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The physiological linkage between molar inclination and dental macrowear pattern

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ABSTRACT

Objectives: Exact symmetry and perfect balance between opposite jaw halves, as well as between antagonistic teeth, is not frequently observed in natural masticatory systems. Research results show that asymmetry in our body, skull, and jaws is often related to genetic, epigenetic, environmental and individual ontogenetic factors. Our study aims to provide evidence for a significant link between masticatory asymmetry and occlusal contact between antagonist teeth by testing the hypothesis that tooth inclination is one of the mechanisms driving distribution of wear in masticatory phases in addition to dietary and cultural habits.

Materials and Methods: The present work investigates the relationship between dental macrowear patterns and tooth inclinations on a sample of complete maxillary and mandibular 3D models of dental arches from 19 young and adult Yuendumu Aboriginal individuals. The analysis was carried out on first molars (M1) from all quadrants. Occlusal Fingerprint Analysis was used for the quantification of macrowear patterns, and 2D cross-sectional geometric analysis was carried out to investigate asymmetry in dental arches.

Results: The asymmetry is highly variable on both arches, and it is associated with differences in the inclination of upper M1 crowns. Each molar has variable inclination (buccal/lingual) which influence tooth to tooth contact, producing greater or lesser variation in wear pattern. Inter-individual variability of morphological variation of the occlusal relationship has to be considered in macrowear analysis.

Discussion: Our results suggest that overall asymmetry in the masticatory apparatus in modern humans affects occlusal contact areas between antagonist teeth influencing macrowear and chewing efficiency during ontogeny.

Tooth wear is a physiological and adaptive phenomenon of dental tissue loss (Benazzi et al. 2013). In anatomically modern humans, numerous factors contribute to creating and modifying wear on the occlusal surface of teeth. Such factors comprise, but are not limited to, tooth position in the dental arch (Molnar & Molnar 1990), diet (El Zaatari et al., 2011, El Zaatari & Hublin 2014, El Zaatari, 2010, 2008; Fiorenza et al., 2011a,b; Fiorenza, 2015; Hinton, 1982; Molnar, 1972; Smith, 1984), endogenous and exogenous chemical factors (Grippio et al., 2004), bruxism (Sameera et al., 2017), para-masticatory activities (Fiorenza et al., 2011a; Fiorenza & Kullmer, 2013, 2015), and cultural practices such as dental treatment (Bennike & Alexandersen, 2003; Coppa et al., 2006; Lozano et al., 2013; Ortiz et al., 2016; Oxilia et al. 2015, 2017; Ricci et al., 2014; Schwartz et al., 1995; Seidel et al., 2005; Turner, 2004; White et al., 1997) or food processing (Fiorenza et al., 2018). The above mentioned factors have been extensively used to investigate dietary habits and behavioral patterns across prehistoric populations and extinct human species (El Zaatari et al., 2011; Fiorenza et al., 2011a,b, 2018; Fiorenza & Kullmer, 2013, 2015; Hinton, 1982; Molnar, 1972; Smith, 1984), behavioral patterns of historic and modern hunter-gatherers (Hinton, 1982; Kaidonis, 1993; Molnar, 1971, 1972), predominant occlusal movements performed during masticatory and paramasticatory activities (Kullmer et al., 2012; Oxilia et al., 2015, 2017), and the biomechanical effects of occlusal loading (Benazzi et al., 2011, 2014, 2015, 2016; Dejak et al., 2003) and the functional restoration of fossil dental arches (Benazzi et al., 2013c; Kullmer et al., 2013).

Nevertheless, the presence of asymmetry in masticatory systems may also offer additional insights to explain the distribution of tooth wear. Asymmetry in maxilla emerges as the result of many potential factors including tongue movements involved in swallowing (Anagnostara et al., 2001; Hartl et al., 2003; Lear et al., 1965; Mosier et al., 1999; Palmer et al., 2008; Pameijer et al., 1970), speech, and postural stability, all of which influence the alteration of both upper and lower jaw morphology (Alghadir et al., 2015; Hiiemae & Palmer 2003; Hori et al., 2013; Palmer et al.

1997). In particular, by pushing upwards, the tongue exerts a pressure on the palate that is then transmitted through maxillary bones and potentially resulting in tooth inclination (Proffit 1978). At the same time, this alteration involves the palate, vomer and the sphenoid bones (Brodie 1946; Fishman 1969; Kapoor et al., 1979; Rakosi 1978).

