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The Non-Masticatory Use of the Anterior Teeth Among Late Pleistocene Humans

by

John C. Willman

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Abstract of the Dissertation

The Non-Masticatory Use of the Anterior Teeth Among Late Pleistocene Humans
by
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Doctor of Philosophy in Anthropology
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Characteristic patterns of dental wear form through the use of the dentition for non-masticatory manipulative behaviors. The use of “teeth-as-tools” or the dentition as a “third hand” for manipulative behaviors emphasizes the importance of the human dentition in our otherwise extrasomatic tool-kit. The extreme pattern of anterior dental wear found in many Neandertals, together with their large anterior teeth, has led researchers to suggest that the unique craniofacial morphology of Neandertals is the result of functional adaptation to the habitual use of the dentition for manipulative tasks. However, decades of research investigating the adaptive significance and biomechanical properties of Neandertal and modern human craniofacial morphology has not convincingly demonstrated whether non-masticatory behavior was a significant selective force during the Late Pleistocene. Studies addressing non-masticatory behavior among Late Pleistocene archaic and modern humans through the direct study of dental wear are equally equivocal in this regard. The few studies that have attempted to systematically quantify non-masticatory dental wear among Neandertals and early modern humans are constrained by different analytic methods that prevent cross-study comparisons, contain small early modern human samples, and/or differ in conclusion as to the implied patterning and magnitude of behavioral shifts in the Late Pleistocene.

The aims of this thesis are to address non-masticatory manipulative shifts in the Middle to Late Pleistocene through the analysis of non-masticatory dental wear using both macroscopic and microscopic techniques. Scaled macrowear gradients, enamel chipping, and instrumental cutmarks on labial tooth surfaces were documented to understand differences in degree, magnitude, and repetition of non-masticatory behaviors between morphologically and temporally partitioned groups of Middle and Late Pleistocene humans. Data from Middle and Late Pleistocene fossils are studied directly rather than using recent human groups as proxies for Pleistocene behavioral variation.

Changing technological, cultural, and socioeconomic organization during the Middle to Upper Paleolithic Transition is often used to explain craniodental structural reduction across the morphological transition from archaic to fully modern human morphology during the Late Pleistocene. The results of this thesis challenge this view by documenting a high degree of wear among both archaic and modern human groups in the Pleistocene. Archaic humans benefit from having large anterior dentitions to withstand a lifetime of anterior tooth-use, but there is little evidence from anatomy or dental wear to indicate that the forces exerted, or non-masticatory activities engaged in, differed greatly from those of early modern humans. Instead, a high degree of anterior versus posterior dental wear is characteristic of hunter-gatherers generally. Thus, explanations relying on technological innovation as a means of relaxing selection on the body/dentition for manipulative tasks fall short in this regard. Anterior dental reduction (and craniofacial reduction, generally) occurred despite evidence suggestive of persistent use of the dentition for manipulative tasks throughout the Pleistocene and into the Holocene by modern humans. It is implausible that anterior tooth-use or extreme dental wear would have produced selective pressure on craniodental anatomy in humans since most problems related to extreme tooth-use among hunter-gatherers will affect individual morbidity late in life but not necessarily affect reproductive fitness. There is a paradox in that anterior dental reduction occurred among early modern humans despite high-levels of anterior tooth use. Therefore, we are left with another example of how modern humans are derived with respect to Middle and Late Pleistocene archaic humans.

Chapter 1. Introduction

The spread of early modern humans and the eventual replacement or absorption of the Neandertals in Western Eurasia is often explained by the advent of cultural practices among early modern humans that provided more effective technological and socioeconomic strategies than possessed by their archaic counterparts (Mellars 2005; Kuhn and Stiner 2006; Klein 2008; Shea and Sisk 2010; Marean 2015); however, defining the spatiotemporal details and nature of the purported technological or socioeconomic advantages that early modern humans may have possessed over the Neandertals remains widely debated (Kuhn and Stiner 2001; Teyssandier 2008; Caron et al. 2011; d'Errico et al. 2012; Langbroek 2012; Roebroeks et al. 2012; Villa and Roebroeks 2014; García-Diez et al. 2015; Roebroeks and Soressi 2016). Historically, many approaches to understanding the behavioral differences between archaic and modern humans have focused on the analysis of archaeological material culture (e.g., faunal remains, stone and osseous tools, objects of symbolic expression – beads, pendants, engravings, cave art, etc.) and human paleobiology. This thesis takes an integrative biocultural approach that combines insights from human paleobiology in light of the archaeological record of human technological and socioeconomic variation.

Biocultural approaches emphasize the dynamic relationships and interactions between human biology and the physical and sociocultural environments humans are exposed to (Zuckerman and Armelagos 2011). In this sense, a biocultural approach provides compelling framework for the exploration of the biological consequences of anterior tooth-use (e.g., craniofacial structural adaptation, dental metric evolution, dental wear-induced pathology and morbidity, etc.) among morphologically-defined groups of Pleistocene humans across time and space. Biocultural approaches focusing on human manipulative behavior are particularly well-poised to provide nuanced understanding of the complex interplay between technocultural variation and human paleobiology. Biocultural approaches rely heavily on skeletal evidence of physiological stress, skeletal loading, disease, longevity, morbidity, and other paleobiological indicators of past human experience and habitual behavior which is further informed through a detailed reading of archaeological evidence on technocultural and socioeconomic variation such as those related to subsistence practices (Niewoehner 2006; Shackelford 2007; Holt and Formicola 2008; Trinkaus 2008; Rhodes and Churchill 2009; Villotte et al. 2010; Krueger 2011; Maki and Trinkaus 2011; Di Vincenzo et al. 2012; Fiorenza and Kullmer 2013; Lacy 2014; Villotte and Knüsel 2014; Macias and Churchill 2015; Sládek et al. 2016). For instance, changes in manipulative behavior during the Late Pleistocene have been inferred from a variety of analyses of the upper limb which emphasize reduced skeletal hypertrophy among early modern humans compared with Neandertals (Trinkaus and Churchill 1988; Niewoehner 2001; Churchill and Rhodes 2006; Trinkaus 2006b; Maki and Trinkaus 2011). Less reliance on the upper limb for manipulation among early modern humans is paralleled by evidence for less intensive use of the anterior teeth for non-masticatory[1] activities – evident as a reduction in anterior dental wear and structural reduction of the anterior teeth (Smith and Paquette 1989; Trinkaus 1992; Frayer et al. 2006; Cartmill and Smith 2009; Doboş et al. 2010; Krueger 2011). Thus, multiple

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[1] "Non-masticatory" is one of many terms frequently used in the literature to discuss the use of the dentition for purposes other than normal mastication. Other terms include paramastication, extra-mastication, non-dietary tooth-use, using the teeth-as-tools, non-alimentary tooth use, etc.

forms of paleobiological evidence, namely those related to the use of the upper limb and anterior dentition, suggest decreased reliance on the body for manipulative behavior across the Middle to Upper Paleolithic Transition – probably related to technological and cultural shifts related to manipulative behaviors[2].

Following the trend set by other researchers interested in the study of paleobiological reflections of technological and socioeconomic variation, a biocultural approach is adopted in this thesis to discern the degree to which the body, specifically the anterior dentition, was relied on for manipulative behavior among morphologically defined groups of archaic and modern humans. Of primary interest is the collection of paleobiological data on non-masticatory behaviors through analyses of dental wear to address the degree to which Pleistocene humans relied on the anterior dentition for manipulative behavior in lieu of technological or cultural solutions.

Biocultural adaptation and non-masticatory behavior

The use of "teeth-as-tools" as a "third hand" to assist the hands in manipulative behaviors has a long history of study in paleoanthropology (Koby 1956; Patte 1960, 1962; Brace 1962b, 1964, 1975; Coon 1962; Brose and Wolpoff 1971; Molnar 1972; de Lumley 1973; Wallace 1975; Frayer 1978; Wolpoff 1979; Trinkaus 1983). In many ways the use of teeth-as-tools has become a quintessential feature of Neandertal behavioral reconstructions[3]. The

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[2] Leslie White's (1959) classic definition of culture as "man's extrasomatic means of adaptation" is particularly apt in this context.

[3] Reconstructions of Neandertals engaging in non-masticatory behaviors have even appeared in television documentaries, permanent museum exhibits (The Spitzer Hall of Human Origins in the American Museum of Natural History has a classic reconstruction of a "Neanderthal Camp" depicting a seating woman gripping animal hide between her teeth and one hand while scraping the hide with a stone tool held in her free hand. Another

prominent place of non-masticatory behavior in discussions of Middle and Late Pleistocene human behavior is further emphasized in the extensive literature surrounding the *anterior dental loading hypothesis* (ADLH) which attempts to explain the apparent structural adaptations of the face, jaws, and anterior dentition among archaic humans and the reduction of these features in early modern humans in terms of non-masticatory loading (or lack thereof) of the anterior dentition.

The ADLH suggests that high magnitude and/or repetitive loading of the anterior dentition through the habitual use of teeth-as-tools provided a significant selective force in Neandertal craniofacial and dental evolution (Smith 1983b; Rak 1986; Demes 1987; Trinkaus 1987; Smith and Paquette 1989; Spencer and Demes 1993; Brace 1995; Le Cabec et al. 2013). The behavioral basis of the ADLH was provided by qualitative descriptions of the labially worn, rounded, and non-occluding anterior teeth in some older adult Neandertal fossils; documentation of stone tool-induced cutmarks on labial enamel of incisors and canines[4]; and the large, morphologically robust anterior tooth crowns and roots of archaic compared to modern human dentitions (Brace 1962b, 1964; Coon 1962; Smith 1983b; Trinkaus 1983; Smith and Paquette 1989; Cartmill and Smith 2009). However, more recent biomechanical analyses repeatedly show that Neandertals are unlikely to have been capable of producing higher magnitude bite forces or exhibit more efficient anterior bite force production than modern humans despite their seemingly elevated degree of anterior tooth use for manipulative

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reconstruction of Shanidar 1 displays him chewing hide cordage at the Gallo-Romens Museum, Tongeren, Belgium), and even popular culture via comic books (DC's Showcase Presents: Anthro, Issue #74 from 1968; Joe Kubert's TOR, Issue 1 of 6 from 2006).

[4] A result of behaviors frequently referred to as "stuff-and-cut" (Brace 1975) – see Chapter 2.

purposes (Antón 1990, 1994, 1996; Couture 1993; Dobson and Trinkaus 2002; O'Connor et al. 2005; Clement et al. 2012). Instead, many researchers suggest that the morphological evolution and differentiation of Late Pleistocene human craniofacial complexes are the result of neutral evolutionary processes (e.g., gene flow and genetic drift) and/or climatic adaptation rather than functional adaptations to non-masticatory anterior tooth-using behaviors (Antón 1994; Maureille and Houêt 1998; Hublin 2002, 2009; Franciscus 2003; O'Connor et al. 2005; Weaver et al. 2007; Holton and Franciscus 2008; Weaver 2009; Holton et al. 2011; Rae et al. 2011a).

Despite the extensive historical interest in understanding functional adaptation to anterior dental loading, research on non-masticatory behavior among Middle and Late Pleistocene humans has rarely observed the behavioral correlates of these behaviors from direct, quantitative analyses of the patterning of the dental wear in and of itself. Most detailed research focused on anterior dental wear as a means of addressing the ADLH is largely a product of efforts in the last decade. There are copious, qualitative descriptions of the degree and form of dental wear for particular archaic human fossils, but few studies that attempt quantification and comparisons across Neandertals and early modern humans (reviewed in Chapter 3). This is due in part to a historical tendency to focus on research questions that address morphological and functional adaptation to non-masticatory behaviors. The degree to which Neandertals or early modern humans engaged in non-masticatory behaviors was either assumed or thought to be testable from analyses of morphology – qualitative descriptions of anterior wear merely provided the reason to test hypotheses about biomechanical models of craniodental function or provide support for the ADLH more generally. Given past tendencies to value research approaches focused on craniodental morphology rather than the patterning of dental wear, much can be gained by refocusing attention on wear. Therefore, the direct study of dental wear will provide an independent assessment of the degree to which the teeth were used for manipulation in addition to providing information on the nuanced behaviors that produced particular wear features.

Furthermore, there is still no satisfactory explanation for why the demonstrably larger anterior dentitions of archaic humans were maintained in contrast to the drastic reduction of the anterior dentition in early modern humans. The magnitude and patterning of the manipulative shift in non-masticatory tooth use and its relationship to cultural transformations during the Late Pleistocene remains unclear due to conflicting conclusions in recent quantitative analyses of anterior dental wear, the paucity of direct comparisons between Neandertals and early modern humans, and the relatively small samples of early modern human fossils analyzed to date (when examined at all).

Analogy, extrapolation, and generalization: Issues of interpretation in paleobiology

> *"We know that variation is not constant through time, and that using extant models of variation as ''yardsticks'' against which we judge fossil samples is problematic. Yet, because we all (myself and colleagues included) work within a uniformitarianist paradigm, we must carefully consider the biases and assumptions inherent in this system, and clearly account for them – either in discussion or, when possible, in methodological design."* – Ackermann 2005:646

Ethnographic analogy is a necessary starting point for the study of non-masticatory behaviors. Generally, idiosyncratic wear features and consistent patterns of wear are attributed to non-masticatory behaviors through analogy with observed behaviors in the ethnographic present[5] (Molnar 1972; Barrett 1977; Milner and Larsen 1991; Alt and Pichler 1998; Erdal 2008; Clement et al. 2009b; Krueger and Ungar 2009; Fiorenza et al. 2011a; Molnar 2011; Berbesque et al. 2012; Clement and Hillson 2012; Krueger 2015; Stojanowski et al. 2016). In fact, instrumental cutmarks on the labial enamel of Neandertals (specifically, the La Quina 5 and Saint-Brais Neandertals) were first attributed to non-masticatory behaviors through the use of behavioral analogy from high-latitude hunter-gatherers (Koby 1956).

Comparative studies of hunter-gatherer behavioral diversity are used to build interpretive models to understand aspects of prehistoric foraging behaviors (Binford 2001) that go beyond the one-to-one correlation of ethnographically documented behaviors (e.g., “stuff-and-cut” activities – see Chapter 2) with a particular wear feature (e.g., labial cutmarks). These analogical and comparative frameworks are a central theme for many biocultural approaches to behavioral reconstructions. One method is to study the co-variation between particular behaviors and their reflections in aspects of human biology across multiple groups of hunter-gatherers from diverse climatic, ecological, and socioeconomic backgrounds. The patterning of variation in the comparative framework is then used to explore variation and patterning for variables of interest in prehistoric materials for which little is known.

Several comparative frameworks have been developed for the study of aspects of non-masticatory dental wear using skeletal material from ethnographic and Holocene collections that have well-documented contextual information (Lalueza-Fox 1992; Krueger and Ungar

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[5] The “ethnographic present” is used to denote the use of both historic documents and ethnographic studies occurring up until the present day. There are many issues created by the approach, the most obvious being the time averaging of decades or in some cases hundreds of years of historic accounts, but it is a largely inescapable fact in using the “present” as a means of understanding variation in the past (see discussion in Speth 2010)

2009; Fiorenza et al. 2011a; Krueger 2015), which have subsequently been used to explore and interpret non-masticatory variation among Pleistocene fossils (Krueger and Ungar 2012; Fiorenza and Kullmer 2013; Hlusko et al. 2013; El Zaatari et al. 2014; Fiorenza 2015; Krueger 2016). Dental microwear texture analysis (Krueger and Ungar 2009, 2012; Hlusko et al. 2013; El Zaatari et al. 2014; Krueger 2014, 2015, 2016) and occlusal fingerprint analysis (Fiorenza et al. 2011a, b; Fiorenza and Kullmer 2013; Fiorenza 2015) are particularly reliant on comparative analogical frameworks due in part to these technologically-innovative approaches only recently being applied to non-masticatory wear research. For instance, a recent publication (Krueger 2015) on microwear texture analysis refined previous interpretations of microwear variability among five bioarchaeological samples (Krueger and Ungar 2009) through the inclusion of six newly analyzed bioarchaeological samples. Continued refinement of interpretations is to be expected as these methodologies are continually used to study non-masticatory wear in additional samples.

While the above examples illustrate the utility of comparative approaches when inferring prehistoric human behavior, many problems still exist in using behavioral variation from the ethnographic present to understand behavioral variation in the Pleistocene (Kusimba 2005; Speth 2010). For instance, the extent to which the environments (or perceived marginality) of hunter-gatherers from the ethnographic present compare to the “pristine” environments Pleistocene humans lived in is widely debated (Marlowe 2005; Porter and Marlowe 2007; Speth 2010). So too is our ability to assess aspects of Pleistocene population demography through the use of population densities from ethnographic peoples with complex technologies that provide the means by which they can live in relatively high density populations (Speth 2010; Holliday et al. 2014; Gautney and Holliday 2015). Regardless of the numerous biases in the use of ethnographic literature, it is not without utility (Marlowe 2005; Speth 2010; Kelly 2013). However, the comparisons made between past and present hunter-gatherers regularly ignore or diminish important variability (behavioral, morphological, ecological, etc.) in order to simplify models to interpret the behaviors of Pleistocene peoples (see Owen 2005; Hardy 2010). Approaches that ignore the historical contingencies influencing social, cultural, and technological axes of variation in behaviors of individuals and groups relegate hunter-gatherers as little more than relicts of a stone age past.

The study of the origins of “behavioral modernity”, almost without exclusion, relies on the ethnographic record of recent hunter-gatherers as a starting point from which to test hypotheses related to the emergence of a supposed suite (or laundry list) of characteristics that apparently denote modern behavior (for a thorough review of research on the "origin of behavioral modernity" and a refutation of its basic tenets see: Villa and Roebroeks 2014; Roebroeks and Soressi 2016). General adherence to linear evolutionary models of hominin behavior characterize studies of behavioral modernity, but there is also a problem in conflating behavioral modernity with *behavioral variability* – only the latter is observable and testable using the archaeological record (Shea 2011; Langbroek 2012, 2014).

The use of trait lists to assess modernity or studying actual behavioral variability will be affected by the inherently imperfect resolution of the archaeological record of past human behaviors. However, the way in which the presence, absence, or degree to which a behavior is represented in the past compared to observations in the ethnographic present can be, and is, interpreted in a number of ways. For instance, ethnographic analogy was used as a starting point to evaluate archaeological evidence for the emergence of the division of labor (a "modern" behavior) in the Late Pleistocene (Kuhn and Stiner 2006:954):

> *"Generalizations about recent hunter-gatherers are most helpful when they reveal points of discordance between what we expect from historical experience and what seems to have gone on during the Pleistocene. In other words, models developed from data on recent hunter-gatherers are most informative precisely when they prove to be inadequate predictors of patterns encountered in the Paleolithic record. Where they fail to account for what we know about earlier hominins, modern human analogs show us more specifically how our ancestors were not like us and what we need to explain about human evolution."*

This approach is not unlike what Wobst (1978:303) coined "ethnography with a shovel" or the "tyranny of the ethnographic record" whereby evidence from ethnography is fitted to observations in the archaeological record. The difficulty (and some might say impossibility) of determining the point in prehistory when the archaeologically observed behaviors of hunters and gatherers coalesce with the behavioral repertoire of foragers from the ethnographic present (Kuhn and Stiner 2001; Kusimba 2005; Kelly 2013) is reason enough to use such approaches with extreme caution. But, we must also consider that behaviors found in the ethnographic present may be very recent innovations (Marlowe 2005; Speth 2010); or that the limited number of ethnographic examples of hunting and gathering behaviors may not encompass the complete range of variation that was present in the past (Lieberman et al. 2007; Kelly 2013). This is especially relevant when dealing with the time depth of the Pleistocene and possibility of human adaptation to no-analog paleoecological conditions.

Generalizations are no less common when a comparative framework to interpret paleobiological data is based on human skeletal material from ethnographically documented groups, or Holocene skeletal material with a high-resolution archaeological context for past behaviors. It is common practice to interpret data from a particular individual or sample as representative of an entire chronologically, geographically, or morphologically defined fossil group. This latter issue is directly relevant to the research goals of this thesis and is discussed using an example derived from recent literature on instrumental cutmarks on the labial surfaces of anterior teeth.

Instrumental striations, or “cutmarks” on the labial surfaces of anterior teeth are incurred when the teeth are used like a vise to hold materials (e.g., meat or hide) while cutting the item with a stone tool close to the mouth. Incidental contact between the stone tool and enamel is not uncommon and leaves characteristic cutmarks on the labial enamel (Chapter 2). The use of teeth-as-tools for this kind of “stuff-and-cut” behavior has recently been used to test hypotheses about aspects of visuospatial integration among archaic and modern humans (Bruner and Lozano 2014b, 2015; Bruner and Iriki 2016; Bruner et al. 2016). Bruner and Lozano (2014b, 2015) have proposed that morphological differentiation in the archaic and modern human brains (attributed to the apparent expansion of the parietal lobes in the latter group) has left archaic humans with a mismatched, or impoverished, form of visuospatial integration. The ubiquitous presence of cutmarks on the incisors and canines of archaic *Homo* from Sima de los Huesos (a proposed ancestor of Neandertals: [Arsuaga et al. 2014]) and Neandertals is starkly contrasted by the percentage of individuals (46%) with cutmarks on their dentitions in a comparative group of Australian Aboriginal hunter-gatherers. They see the low frequency of this particular manipulative behavior among modern humans as evidence for a less intensive use of the body for manipulation among *Homo sapiens* – or evidence of superior visuospatial integration. Archaic *Homo,* with 100% of individuals exhibiting evidence of stuff-and-cut behaviors, are viewed in a different way. As stated by the authors (Bruner and Lozano 2014b:276):

> *“Taking into consideration the evidence of a specific increase in the use of teeth for handling functions in the Neandertal lineage, we hypothesize that these species may have suffered a mismatch between cultural and neural complexity, in which additional anatomical elements were involved as a body interface to overcome insufficient visuospatial integration processes.”*

This study will be considered again later (Chapter 7), but the important issue in this discussion is an underlying assumption about the modern human comparative sample. The authors are attributing cutmark prevalence from a single sample of recent Australian Aboriginal hunter-gatherers to the entirety of *Homo sapiens* (Bruner and Lozano 2014b, 2015; Bruner and Iriki 2016; Bruner et al. 2016). The primary problem with a generalization of this sort is that it implies behavioral equivalence across a morphologically defined group, *Homo sapiens*, without taking into account issues of temporospatial or technocultural variation. Without any additional qualifier, the use of “*Homo sapiens*” implies that the inferred difference in cognition, based on the prevalence of instrumental striations on the teeth of archaic humans and Australian Aboriginals, is a difference that can be extrapolated to all *Homo sapiens* from the Late Pleistocene to present day. Other explanations for differences in instrumental striation prevalence between the archaic human and Australian Aboriginal samples will be discussed in Chapter 7. It should be noted that the hypothesis put forth by Bruner and colleagues (Bruner and Lozano 2014b, 2015; Bruner and Iriki 2016; Bruner et al. 2016) is testable with new data, and that no comparative data on early modern human instrumental striations had been published when the hypothesis was first formulated.

The assumption that the behavior of the earliest modern humans can be attained from the analysis of skeletal materials from the recent past is not uncommon in paleoanthropological research. Many paleoanthropologists still adhere to the outdated notion that "behavioral modernity" is attributed to "anatomical modernity" which assumes that the behaviors of recent hunter-gatherers can be unquestionably used as a proxy for the behaviors of *Homo sapiens* in the distant past. It is important to remember that there are a number of uncertainties about the degree to which hunter-gatherers of the ethnographic present are representative of Pleistocene foragers given the incredible degree of change that has taken place in socioeconomic and technocultural organization since the Pleistocene – much of which has taken place recently (Kuhn and Stiner 2001; Kusimba 2005; Marlowe 2005; Speth 2010; Kelly 2013). Common issues of interpretation are succinctly stated by Kusimba (2005:354):

> *"More broadly, though, a research agenda driven by identifying hunter-gatherers either in general or with reference to ethnographically known groups misses the goal of understanding ancient ways of life in and of themselves and sets up a circularity of interpretation where the nature of the society in question is assumed from the start. Modern hunter-gatherers are contrasted against their opposites—against the archaic or against the farmer—even though the features that distinguish them are unclear. […] The consensus view has been to retain the concept of the hunter-gatherer but to emphasize its diversity."*

Thus, the above review illustrates the need for critical evaluations of the use of ethnographic comparisons in paleoanthropology, broadly speaking. A focus on behavioral variability, in the past and present, is one way of avoiding these common interpretative pitfalls. However, through research design we can also avoid problems of uniformitarian comparative frameworks (see opening quotation for this section). For instance, this thesis makes use of ethnographic comparisons to illustrate the range of behaviors that produce non-masticatory wear features among hunting and gathering peoples (see Chapter 2), but the interpretation of Pleistocene behavioral variability is based on paleobiological data derived directly from Middle and Late Pleistocene human fossils. Thus, the interpretations of behavioral variation in this thesis are not reliant on an assumption that behavioral variation in the ethnographic present is, or is not, representative of behavioral variation of morphologically or chronologically defined groups of Middle and Late Pleistocene humans.

Research questions

Despite a long history of research and interest in non-masticatory behaviors among Middle and Late Pleistocene archaic humans, comparatively little is known about the use of teeth-as-tools among early modern humans. There are few direct studies of early modern human fossils, but it is generally assumed that modern humans engaged in manipulative behaviors involving the anterior teeth to a lesser extent than archaic *Homo* and late archaic Neandertals. Several recent studies have addressed variation in non-masticatory dental wear among Neandertals and early modern humans (Krueger 2011; Clement et al. 2012; Fiorenza and Kullmer 2013), but these studies are driven by relatively recent methodological approaches, and are not directly comparable to previously published data on Middle and Late Pleistocene archaic humans.

As outlined above, a major shortcoming of previous research on non-masticatory behavior has been a lack of focus on early modern human fossils or the use of Holocene samples as proxies for early modern human behavioral variability. This issue is easily rectified through the inclusion a large sample of early modern human fossils in the present study (see Chapter 4). Thus, the behavioral variation studied here is a direct representation of Middle and

Late Pleistocene human paleobiology. A biocultural approach to non-masticatory behavior is adopted to explore the degree to which Pleistocene humans relied on the anterior dentition for manipulative behaviors. The null hypothesis addressed in each analysis is:

> *H_0: There are no significant differences in anterior tooth-use between archaic Homo and Neandertals compared to early modern humans.*

And three main sets of questions will be addressed in relation to the null hypothesis:

1. *Are differences in anterior tooth use for manipulative behavior evident across morphologically defined or temporally partitioned groups of Middle and Late Pleistocene humans? If so, what is the magnitude or degree of change in the behavioral shift?*
2. *To what degree can anterior dental morphology be attributed to functional adaptations to the high magnitude and/or repetitive loading of the dentition through non-masticatory behaviors?*
3. *To what extant does the presence of labial cutmarks on the anterior dentition differ across morphologically defined and temporally partitioned groups of Middle and Late Pleistocene humans?*

These questions will be addressed through direct assessment of dental wear related to the degree of wear (macrowear gradients), magnitude of bite forces (chipping), and a particular form of wear (labial cutmarks) to explore patterns of anterior tooth-use for manipulative behaviors among Middle and Late Pleistocene humans. The results will be used to comment on hypotheses of craniofacial and dental adaptation to non-masticatory behavior among Middle and Late Pleistocene humans with a particular emphasis on patterns of anterior dental reduction in the Pleistocene.

Thesis outline

Chapter 2 presents a brief review of the mechanisms that cause dental wear and the biological factors that must be taken into account when studying dental wear.

Chapter 3 addresses issues of dental functional morphology and wear that are directly relevant to the topic of non-masticatory behaviors during the Middle and Late Pleistocene. A thorough review of research on non-masticatory dental wear assessed from Middle and Late Pleistocene fossils is presented.

Chapter 4 introduces the human skeletal materials used in all analyses and provides a rationale for the subgrouping of the fossils for analyses. A brief synopsis of the methods used to clean, mold, cast, and prepare dental specimens for scanning electron microscopy (SEM) is also presented. The methods used for each stand-alone analysis are provided in their respective analysis chapters.

Chapter 5 is concerned with macroscopic occlusal wear gradients scaled to buccolingual crown dimensions. The analysis is focused on understanding how anterior relative to posterior dental wear varies among and between groups and what this says about the degree to which groups differentially engaged in anterior tooth use. The importance of crown size is emphasized.

Chapter 6 emphasizes aspects of anterior dental loading by analyzing enamel chipping and fracture found on incisors and canines. The simple premise is that a higher frequency of chipping is related to more frequent loading of the anterior teeth and contact with hard objects. The size of chips reveals insights into bite forces exerted to fracture the enamel. This chapter is a compliment to the analysis of degree of wear established in Chapter 6.

Chapter 7 examines the presence of stone-tool induced instrumental striations/cutmarks on the labial enamel of maxillary central incisors. A single tooth type is used to ensure that comparisons are made between equivalent data – a point that was not always considered in previous research. This chapter is aimed at understanding whether early modern humans used their dentitions for “stuff-and-cut” behaviors that are ubiquitous among archaic *Homo* and the Neandertals.

Chapter 8 discusses the results of each analysis in detail and frames them within the current knowledge of manipulative behavior in the Middle and Late Pleistocene, functional adaptation, and cognition. A conclusion follows.

Chapter 2. An introduction to dental wear

Introduction

This chapter focuses on the definition and mechanisms of dental wear. A discussion of dental development, eruption, and dentoalveolar compensatory mechanisms to dental wear throughout the lifetime are presented to illustrate the universality of dental wear among different groups of Pleistocene humans. Dental wear is a complex process with many causal factors and influences interacting to produce an overall degree of wear as well as distinct dental wear features that can be attributed to certain types of behaviors – such as manipulative tasks related to the use of teeth-as-tools. This chapter introduces the basic concepts and terminology for describing, discussing, and understanding the progressive dental wear and mechanisms that produce wear; the biological factors that influence dental wear patterning and their similarities and differences among Late Pleistocene humans; the environmental influence on dental wear; how the anterior teeth are used for both dietary and non-masticatory, manipulative behaviors; ethnohistoric examples of the use or teeth-as-tools; and finally, a discussion of individual dental wear features that are often attributed to manipulative behavior (albeit, sometimes overlapping with dietary behaviors). The chapter ends with a discussion of anterior dental wear as a palimpsest of ingestive/dietary and non-masticatory/manipulative behavior and suggests a multifactorial approach to understanding the human use of teeth-as-tools for manipulative behaviors in prehistoric contexts.

Some functional characteristics of Middle and Late Pleistocene human dentitions may have evolved through natural selection to compensate for high rates of wear or a high prevalence of certain types of wear (e.g., chipping or fracture). Likewise, selection for certain characteristics may be relaxed through altered behavioral and technological change. Dental loading also has functional implications for the evolution of craniofacial morphology in the Pleistocene. Thus, the discussion of dental wear in this chapter will ground the discussion of the relationship between tooth-use and functional morphological in Chapter 3.

Dental tissues

Teeth are composed of four primary tissues: enamel, cementum, dentin, and pulp. The enamel crown is the most mineralized of these tissues, largely composed of hydroxyapatite, making it both hard and brittle. While the hardness of dental enamel is often stressed in the literature, it is becoming apparent that enamel toughness is also of consequence, especially as research moves forward to understand the relative influence of wear resistance versus fracture resistance related to the evolution of enamel material properties (Lucas et al. 2013, 2016; Lucas and van Casteren 2015; Ungar 2015; Xia et al. 2015; Constantino et al. 2016). Deep to, and less mineralized than enamel, is dentin with soft-but-tough physical properties. The pulp is the living tissue surrounded by dentin that contains the nerves and blood vessels that feed the tooth. As wear progresses from the enamel to the dentin, odontoblasts in the pulp will deposit secondary dentin and protect the receding pulp chamber. If the rate of wear proceeds beyond the rate at which secondary dentin is deposited, the pulp chamber may become exposed (**Figure 2.1**) and infection is probable (Larsen 2015). Any inflammation due to pulp exposure is referred to as *pulpitis* (Soames and Southam 2005). The third calcified dental tissue is the thin layer of cementum that surrounds the entire root surface. Periodontal ligaments attach to the cementum and anchor the tooth to the alveolar bone. The proportions of these tissues in Middle and Late Pleistocene humans and their influence on dental wear will be discussed in Chapter 3.

Figure 2.1 Marked occlusal attrition and exposed pulp chambers.
Occlusal view of anterior maxillary dentitions of La Ferrassie I (top) and Shanidar 1 (bottom) Neandertals with red arrows indicating teeth with exposed pulp chambers. The right I^2 and C^1 were incorrectly reconstructed for La Ferrassie I and their positions should be switched. Photographs by Erik Trinkaus.

Dental wear basics: attrition, abrasion, and erosion

Dental wear is the cumulative loss of dental tissue volume throughout the life of an individual caused by the movement of two or more textured surfaces against each other. Friction occurs because no surface is completely smooth although surface asperities may be imperceptible without the aid of high-resolution microscopy. Dental wear begins at the damage-tolerant and wear-resistant enamel surface before progressing to the softer-but-tougher dentin (Chai et al. 2009; Lawn et al. 2010). The loss of dental tissue is primarily a microscopic process (Lucas et al. 2013), and the accumulation of microscopic wear is observed macroscopically as enamel polishing or faceting and eventually as the exposure of underlying dentin. The ratio of enamel to dentin has wide applicability in mammalian paleobiology and is widely used in paleoanthropology and bioarchaeology to assess dietary habits, individual ages-at-death, and cultural behaviors (Miles 1963; Molnar 1971; Scott 1979; Smith 1984; Lovejoy 1985; Clement et al. 2012; Gilmore and Grote 2012). Dental wear has been traditionally described in terms of attrition, abrasion (both masticatory/dietary and non-masticatory/manipulative), and erosion in the anthropological literature – to which some researchers add dental fracture (e.g., Kaidonis et al. 1993). It should be noted that it has become increasingly common for researchers to adopt terminology derived from *oral tribology* (tribology is the study of wear, friction, and lubrication) to describe the underlying mechanisms that produce particular patterns of dental wear (Mair 2000; Zhou and Zheng 2006; Mair and Padipatvuthikul 2010; d'Incau et al. 2012; d'Incau and Saulue 2012; Lucas and Omar 2012). This summary will largely focus on the general, descriptive terms common in the anthropological literature, and while oral tribology terminology is not explicitly adopted here it will be used to illustrate the mechanisms that cause wear as needed.

Attrition: Attrition[6] is a form of abrasion caused by tooth-to-tooth contact and is evident by smooth, shiny wear facets, with clearly delineated edges, on the occlusal surfaces of opposing maxillary and mandibular teeth (d'Incau et al. 2012). Microscopic striations occurring in parallel orientation to each other are often found within the borders of attrition facets (Kieser et al. 2001; Kaidonis 2008). Attrition facets have clinical relevance in that they assist in the diagnosis of departures from ideal occlusion and bruxism[7] (Kaidonis et al. 1993; De Luca Canto et al. 2013). The dynamic nature of dental wear throughout the life of an individual leads to changes in shape, size, or visibility of attrition facets as dental wear progresses, human behavior changes, or other factors, like abrasive load, change (Kaidonis et al. 1993).

Attrition also occurs at the interproximal (also referred to as approximal or interstitial) contacts between adjacent teeth in an arcade (**Figure 2.2**). At a gross level, interproximal contact facets are also characterized by a smooth, shiny appearance with strongly defined facet boundaries and variable facet curvature. Microscopically, interproximal contact facets have a roughened texture caused by the accumulation of small pits and the absence of any striations (Pérez-Pérez et al. 2003). The size and shape of an interproximal contact facet changes with progressive interproximal and occlusal wear (Deter 2012), and can lead to substantial reduction in the mesiodistal length of a tooth (Begg 1954; Wolpoff 1971b). Both anterior and posterior

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[6] There is some confusion surrounding the use of the term attrition since it is often used as a synonym for generalized loss of tooth volume through cumulative crown wear. However, others will use a strict definition of attrition to designate wear derived from tooth-to-tooth contact only. This latter definition is what is being defined above.

[7] Bruxism is the "repetitive jaw-muscle activity characterized by clenching or grinding of the teeth and/or by bracing or thrusting of the mandible" (Lobbezoo et al. 2013:3) that results in characteristic attrition facets.

teeth tilt mesially when subjected to loads (Picton 1962) and interproximal contact facet formation is generally attributed to the mesial movement of adjacent teeth as they are subjected to occlusal forces – dietary or otherwise (Osborn 1961; Wolpoff 1971b; Kaidonis et al. 1992).

Figure 2.2 Marked interproximal wear.
The Tabun C1 right I^1-left I^2 (top) and the Tabun C1 right P$_3$-M$_1$. The lateral edge of the left I^2 has a postmortem enamel spall.

Some interproximal contact facets display small furrows or channels, known as subvertical grooves (Kaidonis et al. 1992; Villa and Giacobini 1995a; Estalrrich et al. 2011), but the ultimate cause of their formation remains unclear (**Figure 2.3**). Interproximal contact facet morphology has recently proven useful in the analysis and association of teeth that are found mixed within archaeological sites rather than *in situ* within the jaws or distinct contexts (Benazzi et al. 2011a; Rosas et al. 2013).

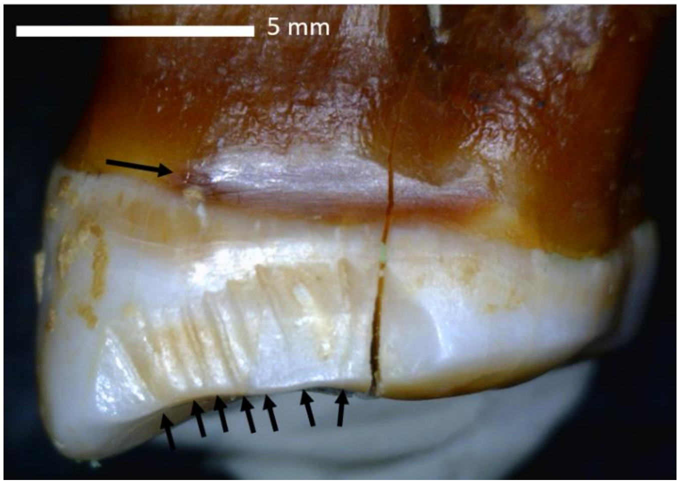

Figure 2.3 Subvertical grooves on an interproximal contact facet (mesial view). Neandertal (N31 from Feldhofer, Germany) right M^2 surface showing multiple subvertical grooves or furrows. Upper arrow is pointing to an interproximal “toothpick” groove (discussed below).

Abrasion: Abrasive wear occurs when teeth are in contact with exogenous material – generally particles contained in food (Mair and Padipatvuthikul 2010; d’Incau et al. 2012), but also other materials that are manipulated with, or come into contact with, the dentition (e.g., cordage, sinew, toothpicks, pipe stems, arrow shafts, labrets, etc.). Mastication breaks down the bolus and creates microscopic pits and scratches on tooth surfaces. The orientations of the striations are generally “cross-hatched” and random in contrast to the parallel striations formed through attrition (Kieser et al. 2001; Kaidonis 2008). The size, shape, and hardness of the particles introduced with the bolus influence the density and size of microscopic pits and scratches on tooth surfaces (d’Incau et al. 2012). These pits and scratches are commonly referred to as microwear and are analyzed by paleoanthropologists and bioarchaeologists to reconstruct the diets of human and non-human primates (Teaford 2007). Dietary abrasion also has distinctive macroscopic signals. With high levels of dietary abrasion, the soft, exposed dentin is preferentially worn away, leaving an enamel rim that forms a “cupped” occlusal surface (Molnar 1971; Kaidonis 2008). Importantly, the enamel rim and cupped dentin remain decorated with randomly oriented striations further illustrating dietary abrasion. Abrasive wear caused by non-dietary objects and manipulative behaviors can produce many distinctive wear features which will be discussed subsequently.

Erosion: Erosion is caused by the presence of acid in the mouth that dissolves tooth surfaces. The exposure to oral acids can be voluntary (dietary) or involuntary (e.g., the regurgitation of stomach acid or the presence airborne acids in some occupational settings) (Johansson et al. 2012). Erosion is identified by cupped surfaces with rounded, but non-striated, edges (d'Incau et al. 2012). Erosion is well known in clinical cases (Johansson et al. 2012) but remains relatively rare in human groups prior to the introduction of a heavily processed, "Westernized" diet (Kaidonis 2008). Erosion has also been successfully characterized and differentiated from other forms of wear using microwear texture analysis (Hara et al. 2016). Oral bacteria subsisting on food particles in the mouth produce acids that dissolve dental tissues (Temple 2016); however, this is not generally discussed in terms of dental wear.

Mechanisms that cause dental wear: Materials that are as hard as or harder than enamel (and dentin) will initiate wear. As discussed above with respect to attrition, tooth-to-tooth contact can cause enamel wear as can dentin-to-dentin, or enamel-to-dentin contact given the tissues are as hard as, or harder, than each other. Environmental grit and dust, namely quartz, is another commonly cited cause of dental wear (Jardine et al. 2012; Lucas et al. 2013; Wood 2013; Damuth and Janis 2014). Silica phytoliths, the microscopic silicon dioxide bodies formed in plants, have long been thought to induce dental wear as well (Walker et al. 1978; Teaford 1988; Ciochon et al. 1990; Lalueza-Fox et al. 1994, 1996; Ungar 1994; Gügel et al.

2001; Reinhard and Danielson 2005; Rabenold and Pearson 2011, 2014), but recent experimental studies challenged this assertion (Lucas et al. 2013, 2014). Lucas and colleagues (2013) used nanowear experiments to perform controlled sliding of starch grains, enamel pieces, grass phytoliths, and quartz (sand) grains across flat enamel surfaces. Unsurprisingly, quartz and enamel induced wear (i.e., the chipping, fracture, or removal of material from a body) while starch grains did not (Lucas et al. 2013). On the other hand, sliding phytoliths across enamel only created “prows” in the enamel surface, and this displacement without the removal of enamel was termed “rubbing” as it did not conform to the classic definition of wear (Lucas et al. 2013).

The findings of Lucas and colleagues (2013) have been challenged on semantic grounds, but also with regard to the role that repetitive displacement through rubbing may contribute to accumulated wear over a greater length of time than is shown by individual nanoindentation events (Rabenold and Pearson 2014). Indeed, rubbing would change the surface texture, create additional microasperities, which increases friction and abrasive potential. Cumulative rubbing events could also contribute to fatigue wear (Zum Gahr 1987; d’Incau et al. 2012; d’Incau and Saulue 2012). Additional experiments by Xia and colleagues (2015) examined the removal of enamel by aluminum (which is softer than enamel) in microscale experiments and by silicon dioxide (i.e., phytoliths) in nanoscale experiments. The “piling up” of enamel debris found by Lucas and colleagues (2013) could be washed away with water which showed that the enamel had truly been removed after each sliding experiment (Xia et al. 2015). Others have contributed to the discussion and confirmed that even very modest microcontact events between an indenter and enamel in silica-slurry can remove (i.e., wear) enamel (Borrero-Lopez et al. 2014, 2015; Constantino et al. 2016).

The action of thousands of chewing cycles involving exogenous particles (grit, silicates, enamel fragments, etc.) contributes to microwear and eventually macrowear. By extension, repetitive non-masticatory behaviors that involve the manipulation of materials with the anterior teeth are expected to include abrasive particles that will contribute to micro and macrowear over time.

Finally, dentin is largely ignored in anthropological studies of (dietary) microwear because it does not display microwear features in the same manner as enamel due different biomechanical properties of enamel and dentin. Other studies concerned with non-masticatory, manipulative dental wear more commonly observe microscopic wear features on enamel *and* dentin (Ryan 1980b; Ryan and Johanson 1989; Lozano et al. 2008), but these studies are not as concerned with the causal mechanisms of dental wear at the microscopic level. It has been noted that experimental studies should move toward considering causal mechanisms of dentin microwear (Lucas et al. 2013). After all, a large portion of a long-lived primate's life will involve wear on exposed dentin.

Many dental wear studies cite wear as a limiting factor in the lifespan of primates and other mammals (see: Logan and Sanson 2002; King et al. 2005, 2012; Cuozzo and Sauther 2006), and thus understanding the mechanisms that cause enamel *and* dentin wear are of particular importance to understand the evolutionary adaptiveness of dentitions and their relationship to life history patterns and potential environmental mismatches. Dental size (larger molars) has been linked to increased fitness in mantled howler monkeys (DeGusta et al. 2003), but selection for resistance to wear in and of itself is understudied. Much research still needs to be done to link the causal mechanisms of dental wear with dental size, tissue proportions, and rates of wear before selective advantages can be determined for interspecies comparisons. Simulation studies are making progress in this direction and show promise in linking the microscopic removal of dental tissue to the accumulation of macroscopic wear over time (Borrero-Lopez et al. 2014, 2015; Constantino et al. 2016). In sum, the use of innovative methods, such as those described, that incorporate observations of wear from the nanoscale to the macroscale are revolutionizing the study of dental wear and its utility for reconstructing prehistoric behavior (Lucas et al. 2013, 2016; Borrero-Lopez et al. 2014, 2015; Lucas and van Casteren 2015; Ungar 2015; Xia et al. 2015; Constantino et al. 2016).

The multifactorial nature of dental wear: Attrition, abrasion, and erosion are rarely found in isolation; instead, they interact in complex ways to generate an overall pattern of dental wear related to physiological, mechanical, and cultural factors (Kieser et al. 2001; Addy and Shellis 2006; Kaidonis 2008; Mair and Padipatvuthikul 2010; Khan and Young 2011; d'Incau et al. 2012). However, there are distinctive characteristics of each of these forms of dental wear that allow researchers to determine the relative contributions of attrition, abrasion, and erosion to the overall pattern of dental wear.

The effects of dental eruption sequence and timing on dental wear

An understanding of the timing and sequence of dental crown formation and subsequent eruption is of particular interest in biological anthropology as a means of determining the relative age of immature fossil specimens as well as maturation rates. Dental crown formation is of little interest here as unerupted teeth are not subject to dental wear. However, the sequence and timing of permanent tooth eruption is of great importance for the understanding of dental wear gradients and age-related rates of wear.

Both the sequence and timing of dental mineralization and eruption include significant variation among and between individuals, sexes, and populations; although, there are three consistent phases for the timing and sequence of dental emergence for the permanent dentition in humans (Hillson 1996:140):

1. Around 5 to 8 years of age the incisors and first molars erupt.
2. Around 9.5 to 12.5 years of age the canines, premolars, and second molars erupt.
3. Around the late teens to early twenties the third molars erupt.

In general, mandibular teeth erupt earlier than their maxillary counterparts, and teeth that erupt more closely in time have more commonly reversed eruption sequences (modified from Hillson 1996:141; parentheses indicate common reversals in eruption sequence):

- Maxillary: $M^1 – I^1 – I^2 – (P^3 – C – P^4) – M^2 – M^3$
- Mandibular: $(M_1 – I_1) – I_2 – (C – P_3) – (P_4 – M_2) – M_3$

The pattern and sequence of dental mineralization and eruption is known to vary both within Late Pleisotcene humans and relative to Holocene human groups (BH Smith 1991; Tompkins 1996; TM Smith et al. 2007b; Bayle et al. 2009b, b, 2010; Guatelli-Steinberg 2009; Shackelford et al. 2012). Unfortunately, conclusions regarding the relative differences in pattern and timing of Neandertal and early modern human dental development are far from consensus given the paucity of younger individuals in the fossil record suitable for study and differences in methodology between studies. For example, some studies of incremental growth suggest that Neandertals have relatively rapid rates of growth relative to recent modern humans (Ramirez Rozzi and Bermúdez de Castro 2004; Smith et al. 2007a), while others suggest that incremental growth rates are within the recent human range of variation (Guatelli-Steinberg et al. 2005, 2007; Macchiarelli et al. 2006). Furthermore, the issue has been raised as to whether it is suitable to apply recent human developmental standards to immature Late Pleistocene fossils (Guatelli-Steinberg 2009; Shackelford et al. 2012). Despite the above disagreements there is some support for delayed mineralization of the incisors and third premolars relative to the molars in Neandertals compared to early modern humans and Holocene human groups, as well as evidence for the precocious eruption of maxillary and mandibular third molars among both Neandertals and early modern humans, all of which indicate that dental development continued to evolve since the Late Pleistocene (Tompkins 1996; Smith et al. 2007a; Bayle et al. 2010).

The above discussion on the sequence and timing of dental mineralization and eruption is a necessary prelude to the discussion of dental wear despite the rather intuitive conclusion: *earlier erupting teeth attain occlusion and are exposed to wear agents for a longer period of time than later erupting teeth*. When combined, dental eruption and dental wear gradients along a tooth row can be used to record the relative ages of deceased individuals (Miles 1963; Scott 1979; Lovejoy 1985; Brothwell 1989; Ubelaker 1989; Buikstra and Ubelaker 1994; Mays et al. 1995; Mays 2002), as well as to infer relative differences in diet and behavior within and between different groups (Molnar 1971; Smith 1984; Alexandersen 1988; Skinner 1997; Deter 2009; Clement et al. 2012). Diet, environment, and biological factors (e.g., such as tooth size, tissue proportions, and relative eruption sequences) influence the overall rates of attrition among groups, and therefore ages obtained from dental wear gradients are generally population-specific (and often most useful in bioarchaeological settings where large sample sizes are more common). However, most ordinal scales have relatively broad age categories (e.g., 8 ordinal values in the widely-used Smith 1984 system) which encompass several years of life in each category. The imprecise nature of ordinal scores is particularly useful when estimating age in fossil humans since biological "populations" are non-existent, and small fossil samples must be grouped into categories often defined by broad temporospatial criteria. However, the relative differences in eruption sequences (see discussion of dental tissue proportions in Chapter 3) between Neandertals, early modern humans, and Holocene human groups could affect interpretations of Late Pleistocene demography and life history that rely heavily on dental aging techniques (e.g., mineralization, eruption, and wear gradients). Nonetheless, most broad-range assessments of Late Pleistocene demography and life history generally focus on few age categories due to the obvious sampling limitations in the Pleistocene fossil record (e.g., Trinkaus 1995, 2011; Caspari and Lee 2004). Thus, criticism of the use of dental aging techniques for Late Pleistocene fossils (e.g., Smith et al. 2012) is largely unfounded due to the necessity of using broad age categories encompassing several, averaged wear categories.

Dentoalveolar compensatory mechanisms in relation to dental wear

Marked dental wear is a naturally occurring process that was ubiquitous in hominin evolution until relatively recently (Kaifu 2000b). Dental crowns decrease in height, breadth, and length as wear progresses and a series of skeletal compensatory mechanisms occur in the jaws to maintain efficient occlusion throughout the lifetime of an individual. Research encompassing the study of mismatches between high attrition oral environments in our evolutionary past and the generally low attrition oral environments of the present (and also including the study of shifts in oral pathology from prehistory to present) have been increasingly studied under the umbrella of “evolutionary dentistry”, or more generally, evolutionary medicine (Corruccini 1999; Kaifu et al. 2003; Rose and Roblee 2009; Gibbons 2012; Ungar et al. 2012; Benazzi et al. 2013). A description of the mechanisms related to progressive dental wear and maintenance of functional occlusion are discussed below.

Continuous eruption: Gottlieb (1927) first proposed that teeth continually erupt throughout the course of an individual’s lifetime, and this conjecture has been continually supported by studies from worldwide samples of human skeletal material dated to prehistoric and recent contexts (Murphy 1959a; Hylander 1977b; Newman and Levers 1979; Whittaker et al. 1982, 1985; Levers and Darling 1983; Varrela et al. 1989, 1995; Danenberg et al. 1991; Glass 1991; Kerr 1991; Margvelashvili et al. 2013), in clinical settings (Crothers and Sandham 1993), among the great apes (Dean et al. 1992; Villmoare et al. 2013), and other hominins (Martinón-Torres et al. 2011; Margvelashvili et al. 2013; Villmoare et al. 2013). This proposed compensatory mechanism is called *continuous eruption* (also commonly referred to as supereruption or supraeruption). The apposition of cementum at the root apices is thought to cause or co-occur with continuously erupting teeth (Hopewell-Smith 1920; Azaz et al. 1974, 1977; Levers and Darling 1983; Leider and Garbarino 1987). Three continuous eruption scenarios are generally agreed upon (Berry 1976; d’Incau et al. 2012):

1. The rate of continuous eruption closely approximates the rate at which occlusal crown height is lost through lifelong attrition. Functional occlusion is maintained without a significant loss of the occlusal vertical dimension or interocclusal space. This explanation is the most commonly cited scenario in anthropological studies of dry skeletal material. A distance greater than 2 mm between cementoenamel junction (CEJ) and the alveolar crest (AC) is generally taken as evidence of supereruption (Ogden 2008), but root exposure may not be present if healthy alveolar bone migrates with the supererupting teeth making continuous eruption difficult to assess without longitudinal or cross-sectional studies using methods that do not rely on root exposure (Kaifu et al. 2003).
2. Continuous eruption occurs with little occlusal attrition and increases the occlusal vertical dimension while maintaining a relatively constant interocclusal space. In this case, the alveolar bone migrates with the supererupting teeth. Again, this type of continuous eruption is only detectable in longitudinal studies (and to a lesser extent, cross-sectional studies) rather than measuring the distance between CEJ and AC (e.g., Whittaker et al. 1990).
3. Continuous eruption occurs at a slower rate than dental wear, typical of later stages of wear when the softer dentin is worn, and causes a decrease in occlusal vertical dimension and increase in interocclusal space. The presence of oral pathologies (e.g., periodontitis or periapical lesions) are common if this scenario occurs, making root exposure as an indicator of supereruption less reliable.

Continuous eruption is a difficult phenomenon to study given that it can be accompanied by essentially no root exposure, exceptional root exposure, or be associated with alveolar pathology. It is further complicated by the fact that many studies are concerned with periodontal disease *or* supereruption and each are often measured the same way (CEJ-AC height). If there is no root exposure, and there is healthy alveolar bone, there is no way to detect supereruption in anything but longitudinal or cross-sectional studies. One possible method of detecting continuous eruption in these cases could be addressed by assessing the position of molar roots relative to the inferior alveolar nerve canal (e.g., Margvelashvili et al. 2013), and/or examination of cementum deposition along root apices using radiographs or computed microtomography methods.

An interesting case of supereruption with migrating alveolar bone comes from instances of *ablation* – the practice of removing anterior teeth for symbolic, ritual, medicinal, and other cultural motives that often expresses aspects of social identity (Stojanowski et al. 2014; Willman et al. 2016). In cases of maxillary incisor ablation the unopposed mandibular incisors continually erupt forming a pronounced occlusal "arch" (Humphrey and Bocaege 2008); but importantly, the mandibular alveolar bone generally remains healthy and migrates with the teeth revealing little to no root exposure (**Figure 2.4**). The antemortem loss of teeth also frequently leads to individual teeth supererupting as seen in the mandible of the Early Upper Paleolithic specimen Tianyuan 1 (Shang and Trinkaus 2010) (**Figure 2.4**). Clinical implant cases also provide strong support of continuous eruption of teeth adjacent to the static implants (Heij et al. 2005). Again, it is important to note that root exposure is not seen in the clinical cases unless related to pathology; instead, supereruption is documented through studies capable of determining facial height growth or in comparison to implants.

Finally, one clinical study showed that continuous eruption is accompanied by other compensatory changes in anterior occlusion, which include a shift from incisor over-bite to edge-to-edge occlusion along with some increase in mandibular incisor prognathism (Crothers and Sandham 1993).

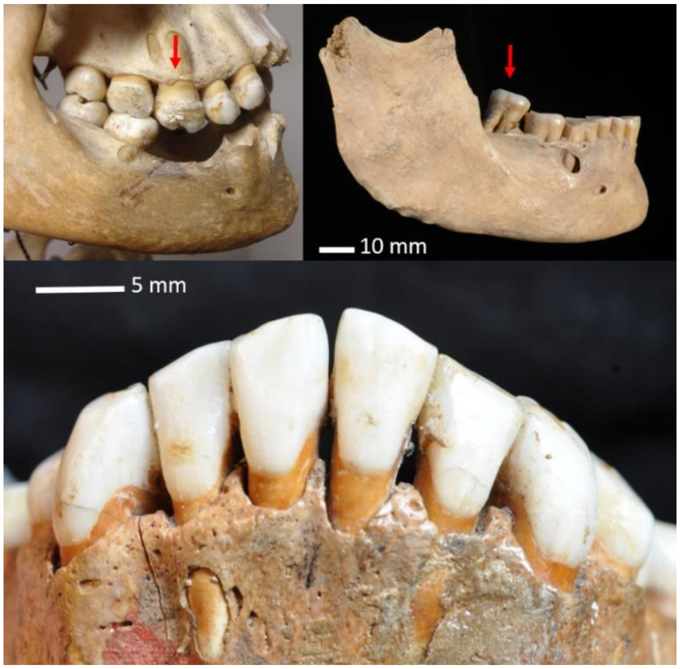

Figure 2.4 Examples of supereruption.
Top left: recent anatomy collection specimen showing antemortem loss of the left M_1 and supereruption of unrestricted M^1. Top right: Tianyuan 1 early modern human showing supereruption similar to specimen on left (photo by Erik Trinkaus). Bottom: Late Upper Paleolithic individual from Afalou showing compensatory supereruption of the incisors due to maxillary central incisors ablation (maxilla not shown). Slanted wear is also common.

***Mesial drift*:** The mesial migration of the dentition occurs in conjunction with the loss of dental tissue at the interproximal spaces (Kaifu et al. 2003; d'Incau et al. 2012). Histological examination shows resorption of alveolar bone mesial to each tooth and apposition distal to each tooth (Saffar et al. 1997), and distal cementum apposition matches mesial drift (Dastmalchi et al. 1990). The mesial drift of the dentition, as well as a concomitant decrease in total arch length, has been investigated substantially in prehistoric and recent human groups through the analysis of dry skeletal materials and contemporary clinical studies (Begg 1954; Beyron 1964; Murphy 1964; Wolpoff 1971b; Fishman 1976; Hylander 1977b; Hinton 1982; Corruccini 1990; Nara et al. 1998; Watanabe et al. 1998; Deter 2012). Mesial drift is typically discussed in relation to the postcanine dentition while incisor lingual tilting (discussed below) is the mechanism more often cited for maintaining close proximity between the anterior teeth.

However, the maintenance of tight, mesiodistally abutted teeth often does not occur in individuals with exceptional dental wear (i.e., Smith [1984] scores 7-8), especially in the anterior teeth (but see *incisor lingual tilting* below), where small spaces are present between adjacent tooth roots (Willman, personal observation) (**Figure 2.5**). A possible explanation is that heavily worn teeth are more frequently found in older individuals and the aging of osteoblasts, osteoclasts, and osteocytes impairs function of these cells or leads to cell death (for a discussion of cell aging in bone see: Boskey and Coleman 2010); and thus diminish the capacity for normal apposition and resorption associated with mesial movement. A second explanation is that the rate of dental wear increases with the exposure of the softer dentin and the rate of wear progresses more quickly than the rate of alveolar bone resorption and apposition associated with mesial drift can occur. These two explanations need not be mutually exclusive.

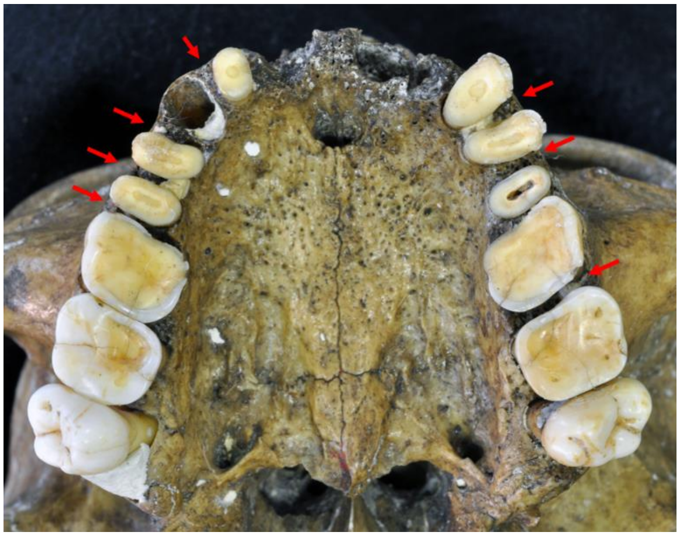

Figure 2.5 Interdental spaces formed through excessive occlusal wear.
Palate of Ortucchio 1 (Late Upper Paleolithic, Italy). Red arrows indicate spaces between teeth that fail to close through mesial drift. It is most likely a product of an extreme rate of occlusal wear. Missing teeth were lost antemortem despite extensive alveolar pathology.

Incisor lingual tilting and anterior occlusion: As progressive interproximal and occlusal wear occurs throughout a lifetime, the anterior teeth maintain tight contacts at the interproximal spaces through a process of mesial drift and lingual tilting (also referred to as posterior tipping) whereby the anterior teeth obtain a more axial orientation. The process has been documented in many skeletal collections and clinical settings of individuals with little wear to individuals with extensive wear (Lundström and Lysell 1953; Lysell and Filipsson 1958; Hasund 1964; Hylander 1977b; Forsberg 1979; Seddon 1984; Krogstad and Dahl 1985; Varrela 1990; Johansson et al. 1993; Crétot 1997; Kaifu 2000a), as well as among the great apes (Dean et al. 1992; Villmoare et al. 2013), and some hominins (Margvelashvili et al. 2013; Villmoare et al. 2013).

Changes in anterior occlusion occur in conjunction with progressive occlusal wear and lingual tilting. In unworn, normally occluding anterior teeth, both overjet and overbite are greater than zero resulting in a slight overlap of the maxillary anterior teeth over the mandibular anterior teeth in "scissors occlusion" (Reinhardt 1983a; Kaifu 1996). As the anterior teeth undergo further wear and axial inclination, overbite will become zero and overjet will continue to diminish producing "edge-to-edge" occlusion (Reinhardt 1983a; Kaifu 1996). Scissors occlusion is evident in the deciduous dentition of the Roc du Marsal infant (Madre-Dupouy 1992:111), the mixed dentition of the Teshik Tash child (Weidenreich 1945:163), and the slightly worn dentition of Le Moustier 1 (Thompson and Illerhaus 1998:653-5; Ponce de León and Zollikofer 1999:481-2). The development of edge-to-edge occlusion through progressive wear and compensatory mechanisms occurs by the same means in both Neandertals and modern humans, and thus occlusal differences cannot be a cause of distinct dental wear patterns among or between these groups. These lifelong changes in incisor procumbency through wear and lingual tilting have also been documented through the analysis of incisor beveling angles in recent humans, Late Pleistocene humans, *Paranthropus robustus,* and *Australopithecus africanus* (Ungar and Grine 1991; Ungar et al. 1997).

Hypercementosis: Many possible scenarios have been presented for the apposition of tooth root cementum beyond normal physiological limits, generally referred to as hypercementosis (Pinheiro et al. 2008; d'Incau et al. 2015). Recent research has lent support to the idea of "compensatory hypercementosis" to repeated or high levels of stress on tooth roots due to masticatory and non-masticatory behaviors (Pedersen 1949; Le Cabec et al. 2013). However, hypercementosis co-occurs with heavy attrition (Gardner and Goldstein 1931;

Comuzzie and Steele 1989; Trinkaus et al. 2008), periodontal disease (Corruccini et al. 1987; Comuzzie and Steele 1989; Bosshardt and Selvig 1997; Pinheiro et al. 2008; Martinón-Torres et al. 2011; Zhou et al. 2012), occlusal stress (Thomas 1921; Gardner and Goldstein 1931; Corruccini et al. 1987; Comuzzie and Steele 1989), and continuous eruption (Hopewell-Smith 1920; Kronfeld 1938; Azaz et al. 1974, 1977) among other influences (Pinheiro et al. 2008). With the exception of periodontal disease all of the above factors are also influenced by age, further complicating simple associations between prevalence and etiology. While hypercementosis does appear to indicate physiological compensation for repetitive or heavy loading of the dentition in some cases, periodontal disease is also a plausible cause, and caution should be taken when interpreting the etiology of hypercementosis for isolated teeth, since the alveolar bone is necessary for determining periodontal status.

Compensatory mechanisms summary: Compensatory mechanisms, related to the maintenance of ideal occlusal relationships with progressive wear, are well documented in clinical and skeletal analyses of recent humans. Continuous eruption, mesial drift, and lingual tilting are particularly well understood; and the role of normal cementum remodeling and hypercementosis has become better understood in recent years. Several studies have greatly expanded our knowledge of compensatory mechanisms beyond recent human samples, and it is now becoming clear that these mechanisms are also at work among the great apes (Dean et al. 1992; Villmoare et al. 2013), australopithecines and paranthropines (Villmoare et al. 2013), and Early and Middle Pleistocene *Homo* (Martinón-Torres et al. 2011; Margvelashvili et al. 2013). Evidence of compensatory mechanisms in Late Pleistocene humans are also documented through individual cases of continuous eruption, maintenance of tight interproximal contacts in the presence of heavy interproximal and occlusal wear through mesial drift, and the indirect measure of lingual tilting through incisor beveling angles and anterior root functional morphology. Thus, there is no reason to assume that the physiological processes occurring with progressive dental wear among Neandertals, early modern humans, and recent humans would lead to anything other than differences in degree of wear and compensation rather than unique patterns of wear and compensation between groups.

Dental occlusal variation

Dental occlusal variation describes the position of individual teeth, spatial relationships between adjacent teeth, and form of contact between maxillary and mandibular teeth. Departures from "ideal" occlusion are generally referred to as "malocclusion", but such departures from ideal occlusion are so common in contemporary populations that it is more appropriate to discuss the spatial relationships between teeth in terms of "occlusal variation" in clinical discussions (Harris and Corruccini 2008). In fact, no less than 70% of American youths today exhibit some form of malocclusion (Proffit et al. 2007), and the percentage exceeds 50% among global populations consuming "Westernized" diets (see citations in: Corruccini 1991; Corruccini 1999; Larsen 2015). Environmental factors such as a shift from mechanically tough and/or wear-inducing diets widely cited as the primary cause of malocclusion in today (Corruccini 1991, 1999; Rose and Roblee 2009). While there is a genetic component that dictates the potential size of the jaws in adults (ones that would accommodate the entire dentition in ideal occlusion), it is the stimulation of jaws during development that will ultimately influence whether that potential is achieved (Corruccini 1991, 1999). Similarly, occlusal and interproximal wear can decrease tooth size in abrasive environments preventing malocclusion (Rose and Roblee 2009). The diets and non-masticatory behaviors of most hunter-gatherers and pre-industrial populations provided sufficient stimulation and/or abrasive loads to combat the contemporary problem of rampant malocclusion.

Examples of malocclusion or dental crowding among Archaic *Homo* are virtually unknown. A single mandible dentition from Krapina exhibits incisor crowding (Wolpoff 1979; Frayer and Russell 1987), and while premolar rotations are relatively common among Neandertals they are most likely of hereditary, rather than environmental, origin (Rougier et al. 2006; Willman et al. 2012). Interestingly, malocclusion is far more common in modern human fossils (although the frequency is far from that of post-agricultural and contemporary populations). Malocclusion has been documented in several Middle Paleolithic modern humans from Qafzeh (Sarig et al. 2013; Sarig and Tillier 2014, 2016), and dental crowding and malocclusion is becoming increasingly well-documented in Early Upper Paleolithic specimens (Hillson 2006; Trinkaus et al. 2014). Malocclusion is also noted in several Late Upper Paleolithic contexts (Anderson 1968; Angel and Kelley 1986; Kramar 2008; Willman et al. 2016), and rates appear to be higher than in earlier periods (Willman, personal observation).

The rarity of malocclusion among Late Pleistocene humans, and for that matter, most pre-industrialized populations suggests that its occurrence will have a negligible effect on the present analyses. Occlusal alignment may bias some analyses that rely on the identification of and functional interpretations of wear facets, but this is still a matter of debate (Sarig and Tillier 2014; Fiorenza and Kullmer 2015; Sarig and Tillier 2016). The crowding and misalignment of anterior teeth in the early modern human specimen Dolní Věstonice 15 may have contributed to the smaller amount of instrumental striations on the right I^2 compared to the remaining three maxillary incisors, but the instrumental striations were present nonetheless (Willman 2016). However, the analyses undertaken in this thesis should not be greatly affected by occlusal variation. Furthermore, tell-tale signs of malocclusion will be evident from the examination of abnormal attritional facets and can therefore be removed from consideration in particularly analyses as necessary (e.g., Sarig et al. 2013).

Environmental factors influencing dental wear

Environment is a particularly important factor in comparative dental wear studies of temporally and ecogeographically disparate human groups. In the simplest sense, environment dictates local food availability, locally adaptive technocultural strategies, and exogenous abrasive loads – there is also extensive interplay between these factors.

Ungar and colleagues (1995) were able to show that both quantity and particle size of exogenous grit varied by environment, position in canopy, and season at two study sites. Galbany and colleagues (2014) compared macrowear among forest-dwelling mandrills and savannah yellow baboons while controlling for age to show that the environmental quartz load was particularly important (it is higher in the mandrill environment) in the faster rate of dental wear in mandrills. While molar wear seems less affected, howler monkeys (*Alouatta palliata*) in areas with considerable volcanic ash contribution to exogenous environmental grit experience more extensive anterior dental wear than those in areas without volcanic ash (Spradley et al. 2016). Disturbed versus pristine habitats also contribute subtle differences to microwear, but the strength of the relationship is stronger in the more frugivorous capuchins (*Sapajus paella*) than folivorous Howler monkeys (*Alouatta belzebul*) in another study sample (Estalrrich et al. 2015). A study of incisor microwear in shrews (Withnell and Ungar 2014) with various diets and habitats found small but significant differences in microwear when controlling for diet (e.g., omnivory, faunivory, and insectivore) and habitat. The study also showed that shrews living in the same habitats but eating different diets had the strongest contrasts in microwear which suggests that controlling for habitat type will provide a better dietary signal (Withnell and Ungar 2014). Similar research on incisor microwear in rodents is beginning to tease out the effect of diet, habitat, and substrate on microwear signals for paleoecological reconstructions (Caporale and Ungar 2016).

An extreme example from contemporary settings has been documented in miners compared to white-collar workers (Enbom et al. 1985). Miners working more than 10 years had significantly more dental wear than miners with shorter work histories and white-collar workers illustrating the effect airborne dust can have on wear patterning (Enbom et al. 1985).

Controlled grouping of samples by location, ecogeography, and/or climate is increasingly common in dental wear studies. Many bioarchaeological and paleoanthropological studies show significant differences in dietary and non-masticatory behaviors as reflected in dental macro and microwear when controlling for environmental categories (Pérez-Pérez et al. 2003; El Zaatari 2008, 2010; Deter 2009; Krueger and Ungar 2009; El Zaatari et al. 2011, 2016; Fiorenza et al. 2011b; El Zaatari and Hublin 2014; Krueger 2015, 2016).

Non-masticatory, manipulative behavior and dental wear

The human dentition has long been considered to be an integral component of the mostly extrasomatic human tool-kit (Brace 1962b; Dahlberg 1963; S Molnar 1972; Larsen 1997; Clement et al. 2009a; P Molnar 2011), and ethnographic and ethnohistoric documentation of the use of teeth-as-tools to manipulate cultural artifacts is widespread. For instance, the Hadza (contemporary hunter-gatherers from Tanzania) are known to use their teeth to straighten arrow shafts, cut string, strip bark from branches, tighten bow strings, soften leather, fletch arrows, peel tubers, and preform stuff-and-cut behaviors (Woodburn and Hudson 1966; Woodburn 1970; Marlowe and Berbesque 2009; Berbesque et al. 2012). A similar range of behaviors are known among various groups of Kalahari hunter-gatherers (Marshall and Gardner 1957; Marshall 1971) (**Figure 2.6**).

Similarly, aboriginal Australians straightened spear shafts, softened sinew, and stripped bark with their dentitions; but also used their teeth to retouch stone tools, sharpen the ends of digging sticks or spears in absence of a knife, or grasp an object being manipulated with the hands (Gould 1968; Molnar 1972; Barrett 1977; Hayden 1979; Dunlop and Martin-Jones 2011 [1967]).

Eskimo and Inuit hunter-gatherers of the Arctic are perhaps the most widely cited groups with reference to the non-masticatory use of teeth (**Figure 2.7**). They used their teeth to stabilize bow-drills, soften leather, and work sinew as well as a variety of other tasks (Pedersen 1947; Pedersen 1949; Merbs 1968, 1983; Molnar 1972). The use of the dentition as a 'third-hand' to grasp and hold materials while cutting them into smaller pieces with a free hand, i.e. "stuff-and-cut", was particularly pervasive among Arctic hunter-gatherers (Koby 1956; Brace

1975; Lalueza-Fox and Frayer 1997); but this behavior is also commonly documented in disparate human groups of the ethnographic present (Uomini 2008).

Figure 2.6 Examples of non-masticatory behaviors among !Kung hunter-gatherers. "Stuff-and-cut" behavior (top, middle, and bottom, left) being used to reduce meat gripped between the teeth for consumption (Marshall and Gardner 1957). Using the dentition to manipulate cordage (top and middle, right) and to shape wood (bottom, right) in the making of a snare (Marshall 1971). [Used with permission, Documentary Educational Resources]

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Many more ethnographic examples can be drawn upon, but the trend is clear: humans use their teeth to manipulate artifacts by clamping and grasping materials between the teeth or chewing and dragging abrasive-laden materials like hide, fiber, and cordage across the dentition. These abrasive activities result in a variety of dental wear features.

Ethnographic analogy is useful in documenting the types of non-masticatory activities that form distinct patterns on the teeth of prehistoric human groups. However, many activities can lead to similar patterns of wear (S. Molnar 1972; P. Molnar 2011). Therefore, we generally cannot know what specific activity or task created a particular non-masticatory wear feature; but, recording non-masticatory wear *features* allows researchers to compare the degree and pattern of non-masticatory tooth use across spatiotemporally variable human groups (Molnar 2011). In addition to ethnohistoric examples of non-masticatory dental wear, bioarchaeological studies of human dental wear have thoroughly documented many non-masticatory dental wear features among temporospatially disparate human groups. Case studies are described below in relation to specific types of dental wear features.

Figure 2.7 Softening of sealskin boots and use of bow-drill (Netsilik).
Gripping, clenching, and pulling motions used to soften boots before wearing (Left). Use of composite bow-drill clenched between anterior teeth (Right). (Brown and Balikci 1967). [Used with permission, Documentary Educational Resources]

<u>Dental wear features and their interpretations</u>

Occlusal macrowear: The measurement of occlusal enamel loss and concomitant dentin exposure is the simplest description of macroscopic dental wear. Generally, pictorial representations accompanied by written descriptions of discrete wear stages are used to assign an ordinal wear score to a tooth (Miles 1963; Molnar 1971; Scott 1979; Smith 1984; Lovejoy 1985; Alexandersen 1988), or the ratio of exposed dentin relative to remaining enamel is calculated using occlusal photographs (Richards and Brown 1981; Clement 2007; Deter 2009; Galbany et al. 2011; Pinilla and Trinkaus 2017a). The methods both have benefits and drawbacks. Ordinal scores are easily and quickly collected data, and there is little margin for error when estimating a wear stage for a tooth that presents a partial occlusal surface due to either antemortem (e.g., chipped or fractured) or postmortem damage. Ratios of dentin exposure relative to enamel allow for more precision in analyses, while ordinal scales can mask some variation. Currently there are two means of calculating the ratio: (1) reconstruct the full occlusal surface by adding surface area for interproximal wear or missing area due to chipping, fracture, or damage; and (2) ignore all but postmortem damage and record the ratio with the remaining enamel and dentin. Furthermore, there can be issues of comparability between studies depending on whether the full crown border is considered to be the surface area or whether only the occlusal surface is considered to be the area in direct contact opposing teeth – as indicated by wear facets. Ordinal scores are readily comparable and can often be assessed from published photographs.

Macrowear is particularly useful for standardizing other dental wear features. For instance, some features are thought to intensify with wear, such as dental chipping, whereby the enamel rim on well-worn teeth could be more easily spalled than in teeth with more occlusal enamel (Scott and Winn 2011). Other dental wear features may be underrepresented in more heavily worn teeth, such as labial cutmarks (see below), since a shorter labial face means less surface area for cutmarks or the erasing of labial cutmarks close to the occlusal edge with advanced attrition. Making comparisons across similarly worn teeth can explore the potential biases in feature representation across the use-life of the dentition.

The gradient of anterior (incisor and canine) relative to posterior (premolar and molar) dental wear can be used to examine the intensity of anterior tooth use within and between groups. For instance, anterior dental wear is known to decrease with the adoption of an agricultural lifestyle in many parts of the world (Hinton 1981; Smith 1984; Kaifu 1999; Eshed et al. 2006; Deter 2009; Larsen 2015), while both anterior and posterior wear are greatly reduced in “traditional societies” that are introduced to manufactured materials and processed diets (Corruccini 1999; Kaifu 1999). Since anterior teeth are involved in the initial processing of food and manipulative behavior, anterior occlusal macrowear is an amalgamation of dietary and non-masticatory behaviors.

Figure 2.8 Incisor and canine wear showing extreme beveling angle (Shanidar 1).
Photograph credit: Erik Trinkaus.

Incisor beveling angles: Incisor beveling angles are a measure of the incisal wear plane orientation relative to the tooth cervix (Ungar and Grine 1991). With high levels of occlusal and interproximal wear the incisors will maintain occlusion through lingual tilting ("posterior tipping") (Ungar et al. 1997). The extreme results of incisor beveling are labially open, rounded, and non-occluding incisors – characteristics seen in several older Neandertal specimens (Brace 1962b, 1964; Wallace 1975; Trinkaus 1983) (**Figure 2.8**). Incisor beveling angles are a result of non-masticatory and dietary behaviors, and differential rates of beveling are known to differentiate human groups (Ungar et al. 1997).

Enamel chipping and fracture: Enamel chipping and fracture occurs when the occlusal surface is subjected to high bite forces on large and/or hard artifacts (Constantino et al. 2010). Chipping and fracture are commonly recorded in bioarchaeological studies (Turner and Cadien 1969; Bonfiglioli et al. 2004; Belcastro et al. 2007; Molnar 2008; Scott and Jolie 2008; Scott and Winn 2011; Tanga et al. 2016). The chipping of anterior teeth is related to non-masticatory activities and the initial processing of hard food items (e.g., frozen foods, bone, nuts, seeds, etc.). Lithic retouching with the anterior dentition, strong axially-inclined biting on hard-objects, or clamping materials (e.g., hide, leather) while applying external forces (e.g., pulling the material away from the mouth) are some possible scenarios that could produce enamel chipping.

Chipping on the posterior teeth is more frequently associated with the mastication of food with high levels of grit or hard particles. However, chipping may also occur through forces generated during non-masticatory behaviors that use the posterior teeth as vises and clamps while manipulating the object through “levering” motions with the free hands (e.g., spear shaft straightening).

Recent experimental research found a close relationship between the size of dental chips on the posterior dentition and bite force using ideal glass dome models and bunodont teeth of some mammals (e.g., peccaries, sea otters, monkeys, apes, and humans) (Chai and Lawn 2007ba, b; Lawn and Lee 2009; Lawn et al. 2009; Lee et al. 2009; Myoung et al. 2009; Chai et al. 2010, 2011; 2011; Constantino et al. 2011; Ziscovici et al. 2014). Experimental research have generated models that allow estimates of bite forces to be calculated on the basis of tooth dimensions and chip dimensions, and these equations have been used to calculate bite force estimates both hominins and non-human primates (Constantino et al. 2010, 2012). While no equations have been developed for the estimation of bite force from chips on the anterior dentition, ordinal scores have been developed for chip size classes (Bonfiglioli et al. 2004). Chip size classes in addition to presence/absence data can therefore be used to understand the relative loads placed on the anterior dentition.

Occlusal Grooves: Occlusal grooves are caused by the abrasion of materials against the occlusal surfaces of teeth in a unidirectional orientation. Grooves are generally attributed to the processing of pliable materials like sinew, fibers, basketry materials, and cordage (Cybulski 1974; Schulz 1977; Pedersen and Jakobsen 1989; Larsen et al. 1998; Bocquentin et al. 2005; Molleson 2005; Erdal 2008; Lorkiewicz 2011). Abrasion from the movement of materials across tooth surfaces produces characteristic, parallel striations within the boundaries of the grooves and can often be traced across several occlusal tooth surfaces (Larsen 1985; Minozzi et al. 2003; Waters-Rist et al. 2010).

Notches: Notches are indentations on the occlusal edge of a tooth (Bonfiglioli et al. 2004; Tanga et al. 2016) most likely derived from the habitual biting or clenching of hard objects in the same location. Abrasion, repeated chipping, and fatigue wear are all possible causal factors. Pipe stems, carpenter’s nails, and sewing needles among other objects are examples of materials producing notches in ethnohistoric and contemporary occupational settings (Corruccini et al. 1982; Alt and Pichler 1998; Prpié-Mehiéié and Buntak-Kobler 1998; Turner and Anderson 2003); but activities involving the habitual gripping, working, or breaking bone and wooden tools between the teeth are other possible causal factors in notch formation. Clinical settings have also documented seed processing (e.g., pumpkin, sunflower, and melon) as a cause of notches on the anterior teeth (Kaidonis et al. 2012).

Occlusal striations: Occlusal striations are microscopic striations that occur in groups and are aligned in parallel on occlusal surfaces (**Figure 2.9**). They differ from grooves in that they are much smaller and may not be continuous across an entire occlusal surface, and they can be differentiated from striations on attritional facets because they are not limited to facet boundaries. They are most likely the result of grit and silica particles that adhere to materials dragged across the anterior teeth (e.g., plant fibers or leather softened with the dentition) (Ryan 1980a; Lozano et al. 2008) rather than cordage or sinew which tends to create macroscopic grooves and notches with parallel striations within the boundary of the wear feature.

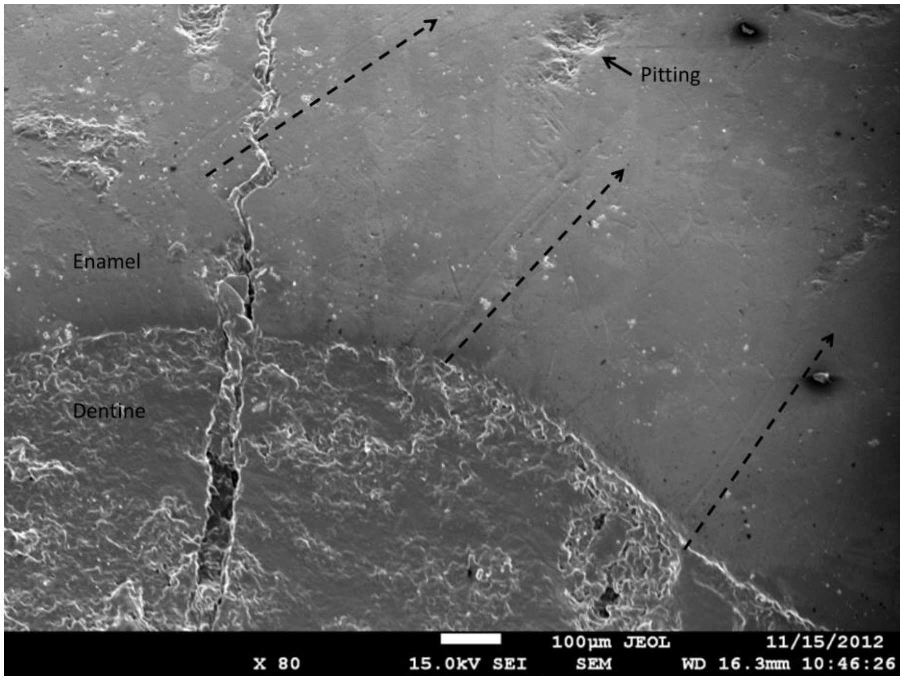


Figure 2.9 Occlusal striations (right C^1, Picken's Hole 1a, Neolithic).
Occlusal striation probably related to pulling abrasive material across the occlusal surface.

Enamel polishing: Enamel polishing is associated with an absence of features in a localized area and is thought to relate to the working of pliable materials like leather or hide (Puech 1982; Lozano et al. 2008) (**Figure 2.10**). There may be some wear features (e.g., pits) that may still be visible within the polished area but often exhibit polishing as well. Likewise, other wear features could overlay the polished surface while the polished margins still provide evidence of the features. Some tough materials (e.g., wood, leaves, and keratin) also appear to polish enamel surfaces (Lucas 2004). One study has suggested that the use of abrasive plant-based toothbrushes can leave characteristic polishing traces (Cook et al. 2015).

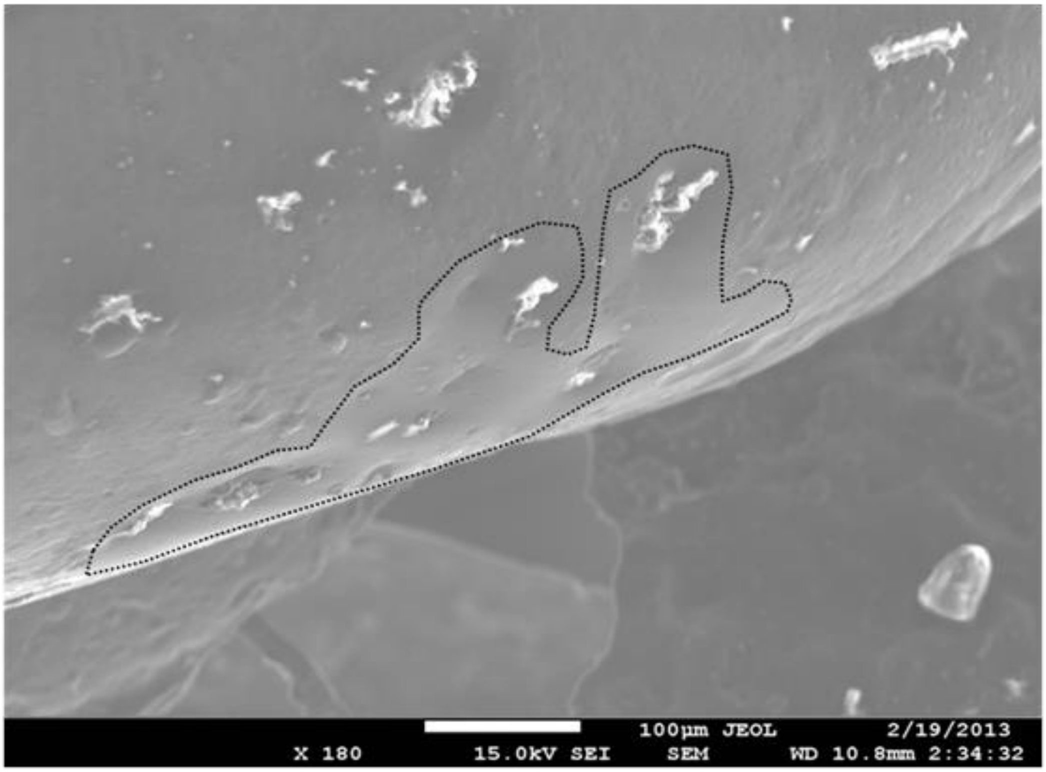


Figure 2.10 Enamel polishing (right I^2, Sunghir 2, Early Upper Paleolithic).
Enamel polishing is indicated within the black outline. Some pitting of the surface is also present.

Interproximal grooves: Interproximal grooves are frequently found at or near the cementoenamel junction of premolars and molars (Lukacs and Pastor 1988; Formicola 1991; Milner and Larsen 1991), and current consensus supports their presence as an indication of dental probing or "toothpick" use (Ungar et al. 2001; Lozano et al. 2013). However, some posterior tooth interproximal grooves seem more indicative of working materials such as sinew or cordage as evinced by mirrored grooves on antimeres, or the wrapping of the groove around the mesial edges of the tooth as if a cord is being working back and forth with the hands (e.g., Brown and Molnar 1990). Seemingly rarer still, are interproximal grooves that occur on the enamel and not the dentin (Molnar 2008) which negates their interpretation as palliative in nature since the gingival tissue is not near the feature. Occasionally, these grooves are found on the anterior teeth and some of the groove wraps around the edges of a tooth as if fiber or sinew has been dragged around the tooth (Frayer and Russell 1987; Formicola and Repetto 1989; Molnar 2008; Willman, personal observation) (**Figure 2.3** and **Figure 2.11**).

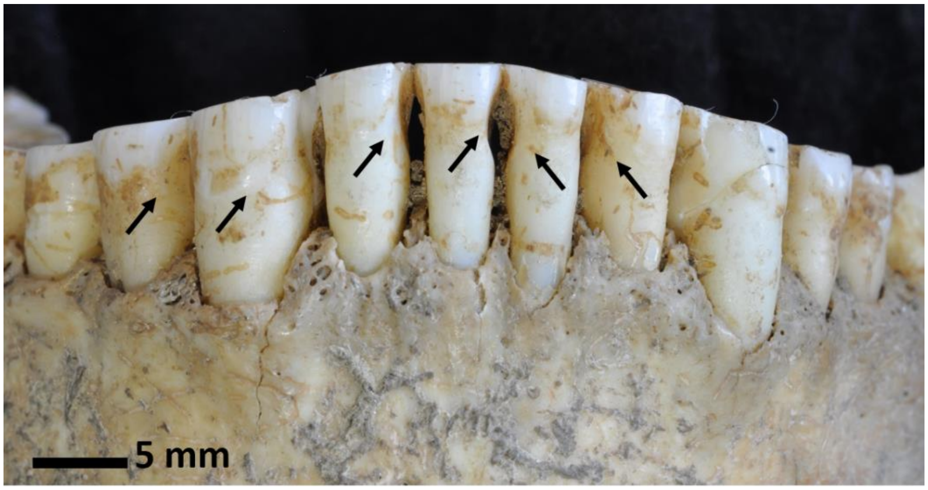


Figure 2.11 Interproximal grooves on mandibular anterior teeth.
Specimen from Schela Cladovei (Mesolithic, Romania). Arrows indicate location of interproximal grooves. They are present on each tooth in this mandible but not all are marked in this view.

Experiments have attempted to elucidate how interproximal grooves were formed and what materials were used. One study replicated interproximal grooves with grass stalks (Hlusko 2003) while another used deer bone and antler, calf sinew, and wood all with and without the addition of abrasive particles (Bouchneb and Maureille 2004). Of all materials used, calf sinew is the only material to produce grooves that do not look like known grooves from Pleistocene fossils (Bouchneb and Maureille 2004).

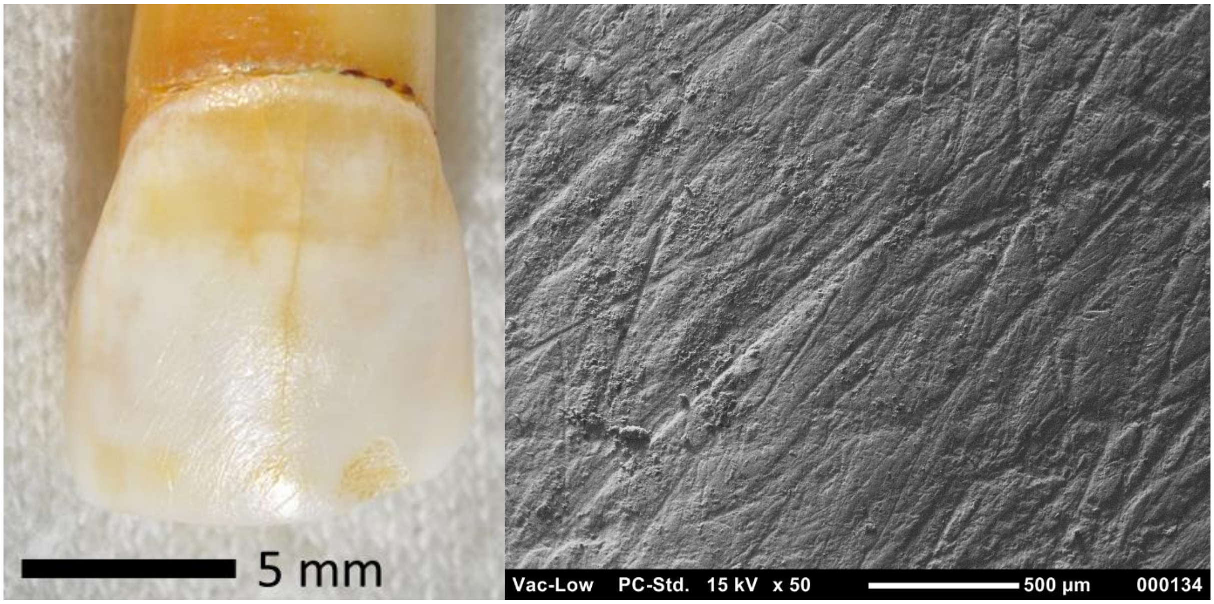


Figure 2.12 Extensive instrumental striations on the Saint-Brais Neandertal (left I^1). The cutmarks are so distinct that they are visible macroscopically (left image). A large, scallop-shaped enamel chip is also visible lateral to midline on the labio-occlusal edge (left image). Right image: SEM micrograph showing extensive striations at 50x magnification.

Labial Instrumental Striations: The “stuff and cut” behavior (Brace 1975) is often evoked to explain the presence of striations on the labial surfaces of the anterior teeth (**Figure 2.12**). Accidental contact between a cutting tool and the labial enamel produces distinct cutmarks that have been experimentally replicated (Bromage and Boyde 1984; Bermúdez de Castro et al. 1988; Lozano et al. 2004; Frayer et al. 2010), and are similar in morphology to stone-tool induced cutmarks on butchered animal bones (Shipman and Rose 1984; Bromage et al. 1991). Instrumental striations are known from many paleoanthropological and bioarchaeological contexts. The orientation of each instrumental striations is generally categorized into one of four categories (horizontal, right oblique, vertical, or left oblique), but the emphasis in the literature tends to be on determining handedness of individuals based on the predominance of left or right oblique orientation striations (Koby 1956; Trinkaus 1983;

Bermúdez de Castro et al. 1988; Lalueza Fox 1992; Lalueza-Fox and Frayer 1997; Lozano et al. 2004, 2008, 2009; Volpato et al. 2012; Estalrrich and Rosas 2013; Fiore et al. 2015; Willman 2016, 2017). The ratio of right to left handedness (~10:1) inferred from striation orientation among Middle and Late Pleistocene archaic *Homo* is consistent with that seen in humans today, associated with hemispheric dominance, and viewed as a probable indicator for a spoken language capacity among archaic Homo (Lalueza-Fox and Frayer 1997; Lozano et al. 2009; Frayer et al. 2010, 2012; Volpato et al. 2012; Fiore et al. 2015; Willman 2016, 2017). However, vertical and horizontal striations also reveal important information about behaviors that may not be related to cutting materials at oblique angles (Lalueza-Fox 1992; Molnar 2008; Willman 2017). The behaviors are not always readily interpretable but the difference in patterns at least confirms that the task involved different motions of the instrument-wielding hand when contact is made with the labial enamel. A preponderance of vertical striations have recently been interpreted as a product of downward scraping motions related to hide/leather-working among the early modern humans at Dolní Věstonice II (Willman 2016). Hence, the preference for general terms such as "instrumental striations" to describe these wear features *sensu lato*, and specific terms like "labial cutmarks" to describe the marks left by stuff-and-cut behaviors.

Lingual surface attrition of the maxillary anterior teeth (LSAMAT): LSAMAT describes the marked wear of the lingual surfaces of maxillary incisors and canines without concomitant wear on the lingual surfaces of mandibular incisors and canines (Turner and Machado 1983; Irish and Turner 1987). The behavior is often thought of as a product of peeling, processing, and/or consuming fibrous vegetable foods like roots or tubers (Turner and Machado 1983; Irish and Turner 1987; Larsen et al. 1998; Berbesque et al. 2012), but in some circumstances LSAMAT is thought to be a result of processing or softening of hide and leather or other pliable materials with the anterior dentition (Alt and Pichler 1998; Porr and Alt 2006; Willman 2016). **Figure 2.13** shows recently described LSAMAT examples from the Early Upper Paleolithic sites of Dolní Věstonice II and Pavlov I as well as a previously undescribed case from the Late Upper Paleolithic of Croatia.

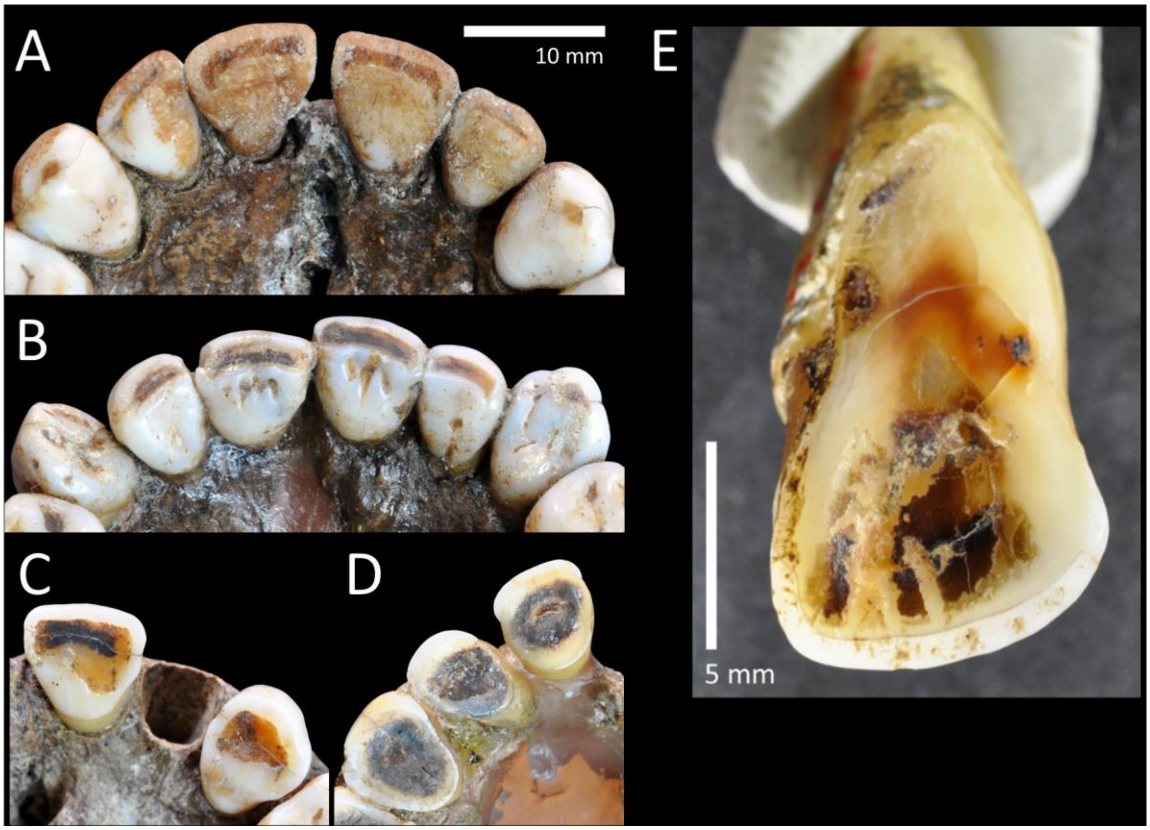


Figure 2.13 Lingual surface attrition of the maxillary anterior teeth (LSAMAT).
Examples range from incipient (A) to extreme (D and E). (A) Dolní Věstonice (DV) 14 has lingual faces with smoothly-worn surfaces. Latero-lingual extensions of dentin visible of several incisors. (B) DV 15 has a wellworn tuberculum on each incisor. Major rotation of right canine and incisor irregularities are also evident. (C) DV 13 has extensive exposure lingual dentin. (D) Pavlov 1 has lost nearly all of the lingual enamel. (E) Extreme example from a Late Upper Paleolithic individual from Vindija, Croatia.

Lingual surface attrition is also present on some anterior teeth with little occlusal wear. I suggest that this is due to normal anterior occlusal relationships and the transition from scissors occlusion to edge-to-edge occlusion with progressive wear. If non-masticatory activity such as clamping, gripping, and pulling occurred in the presence of a slight overbite and overjet, wear would occur on the lingual surface of the maxillary anterior teeth and to a lesser extent on the labio-occlusal edge of the anterior mandibular teeth. This type of wear is quite different from the LSAMAT, and distinctions will be made when referring to either manifestation of lingual surface attrition.

Labial microwear: Microwear is most commonly studied with the goal of reconstructing diets. Dietary studies typically focus on the occlusal and buccal surfaces of premolars and molars using SEM to document the size, frequency, and orientation of microscopic pits and striations; or confocal light microscopy and scale-sensitive fractal analysis to examine microwear textures (Pérez-Pérez et al. 2003; Teaford 2007; Ungar et al. 2008; Romero and De Juan 2012; Krueger 2016). However, both of these methods have been used to examine the labial surfaces of anterior teeth in attempts to reconstruct patterns of dietary and non-masticatory behaviors in fossil and bioarchaeological groups (Ungar and Spencer 1999; Teaford et al. 2001; Romero and De Juan 2003; Henry et al. 2006; Krueger and Ungar 2009, 2012; Hlusko et al. 2013; El Zaatari et al. 2014; Krueger 2014, 2015, 2016). Non-masticatory studies examine an area of labial enamel at the incisal or canine edge, under high-magnification, with a total field of view of ~0.02 mm^2. As stressed above, the incisors and canines are involved in both dietary and non-masticatory behaviors, and this combination of activities makes it difficult to discern the relative influences of diet and non-masticatory behaviors in labial microwear studies (Teaford et al. 2001; Henry et al. 2006).

Krueger (Krueger and Ungar 2009, 2012; Hlusko et al. 2013; El Zaatari et al. 2014; Krueger 2014, 2015, 2016) has made the most progress in teasing apart the relative influence of diet, environmental abrasive loads, and non-masticatory behavior on microwear texture signals through a broad, ethnohistoric comparative framework. Unfortunately, but to be expected, early ethnographers were not thinking about how their behavioral descriptions would aid the interpretation of non-masticatory dental microwear research and descriptions of anterior tooth-use can be vague. As discussed earlier (Chapter 1), the use of microwear texture analyses to address non-masticatory behavior is relatively recent and continues to be refined with the addition of new samples. Thus, there is an assumption that the range of microwear texture variation represented in the ethnohistoric samples is broad enough to encompass the behaviors of Pleistocene humans.

Occlusal and buccal microwear studies have documented the effects of food-processing on the formation of microwear in humans and primates showing links to levels of abrasives and feature density (Teaford and Oyen 1989; Teaford and Lytle 1996; Romero et al. 2012). Turnover rates in occlusal microwear features occur within 7-14 days depending on the nature of the abrasives in the diet (Teaford and Oyen 1989), and buccal microwear has a slower turnover rate (Romero et al. 2012). How much these turnover rates on the postcanine teeth can be extrapolated for the anterior teeth, whose function is different, is unknown. However, turnover does occur and in individuals using teeth-as-tools it may be even more accelerated than is seen on the posterior teeth given the size discrepancies between microwear and many non-masticatory dental wear features.

A further consideration of microwear analyses is the small area of a tooth analyzed in labial microwear studies there are several issues that are missed when only microwear is considered. First, many dental wear features (e.g., enamel chipping or instrumental striations) are often larger than the entire area analyzed in microwear studies. Second, the focus on wear near the labial edge ignores features that may be more densely packed on the labial midface or higher (e.g., labial cutmarks). Last, the mesial, distal, occlusal, and lingual surfaces are completely ignored in microwear analyses, and all of these surfaces can have diverse dental wear features indicative of non-masticatory behaviors. Future research comparing microwear alongside additional wear variables will help parse out these discrepancies.

Conclusions

From this broad review of dental wear, and the factors that contribute to its patterning, it has been made clear that the process is a dynamic one – changing throughout the lifetime of an individual; and it is influenced by a great many biological, environmental, and behavioral stimuli. Dental wear can be thought of as a palimpsest of human dietary and non-masticatory manipulative behaviors, where the size and depth of the feature, tissue affected, and abrasive loads will all affect that rate at which features are erased (turnover) or remain.

Most dental wear studies in paleoanthropological contexts focus on a single method or wear feature. In such studies entire dental surfaces and informative wear features are overlooked, greatly reducing the behavioral resolution one can glean from more holistic approaches. However, there are limitations related to access to fossils, time needed for specific analyses, and cost. All of these factors play into researcher decisions to focus on certain aspects of wear or methodologies. Finally, many of the dental wear features associated with non-masticatory behavior are related to the processing of perishable archaeological materials such as leather, wood, sinew, cordage, plant fibers, etc. Thus, careful focus on wear features, while not being able to directly comment on the precise task being performed (Molnar 2011), can reveal something about the types of materials being manufactured or worked with the anterior dentition.

Chapter 3. Non-masticatory tooth-use in the Pleistocene

Introduction

The extent to which non-masticatory tooth use, inferred largely through the patterning of dental wear, has been used to support or refute interpretations of behavioral variability, cognitive ability, language capacity, or morphological evolution and adaptation of morphologically defined archaic and modern human is rather astounding (Brace 1962b, 1995; Brose and Wolpoff 1971; Frayer 1978; Smith 1983b, 2015; Rak 1986; Demes 1987; Trinkaus 1987; Smith and Paquette 1989; Antón 1990, 1994, 1996; Spencer and Demes 1993; Lalueza-Fox and Pérez-Pérez 1994; Lalueza-Fox and Frayer 1997; Dobson and Trinkaus 2002; Bermúdez de Castro et al. 2003; O'Connor et al. 2005; Bailey 2006; Lozano et al. 2008, 2009, nd; Cartmill and Smith 2009; Weaver 2009; Frayer et al. 2010, 2012; Krueger 2011; Uomini 2011; Clement et al. 2012; Krueger and Ungar 2012; Volpato et al. 2012; Estalrrich and Rosas 2013, 2015; Fiorenza and Kullmer 2013; Hlusko et al. 2013; Le Cabec et al. 2013; Bruner and Lozano 2014b; El Zaatari et al. 2014; Bruner and Lozano 2015; Fiore et al. 2015; Fiorenza 2015; Bruner and Iriki 2016; Bruner et al. 2016; Krueger 2016). However, the majority of research to date is biased toward the study of non-masticatory wear among Middle Pleistocene archaic *Homo* and the Neandertals. Research within the last decade has started to include samples of early modern humans (Krueger 2011; Clement et al. 2012; Fiorenza and Kullmer 2013), but most studies are driven by particular methodologies (e.g., dental microwear texture analysis or occlusal fingerprint analysis), which makes it difficult to compare with approaches using light or scanning electron microscopy to document specific wear features (Ryan 1980b; Ryan and

Johanson 1989; Lozano et al. 2008; Lozano et al. 2015; Sarig et al. 2016; Willman 2016). The following review discusses the current state of non-masticatory dental wear research on Pleistocene humans and illustrates the current gaps in the literature that will be addressed in the present study.

Neandertal and early modern human craniofacial shape, bite force, and dental wear

Functional adaptation, climatic adaptation, or neutral evolutionary processes are frequently invoked to explain the differences between archaic and modern human craniofacial morphology during the Late Pleistocene (e.g., Weaver et al. 2007; Weaver 2009; Holton et al. 2011; Rae et al. 2011ba, b). The "*Anterior Dental Loading Hypothesis*" (ADLH), one of the more influential hypotheses in the literature, posits that high magnitude and/or repetitive loading of the anterior dentition through the habitual use of teeth-as-tools provided a strong selective force in Neandertal craniofacial and dental evolution (Smith 1983b; Rak 1986; Demes 1987; Trinkaus 1987; