For consistency, lefts molars were preferentially chosen over rights, though the sample did include a small number of right molars ($n = 2$; one M_2 and one M_3). The molars were cleaned and then soaked in alcohol. Only one section was taken from each tooth from close to the mesial cusp tips using a Beuhler Isomet$^{\text{TM}}$ diamond wafering-blade saw. Each section was mounted on a microscope slide and then lapped down through a graded series of coarse papers (ensuring that the section plane traversed both cusp tips and dentine horns), rinsed in alcohol, placed in an ultrasonic bath to remove surface debris and polished yielding a final section thickness of 100–120 μm. The resultant thin sections were then mounted in xylene-based DPX$^{\text{TM}}$ mounting medium, photographed and montaged from ×15 images. Four linear measures of enamel thickness were recorded for each specimen (Fig. 2). These measurements include the enamel thickness at the lingual and buccal cusp tips (LCT and BCT, respectively) and the lingual and buccal slopes of the occlusal basin (LOB and BOB, respectively); all measurements have been used in previous studies of enamel thickness in modern great apes, humans and fossil hominids and characterize the linear thickness of enamel at corresponding functional regions of the molar crown (e.g. Macho and Berner, 1993, 1994; Spears and Macho, 1995; Schwartz, 1997).

Comparisons of morphological differences and similarities within or among species that differ in body/

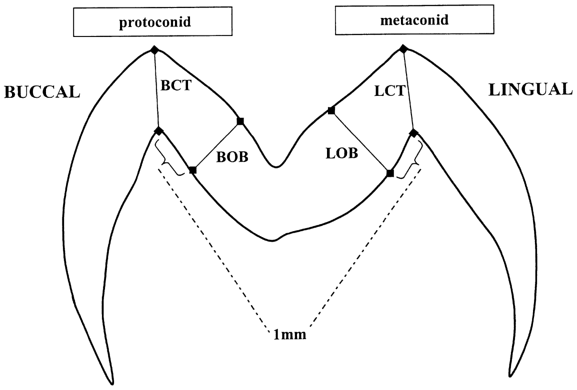

Fig. 2. Schematic diagram of a cross-section through the mesial cusp region of a modern human mandibular molar indicating the four enamel thickness measurements used in this study. Maximum cuspal thicknesses (LCT and BCT) are recorded from the tip of the dentine horn to the tip of the associated cusp at the outer enamel surface. Maximum enamel thicknesses in the occlusal basin (LOB and BOB) are recorded 1 mm from the dentine horn (see Schwartz, 1997).

tooth size require that the data be 'size-corrected' in one way or another; i.e. the linear covariation of the measurement variable with size removed. As all of the specimens in this study belonged to *Homo sapiens*, raw measurements of enamel thickness were used throughout. Even though differences in molar size are evident between individuals and even within an individual (i.e. along the molar row), it is interesting that the results reported here do not change whether enamel thickness measurements were scaled by the area of the enclosed dentine cap (as in Martin, 1983; Grine and Martin, 1988; Dumont, 1995; Shellis et al., 1998), a standardized buccolingual dimension (as in Spears and Macho 1998; Macho and Spears, 1999), or the width of the cervical margin (Schwartz, 1997).

Given the relatively small samples of teeth analysed here, especially when separated by tooth category, the lack of a significant result from parametric tests may be an artefact of non-normality or the result of limited power. To avoid this phenomenon, two non-parametric tests, Kruskal–Wallis and Wilcoxon signed-rank, were used to test for gradient-related changes in each measure of enamel thickness along the molar series and for differences between corresponding functional regions of the crown at each molar position, respectively. It is important to bear in mind that any statistical analysis of small samples has relatively low power and is therefore prone to type II errors (i.e. the acceptance of a false null hypothesis). As a result, greater emphasis is placed on the pattern of differences rather than differences in absolute values of enamel thickness.

Table 1
Descriptive statistics of enamel thickness measurements (mm) of modern human mandibular molars[a]

Measurement	M_1	M_2	M_3	H	*P*
LCT					
Mean	1.77	1.80	1.81	0.202	0.904
SD	0.48	0.32	0.39		
N	9	13	7		
BCT					
Mean	1.98	2.05	2.26	0.942	0.625
SD	0.74	0.49	0.61		
N	9	13	7		
LOB					
Mean	1.53	1.55	1.59	0.083	0.959
SD	0.34	0.31	0.34		
N	9	13	7		
BOB					
Mean	1.91	1.81	1.96	0.742	0.689
SD	0.55	0.44	0.51		
N	9	13	7		

[a] Results of Kruskal–Wallis and probability values are also listed. Abbreviations: LCT, metaconid tip; BCT, protoconid tip; LOB, buccal slope of metaconid; BOB, lingual slope of protoconid.

3. Results

Descriptive statistics of enamel thickness at each region across the molar crown for each molar type are listed in Table 1 along with the results of Kruskal–Wallis tests to establish the presence of significant gradients of enamel thickness towards the posterior molar region. Paired statistical (Wilcoxon signed-rank) tests of enamel thicknesses at corresponding functional regions of the crown are provided in Table 2, and Fig. 3 illustrates the gradient-related changes in mandibular molars at the cusp tips and across the occlusal basin [previously recorded data for maxillary molars from Spears and Macho (1995) are included for comparative purposes].

As expected, functional cusps (i.e. protoconids) possessed thicker enamel than non-functional cusps (i.e. metaconids) across the entire tooth crown at all mandibular molar positions (Table 1). On average, enamel thicknesses at the cusp tips and lingual occlusal basin increased posteriorly, though none of these changes at any position across the crown was statistically significant [Table 1; Fig. 3(a)]. Alternatively, a trend existed whereby the disparity between functional and non-functional regions of the crown became more highly significant posteriorly, especially with regard to the cusp tips [Table 2; see Fig. 3(a)]. This resulted in the disparity between corresponding functional regions (most notably, the cusp tips) of the mandibular molar crown to increase posteriorly; this pattern was in marked contrast to that observed in modern human maxillary molars [see Fig. 3(b)], where differences in enamel thickness at the cusp tips and occlusal basin became progressively less towards M^3.

Table 2
Paired statistical tests of enamel thickness measurements recorded at corresponding regions of functional (protoconid) and non-functional (metaconid) cusps[a]

		LCT/BCT		LOB/BOB	
	Molar	Z	*P*	Z	*P*
H. sapiens	M_1	−1.24	0.214	−2.43	0.015
	M_2	−1.96	0.050	−3.08	0.002
	M_3	−2.37	0.018	−2.20	0.028

[a] Results from Wilcoxon signed-ranked test with probability values are listed. Variable abbreviations are the same as in Table 1.

4. Discussion

Helicoidal occlusion is known to occur in modern human populations as well as early hominids, especially early *Homo* (Campbell, 1925; Ackerman, 1953; Murphy, 1964; Hall, 1976; Tobias, 1980; Osborn, 1982; Richards and Brown, 1986; Smith, 1983, 1986; Spears and Macho, 1995). Helicoidal wear was believed to be caused by the relation between the width of the mandibular and maxillary arches. Wider maxillary arches along the entire molar row would cause the mandibular molars to 'fit inside' that of the maxilla. However, this would result in wear occurring solely along the lingual aspect of maxillary crowns and the buccal aspects of mandibular molar crowns (Campbell, 1925). This pattern accords well with the observed distribution of enamel thickness in many species of primates, including humans and early hominids; i.e. in general enamel is thickest over these corresponding regions of maxillary and mandibular molars. In cases where the mandibular arch becomes wider than the maxillary arch (i.e. orthodontic 'cross-bite'), the location of greatest wear would change such that buccal slopes of maxillary molars, for example, would be subjected to increased wear in regions where the mandibular arch is relatively wider. Wider maxillary arches anteriorly and wider mandibular arches posteriorly then would result in a spiraling of wear along the molar series (see Fig. 1).

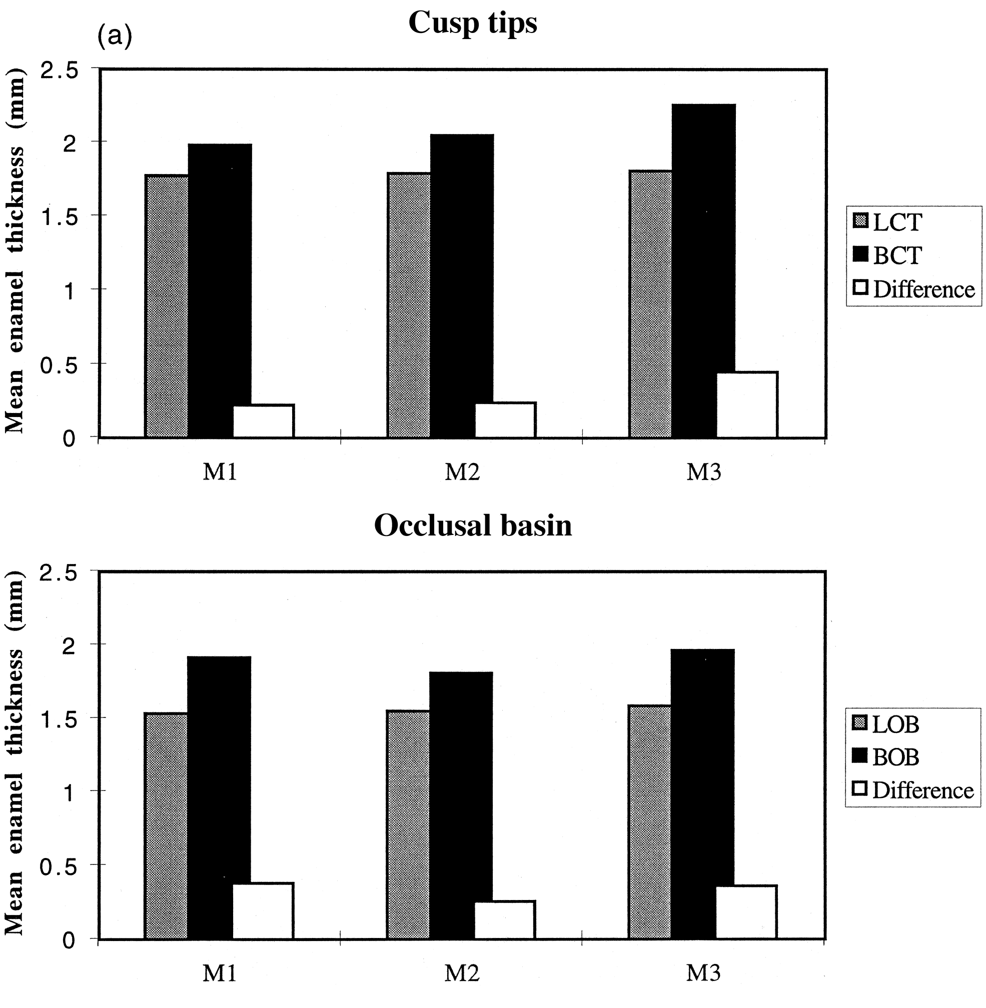

Fig. 3. (a) Gradient-related changes in enamel thickness at the cusp tip region (top) and the occlusal basin (bottom) for modern human mandibular molars. The vertical bars represent mean values while the white bar represents the difference between enamel thickness measurements at corresponding functional regions at each molar position. (b) For illustrative purposes, the same as in (a), except for maxillary molars (adapted from Spears and Macho, 1995). Abbreviations as in Fig. 2.

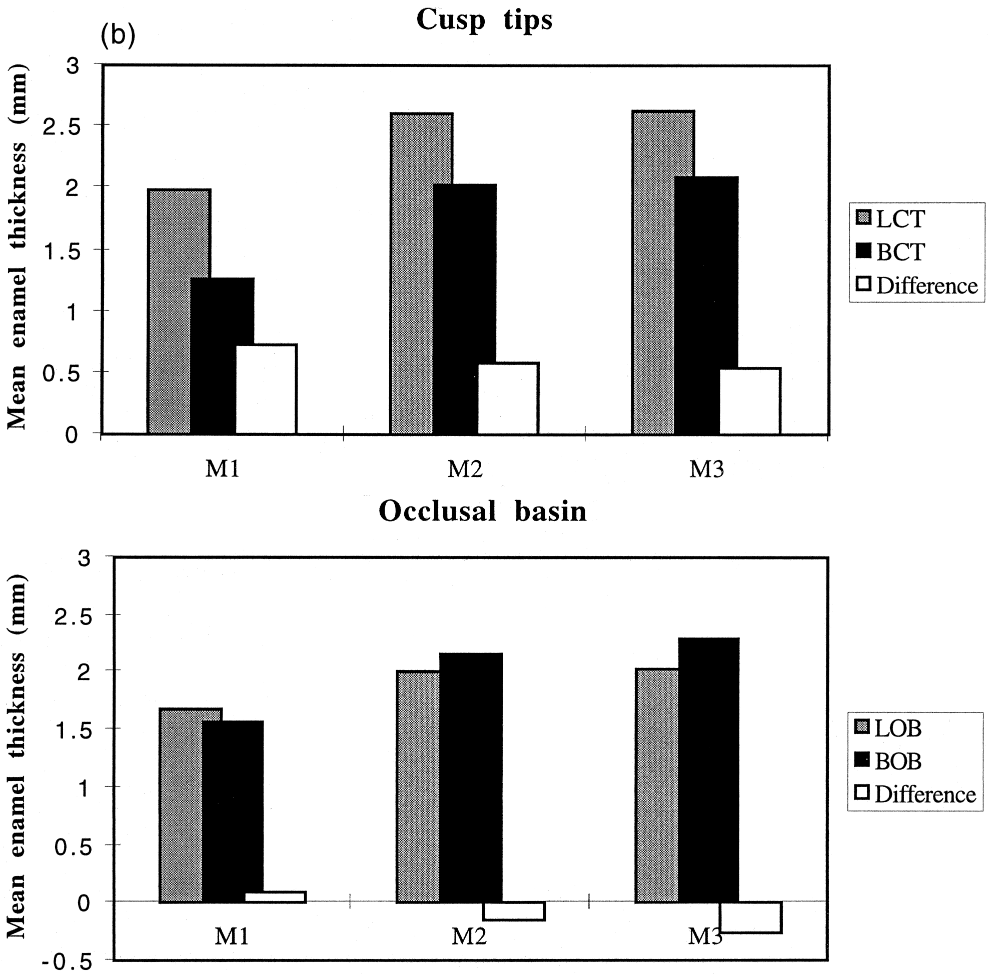

Fig. 3 (*continued*)

The presence of a strong gradient in enamel thickness in modern human maxillary molars coupled with the trend towards minimizing the discrepancy between enamel thickness within the occlusal basin between functional (protocone) and non-functional (paracone) cusps supports previous claims of an increase in masticatory loads posteriorly (Mansour and Reynick, 1975; Osborn and Baragar, 1985; Koolstra et al., 1988; Osborn, 1996). This is supported by the data presented here for mandibular molars, as enamel thickness at the cusp tips, and to a lesser extent within the occlusal basin, exhibits a positive gradient from anterior to posterior. This results in both maxillary and mandibular posterior molars having relatively thicker enamel, a necessary arrangement for the effective dissipation of increased loads incurred in this region.

Changes in enamel thickness across corresponding functional regions of the occlusal basin in maxillary molars are such that molars would tend to wear in a helicoidal manner. In other words, if proportional increases in enamel thickness are taken as indirect evidence of increased wear resistance, then the ‘switch’ to relatively thicker enamel across the buccal aspect of the paracone [BOB in Fig. 3(b)] would indicate higher wear gradients along the lingual aspect of anterior maxillary molars, switching to become higher along the buccal aspect of posterior maxillary molars, resulting in a spiraling of the wear plane. As enamel is consistently thicker over the buccal aspect of the occlusal basin [BOB in Fig. 3(a)] at all three mandibular molar positions, there is no evidence of a reversal such that thicker enamel occurs buccally in M_1 and lingually in M_3.

The disparate results for mandibular molars would seem to suggest several alternative explanations for the role of enamel thickness distribution in mediating helicoidal wear. It is likely that the degree to which arcades contribute to helicoid occlusion may vary among populations so that more work is needed to document this feature in other contemporary human groups. It is also possible that factors other than the distribution of enamel thickness, such as the position of the temporomandibular joint, occlusal area, the relative degree of prognathism, relative canine size, palatal width, the length of time between serially erupting molars and the degree of axial molar angulation, are equally, if not more, critical for developing and maintaining the spatial relation of mandibular molars to their maxillary counterparts in order to promote a helicoidal wear plane. While it is difficult to integrate all of these factors into any one study of orofacial architecture and mastication, especially a study focusing on enamel thickness, it is possible to tie in the observations presented here with recent biomechanical appraisals of tooth form and function.

At first glance, these results indicate that the distribution of enamel thickness in mandibular molars plays little part in contributing to the development of a helicoidal wear plane and that it is the morphology of maxillary molars which is more important in mediating this unique pattern of wear. In other words, the proportional distribution of enamel thickness within the occlusal basin of maxillary molars may be the key to the development of helicoid occlusion. At first, this seems unlikely as both arcades would undoubtedly contribute equally to the occurrence and maintenance of a helicoidal wear plane. However, the lack of any association between enamel thickness and helicoidal wear may corroborate recent biomechanical interpretations of mandibular molars as ‘pestles’ compared to the ‘mortar-like’ function of maxillary molars (Spears and Macho, 1998; Macho and Spears, 1999).

It should be kept in mind, however, that enamel thickness is only one factor contributing to long-term abrasion resistance, which in and of itself, is only one factor contributing to the development of helicoidal wear. As such it is necessary to incorporate other aspects of orofacial architecture into any model attempting to explain the presence of helicoid occlusion. For some time it was believed that the spatial relation of maxillary and mandibular arches could provide a useful morphological explanation for the development of helicoidal occlusion, and has been used to explain its appearance in modern humans relative to our early human ancestors, the australopithecines (e.g. Campbell, 1925; Tobias, 1980). However, some have proposed that relative arch widths are not as important in the development and maintenance of helicoidal wear as is the angle of molar implantation (Drennan, 1929; van Reenan, 1964; Ward, 1981; Osborn, 1982; Smith, 1986). More pronounced axial molar angulation in the posterior mandibular molar region relative to that in the anterior molars would help maintain the relation of maxillary and mandibular molars along the molar series necessary for the development of a helicoidal wear plane. Pronounced axial angulation of posterior molars has been noted in certain early hominids (Ward et al., 1982), apes and humans (Osborn, 1982). It is now thought that this arrangement serves to limit the range of possible loads experienced during mastication: anterior maxillary molars with little to no axial inclination are capable of resisting a variety of loads (as the mandibular molars enter phase I of the chewing cycle) from a host of different angles, whereas posterior maxillary molars are able only to distribute effectively near-vertical loads (Spears and Macho, 1998; Macho and Spears, 1999). The pronounced inclination of the mandibular molar ensures that the cusp most effective in dissipating loads (the mesiobuccal cusp, or protoconid) approaches the occlusal aspect of the maxillary molar’s guiding cusp (i.e. paracone), as this is the region of the maxillary molar most effective at dissipating loads (Spears and Macho, 1998; Macho and Spears, 1999). This coordinated biomechanical setup therefore suggests that the maintenance of thicker enamel on the buccal aspect of posterior mandibular molars would be expected, as is borne out by the data presented here. Thus, it seems that the complicated distribution pattern of enamel thickness in posterior mandibular molars of modern humans could more likely be an adaptation to promote and maintain high, compressive occlusal loads directed towards to the region of the maxillary molar most able to effectively resist high-magnitude occlusal forces.

In conclusion, the thickness of enamel along the molar row has been directly related to the magnitude of occlusal loads generated during mastication. Theoretical and experimental models predict that modern humans should possess thicker enamel in posterior molars as this is the region where the greatest loads occur and this is supported by the data presented here.

The region of the crown subjected to greatest wear is known to change along the molar row in certain species. For instance, modern humans and some early hominids are characterized by a complicated wear pattern, referred to as the helicoidal plane of occlusion. Proportional changes in enamel thickness from anterior to posterior indicate that modern humans show a structural reorganization of maxillary molars, which may help to explain the tendency for the curve of wear to reverse in the posterior region, but that no such evidence is present in mandibular molars. As a reversed curve of wear is a necessary element to the formation and maintenance of helicoid occlusion, the data presented here suggest that the morphology of maxillary molars of modern humans accommodates a helicoidal wear plane, but that other factors are likely to account for the part mandibular molars play in the formation and maintenance of this feature. In particular, it seems that the maintenance of thicker enamel buccally on mandibular molars, coupled with increased axial angulation in this region, provides a coordinated biomechanical set-up to help deliver high loads directed at the occlusal slope of the paracone, which is the region of the maxillary molar crown most effective in dissipating occlusal forces.

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