As far as the mandible is concerned, there are three main forces responsible for tooth inclination: a) lingual force (the muscles of the tongue); b) buccal force (*M. buccinator* and *M. masseter*); and c) occlusal force (loading during mastication) (Koc et al., 2010). Initially, mandibular molars erupt lingually. They then move buccally due to tongue pressure and *M. masseter* function (Janson et al. 2004). Finally, the molars reach a balance position (Masumoto et al., 2001) that will change during life due to the pressure of tongue and other muscles. It can be safely assumed that occlusal contacts between antagonist teeth with varying inclinations will result in macrowear patterns that are specific for that occlusion (Kasai & Kawamura 2001).

At present, however, there has been no substantial contribution to exploring the effect of asymmetry on tooth wear. In this preliminary work, therefore we aim to assess whether the impact of non-pathological asymmetry on wear patterns can represent an additional explanatory variable for the emergence and distribution of dental wear. More specifically, by using digital casts of upper and lower dental arches of Aboriginal individuals from Yuendumu (Australia; Brown et al., 2011), we provide evidence of linkage between dental macrowear and tooth inclination in first molars (M1), showing that structural factors such as bone asymmetry are responsible for the development of wear pattern in addition to the already explored external factors.

MATERIALS AND METHODS

Sample

The Yuendumu collection consists of measurements, radiographs, family data, and 1717 sets of dental casts representing 446 individuals that were produced from alginate impressions (Brown et al., 2011). This is one of the most widely studied dental collections in the world (with over 250

scientific publications), and represent an ideal sample for the present study. The Yuendumu collection was created from a unique longitudinal research project in which data on dentition and growth of Aboriginal children and young adults from Yuendumu (Northern Territory, Australia) were collected annually between 1951 and 1971. This indigenous population was at an early stage of transition from a nomadic and hunter-gatherer way of life to a more settled existence (Campbell & Barrett 1954), with limited contacts with Europeans (Brown et al., 2011). Their dentition was mostly characterized by a normal occlusion (or Angle Class I; Barrett, 1969; Beyron 1964; Nakahara et al., 1997, 1998a, 1998b, 1999) and alternate intercuspation (Brown, 1987; Corruccini, 1990; Richards & Brown 1986) with little evidence of pathological conditions (Campbell, 1923), such as caries (Barrett & Williamson, 1972; Brown, 1974), tooth crowding (Björk & Helm 1969, Helm, 1979), malocclusions (Corruccini et al., 1990), molar agenesis (Macintosh & Barker, 1978), periodontal diseases (Barrett & Williamson, 1972), and asymmetry (Campbell, 1925; Proffit et al. 1975; Proffit, 1975, Townsend & Brown, 1980). Dental wear of Aboriginal people is characterized by evidence of non-masticatory activity (Barrett, 1958; Barrett & Williamson, 1972, Clement et al., 2009) bruxism (Barrett, 1960) and traces of function in eccentric jaw positions (Kaidonis et al., 1993).

The sample used in this study consists of complete casts of maxillary and mandibular dental arches belonging to 19 adult and sub-adult individuals (Table 1), all of which are characterized by slight or moderate M1s wear (up to wear stage 2 on Smith 1984 (Supporting information Figure S1). The sample comprises younger individuals (ca 30 years old and below), because older Australian aboriginals show an increase in tooth wear (stage 3-5; Smith, 1984), with extended dentine areas that compromise the identification of macrowear patterns. The number of selected individuals was further reduced by the exclusion of all damaged samples.

Table 1. Individuals analyzed from the Yuendumu Aboriginal group.

Specimen	Age	Sex	Mandible dentition	Maxilla dentition
751	8	male	mixed	mixed
640	9	male	mixed	mixed
247	10	male	mixed	mixed
716	10	male	mixed	mixed
869	10	male	mixed	mixed
288	11	male	mixed	mixed
634	11	female	mixed	mixed
859	12	male	permanent	permanent
359	15	male	permanent	permanent
251	16	male	permanent	permanent
183	17	male	permanent	permanent
305	17	male	permanent	permanent
307	17	male	permanent	permanent
549	17	female	permanent	permanent
243	19	male	permanent	permanent
294	21	female	permanent	permanent
421	26	male	permanent	permanent
338	29	male	permanent	permanent
466	30	male	permanent	permanent

Digital acquisition of upper and lower arches derived from dental casts

We digitized the specimens from dental cast collection using a white-light scanning system with a xy resolution of 45 μm based on structured-light technology (smartSCAN3D C-5, Breuckmann, GmbH). Collection and alignment of scan-data was carried out using the integrated scanning software optoCAT (Breuckmann, GmbH). Generated virtual 3D models were further post-processed using PolyWorks® V12 (InnovMetric Software Inc.), a 3D metrology software package. The limited size and high resolution of the polygonal models allowed us to avoid the use of smoothing on the meshes and therefore to preserve the original surface. Each raw data polygonal model was imported into the IMEdit™ module where topology errors, artifacts, and degenerate/duplicate triangles were manually identified and removed.

