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Dental morphology and dental wear as dietary and ecological indicators: sexual and inter-group differences in traditional human populations

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Dental morphology and dental wear as dietary and ecological indicators: sexual and inter-group differences in traditional modern human populations

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“*Now is no time to think of what you do not have.*

Think of what you can do with what there is.”

The Old Man and the Sea, Ernest Hemingway (1952).

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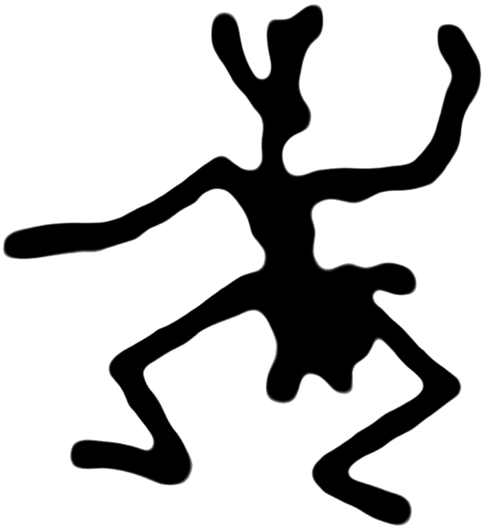


INTRODUCTION

Dental anthropology offers an excellent insight into understanding individual and population behavior, living conditions and environmental influences through biological, ecological and cultural settings. Teeth constitute an excellent multidisciplinary material for research in dentistry, comparative anatomy, paleontology and paleoanthropology, genetics and forensic science, among others. They can be used to make inferences on hominid evolution, ecological adaptations, biological affinities among species, cultural practices and overall health and pathological conditions, as well as to identify individuals in the field of forensic dentistry (Alt et al., 1998).

Dental studies are a particularly important branch of physical anthropology, because teeth are very special structures of human anatomy that play an essential role in nutrition. Their main function is to tear, grind, crush and chew food items to facilitate their intake and digestion. Teeth are the only skeletal part of human anatomy in direct contact with the external environment. As a consequence of this daily activity, the enamel surfaces of teeth can be scratched in various ways reflecting certain aspects of human-nature interactions (Brothwell, 1981; Molnar, 1972, Wood, 1992). As a result, teeth can be used as mirrors of individual´s diets, lifestyles and cultural practices.

Two other very important characteristics account for the fact that teeth are used in a wide range of anthropological studies. In the first place, teeth show an excellent preservation in the archaeological deposits due to the resistance of the enamel tissue, their major, external component. As a consequence, teeth are one of the most common, often the only, fossil remain encountered at an excavation site. On the other hand, teeth are the only structure of the human body that is not affected by the remodelling process once their mineralization is completed (Dahlberg, 1971; Kelley and Larsen, 1991; Thomason, 1997; Riga et al., 2013). Therefore, they are significantly less sensitive to environmental fluctuations than any other skeletal part of the body, which provides a high ontogenetic stability to certain anatomical traits (Alt et al., 1998) that can be used in studies of taxonomical relationships among modern humans or fossil species. Other traits, however, strongly reflect environmental conditions, such as dental wear, hypoplastic stress indicators, dietary habits or ecological adaptations.

Additionally, teeth play an important role in communication, as certain sounds of our language can be pronounced only with the involvement of teeth. This function is crucial in the development of social aspects of human behavior. Teeth also possess other, more secondary functions: tongue protection and support of facial muscles that indirectly determine one's appearance.

Humans are *diphyodont*, which means that they develop two successive sets of teeth during their lifetime: deciduous and permanent. Deciduous teeth start to erupt around the age of 6-12 months and last until 12 years old, when the last deciduous tooth is replaced by its permanent substitute. The complete deciduous dentition consists of 20 teeth: two incisors, one canine and two molars in each quadrant. The function of the deciduous dentition is basically to help in eating and speaking before the permanent teeth erupt. Due to the fact that teeth do not grow in size, once formed, they maintain their original size, so the child's mouth is too small to fit permanent teeth, and the adult's mouth is too big for the deciduous dentition. Therefore, deciduous teeth play the same role as the permanent ones until the tooth arch is big enough to fit the permanent dentition. This process starts around 6 years old, when the first permanent molar erupts, usually the lower one, and ends at the age of 18-25 when the last permanent tooth, the third molar, is expected to emerge (otherwise, the second permanent molar erupts around the age of 12). After this dental transition, permanent teeth remain functional in the mouth during the rest of an individual's life, and the only natural modification they suffer is wear, being the result of their function. The permanent dentition includes 32 teeth: two incisors, one canine, two premolars and three molars in each quadrant.

Teeth are also very specialized structures. Humans are *heterodont,* which means that they have more than one tooth kind within each set. Human teeth are divided into four classes: incisors, canines, premolars and molars, and each one of them has a distinct morphology and a specialized function. Incisors are the first teeth to contact food and are used to bite and separate the portions of food for its later processing in the mouth. Canines help the incisors in their role and are also used for tearing and ripping food pieces. Premolars, and especially molars, are used to grind and chew food portions.

1. Tooth morphology

Each tooth consists of a crown and a root, covered with enamel and cementum, respectively (*Figure 1*). Both structures meet at the cement-enamel junction (CEJ), also referred to as the cervical line. The root is placed into the alveolar socket of the jawbones (maxilla and mandible) supported by the alveolar process, whereas the crown emerges into the oral cavity. Below the enamel and cementum layers lies the dentine tissue that surrounds the pulp cavity, which is the only soft dental material.

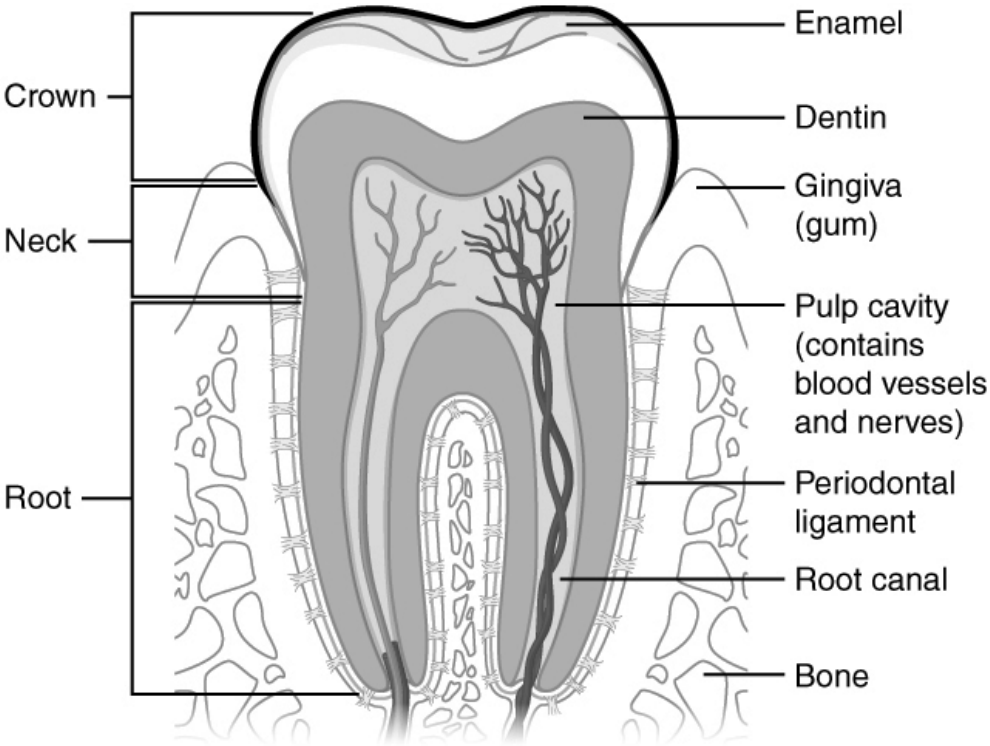


***Figure 1**. Dental morphology of human teeth*

Apart from these overall similarities in dental structure, tooth morphology varies depending on the tooth type, as well as on the maxillary bone in which the tooth is placed (upper or lower), which is especially visible in the incisors (larger in the maxilla) and molars (with different cusp patterns). I shall now describe the overall morphology of each tooth in the permanent dentition.

a. Incisors

There are eight incisors (*Figure 2*) in the mouth, four in each jaw and two in each quadrant (central and lateral incisors), placed next to each other. The maxillary and mandibular central incisors connect both arcades of the jaw, while the lateral/second incisors contact with the canines on their distal side. Incisors are the only teeth without evident cusps (the vestiges of three cusps, the *mamellons*, disappear very fast after eruption). Their incisal surface forms a sharp edge that serves as a cutting "blade". The role of the incisors is to shear, cut and separate pieces of food for their later processing during mastication.

The maxillary central incisors are characterized by their wide mesio-distal dimension, the widest of all teeth (Nelson and Ash, 2010), and rectangular shape of the crown from the labial aspect, with a slightly convex surface. The mesial outline of this tooth, forms a labial view, and is generally straight or slightly convex, whereas the distal outline is frequently much more convex. The incisal plane is usually straight and sharp. From the lingual aspect the tooth is concave in the upper part and shows mesial and distal borders forming marginal ridges that surround the concavity called *lingual fossa*, while the lower part is slightly curved, forming a structure called *cingulum*.

The maxillary lateral incisors, complement the function and present similar characteristics to their central counterpart, however they are significantly smaller in most dimensions. Its labial surface is slightly more convex, while the lingual one is usually not as concaved but with marked marginal ridges and a prominent *cingulum*.

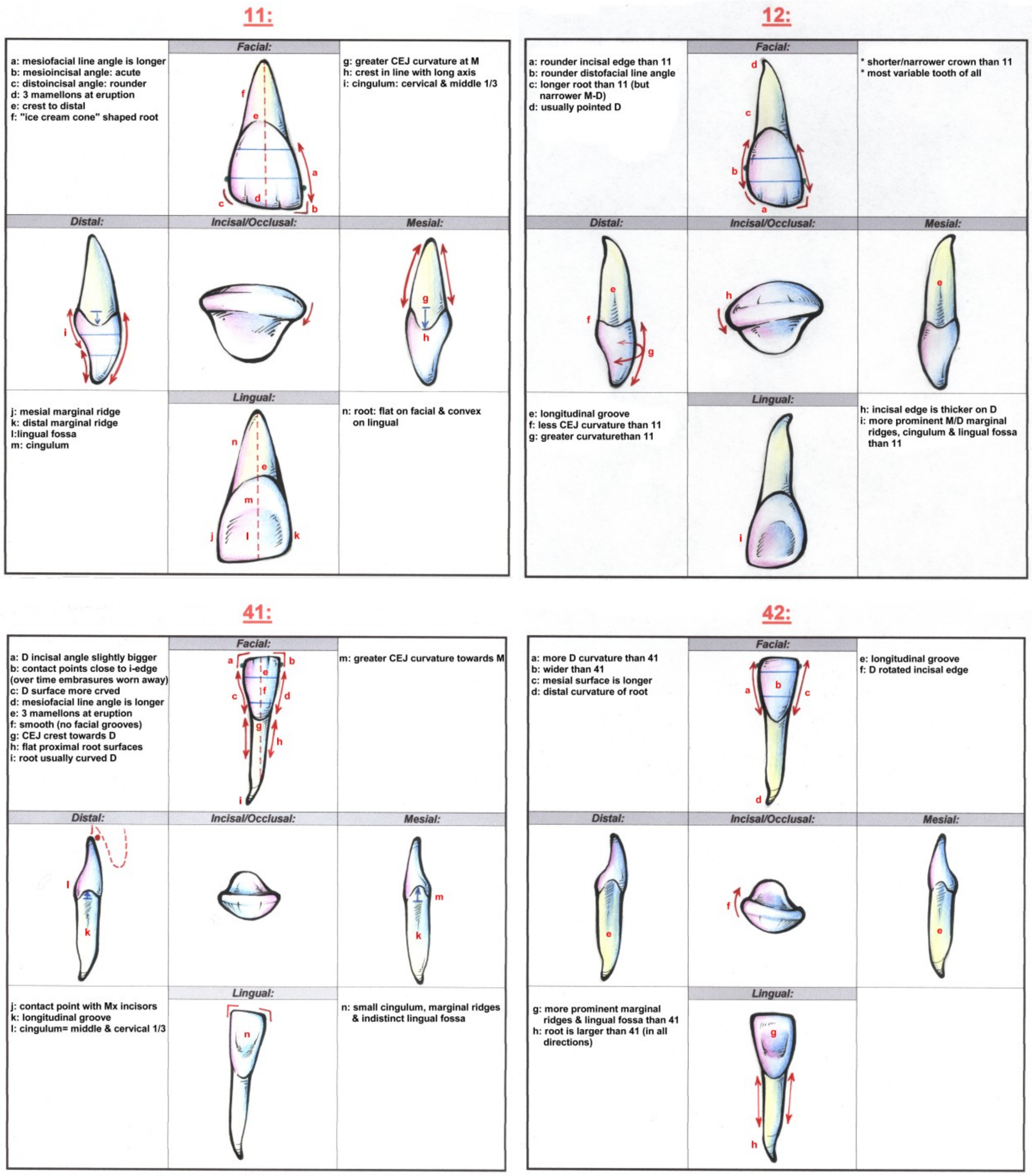


***Figure 2**. Dental morphology of the human right upper first (11, I^1) and second (12, I^2) incisors, and lower first (41, I_1) and second (42, I_2) ones.*

The mandibular central and lateral incisors have a very distinct morphology compared to their upper counterparts, but they are very similar to one another. They are usually the most mesio-distally narrow teeth in the whole set, and the central incisor tends to be somewhat narrower than the lateral. In fact, the mandibular central incisor is very often the smallest tooth of all. The labial surface of these teeth is regular, elongated and only slightly curved. The lingual surface is not as concave, as in its upper counterpart, but the *cingulum* is still present. The marginal ridges are not as prominent as in the maxillary central incisor. All the incisors have only one root, though their length and width may vary.

b. Canines

Canines, placed between incisors and premolars, have a dual function. In addition to tearing pieces of food, they complement both of their neighbors in their actions. Upper and lower canines are quite similar in their morphology, but slightly differ in size as the upper are wider than the lower ones (*Figure 3*). They only have one, single and prominent cusp and one root. They are usually the longest/highest teeth in the whole set. Most of their surfaces are strongly convex, with marginal ridges visible on the lingual surface, and show a prominent *cingulum*, especially in the upper canine. The lingual surface of the mandibular canine is flatter than that in the upper canine, with only a slightly developed *cingulum* and marginal ridges.

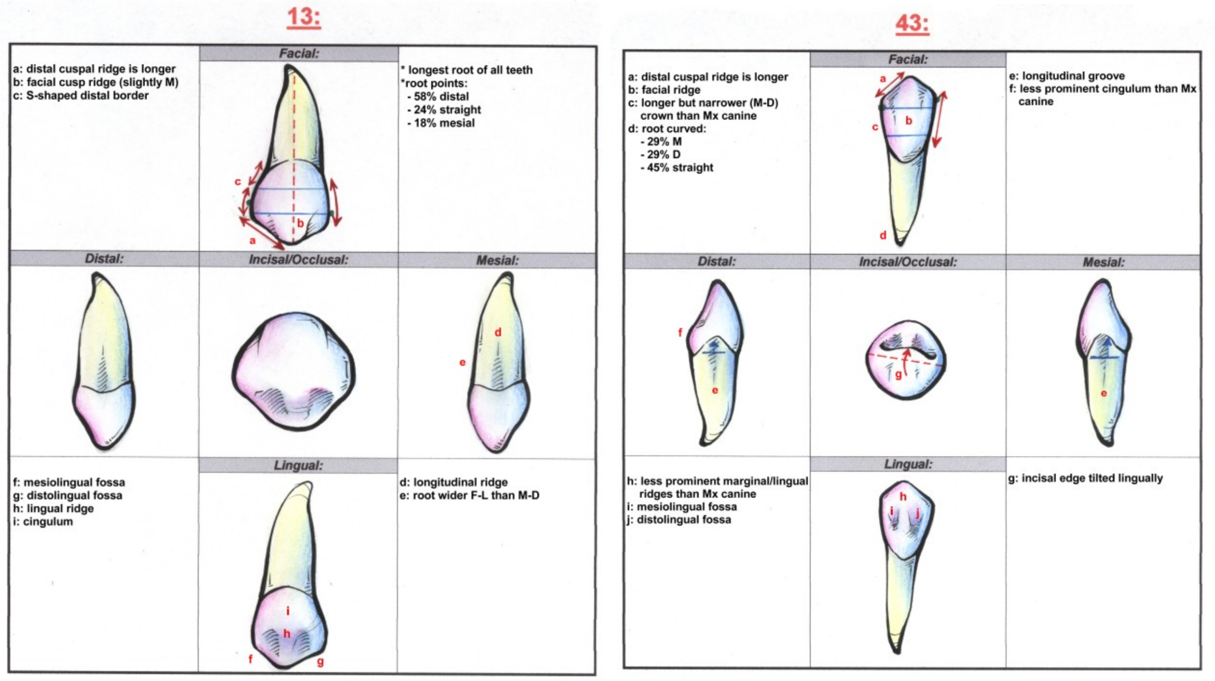


***Figure 3**. Dental morphology of the human right upper (13, C') and lower (43, $C_{,}$) canines.*

c. Premolars

Premolars occupy the place of the deciduous molars, behind the canines. There are two premolars per quadrant, respectively referred to as the third and fourth premolar, due to the fact that primitive mammals had four premolars, the first two of which were lost during evolution of the clade. Premolars (*Figure 4*) most frequently have two cusps (although they can vary in this matter from one to three cusps, especially mandibular premolars) and one or two roots. The crown is frequently more elongated bucco-lingually than mesio-distally. Their function combines the function of canines (shearing food) and molars (grinding food). Additionally, they support and maintain face verticality (Woelfel, 1990). Premolars and molars are very often referred to as posterior teeth. Both lack incisal cutting edges because their crown is flat and shows a broader occlusal surface. The upper third premolar (P^3) is usually bigger than the fourth (P^4), both in crown and root dimensions.

From a buccal view, the crown of premolars has a somewhat pentagon shape with the distal ridge being longer than the proximal. The buccal surface is slightly curved and shows two facial grooves. The mesial ridge of the main cusp is longer than the distal one in the upper first premolar, though shorter in the other ones. The lingual surface is convex, although slightly narrower than the buccal one. The lingual cusp is sharp, but noticeably smaller than its buccal counterpart, with the tip bending mesially, except in the upper fourth premolar, in which they are similar in size. This cusp size difference is more marked in the mandibular premolars because the crown tends to bend lingually, whereas it is strait in the upper premolars. The mandibular fourth premolar is frequently slightly bigger than the third one, although its crown is usually a bit shorter. The buccal surface of the mandibular third premolar is convex and shows well-marked facial grooves, lees visible on the other premolars.

From an occlusal perspective, the central groove and mesial and distal fossa are well marked, more centrally placed (bucco-lingually) in the upper premolars than in the lower ones that show a smaller lingual cusp and a diamond-shape occlusal contour. An occlusal Y-type cusp pattern, with two lingual cusps in addition to the buccal main cusp, may be observed in the lower fourth premolar. One or two roots may be present at the upper third premolar, though with a furcation at the apical third of the root, whereas the other premolars are single-rooted with the root more frequently curved distally than mesially.

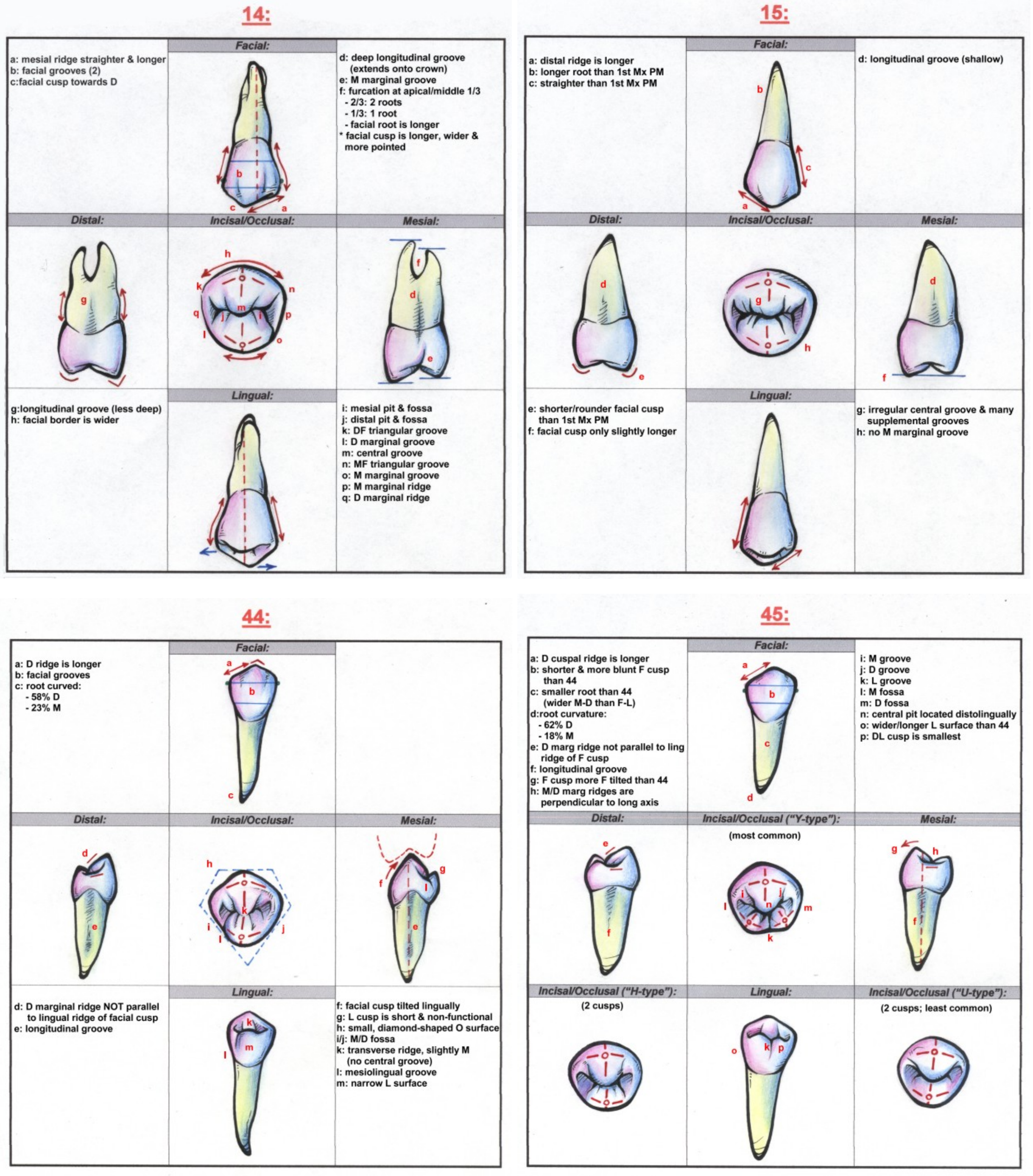


***Figure 4**. Dental morphology of the human right upper third (14, P^3) and fourth (15, P^4) premolars, and lower third (44, P_3) and fourth (45, P_4) ones.*

d. Molars

There are twelve molars in the human mouth, three each quadrant. Their main function is chewing and grinding food particles during the process of mastication. They are also very important in maintaining the verticality of the face and filling the cheeks (Woelfel, 1990). The molar teeth have no antecedents in the deciduous dentition and are the biggest teeth in the mouth, summing up to almost half of the dental arch length (51% mandibular and 44% maxillary) (Woelfel, 1990). Molars present the most complicated morphology, which varies notably both between the jaws and among teeth (*Figure 5*).

The first upper molar has the most stable morphology of all molar teeth (Scott and Turner, 1997; Bailey, 2004; Gomez-Robles et al., 2007). It usually has four main cusps, two buccal (protocone and paracone) and two lingual (metacone and hypocone), and sometimes presents an extra Carabelli's cusp (although not a true cusp) located on the lingual surface of the metacone. In this tooth the hypocone (the disto-lingual cusp) is well defined by a distal oblique groove and the paracone and metacone are connected through a transverse groove of the oblique ridge that joins them. Most frequently the first upper molar has three roots of a similar length, two buccally and one lingually placed. From an occlusal view the tooth has an overall squared aspect that is usually larger bucco-lingually than mesio-distally. The mesio-buccal cusp (protocone) is usually the biggest cusp and the disto-lingual one (hypocone) the smallest.

The second upper molar, generally smaller than the first one, shows a much more variable morphology. Although four cusps is the norm, it can show a reduced hypocone or even lack it. From an occlusal view, the proximal side is wider than the distal. The mesio-lingual cusp is usually the biggest and the disto-lingual, if not missing, is the smallest. The oblique ridge is wide and the proximal and distal foveae are deep and well-marked as in the first molar. The tooth also shows three, well-developed roots.

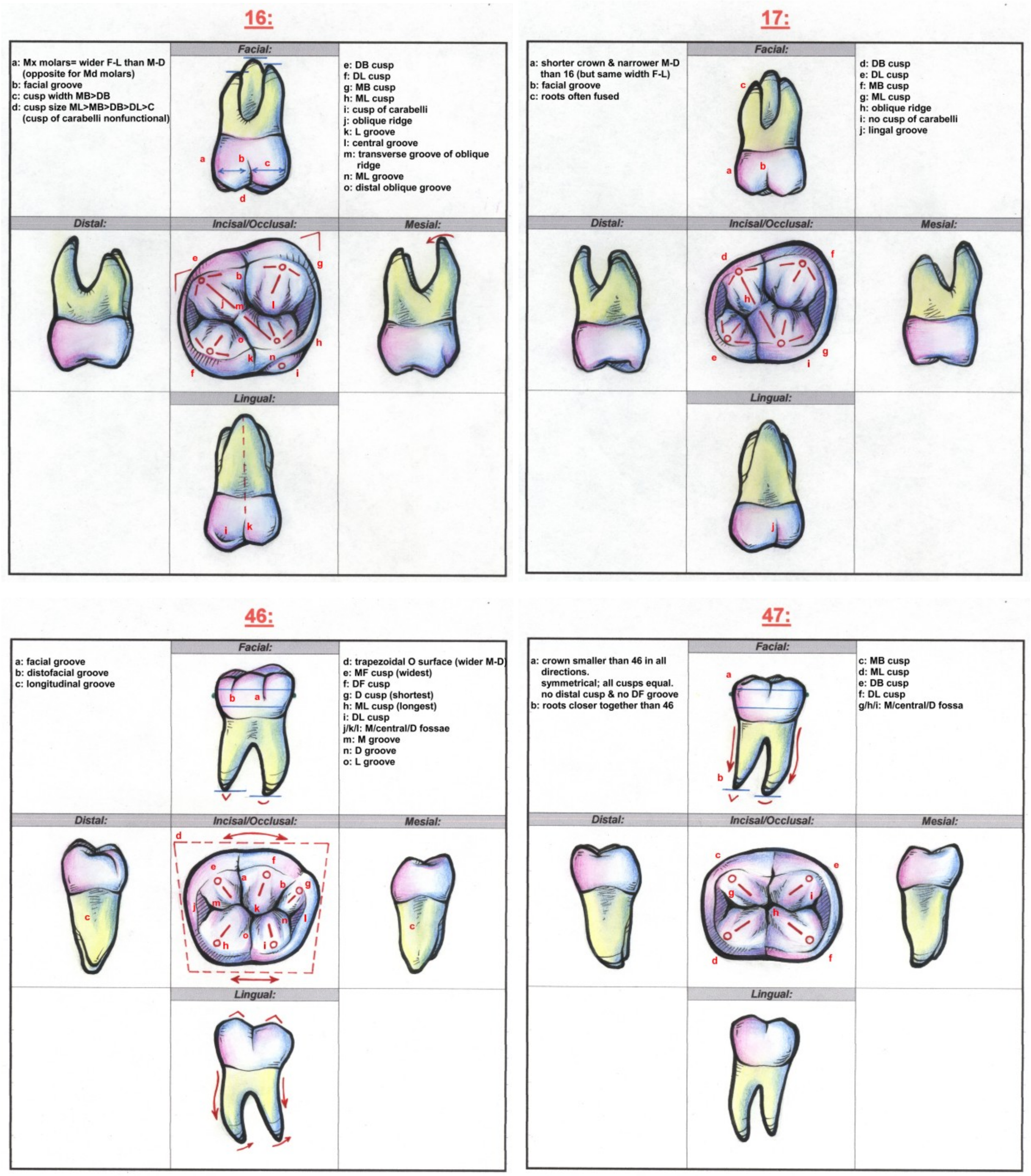


***Figure 5**. Dental morphology of the human right upper first (16, M^1) and second (17, M^2) molars, and lower first (46, M_1) and second (47, M_2) ones.*

The third upper molar is the last one in the dental arch and the last maxillary tooth to erupt. This tooth shows the greatest morphological variability of all other teeth (Woelefel, 1990) and is the smallest of all molars.

The lower molars also have large occlusal surfaces but, contrary to the upper ones, they are elongated mesio-distally, not bucco-lingually. This is because their morphology derives from a Y5 occlusal pattern with 5 main cusps (instead of 4), 3 buccal and 2 lingual. Their crown relief is relatively low and flat and the tooth usually has two roots (mesial and distal) that tend to curve distally.

The lower first molar is the largest in the mandible, especially in the mesio-distal dimension. It has three buccal cusps (protoconid, paraconid and hypoconulid) and two lingual cusps (entoconid and hypoconid). The mesio-buccal cusp (protoconid) is the biggest and highest of all, and the distal cusp (hypoconulid) is the smallest. Usually, the lingual cusps of the lower molars are more pointed than the buccal ones. The crown is usually wider on the buccal than the lingual side. The occlusal view shows three major fossae (central, mesial and distal) and several grooves (central, mesio- and disto-buccal, and lingual), as well as various ridges (mesial and distal marginal ridges). The pattern of these discreet features can show considerable variation. Depending on the number of cusps and the groove relationships, three main patterns have been defined: Y (the most frequent with 5 cusps), + and × (both with 4 cusps). Some mandibular first molars can present a *tuberculum sextum* –an additional, small sixth cusp located between the distal and disto-lingual cusp and the *tuberculum intermedium*–, an extra, seventh cusp located between the lingual cusps.

The lower second molar is usually smaller than the first one and in modern humans it only shows four cusps, with a +4 occlusal pattern, somewhat wider mesio-distally than bucco-lingually but not as much as in the first lower molar. The mesial cusps are generally larger than distal ones. On the occlusal view, three main fossae are frequently present (central, mesial and distal), as well as three main grooves (central, buccal and lingual). The Y5 patterns (with 5 cusps) are rare in the second lower molars but can be observed in some human populations (Chinese and African groups). The two roots are closer to each other than in the first lower molar and also tend to more pronouncedly bend distally.

The lower third molar is the tooth with the highest morphological variation. It is most frequently characterized by very convex buccal and lingual crown surfaces, with three, and sometimes four, cusps, of which the lingual ones are larger than the buccal ones. The groove pattern is very irregular with numerous pits and grooves that provide a wrinkled impression. The tooth roots are rather short and tend to fuse.

2. Dental wear

Dental wear is a physiological, cumulative process of gradual loss of tooth crown surface due to the normal dental activity. It reflects the constant contact of abrasive particles with dental surfaces, as well as tooth-to-tooth contact, and the mastication forces employed in food processing. Both factors act upon the enamel, and later upon dentine, slowly wearing down its layers.

a. Attrition, abrasion and erosion

Dental wear is often classified into three distinct processes depending on the causing mechanism. *Attrition* is the result of the tooth-to-tooth contact while grinding the food. Attrition involves occlusal dental surfaces and causes flat wear facets on the enamel of the teeth involved (Kaidonis, 2008). *Abrasion* results from the contact of dental enamel surfaces with abrasive particles, either included in food items or exogenous contaminants (Hilson, 1996; Kaidonis, 2010). Depending on the hardness of the abrasive particles, they may require a variable amount of bite forces to be able to cause enamel loss on dental surfaces. Abrasion is not anatomically specific and can, thus, occur on the whole dental crown surface (either occlusal, buccal or lingual), resulting in hollow wear spots (Kaidonis, 2008). Abrasion is the principal wear mechanism and its positive correlation with age has long been established (Richards and Brown, 1981). The third process involved in dental wear is *erosion*. It is triggered by chemical factors (usually acids, both external and internal) that act upon the enamel surfaces causing a gradual dissolution of its structure (Kaidonis, 2010). The three processes (attrition, abrasion and erosion) act both alternately and simultaneously on dental surfaces resulting in a broad range of dental wear patterns (Kaidonis, 2008).

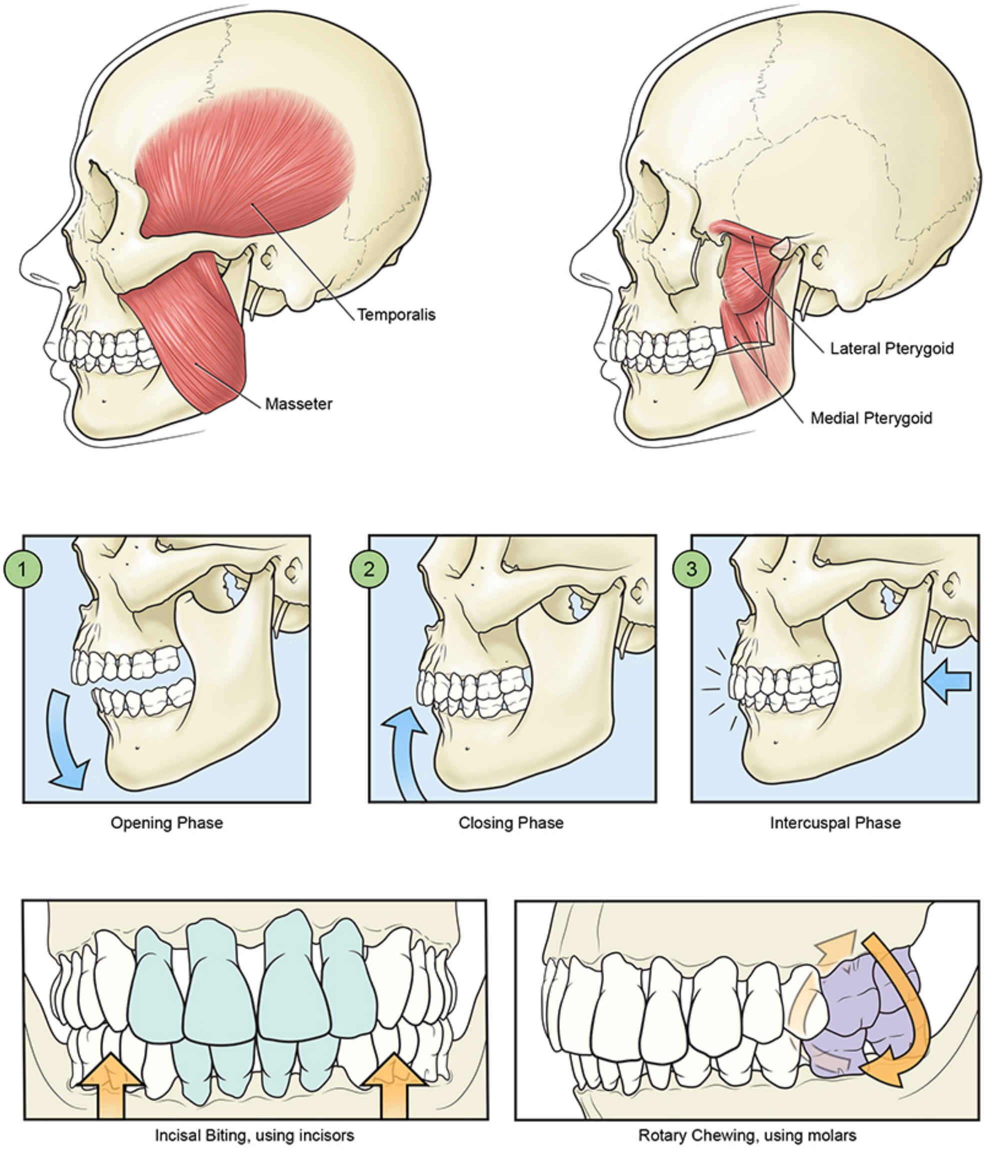


***Figure 6**. Chewing phases involve the temporalis, masseter and pterygoid muscles to open and close the mouth during food processing. The puncture-crushing phase (1 and 2) does not involve tooth-to-tooth contact, whereas the intercuspal phase (3) involves attritional processes between opposed molar teeth in the rotary chewing process (modified from Ellen Davis, 2013)*

The mechanics of food chewing has been well described. It can be divided into two alternating phases (*Figure 6*): 1) the *puncture-crushing* phase is characterized by relatively fast jaw movements in which teeth change their position from 'open' to 'near contact', chopping the food and producing smooth, flat wear on the entire tooth surface (Smith, 1984). 2) The second phase is *chewing* or *intercusp* phase, during which the teeth shear and grind against each other in lateral movements (rotary chewing) while stronger bite forces are applied to break down food pieces. In this phase teeth come into contact, and abrasive particles scratch and score enamel surfaces (Mair et al., 1996). This second phase mainly results in oblique wear facets on the buccal surfaces of the cusps of lower mandibular and on the lingual cusps of the upper molars that wear down on both faces, while the remaining cusps wear down only on the lingual side (Smith, 1984).

As mentioned above, enamel abrasion is produced during food processing when teeth contact abrasive particles, either included with foodstuffs or not related to nutritional process. Such exogenous elements may cause not-diet related dental abrasion that is generally referred to as non-masticatory dental wear. It has been widely noticed that in many modern human populations teeth are used in various culture-related activities. These can include the use of teeth as a third hand, to handle or hold various objects, or their use as tools, for instance to cut or soften animal hide or other materials for clothing production. These actions mostly involve the use of anterior dentition, highly overloading teeth and dental support structures, consequently resulting in quicker and more pronounced dental wear than that caused by food processing (Turner and Cadien 1969; Molnar 1972; Pedersen and Jakobsen 1989; Clement and Hillson 2012). Nevertheless, diet composition also plays an important role in dental wear. The consumption of highly abrasive and fibrous foods, such as dried or frozen meat, seeds or tubers, requires high masticatory loads and prolonged chewing, which accounts for more pronounced dental wear than if softer foods are consumed (Molnar, 1971, 1972; Hinton, 1982; Kaifu, 1999; Deter, 2009). Additionally, external particles, such as sand, ash or grit, may be incorporated into consumed foods during storage or preparation techniques, greatly contributing to enamel destruction, production of wear facets, and eventually dentine exposure (El-Zaatari, 2008; Lucas, 2004; Hillson, 1996).

The relationship observed between dental wear and cultural practices has favoured its use as a diagnostic feature in anthropological research. Dental wear has long been used as an indicator of diet and dietary-related practices, as well as an indicator of non-masticatory use of teeth in modern humans (Larsen, 1997; Rose and Ungar, 1998, Scott and Turner, 1988, Kaifu, 1999; Hinton, 1982, Deter, 2009; Dahlberg, 1963, Molnar, 1972, Anderson, 1965; Mickleburgh, 2009; Turner and Machado, 1983; Smith, 1984) and for the age at death in archaeological samples (Miles, 1962, 1963, 1978). In the present thesis dental wear analysis is used in three different contexts: 1) it was applied to investigate the effect of sexual division of labour on dental wear; 2) crown complexity and crown relief were analysed to test their association to dental wear; and 3) dental wear was compared between hunter-gatherer and agricultural populations.

b. Sexual division of labour

Dental wear has been especially relevant for studying the consequences of sexual division of labour in modern humans. This is based on the hypothesis that sexual division of labour, strongly present in hunting and gathering societies (Marlowe, 2007) in relation to food acquisition activities, would determine a differential access to food resources by both sexes and, in consequence, they would show distinct degrees of dental wear (Molnar, 1971).

In traditional hunter-gatherer communities, men are primarily responsible for hunting prey, while women usually perform activities related to gathering roots, seeds, nuts or fruits, and take general care of the household (*Figure 7*). Meat is a fibrous, tough but not very abrasive food, whereas seeds and roots are much more abrasive because they contain hard, coarse particles that may more easily scratch and wear down the enamel. Molnar (1971) suggested that sex differences in food procurement roles are also related to differences in food consumption with women consuming greater amounts of the fibrous plants and abrasive roots they collect than men, who would consume a larger amount of the animals they hunted. It has been reported that, in some societies, men would consume part of the prey directly on the spot (Minter, 2010), while women would consume fibrous and tough plant foods as a snack during gathered activities throughout the day (Molnar, 1972). As a result, women would have a constant access to such food items and would exhibit greater degrees of dental wear when compared to men, who would have greater access to meat and its derivatives. Nevertheless, it has also been suggested that women's gathering activities also involve the hunting of small animals, such as snakes, turtles or small rodents, which would compensate the protein intake of women.

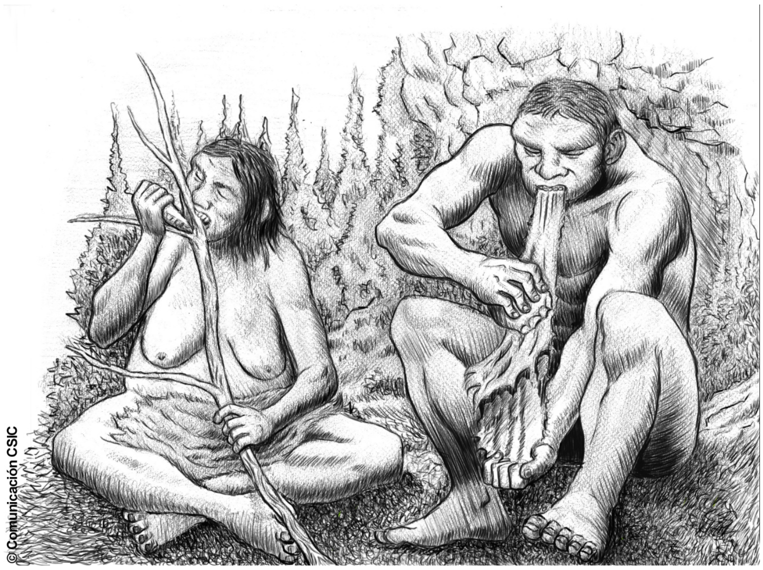


***Figure** 7. Sexual division of labour might result in a differential access to foods in modern human hunter-gatherer populations*

Sexual division of labour has been the focus of many researchers. The origin of this phenomenon is not ultimately explained, although there are various hypotheses regarding its origin. Murdock (1949) suggested that the biological differences between men and women was one of the basic factors determining the division of labour and, consequently, the improvement of the cooperation between the sexes. Levi-Strauss (1956) did not support such view and suggested that sexual dimorphism was the basis of labour division in a pure cultural concept. He argued that the division of labour serves for sustaining the mutual dependence of the sexes by culturally forbidding and putting certain taboos on the work and activities of the opposite sex. From a different perspective, both Malinowski (1913) and Mead (1949) advocated for psychological aspects of sexual division of labour. The former stated that the issue is based on forcing the 'weaker' sex by the 'stronger' one to perform dull and boring activities, such as gathering (Brown, 1970), while the latter argued that both sexes possess different physical and psychological capacities for performing certain tasks: women would possess the ability for performing monotonous and boring work not shared by men, and men would be more capable for performing activities demanding rapid and intensive calories use, followed by periods of rest, such as hunting.

The debate will probably continue, as the subject is complex and does not show a homogenous pattern across all human populations. Are any of these theories better than the rest? Or do they altogether make for the best explanation of the phenomenon? Either case, we do not intend to answer the question about the origin of the sexual division of labour, but to verify whether the different access to food during daily activities explains the different pattern of dental wear observed between the genders in some hunter-gatherers societies.

3. Dental microwear and dental topography

Using Mohs' 1-10 relative scale of mineral hardness (Mohs, 1824), enamel is rated a 4.5 to 5.0 score. Food particles equally hard or even harder than enamel (e.g. phytoliths, calcium oxalate, silicon or quartz) may cause dental microwear (Lee et al., 2011; Romero et al., 2012). Such abrasive particles, depending on their origin, can be classified as intrinsic or extrinsic. Intrinsic particles are those that form a part of the plant tissues or seed that are ingested. Extrinsic particles are those that are incorporated into food during preparation or storage, such as dust, ash or sand grains. Dental microwear features, produced as a result of the interaction of abrasive particles with enamel surface during mastication (Schimdt, 2001; Romero and De Juan, 2003; Perez-Perez et al., 2003; Mahoney, 2006), mainly consists of either *pits*, which may only be observed on the occlusal tooth surfaces because they require tooth-to-tooth contact to be formed, or *scratches* or *striations*, which can be observed on both occlusal and buccal surfaces. Dental microwear is the microscopic evidence of enamel wear and requires the use of a Scanning Electron Microscope (SEM) for observation.

Since Puech (1976, 1979) suggested that microwear features might be indicative of dietary habits, both occlusal (Ungar et al., 2003; Scott et al., 2005) and buccal (Perez-Perez et al., 2003; Romero et al., 2012) dental microwear research has been widely applied to the characterization of the dietary habits of primates, including fossil hominines (Perez-Perez et al., 1994; Spencer, 1999; Schmidt, 2001; Alorusan, 2005; Mohany, 2006; Alorusan and Perez-Perez, 2008), not without a certain controversy.

Dental topography analysis, on the other hand, tries to correlate tooth function with dental wear based on the fact that the morphology and shape of the dental crown changes through time while crown height decreases due to overall dental wear. This approach has been widely explored in primate species and early human populations (Kay, 1973, 1975, 1978; Kay and Hylander, 1978; Rosenberger and Kinzey, 1976; Kinzey, 1978; Lucas, 1979; Maier, 1984; Ungar, 2004). It has been noted that dietary habits greatly affect dental crown loss, and thus natural selection has favoured different dental morphologies depending on the foods consumed. Folivorous and insectivorous species tend to have high-cusped, long crested teeth adapted to shearing and slicing, while frugivorous species and those that consume relatively hard objects, such as seeds, would rather have flatter and more rounded occlusal surfaces, better adapted for grinding and crushing (Kay, 1973; Ungar, 2004).

The analysis of dental shape can thus be especially informative in terms of dietary adaptations, a research line that has not yet been widely applied to characterize dietary adaptations of modern human populations. Most researchers studying the functional morphology of teeth have focused on unworn samples (Ungar, 2004). The development of three-dimensional topographic techniques, such as landscape GIS (Geographic Information System) analysis (Zuccotti et al., 1998), has facilitated research of both unworn and worn teeth (Ungar, 2004, 2015). Two measures of dental topography are especially relevant in this regard. As wear proceeds during the puncture-crushing phase of food chewing, wear facets are formed on the cusp tips of molars showing a distinct orientation depending on cusp contact during rotary chewing. Dental complexity can be measured by the *Orientation Patch Count* (OPC) that measures the total number of patches with varying orientations in a given tooth crown. The GIS analysis groups the 3D grid points that are orientated in the same direction up into a single patch and counts the total number of distinct patches. There is a consistent increase in the dental complexity when moving from meat-feeding through omnivory (meat and plants) to herbivory (plant material such as leaves and grasses). The standardization and rotation of all studied specimens for comparison, provides an OPC ration (OPCR, Evans, 2013) that has been used to test dietary hypotheses in primates, rodents, or bats (Evans et al., 2007; Boyer et al., 2010; Godfrey et al., 2012; Santana et al., 2011). The method has the advantage that it can be used for both unworn and worn teeth (Ungar and Williamson, 2000).

Another measure of crown complexity is the *Crown Relief In*dex (CRI) that is defined as a ratio between the 3D surface area to its 2D projection (Ungar and Kirera, 2003; Dennis et al., 2004; Evans, 2013). The higher the occlusal surface is, the greater CRI value will have. Tooth wear therefore has a significant influence of the crown relief index, for cusp height diminishes as dental wear progresses (Evans, 2013). Dental wear should always be accounted for when crown relief is being explored. This approach has been employed in various studies on primates and has shown to be very useful in diet differentiation (Boyer et al., 2010; Godfrey et al., 2012).

4. Dental dimensions

A substantial reduction in teeth dimensions within the *Homo* genus has been observed over the last 100,000 years (Fitzgerald and Hillson, 2008). This trend has been attributed to various factors: a probable mutation effect (Brace, 1963, 1967; Brace and Mahler, 1971), a population increase effect (Macchiarelli and Bondioli, 1986), a selective compromise effect (Calcagno, 1986, 1989), or to dietary changes and technological innovations through time (Brace, 1976). At present, a certain divergence among scholars remains on whether dental size can be considered as a distinctive feature in modern human populations. Many authors have reported both intra- and intergroup variability in dental size (Barrett et al., 1963; Bishara et al., 1989; Brook et al., 2009; Hanihara, 1977; Hanihara and Ishida, 2005; İşcan and Kedici, 2003; Keene, 1979; Otuyemi and Noar, 1996; Richardson and Malhotra, 1975; Schwartz and Dean, 2005; Turner and Richardson, 1989), while others claim that dental size cannot significantly discriminate modern human populations (Ates et al., 2006; Castillo et al., 2011; Garn et al., 1964; Harris, 2003; Hillson, 1996; Scott and Turner, 1997; Suazo et al., 2008).

Tooth size analysis is of great importance in Physical Anthropology, as it can serve as an indicator of evolutionary change and adaptation processes. The variation in dental size among and within modern human populations has been related to various genetic and environmental factors (Bailit, 1975). The most common method of investigating dental size variability is the use of simple linear measurements (distances, angles, etc.), such as crown length and breadth, and their indices (Kieser et al., 1985). Mesio-distal (MD) and bucco-lingual (BL) diameters are the most common measurements used for dental size characterization. A third measurement, the cervical-incisal diameter (crown height), has also been widely used, although it is very often affected by occlusal wear, which poses some limitations to its use (Brace, 1967). The mesio-distal diameter, often referred to as tooth width (Moorrees et al., 1957) or mesiodistal width (Bolton, 1958), is the maximum distance between the contact points of the tooth with its neighbors, either in physiological occlusion (Goose, 1963; Wolpoff, 1971) or parallel to the occlusal surface of the tooth (Moorrees e al., 1957). However, this measurement is quite often affected by interproximal wear

(Kieser, 1990). Therefore, it is always advisable to use at least one other tooth dimension in order to obtain a more reliable account of tooth size (Brace, 1967). The bucco-lingual diameter is also known as a tooth breadth (Kieser et al., 1985) and is usually measured as the maximum bucco-lingual dimension, perpendicular to the mesio-distal width (Moorrees et al., 1957; Lavelle, 1971). The cervical-incisal distance, also referred to as occlusogingival dimension (Al-Shahrani, 2012), incisogingival height (Bolton, 1958) or simply crown height (Lavelle, 1968), is measured between the lowest point of the cement-enamel junction and the top of the crown rim or the highest tip in incisors, canines and premolars (Lavelle, 1968), and on the mesiolingual cusp tip in molars (Volchansky et al., 1981).

All these measurements can be obtained from the actual tooth or its replica with the use of traditional measurement tools, such as dividers or calipers (sliding, digital). However, 2D images of occlusal and lateral views of the teeth can also be used to measure dental dimensions with the use of specific computer software. More recently, 3D scanning techniques have allowed for the implementation of 3D dental models in dental size analysis. The measurements may be obtained from the three-dimensional scan of tooth crown with the use of special 3D imaging software. This virtual method allows for repeated analyses without damaging the original specimen. Each of these methods has its own advantages and limitations and the choice of a technique highly depends on the investigator and the objectives of the study.

5. Dental shape

Dental crown shape can be analysed using indices computed from the linear measurements. The most commonly used is the *crown index* (Lavelle, 1968), defined as the ratio of bucco-lingual to mesio-distal diameter expressed as percentage (BL×100/MD). A dental *crown module* index has also been defined, calculated as the average of the two main dental dimensions: (BL+MD)/2, as well as a *crown area* index, obtained by multiplying both measurements

(BL×MD) (Lovelle, 1968). However, these indices are seldom applied. The crown module is often used to express the mass of the crown and the crown area index illustrates the robustness of the tooth (Mayhall, 1992). These indices are sometimes used to describe the shape of the tooth crown (Lavelle, 1968), but they have some limitations, as they are unable to account for shape variations in dental morphology. Recently though, a new method of Geometric Morphometrics (GM) has been developed that allows for analyzing tooth shape independently of size, and the influence of size (*centroid size*) upon shape. The centroid size concept, first introduced by Bookstein (1989), is calculated as the square root of the sum of squares of the distances of all the points from their center of gravity, and it was later referred to in a series of publications (Bernal, 2007; Robinson et al., 2001, Zelditch et al., 2004).

Shape is defined as the geometric property of an object that is stable independently of the object's position, orientation and size (Kendall, 1977). Analysis of the shape of teeth has long been used to infer affinities among human populations. Since teeth are directly involved in food processing, their shape is strictly related to the function they carry and, thus, dental shape should consequently allow for inferring adaptations to different kinds of foods (Evans, 2013).

Dental shape analyses can be either qualitative or quantitative. Qualitative techniques are based on observation and description of discreet characteristics of tooth morphology (i.e. ASUDAS, *Arizona State University Dental Anthropology System*) and have been widely employed in dental studies. The quantitative Geometric Morphometrics method (Bookstein, 1986) of shape analysis was quickly adopted by dental anthropologists. It is based on the premises that the shape is represented by a spatial configuration of *landmarks*, which by definition are "*precise locations on biological forms that hold some developmental, functional, structural or evolutionary significance*" (Richtsmeier et al., 2002:65) and represent homologous points on the studied objects. The definition of the landmarks can be anatomical, topographical or developmental, depending on the type of problem it is being applied to (Oxnard and O'Higgins, 2009), and the choice of landmarks must be in relation to the hypothesis being tested (Richtsmeier et al., 2002). Shape variation within a sample is studied by interpolating the displacements of the landmark configuration using *thin plate spline* (TPS) or *superimposition* methods to derive *partial* and *relative warps*. The landmark configuration defined by the *partial* or *relative warps*, can be projected onto a two-dimensional space for visualization. Although the use of geometric morphometrics is very common and provides a wide range of useful information, it also has certain back draws. For example, the use of landmarks does not account for the space, curves, angles or surfaces that exist between them. To include the contours/outline of the studied structure into the analysis, the *semilandmark* method has to be used. Semilandmarks are equally spaced points along the outline or curve that have only one fixed coordinate, thus they can "slide" along the curve to produce a set of points that represents the smoothest possible deformation of the curve in relation to the reference form. In other words, it is the minimum distance between the curve on each individual and the reference form. The obtained data can be compared using traditional statistical methods, such as ANOVA or Multivariate Analyses (PCA, DA).

Landmarks can be recorded as coordinates in a two or three-dimensional space. Three main types of landmarks have been established- Type 1 landmarks are points on the studied object in which three structures meet (i.e. connection point of bone sutures). Type 2 landmarks are usually placed on tips or valleys of a structure (i.e. tip of a tooth cusp) and despite that they also are homologous, they may move along the curvature of the structure. Both types, 1 and 2, are likely to be called anatomical landmarks for they refer to easily recognizable anatomical points. Type 3 landmarks, on the other hand, are often called mathematical landmarks because their locations usually involve calculations such as the maximum curvature (Bookstein, 1991).

Geometric Morphometrics techniques were initially applied to 2D structures or projections of 3D models (e.g. photos). Recently though, 3D imaging techniques have allowed for 3D landmark configurations in biological investigation (Witter et al., 2003; Ulhaas et al., 2004; Benazzi et al., 2009; Cooke, 2011). In Dental Anthropology, due to small size of teeth, the use 3D GM methods is especially advisable to obtain more complete data that would increase the possibilities of the research.

OBJECTIVES and JUSTIFICATION

The main objective of the present dissertation is to investigate the dental variation among modern human populations. It focuses particularly on dental wear, but also analyses other characteristics of the human dentition, such as dental size, dental shape, dental microwear, dental crown complexity and crown relief. The research represents a unique opportunity to characterize dental variability in a large set of modern, hunter-gatherer and agriculturalist human populations from all over the world, living in distinct ecological environments and with different cultural traditions. Previous research has applied varied techniques that have shown contradictory results. We aim to contribute to a deeper understanding of the causes of the variability of dental form and function in modern human populations.

Four specific objectives were assessed:

1. Determine if sexual division of labour affects dental wear on the M_1 tooth. Males and females from the Eskimo population from Point Hope (Alaska) are not expected to show significant differences in dental wear on the first lower molar because 1) sexual division of labour has been shown to primarily affect the anterior dentition (Wood, 1992; Lozano et al., 2008; Mickleburgh, 2009, Clement and Hillson, 2012) and 2) dietary differences between sexes in this group have not been reported (Costa, 1977, 1982; Madimenos, 2005).

2. Explore other techniques of dental enamel loss characterization, such as overall wear, microwear, crown relief and crown complexity, to test for intrapopulation differences and correlations in the Eskimo group from Point Hope. Similar results to those obtained from the previous objective were initially expected.

3. Test if the wear patterns observed in the Eskimo population from Point Hope resemble those in other human populations, both hunter-gatherers and

agricultural groups, using the same standardized, methodological procedures so data comparison is possible. Dietary differences, conditioned by the sexual division of labour in these groups and by the distinct subsistence strategies of hunters-gatherers and agriculturalists, are expected to greatly influence the dental wear variability.

4. Conduct a three-dimensional geometric morphometric analysis in order to investigate shape differences among modern human populations of different geographic origins. Dental shape of unworn teeth is expected to reflect the geographic dispersion of human populations through time. This approach has never been applied before to modern human groups, which may open new perspective for further investigation.

The proposed studies attempt to explore the subject of modern human dental variation from four different perspectives: dental wear, crown complexity, tooth size, and tooth shape.

The methods generally used by researchers, especially in dental wear and dental size analyses, are very heterogeneous, which causes great confusion in the interpretation of results and drawing comparative conclusions. In the present work, we apply standardized and quantitative methods of dental wear assessment to a cross-cultural sample, which can provide important insights into the process of enamel loss between the sexes and among populations with different subsistence strategies. A single method for tooth size variation analysis was applied to all the populations considered, which can assure to eliminate the possible influence of differences in methodological procedures that have been so far applied to investigate this feature in modern humans, providing contradictory results on whether tooth size can be a distinctive characteristic among modern human populations.

Tooth shape variation analysis in modern human population with the use of a three-dimensional geometric morphometric approach is, to our knowledge, still an unexplored area of anthropological studies. The analysis made is therefore highly innovative and opens new perspectives for further and more profound investigations on this subject. In addition, the analysis of the correlations between macro and microwear, crown complexity and relief are not common. Thus, the results of this study are very interesting in terms of providing new insight into the process of gross and micro enamel loss and their relationship to general dental morphology and function of teeth.

Apart from the methodological aspects of this dissertation, it is also important to mention that studies focusing on modern hunter-gatherer populations are of extreme importance. For 99% of our history as a species we have been living under this lifestyle model, and only the invention of agriculture ca. 10,000 years ago has switched our basic subsistence strategy. However, there are still living human populations that practice this ancestral way of life, basing their subsistence on hunting, fishing and gathering. By investigating these populations we gain an invaluable opportunity to understand archaeological data (Stiner and Kuhn, 2006; Yellen, 1977; Berbesque, 2010). They provide us with information about the nutritional ecology of our pre-agricultural ancestors as well as with an insight into our modern nutritional status and needs.

Traditional groups also represent an important link between contemporary human populations and our ancestors, in terms of social and economic structure, subsistence methods and dietary patterns. Therefore, their knowledge may reveal the evolutionary outlines that occurred in human evolution within the last 10,000 years, since the invention of agriculture. According to Kuhn and Stiner (2006), the studies of modern hunter-gatherers are most informative when they actually fail to predict the patterns encountered in Palaeolithic records and when they expose certain divergences of what would be expected and what probably occurred during that period. They show us how our ancestors differ from us and what still needs to be explained in human evolution.

MATERIALS

The research was done using the dental cast collection of hunter-gatherers and agriculturalist modern human populations available at the University of Barcelona and the University of Alicante. The casts were obtained from the original specimens curated at the *American Museum of Natural History Museum* (*AMNH*), New York (USA), and at the *Musée de 1'Homme Paris* (*MH*). A total of 251 teeth were analysed (*Table 1*). They belonged to 188, young adults or adult individuals from 9 different modern human populations: Agta, Australian Aborigines, Batéké-Balali, Eskimo, Hutu, Javanese, Khoe, Navajo and San. The Eskimo was the most represented group and the sample was used as a reference collection to test hypotheses on dental wear, size and shape. The sample used in each analysis varied depending on the purpose of each research and the characteristics required and preserved in each sample (e.g. presence of microstriations, absence or presence of occlusal gross wear, etc.).

Below, we will present a brief characterization of each of the analysed groups, in terms of social and economic patterns. A special emphasis is put on the diet and the sexual division of labour, if present, and if data on this matter is available.

1. Agta (Philippines, hunter-gatherer)

Agta are the indigenous inhabitants of the Philippine islands, who have been living there for at least 35,000 years. Their number has dramatically decreased in recent times, reaching to about 9,000 individuals at present (Minter, 2010). Agta are unique among other hunter-gatherer groups because there have been reported regular hunting activities performed by women (Estiko-Griffin and Griffin, 1981). The most preferred hunted animals are the Philippine warty pig and brown deer, although the latter is almost extinct. They also hunt long tailed macaque, the water monitor lizard and Gray´s monitor lizard, which is obtained less often, as well as the rufous hornbill, tarictic hornbill and red jungle fowl, which are hunted more regularly but are less desired (Minter, 2010). There is no

***Table 1**. Sample sizes of the human populations (GROUP) studied. The columns indicate the population acronym (ID), provenance, subsistence strategy (STR: hunter-gatherers - HG; agriculturalists with or without raising animal and/or fishing - AGR), N: total number of individuals (N); total number of studied teeth (n), sample sizes of upper first molar (M^1) and lower first molar (M_1), institution where the remains are curated (INST: American Museum of Natural History - AMNH; Musée de 1’Homme Paris - MH), and reference of publication, if available.*

GROUP	ID	PROVENANCE	STR	*N*	***n***	M^1	M_1	INST	REF
Agta	**AGT**	Luzon, Philippines	**HG**	19	30	16	14	*MH*	Genet-Varcin, 1949
Australian Aborigines	**AUS**	North and SE Australia	**HG**	27	34	17	17	*AMNH*, *MH*	
Batéké-Balali	**BAT**	Congo, Africa	**AGR**	10	13	8	5	*MH*	Trezenem, 1940
Eskimo	**ESK**	Point Hope, Alaska	**HG**	80	100	39	61	*AMNH*	Costa, 1977
Khoe (Hottentot)	**KHO**	South Africa	**AGR**	11	17	10	7	*AMNH*, *MH*	
Navajo	**NAV**	Canyon del Muerto, Arizona	**AGR**	20	32	16	16	*AMNH*	
San	**SAN**	South Africa	**HG**	6	10	6	4	*AMNH*, *MH*	
Hutu	**HUT**	Rwanda	**AGR**	11	11	11	-	*MH*	
Javanese	**JAV**	Java, Indonesia	**AGR**	4	4	4	-	*MH*	
		Total	**188**	**251**	**127**	**124**			

data available on the contribution of gathered foods to Agta's diet (Minter, 2010), though it is known that they collect at least 29 plant species (Garcia and Acay, 2003). The most common plant foods gathered are fern shoots. A significant part of the plant food acquisition is formed by wild tubers, which were and still are a very important part of Agta's diet.

At the end of the rainy season fruits become very popular. Garcia and Acay (2003) identified 60 different fruits collected by Agta women, among them the rattan fruits, wild rambutan, wild guava, pudo balo and balagwesan. There is one, much-desired product in which collection men are the dominant sex: honey. Guimares de Souza (2007) reported that most Agta people eat three meals per day: early in the morning, early in the afternoon and early at night.

Back in time, the hunter's wife would wait until her husband came back to the camp to eat together. Nowadays, since hunting expeditions are less successful, women try to provide as much as possible of other kinds of foods for herself and her children, while the husband hunts (Minter, 2010). The hunters sometimes butcher the game right at the place where it was caught and eat some parts yet in the forest (Minter, 2010). Similarly, during foraging trips it is very common for women to consume different kinds of "snacks" (berries, fruits, nuts, roots etc.).

2. Australian Aborigines (Australia, hunter-gatherer)

It is believed that the first Aborigines arrived in Australia around 40-50,000 years ago from Southeast Asia (Flood, 1983). They lived exclusively as hunter-gatherers all over the continent until the European colonization. Australian Aborigines are omnivorous –all animals are potential food sources. Each edible part of the animal's body can be consumed, with the exception of the intestinal content. Insects provide an important contribution to the diet, and are eaten directly or through their honey production. Both genders contribute equally to the subsistence, but they differ in their procurement activities. Labour is divided as in a typical hunter-gatherer group: women are mainly responsible for gathering wild plants and collecting honey or eggs, and men are primarily big game hunters. They hunt alone or in pairs, and provide irregular but valuable meat from big mammals, such as kangaroos, birds, such as emus, or reptiles, such as turtles (O´Dea, 1991).

3. Batéké-Balali (Congo, agriculturalist)

Not much is known about the Batéké-Balali tribe. They belong to a broader ethnic group, the Bantu, and inhabit mainly the territory of Congo (White et al., 1981). Their subsistence is based almost exclusively on agriculture. The main cultivated crops are maize, millet and tobacco. Trezenem (1940) published a monograph on the Batéké-Balali tribe, but focused mainly on the physical and morphological aspects of these people.

4. Eskimo (Alaska, hunter)

The studied sample of Eskimo hunter-gatherers came from the population of Tigara from Point Hope in Alaska. The area is located 200 *km* above the North Polar Circle and is inhabited by some 300 different animal species, including sea and terrestrial mammals, fish, birds and invertebrates. Around 70 of these form the diet of the Eskimo people (Anderson, 1984; Keenleyside, 1998), especially the bowhead whale, walrus, seal, caribou, different kinds of fish, grizzly and polar bear, some birds and also invertebrates. Sea mammals are the main source of food, especially in the period between December and June, when they are most abundant. During the rest of the year the Eskimo people tend to depend on frozen and stored meat or hunted caribou and other terrestrial mammals and fish.

The Tigara (1,200-1,700 AD) economy was almost exclusively based on the exploitation of land and sea mammals and fish, including the bowhead whale, walrus, and seal (Keenleyside, 1998, Larsen and Rainey, 1948). Thus, their diet, composed 95% of animal protein and fat, consisted mainly of land and sea mammals and fish, eaten raw, dried or frozen (Keenleyside, 1998; Larsen and Rainey, 1948). Very little amounts of carbohydrates were consumed (Waugh, 1937), only some roots often eaten raw. In this society sexual division of labor did not focus on the subsistence strategy. Very harsh climatic conditions significantly limited the availability of plant foods that could be eaten to rare tubers on a seasonal basis. Therefore, women did not participate in the food quest and all the responsibility for providing food laid on the hands of men-hunters. Nevertheless, women were involved in all possible household activities. They took care of the children, managed the game brought by men (conservation of meat or cleaning furs), prepared clothes, gathered the limited roots available and kept the fire (Anderson, 1984; Frink, 2009). Differences in daily activities, according to Costa (1982) did not differentiate the access to food in this group, but the tasks performed by women heavily overcharged teeth, which may influence the degree of observed dental wear.

The name *Eskimo* is widely accepted by the indigenous inhabitants of Alaska, but for *Inuit* and *Yupik* people living in Canada, Greenland and Siberia this name is considered to be derogatory, as it was introduced by non-Inuit people (Kaplan, 2011). Samples of both Eskimo (Point Hope) and Inuit (from other territories) were included in the analysis and both names are used to distinguish between them.

5. Hutu (Central Africa, agriculturalist, herding)

Hutu is the major population inhabiting Rwanda and Burundi. This tribe belongs to the Bantu language group, together with *Tutsi* and *Twa*. They are most likely Bantu descendants that arrived in the area from the Great Lake region in West Africa during the great Bantu expansion (Luis et al., 2004).

The basis of their economy is mainly farming, with beans, corn, millet, sorghum, sweet potatoes, and cassava being the basis of their diet. Cattle herding is considered to be of higher social status. Beef and cow milk are more refined foods than goat milk and meat that is usually consumed by lower class people. Sexual division of labour is significant. Men usually take care of the livestock and prepare the fields for planting, while women perform household activities and help in planting and harvesting the crops.

6. Javanese (Java, farmers and fishers)

Java is an island of Indonesia, an archipelago of more than 17,500 islands, of which around 6,000 are inhabited. Javanese people constitute some 45% of the island inhabitants, living mainly in the central and northern areas (*Marshall Cavendish,* 2008). They are descendants of Austronesian migrations from Taiwan to Java, through the Philippines (Spiller, 2008), between 1,500 and 1,000 BC (Taylor, 2003). Until relatively recently, the inhabitants of Java were mainly tropical hunters and gatherers (Taylor, 2003), but they switched into farming, as the volcanic soil of Java is exceptionally fertile. The most common crop cultivated in Java is rice, but cassava is also popular (Dunham and Dewey, 2008). Fishing is also an important subsistence activity, especially in coastal areas. Big scale animal husbandry was never introduced due to very limited space (Martin, 1996).

The social structure of the traditional Javanese communities was egalitarian in rural areas, though more hierarchical in urban areas. The sexual division of labour was especially visible in fishing villages. Men were mostly responsible for fishing, mending fishing nets, building boats for deep-see fishing, hunting turtles and searching for pearls. Women once collected shellfish from the shore and prepared foodstuffs by drying, smoking or boiling it. In the rice farming communities, men usually prepared the fields, planted, watered and harvested the crop, while women would take care of the cooking.

7. KhoeSan

KhoeSan is the common name for two separate but closely related ethnic groups from South Africa (Draper, 1975; Lee, 1978; Schapera, 1930): *Khoe* (Hottentott) and *San* (Bushmen). They share physical and linguistic features that separate them from the Bantu –the most abundant ethnic group in the region– and differ from each other in the mode of subsistence: The Khoe are traditionally pastoralists while the San were primarily foragers, but from the 1950' to 1990', under governmental pressure, they increasingly practice farming.

a. Khoe – Hottentott (South Africa, pastoralist)

Originally they come from northern Botswana but they migrated southwards to the Cape. Their subsistence is based on husbandry of sheep and goat. Cattle breeding provides a balanced diet and stability of food supply. This kind of pastoral economy allows them to live in more numerous groups than the San. Even though they base their economy on pastoralism, hunting and collecting wild plants is also practiced, but to a limited extent. Hottentots do not represent a typical hunting and gathering society, but the gender roles are also divided. Women are responsible for milking the cows and ewes, collecting plants while herding, and occasional hunting, which is men's domain. Sexes also divide their responsibilities in house building: men usually build up the house construction, from saplings and leather thongs and women prepare mats for the cover.

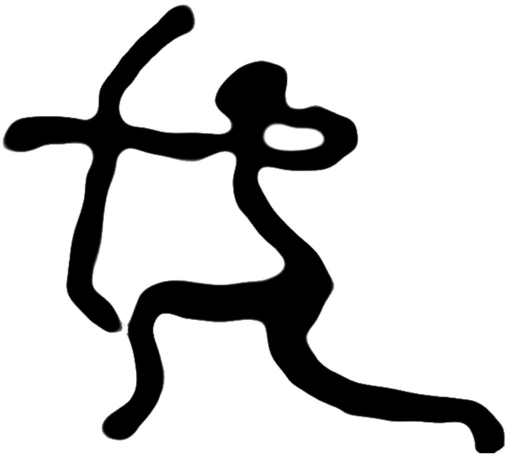
b. San – Bushmen (South Africa, hunter-gatherer)

San are indigenous and the oldest inhabitants of South Africa, living mainly on the territory of Angola, Botswana and Namibia. Their traditional subsistence is based almost entirely on hunting and gathering. Plant foods, which are abundant, nutritious and predictable, are the base of their diet, while meat, which is scarce and unpredictable, is of secondary importance. The Bushmen, and especially the !Kung, are very egalitarian societies, where the sex is the only factor of differentiation in economic and social patterns. Nevertheless, there exists a certain overlap in the activities previously attributed only to men or only to women. Women contribute relatively more to the subsistence than do men. Although the sexual division of labor is not too strict in San society, only men are involved in hunting, and they prefer to hunt alone or in pairs, and rarely stay overnight.

8. Navajo (North America, agriculturalists)

The Navajo was the largest indigenous tribe in North America, numbering about 70,000 individuals (Underhill, 1956). The studied sample comes from the Cañón del Muerto area. Even before the Spanish colonization, most American

Indian tribes were farmers, but they also hunted with bows and arrows from time to time. The most commonly hunted game was deer and rabbits. No domestic animals were present at that time. Only after the arrival of the Spaniards (~1,589 AD), the Navajo people became shepherds and excellent horsemen. In the villages, men were responsible for taking care of the crops in the nearby fields (mainly corn, beans, squash, sunflowers, tobacco and cotton), as well as for preparing the wooden framework for the Hogan. Women, on the other hand, worked in the village grounding the crops into flour and preparing food out of it in many different ways. Women also made handcrafts, produced clothes, mats to cover the tent, baskets and pottery. During harvesting months they helped men in the field, although performing different tasks, and during the rest of the year they also occupied themselves with collecting wild seeds or *piñón* nuts. Nevertheless, certain crossovers in gender roles existed. Women were free to join hunting expeditions and work in the field while men also cooked or prepared handcrafts. The basis of the traditional Navajo economy was agriculture. Traditionally, hunting was also an important subsistence activity, but after the introduction of sheep it played a more ritual role, rather than subsistence activity.



METHODS

In the present dissertation a set of methods was used to investigate the diversity of dental wear, size, and shape among modern human populations: 1) a non-discrete, actual measurement procedure for dental wear measuring was implemented in the examination of sex-related differences in dental wear, as well as among different human groups; 2) a comparison of gross wear, enamel microwear, and dental crown complexity and relief was designed to test within population hypotheses. Traditional morphometric techniques were used to study dental size variation between and within populations; and 3) three-dimensional geometric morphometrics was used to investigate the possible differences of dental shape among modern human populations.

Below, a brief description of each method is presented. More detailed descriptions of the methods used will be included the corresponding chapter. For greater clarity of the presentation of the results section, each chapter includes a description of the sample and methods used in each research analysis, as well as the discussion of the main results obtained. This will facilitate the overall presentation of the four main objectives of this thesis, which is structured in a classical way but is comprehensive within each analysis made.

All the analyses were performed on positive dental casts obtained from the original specimens curated at museum collections. Standardized moulding and casting procedures (Galbany et al., 2006) were used to prepare the high-resolution replicas of the dental crowns of all specimens. The original molar crowns were first cleaned with pure acetone and ethanol and negative dental impression molds were made using President-Jet MicroSystem Affinis *Regular body* (Coltène-Whaledent) polyvinylsiloxane. Once hardened, the molds were filled with Feropur PR-55 (Feroca Composites) polyurethane or Araldite 2020 epoxy resin to obtain the positive cast of the original tooth, following previous procedures (Galbany et al., 2006; Romero et al., 2012). The casts were mounted on aluminum stubs for analysis.

1. Dental dimensions

All metric analyses were performed on digital images (300 dpi) obtained from tooth replicas. The photos of occlusal crown surfaces, including a linear scale for calibration, were taken with a Nikon D40 camera attached to a camera stand at a focal distance of 50 cm. Teeth were orientated in a way that the occlusal plane was placed parallel to the camera lens to prevent image distortions. The scale was placed parallel and at the same height as the occlusal crown surface. Images were calibrated with the use of *ImageJ* software (Abramoff et al., 2004) and 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 crown 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.

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).

2. Dental wear

The amount of dental wear might dependent on tooth size. Therefore, in order to eliminate the size effect, the percentage of dentine exposure relative to total crown area was calculated. Total occlusal area was calculated from the outline of the perimeter of the occlusal surface using *ImageJ*. The outline polygon was drawn with a minimum of 30 points to define the crown perimeter.

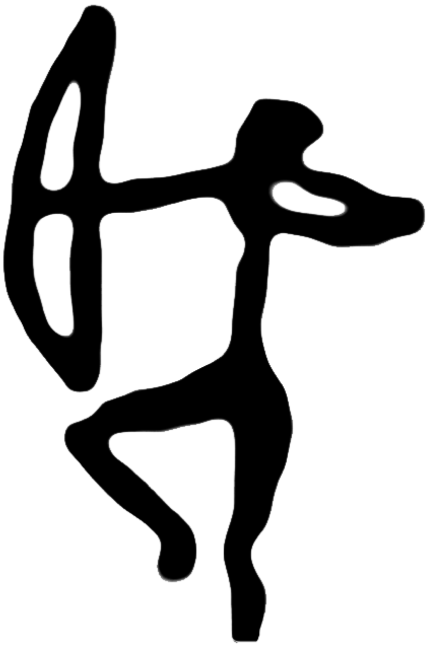
The area of dentin exposure was measured in the same way, outlining all possible dentin exposure areas, visible as depressed surfaces in the dental replicas (Galbany et al., 2011). If several spots of dentin exposure were present in one tooth, each was measured separately and the sum of all areas was calculated to define the total area of dentin exposure (*ADE*) to be used in further analyses. Finally, the percentage of dentin exposure (*PDE*) with respect to total occlusal area (*TOA*) was computed as follows: $PDE = ADE \times 100 / TOA$.

3. Dental microwear, crown complexity and relief

The analyses of dental topography were conducted on the dental replicas. The selected teeth were scanned in three dimensions (3D) with a Pizca (Roland®) scanner and saved as *.txt* files. The *Surfer Manipulator* (Golden Software, Inc.) software was used to obtain the variables *crown complexity* and *crown relief*, as explained in Evans (2013). For the dental microwear analysis, the epoxy casts were coated with a ~15 *nm* gold layer (Balzers® SCD 004 Sputter Coater) and a colloidal silver bridge was applied in some parts of the holding stub to minimize the electron charges (Galbany et al., 2006). A *Hitachi* S3000N scanning electron microscope in SE (secondary electron) mode was used to obtain 100× magnification images of enamel surface (1280×960 pixel image file in BMP format). The images were obtained at the middle third of the vestibular surface, preferably under the protoconid cusp (Pérez-Pérez et al., 1994; Romero et al., 2012). All images were processed with *Adobe Photoshop®* CS3 in order to analyse a standardized 0,56 mm^2 enamel surface patch in which the density (NT) and average length (XT in μm) of striation (all features with a 3:1 length to width ratio) were measured in each analysed tooth following standard procedures (Romero et al., 2012).

4. Dental shape

The dental crown shape was studied with the use of three-dimensional (3D) geometric morphometric (GM) methods. A *NextEngine*© scanner was used to digitalize the surface of the selected dental casts [the scan settings were: scan positioning: 360°; scan divisions: 6; tilt: 0° (scan A), 45° (scan B); points: HD; target: neutral, macro]. The 3D scans obtained were saved in *.ply* (Ascii) format and uploaded into the *Landmark Editor* software for landmark digitalization. A 10 landmark configuration protocol was used and the 3D coordinates were exported in *.dta* format into the *MorphoJ* software (Klingenberg, 2011) for semi-automated 3D geometric morphometrics analysis. For the purpose of unambiguous landmark identification and digitalization, only teeth lacking any dental wear or with minimal enamel loss on cusp tips (dental wear scores 1 and 2, after Smith, 1984), and without dental caries and no visible damage were selected.



RESULTS

1. Sexual division of labour and dental wear

Dental wear processes are determined by complex interactions between tooth morphology and biomechanical factors (Benazzi et al., 2011; Larsen, 1997; Smith, 1984). Dental wear results in a loss of occlusal relief and height of teeth. It is a normal, cumulative process reflecting the results of multiple abrasive factors acting upon the individual's dentition along its lifespan (Mickleburgh, 2009). Two main types of dental wear can be established based on the nature of causing factors: masticatory and non-masticatory. Non-masticatory dental wear occurs when teeth are used in actions other than food mastication, for example cultural modifications, the use of teeth as third hand, etc. (Dahlberg, 1963; Molnar, 1972; Larsen, 1985).

Such activities overload dental structure (mainly the anterior dentition), resulting in faster and more pronounced dental wear (Turner and Cadien, 1969; Molnar, 1972; Pedersen and Jakobsen, 1989; Clement and Hillson, 2012). Masticatory dental wear is the result of the use of teeth for food processing. Dental wear is often categorised regarding the nature of processes that act upon the enamel mainly by three different mechanisms: attrition, abrasion and erosion. Attrition is defined as a gradual loss of dental enamel due to tooth-to-tooth contact, while abrasion is the result of tooth-to-food contact (Hilson, 1996). Erosion, on the other hand, results from mineral loss due the action of acid substances (external or internal) (Hilson, 1996). All the above-mentioned processes act together, but with different intensities and duration producing a wide range of different wear patterns (Kaidonis, 2008).

It has been reported that different wear patterns or differences in dental wear degrees can be informative of dietary habits of populations (Anderson 1965; Turner and Machado 1983; Smith 1984). More abrasive and fibrous diet (seeds, wild plants and tubers, not processed, frozen or dried animal meat, etc.) requires higher mastication forces and prolonged chewing which results in a higher degree of dental wear (Molnar, 1971, 1972; Hinton, 1982; Kaifu, 1999; Deter, 2009). Apart from the intrinsic abrasives of food items, there are also external, environmental particles that may be incorporated into food during its preparation or storage (dust, ashes or grit) that may also significantly contribute to enamel wear and dentine exposure (El-Zaatari, 2008; Lucas, 2004; Hillson, 1996).

Dental wear has thus been extensively used as an indicator of diet, dietary-related habits and non-masticatory actions in human populations (for reviews see Larsen, 1997; Rose and Ungar, 1998; Scott and Turner, 1988; Kaifu, 1999; Hinton, 1982; Deter, 2009; Dahlberg, 1963; Molnar, 1972; Anderson, 1965; Mickleburgh, 2009; Turner and Machado, 1983; Smith, 1984). Early analyses reported significant differences in wear rates between agricultural and foraging populations, caused by their distinct subsistence strategies and food preparation techniques (Hinton, 1982; Smith, 1984; Rose and Ungar, 1998; Kaifu, 1999; Eshed et al., 2006; Deter, 2009), as well as between individuals of the same population (Molnar, 1971; Molnar et al., 1983; Clement and Hillson, 2012). Molnar (1971, 1972) suggested that since tooth wear is the result of the interaction between teeth and specific items of the surrounding environment, it should reveal information about the distinct use of teeth among individuals, such as food choice, food processing specializations, or food chewing differences.

High degrees of dental wear rates in Eskimo/Inuit populations have been noted for centuries by Artic travellers (Cook and King, 1784) and described in anthropological reports (Clement and Hillson, 2012; Costa, 1982; Poncins, 1942; Turner and Cadien, 1969). Various reports indicate that Eskimo/Inuit females present heavier dental wear, especially on the anterior dentition, compared to males (Turner and Cadien, 1969; Pedersen and Jakobsen, 1989; Clement and Hillson, 2012). This has been attributed to differential cultural practices and more extensive use of teeth by females (i.e. hide chewing by women), rather than to dietary differences (Clement and Hillson, 2012; Merbs, 1968; Poncins, 1942; Steensby, 1910; Madimenos, 2005). Since it is mostly the anterior dentition that is involved in non-masticatory actions (Wood, 1992; Lozano et al., 2008; Mickleburgh, 2009; Clement and Hillson, 2012), in the present research we hypothesize that teeth that are theoretically not involved in cultural practices in this group –M1 in particular– will not show sex-related differences in the degree of dental wear. Costa (1977, 1982) and Madimenos (2005) reported a lack of statistically significant sexual dimorphism in dental wear among Point Hope Eskimo populations, which they interpreted as minor or absent dietary differences.

This study aims to verify this hypothesis by analysing the Tigara archaeological (1,400-1,850 AD) population from Point Hope (Alaska), controlling for age variability and recording quantitative ratios of dentine exposure to total crown size (Clement and Hillson, 2012; Galbany et al., 2011) instead of discrete class-groups of dental wear. We will also compare our results with previous studies on sexual dimorphism of dental wear in this population. To our knowledge, no other studies have used a quantitative approach to document inter-individual and intra-group dental wear variability in the Point Hope Eskimo population.

a. Point Hope Eskimo

Point Hope lies at the western tip of the Alaska Peninsula, in the Chukchi Sea, 200 *Km* north of the Arctic Circle and 140 *km* north of latitudinal 3º (*Figure 8*).

The climate of the region is arctic, with short and dry summers (–1ºC to 10ºC) and cold winters (–50ºC to 0ºC); precipitation is quite limited –ca. 25-30 *cm* per year– with an average snowfall of 90 *cm*; the sea is covered with ice from September until June. Vegetation consists of tundra, including dwarfed ground willows, saxifrage, dandelion, reindeer moss, lichens and some flowers (Larsen and Rainey, 1948).

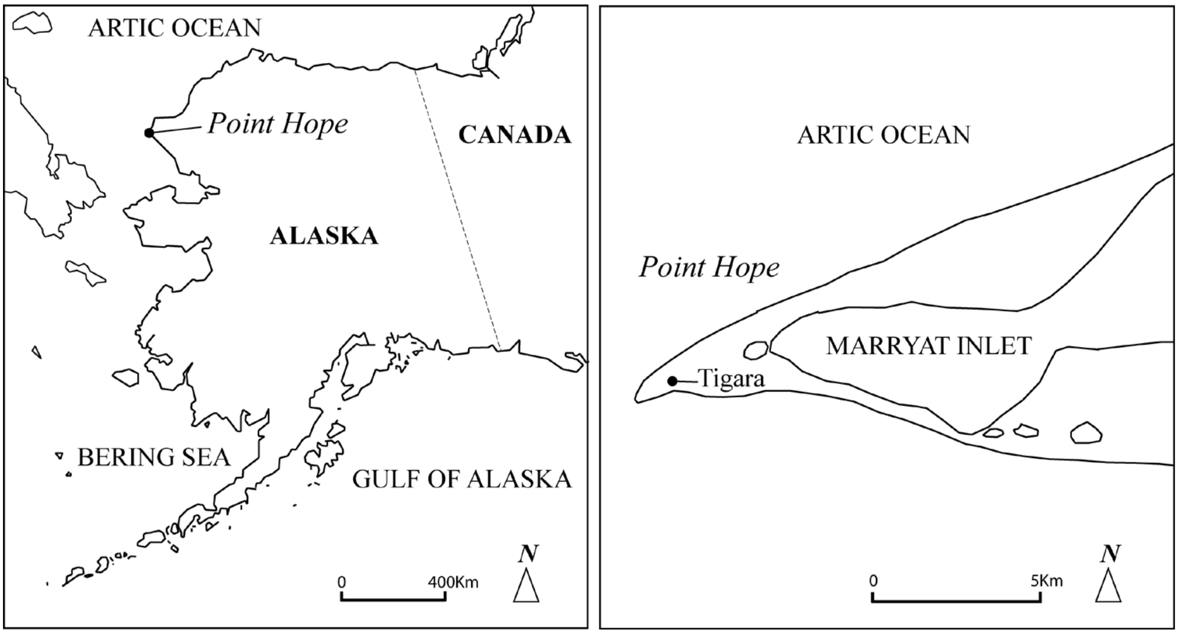


Figure 8. *Map of northern coastal Alaska and location of Point Hope (redrawn from Larsen and Rainey, 1948).*

Between 1939 and 1941, Froelich Rainey and Helge Larsen, as part of an *American Museum of Natural History* expedition, together with the *University of Alaska* and the *Danish Museum*, discovered several archaeological sites at Point Hope. The excavations indicated two chronologically and culturally distinct settlements (Larsen and Rainey, 1948): Ipiutak (100 BC to 500 AD) and Tigara (1,400-1,850 AD). Around 600 house remains and over 10,000 artefacts were discovered, along with some skeletal remains of around 500 individuals. Grave goods and burial typology were primarily used to define the two cultures. Tigara populations proved to be specialized whale hunters, whose unearthed archaeological remains included household ruins and a cemetery with hundreds of graves. Tigara individuals were buried separately, in a supine position, with the head facing towards the West and with flexed arms and legs (Larsen and Rainey, 1948). The objects associated with the remains place the Tigara population from Point Hope in the late Thule period (1,400-1,850 AD) and suggest that these people were primarily marine-based hunters and whalers (Larsen and Rainey, 1948). Their overall material culture resembles that of modern Point Hope Eskimo populations that, as part of a broader Thule culture, are characterized by permanent settlements for whale hunting activities (Larsen and Rainey, 1948). The overall Tigara sample from this site consisted of a total of 355 individuals, from which 124 were males, 122 females, 24 adults of doubtful sex, and 85 subadults (Dabbs, 2009).

The settlement and land use pattern of Point Hope Tigara inhabitants was strongly influenced by game movements. The area was inhabited by some 300 different animal species, including sea and terrestrial mammals, fish, birds and invertebrates, 70 of which still constitute part of the present day Eskimo diet (Anderson, 1984; Keenleyside, 1998). Among other fauna, bowhead whale, walrus, seal, caribou, different kinds of fish, grizzly and polar bear, as well as some bird species, have been documented. Sea mammals were, however, their main food source, hunted during spring and early summer when they abound, and then frozen and stored underground for the rest of the year.

During the winter they more intensively preyed on terrestrial mammals, including seals, polar bears or caribou, as well as on fish (Larsen and Rainey, 1948). However, the Tigara economy was almost exclusively based on seafood exploitation. Their diet consisted of 95% animal protein and fat, and included mainly raw, dried or frozen meat of whale, walrus, seal, caribou, polar bear and various fish (Keenleyside, 1998; Larsen and Rainey, 1948), with very little carbohydrates from a limited number of roots that were often eaten raw (Waugh, 1937).

Sex-related differences in daily activities did not seem to condition access to foodstuffs and the rates of dental caries were low in both sexes (Costa, 1982). Dried or raw meat, which was a major food source, required extensive and prolonged chewing that would be responsible for heavy masticatory loadings (Holmes and Ruff, 2011; Waugh, 1937) and for enhanced dental enamel loss (Tomenchuk and Mayhall, 1979).

b. Analysis of dental wear

The studied Tigara Eskimo archaeological collection (1,400-1,850 AD) is curated at the *American Museum of Natural History* (*AMNH*) in New York (USA). High-resolution replicas, stored at the University of Barcelona (Faculty of Biology, Anthropology Unit), of 92 permanent maxillary (M^1, n=31) and mandibular (M_1, n=61) first molars of both female (14 M^1 and 36 M_1) and male (17 M^1 and 25 M_1) individuals (16-45 years old range) were studied (*Table 2*). The total number of individuals included in the analysis was 72. The left side of the jaw was arbitrarily chosen for the analysis, except when the left molar was missing or damaged, in which case its right antimere was used, if available. Only 14 right side first molars were used for this purpose. This practice might affect the analysis of dental wear since some individuals might prefer to use one side of the jaw for chewing than the other, consequently showing more pronounced dental wear on the preferred side and causing an intra-individual dental wear asymmetry (Molnar et al., 1983). However, no other alternative was considered suitable as a means for increasing the sample size. Only teeth with dentin exposure were considered for the comparisons because very light enamel wear, without dentine exposed, could not be recorded by the method applied.

Since the anterior teeth have been shown to highly reflect paramasticatory actions (Wood, 1992; Lozano et al., 2008; Mickleburgh, 2009) we focused the analysis on the first molars. The main objective was to test the hypothesis that teeth not involved in cultural practices would not show sexual dimorphism in dental wear because in this society no differences in diet between sexes have been reported. The first molar was chosen for the analysis because it is the first of the postcanine teeth to erupt (average ca. 5.5-6 years) (Hillson, 1996) and, consequently, would generally show larger areas of dentine exposure than the other molars (Shykoluk and Lovell, 2010).

Tooth replicas, were made following standard casting procedures (Galbany et al., 2006). Molar crown surfaces were cleaned with pure acetone using cotton ear-cubes and rinsed with ethyl alcohol. The molding was performed with President microSystem Affinis regular body (Coltène-Whaledent®) polyvinylsiloxane and the replicas were made with Feropur PR-55 (Feroca®) polyurethane resin. Sex attribution, based on cranial and pelvic measurements, and age-at-death, based on changes in the pubic symphysis, was obtained from Costa (1977). Age group classification categories by Costa (1977) were also used, which included six 5-year-range categories: 16-20, 21-25, 26-30, 31-35, 36-40, and 41-45 years old. However, since sample sizes of age groups older than 30 were very small, we combined the oldest groups into a single category (>30) and used four age-groups categories as follows: 16-20, 21-25, 26-30, and >30.

Digital images (1,200×900 pixels) of occlusal crown surfaces, including a millimeter scale for calibration, were recorded using a Nikon D40 camera attached to a stand at a focal distance of 50 *cm*. The scale was placed parallel to the camera lens and at the same height as the occlusal plane of the dental crown. Calibrated images (in *mm*) were processed using *ImageJ* (Abramoff et al., 2004). Total occlusal crown area (TOA, mm^2) and the dentin exposure area (mm^2) were recorded by outlining their perimeters on the occlusal surface (*Figure 9*). A minimum 30 points were recorded for the crown outline and a similar point density was used for the dentine exposure perimeters, visible as depressed surfaces on the tooth replicas (Clement and Hillson, 2012). When several dentin exposure areas were present, each one was measured separately (Shykoluk and Lovell, 2010) and the sum of all the areas was accounted as the total dentine exposure area (ADE). The percentage of dentine exposure (PDE) with respect to total occlusal area (TOA) was computed as PDE = ADE × 100 / TOA (Galbany et al., 2011). To represent the PDE variation by sex, a sexual dimorphism index (PDE_{sex}) was calculated by scaling the PDE differences between sexes with the male total occlusal area: $PDE_{sex} = [PDE_m - PDE_f] \times 100 / TOA_m$. PDE_m is the median of PDE in men, PDE_f is the median of PDE in women, and TOA_m is the mean value of TOA in men. Median values were used instead of mean values to minimize the effect of outlyers. All the measurements were taken by a single researcher (KG) and her intra-observer measurement error was calculated. All descriptive and comparative statistics were made with the *PAST* v.18 software.

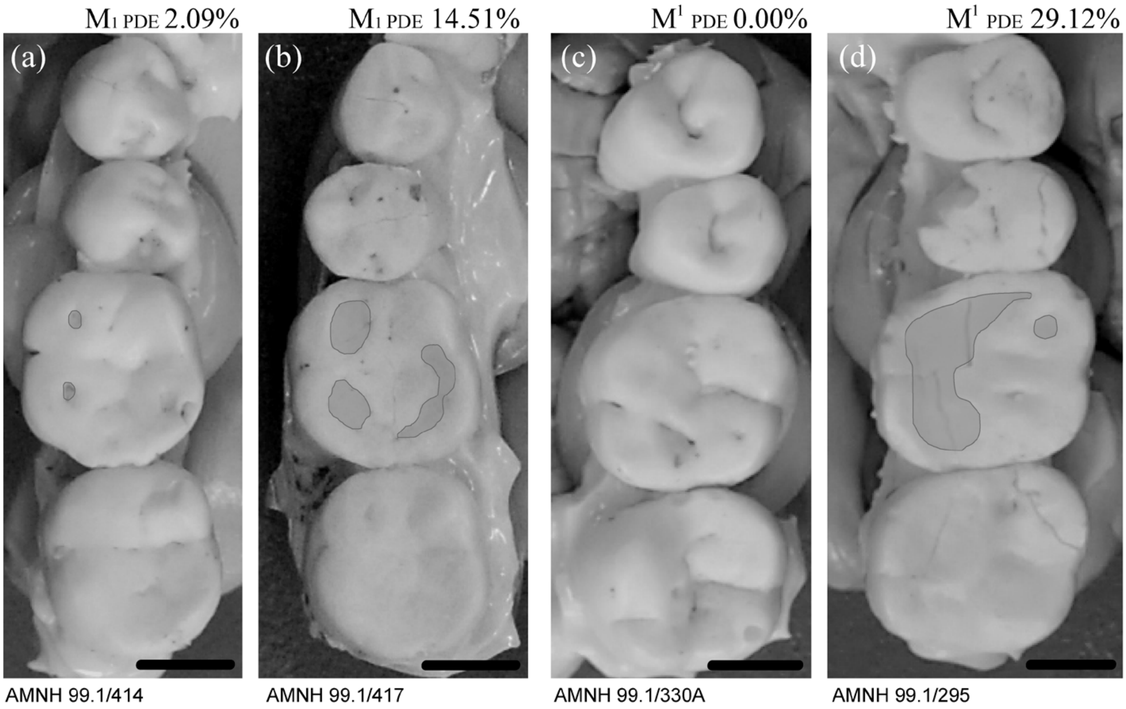


Figure 9. *Occlusal view of high-resolution tooth replicas (P4-M2) of both lower (M_1) and upper (M^1) first molars. Percentages of dentine exposure (PDE) are indicated by the shaded areas: a) AMNH 99.1/414, 21-25 years old female, PDE=2.09%; b) AMNH 99.1/417, 26-30 year-old female, PDE=14.51%; c) AMNH 99.1/317, 16-20 year-old male, PDE=0.67%; d) AMNH 99.1/349, 41-45 year-old male (PDE=52.33%). Solid outlines delineate dentine-exposed regions. PDE was defined as the sum of all dentine exposure areas times 100 divided by total crown area (TOA) (%). Scale bar: 0.5 cm.*

The reliability of the method for estimating the percentage of dentine exposure was examined by calculating the relative measurement error (*RME*) [$RME = \frac{\Delta\bar{x}}{\bar{x}}\times 100$; $\Delta\bar{x} = \frac{\Delta x}{\sqrt{n}}$] (Harris and Smith, 2009) on twenty randomly selected teeth measured three times at one-month intervals. Averaged *RME* for

TOA was 0.56% and for PDE was 3.29%. In both cases the error rate was lower than the 5% value, above which the method is considered unreliable (Weinberg et al., 2005) and consequently the method was considered to be precise and repeatable. Shapiro-Wilk's test ($P<0.05$) was performed in order to test the distribution of the measured variables (PDE, TOA). PDE showed clear asymmetrical distributions for both M^1 and M_1 ($W=0.863$, $P=0.000$ and $W=0.846$, $P=0.001$ respectively) and, therefore, the non-parametric Mann-Whitney U test was used to compare the percentages of dentine exposure between groups.

c. Sexual dimorphism in dental wear

Significant differences in dentine exposure with skeletal age were observed between all age groups except those between 16-20 and 21-25 ($P=0.073$) and 26-30 and >30 ($P=0.209$). Sex comparisons of PDE were thus made within age categories. Median PDE values were somewhat higher in men than women in the older age categories (26-30 and >30) for both M^1 and M_1 (*Table 2* and *Figure 10*). The 21-25 year-old women showed slightly higher PDE values than men for both teeth. The 16-20 year-old group behaved differently for M_1 and M^1 and showed higher values of PDE for women in M^1 and for men in M_1. However, none of these sex differences were statistically significant ($P>0.05$).

The variation in PDE by sex, scaled for male TOA, ranged from –4.7% to 15.1% depending on the age group considered (*Figure 11*). The negative values of this scaled index in younger groups, except 16-20 M_1, indicate higher values of dental wear in women than in men, while the positive values in individuals older than 25 years indicate lower values of dental wear in women than men. No significant differences in PDE were found between M_1 and M^1 teeth by sex and age-groups except for the 16-20 years male group ($P=0.039$; n=6 and PDE median=10.09% for M_1 and n=3 and PDE median=0.67% for M^1), which might be a random fluctuation due to a reduced M^1 sample size (n=3).

***Table 2**. Summary statistics of the percentage of dentine exposure (PDE) by tooth (M^1 and M_1), age and sex groups (Costa, 1977); n: sample size, PDE: average percent dentine exposure (%), e_m: standard error of the mean, σ: standard deviation, range: maximum PDE – minimum PDE, m: median, P: bilateral significance (non-parametric Mann-Whitney U test), P*: exact significance [2 × unilateral significant].*

Tooth	Age	Sex	n	PDE	e_m	σ	range	*m*	P	P*
M_1	16-20	Female	8	3.69	0.75	2.11	5.08	4.03	0.071	0.081
		Male	6	13.88	5.58	13.68	36.40	10.09		
	21-25	Female	12	17.26	5.70	19.75	51.45	7.43	0.434	0.464
		Male	9	10.54	3.52	10.56	26.26	4.42		
	26-30	Female	8	17.62	3.06	8.65	26.67	14.73	0.366	0.414
		Male	6	27.44	8.08	19.78	53.50	31.16		
	>30	Female	8	32.26	5.42	14.34	34.40	32.45	0.571	0.648
		Male	4	36.83	8.68	17.37	39.19	38.22		
M^1	16-20	Female	3	2.55	2.22	3.13	4.43	2.55	1.000	1.000
		Male	4	1.25	0.69	1.19	2.16	0.67		
	21-25	Female	4	9.60	4.52	7.82	15.63	9.20	0.827	1.000
		Male	4	16.86	12.88	22.30	39.24	4.61		
	26-30	Female	6	19.40	7.66	18.77	48.51	12.42	0.144	0.177
		Male	5	39.35	10.29	23.01	54.04	29.12		
	>30	Female	1	23.74					1.000	1.000
		Male	4	29.69	12.26	24.51	48.05	31.07		

Dental wear is mainly caused by the interaction of abrasive particles with enamel surfaces in relation to the biomechanical forces involved in food chewing (Hillson, 1996; Benazzi et al., 2012). Meat processing prior to consumption in Eskimo/Inuit populations involves, among others, open-air drying and underground storage (Larsen and Rainey, 1948; El-Zaatari, 2008; Brubaker et al., 2009). Such practices cause the incorporation of significant amounts of sand grains and gritty contaminants to the food that have been shown to cause extensive dental wear (Davies and Pedersen, 1955; El-Zaatari, 2008).

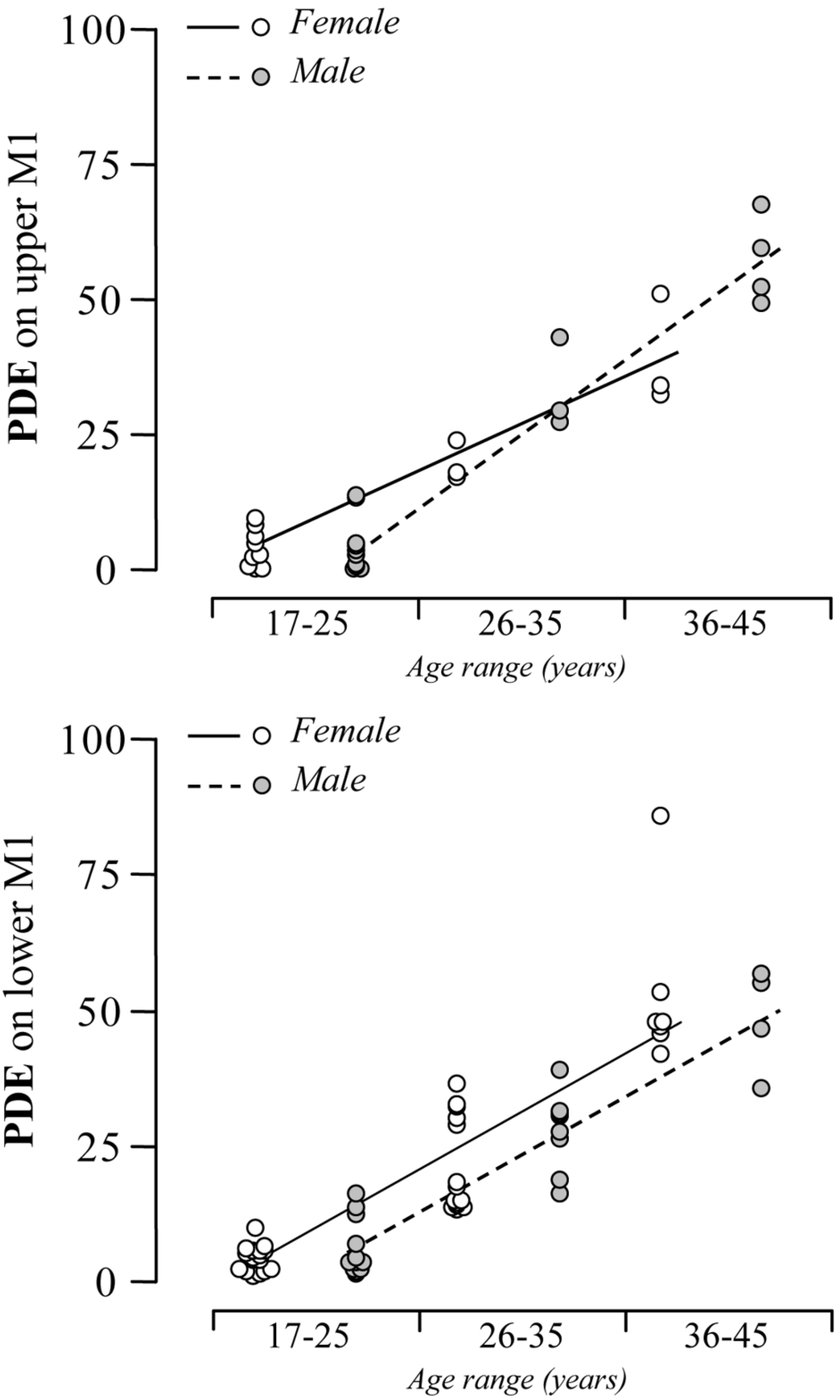


Figure 10. *Regression plot of median percentage of dentin exposure (PDE) by sex, skeletal age groups (defined by Costa, 1977) and tooth (M_1 and M^1). Asymmetric non-Normal distributions indicate that most individuals show low PDE values.*

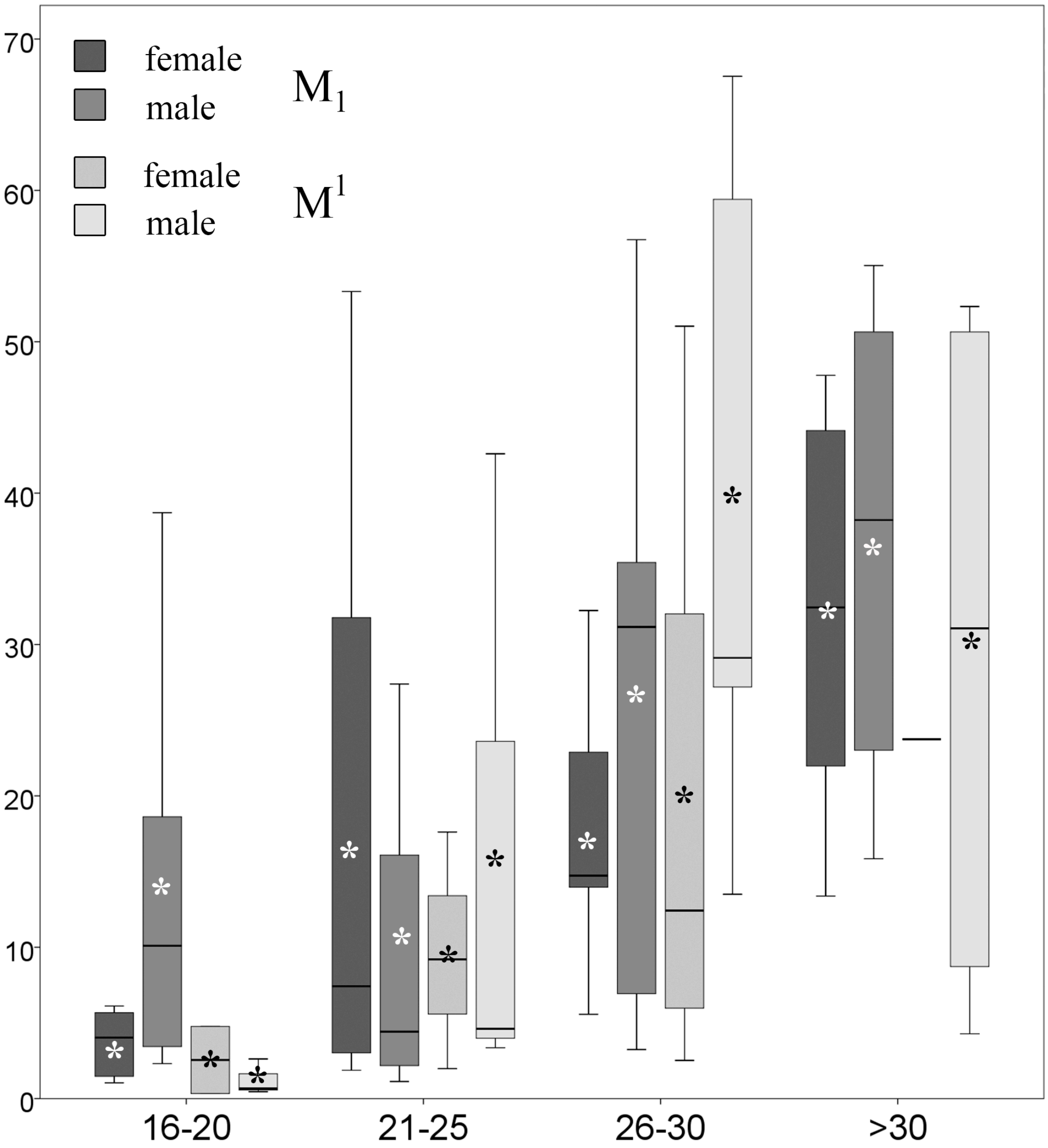


Figure 11. *Box plot of PDE by sex (female, male) and tooth type (M_1 and M^1). The horizontal lines within the boxes show the median PDE values; the * symbols represent mean PDE values; lower and upper limits of the boxes are the 25% and 75% percentiles; and whiskers are minimum and maximum values for each group.*

Enamel loss in meat-eating populations, such as Tigara, greatly depends therefore on the presence of exogenous abrasive particles along with ingested foods. Occlusal texture studies in Tigara molars (El-Zaatari, 2008) have shown significant amounts of microwear features on enamel surfaces consistent with the consumption of substantial quantities of exogenous abrasive particles. However, the effect of food chewing on enamel surfaces depends not only on the composition of the diet but also on the intensity of tooth-food-tooth contact. The Tigara population based their diet mainly on whale and other sea mammals' meat (Larsen and Rainey, 1948). Raw meat is a non-abrasive, although fibrous, tough and difficult to chew material compared with more abrasive plant foods (Molnar, 1972; Scott and Turner, 1988). Meat alone though, is not a hard enough food item to significantly scratch enamel surfaces and wear-down dental crown. Nevertheless, food preparation techniques practiced by Eskimo societies, such as freezing or smoking, change the physical properties of the meat, significantly increasing its toughness (Szmańko et al., 1995; Sigurgisladottir et al., 2000). Consequently, higher biting forces and prolonged mastication is needed to chew it and, as a result, high dental wear is produced (Hylander, 1977; Spencer and Demes, 1993).

It is commonly accepted that traditional Eskimo populations show a strongly defined sexual division of labor (Rudenko 1961; Madimenos 2005; Dabbs 2011). Hide chewing techniques necessary for clothes preparation have been reported to cause excessive degrees of wear in the anterior dentition, especially in women (Turner and Cadien, 1969; Pedersen and Jakobsen, 1989; Clement and Hillson, 2012). At the same time, the sexual specializations in hunting and household activities in Tigara Eskimo have been considered not to affect the access to food resources (Costa, 1977, 1982) and as a consequence, teeth not involved in non-masticatory practices are not expected to show sexual differences in dental wear (Clement and Hilson, 2012). Although it has been suggested that hunting and gathering groups may show non-masticatory dental wear in molar teeth (Fiorenza et al., 2011), our results indicate that dentine exposure on the first molar (both upper and lower) did not present statistically significant sex-related differences. This may point out that in this group the first molar seems not to be affected by non-masticatory, sex-based practices that would cause differential dental wear in both sexes. This is in accordance with the statement made by Costa (1977) that the posterior dentition in Tigara

Eskimo is more involved in grinding and chewing actions related mostly to food processing than in cutting movements more characteristic of the anterior teeth. Dentine exposure of the first molars would be therefore mainly caused by daily tasks related to food grinding and chewing, and the lack of diet differences between sexes implies that the first molar wear was not expected to show sexual dimorphism.

In fact, the lack of sexual differences in dental wear in Tigara is consistent with previous reports on this population. Both Costa (1977) and Madimenos (2005) reported no significant differences between Tigara men and women in terms of dental wear. Both authors used, however, traditional, qualitative dental wear scoring methods, with no quantitative assessment of this feature. Many researchers complained on the lack of precision in these qualitative scales, until a quantitative and more objective approach for scoring dental wear, based on occlusal plane photographs, was first proposed by Beherend (1977) and later developed and successfully applied by other researchers (Walker, 1978; Deter, 2009; Clement and Hillson, 2012). We believe that quantitative measurements of dental wear are more appropriate for such analyses, as they provide more precise and objective data for making comparisons despite this case, in which they are in accordance with the qualitative approach previously made.

In our analysis, we have observed an interesting shift in dental wear between younger women and older men. Young women (16-20) showed more pronounced dental wear, whereas in the older age groups (20-30 and >30) men had the highest values of dentine exposure. We believe that this observation, although the differences were not statistically significant, might be explained by both a higher exposure to wear in young women and an increase in diet abrasivity with age in men. The slightly higher dental wear scores in younger woman might be related to the fact that female dentition tends to erupt somewhat earlier than male dentition (Demirjian and Levesque, 1980; Weld et al., 2004, 2005). As a result, female teeth start being exposed to dental wear earlier than their age-matched male counterpart and therefore present, to some extent, more pronounced dental wear in younger ages. As times goes by, women's teeth are being exposed to excessive use related to cultural practices and wear down at higher speed than in men (Clement and Hilson, 2012). Also, more frequent *ante-mortem* tooth loss has been reported in Eskimo females (Madimenos, 2005). In older women, both facts could condition the need for ingesting softer food items that are easier to chew, producing less dental wear. At older ages women might simply consume less due to the inability for chewing due to severe wear or dental loss. The observation that adult men are generally bigger and poses greater muscle mass than women (Ruff, 2002; Wells, 2007) may explain their need for greater calories intake per day. Such circumstance could require increased dietary processing loadings, in order to meet their caloric needs, resulting in higher wear scores in adult men than women. However, this hypothesis would need a more profound analysis on the diet composition at different ages in Eskimo/Inuit populations in order to verify whether this tendency can be confirmed and if a similar trend can be found in other populations.

2. Dental topography

The nature and physical properties of food and the action of attrition condition enamel loss and dentine exposure affecting the morphology of the tooth (Lucas, 2004). The progressive loss of enamel over an individual's life modifies the topography of the occlusal surfaces and reduces the relief and height of the crown, significantly influencing the biomechanics of mastication (Smith, 1984; Benazzi et al, 2011; Fiorenza et al, 2011; Galbany et al, 2011). The morpho-functional and structural characteristics of the teeth, along with the physical and mechanical properties of food and its hardness and abrasiveness −determined by the nature of the abrasive agents (particles of calcium carbonate or oxalate, crystalline silica or quartz)− are crucial in the process of alteration and small-scale fracture of enamel (microwear) during mastication (Lee et al, 2011; Romero et al, 2012). Microwear dental analysis has shown that the abrasive properties of food also affect the scale of the wear process (Teaford and Tylenda, 1991).

While dentine exposure shows no covariance with microscopic feature densitiess (Schmidt, 2010), there is a clear relationship between the micro-fractures in the occlusal surface and volume loss of enamel (Teaford and Tylenda, 1991; Schmidt, 2010). It has also been shown to produce higher levels of quartz enamel loss phytolith silica (Lucas et al., 2013). Therefore, the abrasion of the enamel depends on the type of food eaten, the quantity and geometry of the abrasives and its coefficient of friction in relation to the force exerted during biomechanical processing (Lucas, 2004; Lee et al. 2011; Romero et al, 2012).

The traditional hunter-gatherers Eskimo and Inuit populations (Alaska, Canada and Greenland) represent a model of interest in the study of macro- and microwear. Their diet, mostly based on consumption of protein and animal fat (marine and terrestrial origin), with a very occasional consumption of plants, mainly roots (Waugh, 1937. Fiorenza et al, 2011), and its strong craniofacial robustness have been linked directly to changes in the occlusal topography (Evans, 2013) and severe degrees of dentin exposure in the teeth (Hylander, 1977; Clement Hillson, 2012). However, its relationship with the vestibular microwear pattern is not known yet. In this work, different lines of analysis are applied to characterize the nature of the loss of enamel, using the ancient archaeological Eskimo population, of known ecology and diet, as a model, with the aim of analysing the long-term factors that determine or affect wear.

A total of 53 first permanent mandibular molars (M_1), preferably on the left side (~80% of the sample) of individuals (one tooth per individual) between ~6-40 years (Costa, 1977) were selected, showing different dentin exposure degrees, from the skeletal remains of the Tigara population, dating from the period Thule (1,400 to 1,850 AD), recovered at Point Hope (Alaska) in 1939 (Larsen Rainey, 1948) and deposited in the *American Museum of Natural History* (AMNH) in New York. This is the same series of previous study but, in this case, a mandibular tooth was selected to correlate tooth wear data with other enamel surface alterations of the tooth crown.

a. The Tigara Esquimo population

The Point Hope Peninsula (Alaska) is located approximately 200 *km* north of the Arctic Circle. Its vegetation is tundra, treeless, with the presence of moss, lichens and small plants. This ecosystem is home to a wide variety of wildlife, both marine and terrestrial, such as the polar bear or caribou (Larsen Rainey, 1948). Next to the ruins and human remains found during excavations in the village of Tigara, different devices used for hunting (Larsen and Rainey, 1948; Costa, 1977) were recovered.

The artifacts found and their analogy to those of the humans that later inhabited Point Hope indicate that the diet of this archaeological population would have been based on a high consumption of animal proteins (~30-60%), both marine and terrestrial, and a low intake of carbohydrates, mainly from roots (Costa, 1977). Meat processing for preservation (especially smoking, drying and freezing) alters its physical and mechanical properties (Waugh, 1937; Larsen Rainey, 1948; Costa, 1977), increasing its abrasive capacity on tooth enamel.

b. Analysis of dental crown

The analysis was performed from high-resolution dental replicas (Galbany et al., 2006). The crown of the original teeth were cleaned with acetone and ethanol and, after air-drying, silicone moulds were made with Affinis (Coltène). From the moulds, two different types of replicas were obtained: polyurethane Feropur PR-55+E-55 (Feroca) and epoxy resin Araldite 2020 cast. The polyurethane replicas were used for the analysis of the dentin exposure and tooth topography, and the epoxy one was used for the analysis of dental microwear.

With the polyurethane replicas, high-resolution digital calibrated images (1200×900 pixel, JPG format) of the occlusal surface of each replica were obtained with a Nikon D40 camera with a focal length of ~50 *cm*. The total occlusal area (TOA) and the area of dentin exposure (ADE) were measured, both in mm^2, with the *ImageJ* software (http://rsbweb.nih.gov/ij/). With these data, the percentage of dentin exposure (PDE = ADE × 100 / TOA) (Galbany et al., 2011) was obtained. With these same replicas, 3D (.txt) moulds were obtained with a *Picza* perfilometer (Roland). The 3D mesh was edited and analysed with *Rhinoceros*, and *Surfer Manipulator* (Golden Software, Inc.) was used to measure the variables of crown complexity (OPRC) and crown relief (CRI) (Evans, 2013).

The dental microwear analysis was made with the epoxy resin replicas, coated with a ~15 *nm* gold layer (Balzers SCD 004 Sputter Coater) and with a colloidal silver bridge to dissipate electrostatic charges (Galbany et al., 2006), with a *Hitachi* Scanning Electron Microscope (SEM) in secondary mode (SE) at 15 *kV*. Images at 100× magnification (1280×960 pixel, BMP) were obtained in the middle third of the labial surface, preferably below the protoconid (Perez-Perez et al., 1994; Romero et al, 2012.). All micrographs were processed with *Adobe* Photoshop CS3, obtaining images of 0.56 mm^2 of enamel in which each scratch (minimum 3:1 length to width ration) was measured.

From the dataset of all observed striations on the buccal enamel surfaces (0.56 mm^2) of teeth, the total density of scratches (NT) and the average length of all observed striations (XT, in microns) on each tooth (Romero et al., 2012) were measured. The correlation between the microwear variables (NT, XT) and the topography (OPCR, CRI) was studied using both univariate and multivariate tests. All the descriptive and statistical analyses were performed with the *Past* v. 2.17 software (http://folk.uio.no/ohammer/past/), usding an $\alpha=0.05$ level of significance for hypothesis testing.

c. Dental wear and topography

The results of overall crown wear analysis revealed, first, that the analysed M_1 show a clear increase in the percentage of dentin exposure (PDE) in relation to the age of the individuals (r= 0.746; *P*<0.0001). Lower values of PDE (from 0% to 13.6%) occurred in individuals of 6-25 years (n=33), showing a significant increase in the PED (from 13% to 56.7%) in individuals of 26-40 years (n=20) (χ^2=8.30; *P*=0.004). The complexity (OPCR) and crown relief (CRI) variables showed a multivariate significant association with the percentage of dentine exposure (PDE) (MANOVA Linear Model λ=0.742; df_{2-50}; F=8.693, P=0.0005), as well as for the univariate correlations of each variable (*Table 3*, *Figure 12*).

Table 3. *Multivariate regression of the percentage of dentin exposure (PDF, dependent variable) in relation to changes in crown complexity (OPCR) and relief (CRI), as independent variables (* P<0.001).*

Variable	**slope**	**error**	**constant**	**error**	**R^2**	***P***
CRI	–0,0048	0,0017	1,8772	0,0369	0,12536	0,0092*
OPCR	0,3068	0,080686	31,789	1,6734	0,22087	0,0003*
MANOVA	**λ**	**gdl_1**	**gdl_2**	**F**	**R^2**	***P***
	0,742	2	50	8,693	0,2208	0,0005*

Both variables behave differently. OPCR showed a significant positive correlation with PDE (r=0.469; *P*<0.01), but negative with CRI (r =–0.354; *P*<0.05), indicating a clear transformation of the topography of the crown that affects particularly the buccal cusps (protoconid, hypoconid, hipoconilid). Similarly, the age of the individuals (according to the categories considered) showed significant correlations with OPCR (r=0.572; *P*<0.001) and CRI (r=–0.380, *P*<0.01), indicating that the age is clearly associated with the percentage of dentin exposure.

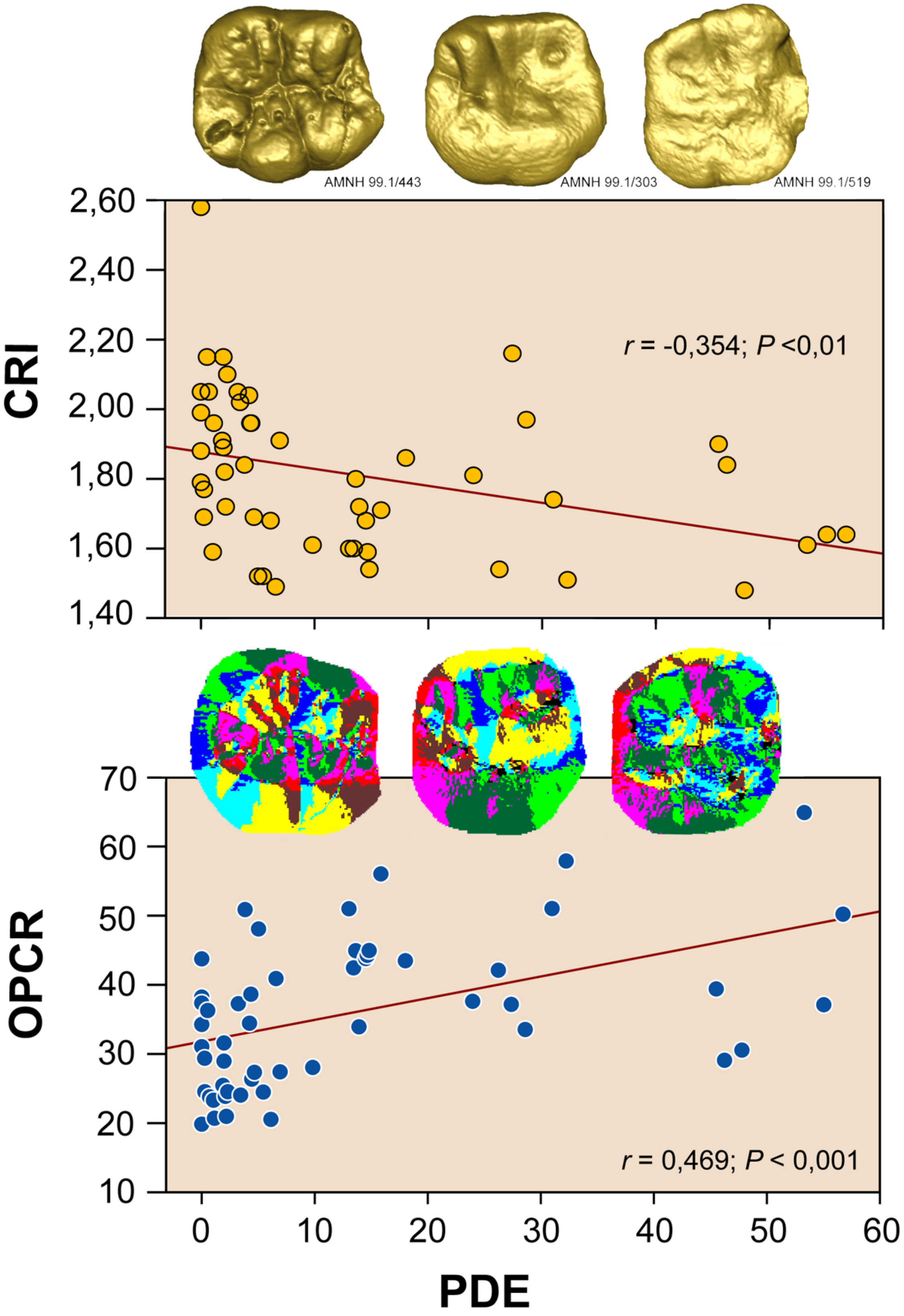


Figure 12. *Graphical representation of the relationship between PDE and changes in the topography of the tooth (CRI and OPCR). 3D models of teeth (AMNH code) and their conformation CRI (bottom) are shown.*

Thus, young people show less complex dental crowns (31.08±8.41) than older individuals (43.53±9.41), but higher profiles (1.87±0.22) than these (1.70±0.17), with the differences being significant in both cases (OPCR, $\chi^2=16.594$, $P<0.0001$; CRI, $\chi^2=7.839$, $P=0.005$). As expected, tooth wear increases with age and causes increased complexity and a decrease of the relief of the tooth crown.

No significant correlations were observed between vestibular microwear (NT and XT) and PDE ($\lambda=0.948$; $df_{2\text{-}50}$; $F=1.37$; $P=0.263$) (*Table 4*), so that the microscopic pattern of abrasion and percentage of dentin exposure appear distinct wear processes. When the correlations of the microwear variables (NT, XT) with OPCR (complexity) and CRI (relief) are analysed, only a significant correlation ($r=-0.372$, $P<0.01$) is obtained, which indicates a substantial change in the occlusal relief (CRI) in relation to enamel loss that affects only to the average length of striations (XT). However, changes in OPCR and CRI are not associated with the density (NT=110.54±32.17) of enamel scratches. Only their average length (XT, range 53.45 to 129.*71μm*) is higher as CRI values increases ($r=-0.465$, $P<0.001$) (*Figure 13*). This means that teeth with less wear (lower loss of crown relief) have longer scratches. This is an expected result as the accumulation of scratches over time tends to fragment existing striations, thus reducing their length.

Enamel loss depends on the use (mostly in relation to dietary activities for the posterior dentition) of the tooth along its functional life and therefore significantly correlates with the age of the individual (Smith, 1984; Fiorenza et al., 2011). However, the process of enamel loss, through dental wear, also depends on the type of diet and the ingested foods. The physical and mechanical characteristics of foods greatly affect the biomechanics of mastication and food chewing (Lucas, 2004), producing varying degrees of dentin exposure.

Our results confirm the association between dentin exposure and crown relief in the Tigara Eskimo populations, showing that the increased exposure of dentin with age is significantly corelated to the loss of height of the tooth crown, unlike that previously observed by Costa (1977). In his analysis, the height of the crown showed no significant changes in dental wear in relation to the age of the individuals. However, this was probably the case because in his analysis he mixed anterior and posterior teeth, without considering that dental wear may differentially affect both classes of teeth,

Table 4. *Multivariate regression of density (NT) and average length (XT) of vestibular microwear with the percentage of dentin exposure (PDE), complexity (OPCR) and crown relief (CRI). P<0.01 (*)*

PDE

variable	**slope**	**error**	**intercept**	**error**	***r***	***P***
NT	0,4303	0,2699	104,94	5,5976	0,2179	0,1169
XT	–0,0026	0,1667	84,49	3,4572	–0,0022	0,9875

MANOVA	**R^2**	**λ**	**df1**	**df2**	**F**	***P***
	0,0348	0,948	2	50	1,37	0,2635

OPCR

variable	**slope**	**error**	**intercept**	**error**	**r**	***P***
NT	0,6786	0,4128	86,26	15,401	0,2243	0,1063
XT	0,1019	0,2549	80,807	9,511	0,0559	0,6908

MANOVA	**R^2**	**λ**	**df1**	**df2**	**F**	***P***
	0,03775	0,9496	2	50	1,327	0,2746

CRI

variable	**slope**	**error**	**intercept**	**error**	***r***	***P***
NT	–9,4919	20,26	127,77	37,028	–0,065462	0,6414
XT	–40,655	10,834	158,22	19,801	–0,46515	0,0004*

MANOVA	**R^2**	**λ**	**df1**	**df2**	**F**	**P**
	0,0608	0,7788	2	50	7,1	0,0019*

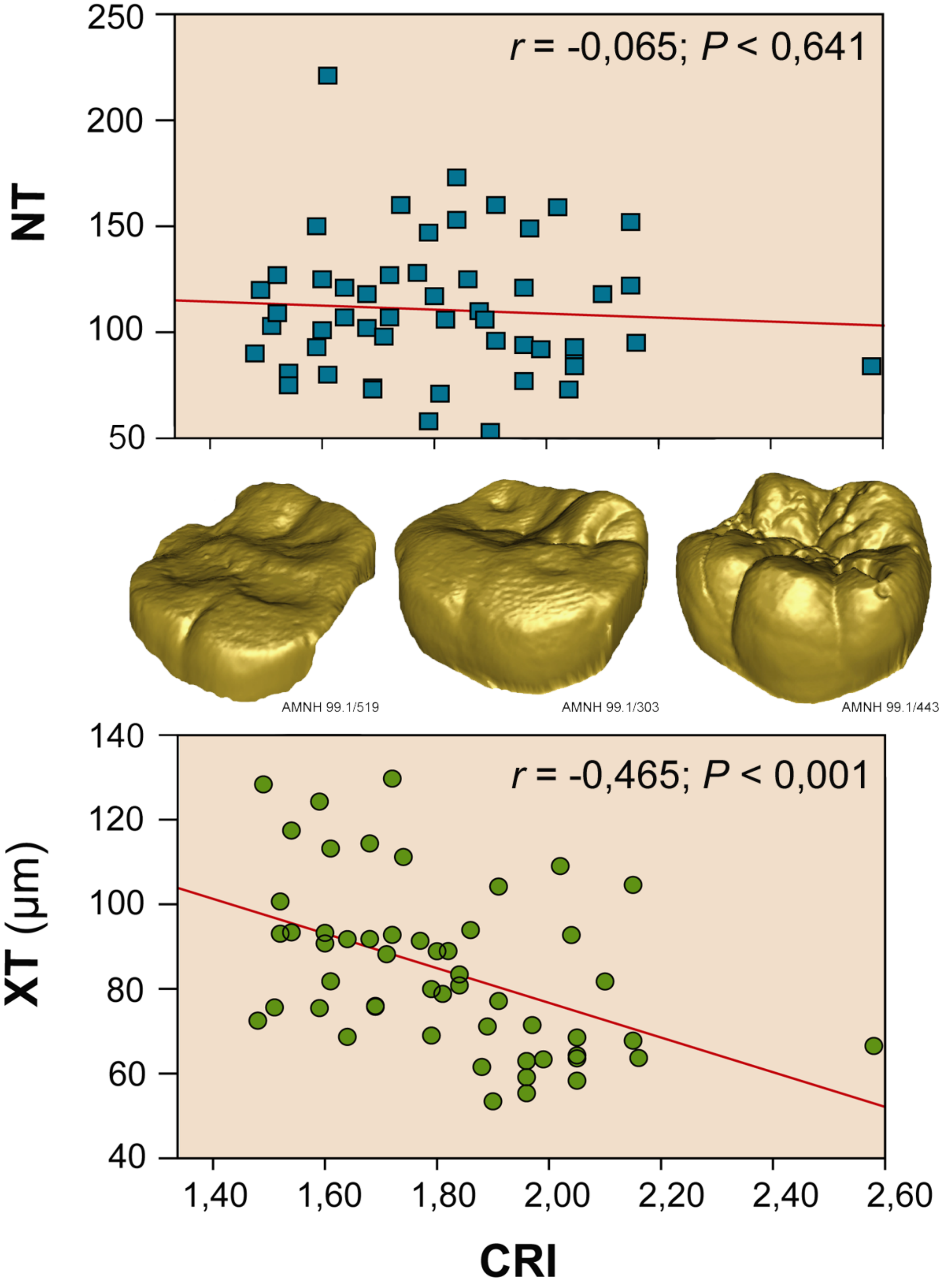


Figure 13. *CRI changes in relation to microwear density (NT) and average length (XT) in the buccal tooth surface. 3D teeth (AMNH code) models are shown to illustrate that CRI values are linked to changes in topography.*

In contrast, Smith (1984) for M_1 documented that enamel loss in a vestibular direction is smaller in Arctic hunter-gatherer environments (Canada and Alaska) than in agricultural groups. The model of dental wear in Igloolik Eskimos (Canada) also shows a reduction in the height of the crown with the increase of PDE from 21 to >50 years age groups (Tomenchuk and Mayhall, 1979). In this population, relative to the eruption of the first molar, dentine exposure was greater in the anterior dentition than in the postcanine one, but the upper and lower molars did not differ in dental wear (Clement Hillson, 2012).

Analysis of the 3D topography in molars shows, in fact, that more wear occurs in occluso-vestibular enamel facets in hunter-gatherer groups mainly consuming meat, such as Eskimos and Inuit (Alaska, Canada and Greenland) than in populations of mixed diet, such as the Khoe-San (Kalahari, South Africa) or the Australian Aborigines (Fiorenza et al., 2011). Although the wear on the anterior dentition, generally more marked than in the postcanine dentition, is mainly caused by either anatomical features of the skull, biomechanical processes or cultural practices, such as those described in the Eskimos groups (Waugh, 1937; Hylander, 1977; Holmes and Ruff, 2011; Clement and Hillson, 2012), the causes of wear in molar teeth are poorly known yet. Although the data from our study require comparative analysis with other groups of known diets, the observed relationship between PDE and the changes in the topography of the tooth are evident and consistent with the pattern of dental wear described in Eskimo populations in previous studies (Tomenchuk and Mayhall, 1979 Fiorenza et al, 2011).

Cranio-functional variables, the type of diet and techniques of food preservation and preparation, are the key factors in the formation of dental wear in Eskimo populations (Hylander, 1977). The abrasive properties of the ingested diet, dried meat with lots of extrinsic abrasive particles, require large power during biomechanical masticatory processing, which is evidenced in the large dimensions of the condyles and jaw muscles that, together, are indicative of strong vertical pressure during mastication (Hylander, 1977; Holmes and Ruff, 2011). Changes in the size of the jaw during growth, documented in the town of Tigara (Holmes and Ruff, 2011), are consistent with the results obtained in this thesis regarding the decrease in CRI with the increase in PDE in adult individuals (>25 years old) compared to younger ones. The Eskimo generate forces of mastication (lb/in^2 or *psi*) higher (240-280 *psi*) than the European populations (90-120 *psi*), which is linked to distinct craniofacial features (Hylander, 1977). Recent analyses also show that the force exerted during mastication (tooth-tooth and tooth-food-tooth) influences dental wear in M_1 teeth, affecting the topography and morphology of the occlusal surface of the tooth crown, on which tensile forces are distributed (Benazzi et al, 2011; Lee et al., 2011). Thus, the occlusal macro and micro-wear have a marked influence on enamel loss, with long-term effects on the enamel tissue and tooth crown (Teaford and Tylenda, 1991; Schmidt, 2010; Lee et al., 2011).

The vestibular microwear is not produced in occluding facets of enamel, with interdental contact, whereby wear patterns have a direct relationship with the abrasive nature of the diet (Romero et al., 2012). In the sample analysed, the percentage of dentin exposure (PDE) and the density of the enamel microwear (NT) are not significantly correlated. However, the average length of these scratches (XT) is significantly lower in teeth with lower occlusal relief. Previous studies (Perez-Perez et al., 1994; Romero and John, 2007) showed a wide dispersion in the average length of the buccal marks on agricultural populations, which have a high density of striations. However, since it has been shown that the dynamics of formation of the microwear pattern is linked to the abrasive nature of the diet (Romero et al., 2012), analyses of intergroup differences must consider the physical and mechanical characteristics of the food consumed by each population. Thus, in the Tigara population the changes that occur in the crown relief of the occlusal topography, which is directly related to the percentage of dentine exposure, appears to be due to the abrasive effect of the extrinsic particles incorporated into foodstuffs, acting on enamel surfaces during mastication and producing a differential microscopic fracture process. It is therefore necessary to establish comparative models on other groups with known diets to more accurately document the changes in the topography of the tooth and its connection with the vestibular dental microwear patterns in the vestibular enamel surfaces. The results obtained suggest that the process of enamel wear, either macro or microscopic, may have distinct causes.

3. Molar size and wear in traditional populations

Dental variation among and within modern human populations has been attributed both to genetic and environmental factors (Bailit, 1975). Crown length-breadth measurements have been widely used to analyze inter- and intragroup variability in dental size (Bishara et al., 1989; Brook et al., 2009; Hanihara, 1977;Keene, 1979; Otuyemi and Noar, 1996; Turner and Richardson, 1989). Hanihara and Ishida (2005) made a significant study of tooth size differences in modern human populations. They analysed mesio-distal and bucco-lingual tooth crown differences among 72 major human populations and concluded that the Australian Aborigines possess the largest and Philippine Negritos the smallest teeth of all groups considered. They 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;˙Işcan 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; Garn, 1977; Hillson, 1996; Mizoguchi, 1988). Harris (2003) reported that sexual variance accounted only for 1.2% of total variation among studied groups. Additionally, Scott and Turner (1997) acknowledged that even if there are differences between sexes, they are very often inconsistent among samples and cannot lead to conclusive statements.

Dental wear and dentin exposure analyses have also been performed. 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 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) analysed mandibular dental wear between the Natufian hunter-gatherers from southern Levant (10,500–8,300 BC) and Neolithic populations (8,300–5,500 BC) and found higher rates of dental wear, for all tooth types, in the forager groups. Finally, Deter (2009) analysed maxillary teeth and reported higher percentages of dentin exposure for all tooth types in North American hunter-gatherers (3,385±365 BC) than in more recent agricultural groups (~1,300 AD). The reduction of dental wear in societies with prevalent food production was associated to a decrease in diet abrasiveness. Sex-related intragroup differences in tooth abrasion have been reported. Generally, women exhibit greater wear on anterior teeth than men, especially in foraging societies (Berbesqueet al., 2012; Clement and Hillson, 2012; Madimenos, 2005; Molnar, 1971; Richards, 1984). Molnar (1971) suggested that differences in roles between sexes conditioned the foods consumed, women consuming greater amounts of fibrous plants and abrasive roots. However, Tomenchuk and Mayhall (1979) reported that Canadian Igloolik men exhibited greater wear rates in maxillary teeth than women, likely caused by prolonged or heavier mastication. However, another study on the same population, based on quantitative analyses of the percentage of dentin exposure (Clement and Hillson, 2012), reported that the wear of anterior teeth in females 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. 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 intra-group 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).

a. Samples studied

We studied a total of 225 first lower (M_1, N=124) and upper (M^1, N=101) molar molds, belonging to 162 individuals from four geographically dispersed hunter-gatherer (Agta, Australian Aborigines, San, and Eskimo) and three agriculturalist (Batéké-Balali, Khoe, and Navajo) populations (*Table 5*).

Two different aspects of dental morphology were investigated: tooth size and dental wear. For each aspect three comparisons were performed: 1) within-group sexual dimorphism, 2) intergroup variation, and 3) 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. 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. The analysis focused on the first permanent molar because it was the most abundant tooth. It is the first tooth to erupt (5.5–6.0 years) in modern humans and, thus, exhibiting the greatest degree of dental wear among postcanine teeth (Clement and Hillson, 2012). Sex estimations were obtained from museum records or previous studies 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 we used cranial and pelvic traits for sex determination (Buikstra and Ubelaker, 1994).

***Table 5**. Human population studied (group), acronym (ID), provenance, subsistence strategy (ST): hunter-gatherers (HG) or agriculturalists (AGR) with or without raising animal and/or fishing;* N*: total number of individuals;* n*: total number of studied teeth; n: 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): first number is the number of teeth showing dentine exposure over (/) the total number of teeth. Collection: institution where the remains are curated, AMNH: American Museum of Natural History (New York), MH: Musée de 1'Homme (Paris).*

Group	**ID**	**Provenance**	**ST**	**N**	**n**	***n***	**M**	**F**	**M^1**	**M_1**	**Collection**	**Reference**
Agta	**AGT**	Luzon, Philippines	**HG**	19	30	9	16	3	4/16	5/14	MH	Genet-Varcin, 1949
Aust. 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
Eskimo	**ESK**	Point Hope, Alaska	**HG**	72	92	88	16	8	27/31	61/61	AMNH	Costa, 1977
Hottentot-Khoe	**KHO**	South Africa	**AGR**	11	17	9	15	5	5/10	4/7	AMNH, MH	
Navajo	**NAV**	Cañon del Muerto Arizona	**AGR**	20	32	29	4	2	14/16	15/16	AMNH	
Bushmen-San	**SAN**	South Africa	**HG**	6	10	7	6	4	3/6	4/4	AMNH, MH	
			Total	**162**	**225**	**171**	**78**	**44**	**66/101**	**105/124**		

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.

b. Subsistence strategies

Hunter-gatherers

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

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).

Eskimo. 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 Cañon 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: Cañon 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).

c. Dental size and wear

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 (*Figure 14*), outlining the dentin exposure areas on the dental replicas (Galbany et al., 2011).

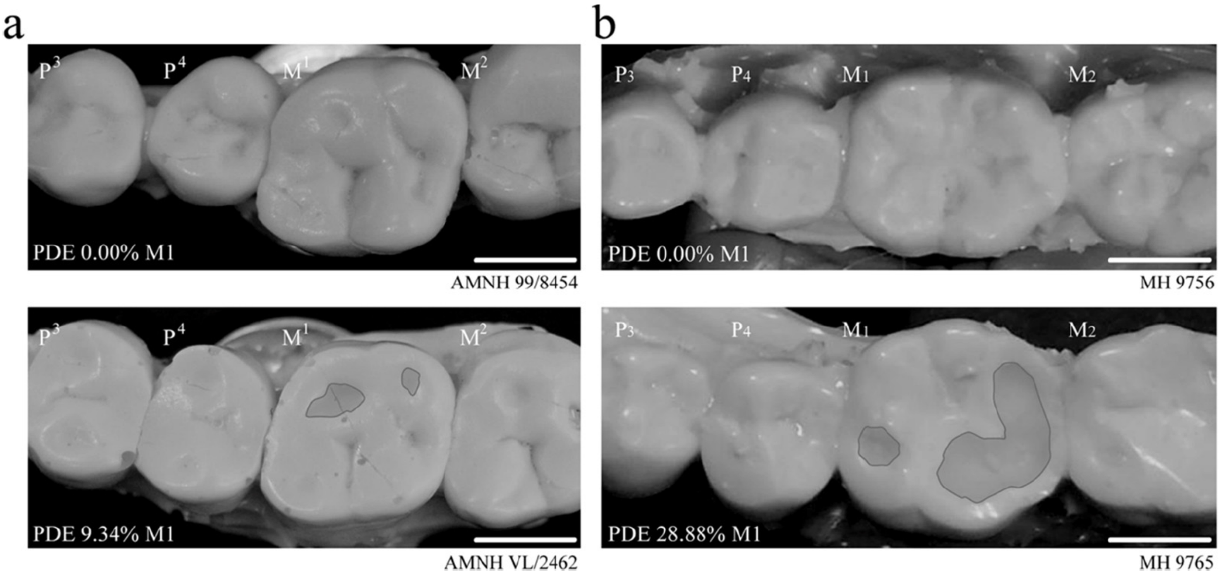


Figure 14. *Occlusal view of upper (a) and lower (b) postcanine (P1–M2) teeth in San (South Africa) and Agta (Philippines) individuals(left and right, respectively) showing different percentages of dentin exposure (PDE) in M1. Code number indicates museumrecord (see Table 1). Mesial: left; buccal: down. Scale bar: 5 mm.*

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 total area of dentin exposure (ADE). The percentage of dentin exposure (PDE) with respect to total occlusal area (TOA) was computed as indicated in the methods section. For measuring the intraobserver error (Harris and Smith, 2009), twenty randomly selected teeth were measured five times, with a 2-week interval between each repetition. Error values higher than 5% 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.

d. Intra and interpopulation variability

Measurement error and normality of variables

The average relative measurement error was smaller than 5% for all measurements: 0.64% for MD, 0.39% for BL, 0.56% for TOA, and 3.29% for DEA. 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 all groups. In most cases, the area and percentage of dentin exposure failed the normality assumption, so they were rank-transformed before being subjected to multivariate analyses of variance.

Sexual dimorphism

Except for the TOA in Eskimo (M_1: $F=7.808$, $P=0.007$; M^1: $F=5.716$, $P=0.024$), no significant sexual differences were found (*Table 7*). Eskimo women had significant smaller TOA and they generally have smaller teeth than men (*Tables 6*).

Table 6. *Multivariate Analysis of Variance (MANOVA) P<0.005 for intragroup differences in dental size (MD, BL, AREA) and dental wear (ADE, PDE).*

Lower	**MANOVA**		**BL**		**MD**		**AREA**		**AED**		**PDE**	
	F	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
AGTA	0.314	0.891	0.145	0.710	1.331	0.271	0.892	0.364	0.948	0.349	0.961	0.346
ESKIMO	2.011	0.091	3.483	0.067	3.322	0.073	7.808	0.007	0.219	0.642	0.053	0.819
KHOE	0.258	0.894	1.496	0.276	1.256	0.313	2.121	0.205	0.000	0.999	0.027	0.876
AUST	0.693	0.640	0.740	0.403	0.015	0.905	0.560	0.466	0.004	0.953	0.013	0.911
NAVA	0.981	0.475	0.002	0.968	0.003	0.960	0.003	0.954	2.573	0.131	2.360	0.147
BUSH	2.352	0.419	8.077	0.105	2.143	0.281	3.494	0.203	0.002	0.967	0.007	0.940
BATE	14.668	0.189	1.489	0.310	.067	0.378	2.101	0.243	0.146	0.728	0.012	0.919
Upper												
AGTA	0.171	0.967	0.091	0.768	0.088	0.772	0.000	0.990	0.988	0.337	1.004	0.333
ESKIMO	1.941	0.123	0.259	0.614	1.961	0.172	5.716	0.024	0.726	0.401	0.468	0.500
KHOE	0.465	0.788	0.234	0.642	0.525	0.489	1.669	0.233	3.182	0.112	3.092	0.117
AUST	0.345	0.872	0.201	0.662	0.045	0.835	0.070	0.796	1.084	0.318	1.182	0.298
NAVA	0.658	0.663	0.117	0.737	1.827	0.198	0.442	0.517	0.007	0.937	0.034	0.856
BUSH	2.984	0.406	0.000	0.995	2.360	0.199	0.837	0.413	0.066	0.810	0.172	0.700
BATE	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 7. *Descriptive statistics for the variables analysed (MD, DM, AREA, ADE and PDE) by population (ID), maxilla (Max, 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	**Max**	**Sex**	**n**	**mean**	**std**	**mean**	**std**	**mean**	**std**	**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

ESK	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

Intergroup variability.

Because only one significant difference between the sexes was found, intragroup variation was analysed with the sexes pooled (Scott and Turner, 1997). A general multivariate analysis of variances revealed significant differences between groups for all analysed 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

Tukey's *post-hoc* pairwise comparison (*Table 8*, upper matrix) 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 7*). In addition, Navajo presented greater mesio-distal dimensions than Eskimo (*P*=0.038). All other groups did not differ in this measurement. The bucco-lingual crown diameter presented higher variation among groups. The Eskimo 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 Eskimo, 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 Eskimo *vs.* Agta and Eskimo *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), Eskimo (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).

Morphology and wear of M_1

Pairwise analysis showed relatively small variation in mesio-distal crown diameters for M_1 (*Table 8*, lower matrix). Only Australian Aborigines compared with Agta (P<0.001) and Khoe (P=0.029) showed significant differences. In both cases greater mesio-distal dimensions characterized the Australian groups. Bucco-lingual crown diameter of M_1, on the other hand, showed somewhat greater variation among the analysed groups as compared to that seen in M^1. Agta had significantly smaller bucco-lingual crown diameter than Eskimo (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), Eskimo (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 M1crown.

Table 8. *Post hoc Tukey analysis ($P<0.05$) among populations for dental size (MD, BL AREA) and wear (AED, PDE) of M_1 lower triangular matrix) and M^1 (upper matrix).*

BL	**AGT**	**AUS**	**BAT**	**ESK**	**KHO**	**NAV**	**SAN**
AGT	-	0.117	0.830	**0.000**	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
ESK	0.000	0.141	0.203	-	0.000	0.485	0.000
KHO	1.000	0.206	0.915	0.000	-	0.048	0.983
NAV	0.000	0.112	0.126	0.984	0.000	-	0.015
SAN	0.996	0.066	0.546	0.000	0.980	0.000	-
MD							
AGT	-	0.025	1.000	0.886	1.000	0.005	1.000
AUS	0.000	-	0.196	0.158	0.162	1.000	0.162
BAT	0.770	0.614	-	0.994	1.000	0.082	1.000
ESK	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	-	0.008	0.922	0.129	0.931	0.010	0.740
AUS	0.000	-	0.242	0.661	0.001	1.000	0.001
BAT	0.433	0.898	-	0.861	0.706	0.302	0.487
ESK	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	-
AED							
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
ESK	0.000	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	**N**						
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
ESK	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	-

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), Eskimo (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 Eskimo (P=0.001). In both cases, the Philippine group was characterized by less advanced dental wear.

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 9*).

Table 9. *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
AED	0.033	0.855	1.148	0.287
PDE	0.022	0.883	1.264	0.264

e. Sexual dimorphism and intergroup variation

As indicated above, 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; Işcan 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 Eskimo for the total occlusal area of the crown. Eskimo 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 analysed 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 (Berbesqueet 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, the 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 analysed 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 Eskimo. 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 (BL and MD crown diameters, and TOA), the analysed 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 evolutionary factors than mesio-distal crown diameter, reflecting the different environments of the analysed groups. The group variation in tooth size could be summarized as follows: Agta, San, and Khoe groups together presented lower values of the analysed features than Australian Aborigines, Eskimo, and Navajo. Although previous authors have proposed that agriculturalists would show reduced tooth size (Hintonet 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 is the rather low values of tooth size variables in the African groups (San and Khoe). Hanihara and Ishida (2005) reported that relatively large tooth dimensions characterize sub-Saharan groups, 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 analysed 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 analysed teeth. In general, the Eskimo, 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-Griffinand Griffin, 1981; Minter, 2010). Eskimo 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 of the Eskimo, 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) 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 (Romero et al., 2013). 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 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 analysed based their economy exclusively on cultivated plants, which might also contribute to the lack of dental wear variation between the two groups.

4. 3D GM of first molars

Dental morphology has been an essential part of anthropological studies (Kieser, 1990). Teeth are strongly genetically controlled development (Scott and Turner, 1997; Bernal, 2007; Bei, 2009), and once formed they do not remodel during the individual's lifetime (Dahlberg, 1971; Kelley and Larsen, 1991; Thomason, 1997; Riga et al., 2013). Thereby, metric and non-metric dental traits have been broadly used to address anthropological and evolutionary questions, extensively contributing to our knowledge of paleontology, ecology, variability and taxonomy of modern and past human populations (Kieser, 1990; Lalueza and Pérez-Pérez, 1993; Hillson, 1996; Scott and Turner, 1997; Irish and Guatelli-Steinberg, 2003; Pérez-Pérez et al., 2003; Hanihara and Ishida, 2005). Studies on monozygotic twins show that apart from a high level of genetic control, epigenetic and environmental factors also contribute to dental development, resulting in morphological variation among and within human populations (Townsend and Brown, 1978; Townsend and Brook, 2008; Townsend et al., 2009, 2011). For these reasons, studies on dental variation of modern humans may reveal interesting information about the impact of various external factors on tooth morphology and contribute to our knowledge of the mechanisms of human dietary adaptations, providing an insight into a variety of ecological, taxonomic or phylogenetic uncertainties.

Advances in geometric morphometric (GM) techniques have opened new perspectives for a wide range of research. The method itself has become a powerful and very useful tool in the studies of shape variations in biological structures and of their effects on ecological adaptations, ontogeny and phylogeny (Jones, 1998; Vidarsdottir et al., 2002; O`Higgins and Harvati, 2003; Witter et al., 2003; Hennessy et al., 2005; Macholán, 2006; Nicholson and Harvati, 2006; Gómez-Robles et al., 2007; Kulmeyer et al., 2009; Skinner et al., 2008; White, 2009; Cooke, 2011; Singleton et al., 2011). Applied to dental anthropology, geometric morphometrics has shifted the interest of researchers from dental size (Bailt, 1975; Hanihara, 1977; Keene, 1979; Bishara, 1989; Turner and Richardson, 1989; Otuyemi and Noar, 1996; Işcan and Kedici, 2003; Hanihara and Ishida, 2005; Harris and Lease, 2005; Matsumura and Hudson, 2005; Kondo et al., 2005; Brook et al., 2009; Khan et al., 2011) to the shape of teeth, an approach that up to recently has not been widely investigated. This method has been widely employed ever since in dental studies. Contrarily to traditional morphometrics, it better describes the object's geometry, and allows for more accurate shape representation and visualization of the shape changes (Rohlf and Marcus, 1993; O'Higgins and Jones, 1998, Bernal 2007). The method is highly sensitive and thus minimal shape differences can be analysed with great precision, even on small objects such as teeth.

Geometric morphometrics is based on a configuration of landmarks, which are very precise points on anatomical structures, homologous and clearly definable on each of the analysed specimens (Bookstein, 1991; Richtsmeier et al., 2002; Zelditch et al., 2004). The configurations of landmarks from all specimens (landmarks coordinates) are rotated and scaled to minimize the intragroup variability, so the size effect is removed and only the shape information remains for analysis (Kendall, 1977; Dryden and Mardia, 1998). The shape variation within a sample is studied by interpolating the displacements of the landmark configurations, which represent the direct differences in the shape configuration between two or more individuals.

Early research in this field comprehend mainly two-dimensional (2D) analyses of dental shape among Hominoidea species and/or Early Modern Humans (Bailey and Lynch, 2005; Martinon-Torres et al., 2006; Gomez-Robles et al., 2007, 2008, 2011, 2012; Liu et al., 2010; Górka et al., 2012). Not much attention, however, has been directed towards studies of dental shape on modern human (*Homo sapiens sapiens*) populations. Kieser et al., (2007) examined the distinctiveness of human anterior dentition for forensic purposes using a geometric morphometric approach and concluded that the morphology of the anterior teeth is a unique and individually distinct feature. Bernal (2007) performed a very interesting comparative study of dental size and shape variation with the use of three different methods: traditional morphometrics, as well as landmarks and semi-landmarks geometric morphometrics. She studied second upper molars (M^2) of three geographically disperse Argentinian populations. The results proved a high correlation between the methods, in terms of centroid size, which suggests that they provide analogous information.

However, when comparing linear measurements with landmark-based geometric morphometrics, the use of the latter increased the amount of information obtained, which was particularly significant given that both methods used the same set of landmarks. Both geometric approaches (landmarks and semilandmarks) were able to discriminate among the analysed populations, whereas traditional metric approach did not separate the groups. Therefore, Bernal (2007) concluded that given that modern human variation is relatively low, geometric morphometrics techniques appear to be more accurate and allow for more detailed analyses, and consequently are more suitable for such studies.

Teeth however are geometrically complex structures and the quantification of their morphological traits is not complete if limited to a two-dimensional space (Ulhaas et al., 2004). Implementing three-dimensional (3D) geometric morphometrics in dental research would allow for a more complete data collection and thus expand research possibilities. This approach has already been used in dental studies (Witter et al., 2003; Ulhaas et al., 2004; Benazzi et al., 2009; Cooke, 2011). However, to our knowledge, a 3D geometric morphometric approach has not yet been applied to research on dental shape of modern human populations variation. The aim of this analysis is, therefore, to develop a three-dimensional (3D) geometric morphometrics (GM) procedure to characterize molar shape variability in five geographically dispersed archaeological human populations. We hypothesize that dental shape, having a very strong genetic component, may carry information on the phylogenetic affinities among populations, although other factors, such as geographic isolation, climatic conditions, or dietary habits may have also influenced the evolution of molar shape through time on recent modern humans.

a. Sample studied and methodological procedures

The selected teeth and analysed for this purpose was the upper first molar (M^1). Early reports have shown its usefulness in the discrimination of contemporary human groups (Morris, 1986). Additionally, this tooth has a more stable morphology than for example its lower analogous (Scott and Turner, 1997; Bailey, 2004; Gomez-Robles et al., 2007), and therefore seems to be a better marker for population affinities (Turner, 1969).

As in previous studies, the analysed sample comes from the dental casts collection curated at the *University of Barcelona*, originally obtained from the *American Museum of Natural History* (New York) and the *Musée de 1'Homme* (Paris). The dental crown replicas were obtained following standardized procedures (Galbany et al., 2006), as explained in the previous chapter. Dental impression molds were made using the *President MicroSystem* (Affinis) Regular body (Coltène-Whaledent) polyvinylsiloxane and the casts were made with polyurethane resin Feropur PR-55 (Feroca Composites).

The total available sample was 98 teeth (M^1), one tooth per individual. However, the 3D GM analysis designed required the use of unworn teeth, so only the anatomical variation was analysed, excluding dental wear. Therefore, for the purpose of unambiguous landmark identification and digitalization, only teeth with minimal or no enamel damage, lacking significant enamel wear facets on cusp tips (dental wear scores 1 and 2, after Smith, 1984) or any pathological conditions, such as dental caries, were selected. The process of teeth selection was consequently highly time consuming during a great deal of the research period. However, such selection was required to avoid interference of ecological factors on the results. Eventually, the analysed sample (*Table 10*) only consisted of 36 individuals, and one tooth per individual was studied (the first upper molar, M^1). The represented modern human populations were: Agta (Luzon, Philippines, SE Asia, N=8), Australian Aborigines (N and SE Australia, N=5), Hutu (Rwanda, Africa, N=11), Eskimo/Inuit (Canada, Alaska, and Greenland, N=8) and Javanese (Java, Indonesia, South Asia, N=4). Unfortunately, museum records from which the samples were obtained did not have information on the sex of all analysed individuals, and thus this factor could not be accounted for.

***Table 10**. Detailed description of the sample used in the 3D GM analysis. N: Number of teeth analysed. *AMNH: American Museum of Natural History (New York); MH: Musée de l'Homme (Paris).*

Provenance	**Area**	**Climate**	**Subsistence**	**N**	**Museum***
Luzon	SE Asia	tropical	hunter-gatherer	8	MH
Australia	Australia	Dry-warm	hunter-gatherer	5	AMNH, MH
Rwanda	Africa	tropical	mixed	11	MH
Eskimo/Inui	N America	arctic	hunter-gatherer	8	AMNH
Java, Indonesia	SE Asia	tropical	mixed	4	MH

Tooth-replicas were scanned using the *NextEngine* scan [Positioning: 360°; Divisions: 6; Tilt: 0° (A scan), 45° (B scan); Points: HD; Target: neutral, macro], and saved in *.ply* (ASCII) format.

The scanned 3D images were uploaded into *Landmark Editor* software to digitize a set of 10 landmarks defining dental crown homologous points (*Table 11*, *Figure 15*).

The configuration of chosen landmarks was later exported in .dta format and uploaded in MorphoJ (Klingenberg, 2011) for 3D geometric morphometrics analysis. The size effect on shape (allometry) was tested with regression analysis. Canonical Variate Analysis (CVA) was performed, based on the Covariance Matrix of Procrusters Coordinates, to find these shape characteristics that the best differentiate analysed groups. To increase the accuracy of discrimination the data was subjected to a pair-wise jackknife cross-validation by requesting Discriminat Function (DF) in MorphoJ.

Mahalanobis distances obtained during the Discriminant Function Analysis were later used in generating a phylogenetic tree with PHYLIP software (Felenstein, 2005) to investigate whether encountered differences can serve to estimate phylogenetic relationships among studied groups.

***Table 11**. Landmarks definitions for the 3D GM analysis made.*

Landmark #	Definition
1	Paracone tip
2	Metacone tip
3	Hypocone tip
4	Protocone tip
5	Intersection of buccal groove with central fossa
6	Intersection of central fossa with distal fossa
7	Mesial endpoint of mesio-distal (MD) distance
8	The most flat point in the intersection of the distal fossa with the distal border of occlusal surface
9	The most flat point in the intersection of the buccal groove with the buccal crown surface
10	The most flat point in the intersection of the distal fossa with the lingual surface of the crown

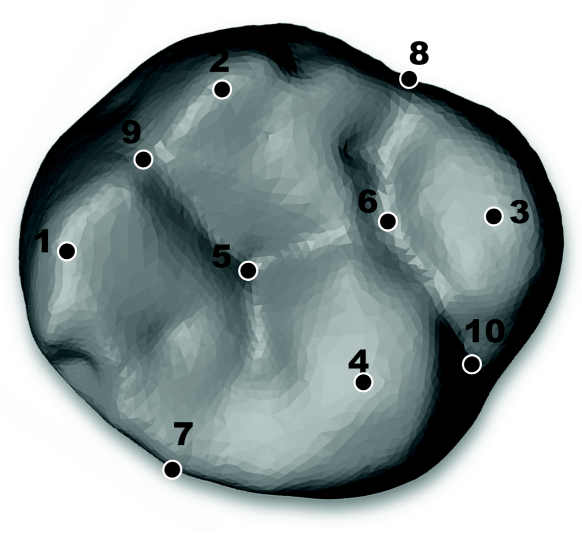


***Figure 15.** Digitized three-dimensional anatomical landmarks for the upper first molar. Landmark numbers correspond to those listed in Table 1. Mesial: left; buccal: top.*

b. 3D Geometric Morphometrics

The regression analysis revealed that the size effect on shape was not significant (*P*=0.377) and only 2.34% of the total shape variance was explained by size. Therefore, for the upper first molar, shape differences do not result from differences in size among populations, and there exists other factors responsible for the observed variation. The results of the Canonical Variate Analysis (CVA), within the *MorphoJ* Procrustes fit, are illustrated in the *Figure 16* and the comparisons of molar shape between groups are shown in *Table 12*. The first canonical variate (CV1) explains 55.19% of shape variance, and CV2 explains 29.40%. Both discriminant functions together explained 84.59% of total variance among groups. All groups showed highly significant pairwise shape differences among them, which indicates that substantial variation of the upper molar shape exists in modern human populations, despite otherwise indicated.

***Table 12**. Results obtained for Canonical Variate Analysis (CVA). The lower triangular matrix shows the Mahalanobis distances among groups; the upper triangular matrix shows the P-values (in italics) for the ANOVA comparisons between groups using Procrustes permutation tests (10000 permutation rounds).*

	AGTA	**AUST**	**HUTU**	**ESK/INU**	**JAVA**
AGTA	-	*0.0006*	*<0.0001*	*0.0001*	*0.0008*
AUST	5.4128	-	*0.0003*	*0.001*	*0.0034*
HUTU	6.9175	8.0724	-	*<.0001*	*0.0005*
ESK/INU	5.2878	7.9216	8.5041	-	*0.0014*
JAVA	4.8141	5.5330	5.6324	7.2724	-

The equiprobable ellipses in *Figure 16* include an 85% confidence interval of the group samples, which approximately spans an interval of 1.5 standard deviation around the group means. Since small sample sizes greatly affect the GM analysis and, therefore, a *leave-one-out*, a Jackknife test was performed for a more accurate discrimination (*Table 13*). Significant shape differences were confirmed between Hutu and Eskimo/Inuit ($P<0.001$), Australian Aborigines ($P=0.041$) and Agta ($P=0.005$), and between Eskimo/Inuit and Javanese ($P=0.038$).

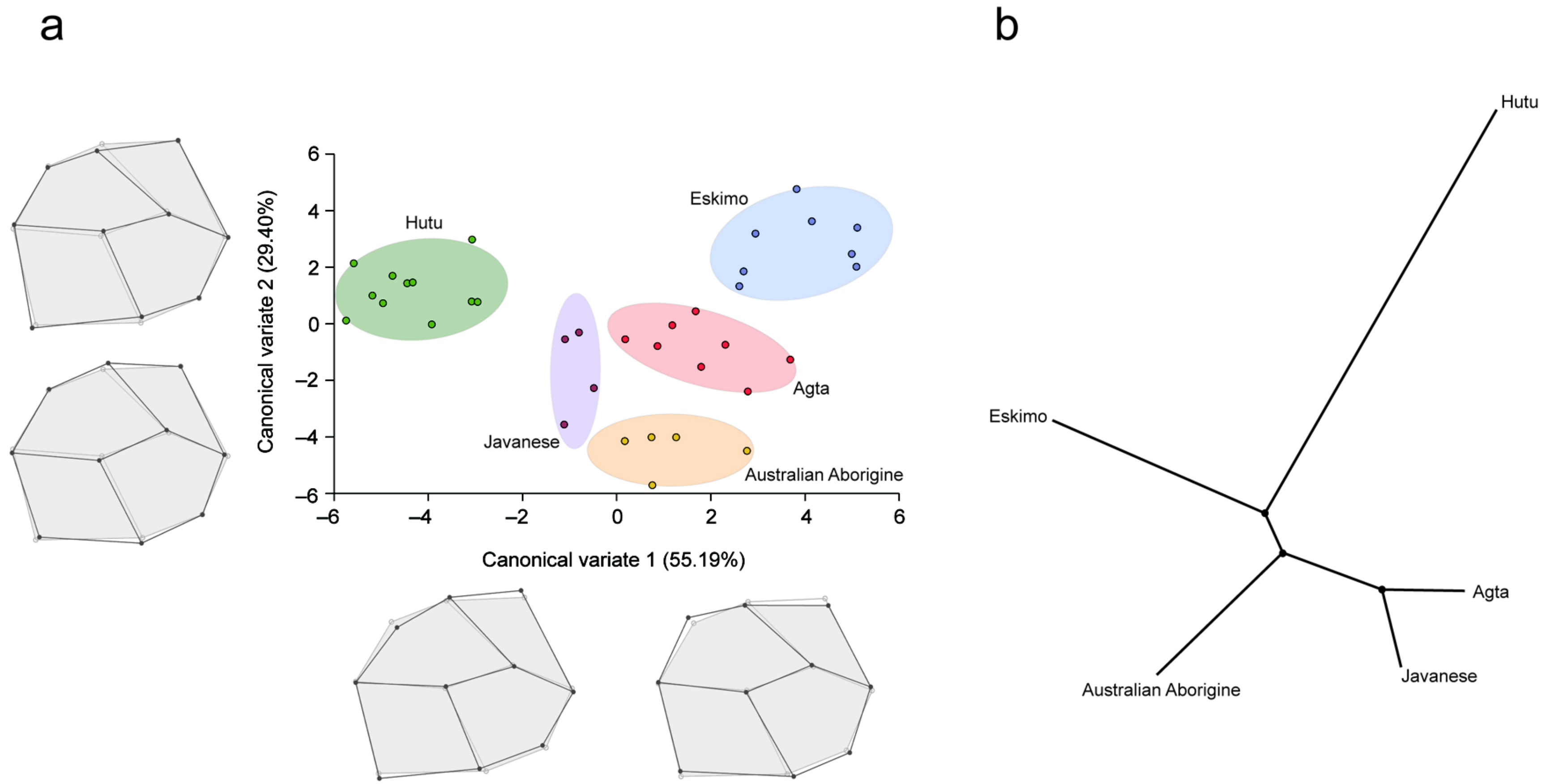


Figure 16. *a) Scatter plot of the first two canonical variates (CV1, CV2) showing molar shape changes between populations. Wireframes represent the morphology associated with the specimens located on the extremes of the canonical scores in comparison to the mean shape (0 scores) of the sample (grey base wireframes). Ellipses comprise 85% confidence intervals. b) Neighbor-Joining tree displaying relationships between populations obtained from the Mahalanobis distances between groups.*

Table 13. *Results of leave-one-out pair-wise Discriminant Function Analysis performed on Canonical Variate Analysis data, for more accurate discrimination.*

Compared groups	Mahalanobis distance	P-value
AGTA-AUST	3.3382	0.526
AGTA-HUTU	5.872	**0.005**
AGTA-ESK/INU	2.0972	0.592
AGTA-JAVA	1.0379	0.988
AUST-HUTU	4.2413	**0.041**
AUST-ESK/INU	3.8403	0.276
AUST-JAVA	1.3827	0.851
HUTU-ESK/INU	5.6206	**< 0.0001**
HUTU-JAVA	3.2568	0.253
ESK/INU-JAVA	3.0057	**0.038**

The wireframe variations along the canonical variates show the main tooth shape differences among the analysed groups. Eskimo/Inuit and Hutu clearly differed for CV1 ($P<0.0001$), whereas Eskimo/Inuit and Australian Aborigines, clearly separated for CV2, did not differ significantly ($P=0.276$) in terms of molar shape, most likely because they highly overlapped for CV1, which was the main function obtained. The similarities among groups can be clearly seen in *Figure 16a*. Agta, Australian Aborigines and Javanese are centrally placed on CV1 (around the 0 score or slightly to the positive values) and in the negative values for CV2. These three groups form a cluster in which no tooth shape differences were observed among the groups. On the contrary, Hutu and Eskimo are located at both extremes of CV1, significantly differing from each other ($P<0.0001$). The former group is characterized by the most negative values of CV1 and positive loadings for CV2, while the latter lies on the positive CV1 extreme and is characterized by highly positive values also for CV2.

The shape variations of the landmark configuration along the CVs are also shown in *Figure 16a*. The wireframes shown with a solid black line depict various shape modifications along specific CV values: 6 and −6 for CV1, and 6 and −6 for CV2. The main landmark displacements with positive values of the first canonical variate (CV1) are: 1) displacement in a buccal direction of the intersection of the buccal groove of the crown (landmark 9); 2) a movement of the intersection of the distal fossa with the distal border of the occlusal surface (landmark 8) towards the middle of the distal border of the crown; 3) a subtle drift of the protocone tip (landmark 4), shifting lingually, and 4) the mesial endpoint of mesio-distal (MD) distance (landmark 7) moving slightly towards the middle of the mesial border of the tooth crown. The most visible changes represented by CV2 (towards positive values) occur for: 1) the metacone (landmark 2) and protocone (landmark 4) tips that show a small shift of both cusps towards the center of the tooth crown; 2) the mesial endpoint of mesio-distal (MD) diameter (landmark 7) that slightly moves in a distal direction; and 3) the intersection of the buccal groove with the central fossa (landmark 5) that shifts in the direction of the center of the tooth crown.

Figure 16b shows an unrooted phylogenetic tree obtained with PHYLIP based on the Mahalanobis distances between the centroids of the analysed groups. As can be observed, the relationships reflect the possible evolutionary history of the populations, with Hutu, an African tribe, being the most distinct group, and the inhabitants of SouthEast Asian islands clustering together in a relative proximity with the Australian Aborigines. Eskimo/Inuit, who are the only representatives of an Arctic habitat, are also clearly separated in the diagram.

c. Molar shape affinities among hunter-gatherers

The main objective of this research was to investigate shape differences in the first upper molars of contemporary humans by applying a new technological advance: three-dimensional geometric morphometrics (3DGM). This was done both to evaluate the usefulness of this method in dental studies and to investigate whether modern human groups of different geographic origins vary among themselves in terms of M^1 tooth shape. The results indicate the dental anthropology can significantly benefit from 3D GM applications.

As already indicated, traditional metric techniques have been shown to be insufficient and limited in detecting dental variation in modern humans (Bailey, 2004; Bernal, 2007; Ulhaas et al., 2004), while 3D GM methods provide more complete and detailed data (Bernal, 2007; Ulhaas, 2004) that allow for intergroup variation analysis in human populations. Also, odontogenesis is a process that occurs in all three dimensions and as such, three-dimensional studies are more than adequate for better understanding dental structure. Such studies can greatly expand our knowledge of the biological interactions and the effects of genetic and environmental factors influencing dental development (Townsend and Brook, 2008; Townsend et al., 2009, 2011). Moreover, 3D GM presents a several advantages over the 2D approach. It allows for a legitimate representation of the third dimension, which substantially increases the amount of potential information obtained for the analysis. In addition, difficulties in a precise orientation of teeth for obtaining a 2D image for GM have been repeatedly reported (Martinón-Torres et al., 2006; Gómez-Robles et al., 2007; Benazzi et al., 2009, 2011). 3D GM easily overcomes this obstacle, as the dimensionality of the objects is not reduced and the 3D coordinates of the landmark configuration do not depend on the orientation of the tooth crown.

There is a consistent amount of evidence on the high genetic control over dental development (Scott and Turner, 1997; Bernal, 2007; Townsend and Brook, 2008; Bei, 2009; Townsend et al., 2009; 2011), but research has also shown that environmental factors may cause dental size and shape variation (Scott and Turner, 1997; Townsend and Brook, 2008; Townsend et al., 2009; 2011). However, Scott and Turner (1997) pointed out a scarcity of studies about such possible environmental influences affecting dental morphology. Our analysis confirms that a substantial variation in the first upper molar shape exists among modern human populations, which is likely due to genetic diversification as a result of environmental adaptations through selective pressures upon the different groups studied.

The unrooted phylogenetic tree (*Figure 16b*), obtained from Mahalanobis distances between the centroids of the analysed groups, shows the average morphological affinities (or distances) between groups based on the shape of their first upper molars. The clustering is congruent with the described pattern of dispersal and migration of modern humans (Cavalli-Sforza et al., 1994, Crow, 2002; Gugliotta, 2008). The African Hutu tribe is the most distinct group, clearly separated from the other groups, which may reflect the ancestral characteristics of their tooth morphology. It has been reported that Sub-Saharan Africans differ significantly in their dental morphology from North American, European, Asian and Australian samples and that they exhibit a variety of ancestral traits, shared with archaic *Homo sapiens* and other early hominids (Irish, 1997, 1998; Irish and Guatelli-Steinberg, 2003).

According to our analysis, compared to other populations, the archaic traits of the M^1 present in the Hutu would include: a) a protocone tip located more distally; 2) a hypocone tip displaced lingually; 3) a mesio-lingually moved mesial endpoint of the MD dimension; 4) a shift in a disto-buccal direction of the intersection of the distal fossa with the distal border; and 5) a displacement of the buccal and lingual landmarks (landmarks 4, 9, 10) towards the center of the crown (*Figure 16a*). These shape changes result in a molar M^1 tooth with a relatively more oval crown shape (from occlusal view) compared to those represented by the other studied groups that show more quadrangular tooth crowns.

A clear separation between Eskimo/Inuit and the Austral-Asian populations clustering together is also evident. The two groups have been classified by

Turner (1990) into distinct dental categories: Sinodont (Eskimo/Inuit) and Sundadont (South East Asians). Our analysis suggests that this classification between both dental patterns has a reflection in the shape of the first upper molar. Australian Aborigines are considered to be representatives of a "proto-sundadont" dental pattern (Turner, 1990; Matsumura and Oxenham, 2014) that very likely shares a common ancestor with Negritos and Java Indonesians, who occupy the Southeast Asian islands and are characterized by a more advanced Sundadont pattern (Turner, 1990). Our results are in accordance with the recently published work by Matsumura and Oxenham (2014). In their study, the authors analysed an impressive number of individuals (7,247) belonging to 58 Asian samples in order to establish a possible evolutionary relationship between them. For that reason they used a great number of non-metric dental traits. As a result of their investigation, they produced a genetic tree in which the Australian population and Southeast Asian Sundadont populations (*ie*. Philippine Negritos and Indonesians) share a close relationship, clearly separated from Northern Asian Sinodont (including Native Americans) groups.

Our results on the upper first molar are concurrent with those analyses and thus suggest that the 3D GM of dental shape is a highly sensitive procedure to infer evolutionary affinities and migratory patterns of human populations. Turner (1990) described 28 ASUDAS dental traits used for the characterization of the Sundadont and Sinodont dental patterns, out of which 8 significantly differentiate both groups. These traits are: I^1 shovel, I^1 double-shovel, P^3 one root, M^1 enamel extension, M^3 P/R/CA, M_1 deflect wrinkle, M_1 three roots and M_2 four cusps. Only one of these traits refers to the upper first molar (the tooth analysed here). Our findings on M^1 add some anatomical traits that differentiate the two dental groups, at least in terms of molar crown shape. Rather than clear discrete differences we could observe a trend towards a more rounded/squared and symmetrical tooth crown shape (from occlusal view) in the Sinodont Eskimo, while the first upper molars of the Sundadont groups would retain a more oblong and irregular crown shape. However, to confirm this statement, a research including more samples of both dental patterns should be carried out. Whether our suppositions would become confirmed or not, we may certainly state that the shape of the first upper molar carries relevant information about human phylogenetic affinities, geographic dispersion and population diversity. More studies are needed in order to complete the knowledge and expand our understandings of the mechanisms behind these processes.

We may also hypothesize about the possible effects of environmental factors on the encountered variation in the first upper molar crown shape. By environmental factors we understand the differences in geographic and climatic conditions affecting human populations. Scott and Turner (1996) indicated the lack of studies about the possible influences of these factors on dental morphology; however, they did not reject them. The populations studied include individuals representative of four continents with dramatically different climatic conditions: from arctic (Eskimo) to tropical (Hutu, Agta, Javanese) or hot and dry habitats (Australian Aborigines). As indicated before, tooth shape variation has been shown to be indicative of adaptations to changes in the *internal* characteristics of foodstuffs, such as toughness, strength and deformability (Ungar and Teaford, 2002). Since climate has a great impact on availability of food resources, we may assume that some of the observed variation in dental shape may be a reflection of adaptations to chew different diets, conditioned by distinct climatic circumstances. However, in order to state more grounded conclusions, a broader study should be performed including populations with well-documented diets and greater numbers of individuals.

Although it has provided new insight into our understanding of human diversity, the applied methodology contains certain flaws that may inconvenience its application to dental studies. Above all, the very rigorous criteria (dental crown preservation and lack of dental wear) of tooth selection result in a great reduction of the available sample, which greatly affected the present study, in addition to the complication in the process of the selection of teeth. Archaeological material is very often affected by dental wear and/or damaged; therefore it is very problematic to collect a representative sample for statistical analysis. We are aware that in the present study the sample size is severely reduced and that this may bring certain critiques in relation to the statistical estimations and their accuracy. We strongly encourage all scholars interested in this kind of investigation to implement three-dimensional analyses to their research to broaden our knowledge of dental morphology variability.

GENERAL DISCUSSION

At first sight, teeth may seem to be simple and ordinary tools for food processing that would rather not deserve much attention. However, dental anthropological studies have long proved that their detailed analysis may reveal noteworthy evidences and lead to important conclusions about people's lifestyle, health, cultural practices and biological adaptations, and allow for inferring evolutionary relationships between various groups.

In this dissertation I focus on dental variation within and among several modern human populations. The study was performed on a multifactorial level, combining the analysis of several methodologies: dental wear, microwear, dental crown size, complexity and relief, and tooth shape. With a deliberate spotlight on modern hunter-gatherer populations, we tried to analyse the possible effects of sexual division of labour, still highly present in these societies, on dietary habits of both sexes through the study of sex-related differences in various dietary and ecological indicators, such as dental wear, buccal microwear, crown complexity, tooth size and shape.

The study entirely focused on the first molar. The reason for this was twofold. On the one hand, first molars are the first permanent teeth to erupt, and consequently they are exposed longer to factors that may cause enamel loss. As a result, they are more apt to reveal higher amounts of information regarding dental wear processes. On the other hand, they are the most morphologically stable teeth of the entire set (particularly the first molar), (Scott and Turner, 1997; Bailey, 2004; Gomez-Robles et al., 2007) and can, thus, be informative of genetic affinities among groups (Turner, 1969).

In general, the results indicate an exceptional usefulness of the analysed tooth in characterizing modern human populations. Below, I will present a general discussion on the main results obtained. First, I will discuss the studies made on the Tigara group from Point Hope, the most abundant sample that was used in most of the research made. Then I will concentrate on the main topic of this thesis, which is the sexual division of labour and its impact on dental wear, as well as on the inter-population differences in dental wear. Finally, I will address the topics of tooth size variability and dental shape differences among modern human populations and its implications to dental anthropology.

1. Dental wear

The Tigara (Point Hope, Alaska) dental sample is the best preserved and most abundant skeletal collection of traditional Eskimo culture, which is of great importance in the context of this thesis because a significant amount of information regarding sex and age-at-death of many individuals is available (Costa, 1977). Such data are essential for the dental wear and sexual dimorphism studies that form a great part of present research.

Eskimo/Inuit culture is quite peculiar among other traditional societies in great part due to the climatic condition in which these groups live: the Arctic coast. Such environmental circumstances influence daily life activities, shape cultural behaviour and condition the type of food available for consumption. Eskimo diet is almost entirely based on animal protein and the fat of sea mammals and fish, and only very limited plants, mainly roots, are sometimes encountered and eaten (Keenleyside, 1998; Larsen and Rainey, 1948). As a consequence, the possible sexual differences in diet are almost non-existent in this society (Costa, 1977) and although sexual division of labour exists, it does not focus on the subsistence. In this population men are almost entirely the only food providers. They hunt and quest mostly sea mammals that form the base of the diet of these people and provide materials for clothing and house building. In general, women are responsible for the hunted game management, preparing, drying and storing the meat and treating the hides for their subsequent use. The latter has been reported to be performed almost exclusively by women (Waugh, 1937; Pedersen, 1947; Molnar, 1971; Mayhall, 1972; Tomenchuk and Mayhall, 1979; Merbs, 1968; Richards, 1984) and involves slow chewing of the raw hide in order to soften it enough to be used for clothing (Steensby, 1910; Leigh, 1925; Pedersen, 1947; Davies and Pedersen, 1955; Mayhall, 1972; Merbs, 1968). Hide chewing heavily overcharges teeth and leads to fast and very pronounced dental wear. Hide preparation is mostly performed with the anterior dentition (Leigh, 1925; Waugh, 1937; de Poncins, 1942; Turner and Cadien 1969; Mayhall, 1970; Hylander, 1977; Hinton, 1981; Pedersen and Jakobsen 1989; Clement and Hillson 2012) and not much is known about how this practice may affect the posterior teeth, as no especially designed research has been performed in this regard, and only few researchers mention this aspect as a part of broader studies (Wood, 1992; Clement and Hillson, 2012). This question was examined as a principal part of the current research.

In this research we used the Tigara sample to infer the influence of non-masticatory use of teeth on the posterior dentition by analysing the sex-related differences in dental wear on the first molars between men and women. Our results are in accordance with those previously reported by Clement and Hillson (2012) and confirm the hypothesis that the posterior dentition is not being used in non-masticatory actions and no significant differences were found between men and women in the degree of enamel loss on the first molars. Therefore, it can be concluded that hide chewing practices that produce greater wear on the anterior teeth of women do not affect the first molars. However, we cannot totally exclude that other non-masticatory dental uses do. Still, considering the position and location of post-canine dentition and the fact that the cheek muscles protect them, it is quite unlikely that they would be used in practices other than food mastication. This observation confirms previous reports indicating that the non-masticatory use of teeth in Inuit/Eskimo populations is performed mainly by the anterior dentition (Leigh, 1925; Waugh, 1937; de Poncins, 1942; Turner and Cadien, 1969; Mayhall, 1970; Hylander, 1977; Hinton, 1981; Pedersen and Jakobsen, 1989). These authors however, mostly used descriptive methods of evaluating dental wear. Our analyses, using standardized metric procedures, show a lack of differences in the percentage of dentin exposure in first molars between men and women of Tigara population. Clement and Hillson (2012) obtained similar results in the Iglookik Inuit population from Canada that showed an extremely pronounced wear on anterior dentition, with women presenting much higher median wear rates, especially in the maxillary teeth. However, the posterior dentition, except for the third premolar that was affected by a non-masticatory tooth use, showed no sex-related differences in wear rates. The authors concluded that the anterior dentition forms an important part of the tool kit employed by these people, thus reflecting sexual division of tasks.

In the present analysis, the objective was to verify the hypothesis that the first molars are not used in non-masticatory actions. The Tigara population was a perfect model to study this question and the results suggest that the main function of first molars is to chew food pieces, without significantly taking part in other paramasticatory practices.

2. Dental wear and topography

Since a significant amount of data on the sex and age-at-death was available for most individuals from the Tigara Eskimo population, we analysed the relationship between dental wear, dental microwear and dental topography (crown complexity and crown relief). Several important correlations between variables could be detected.

Dentine exposure is the result of enamel destruction due to the action of abrasive particles on enamel surfaces during mastication. Both physical and mechanical properties of chewed foods influence the biomechanics of mastication (Lucas, 2004) resulting in different levels of dentine exposure and distinct patterns of dental topography (Smith, 1984; Fiorenza et al., 2011). A significant correlation between dentine exposure and crown relief was exposed in our analysis of the Tigara group. Patterns in crown complexity and crown relief suggested that in this population tooth wear mostly affected the protoconid, hypoconid and hypoconulid cusps. Smith (1984) reported important differences in the patterns of dental wear between hunter-gatherer and agricultural populations, the latter showing a more advanced, oblique wear (in a buccal direction). Fiorenza et al., (2011) enriched the findings by Smith and indicated that groups with meat-based diets, such as the Eskimo from Alaska, Canada or Greenland, had more advanced dental wear in an occluso-vestibular direction than groups with mixed diets, such as Khoe-San or Australian Aborigines, which most likely implies that dentine exposure affects dental topography. However, analysis of other groups of known diet would be important to provide a broader perspective on this.

Another conclusion driven from this study was the confirmation of the increase of the percentage of dentine exposure with age. Since dental wear is a natural, continuous and cumulative process, older individuals tend to show higher values of dental wear than younger ones (Richards and Brown, 1981). This correlation was clearly reflected in our study. A similar observation was made by Costa (1977) in the same population. However, in his analysis the results were not significant, probably because they derived from a joint examination of both anterior and posterior teeth. Costa also reported a positive correlation between age and dentine exposure and a negative association with tooth crown height. Similar findings have been reported in other traditional populations (Tomenchuk and Mayhall, 1979; Richards and Brown, 1981; Molnar et al., 1983; Richards and Miller, 1991; Walker et al., 1991).

Eskimo groups are exceptionally interesting for analysing dental wear given their distinct craniofacial anatomy and biomechanical and cultural factors involved in enamel and dentine loss (Waugh, 1937; Hylander, 1977; Holmes and Ruff, 2011; Clement Hillson, 2012). In previous part of this thesis, I proposed that the first molars in the Tigara group were very likely exclusively involved in food processing. Therefore, the type of diet would be the main factor involved in the wear patterns of molar teeth, which includes techniques of food preparation and conservation (Hylander, 1977). The ecological circumstances condition the type of diet of this people to mainly raw, dried and frozen meat containing high amounts of extrinsic abrasive particles. Such foods require heavy mastication forces for biomechanical processing, responsible for generating vertical pressures during the process of mastication that exceed two to three times the average in European population (Hylander, 1977).

Dental microwear is another aspect that has been investigated. As Romero et al. (2012) demonstrated, buccal microwear patterns show a direct connection with the abrasive character of the diet. Our results indicated that the length of microwear striations is negatively correlated with crown relief. Since microwear formation is associated with diet abrasiveness, the obtained results can lead to conclude that intergroup differences in crown relief could be related to the variation in physical and mechanical properties of foods consumed by each population, since various aspects of dental wear are mutually inter-correlated. The power stroke in the process of food mastication significantly influences the wear of the first lower molar, causing changes in occlusal topography and buccal microwear. Consequently, both macro and microwear affect crown complexity and relief (Teaford and Tylenda, 1991; Schmidt, 2010; Benazzi et al., 2011; Lee et al., 2011).

3. Sexual division of labour and dental wear

Duties resulting from sexual division of labour differentiate the access to food resources in most foraging populations (Molnar, 1972). This author suggested that women generally targeting more fibrous and hard materials would constantly test and sample the acquisition. Such increased contact with abrasive food, compared with men that are more often in contact with less abrasive meat, would demand heavier mastication loads on female teeth leading to faster and more pronounced dental wear. This would however be true for groups in which the sexual division of labour focuses on subsistence and affects diet composition. In Arctic populations, such as the Eskimo or Inuit, the climatic conditions highly restrict the access to any type of plant food. The diet is based almost entirely on sea mammals' meat, mostly provided by men. As a result, the diet factor cannot be accounted for while analysing the sexual dimorphism of dental wear in these populations.

It is commonly accepted that dental wear of the anterior dentition may exhibit sexual dimorphism, especially in hunting and gathering populations (Molnar, 1971; Richards, 1984; Berbesque et al., 2012; Clement and Hillson, 2012). However, sex-related studies on tooth wear in the posterior teeth have not been reported to show significant variation (Kieser et al., 2001; Lovejoy, 1985; Berbesque et al., 2012; Clement and Hillson, 2012; Madimenos, 2005). We have investigated if the reported sexual division of labour influences the diet of each sex, as suggested by Molnar (1972), thus causing differential patterns of dental wear between sexes in various traditional modern human populations from different climatic origins and with different subsistence strategies. The results confirm the previously mentioned findings and indicate that the first molar does not show significant sexual dimorphism regarding dental wear, independently of the geographic origin of a sample and the model of sexual division of labour in food acquisition.

Climatic conditions are also believed to influence the pattern of sexual division of labour. Frayer (1980) proposed a theory in which he related environmental conditions with the intensity of labour division. He argued that harsh environmental conditions in which hunting and gathering tribes live would provoke a stronger separation of duties between the sexes in contrast to agricultural populations, where sexual division of labour would not be as marked. According to this hypothesis we would expect the hunter-gatherer groups, in which sex roles are focused mainly on food quest, to show more pronounced sexual dimorphism in dental wear than the agro-pastoral populations. Moreover, groups in which the sexual division of labour follows the standard pattern (men hunt and women collect, eg. San or Australian Aborigines) should present greater differences between sexes than those societies where gender roles are blurred (e.g. Agta) or where men are entirely responsible for food provision (e.g. Eskimo). Independently of the climatic conditions, economic strategy or intensity of sexual division of labour, no sexual dimorphism in the percentage of dentine exposure was encountered among the analysed samples. The obtained results do not therefore confirm the hypothesis that sexual division of labour would influence the diets of both sexes.

Traditional division of labour usually places men as the main meat providers while women target all other kinds of food (seeds, roots, tubercles, fruits, etc.). However, in most modern human tribes, at the end of the day, all acquired goods are shared among all the members of the family and often also within the whole community (Draper, 1975; Guimares de Souza, 2007; Hawkes et al., 2001; Lee, 1978; Minter, 2010; Schapera, 1930). This fact could simply obliterate the differential access to food resources resulting from the sexual division of labour. Even though patterns of dental wear may reflect relatively low differences in behaviour (Clement and Hillosn, 2012), it seems that in the studied populations the differences were not strong enough to be significantly projected on tooth crowns, at least in the foraging groups since in the agricultural populations the sexual division of labour does not necessarily focus on food provisioning. With the invention of agriculture, the technological advances also changed the food preparation techniques and allowed for the development of more refined food processing methods. Aliments, either cultivated crops or vegetables, as well as animal livestock meat, almost always undergo a process of preparation before being consumed. This practice probably diminishes the possible differences in diet composition that could differentially overcharge tooth surfaces, due to variation in food hardness, which could explain the lack of sexual dimorphism observed in the agricultural populations included in the present study.

The obtained results indicate that dental wear measurements are not suitable for detecting differences in access to food resources caused by sexual division of labour. In fact, the results suggest that although reported, sexual division of labour is not reflected in the wear of the first molar, neither among hunter-gatherer societies nor among agro-pastoral communities.

4. Inter-population variation in dental wear

Dental wear has been focused in various ways: 1) differences in dental wear were used to infer the impact of sexual division of labour dietary habits in Tigara Eskimo population; 2) the correlations of dental wear with dental microwear, crown complexity and crown relief were analysed; and 3) the effect of sexual division of labour was compared in several modern human populations. Finally, dental wear was studied in both hunter-gatherer and agricultural-based modern human population to study the inter-population variability.

a. Inter-group differences

Climatic conditions are highly responsible for the food resources available to each population. They significantly influence the flora and fauna of the region. Arctic latitudes are almost totally devoid of plants. Therefore, people living in these areas rely almost entirely on animal resources. On the other hand, tropical regions abound in a variety of edible plant species, as well as in diversity of animals. In consequence, tribes that inhabit these habitats have much more diverse diets. As diet is one of the major factors responsible for the pattern of dental wear, we might suspect that groups living under different climatic conditions would be characterized by distinct diets and as such show diverse patterns of dental wear.

The overall results of the inter-group variation in the amount of dental wear among several hunter-gatherer and agro-pastoral populations indicated, however, only few significant differences. The percentage of dentine exposure differentiated the Agta group from Eskimo and Batéké-Balali when analysing the lower first molar and additionally the Navajo population when the upper first molar was considered. For both teeth, the Negritos from the Philippines were characterized by lower values of dental wear. No other significant variation was encountered among analysed groups. Such an outcome is somewhat surprising as certain differences, especially differentiating hunter-gatherer and agro-pastoral populations, were expected, for such findings have been reported elsewhere (Hinton, 1982; Eshed et al., 2006; Deter, 2009). However, several explanations can be proposed in order to address these outcomes.

The indigenous Negrito tribe of the Philippines, the Agta, are inhabitants of a warm, tropical climate and represent a typical hunter-gatherer society. Their diet is based on hunted animal meat and gathered roots, fruits, seeds and other edible plants (Estiko-Griffin and Griffin, 1981; Minter, 2010). On the other extreme, the Eskimo Tigara tribe represents a traditional Arctic culture, with a diet based almost entirely on hunted sea mammals (Costa, 1977; Larsen and Rainey, 1948; Tomenchuk and Mayhall, 1979). These two groups clearly show that climatic circumstances significantly condition the diet of indigenous inhabitants.

Although meat is, by itself, not a highly abrasive aliment, the methods of its preparation, storage and consumption used by the Eskimo increase its overall abrasiveness (Brubaker et al., 2009; El-Zaatari, 2008) by modifying the physical properties of meat and significantly increasing its toughness (Szmańko et al., 1995; Sigurgisladottir et al., 2000). In consequence, higher biting and chewing forces are demanded in order to effectively chew such tough meat pieces. Eskimos have been reported to possess extremely developed facial muscles that are capable of producing extraordinary mastication loads (Hylander, 1977). These are significantly higher than those produced by Agta, as their diet, although based on abrasive raw plants and meat, is much less tough than dried or frozen meat. Great forces acting upon enamel would lead to more pronounced dental wear in the Arctic population than in the Agta.

Dental wear is caused by the abrasiveness of both intrinsic particles included in food items, and extrinsic particles incorporated to the consumed food during its storage and/or processing. It has been reported that underground storing techniques and open-air drying processes result in the incorporation of high amounts of contaminant abrasive particles to the meat consumed by Eskimo (Brubaker et al., 2009; El-Zaatari, 2008; Larsen and Rainey, 1948). They act upon the enamel producing a significant amount of occlusal microwear features (El-Zaatari, 2008). Such microscopic defects reduce enamel resistance and leave the teeth more susceptible to macroscopic wear (Davies and Pedersen, 1955; Lucas, 2008). The Agta population, on the other hand, does not depend as much on stored food, because food is searched for and consumed directly due to climatic conditions. High temperatures and humidity impede long-term storage of daily acquisition. This fact diminishes the possible effect of an extrinsic contaminant being incorporated into the consumed food and consequently may lead to less advanced enamel destruction in this group.

In contrast, the Navajo and Batéké-Balali represent a sedentary way of life and their diet is based on cultivated crops and other gathered plants. They also have domesticated animals that are the source of protein, and although the Navajo are excellent hunters, they do so more for ritual purposes than as a way of obtaining aliments (Underhill, 1956). Agricultural practices result in diets that are *a priori* relatively softer than those of typical hunter-gatherer regimes, but cultural practices in agriculturalist groups can significantly incorporate abrasive particles to the diet. The use of grinding stones leads to the incorporation of extraneous grit particles into the flour responsible for important dentine exposure levels (Larsen, 1995; Molleson and Jones, 1991). Smith (1984) indicated that both hunter-gatherers and agricultural populations are characterized by diets with similar abrasive potential and, thus, no differences in dentine exposure should be expected. However, agricultural groups showed more oblique wear surfaces than foragers that demonstrated flatter patterns of dental wear. This aspect has not been investigated here, yet contrary to Smith's suggestion, the agricultural groups showed more advanced dentine exposure than the hunter-gatherer representatives.

Various hypotheses could explain the lower amounts of dental wear observed in the Agta tribe when compared to the Eskimo, Navajo and Batéké-Balali. Dental wear differences might be related to the better nutritional status of the hunting and gathering Agta compared to the Navajo and Batéké-Balali agriculturalists, or to the exclusively meat-based diet of the Tigara. A typical foraging diet is highly diverse in the types of foods consumed. Plants, vegetables and fruits eaten raw are sources of many vitamins and microelements that restricted diets, such as meat-based lack. In addition, food processing prior to consumption may eliminate many of the valuable vitamins from the food. The transition from foraging to farming has been related to a decrease of the nutritional quality of the diet (Larsen, 1995). Agricultural populations have been observed to have a higher prevalence of dental caries and other dental problems (Turner, 1979; Larsen, 1995). This may reveal that a typical forager diet, as observed in the Agta, could lead to a healthier, hence harder enamel that is more resistant to forces causing dental wear.

Another possible explanation would be related to enamel adaptation to the physical properties and the structure of consumed food. Lucas (2008) proposed that enamel thickness could be a reflection of an adaptation to diet hardness. The harder the objects that are being consumed, the thicker the enamel will be as a result of such evolutionary stress. The Agta diet abounds in hard objects, such as seeds and tubers, while the Eskimo diet consists mainly of tough but not hard meat, and agricultural foods tend to be relatively soft due to different processing techniques used for its preparation before consumption (even though abrasive contaminants are incorporated to processed foods). As indicated by Smith

(1984), due to differential preparation and processing techniques, the diets of Navajo and Batéké-Balali, two agricultural cultures, are softer than the diet of the Agta that eat most foods raw. This fact could lead to a selective pressure towards thicker enamel in the Philippine tribe that would better resist the consumption of hard and tough foods, and consequently result in lower rates of dental wear and a delay in functional dental loss (Lucas et al., 2012).

Theses hypotheses however need to be confirmed with a detailed study on enamel thickness in these modern human populations, as well as on their diet composition, its impact on the enamel structure, and on the effect of health status and non-masticatory use of teeth on enamel wear in order to explain why no other significant differences in dental wear were observed among the analysed groups. Despite the analysis of other hunting and gathering populations (showing diets similar to that of the Agta), no differences were found, on an individual basis, between these groups and those having farming as a subsistence base. This fact is difficult to address since it could be due to many biological factors, not discarding small sample sizes of the studied groups or lack of age assessment for the individuals considered.

b. Hunter-gatherers and agriculturalists

As only very few significant differences in dental wear were found between the analysed groups, tribes representing a similar subsistence strategy were pooled together in order to evaluate the possible differences in dental wear regarding the general subsistence pattern. Hunting and gathering diets, assumed to be less processed, would be somehow more abrasive than the diets consumed by agricultural populations, where food processing prior to consumption is more intense (Brace, 1962; Smith, 1984; Larsen, 1995). However, no significant differences were found when groups representing the hunting and gathering way of life were lumped together and compared to those representing sedentary, agro-pastoral cultures.

Such a result is somewhat surprising and unforeseen. Several authors have indicated that greater levels of dental wear should be expected among hunter-gatherer groups compared to agro-pastoral populations (Hinton, 1982; Eshed et al., 2006; Deter, 2009). Several explanations can be proposed in order to address these findings.

Until the invention of agriculture, ca. 10,000 years ago (Harris and Hillman, 1989; Weisdorf, 2005), all human populations had a hunting and gathering way of life (Gupta, 2004). Foods were obtained mostly from gathering plants, roots and seeds and from animals hunted to provide the necessary protein intake. With the adoption of agriculture, the dietary habits and lifestyles underwent an important transition. A sedentary way of life became predominant and food was no longer a product of the everyday quest but started being produced and stored. Plants and crops became widely available and animals were domesticated. Agriculture and animal domestication resulted in an important change in subsistence methods and consequently in the diet. The lack of the need to search for food allowed for the invention of new techniques of food processing (grinding of crops, cooking, baking, etc.). Such modifications of the traditional diet resulted in a change of the texture and consistence of the consumed food (Smith, 1984). Several scholars have suggested that changes in food preparation techniques affect the dental wear pattern (Brace, 1962; Greene et al., 1967; Molnar, 1972). However, Smith (1984) indicated that even tough farmed foods are relatively soft, and they can cause similar enamel abrasion as foraged foods because the use of grinding stones in the preparation of flour from the cultivated crops may introduce a significant amount of abrasive particles, grit, sand and ash to the produced flour. Foods prepared with such ingredients may cause severe damage and dentine exposure (Molleson and Jones, 1991; Larsen, 1995). Our results reflect that the two dietary groups show similar wear scores, which seems to support Smith's assumption of similar food abrasiveness in both groups. Yet when the groups were analysed separately, most agriculturalists showed higher rates of dental wear than the hunting and gathering Agta, as explained in the previous section. Nevertheless, when all groups of a similar subsistence strategy were mixed together, the differences disappeared. This most likely could be caused by the limited sample sizes available for the majority of groups. Probably, with a higher number of individuals per population, inter-group analysis would reveal more significant results, and consequently, subsequent pooling would remain significant. However, it may also be the case that the pooled groups are in fact heterogeneous, despite clearly including either agriculturalists or foragers. Most of the analysed farming societies were not exclusively dependent on cultivated plants and domesticated husbandry. They also occasionally performed foraging and even hunting activities that could additionally contribute to the similarity of diet abrasiveness and lack of dentine exposure differences when compared with hunter-gatherers.

The potential differences in dental wear between these two big groups are more likely to be observed in the way the teeth are being worn, as suggested by Brace (1962) and Smith (1984). The transition from a traditional hunting and gathering based diet to one centered on cultivated cereals is associated with various technological advances, especially the use of grinding stones and pottery that appeared in the Neolithic. Such modifications of food preparation techniques very often are correlated with a significant decrease in food toughness and fibrousness (Brace, 1962). Masticatory forces required in the process of chewing such processed products are lower than for products eaten without any earlier processing. However, this aspect was not analysed in the present study.

5. Dental dimensions

In addition to dental wear, differences in dental size were also investigated. Sexual dimorphism and inter-group variation in dental size were evaluated.

a. Sexual dimorphism

There is no general agreement on whether dental size is a sexually dimorphic feature in modern humans. There are abundant references reporting the existence of sexual differences in dental dimensions in modern human populations (Barrett et al., 1963; İşcan and Kedici, 2003; Richardson and Malhotra, 1975; Schwartz and Dean, 2005). Other authors, however, argue that the tooth size of modern people does not present significant sexual dimorphism (Hillson, 1996; Harris, 2003; Suazo et al., 2008; Ates et al., 2006; Castillo et al., 2011). Our results are in accordance with the latter as no differences in dental size dimensions (bucco-lingual and mesio-distal) were found between men and women within most studied groups. The only feature that showed sexual dimorphism was the total occlusal area of the crown in the Eskimo population (men showed bigger teeth than women). Lack of similar findings in the other populations analysed could either be due to the fact that their sample sizes were relatively limited compared to the Eskimo group or to a significant reduction of overall sexual dimorphism in modern human populations, including the Australian Aborigines.

Sexual dimorphism in dental size is visible among most primate species, especially in the size of canines, as well as in our hominid ancestors (Brace and Ryan, 1980; Schwartz and Dean, 2001). Sex differences in the size of teeth have been interpreted from a reproductive perspective related to male competition for mating (Kay et al., 1988, Kieser, 1990). Modern humans are however subjected to lower levels of reproductive competition, at least from a biological perspective compared to cultural behaviours, and as a consequence the sexual dimorphism in the size of teeth has decreased (Castillo et al., 2011; Schwartz and Dean, 2001). Our analysis has focused on one single tooth, the first molar, and thus sex related differences in dental size in other types of teeth, for example the canines, cannot be ruled out.

İşcan and Kedici (2003) reported that Turkish males significantly exceeded females (with a total sample of 100 individuals, 50 of each sex) in bucco-lingual dimension in all tooth types for both maxilla and mandible. The most dimorphic tooth was the canine, and the least one was the lower first molar. The authors concluded that tooth size shows a clear sexual dimorphism, yet they also indicated that sexual dimorphism *per se* is a continuous trait and therefore overlap between sexes is always expected. Brace and Ryan (1980), on the other hand, analysed primate species together with Upper Palaeolithic and modern human populations. They suggested that sexual dimorphism in tooth size is simply the reflection of the general variation of body size. According to the authors, during the Upper Palaeolithic period, when big game hunting was still a part of the subsistence strategy, differences in body and dental size were significant. Such a mode of subsistence was a selective pressure towards a significant sexual dimorphism in terms of size. With the adoption of more sophisticated methods of food preparation the between-sex variation decreased and in modern humans it does not surpass 4% (Bryce and Ryan, 1980). Such reduced dimorphism in small structures such as teeth is very unlikely to be detected in relatively small samples.

b. Inter-group variation

Because no sexual variation was encountered in terms of bucco-lingual and mesio-distal diameters of tooth crown, the sexes were combined within each group in order to analyse possible intergroup differences. Some significant differences were found between the analysed groups. The bucco-lingual diameter showed a greater between-group variation that the mesio-distal distance. This is in accordance with previous reports (Bishara et al., 1989; Otuyemi and Noar, 1996). However, few significant differences were detected: Agta, San, and Khoe showed smaller dental dimensions than the Australian Aborigines, Eskimo and Navajo. The Philippine Negritos tend to have small dental dimensions, while the Australian Aborigines and Native Americans tend to have the largest teeth of all modern human populations (Hanihara and Ishida, 2005). Our findings confirm this tendency. At the same time, it is quite surprising that the Navajo, an agro-pastoral group, had bigger teeth than the hunting and gathering tribes, since various authors have suggested that the transition to agricultural subsistence results in a reduction of dental size (Hinton et al., 1980; Larsen, 1995; Y'Edynak, 1989). This hypothesis is however not clearly reflected in our results, as Agta and San, who are typical hunting and gathering groups, have smaller teeth than the Navajo. It is also interesting to note that the San and Khoe groups, in this analysis, showed relatively reduced dental dimensions when compared with other groups. This contrasts with earlier reports that indicate that sub-Saharan tribes show relatively large teeth (Hanihara and Ishida, 2005). However, the Khoe-San are reported to have small body size in comparison with other sub-Saharan ethnic group (Schapera, 1930), and tooth size is positively correlated with body size (Lauer, 1975; Gingerich, 1977, Brace and Ryan, 1980). Nevertheless, there are many scholars who reject such correlation, claiming that both features are independent and that tooth size is not indicative of body size (Garn and Lewis, 1958; Bailit and Friedlaender, 1966).

c. Hunter-gatherers *vs.* agriculturalists

While certain variation in dental size was found among some of the analysed populations, when the samples were pooled together into general subsistence strategy groups, no differences in the bucco-lingual and mesio-distal dimensions were found.

The implementations of new techniques of food processing that were developed together with the adoption of agriculture and sedentary lifestyle, as well as the subsequent changes in diet have been associated to a general reduction of dental size (Hinton et al., 1980; Larsen, 1995; Y'Edynak, 1989).

The decline of the nutritional status of foods consumed by agricultural populations has been claimed to result in smaller permanent teeth (Larsen, 1995). Consequently, groups which have agriculture as a predominant subsistence would be expected to show smaller tooth dimension, as a result of the selective pressure of lower nutritional status, than traditional hunting and gathering groups, with a diversified and less processed diet. The results obtained, however, do not support this hypothesis. In fact, differences in diet and nutritional intake between hunters-gatherers and farmers, at least among the analysed groups, might not be significant enough to cause dental size differences. Additionally, the farmer groups were not entirely relying on cultivated and processed foods, as they would probably also gather wild plants, and the hunter-gather groups, to a certain extent, also processed some of the food they consume. Therefore, differences between the two groups might be less evident than expected.

6. Dental shape

The last part of the research made involved the implementation of 3-dimensional geometric morphometrics to the study of modern human tooth shape variation. The obtained results are highly preliminary and the main objective of the analysis was the evaluation of such a method in modern human dental studies. The results point toward an important capacity of this methodology for detecting even very subtle shape changes in modern human teeth. They also indicate a substantial variation in the shape of the first upper molar among contemporary human populations.

Shape changes can be the results of growth, evolution or medical treatments (Rolf and Marcus, 1993). In dental anthropology tooth shape variation has been mostly used to infer evolutionary affinities (Bailey, 2004; Marition-Torres et al., 2006; Bernal, 2007; Gómez-Robles et al., 2007), genetic or environmental control over dental development (Townsend and Brook, 2008; Townsend et al.,

2011) or for forensic purposes (Kieser et al., 2007). Up to relatively recently, shape was studied with the use of traditional metric methods that very often showed a limited potential to represent the variability of the human dentition. The first studies of hominid dental shape were performed on two-dimensional projections (Bailey and Lynch, 2005; Martinon-Torres et al., 2006; Gomez-Robles et al., 2007; 2008; 2011; 2012; Liu et al., 2010; Gorka et al., 2012). Soon, three-dimensional imaging techniques become accessible and started to be used in biological and dental studies (Witter et al., 2003; Ulhaas et al., 2004; Benazzi et al., 2009; Cooke, 2011). However, no research has until now been conducted on modern human dental variation. The results of this primary analysis showed the 3D methodology applied is highly appropriate for dental investigations and can be successfully applied in fields like forensic odontology, physical anthropology, paleodontology or even clinical dentistry, especially because it takes into account the third dimension of the tooth crown, thus expanding our current knowledge of the factors involved in tooth development (Townsend and Brook, 2008; Townsend et al., 2009; Townsend et al., 2011).

The analysis was conducted on upper first molars from five geographically dispersed modern human tribes as this tooth was reported to be the most genetically stable of the whole set (Scott and Turner, 1997; Bailey, 2004; Gomez-Robles et al., 2007). The results indicated a substantial variation in the shape of this tooth among the analysed groups. Genetic control over dental development can be used as an indicator of phylogenetic affinities (Scott and Turner, 1997; Bernal, 2007; Townsend and Brook, 2008; Townsend et al., 2009; 2011). Therefore, in our study, Mahalanobis distances between groups were used to derive an unrooted UPGM tree reflecting similarities between the samples considered, in order to speculate about the probable evolutionary relationships between them.

The results obtained are compatible with reports about the migratory patterns and phylogenetic connections among groups (Cavalli-Sforza et al., 1994, Crow, 2002; Gugliotta, 2008). The Hutu clustered at the root of the tree, thus representing the ancestral traits in dental shape. In addition, the populations representing Sundadont and Sinodont dental patterns clustered separately and, therefore, confirm that dental shape analysis can significantly contribute to the investigation of modern human migratory patterns. The traits that characterised both groups for the upper first molar could be added to the characterization proposed by Turner (1990), even though he based his description on the characterization of discrete ASUDAS traits. Among these traits, the Sinodonts would be characterized by a more regular, rounded molar outline, whereas the Sundadont would show a more oblong and irregular first upper molar crown.

The environmental influence on dental shape should also be taken into consideration when interpreting the differences observed in first upper molar crown shape (Scott and Turner, 1997; Townsend and Brook, 2008; Townsend et al., 2009; 2011). Some researchers do not reject the possibility of climate triggered dental morphological variation (Scott and Turner, 1996) but point out the scarcity of studies on this matter. All groups included in our study were the representatives of different climatic conditions. Climate is one of the most important factors determining the fauna and flora of the region and consequently, it significantly influences the diet of its inhabitants. Ungar and Teaford (2002) suggested that changes in tooth shape might be the reflection of evolutionary adaptation process to the toughness, deformability and strength of consumed foods. Therefore, the observed variation could be interpreted as an adaptation to regional specific diets. Further studies on adaptation to ecological conditions are required, especially in populations of well-known climatic and environmental conditions (Scott and Turner, 1996).

7. Age issues and other drawbacks

No research is perfect. There are always aspects that may be questioned or need more detailed analyses. Various obstacles may appear in the way of the investigation process and sometimes even the hardest trials and best will not be sufficient to overcome them. Yet, it is very important for the researcher to be aware of such occurrences and to acknowledge their existence. This can help others researchers to avoid similar issues and also indicate where progress and improvement can be made in future research.

Dental wear is highly correlated with age, especially in indigenous populations (Tomenchuk and Mayhall, 1979; Mays, 2002; Pinto Vieira et al., 2015). Therefore, it is preferable that teeth included in an analysis of dental wear would have a known, independent estimation of age-at-death, to prevent the circular argument that dental wear correlates with age because age was determined from dental wear scores. On the other hand, unfortunately, no fully reliable and independent methods exist for precisely establishing the age-at-death if unknown previously (Clement and Hillson, 2012). For the Eskimo population independent estimations of age were available for some individuals (Costa, 1977), but this was not the case for the other samples considered. Teeth-independent methods for age and sex determination, mainly based on cranial and pelvic traits, were used whenever possible and overall estimates of sex and age could be obtained for many individuals. Despite this, the lack of a precise address of an individual's age may affect the results obtained, at least to a certain extent. However, I strongly believe that the analyses made, despite the limitations, still provide valuable information and greatly contribute to the knowledge of the variation of dental wear, since a single and standardized methodology was used in all the populations studied, from different geographic origins, with different patterns of sexual division of labour, as well as different subsistence strategies.

Another limitation is the focus on a single tooth for the examination of the factors involved in dental wear. Only the first molar was analysed because the research included several methodological procedures and collections, yet I am aware that an analysis based on a single tooth cannot profoundly examine such a complex and multifactor process as dental wear. Anterior and posterior teeth and also mandibular and maxillary counterparts participate in different processes that may cause different patterns of dental wear (Murphy, 1959a, b; Pal, 1971; Lunt, 1978; Molnar et al., 1983; Lovejoy, 1985; Molnar et al., 1989). Our research has focused on these aspects of dental wear only for the first molars and the conclusions refer only to this particular tooth.

The last important disadvantage that I find important to acknowledge, already mentioned on various occasions, was the limited sample size. This problem affects a lot of anthropological research that deals with archaeological material, including teeth. Very often anthropological collections are severely fragmented and collecting a representative sample is extremely difficult. This was unfortunately, the case in my research. We have carefully analysed the dental cast collections available at the Department of Anthropology, University of Barcelona, and at the University of Alicante, and the first molar was the most abundant tooth. It is also the first tooth to erupt and, thus, the one showing higher dental dentin exposure values. Other teeth were very randomly distributed among the individuals and completing a representative sample consisting of the whole set was simply impossible. Not all the individuals were equally preserved in the collections studied but the studied sample represents the best of all possible samples from the collections studied. From all the molars available, we selected those that fulfilled the selection criteria for each part of the research. Unfortunately, it was impossible to increase and complete the samples with collections from other museums or institutions. It was therefore physically impossible to obtain more individuals, especially from additional populations because specimens from the same populations at different institutions are rare. The *American Museum of Natural History* (New York) and *The Musée de l'Home* (Paris) hold the best and largest collections of modern human populations from all over the world. These institutions were visited and the collections were studied under the joint research projects CGL2010-15340, CGL2011-22999 and 2009SGR884 (funded to APP as a Principal Investigator).

Despite the limitations, I considered that it was important to carry on the analyses, for I believe they provide a significant contribution to our understanding of modern human dental variation and the factors involved in dental wear in traditional, indigenous populations.

CONCLUSIONS

1. Sexual division of labour involving the use of teeth in non-masticatory activities in the Tigara population form Point Hope did not affect the wear of the upper and lower first molars and therefore food chewing was the main factor causing dental wear in this population.
2. No sexual differences were found in the percentage of dentine exposure of the first molars, which is indicative that both sexes in the Tigara populations consumed very similar diets despite sex differences in the dental wear on the anterior dentition have been reported.
3. The percentage of dentine exposure was positively correlated with the age group categories of the individual in the Tigara population, proving that dental wear is a cumulative process throughout lifespan.
4. Crown relief of the first molars was negatively correlated with the percentage of dentine exposure, which shows that dental wear causes a decrease in cusp and crown heights. Crown relief is a continuous variable significantly correlated with age at death.
5. Crown complexity, on the other hand, was greater in teeth with high levels of dentine exposure, showing that wear facets significantly contribute to food processing during mastication.
6. No significant correlations were found between the percentage of dentine exposure and the density and average length of buccal scratches.
7. However, a trend towards shorter scratches on buccal enamel surfaces was observed with decreasing values of crown relief, which demonstrates that the progressive accumulation of buccal scratches caused by enamel abrasion, which results in a reduction of their average length, is a parallel process with respect to the reduction of crown height.

8. No significant differences on dentine exposure by sex were observed in any of the traditional modern human populations studied, which might be indicative that dental wear on molar teeth is not an adequate measure of the impact of sexual division of labour on the diet of both sexes.
9. No significant differences in dental wear were found between the hunter-gatherer and agro-pastoral groups, despite that they had very distinct diets and cultural practices in relation to food acquisition and processing.
10. Such lack of significant wear differences among populations could be indicative that different diets may result in similar wear patterns and that the physical properties of chewed food particles might be more informative on dental wear processes than discrete classifications of dietary habits.
11. First upper molar shape differences from all the modern human populations studied reflected the patterns of human migration and dispersal, although retaining a significant phylogenetic signal.
12. The shape of the upper first molar in the Hutu population may be considered ancestral to the other groups compared that show derived conditions consisting in more quadrangular and less oval shaped molars.
13. Molar shape variability clearly discriminated the Sundadont and Sinodont populations. The Sinodont upper first molar would be characterized by more regular, rounded outlines, whereas the Sundadont would show more oval and irregular crown shapes.

RESUMEN

1. Introducción

La antropología dental es una importante herramienta para estudiar comportamientos individuales y colectivos de las poblaciones humanas, sus condiciones de vida e influencias ambientales que actúan sobre el organismo. Los dientes constituyen un material de estudio multidisciplinar y son usados en varias áreas de la ciencia: odontología, anatomía comparativa, paleontología, paleoantropología, genética y ciencias forenses, entre otras. Un análisis profundo y completo de los dientes puede proporcionar información relevante sobre la evolución de los homínidos, las prácticas culturales y el estado de salud general, tanto de los individuos como de las poblaciones, así como identificar los individuos en el campo de odontología forense (Alt et al., 1998).

Estudios dentales son especialmente importantes en el campo de antropología física, puesto que los dientes juegan un papel importante en el proceso de alimentación. Su principal función es el procesamiento mecánico de los alimentos, lo que facilita su ingestión y digestión. Esta tarea implica que los dientes son la única parte del esqueleto humano que tiene contacto directo con el medio ambiente. En consecuencia, la superficie de los dientes puede mostrar el efecto de la interacción entre el individuo y su entorno (Brothwell, 1981; Molnar, 1972, Wood, 1992). Los dientes aportan información sobre la dieta del individuo, su estilo de vida y las prácticas culturales de cada población.

Los diente muestran una alta preservación en el registro fósil por la excepcional resistencia del esmalte. A menudo los dientes son los restos más abundantes y muchas veces los únicos encontrados en un yacimiento arqueológico. Por otro lado, los dientes constituyen la única parte del esqueleto humano que no sufre remodelación una vez completada su mineralización (Dahlberg, 1971; Kelley y Larsen, 1991; Thomason, 1997; Riga et al., 2013). En consecuencia, son mucho menos sensibles a las fluctuaciones ambientales que otras partes del cuerpo humano. Además, tienen una gran estabilidad ontogenética (Alt et al., 1998), por lo que pueden ser usados en el estudio de las relaciones filogenéticas entre poblaciones, ya que su morfología dental refleja los procesos de adaptación alimentaria y ecológica.

a. Desgaste dental

El desgaste dental es un proceso fisiológico acumulativo de pérdida gradual de la superficie del diente causado por la actividad normal de los dientes. El desgaste refleja el contacto constante de las partículas abrasivas con la superficie dental en relación con las fuerzas de masticación usadas en el procesamiento de los alimentos. El desgaste dental se clasifica en tres procesos diferenciados por el mecanismo que causa la pérdida del esmalte. La atrición es el resultado del contacto de los dientes entre sí, sin presencia de alimento entre ellos. El resultado de este proceso es la formación de facetas planas de desgaste en las cúspides de la corona dental (Kaidonis, 2008). La abrasión, por otro lado, es el resultado del contacto de los dientes con los alimentos u otros objetos extrínsecos (Hilson, 1996; Kaidonis, 2010). Dependiendo de la abrasividad y la dureza, los elementos masticados pueden demandar fuerzas de diferente potencia para ser procesados, lo que en consecuencia resulta en grados de desgaste diferente. Este proceso no es específico anatómicamente, por lo que puede ocurrir en toda la superficie oclusal del diente hasta formar zonas de exposición de dentina (Kaidonis, 2008). La abrasión es considerada el principal mecanismo en el desgaste dental y su correlación positiva con la edad ha sido claramente establecida (Richards y Brown, 1981). El tercero mecanismo involucrado en el proceso de desgaste dental es la erosión. Este mecanismo está causado por factores químicos (sobretodo ácidos, tanto externos como internos al alimento) que actúan sobre la superficie del esmalte produciendo la gradual disolución de su estructura (Kaidonis, 2010). Todos estos procesos actúan alternativamente sobre la superficie dental produciendo una gran variedad de patrones del desgaste (Kaidonis, 2008).

La composición de la dieta tiene un papel importante en el proceso del desgaste dental. La ingestión de alimentos abrasivos y fibrosos, como por ejemplo carne seca o congelada, semillas, tubérculos, etc., requiere fuerzas de masticación altas y una masticación prolongada, lo que resulta en un desgaste más intenso (Molnar, 1971, 1972; Hinton, 1982; Kaifu, 1999; Deter, 2009). Además, las partículas externas, como por ejemplo arena, polvo o ceniza, pueden ser incorporadas al alimento durante su preparación o almacenaje, contribuyendo de forma significativa a la destrucción del esmalte y la exposición de dentina (El-Zaatari, 2008; Lucas, 2004; Hillson, 1996).

El desgaste dental ha sido utilizado como indicador de la dieta y de las practicas relacionadas con alimentación, así como del uso no-masticatorio de los dientes en diferentes poblaciones humanas (Larsen, 1997; Rose y Ungar, 1998; Scott y Turner, 1988; Kaifu, 1999; Hinton, 1982; Deter 2009; Dahlberg, 1963; Molnar, 1972; Anderson, 1965; Mickleburgh, 2009; Turner y Machado, 1983; Smith, 1984). El desgaste dental ha sido utilizado también como indicador de la edad de los individuos en muestras arqueológicas y de poblaciones contemporáneas (Miles, 1962, 1963, 1978).

En el presente trabajo, el desgaste dental ha sido analizado en tres contextos diferentes. El primero fue el estudio de la posible influencia de la división sexual del trabajo sobre el patrón del desgaste del primer molar en la población de esquimales de Point Hope, Alaska. A continuación se analizó la correlación del desgaste con variables del microdesgaste vestibular, relieve oclusal y la complejidad de la corona del primer molar en la misma población, para estudiar sus posibles interacciones. Al final, el desgaste dental se comparó entre inter-cultural en diferentes grupos de cazadores-recolectores y agricultores.

b. División sexual del trabajo

La presente tesis se centra en especial en la influencia de la división sexual del trabajo en la dieta mediante análisis de los patrones de desgaste dental. El estudio se basó en la hipótesis de que la división sexual del trabajo, aun presente en las poblaciones de cazadores-recolectores modernos, está relacionada en gran parte con las actividades de obtención del alimento y, por lo tanto, produce un acceso diferencial a los recursos alimentarios entre los sexos (Molnar, 1971), lo que en consecuencia resultaría en un patrón diferente de desgaste dental.

En los grupos tradicionales e indígenas los hombres son en su mayoría responsables de la caza y de la obtención de las proteínas animales, mientras las mujeres normalmente realizan las labores relacionadas con la recolección de raíces, semillas, nueces, frutas, tubérculos, etc., así como otras actividades domésticas. La carne es un alimento fibroso pero relativamente poco abrasivo en comparación con las raíces, tubérculos, semillas u otros alimentos procedentes de la recolección practicada sobre todo por las mujeres. Molnar (1971) sugirió, que las diferencias en las tareas diarias entre los hombres y las mujeres podrían condicionar el tipo de alimentos consumidos, con las mujeres consumiendo sustancias más abrasivas, como raíces y plantas recolectadas. En algunas sociedades se ha descrito que los hombres, al capturar un animal, comen una parte de la presa *in situ* (Minter, 2010) y las mujeres prueban los alimentos que recolectan (Molnar, 1972). En consecuencia, las mujeres teniendo acceso prácticamente constante a alimentos más duros, rígidos y fibrosos, por lo que cabría esperar que tuviesen grados de desgaste dental más altos que los hombres, que tienen un mayor acceso a la carne y sus derivados. La presente tesis tiene como uno de sus objetivos verificar si este fenómeno se refleja en los patrones de desgaste dental entre los sexos en diferentes grupos de cazadores-recolectores.

c. Microdesgaste y topografía de la corona

El microdesgaste es una manifestación del degaste dental que puede ser observada únicamente con la ayuda de microscopia electrónica. Las propiedades físicas de algunos alimentos y la abrasividad de las partículas que contienen (fitolitos, oxalato de calcio, sílice o cuarzo), pueden causar micro-alteraciones en la superficie del esmalte dental y llegar a producir microdesgaste (Lee et al., 2011; Romero et al., 2012). Dado que la densidad y la longitud de las estrías del microdesgaste pueden ser informativas de la dieta (Puech, 1976, 1979), el análisis del microdesgaste ha sido utilizado para reconstruir el comportamiento relacionado con el consumo de los alimentos en las poblaciones Paleolíticas (Perez-Perez et al., 1994; Spencer, 1999; Schmidt, 2001; Alorusan, 2005; Mohany, 2006; Alorusan y Pérez-Pérez, 2008; Teaford y Tylenda, 1991).

La topografía dental intenta relacionar la morfología dental general y la forma del diente con su función. Esto ha sido explorado en diversos estudios de primates y poblaciones humanas (Kay, 1973, 1975, 1978; Kay y Hylander, 1978; Rosenberger y Kinzey, 1976; Kinzey, 1978; Lucas, 1979; Maier, 1977, 1984; Benefit, 1987; Ungar, 2004). Se ha demostrado que el tipo de dieta influye en la morfología de los dientes (Kay, 1973; Ungar, 2004), por lo que el análisis de la topografía dental puede informativo de las adaptaciones alimentarias.

d. Tamaño dental

El tamaño dental es un indicador de cambios evolucionarios y de procesos de adaptación. La variación dental dentro y entre las poblaciones humanas modernas ha sido atribuida a diferentes factores genéticos y ambientales (Bailit, 1975). Durante los últimos 100.000 años en la especie humana se ha producido una importante reducción del tamaño dental (Fitzgerald y Hilson, 2008). Además, los grandes simios y homínidos presentaban cierta variación morfológica entre los sexos (Brace y Ryan, 1980; Schwartz y Dean, 2001). Sin embargo, dado que los humanos modernos están sometidos a niveles de presión selectiva mucho más bajas, el dimorfismo sexual, sobretodo en el tamaño dental, prácticamente ha desaparecido (Castillo et al., 2011; Schwartz y Dean, 2001). Actualmente, no hay un acuerdo claro entre los académicos sobre si el tamaño dental puede ser una característica distintiva entre los seres humanos (Barrett et al., 1963; Garn et al., 1964; Richardson y Malhotra, 1975; Hanihara, 1977; Keene, 1979; Bishara et al., 1989; Turner Richardson, 1989; Harris, 2003; Hillson, 1996; Otuyemi y Noar, 1996; Scott y Turner, 1997; İşcan y Kedici, 2003; Hanihara y Ishida, 2005; Schwartz y Dean, 2005; Ates et al., 2006; Suazo et al., 2008; Brook et al., 2009; Castillo et al., 2011).

El método más común para investigar la existencia de variabilidad en el tamaño dental es el uso de mediciones lineares (distancias, ángulos, etc.) y varios índices (Kieser et al., 1985). Existen diferentes tipos de mediciones que pueden ser tomados de los dientes (diámetro mesio-distal, diámetro bucco-lingual, diámetro cervio-incisal y sus índices), pero con el desarrollo de la morfometría geométrica se ha introducido un nuevo concepto del tamaño representado por el *centroid size*, que se utiliza en los análisis de la forma de las estructuras biológicas (Bookstein, 1989). En esta tesis se ha estudiado, junto con el análisis del desgaste dental, la variabilidad intra- e inter-poblacional en relación con el tamaño dental en varios grupos de cazadores-recolectores y agricultores.

e. Forma dental

La forma de un objeto se define cómo la propiedad que permanece estable independientemente de la posición, orientación o tamaño del mismo (Kendall, 1977). Los estudios de la forma dental han sido ampliamente utilizados para la investigación de las relaciones bilógicas entre las especies. Como los dientes son la herramienta principal en el procesamiento de los alimentos, su forma está estrictamente relacionada con su función. Por lo tanto, el análisis de la forma de los dientes debe proporcionar información sobre los procesos adaptativos a diferentes tipos de dieta (Evans, 2013).

Los métodos para el estudio de la forma dental pueden ser tanto cualitativos como cuantitativos. Los métodos cualitativos incluyen la descripción de varias características discretas de la morfología dental (por ejemplo el sistema ASUDAS) y han sido abundantemente empleados en estudios dentales. Por otro lado, recientemente ha sido desarrollada una técnica de medición cuantitativa de la forma de los objetos: la morfometría geométrica (Bookstein, 1986). El método está basado en la representación de la forma de los objetos mediante una serie de *landmarks,* que son puntos homólogos en todos los objetos analizados. La correspondencia de estos puntos puede ser tanto anatómica, topográfica como evolutiva y su selección depende del problema que se está analizando (Oxnard y O'Higgins, 2009). Los landmarks de cada objeto son interpolados y los efectos del tamaño, posición y orientación son eliminados. Así, las diferencias entre poblaciones son atribuidas a las diferencias en la forma y pueden ser analizados con métodos estadísticos tradicionales, como el Análisis Multivariante.

La morfología geométrica ha sido utilizada sobre todo en modelos bidimensionales (fotos) pero recientemente el desarrollo de tecnologías tridimensionales ha permitido la utilización de representaciones tridimensionales de los objetos estudiados (Witter et al., 2003; Ulhaas et al., 2004; Benazzi et al., 2009; Cooke, 2011). En antropología dental, debido al limitado tamaño de los dientes, es especialmente útil la implementación de modelos tridimensionales con el fin de obtener datos más completos y aumentar las posibilidades del estudio.

2. Objetivos

La presente tesis tiene como objetivo principal investigar la variabilidad dental en populaciones de humanos modernos desde una perspectiva multimetodológica. El enfoque principal fue el desgaste dental, aunque también se analizaron otras características, como la variabilidad métrica, la forma dental, el microdesgaste, el relieve o la complejidad de la corona. Este objetivo principal fue dividido en cuatro objetivos específicos:

1. Valorar si la división sexual del trabajo presente en los esquimales de Point Hope puede afectar al desgaste del primer molar. La hipótesis de partida fue que hombres y mujeres no deberían presentar diferencias significativas en el desgaste del primer molar, debido a que la división sexual del trabajo en este grupo afecta principalmente a la dentición anterior (Wood, 1992; Lozano et al., 2008; Mickleburgh, 2009, Clement y Hillson, 2012) y no se han descrito diferencias substanciales en la dieta entre los dos sexos (Costa, 1977, 1982; Madimenos, 2005).
2. Siendo el grupo más abundante, los esquimales de Point Hope han sido sometidos a un análisis de las correlaciones entre marcadores del macrodesgaste, microdesgaste, relieve y complejidad de la corona dental para explorar las diferentes líneas de estudio de la pérdida del esmalte y sus correlaciones.
3. Además, se analizó si otras poblaciones de cazadores-recolectores mostraban un patrón similar a los esquimales y confrontarlos con grupos de cultura agricultora para investigar la posible influencia de la división sexual del trabajo sobre la dienta en estas poblaciones. Este análisis se centró en primer lugar en las diferencias entre hombres y mujeres en función de la división sexual del trabajo y a continuación en las diferencias entre grupos de cazadores-recolectores y agricultores.
4. Al final, decidí llevar a cabo un análisis de la forma de los primeros molares en varios grupos de poblaciones humanas modernas mediante la innovadora técnica de la morfología geométrica tridimensional. Este abordaje, no ha sido aún empleado en la investigación de la variabilidad de la dentición humana,

consecuentemente los resultados son muy prometedores y abren nuevas perspectivas para los estudios futuros.

3. Justificación

Las propuestas de estudios mencionados intentan explorar la variabilidad dental entre poblaciones de humanos modernos desde diferentes perspectivas: desgaste dental, tamaño dental, forma dental y complejidad de la corona. Las metodologías usadas convencionalmente en estudios, tanto del desgaste dental como del tamaño dental, son muy a menudo heterogenias, lo que produce cierta confusión a la hora de realizar comparaciones entre poblaciones. En el presente trabajo se aplica una metodología estandarizada y cuantitativa al análisis del desgaste dental en una serie de poblaciones con culturas y modelos de subsistencia distintos, lo que puede proporcionar informaciones homogéneas acerca de los procesos involucrados en la pérdida del esmalte entre hombres y mujeres, así como entre grupos con patrones de subsistencia distintos. Este enfoque elimina los posibles efectos de las diferencias metodológicas que han proporcionado resultados contradictorios y no comparables con otras series.

El análisis de la forma de los dientes en humanos modernos con el uso de la morfología geométrica tridimensional es un campo de estudio aun poco explorado. Por lo tanto, el estudio realizado es innovador y abre nuevas perspectivas para estudios más profundos. De la misma forma, el análisis de las correlaciones entre el macro- y microdesgaste, el relieve y la complejidad de la corona dental son poco frecuentes, por lo que aporta nuevas perspectivas en relación con la morfología y el funcionamiento de los dientes.

Es igualmente importante mencionar que los estudios de los grupos de cazadores-recolectores son de extrema importancia. Durante una gran parte de nuestra historia como especie hemos sido cazadores-recolectores, hasta que la invención de la agricultura cambió nuestro patrón de subsistencia. Sin embargo, aún existen grupos que continúan teniendo un estilo de vida ancestral y basan su subsistencia en la caza, pesca y recolección. Diversos estudios de estas poblaciones proporcionan una inestimable oportunidad para entender los comportamientos humanos deducidos a partir de registros arqueológicos (Stiner y Kuhn, 2006; Yellen, 1977; Berbesque, 2010) y nos proporcionan información sobre la ecología nutricional de nuestros antepasados pre-agricultores.

4. Material y métodos

La investigación ha sido realizada únicamente con el material disponible en las colecciones dentales de la Universidad de Barcelona y la Universidad de Alicante. En total 251 dientes, procedentes de 188 individuos de 9 poblaciones diferentes de humanas modernas (Agta, Aborígenes Australianos, Batéké-Balali, Esquimo, Hutu, Javaneses, Khoe, Navajo y San) han sido analizados.

El grupo de esquimales fue el más abundante, por lo que esta muestra se utilizó en todos los estudios realizados. Sin embargo, no siempre los mismos individuos pudieron ser incluidos en todos los análisis. La selección de las sub-muestras para cada análisis dependía sobre todo del objetivo del estudio y de los criterios de inclusión de la muestra (por ejemplo, presencia de micro-estrías o no de exposición de dentina). Los grupos analizados han sido escogidos sobre todo debido a su patrón de la división sexual del trabajo, las posibles diferencias en la dieta entre los sexos y su lugar de origen.

Los métodos para investigar la diversidad del desgaste, el tamaño y la forma dental en varios grupos de humanos modernos has sido muy diversos. A continuación se describen brevemente los método utilizados. Todos los análisis se han llevado a cabo sobre réplicas dentales obtenidas directamente de las colecciones originales de los museos. Estas réplicas se han realizado con técnicas estandarizadas (Galbany et al., 2006). El material original se limpió con acetona pura y etanol, obteniendo tras su secado al aire moldes negativos con silicona Affinis (Coltène®). Luego, a partir de los moldes se realizaron las réplicas con poliuretano Feropur PR-55 (Feroca Composites).

a. Análisis métrico

Todos los estudios métricos han sido realizados a partir de las imágenes digitalizadas (300 *ppp*) de las réplicas dentales. Las fotos de la superficie oclusal, con su escala correspondiente, fueron tomadas con una camera Nikon D40 a una distancia focal de ca. 50 *cm*. Los dientes fueron orientados de manera que la superficie oclusal se situó paralelamente al objetivo de la camera para evitar posibles distorsiones de la imagen. La escala se situó a la misma altura que la superficie fotografiada. Las imágenes fueron medidas con el programa *ImageJ* (Abramoff et al., 2004), Todas las variables se midieron en milímetros: 1) el diámetro mesio-distal, medido como la distancia máxima entre los puntos más distantes en los bordes medial y distal del perímetro oclusal; 2) el diámetro buco-lingual, perpendicular a la distancia mesio-distal, medido como la distancia máxima entre los bordes bucal y lingual del perímetro oclusal; 3) el área total de la superficie oclusal de la corona (mm^2); y 4) el área total de la exposición de dentina (mm^2), como la suma de todas las áreas de exposición de dentina visibles en la superficie oclusal.

b. Análisis del desgaste dental

La cantidad real de la exposición de dentina en un diente depende del tamaño del diente. Dientes menores tendrán menos exposición de dentina en comparación con dientes más grandes. Por lo tanto, para eliminar el efecto del tamaño, que pudiera afectar el análisis, el estudio del desgaste dental se realizó a partir del porcentaje de exposición de dentina respecto al área total de la corona. Para medir el área oclusal total de la corona, se definió el perímetro oclusal con el uso de la herramienta polígono en el programa *ImageJ*, con un mínimo de 30 puntos para definir el contorno de la corona. Las áreas de exposición de dentina fueran medidas de la misma manera, marcando cada zona por separado y sumándolas para obtener el área total de la exposición de dentina, a partir de la cual se calculó el porcentaje de exposición de dentina.

c. Análisis del microdesgaste, complejidad y relieve

El análisis de la topografía dental ha sido realizado sobre las réplicas dentales. Los dientes seleccionados fueron escaneados en tres dimensiones con un escáner Pizca (Roland®) y se utilizó el programa *SurferManipulator* (Golden Software, Inc.) para obtener las variables de la complejidad y relieve de la corona, siguiendo la metodología descrita por Evans (2013).

A continuación las réplicas fueran metalizadas con una capa de oro de ~15 *nm* (Balzers® SCD 004 Sputter Coater) siguiendo la metodología descrita por Galbany et al. (2006). Se utilizó un microscopio electrónico barrido Hitachi en modo secundario (SE) para obtener imagines a 100× aumentos (imágenes de 1280×960 pixeles, formato BMP) del tercio medio de la superficie vestibular, preferiblemente bajo el protocono (Pérez-Pérez et al., 1994; Romero et al., 2012). Todas las imágenes obtenidas de esta manera fueron procesadas con *Adobe Photoshop*® CS3 para obtener áreas estandarizadas de 0,56 mm^2, sobre las que se midieron las estrías (3:1 longitud/anchura). De este modo, se obtuvo el patrón de densidad (NT) y longitud media de las estrías (XT en μm) de cada diente fue calculado (Romero et al., 2012).

d. Análisis de la forma dental

La forma dental ha sido estudiada mediante morfometría geométrica tridimensional. Se utilizó un escáner NextEngine© para digitalizar las superficies de las réplicas dentales seleccionadas. Las imágenes obtenidas fueron grabadas como ficheros *.ply* (Ascii) y procesadas con el programa *Landmark Editor* para la digitalización de los *landmarks*. Un conjunto de 10 *landmarks* fueron seleccionados en el modelo tridimensional. La configuración de los *landmarks* fue exportada en el formato *.dta* e introducida en el programa *MorphoJ* (Klingenberg, 2011) para realizar el análisis de la morfometría geométrica tridimensional. Con el propósito de la identificación inequívoca de los *landmarks* únicamente los dientes sin desgaste dental, o mínimo, sin daños visibles y sin caries fueron utilizados en este estudio.

5. Resultados y discusión

Diversos estudios de antropología dental demuestran que un análisis detallado puede revelar evidencias significativas sobre el estilo de vida, la salud y las prácticas culturales de las poblaciones humanas, así como sobre procesos de adaptación y relaciones evolucionarias ellas. En esta tesis doctoral se analiza la variabilidad dental intra e inter poblacional de diversas poblaciones de humanos modernos. El estudio se ha centrado los cazadores-recolectores modernos con la intención de analizar los posibles efectos de la división sexual del trabajo sobre el desgaste dental. El estudio se realizó exclusivamente sobre el primer molar dado que es el primer diente permanente que aparecer en la cavidad oral y en consecuencia está expuesto durante más tiempo a factores que puedan producir la pérdida del esmalte. Además, este diente, y especialmente el primer molar superior, se caracteriza por una gran estabilidad morfológica comparando con otros tipos de dientes (Scott y Turner, 1997; Bailey, 2004; Gomez-Robles et al., 2007).

a. Desgaste dental

Una parte importante de los análisis realizados se basa en el grupo de esquimales Tigara de Point Hope. Este material pertenece a una de las más completas y abundantes colecciones esqueléticas de la cultura esquimal tradicional. Y, lo que es aún más importante, este material dispone de información acerca del sexo y la edad de la mayoría de individuos (Costa, 1977). Estos datos son esenciales para el estudio del desgaste dental y del dimorfismo sexual.

La cultura esquimal es única entre las otras sociedades tradicionales. Este hecho esta debido, en gran parte, a las condiciones climáticas en las que viven estos grupos, las costas Árcticas. Las circunstancias ambientales influye en las actividades diarias y en el comportamiento cultural y condicionan el tipo de alimento disponible para su consumo. La dieta de los esquimales está, por lo tanto, basada prácticamente exclusivamente en proteínas y grasa animal de mamíferos marinos y pescado, e incluye muy pocas y limitadas plantas (Keenleyside, 1998; Larsen y Rainey, 1948). En consecuencia, las diferencias en la dieta entre los sexos son prácticamente mínimas o no existen (Costa, 1977) y la división sexual del trabajo no se enfoca en la subsistencia, puesto que todos los alimentos son proporcionados por los hombres. El trabajo de las mujeres incluye tareas domésticas, cuidado de los niños, preparación de la comida y procesamiento de las pieles de los animales para su uso en la producción de ropa, que es una actividad exclusivamente femenina que incluye la masticación prolongada de pieles para suavizarlas (Steensby, 1910; Leigh, 1925; Waugh, 1937; Pedersen, 1947; Davies y Pedersen, 1955; Molnar, 1971; Mayhall, 1972; Tomenchuk y Mayhall, 1979; Merbs, 1968; Richards, 1984). Esta práctica sobrecarga sobre todo los dientes anteriores (Leigh, 1925; Waugh, 1937; de Poncins, 1942; Turner y Cadien 1969; Mayhall, 1970; Hylander, 1977; Hinton, 1981; Pedersen y Jakobsen 1989; Clement y Hillson 2012) y produce un desgaste más rápido en las mujeres. Sin embargo, no se conoce bien cómo influye esta práctica en los dientes posteriores porque no existen estudios diseñados especialmente para evaluarlo y pocos autores mencionan este aspecto en sus estudios (Wood, 1992; Clement y Hillson, 2012). Esta cuestión es el tema principal de esta parte del estudio.

Hemos analizado la muestra de esquimales de Tigara para determinar la influencia del uso no-masticatorio de la dentición anterior sobre el dimorfismo sexual en el porcentaje de exposición de dentina en los primeros molares. Los resultados indican la ausencia de diferencias en esta característica entre hombres y mujeres de la población Tigara de Point Hope. Este resultado coincide con los presentados por Clement y Hillson (2012) y reafirma la hipótesis de que la dentición posterior (primer molar) no está siendo usada en el actividades paramasticatorias de los dientes. Sin embargo, este resultado puede ser interpretado también en el sentido de que el uso de los dientes posteriores en prácticas no masticatorias de los alimentos no presenta variabilidad relativa al sexo. Por lo tanto, se puede afirmar que la práctica de masticación de las pieles animales, que produce un desgaste más avanzado en la dentición anterior en mujeres, no afecta a los molares. Este resultado es consistente con estudios previos que indican que el uso no-masticatorio de los dientes en poblaciones esquimales o Inuit involucra sobre todo la dentición anterior (Leigh, 1925; Waugh, 1937; de Poncins, 1942; Turner y Cadien 1969; Mayhall, 1970; Hylander, 1977; Hinton, 1981; Pedersen y Jakobsen 1989). Sin embargo, estos autores utilizan métodos cualitativos para caracterizar el desgaste dental. En el presente estudio, comprobamos que el porcentaje de exposición de dentina, una variable continua, tampoco muestra diferencias entre hombres y mujeres en los primeros molares en la población de Tigara.

b. División sexual del trabajo

La división sexual del trabajo determina un acceso diferencial a los recursos alimentarios en la mayoría de las poblaciones de cazadores-recolectores (Molnar, 1972). Este autor propuso la hipótesis de que las mujeres que recolectan sobre todo alimentos fibrosos, duros y abrasivos consumirían estos productos en mayor medida que los hombres, que tendrían un mayor contacto con la carne, que es menos abrasiva, lo cual debería resultar en un desgaste dental más marcado en las mujeres. Sin embargo, los escasos estudios de la dentición posterior en este ámbito no aportaron ninguna variación significativa (Kieser et al., 2001; Lovejoy, 1985; Berbesque et al., 2012; Clement y Hillson, 2012; Madimenos, 2005). En la presente tesis se intentó averiguar si la división sexual del trabajo influye en la dieta de cada sexo y si esas diferencias se reflejan en el desgaste dental entre los sexos. Los resultados obtenidos indican que no existe dimorfismo sexual en el desgaste de los primeros molares, independientemente del origen geográfico de la población analizada y el modelo de la división sexual del trabajo, tanto en grupos de cazadores-recolectores como los de cultura agricultora como forma predominante de subsistencia.

El modelo tradicional de división sexual del trabajo coloca a los hombres como los principales proveedores de proteínas animales, mientras a las mujeres como proveedoras de otros tipos de alimentos (semillas, raíces, tubérculos, frutas, etc.). Sin embargo, en la mayoría de estas poblaciones, al final del día, la adquisición diaria de alimentos es compartida entre todos los miembros de la familia o incluso de la comunidad (Draper, 1975; Guimares de Souza, 2007; Hawkes et al., 2001; Lee, 1978; Minter, 2010; Schapera, 1930). Este hecho puede compensar el diferente acceso a los recursos alimentarios que resulta de las diferentes tareas de subsistencia entre hombres y mujeres.

Respecto a los grupos agrícolas, la división sexual del trabajo no se enfoca tanto en la provisión y consumo de los alimentos como en su preparación y procesamiento. En estas poblaciones los alimentos prácticamente siempre pasan por un proceso de preparación antes de ser compartidos y consumidos. Estas prácticas disminuyen las posibles diferencias en la abrasividad de la dieta que podrían causar diferencias sexuales en el desgaste dental.

Los resultados obtenidos en este estudio indican que el desgaste dental no es necesariamente una buena medida para detectar diferencias en el acceso a los recursos alimentarios producidas por la división sexual del trabajo. De hecho, los resultados muestran que la división sexual del trabajo no afecta al desgaste dental de los primeros molares tanto en cazadores-recolectores como en agricultores.

c. Diferencias intergrupales en el desgaste dental

Los resultados generales de esta parte de la investigación indican pocas diferencias significativas entre los grupos analizados. En general, los dos dientes estudiados (primer molar inferior y superior) presentan patrones similares en relación a las diferencias intergrupales. El porcentaje de exposición de dentina ha sido significativamente menor en el grupo Agta de Filipinas que en los grupos de esquimales y Batéké-Balali en el primer molar inferior, y Navajo en el primer molar superior. No se han encontrado otras diferencias significativas entre las poblaciones estudiadas. Este resultado es en cierta forma sorprendente, ya que otros investigadores obtuvieron diferencias entre grupos de cazadores-recolectores y agricultores (Hinton, 1982; Eshed et al., 2006; Deter, 2009). Podemos sugerir diversas explicaciones en relación con esta inconsistencia.

La población indígena de los Negritos de Filipinas, los Agta, son habitantes del zona de clima cálido y tropical, y son típicos representantes de una subsistencia basada en la caza y recolección, mientras los esquimales representan una dieta basada exclusivamente en la carne y grasa animal. Está claro que las condiciones climáticas influyen en el tipo de la dieta disponible en cada región. Aunque la carne no es un alimento altamente abrasivo, las técnicas de preparación, almacenaje y consumo en el ámbito Ártico pueden aumentar su abrasividad significativamente (Brubaker et al., 2009; El-Zaatari, 2008). Muy probablemente, las fuerzas de masticación necesarias para el consumo de la carne por los esquimales son mucho más altas que las producidas por los Agta, lo que resulta en el mayor grado del degaste observado en la población de Point Hope. Las técnicas de almacenaje de la carne en el Ártico también causan un aumento significativo de su abrasividad, por la incorporación de diferentes partículas de alta dureza que actúan sobre la superficie dental causando altos niveles del microdesgaste en estos grupos (Brubaker et al., 2009; El-Zaatari, 2008; Larsen y Rainey, 1948). Además, las microfracturas del esmalte reducen la resistencia de este tejido y dejan los dientes más susceptibles al desgaste (Davies y Pedersen, 1955; Lucas, 2008). La población de Filipinas, debido a las condiciones climáticas en la que vive, no depende tanto del almacenaje de los alimentos. Las altas temperaturas y humedad del clima tropical no permiten que la comida sea almacenada por mucho tiempo. Este hecho disminuye los posibles efectos del material extrínseco que pudiera aumentar la destrucción del esmalte, al ser incorporado a la comida y en consecuencia causa los menores niveles de desgaste observados en este grupo en comparación con los Tigara.

Respecto a los otros dos grupos, con un estilo de vida agro-pastoral, presentaron mayor grado de desgaste en comparación con los Agta. Las prácticas agricultoras de preparación de comida pueden determinar, por un lado, una dieta más blanda en consistencia respecto a la dieta típica de los cazadores-recolectores, pero por otro lado puede llegar a ser incluso más abrasiva en función de las prácticas paramasticatorias involucradas, como el uso de las piedras de moler y otras prácticas de preparación de la comida que causen la incorporación de partículas extrínsecas y abrasivas en la harina que llevan a un desgaste dental intenso (Larsen, 1995; Molleson y Jones, 1991).

Otras hipótesis son también posibles para explicar el menor grado de desgaste dental encontrado en los cazadores-recolectores de Filipinas. La primera está relacionada con un mejor estado nutricional de los Agta que de los Navajo y Batéké-Balali, que tienen una dieta más procesada, o de los Tigara, que tienen dieta basada exclusivamente en la carne y grasa de mamíferos marinos. Es posible que el esmalte de los Agta tenga una estructura más resistente a la abrasión que en los otros grupos. La dieta típica de los cazadores-recolectores es relativamente diversa en cuanto a los tipos de alimentos consumidos. Plantas y frutas comidas crudas son fuentes de muchas vitaminas y microelementos, de los que una dienta basada exclusivamente en la carne carece. Además, el procesamiento de los alimentos antes de ser consumidos (como el cocinado) elimina muchas de las vitaminas de la comida. La transición del estilo de vida de forrajero al agricultor está relacionado con una disminución de la calidad nutricional de la dieta (Larsen, 1995). Las poblaciones agricultoras muestran una alta prevalencia de caries y otros problemas dentales (Turner, 1979; Larsen, 1995). Por lo tanto, se puede sugerir que la dieta diversa, rica en frutas y plantas crudas, que caracteriza a los grupos de cazadores-recolectores resulta en un esmalte más 'sano' y por lo tanto más duro y resistente a las fuerzas que causan desgaste dental.

La segunda explicación se relacionaría con la adaptación del esmalte a la estructura y propiedades físicas de los alimentos. Lucas (2008) propuso que el grosor del esmalte puede tener relación con la dureza y rigidez de la dieta. Cuanto más duros sean los productos consumidos, más grueso es el esmalte, como respuesta evolutiva a esta presión selectiva. La dieta de los Agta abunda en objetos duros, como por ejemplo raíces, semillas, etc., mientras que la dieta de los esquimales está basada en carne fibrosa pero blanda, mientras que la dieta de las poblaciones agrícolas tiende a ser relativamente blanda por el efecto de las técnicas del procesamiento de los alimentos antes de su consumo.

Aunque algunos de los grupos incluidos en este estudio son representantes del estilo de vida cazador-recolector, lo que en consecuencia implica que su dieta debe ser parecida a la de los Agta, no se han encontrado diferencias entre ellos y los grupos con subsistencia basada en la agricultura. Esta cuestión es difícil de explicar y puede estar relacionada con factores como el reducido tamaño muestral o la falta de estimación precisa de la edad de los individuos.

d. Cazadores-recolectores *vs.* agricultores

No se han encontrado diferencias significativas en el desgaste dental entre los cazadores-recolectores las poblaciones agro-pastoras, aunque otros autores han detectado un desgaste más marcado en grupos cazadores-recolectores, debido a su hipotética dieta más dura y abrasiva (Hinton, 1982; Inoue et al., 1986; Lucas, 1995; Eshed et al., 2006; Deter, 2009).

La adopción de la agricultura, hace *ca.* 10,000 (Harris y Hillman, 1989; Weisdorf, 2005) estimuló cambios en los hábitos alimentarios, la dieta y el estilo de vida. La comida acabó de ser un producto de búsqueda diaria y comenzó a ser producida en abundancia. Las modificaciones en la dieta tradicional introducidas por la agricultura causaron un cambio en la textura y consistencia de los alimentos (Smith, 1984), lo que podría reflejarse en un desgaste. Smith (1984) argumentó que aunque la dieta de los grupos agrícolas es relativamente más blanda en consistencia, es igualmente o incluso más abrasiva que la dieta tradicional de los cazadores-recolectores, lo que podría explicar la ausencia de diferencias en la exposición de dentina entre ambos grupos. Los resultados obtenidos parecen confirmar la hipótesis de Smith sobre la abrasividad parecida de ambas dietas.

6. Microdesgaste y topografía dental (relieve y complejidad)

En la población Tigara de Point Hope hemos realizado un análisis de las relaciones entre desgaste dental, microdesgaste y topografía dental representada por el relieve oclusal y la complejidad de la corona. Los resultados indican que existe una clara asociación entre algunos de estos factores.

La exposición de dentina depende en gran medida del tipo de la dieta ya que las propiedades físicas y mecánicas de los alimentos influyen en la biomecánica de la masticación (Lucas, 2004). Diversos estudios sugieren que la exposición de dentina está claramente relacionada con la topografía dental (Smith, 1984; Fiorenza et al., 2011). Esta asociación ha sido claramente evidenciada en nuestro análisis en el grupo de Tigara. Los cambios en la complejidad y el relieve oclusal de la corona en esta población están relacionados con un desgaste más pronunciado en la parte bucal que afecta sobre todo a las cúspides protocono, hipocono e hipocolulido, causando cambios en el patrón de topografía dental.

Romero et al. (2012) han demostrado que el patrón del microdesgaste en la cara bucal de la corona del diente presenta una relación directa con el carácter abrasivo de la dieta. Los resultados obtenidos en nuestro análisis indican una correlación negativa de la longitud de las estrías vestibulares con el relieve oclusal de la corona. Las partículas abrasivas que actúan sobre la superficie del esmalte producen diferentes patrones de microdesgaste asociados con la abrasividad de la dieta. Los resultados obtenidos sugieren que las diferencias intergrupales en la exposición de dentina pueden estar relacionadas con la variación en las propiedades físicas y mecánicas de los alimentos consumidos. Las fuerzas generadas durante la masticación influyen tanto en el desgaste del primer molar, como en el microdesgaste bucal y los patrones de la topografía oclusal de la corona (Benazzi et al., 2011; Lee et al., 2011). En consecuencia, tanto el desgaste como el microdesgaste afectan a la morfología de la corona (Teaford y Tylenda 1991; Schmidt 2010; Lee et al., 2011). Este estudio también ha demostrado que el proceso del desgaste de los dientes en complejo y multifactorial, en el cual las diferentes componentes son mutuamente dependientes.

7. Análisis del tamaño dental

a. Dimorfismo sexual

En general no hay acuerdo entre los investigadores sobre si el tamaño dental es una característica que presenta un dimorfismo sexual en los humanos modernos. Numerosos estudios muestran diferencias sexuales en las mediciones dentales en diferentes poblaciones humanas (Barrett et al., 1963; İşcan y Kedici, 2003; Richardson y Malhotra, 1975; Schwartz y Dean, 2005). Sin embargo, otros estudios no muestran tales diferencias (Hillson, 1996; Harris, 2003; Suazo et al., 2008; Ates et al., 2006; Castillo et al., 2011). Los resultados de análisis son coincidentes con estos últimos trabajos, puesto que no se ha encontrado diferencias significativas en las dimensiones dentales entre hombres y mujeres en ningún de los grupos analizados.

Brace y Ryan (1980) indican que las diferencias en el tamaño dental entre los sexos son simplemente el reflejo del tamaño general del cuerpo. Durante el Paleolítico Superior, cuando la caza de animales grandes era un parte importante de la subsistencia, las diferencias en el tamaño del cuerpo y el tamaño dental entre los sexos eran significativas. Este modo de subsistencia funcionaba como una presión selectiva hacia el dimorfismo sexual en el tamaño. Con la adopción de técnicas más sofisticadas de obtención y preparación de la comida, la variación sexual del tamaño ha disminuido significativamente y en los humanos modernos no sobrepasa los 4% (Bryce y Ryan, 1980). En consecuencia, es muy poco probable que en estructuras tan pequeñas como los dientes se observen variación sexuales significativas. Por lo tanto, los resultados confirman las afirmaciones de los investigadores que indican ausencia del dimorfismo sexual.

b. Variación intergrupal

Al no encontrarse diferencias sexuales en el tamaño dental, los dos sexos se han unido para evaluar las diferencias entre las poblaciones analizadas. En general el diámetro buco-lingual mostró mayor variación que el diámetro mesio-distal. Los resultados obtenidos mostraron que los Agta, Bosquimanos y Khoisánidos presentan valores menores en las dimensiones analizados que los Aborígenes Australianos, esquimales y Navajo. Los Negritos Agta de Filipinas se caracterizan por dimensiones dentales pequeñas respecto a otras poblaciones humanas (Hanihara y Ishida, 2005). Nuestros resultados confirman esta tendencia. Sorprende, sin embargo, que los Navajos, siendo un grupo de subsistencia agro-pastoral presenta dientes mayores que otros grupos de subsistencia cazadora-recolectora. Varios autores han afirmado que la transición del estilo de vida de forrajero al cultivo de las plantas indujo una reducción del tamaño dental (Hinton et al., 1980; Larsen, 1995; Y'Edynak, 1989). Nuestros resultados no reflejan claramente esta tendencia porque los grupos cazadores-recolectores, como Bosquimanos y Agta, tienen los dientes más pequeños que los Navajo. Por otro lado, es igualmente sorprendente que los Khoisánidos y Bosquimanos presenten dimensiones dentales relativamente reducidos en comparación con otros grupos. Esto contradice estudios previos que indican que los grupos subsaharianos se caracterizan por dientes relativamente grandes (Hanihara y Ishida, 2005). Un posible explicación de estas discordancias puede ser que los dos grupos africanos tienen un tamaño corporal comparativamente menor que otros grupos subsaharianos (Schapera, 1930), lo que apoyaría la teoría de la correlación entre el tamaño del cuerpo y el tamaño dental (Lauer, 1975; Gingerich, 1977, Brace y Ryan, 1980). Sin embargo, otros autores rechazan esta correlación, argumentando que el tamaño dental no es indicativo del tamaño del cuerpo (Garn y Lewis, 1958; Bailit y Friedlaender, 1966).

c. Cazadores-recolectores *vs.* agricultores

Aunque se han encontrado cierta variación en el tamaño dental entre algunas de las poblaciones analizadas, cuando los grupos con patrón de subsistencia parecido se agrupan, no se observan diferencias significativas en sus dimensiones dentales.

La implementación de nuevas técnicas de procesamiento de los alimentos con la invención de la agricultura y el estilo de vida sedentario, están asociados a una reducción del tamaño dental en los registros fósiles del Pleistoceno (Hinton et al., 1980; Larsen, 1995; Y'Edynak, 1989). Diferentes estudios indican que el procesamiento de los alimentos empeora el contenido nutricional de la comida, aumentando la prevalencia de los problemas dentales, que causan problemas, nutricional en las madres y por lo tanto los niños nacen con dientes más pequeños (Turner, 1979; Larsen, 1995). En consecuencia, los grupos de subsistencia agricultora deberían estar caracterizados por tamaños dentales menores, como resultado de presiones selectivas, en comparación con los grupos de cazadores-recolectores que tienen una dieta más diversa y menos procesada. Sin embargo, los resultados obtenidos no apoyan esta hipótesis. Esto podría ser indicativo de que el patrón de subsistencia, el procesamiento de los alimentos y el estado nutricional de la dieta no influyen en el desarrollo dental. Además, las diferencias en la ingesta nutricional entre los dos tipos de dieta, por lo menos entre los grupos analizados, no parecen ser tan evidentes como para reflejarse en el desarrollo de los dientes. Como alternativa, podría ser que los grupos atribuidos a una subsistencia agricultora no dependieran tan estrictamente de las plantas cultivadas, sino que también obtenían productos de la caza y recolección esporádica. También los cazadores-recolectores, hasta cierto punto, procesan sus aliéntanos, por lo tanto las diferencias teoréticas entre los grupos no serían tam importantes como se habría supuesto.

8. Análisis de la forma de los dientes

La última parte de la tesis se centra en el análisis de la morfometría geométrica tridimensional de los molares. Debido a su alta estabilidad genética (Scott y Turner, 1997; Bailey, 2004; Gomez-Robles et al., 2007) el análisis se ha realizado en los primeros molares superiores de cinco poblaciones geográficamente dispersos. Los resultados muestran una importante variación en la forma del primes molar superior entre ellas. Las distancias de Mahalanobis entre los grupos son compatibles con estudios previos sobre los patrones migratorios y filogenético en las poblaciones consideradas (Cavalli-Sforza et al., 1994, Crow, 2002; Gugliotta, 2008).

9. Conclusiones

La presente tesis tiene un enfoque amplio en diferentes aspectos de la variabilidad dental de los humanos modernos. Se han propuesto cuatro objetivos principales y los resultados pueden ser resumidos de la siguiente manera.

La división sexual del trabajo en el grupo de Tigara de Point Hope no afecta a los primeros molares. Por lo tanto, se puede concluir que el factor principal responsable del desgaste del este dental en esta población está relacionado sobre todo con el procesamiento de los alimentos, el cual no presenta variaciones sexuales. Al examinar las posibles influencias de la división sexual del trabajo en la dieta en otras poblaciones de economía tradicional, no se ha encontrado tampoco diferencias significativas entre hombres y mujeres en ningún de los grupos analizados. Este resultado llevo a la conclusión que el desgaste dental de los molares no es una medida adecuada para investigar el impacto de la división sexual del trabajo a la dieta de ambos sexos.

Tampoco se han encontrado variaciones en el desgaste entre los patrones de subsistencia cazador-recolector y agricultor. Esto podría deberse a variaciones en la dieta, la abrasividad de los alimentos consumidos, el estado nutricional general de los grupos y la adaptación del esmalte a las propiedades físicas de los alimentos.

El estudio de la forma dental conforma la utilidad excepcional del método de la morfometría geométrica tridimensional en la investigación de la variabilidad de la forma de los dientes en humanos modernos. Los resultados demostraron una importante variación de la forma del primer molar superior entre los grupos analizados e indicaron que esta característica puede contener información filogenética.

En definitiva, el análisis dental es una importante fuente de información sobre varios aspectos de la bilogía humana. En la presente tesis nos hemos centrado sobre todo en la variación de la exposición de dentina y la variabilidad de la forma en los primeros molares.

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