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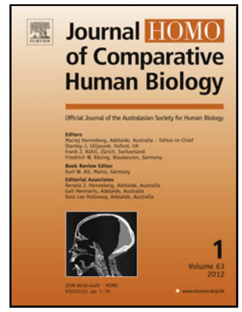

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First molar size and wear within and among modern hunter-gatherers and agricultural populations

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Abstract

Apart from reflecting modern human dental variation, differences in dental size among populations provide a means for studying continuous evolutionary processes and their mechanisms. Dental wear, on the other hand, has been widely used to infer dietary adaptations and variability among or within diverse ancient human populations. Few such studies have focused on modern foragers and farmers, however, and diverse methods have been used. This research aimed to apply a single, standardized, and systematic quantitative procedure to measure dental size and dentin exposure in order to analyze differences among several hunter-gatherer and agricultural populations from various environments and geographic origins. In particular, we focused on sexual dimorphism and intergroup differences in the upper and lower first molars. Results indicated no sexual dimorphism in molar size and wear within the studied populations. Despite the great ethnographic variation in subsistence strategies among these populations, our findings suggest that differences in sexual division of labor do not affect dietary wear patterns.

Introduction

Dental variation among and within modern human populations has been attributed mainly to genetic and environmental factors (Bailit, 1975). Crown length–breadth measurements have been widely used to provide insights into inter- and intragroup variability, and differences in tooth size among modern humans have been reported (Bishara et al., 1989; Brook et al., 2009; Hanihara, 1977; Keene, 1979; Otuyemi and Noar, 1996; Turner and Richardson, 1989). Probably, the most complex study of tooth size differences in modern humans was performed by Hanihara and Ishida (2005), who investigated the mesio-distal and bucco-lingual tooth crown differences among 72 major human populations. The authors have concluded that the Australian Aborigines possess the largest and Philippine Negritos the smallest teeth of all considered groups. They have also stated that Southeast Asians are characterized by dental patterns similar to those of sub-Saharan Africans and that the overall patterns of dental morphology are consistent with genetic and craniometric data. However, many other researchers have argued that the differences in dental measurements do not vary enough to efficiently discriminate contemporary human populations (Ates et al., 2006; Castillo et al., 2011; Harris, 2003; Suazo et al., 2008).

In addition to intergroup differences, the intrapopulation variation in tooth size has also been investigated. In numerous studies, males were found to exceed females in various tooth measurements (Barrett et al., 1963; İşcan and Kedici, 2003; Richardson and Malhotra, 1975; Schwartz and Dean, 2005). Schwartz and Dean (2005) hypothesized that the size difference could be the result of a greater amount of dentin tissue present in male teeth. But other studies found very little sexual dimorphism in tooth size (Garn et al., 1964; Hillson, 1996; Mizoguchi, 1988). Harris (2003) reported that sexual variance accounted only for 1.2% of the total variation among studied groups. Additionally, Scott and Turner (1997) have acknowledged that even if there are differences encountered between sexes, they are very often inconsistent among samples and cannot lead to conclusive statements.

Overall dental wear and dentin exposure analyses have also been performed by dental anthropologists. These features have been used extensively to infer dietary habits, subsistence strategies, food preparation techniques, and cultural practices among ancient human populations (Deter, 2009; Hillson, 1996; Rose and Ungar, 1998; Smith, 1984). The abrasive properties of food have a direct impact on enamel loss and on the rates of tooth wear during an individual's life span (Kieser et al., 2001); that is, tough, fibrous, and abrasive diets require high biting forces during chewing and cause severe dental wear (Kiliaridis et al., 1995).

The transition from forager to agro-pastoral lifestyles implied significant changes in dietary habits and food-processing techniques that decreased the abrasiveness of consumed foods (Deter, 2009; Eshed et al., 2006; Hinton, 1982; Smith, 1984). Smith (1984) reported an increase in the inclination of wear surfaces of lower molars in agricultural populations compared to hunter-gatherers, as a result of a reduction in food toughness with the adoption of agriculture. She also stated, however, that due to similar diet abrasiveness, the two groups could not be differentiated by analyzing dental wear rates alone. Hinton (1982), who compared dental wear scores on first and second molars among Archaic, Woodland, and Mississippian samples from the Tennessee Valley, reported higher degrees of this feature in the Archaic sample (hunter-gatherers), followed by the Woodland group (hunter-gatherers with some cultivation admixture) and Mississippian sample (food production with supplementary hunting and gathering). Eshed et al. (2006) analyzed mandibular dental wear between the Natufian hunter-gatherers from southern Levant (10500–8300 BCE) and Neolithic populations (8300–5500 BCE) and found higher rates of dental wear, for all tooth types, in the forager groups. Finally, Deter (2009), analyzing maxillary teeth, found higher percentages of dentin exposure for all tooth types in North American hunter-gatherers (3,385±365 BCE) than in more recent agricultural groups (~1300 CE). The reduction of dental wear in societies with prevalent food production was generally associated with a decrease in diet abrasiveness.

Sex-related intragroup differences in tooth abrasion have also been reported. Generally, women tend to exhibit greater wear on anterior teeth than do men, especially in foraging societies (Berbesque et al., 2012; Clement and Hillson, 2012; Madimenos, 2005; Molnar, 1971; Richards, 1984). Molnar (1971) suggested that differences in roles between the sexes conditioned the types of food consumed, with women consuming greater amounts of fibrous plants and abrasive roots they collect. Nonetheless, Tomenchuk and Mayhall (1979) reported that Canadian Igloolik Eskimo men exhibited greater wear rates in maxillary teeth than did women, likely caused by prolonged or heavier mastication. However, another study on the same population, based on the quantitative analysis of the percentage of dentin exposure (Clement and Hillson, 2012), reported that the wear of anterior teeth in females highly exceeded that in males, up to the first premolar, and the differences were more pronounced in the maxillary dentition. Nevertheless, no significant sex-related differences in the percentage of dentin exposure were found in the posterior teeth of Canadian Igloolik Eskimos. Similarly, no sexual dimorphism in dental wear was reported either for the Libben population from northern Ohio (Lovejoy, 1985) or for the pre-contact Maori aboriginal groups (Kieser et al., 2001).

Although many researchers have worked toward a general understanding of both inter- and intragroup differences in tooth size and wear, disparities in the results exist. Different impacts of genetic and environmental factors, together with the variation in dietary habits, food acquisition and processing methods, or cultural practices among groups might be partially responsible for the ambiguity. However, differences in methodological procedures might also account for some of the variation in the results.

Considering the variety of approaches and diversity of methods used in dental research (Hillson, 1996), we have attempted to clarify the issue by making inter- and intragroup comparisons based on a single, standardized, and quantitative procedure for measuring tooth size and dentin exposure (Clement and Hillson, 2012).

Materials and methods

We studied a total of 225 first lower (M_1, n=124) and upper (M^1, n=101) molar molds, belonging to 122 individuals from four geographically dispersed hunter-gatherer (Agta, Australian Aborigines, San, and Inuit) and three agriculturalist (Batéké-Balali, Khoe, and Navajo) populations. The sample was obtained from the American Museum of Natural

History (New York) and the Musée de 1'Homme (Paris) and is currently available for study at the University of Barcelona and the University of Alicante's collections (Table 1).

INSERT Table 1 ABOUT HERE

Two different aspects of dental morphology were investigated: tooth size and dental wear. For each aspect three comparisons were performed: within-group sexual dimorphism, intergroup variation, and between subsistence strategies. For the analysis of tooth size, all 225 teeth were included, as once formed teeth do not change their size. In contrast, dental wear analysis was based only on the teeth with visible dentin exposure (see below for explanation). This restriction resulted in a final sample of 171 teeth (76% of the original sample), of which 105 were M_1 and 66 were M^1. Populations were selected to observe diverse subsistence strategies and ecological conditions of their habitats. The analysis focused exclusively on the first permanent molar because it was the most abundant *in situ* tooth available in the studied collections. Additionally, it is also the first molar tooth to erupt (around 5.5 to 6.0 years of age in modern human populations), and consequently it exhibits the greatest degree of dental wear among postcanine teeth (Clement and Hillson, 2012).

Individual sex estimations were obtained from museum records or previous studies of the same collections, when available (Auerbach and Ruff, 2004, 2006; Costa, 1977; Genet-Varcin, 1949; Goldman Data Set: http://web.utk.edu/~auerbach/GOLD.htm; Trezenem, 1940). Otherwise, one of the authors, A.R., used cranial and mandibular characteristics (Buikstra and Ubelaker, 1994) to estimate the sex.

Dealing with age effects

Dental wear is a natural result of tooth function (Molnar, 1972), and therefore older individuals normally possess more heavily worn teeth (Clement and Hillson, 2012; Molnar, 1972). Consequently, when investigating dental wear it is necessary to account for possible age effects by removing this factor from the analysis (Clement and Hillson, 2012; Clement et al., 2012). Unfortunately, dental wear–independent age information was available for only a small subset of the studied material, and statistical analysis performed on such a limited sample would not provide reliable results. Basing the age assessment on dental wear (Brothwell, 1981) would create a circular argument, when comparing tooth wear levels among and within age groups established this way. Another way of removing age from the analysis would be to relate the proportion of dentin exposure to another tooth, as proposed by

Clement and Hillson (2012). However, the collections available for the study are highly fragmented, and it was impossible to collect a representative sample of other types of teeth for such a procedure.

In order to solve this problem, we investigated dental wear variation only among individuals presenting dentin exposure. That is, individuals who presented no visible dentin exposure spots were excluded from the analysis, which ensured that juvenile individuals were not compared with adults, at the expense of several adults with no dentin exposure not being included in the analysis. We acknowledge that this procedure does not strictly eliminate the effects of age on the dental wear results. However, we believe that conducting this study on a heterogeneous sample still provides an important contribution to the subject of modern human dental variation.

Subsistence strategies of the analyzed groups

Hunter-gatherers

Four traditional hunter-gatherer populations were analyzed: Agta (Luzon, Philippines), Australian Aborigines (northern and southeastern Australia), Inuit (Point Hope, Alaska), and Bushmen-San (Kalahari Desert). Each group represents distinct dietary regimen and food processing methods. Sexual division of labor within groups has been described in ethnographic studies, as cited below.

Agta. Origin: Philippines. Climate: tropical. Subsistence: hunter-gatherers. Diet: mixed. Sexual division of labor: low (both men and women hunt and gather; Estiko-Griffin and Griffin, 1981; Garcia and Acay, 2003). Dietary differences: low (Minter, 2010). Number of individuals studied: 19 (16 males, 3 females).

Australian Aborigines. Origin: Northern and southeastern Australia. Climate: hot and dry. Subsistence: hunter-gatherers. Diet: mixed. Sexual division of labor: evident (men hunt and women gather; O'Dea et al., 1991). Dietary differences: high (Molnar et al., 1983). Number of individuals studied: 24 (16 males, 8 females).

Inuit. Origin: Point Hope, Alaska, USA. Climate: arctic. Subsistence: hunters (Larsen and Rainey, 1948). Diet: meat-based. Sexual division of labor: strong but not focused on subsistence (men are the only food providers; Costa, 1977; Tomenchuk and Mayhall, 1979).

Dietary differences: low (Costa, 1977). Number of individuals studied: 32 (16 males, 16 females).

San. Origin: Kalahari Desert (Angola, Botswana, and Namibia). Climate: semi-arid. Subsistence: hunter-gatherers (Lee, 1978). Diet: mixed. Sexual division of labor: present and typical (men mainly hunt and women mainly gather; Draper, 1975; Lee, 1978; Schapera, 1930). Dietary differences: low. Number of individuals studied: 6 (4 males, 2 females).

Agriculturalists

Three populations with productive economies were included in the agriculturalist group: Khoe (Hottentott) from South Africa, Batéké-Balali Bantu group from Congo (Africa), and Navajo Indians from Canyon del Muerto (Arizona, USA).

Khoe. Origin: South Africa. Climate: subtropical. Subsistence: pastoralists (husbandry of cattle, goat, and sheep with small admixture of hunting and gathering; Bernard, 1992; Schapera, 1930). Diet: mixed. Sexual division of labor: present but does not focus on subsistence. Dietary differences: low. Number of individuals studied: 11 (5 males, 6 females).

Batéké-Balali. Origin: Congo, Democratic Republic of Congo, and Gabon. Climate: tropical. Subsistence: exclusively agriculture (Trezenem, 1940; White et al., 1981). Diet: mainly crops (Walters, 2010). Sexual division of labor: present but does not focus on subsistence. Dietary differences: low. Number of individuals studied: 10 (6 males, 4 females).

Navajo. Origin: Canyon del Muerto, Arizona, USA. Climate: hot and dry. Subsistence: agriculture (corn, melon, squash, and beans; Hill, 1938; Underhill, 1956). Diet: mainly crops (Underhill, 1956). Sexual division of labor: present but does not focus on subsistence. Dietary differences: low. Number of individuals studied: 20 (15 males, 5 females).

Dental size and wear analysis

High-resolution replicas of dental crowns were obtained following standardized procedures (Galbany et al., 2006). Molar crowns were previously cleaned with pure acetone and ethyl alcohol. Dental impression molds were made using President MicroSystem Affinis Regular body (Coltène-Whaledent) polyvinylsiloxane and casts obtained with polyurethane resin Feropur PR-55 (Feroca Composites) and hardener.

Digital images (300 dpi) of occlusal crown surfaces, including a linear scale for calibration, were obtained from the tooth replicas using a Nikon D40 camera attached to a camera stand at a focal distance of 0.5 m. The scale was placed parallel and at the same height as the occlusal crown surface. Teeth were orientated in a way that the occlusal plane was placed parallel to the camera lens to prevent image distortions. The left side of the jaw was arbitrarily chosen for the analysis, except when the left molar was missing or damaged, in which case, the right antimere was used, when present. Calibrated images were processed using ImageJ software (Abramoff et al., 2004). Four variables were measured: (1) bucco-lingual crown diameter (mm), measured as the distance between the most distal points on the buccal and lingual edges on the occlusal perimeter in occlusal view, perpendicular to the mesio-distal molar alignment; (2) mesio-distal crown diameter (mm), measured as the distance between the most distal points on the mesial and distal edges on the occlusal perimeter in occlusal view, perpendicular to the bucco-lingual diameter; (3) total occlusal area of the crown (mm^2); and (4) the area of dentin exposure (mm^2), the sum of all areas of dentin exposure surfaces within the dental crown perimeter. In order to measure total occlusal area of the crown, the perimeter of the occlusal surface was outlined using the polygon tool in ImageJ, with a minimum of 30 points to define the crown outline. The area of dentin exposure was measured in the same way (Fig. 1), outlining the dentin exposure areas, visible as depressed surfaces in the dental replicas (Galbany et al., 2011). If several spots of dentin exposure were present in one tooth, each was measured separately and the sum of all the areas was calculated as area of dentin exposure (*ADE*) and used in further analyses. Finally, the percentage of dentin exposure (*PDE*) with respect to total occlusal area (*AREA*) was computed as follows $PDE = ADE \times 100 / AREA$.

INSERT Fig. 1 ABOUT HERE

The relative measurement error (*RME*) was calculated prior to the comparative analyses as follows: [$RME = \frac{\Delta\bar{x}}{\bar{x}} * 100;\ \Delta\bar{x} = \frac{\Delta x}{\sqrt{n}}$] (Harris and Smith, 2009). Twenty randomly selected teeth were measured five times, with a 2-week interval between each repetition. Values of *RME* higher than 5.0% are considered too high, indicating that the method was imprecise and not repeatable (Weinberg et al., 2005).

The Shapiro-Wilk's test was used to check the normality of the variable distributions. Variables that failed the normality assumption were rank-transformed and subjected to multivariate analysis of variance. Descriptive and statistical analyses were conducted using PASW v. 18.0 at the $P<0.05$ significance level.

Results

Measurement error variable distribution

The average relative measurement error was significantly smaller than 5% for all tooth measurements: 0.64% for mesio-distal crown diameter, 0.39% for bucco-lingual crown diameter, 0.56% for total occlusal area of the crown, and 3.29% for area of dentin exposure. Thus, the procedure was shown to be highly precise and repeatable.

The variables measuring tooth crown size (mesio-distal crown diameter, bucco-lingual crown diameter, and total occlusal area of the crown) were normally distributed (Shapiro-Wilk's test). In most cases, the area and percentage of dentin exposure failed the normality assumption, so they were rank-transformed before being subjected to multivariate analysis of variance, together with other variables.

Sexual dimorphism

Except for the total occlusal area of the crown in Inuit (M_1: F=7.808, P=0.007; M^1: F=5.716, P=0.024), no significant sexual differences were revealed in any of the analyzed groups (Table 3). Inuit women had smaller total occlusal area of the crown (Table 2), indicating that they generally have smaller teeth than men.

INSERT Table 2 AND Table 3 ABOUT HERE

Intergroup variability

Because only one significant difference between the sexes was found, intragroup variation was analyzed with the sexes pooled (Scott and Turner, 1997). A general multivariate analysis of variances revealed significant differences between groups for all analyzed variables: M_1 mesio-distal crown diameter (F=4.109, P=0.001), M_1 bucco-lingual crown diameter (F=13.570, P<0.001), M_1 total occlusal area of the crown (F=6.579, P<0.001), M_1 area of dentin exposure (F=5.618, P<0.001), M_1 percentage of dentin exposure (F=5.456, P<0.001), M^1 mesio-distal crown diameter (F=4.419, P=0,001), M^1 bucco-lingual crown diameter (F=8.510, P<0.001), M^1 total occlusal area of the crown (F=7.245, P<0.001), M^1 area of dentin exposure (F=4.648, P<0.001), and M^1 percentage of dentin exposure (F=4.641, P<0.001).

Morphology and wear of M^1

Post-hoc Tukey's pairwise comparison revealed very low intergroup variation in mesio-distal crown diameter. Agta vs. Australian Aborigines (P=0.025) and Agta vs. Navajo (P=0.005) presented significant differences, and in both cases the Philippine indigenous group was characterized by smaller mesio-distal crown diameter (Table 2). In addition, Navajo presented greater mesio-distal dimensions than Inuit (P=0.038). All other groups did not differ in this measurement.

Bucco-lingual crown diameter presented higher variation among groups. The Inuit group was characterized by wider M^1 than Agta (P<0.001) and Khoe (P<0.001). Khoe also differed from Australian Aborigines (P=0.037) and Navajo (P=0.048) in having smaller bucco-lingual crown diameter. Similarly, the San group differed significantly from Inuit, Australian Aborigines, and Navajo (P<0.001, P=0.011, and P=0.019, respectively).

Both bucco-lingual and mesio-distal measurements correlate with occlusal area of the tooth (all three variables refer to general tooth size), so it is not surprising that similar relationships were found when analyzing the total occlusal area of the crown. All the above mentioned pairwise differences remained significant, with the exception of Inuit vs. Agta and Inuit vs. Navajo comparisons, which showed no significant differences in total occlusal area of the crown (P=0.129 and P=0.766 respectively).

Both variables related to dental wear, the area and percentage of dentin exposure showed the same variation pattern. In both cases Agta were characterized by lower values of dental wear than Batéké-Balali (P=0.009 and P=0.006, respectively, for area and percentage of dentin exposure), Inuit (P=0.001 and P=0.001), and Navajo (P=0.031 and P=0.043). All results are presented in Table 4 (upper triangular matrix).

INSERT Table 4 ABOUT HERE

Morphology and wear of M_1

Similar to M^1, pairwise analysis demonstrated relatively small variation in mesio-distal crown diameters. Only Australian Aborigines compared with Agta (P<0.001) and Khoe

(P=0.029) showed significant differences. In both cases, the Australian groups were characterized by greater mesio-distal dimensions and thus longer teeth.

Bucco-lingual crown diameter of M_1, on the other hand, showed somewhat greater variation among the analyzed groups as compared to that seen in M^1. Agta had significantly smaller bucco-lingual crown diameter than Inuit (P<0.001), Australian Aborigines (P=0.012), and Navajo (P<0.001), whereas Inuit had significantly greater values than Khoe (P<0.001) and San (P<0.001) and Navajo values were significantly larger than those of San (P<0.001) and Khoe (P<0.001).

As for the total occlusal area of the crown of M_1, Agta differed significantly from Australian Aborigines (P<0.001), Inuit (P=0.004), and Navajo (P=0.001), in all cases showing a smaller occlusal area. Moreover, Australian Aborigines presented greater values than those of Khoe (P=0.007) and San (P=0.022). Navajo were also found to exceed values of Khoe (P=0.015) and San (P=0.038) in the total occlusal area of the M_1 crown.

Contrary to M^1, the area and the percentage of dentin exposure on M_1 did not present exactly the same patterns. The area of dentin exposure differed between Agta and Batéké-Balali (P=0.006), Inuit (P<0.001), and Navajo (P=0.0038), with the Philippine group being characterized by lower values of dentin exposure in all cases. In addition, Batéké-Balali and Khoe differed significantly (P=0.016), with the Batéké presenting greater dental wear. However, the percentage of dentin exposure revealed differences only between Agta and Batéké-Balali (P=0.008) and Agta and Inuit (P=0.001). In both cases, the Philippine group was characterized by less advanced dental wear. All results of the abovementioned analyses are presented in Table 4 (lower triangular matrix).

Hunter-gatherers vs. agriculturalists

When the samples were combined into subsistence strategy clusters (hunter-gatherers vs. agriculturalists), we found no significant differences in tooth size variables (bucco-lingual crown diameter, mesio-distal crown diameter and total occlusal area of the crown) or dental wear variables (area of dentin exposure, percentage of dentin exposure) for M^1 or M_1 (Table 5).

INSERT Table 5 ABOUT HERE

Discussion

The research was conducted to investigate whether differences exist in dental size and/or dental wear among and within various hunter-gatherer and agricultural populations.

Sexual dimorphism

Although previous research reported sexual differences in tooth dimensions in modern humans (Barrett et al., 1963; İşcan and Kedici, 2003; Richardson and Malhotra, 1975; Schwartz and Dean, 2005), our results indicated no substantial variation in bucco-lingual crown diameter, mesio-distal crown diameter, and total occlusal area of the crown between the sexes. The only group that presented significant sexual differences was the Inuit, for total occlusal area of the crown. Inuit men presented higher values of this feature, indicating the possession of generally larger teeth. Our findings are in line with the assumption of Hillson (1996) and Harris (2003) that tooth size is not a sexually distinctive characteristic in modern humans (Ates et al., 2006; Castillo et al., 2011; Harris, 2003; Suazo et al., 2008).

Due to ontogenetic mechanisms caused by selective evolutionary factors (i.e., competition for resources or mating partners), the great apes and hominids express substantial dental morphological variation between the sexes (Brace and Ryan, 1980; Schwartz and Dean, 2001). However, because modern humans are subjected to lower levels of selective pressure, the sexual dimorphism, especially in dental size, has almost disappeared (Castillo et al., 2011; Schwartz and Dean, 2001). Such weakened selective pressures could help to explain the lack of differences in first molar size between men and women in the analyzed groups.

Several previous studies reported no differences in dental wear between the sexes (Kieser et al., 2001; Lovejoy, 1985; Madimenos, 2005), whereas others did find sexual dimorphism in dental wear, with women generally exceeding males in this feature, especially on anterior dentition (Berbesque et al., 2012; Clement and Hillson, 2012; Madimenos, 2005; Molnar, 1971; Richards, 1984). However, there is no previous evidence of sexual differences in dental wear in posterior teeth. Clement and Hillson (2012) reported a lack of such in their study of Igloolik Eskimo, while reporting extensive differences in wear of anterior dentition. In many hunter-gatherer groups, anterior dentition is often used in various paramasticatory actions, resulting in more pronounced wear. According to Costa (1977), posterior teeth are more involved in grinding and chewing actions related to food processing, rather than other cultural practices not related to food processing. Consequently, the lack of sexual differences in dental wear in the studied populations suggests that the diets of the two sexes do not differ sufficiently to produce a substantial variation in dentin exposure. Therefore, we can assume that the distinct sex roles described in these societies have no significant effect on the overall abrasiveness of the food chewed and/or consumed by each sex.

In traditional hunting and gathering societies, goods from foraging activities are shared among all members of the family and within the whole community after food providers come back to the camp site (Draper, 1975; Guimares de Souza, 2007; Hawkes et al., 2001; Lee, 1978; Minter, 2010; Schapera, 1930). Thus, although men and women target different kinds of foods, at the end of the day they share their acquisitions and consume similar amounts of different food types. In agricultural populations the food quest is not as sexually divided as in hunter-gatherer groups, and agricultural technological advances, especially those related to food processing, shifted the food preparation habits. The crops and other vegetable foods cultivated in agricultural societies, as well as animal husbandry, provide food that is usually processed before consumption. This fact minimizes the dietary differences between the sexes and can result in the absence of sexual dimorphism in dental wear.

Frayer (1980) proposed that hunter-gatherer societies living in harsh environments would be characterized by a stronger separation in sex roles than agriculturalists, where sexual division of labor would not be so strict. If this were the case, we would expect that hunter-gatherers, having a sex-related labor division mainly focusing on the food quest, would show higher levels of sexual dimorphism in dental wear than agro-pastoralists. However, regardless of their economic strategies (hunter-gatherer or agriculturalist), we found no sexual dimorphism in dental wear among the analyzed samples. Moreover, those groups in which men were mainly responsible for bringing meat to the camp and women for the acquisition of other types of foods (mostly plants but also small animals), such as San or Australian Aborigines, would be expected to show greater sex-related differences in molar wear than those with shifted sex roles, such as Agta, or those where men are responsible for providing all food items, such as Inuit. This assumption was not confirmed either. Therefore, our findings suggest that dental wear measures cannot be used as a reliable indicator of differential access to food resources caused by sexual division of labor. In fact, our use of a standardized and reliable method for measuring dentin exposure showed no sexual dimorphism in dental wear in modern non-industrialized human societies, despite the fact that there are differences in dietary and cultural practices between the sexes.

Intergroup variation

In terms of tooth size (bucco-lingual crown diameter, mesio-distal crown diameter, and total occlusal area), the analyzed groups showed some variation. Bucco-lingual diameter seems to present greater variability among modern humans than mesio-distal diameter. This could be interpreted that bucco-lingual crown diameter is probably more sensitive to external factors than mesio-distal crown diameter, reflecting the different environments of the analyzed groups.

The group variation in tooth size could be summarized as follows: Agta, San, and Khoe groups together presented lower values of the analyzed features than Australian Aborigines, Inuit, and Navajo. Although previous authors have proposed that agriculturalists would show reduced tooth size (Hinton et al., 1980; Larsen, 1995; Y'Edynak, 1989), this idea is not clearly reflected in our results, as Agta and San, who are typical hunting and gathering groups, have smaller teeth than Navajo, who have an agro-pastoral subsistence pattern. This inconsistency suggests that genetic factors determine dental size, rather than external or environmental influences (Dempsey et al., 1999; Garn et al., 1977). Australian Aborigines, Native Americans, and Eskimos were reported to have relatively large teeth and the Negritos (Agta) some of the smallest (Hanihara and Ishida, 2005), which is in accord with our results. The decrease of tooth size in Negritos has been associated with their generally reduced body size (Hanihara and Ishida, 2005; Hillson, 1996). An interesting discordance are the rather low values of tooth size variables in African groups (San and Khoe). Hanihara and Ishida (2005) have reported that sub-Saharan African groups are characterized by relatively large tooth dimensions, but our results did not reflect that. This could be due to the fact that these groups were substantially underrepresented in terms of number of analyzed individuals, which could greatly impact our results. However, the coherent pattern for both San and Khoe groups, for both molars, and for bucco-lingual crown diameter and total occlusal area of the crown is at least noteworthy and should warrant additional study. Khoe and San are known to have small body size compared to other Sub-Saharan peoples (Schapera 1930). This may be the reason for their small tooth size.

However, dental wear variables (area and percentage of dentin exposure) presented similar variation patterns in both analyzed teeth. In general, the Inuit, Batéké-Balali, and Navajo were characterized by higher values of dental wear than the Agta group. This result is somewhat surprising, as we would have expected hunter-gatherers to present more pronounced dental wear than agricultural groups, as was reported elsewhere (Deter, 2009; Eshed et al., 2006; Hinton, 1982). Agta are the indigenous inhabitants of the Philippine islands and are typical representatives of the hunting-gathering lifestyle, with a diet based on hunted meat and gathered wild fruits and other plants (Estiko-Griffin and Griffin, 1981; Minter, 2010). Inuit are arctic hunters, basing their subsistence exclusively on sea mammals' meat eaten raw, frozen, or dry (Costa, 1977; Larsen and Rainey, 1948; Tomenchuk and Mayhall, 1979). Batéké-Balali and Navajo are representatives of agricultural societies, with crop-based diets (Trezenem, 1940; Underhill, 1956; Walters, 2010; White et al., 1981). We can therefore assume that the diet types of the Inuit, Batéké-Balali, and Navajo are more abrasive than that of the typical hunting and gathering diet of Agta. Frozen or dried meat stored underground is difficult to chew, which implies prolonged mastication that increases the masticatory loadings (Holmes and Ruff, 2011; Waugh, 1937) and results in greater enamel loss (Tomenchuk and Mayhall, 1979). Additionally, the underground storage of dried and frozen meat (Brubaker et al., 2009; El-Zaatari, 2008; Larsen and Rainey, 1948) results in the incorporation of a significant amount of sand grains and gritty contaminants to the diet, which have been shown to cause extensive dental wear (Davies and Pedersen, 1955). Crop-based diets, although they require food processing prior to consumption, can also be highly abrasive. The use of grinding stones in agricultural populations has been shown to incorporate extraneous grit particles into the flour and result in severe dentin exposure (Larsen, 1995; Molleson and Jones, 1991). However, it cannot be disregarded that dental enamel structure of Agta was more resistant to abrasion.

Hunter-gatherers vs. agriculturalists

While we found differences in dental size among some of the studied populations, no differences were observed when they were pooled into subsistence strategy groups. Dental wear reduction is an evolutionary trend that is usually associated with the implementation of new technologies and methods of food processing and dietary changes (Hinton et al., 1980; Larsen, 1995; Y'Edynak, 1989). These studies revealed a relationship between this trend and the decline of the nutritional status of foods consumed in agricultural populations, which reduced maternal health status and resulted in smaller permanent teeth in children (Larsen, 1995). Consequently, we would expect that agricultural groups would be characterized by smaller teeth. However, our results do not support this, but instead suggest that the subsistence pattern and related food processing techniques do not influence the ontogeny of dental development.

Variation in dental wear between hunter-gatherers and agricultural populations has been widely reported (Deter, 2009; Eshed et al., 2006; Hinton, 1982). Surprisingly, our results for both dental size and dental wear are not consistent with this idea. The general view is that agriculturalists, who use grinding stones and pottery for processing and softening foodstuffs, are characterized by lower degrees of dental wear (Deter, 2009). However, both groups have been shown to have relatively abrasive diets (Smith, 1984), which could equalize the measures in hunter-gatherers and agriculturalists. Additionally, Larsen (1995) and Molleson and Jones (1991) reported that the use of grinding stones may result in highly abrasive grit elements in flour, leading to severe dentin exposure in agricultural populations. Moreover, none of the agricultural populations analyzed based their economy exclusively on cultivated plants, which might also contribute to the lack of dental wear variation between the two groups.

Although this research had several limitations, including the impossibility of addressing tooth age and the focus on only a single type of tooth, we believe that it is still a valuable contribution to the literature on dental wear because of the use of single, standardized, and reliable method of analysis and the wide range of groups analyzed.

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Figure legend

Fig. 1. Occlusal view of upper (a) and lower (b) postcanine (P1–M2) teeth in San (South Africa) and Agta (Philippines) individuals (left and right, respectively) showing different percentages of dentin exposure (PDE) in M1. Code number indicates museum record (see Table 1). Mesial: left; buccal: down. Scale bar: 5 mm.

Table 1. Samples from human populations studied (group), acronym (ID), provenance, subsistence strategy (hunter-gatherers - HG; agriculturalists with or without raising animal and/or fishing - AGR); *N*: total number of individuals; *n*1: total number of studied teeth; *n*2: number of teeth included in the analysis of dental wear (showing dental exposure); sample sizes of M^1 (upper first molar) and M_1 (lower first molar), with the number of teeth showing dentin exposure in brackets; institution where the remains are curated (collection: American Museum of Natural History - AMNH; Musée de 1'Homme (Paris) - MH).

Group	**ID**	**Provenance**	**Strategy**	***N***	***n*1**	***n*2**	**Males**	**Females**	**M^1**	**M_1**	**Collection**	**Reference**
Agta	**AGT**	Luzon, Philippines	**HG**	19	30	9	16	3	(4)/16	(5)/14	MH	Genet-Varcin, 1949
Australian Aborigines	**AUS**	North and SE Australia	**HG**	24	31	17	16	16	(6)/14	(11)/17	AMNH, MH	
Batéké-Balali	**BAT**	Congo, Africa	**AGR**	10	13	12	5	6	(7)/8	(5)/5	MH	Trezenem, 1940
Inuit	**INU**	Point Hope, Alaska	**HG**	32	92	88	16	8	(27)/31	(61)/61	AMNH	Costa, 1977
Khoe (Hottentot)	**KHO**	South Africa	**AGR**	11	17	9	15	5	(5)/10	(4)/7	AMNH, MH	
Navajo	**NAV**	Canyon del Muerto, Arizona	**AGR**	20	32	29	4	2	(14)/16	(15)/16	AMNH	
San	**SAN**	South Africa	**HG**	6	10	7	6	4	(3)/6	(4)/4	AMNH, MH	
			Total	**122**	**225**	**171**	**78**	**44**	**66)/101**	**(105)/124**		

Table 2. Descriptive statistics for the variables analyzed (BL: bucco-lingual crown diameter; MD: mesio-distal crown diameter; AREA: total occlusal area of the crown; ADE: area of dentin exposure; PDE: percentage of dentin exposure) by population (ID; see Table 1), position in the jaw (Jaw: L - lower first molar, U - upper first molar), and sex (M - male; F - female).

				BL (mm)		**MD (mm)**		**AREA (mm^2)**			**ADE (mm^2)**			**PDE (%)**		
ID	**Jaw**	**Sex**	***n***	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	***n***	**Median**	**Mode**	**Range**	**Median**	**Mode**	**Range**
AGT	L	M	12	10.13	0.60	11.11	0.55	94.79	7.81	5	22.26	2.35	26.44	21.91	2.44	27.83
		F	2	10.30	0.00	11.57	0.08	100.21	2.39	0	.	.	.	.	.	.
		Total	14	10.15	0.55	11.18	0.53	95.56	7.48	5	22.26	2.35	26.44	21.91	2.44	27.83
	U	M	13	10.90	0.56	10.71	0.48	98.32	5.40	4	6.57	2.26	9.49	6.64	2.19	9.58
		F	3	10.80	0.56	10.80	0.14	98.28	3.77	0	.	.	.	.	.	.
		Total	16	10.88	0.54	10.73	0.43	98.31	5.03	4	6.57	2.26	9.49	6.64	2.19	9.58
AUS	L	M	11	10.87	0.75	12.30	0.91	110.84	12.40	7	16.65	1.94	35.44	15.41	1.91	29.66
		F	6	11.25	1.11	12.37	1.33	117.01	22.03	4	11.74	6.61	6.90	9.24	7.78	4.77
		Total	17	11.00	0.88	12.33	1.04	113.02	16.03	11	11.96	1.94	35.44	9.68	1.91	29.66
	U	M	8	11.50	1.02	11.50	0.60	111.48	11.57	3	4.74	2.69	17.24	3.59	2.26	15.70
		F	6	11.73	0.87	11.61	1.27	113.58	18.32	3	19.22	8.81	35.52	16.80	7.93	32.82
		Total	14	11.60	0.93	11.55	0.90	112.38	14.23	6	14.01	2.69	41.64	12.37	2.26	38.49
BAT	L	M	2	10.31	0.65	11.38	0.64	98.35	10.49	2	20.15	18.95	2.41	20.70	17.91	5.57
		F	3	11.00	0.60	11.94	0.58	112.07	10.31	3	23.30	16.66	20.81	23.26	14.12	17.63
		Total	5	10.72	0.66	11.71	0.60	106.58	11.71	5	21.35	16.66	20.81	23.26	14.12	17.63
	U	M	6	11.12	0.62	10.61	0.91	97.87	11.98	6	18.11	3.20	29.75	18.73	2.81	32.75
		F	2	11.87	0.41	11.40	0.11	112.45	0.96	1	33.35	33.35	0.00	29.84	29.84	0.00
		Total	8	11.31	0.64	10.81	0.85	101.51	12.17	7	18.11	3.20	30.15	21.06	2.81	32.75

INU	L	M	24	11.67	0.70	11.97	0.45	111.75	9.24	24	16.87	1.24	57.27	14.74	1.13	55.61
		F	37	11.36	0.58	11.68	0.69	105.08	9.01	37	14.17	1.14	86.19	13.38	1.04	84.51
		Total	61	11.48	0.64	11.79	0.62	107.70	9.60	61	14.33	1.14	86.19	13.43	1.04	84.51
	U	M	17	11.99	0.72	11.15	0.82	110.71	10.11	15	17.24	0.49	67.43	13.50	0.46	67.08
		F	14	11.87	0.55	10.78	0.59	102.14	9.71	12	7.86	0.32	52.11	8.60	0.34	50.69
		Total	31	11.94	0.64	10.99	0.74	106.84	10.69	27	16.81	0.32	67.60	13.17	0.34	67.20
KHO	L	M	2	10.91	1.15	11.79	0.91	106.44	20.56	1	9.14	9.14	0.00	7.56	7.56	0.00
		F	5	10.02	0.78	11.12	0.64	91.05	9.67	3	9.42	2.53	7.17	9.65	3.07	8.50
		Total	7	10.28	0.90	11.31	0.72	95.45	13.75	4	9.28	2.53	7.17	8.61	3.07	8.50
	U	M	5	10.71	0.38	10.99	0.65	96.93	7.41	4	11.26	0.85	17.61	11.54	0.88	17.74
		F	5	10.53	0.74	10.67	0.73	90.48	8.36	1	8.36	8.36	0.00	9.13	9.13	0.00
		Total	10	10.62	0.56	10.83	0.67	93.71	8.19	5	9.70	0.85	17.61	11.14	0.88	17.74
NAV	L	M	12	11.63	0.49	11.64	0.78	111.93	8.50	12	12.84	2.86	42.06	12.27	2.76	37.29
		F	4	11.64	0.66	11.62	0.80	112.20	6.88	3	3.36	3.00	35.45	3.24	2.72	30.44
		Total	16	11.63	0.51	11.63	0.75	112.00	7.90	15	10.73	2.86	42.06	9.12	2.72	37.33
	U	M	11	11.56	1.01	11.76	0.53	112.81	12.14	10	9.09	3.02	13.61	8.17	2.52	11.67
		F	5	11.40	0.44	11.39	0.49	108.87	7.36	4	9.32	4.06	37.85	8.72	4.12	32.12
		Total	16	11.51	0.86	11.64	0.53	111.58	10.78	14	9.22	3.02	38.89	8.48	2.52	33.72
SAN	L	M	2	10.41	0.47	11.84	0.75	100.89	10.80	2	13.37	13.35	0.03	13.33	12.33	1.99
		F	2	9.43	0.14	11.00	0.31	86.07	3.00	2	13.54	6.35	14.38	15.54	7.56	15.95
		Total	4	9.92	0.63	11.42	0.67	93.48	10.73	4	13.37	6.35	14.38	13.33	7.56	15.95
	U	M	3	10.31	1.32	10.97	0.27	94.90	13.10	1	23.96	23.96	0.00	21.81	21.81	0.00
		F	3	10.32	0.91	10.43	0.55	86.53	8.89	2	9.67	7.80	3.74	11.93	9.34	5.17
		Total	6	10.32	1.01	10.70	0.49	90.72	11.01	3	11.54	7.80	16.16	14.51	9.34	12.47

Table 3. Multivariate analysis of variance (MANOVA) for sexual differences in dental size (BL: bucco-lingual crown diameter; MD: mesio-distal crown diameter; AREA: total occlusal area of the crown) and dental wear (ADE: area of dentin exposure; PDE: percentage of dentin exposure) for the lower and upper first molar. Significant differences (*P*<0.05) are shown in bold.

LOWER	MANOVA		BL		MD		AREA		ADE		PDE	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
AGT	0.314	0.891	0.145	0.710	1.331	0.271	0.892	0.364	0.948	0.349	0.961	0.346
INU	2.011	0.091	3.483	0.067	3.322	0.073	**7.808**	**0.007**	0.219	0.642	0.053	0.819
KHO	0.258	0.894	1.496	0.276	1.256	0.313	2.121	0.205	0.000	0.999	0.027	0.876
AUS	0.693	0.640	0.740	0.403	0.015	0.905	0.560	0.466	0.004	0.953	0.013	0.911
NAV	0.981	0.475	0.002	0.968	0.003	0.960	0.003	0.954	2.573	0.131	2.360	0.147
SAN	2.352	0.419	8.077	0.105	2.143	0.281	3.494	0.203	0.002	0.967	0.007	0.940
BAT	14.668	0.189	1.489	0.310	.067	0.378	2.101	0.243	0.146	0.728	0.012	0.919
UPPER												
AGT	0.171	0.967	0.091	0.768	0.088	0.772	0.000	0.990	0.988	0.337	1.004	0.333
INU	1.941	0.123	0.259	0.614	1.961	0.172	**5.716**	**0.024**	0.726	0.401	0.468	0.500
KHO	0.465	0.788	0.234	0.642	0.525	0.489	1.669	0.233	3.182	0.112	3.092	0.117
AUS	0.345	0.872	0.201	0.662	0.045	0.835	0.070	0.796	1.084	0.318	1.182	0.298
NAV	0.658	0.663	0.117	0.737	1.827	0.198	0.442	0.517	0.007	0.937	0.034	0.856
SAN	2.984	0.406	0.000	0.995	2.360	0.199	0.837	0.413	0.066	0.810	0.172	0.700
BAT	0.555	0.742	2.467	0.167	1.336	0.292	2.666	0.154	0.536	0.492	0.724	0.428

Table 4. Post-hoc Tukey's analysis among populations in dental size (BL: bucco-lingual crown diameter; MD: mesio-distal crown diameter; AREA: total occlusal area of the crown) and dental wear (ADE: area of dentin exposure; PDE: percentage of dentin exposure) of M_1 (lower triangular matrix) and M^1 (upper triangular matrix). Significant differences (P<0.05) are shown in bold.

BL	AGT	AUS	BAT	INU	KHO	NAV	SAN
AGT	-	0.117	0.830	**<0.001**	0.974	0.193	0.667
AUS	**0.012**	-	0.972	0.766	**0.028**	1.000	**0.009**
BAT	0.665	0.983	-	0.312	0.473	0.995	0.166
INU	**<0.001**	0.141	0.203	-	**<0.001**	0.485	**<0.001**
KHO	1.000	0.206	0.915	**<0.001**	-	**0.048**	0.983
NAV	**<0.001**	0.112	0.126	0.984	**<0.001**	-	**0.015**
SAN	0.996	0.066	0.546	**<0.001**	0.980	**<0.001**	-

MD	AGT	AUS	BAT	INU	KHO	NAV	SAN
AGT	-	**0.025**	1.000	0.886	1.000	**0.005**	1.000
AUS	**<0.001**	-	0.196	0.158	0.162	1.000	0.162
BAT	0.770	0.614	-	0.994	1.000	0.082	1.000
INU	0.060	0.094	1.000	-	0.996	**0.038**	0.967
KHO	1.000	**0.029**	0.960	0.618	-	0.059	0.967
NAV	0.578	0.080	1.000	0.984	0.953	-	0.072
SAN	0.997	0.249	0.996	0.948	1.000	0.998	-

AREA	AGT	AUS	BAT	INU	KHO	NAV	SAN
AGT	-	**0.008**	0.922	0.129	0.931	**0.010**	0.740
AUS	**<0.001**	-	0.242	0.661	**0.001**	1.000	**0.001**
BAT	0.433	0.898	-	0.861	0.706	0.302	0.487
INU	**0.004**	0.541	1.000	-	**0.015**	0.766	**0.015**
KHO	1.000	**0.007**	0.564	0.069	-	**0.001**	0.998
NAV	**0.001**	1.000	0.955	0.783	**0.015**	-	**0.001**
SAN	1.000	0.022	0.532	0.142	1.000	**0.038**	-

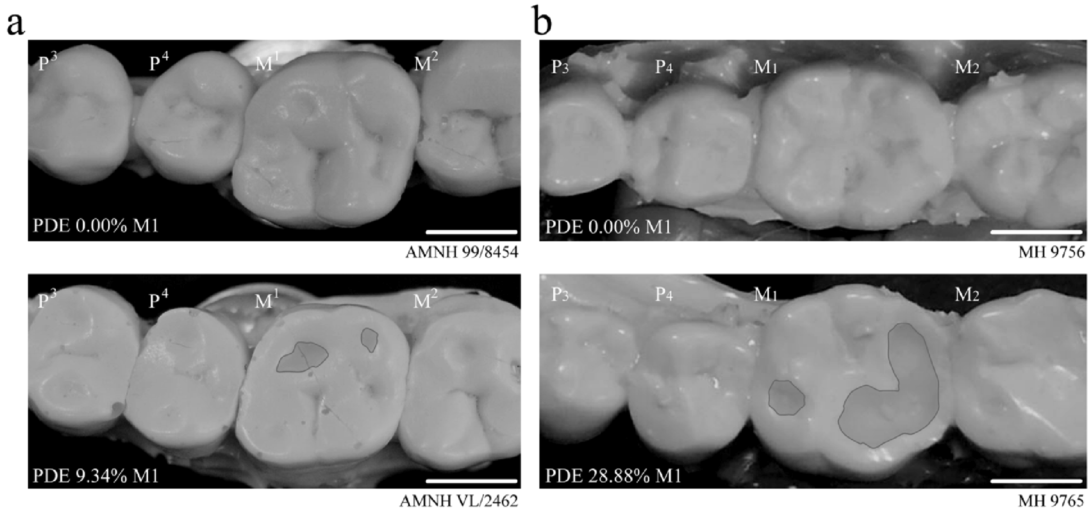
ADE	AGT	AUS	BAT	INU	KHO	NAV	SAN
AGT	-	0.827	**0.009**	**0.001**	0.900	**0.031**	0.797
AUS	0.755	-	0.206	0.121	1.000	0.601	1.000
BAT	**0.006**	0.100	-	0.998	0.259	0.653	0.653
INU	**<0.001**	0.079	0.841	-	0.208	0.990	0.734
KHO	1.000	0.973	**0.043**	0.058	-	0.675	1.000
NAV	**0.038**	0.604	0.719	0.996	0.299	-	0.964
SAN	0.244	0.799	0.971	1.000	0.495	1.000	-

PDE	AGT	AUS	BAT	INU	KHO	NAV	SAN
AGT	-	0.874	**0.006**	**0.001**	0.873	**0.043**	0.728
AUS	0.835	-	0.133	0.103	1.000	0.605	0.998
BAT	**0.008**	0.094	-	0.992	0.234	0.883	0.658
INU	**0.001**	0.068	0.844	-	0.262	0.984	0.825
KHO	1.000	0.987	0.052	0.075	-	0.776	0.999
NAV	0.058	0.608	0.702	0.993	0.371	-	0.990
SAN	0.184	0.655	0.991	1.000	0.415	0.998	-

Table 5. Comparison of variables (BL: bucco-lingual crown diameter; MD: mesio-distal crown diameter; AREA: total occlusal area of the crown; ADE: area of dentin exposure; PDE: percentage of dentin exposure) between subsistence strategies (hunter-gatherer vs. agriculturalist) for the lower and upper first molars. Multivariate analysis of variance was performed at a significance level of $P<0.05$.

	Lower		Upper	
	F	*P*	*F*	*P*
MANOVA	2.037	0.078	2.028	0.082
BL	0.001	0.974	2.112	0.149
MD	1.744	0.189	1.475	0.230
AREA	0.055	0.814	0.046	0.830
ADE	0.033	0.855	1.148	0.287
PDE	0.022	0.883	1.264	0.264

Fig. 1.


a
b
P3
P4
M1
M2
PDE 0.00% M1
AMNH 99/8454
PDE 0.00% M1
MH 9756
PDE 9.34% M1
AMNH VL/2462
PDE 28.88% M1
MH 9765