For each specimen, macrowear pattern of left/right maxillary/mandibular first molars (i.e., 76 M1s), tooth inclination at the level of M1s, and quantification of jaw asymmetry were obtained as detailed below.

Macrowear pattern of the M1s

M1 wear areas were manually outlined on each digital 3D surface models and were labeled according to the wear area terminology and numbering system created by Maier & Schneck (1981). Areas that were affected by wear were then grouped into their respective masticatory cycle phases, i.e. phase I buccal areas (1, 1.1, 2, 2.1, 3, 4), phase II (9, 10, 11, 12, 13, 10.1), and phase I lingual areas (5, 6, 7, 8) (Kay & Hiimeae, 1974). The relative wear area of each chewing phase was computed by summing the absolute areas (in mm²) belonging to the same phase, and dividing this sum with to the total occlusal wear area. The resulting values (proportions) were visually represented by the ternary plot, which is a diagram that describes the proportions of three variables (in this specific case represented by the relative areas of Phase II, and Buccal and Lingual Phase I) which have to sum to 1 or 100%.

M1 crown inclination

A reference plane (hereafter called “RP”) was identified on virtual models. The xy-plane of a Cartesian coordinate system was transformed parallel to the RP. The RP was obtained by observing: i) the apex of the septum between the central incisors; and ii) two points marked respectively on the left and right hypoconid (distobuccal cusp of mandibular M1s) and metacone (distobuccal cusp of maxillary M1s) (Figure 1a, e).

Then, a plane perpendicular to the RP (Figure 1b, f), passing through the hypoconid and metacone (Figure 1c, g), was created in order to obtain a cross-section of dental arch (Figure 1d, h). On the cross-section, a line was drawn for each M1 between the buccal and lingual gingival sulcus

(hereafter called “Gingival Line”). Finally, further an additional line was located at the cross-section perpendicular to the Gingival Line (hereafter called “Vertical Line”). The lingual angle measured at the cross-section between the Vertical Line and the RP was used to establish the buccal or lingual inclination of the alveolar arch at the level of M1s (Figure 1d, h). This measurement is taken as a proxy for the inclination of the M1 crowns. An angle higher or lower than 90° suggests a lingual or buccal inclination of the M1 crowns respectively.

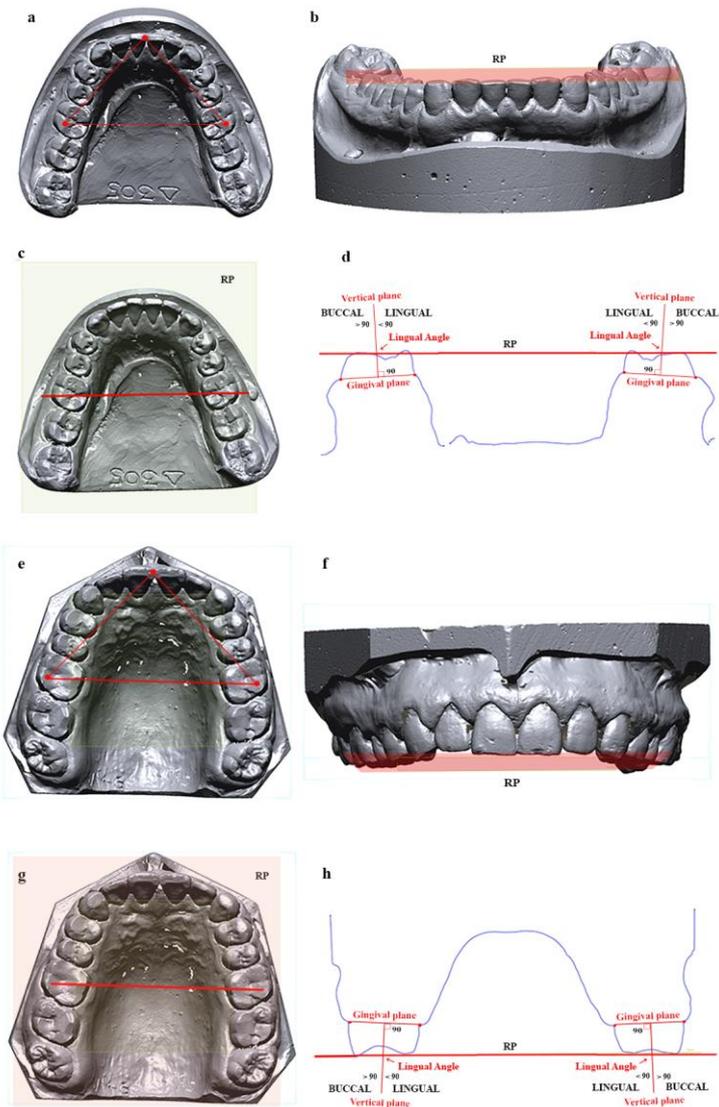


Figure 1. Occlusal reference plane. Three anatomical points were identified on the occlusal surface (a, e) and the plane created from them was taken as reference plane (RP) (b, f). Afterwards a plane was drawn between Hypoconid (c) and Metacone (g) of first molars perpendicular to the

RP. A cross-section of the entire virtual model was obtained (**d, h**) in order to calculate the inclinations of alveolar bone (vertical plane perpendicular to the gingival plane) in relation to RP.

Quantifying palatal arch asymmetry

The cross-sections described above were also used to quantify the asymmetry of the palatal arch. In detail, for both mandibular and maxillary cross-sections, the midpoint (MP) between the left and right M1 lingual gingival sulcus was computed (Figure 2). The midpoint MP was then projected on the parallel reference plane (PRP), thus obtaining a new point called PMP (projected midpoint). The line passing through MP and PMP was used to split the palatal arch in a left and right half-component (Figure 2). The relative area of each half-component (Figure 2) was calculated by dividing the absolute area of each half side by the total palatal area.

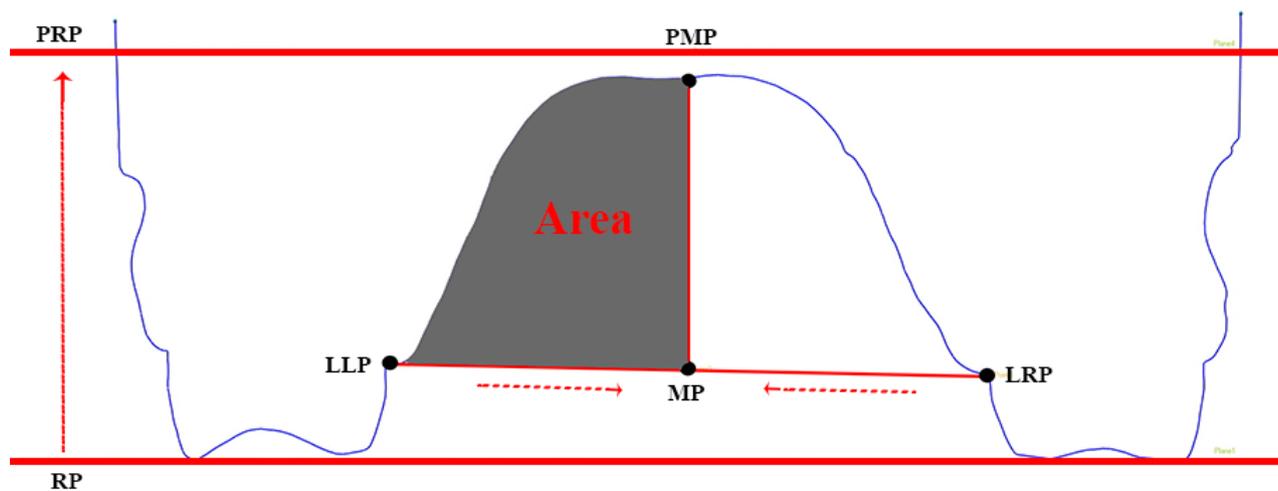


Figure 2. Cross-section of upper jaw. Points used to calculate the relative areas of the palatal arch. (RP = Reference plane; PRP = Projected Reference Plane; LLP = Lingual Left Point; LRP = Lingual Right Point; MP = Middle Point; PMP = Projected Middle Point).

Measures of statistical association

Considering the small size of the present sample (n=19), non-parametric tests were used to formally assess the presence of significant associations between variables. More in detail, Mann-

Whitney-Wilcoxon signed-rank test was used on paired observations to identify significant differences in wear patterns across the masticatory phases of each dental arch.

The potential relationship among teeth inclinations was analyzed using Spearman rank correlation coefficient (ρ). The same statistical analysis was performed to test for significant relationship between tooth inclination and macrowear in each masticatory phase of each quadrant. The latter consist of: Upper Right (UR), Upper Left (UL), Lower right (LR) and Lower Left (LL). For significant cases identified through correlation, we assessed the explanatory power of tooth inclination with respect to wear patterns through an ordinary least squares (OLS) linear regression analysis. Segregation based on age was further explored by computing a Principal Component Analysis (PCA) based on alveolar inclinations, and by performing AMOVA (Analysis of Molecular Variance; Excoffier et al., 1992) based on inter-individual, pairwise Euclidean distances computed on the same alveolar inclinations.

Finally, the presence of significant differences in the distribution of tooth inclination values across classes of palatal asymmetry (symmetric, predominant left, and predominant right) at each position (UR, UL, LR and LL) was explored using a Kruskal-Wallis test. All analyses were performed in R version 3.4.3 (R Core Team, 2017).

RESULTS

Macrowear pattern phase distribution of the M1s

The relative proportion (percentage) of the three masticatory phases identified on the M1s were graphically represented in the ternary plots (Figure 3). Overall distributions of mandibular and maxillary M1s overlap (Figure 3a), even though the latter (black circle) is more scattered (Figure 3b) than the former (red circle) (Figure 3c). Indeed, significant differences between antagonists (Mann-Whitney-Wilcoxon signed-rank test) were obtained for buccal and lingual phase I of both the left (p-value=0.04) and right (p-value=0.03) M1s (Table 2).

When maxillary and mandibular M1s of the same individual are considered separately, there are no significant differences in the pattern of masticatory phases between left and right side (Table

2). Overall, we observed that right maxillary M1s (points) are more variable than left maxillary M1s (circles) (Figure 3b), while such difference was not observed for mandibular molars (Figure 3c).

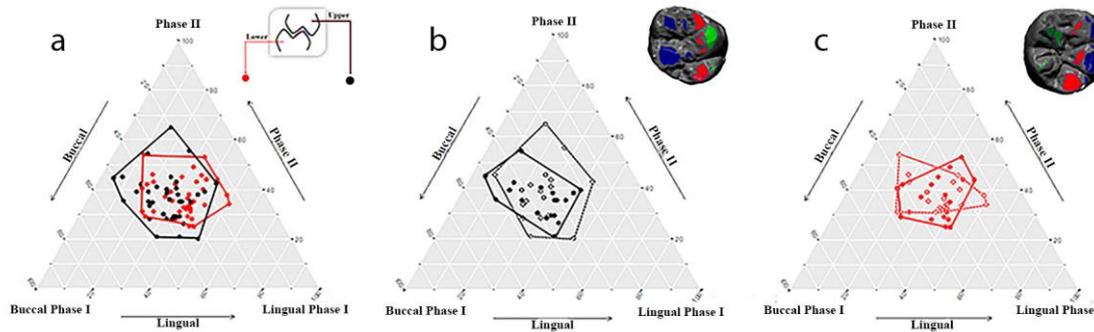


Figure 3. Ternary diagrams showing the proportions (in %) of relative wear areas of buccal phase I areas, lingual phase I areas, and phase II areas, which are positioned in an equilateral triangle. Each base of the triangle represents a ratio of 0% while the vertices correspond to a percentage of 100%. **(a)** Relation between upper (black) and lower (red) molars. **(b)** Relation between right (filled points) and left (empty points) upper molars. **(c)** Relationship between right (filled points) and left (empty points) lower molars.

Table 2. Relationship between masticatory phases of each dental arch measured using Mann-Whitney-Wilcoxon signed-rank test for two-sample, paired study design (T= test statistic; $\alpha=0.05$).

	Phase II		Buccal Phase I		Lingual Phase I	
	T	p	T	p	T	p
UL - UR	109.5	0.3	64	0.6	76	0.7
UL - LL	102	0.8	134	0.04	44	0.04
LR - UR	103.5	0.75	43	0.03	131	0.05
LR - LL	68	0.46	107.5	0.63	88	0.93

UL = Upper Left; UR = Upper right; LL = Lower Left; LR = Lower right

M1 crown inclination

The inclination of maxillary and mandibular M1 crowns are listed in supporting information Table S1. Even though we observe variability between opposite (left and right; Supporting information Table S2a) and antagonist teeth (Supporting information Table S2b), the only significant relationship emerges between tooth inclinations of opposite sides of the upper ($\rho = 0.55$, p-value = 0.016) and lower ($\rho = 0.76$, p-value = 0.00016) dental arch respectively (Table 3).

Table 3. Potential relationship among teeth inclinations expressed as Spearman rank correlation coefficients (ρ). Significant values in bold ($\alpha=0.05$).

	ρ	p-value
UR~UL	0.55	0.016
UR~LR	-0.18	0.46
UR~LL	-0.17	0.46
UL~LR	0.2	0.39
UL~LL	0	1
LR~LL	0.76	0.00016

UL = Upper Left; UR = Upper right; LL = Lower Left; LR = Lower right

Relationship between alveolar inclination and dental wear development

The relationship between molar inclination and wear patterns in each masticatory phase at each position is shown in Table 4. Significant correlations are identified only for the right side, in both the upper and lower arch (quadrants 1 and 4). More specifically, significant negative relationship is identified for phase II in UR position and for buccal phase I in LR position. On the other hand, lingual phase I of the right side always exhibits positive correlation with tooth inclination.

Table 4. Relationship between tooth inclination of each position and the relative masticatory phases measured as Spearman rank correlation coefficient (ρ). Significant values in bold ($\alpha=0.05$).

	Phase II		Buccal Phase I		Lingual Phase I	
	ρ	p-value	ρ	p-value	ρ	p-value
UR	-0.65	0.0026	-0.38	0.1	0.73	0.00035
UL	-0.09	0.7	0.14	0.55	0.006	0.98
LR	0.18	0.44	-0.56	0.011	0.52	0.025
LL	-0.056	0.82	-0.19	0.439	0.14	0.55

UL = Upper Left; UR = Upper right; LL = Lower Left; LR = Lower right

The coefficient of determination (R^2) obtained through OLS regression for the same cases, and the relative F statistic, suggest that variability in tooth inclination is one of the mechanisms driving the distribution of wear in masticatory phases, and the significance of the obtained values suggests that these results may be also generalized in a broader sample (Table 5).

As far as the impact of age is concerned, we computed a PCA on all four inclination values and color-coded individuals based on age classes (“mixed” for subadults and “permanent” for adults; Figure 4, supporting information Table S3, S4 and S5). The first two principal components explain 91% of the total variance and show a certain level of segregation between the two age groups, with the majority of subadults grouped in the right side of the graph while adult individuals tend to be grouped in the left half. Subadults exhibit most of their variability on PC1 (with the exception of specimen 288), while adult individuals – with the exception of two outliers (specimens 359, 243) – seem to vary predominantly along PC2. A closer inspection of variable loadings (Supplementary Table S3) suggests that PC1 may indicate variability in mandibular inclinations, while PC2 refers to maxillary variability.

Results of AMOVA based on the same grouping show that age differences between mixed and permanent dentition explain about 12% of the total variability in tooth inclination in the current sample ($\Phi_{ST}=0.12$, p-value=0.032).

Table 5. Coefficient of determination (R^2) and the relative F statistic produced by linear regression to infer the proportion of variability in wear masticatory phases that could be explained by tooth inclination.

	R ²	p-value	F-statistic for 1 and 17 df
UR_Phase II ~ UR inclination	0.32	0.006	9.579
UR_Lingual Phase I ~ UR inclination	0.42	0.0016	14.09
LR_Buccal Phase I~ LR inclination	0.33	0.006	9.881
LR_Lingual Phase I~ LR inclination	0.17	0.05	4.654

UL = Upper Left; UR = Upper right; LL = Lower Left; LR = Lower right

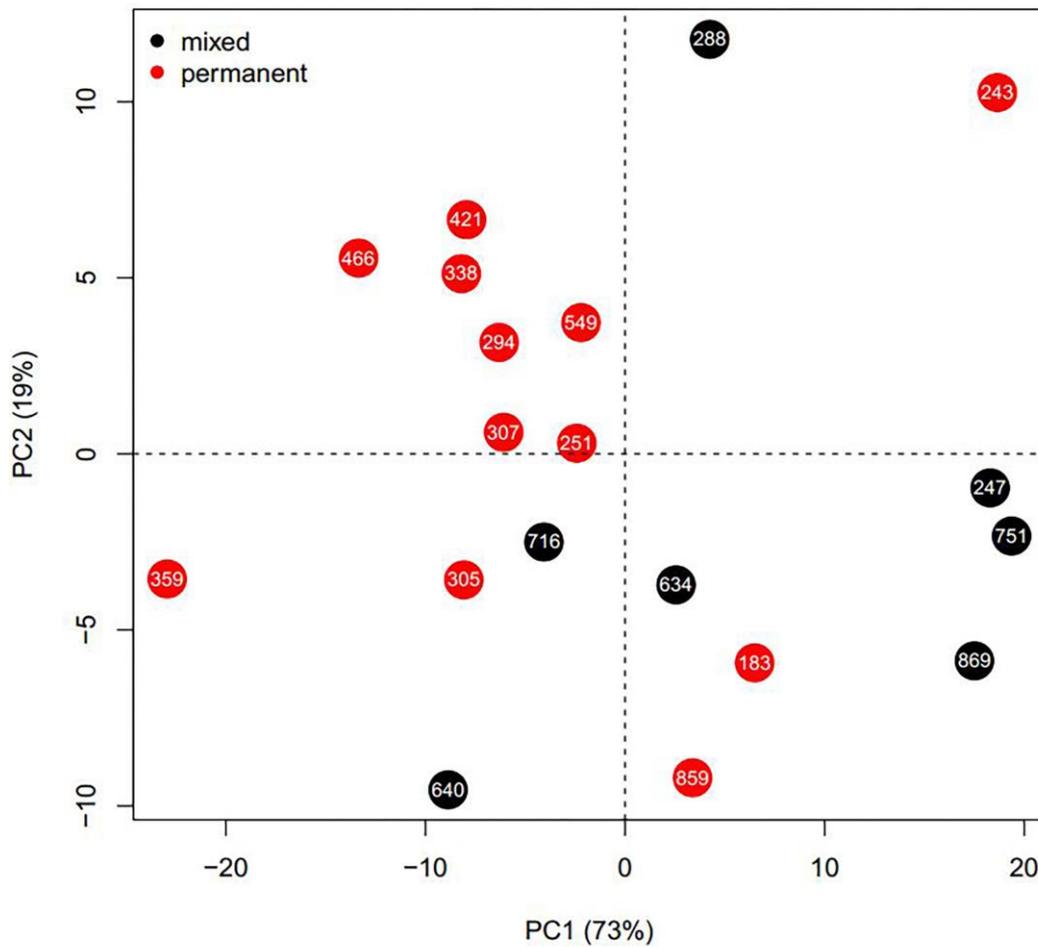


Figure 4. Principal Component Analysis (PCA) based on alveolar inclinations. Individuals are color-coded according to their dentition (mixed=red; permanent=black). Horizontal axis represents PC1 (describing 73% of the total variance) while vertical axis represents PC2 (capturing 19% of the total variance).

Relationship between palatal arch and tooth inclination

The values of the relative palatal areas (Supporting information Table S6) show only six individuals with no difference (50%) between each half. The Kruskal-Wallis test performed to preliminary explore the possible relationship between palatal arch asymmetry and tooth inclination yielded no significant results (Table 6), suggesting that – at least in the present sample– tooth inclination may not be directly linked to palatal asymmetry.

Table 6. Results of Kruskal-Wallis test assessing whether the distribution of alveolar inclinations is significantly different between classes of palatal asymmetry. The latter consist of: 1) symmetric halves; 2) asymmetry with predominant right half; and 3) asymmetry with predominant left half

	Chi-squared	df	P-value
UR	3.4829	2	0.175
UL	2.2418	2	0.326
LR	5.1052	2	0.078
LL	3.1766	2	0.2043

UL = Upper Left; UR = Upper right; LL = Lower Left; LR = Lower right

Discussion

The results described in this study provide evidence that tooth inclination (lingual or buccal) has an impact on the distribution of dental wear. Upper and lower tooth inclinations can produce an increase in tooth wear areas. When tooth inclination presents with an angle greater than 90 degree (buccal tendency) there is a general increase of the area interested by Lingual Phase I, while an angle of less than 90 degrees (lingual tendency) tends to increase wear area of the buccal slope.

Percentage values of dental masticatory phases show differences in wear between antagonistic molars (Table 2). In this respect, it is recommended to separately analyze the areas of wear of maxillary and mandible molars for comparative group studies in order to reduce variability.

Whether this effect depends on particular features of the present sample or on sample size will need to be further tested in the future with larger samples.

Tooth inclination values exhibit a high degree of inter-individual variability when considering the whole of the sample (Supporting information Table S2). Subadults exhibit a more pronounced mandibular variability, while adults tend to vary more in the inclination of maxillary teeth (Figure 4). Although the impact of age on tooth inclination in the present sample is only moderate (~10% of the total variance), results point to a stronger correlation between maxillary dentition and age, as opposed to a more negligible effect of ageing on the mandible. Correlation among inclinations of right and left sides of upper molars is generally lower than the relationship documented between mandible molars of both sides. In view of these results, upper and lower jaws seem to be two separate and yet interdependent elements, and the lack of covariance between upper and lower jaws (Supporting information Table S2, S7 and S8) is also supported by the absence of statistical significance (Table 3). The most relevant result consists of a significant correlation between tooth inclination and tooth wear. Such a relationship is particularly strong on the right side of the present group of individuals. This result can be explained based on the characteristic mode of occlusion observed among Australian Aborigines called: “X-occlusion” or “alternate intercuspation” (Barrett, 1953). Barrett (1953) carried out a study on dental morphology in Yuendumu Aboriginal people, showing that upper and lower teeth could join in maximum contact on either left or right side, but not on both sides at the same time. The latter observation could suggest that Aboriginal individuals probably had a tendency to occlude properly on the right side, producing an increase in occlusal force and thus a more localized evidence of the relationship between wear development and tooth inclination (Table 4). This condition is considered as a malocclusion by orthodontists. Nevertheless, it does not prevent mastication and provides a much wider range of lateral or rotational jaw movements, which can prove to be advantageous when grinding during chewing hard and tough food entailed by the diet of nomadic hunter-gatherers (Brown et al., 2011).

In the present study no statistically significant relationship between palatal asymmetry and tooth inclination could be documented, possibly because of the joint effect of a small sample size and

the absence of parafunctional, pathological conditions. The latter element in particular can increase asymmetry during palatal bone development due to incorrect tongue posture and pressure (Alghadir et al., 2015; Hiiemae & Palmer, 2003; Hori et al., 2013; Palmer et al., 1997).

Since our results suggest that tooth inclination has an impact on macrowear pattern, we must inquire about the processes that are responsible for such asymmetry in the masticatory apparatus. In this respect, elements of particular interest can be the specific role of tongue during important steps of human evolution, such as changes due to locomotion, speech and dietary habits.

As far as the first point is concerned, tongue thrust is a common kind of Orofacial Myofunctional Disorder (OMD) where constant pressure from resting or incorrectly thrusting the tongue away from the hard palate may push teeth out of place and that pressure may later prevent teeth from erupting. The correct posture of the tongue (Van Dyck et al., 2016) seems one of the most promising solutions to this problem, further stressing the importance of tongue in the rehabilitation from oral disorders. Therefore, it could be possible that the physiological asymmetries in the masticatory system of the studied human group is attributable to the posture of the tongue which, in addition to all other muscles involved in swallowing, exerts a force that is absorbed by the hard palate (Anagnostara et al., 2001; Hartl et al., 2003; Lear et al., 1965; Mosier et al., 1999; Palmer et al., 2008; Pameijer et al., 1970). When swallowing takes place correctly, the tip of the tongue presses firmly against the roof of the mouth or hard palate, which is located slightly behind the front teeth. During an incorrect deglutition, the tip and/or sides of the tongue press against or spread between the teeth producing loading asymmetries and affecting bone asymmetry (Matsuov & Palmer, 2008; Van Dyck et al., 2016).

Considering biocultural developments involved in human evolution, on the pathway towards *Homo sapiens* food energy content and quality increased over time, while physical stiffness and toughness were reduced through cultural adaptation (Demes & Creel, 1988), in particular with the development of more and more sophisticated external food preparation techniques (Brace et al.,

1991; Hinton, 1982; Kaidonis, 1993; Lieberman et al., 2004, Lucas et al., 2013; Mariotti et al., 2015; Molnar, 1971, 1972; Shipman & Rose, 1983; Smith, 1984; Straus, 1989; Toth, 1985, Watson, 2008). This general trend led to a reduction of biomechanical loading and forces in our masticatory system during food ingestion and dental processing (Zink & Lieberman, 2016). From a biological perspective, it is likely that through the continuing reduction of biomechanical pressure on our masticatory system, the human organism reacted with a dimensional reduction in the system itself, favoring an increased variability in the emergence of asymmetry during the process of development, growth and remodeling of the entire masticatory apparatus.

The analysis of this specific masticatory context opens a new perspective on dental macrowear development. Endogenous factors such as dental inclination (Table 4) are to be added to the already known, multiple exogenous variables (such as food and environment abrasiveness, as well as cultural adaptation) in order to obtain a comprehensive model for the appearance of occlusal wear patterns.

The role of asymmetry in the masticatory apparatus and its change over time due to the development of various cultural and dietary habits should therefore receive more consideration both in modern dentistry and dental anthropology. In the first case, comparative studies of tongue posture and tooth inclination would be helpful to enhance knowledge on parafunctional influences in jaw asymmetry, on the relationship between alveolar inclination and crown orientation, and on how individual wear areas are produced by loading and pressure during occlusion and swallowing.

As far as dental anthropology is concerned, future studies on dental macrowear would benefit from adding asymmetry to the already known explanatory variables for the distribution of dental wear, i.e. cultural and dietary habits. A more comprehensive evaluation of tooth inclination could also facilitate a better understanding of the mechanisms driving the formation of paramasticatory wear areas (Fiorenza et al., 2011b).

A more holistic view that harmonizes mouth functionality with the rest of the human body (through postcranial posture, chewing, and functional deglutition) is therefore desirable in future occlusal research in order to understand the development of asymmetry in our masticatory system, and to evaluate individual patient situations in dental rehabilitation.

Additional Supporting Information may be found online in the supporting information tab for this article.

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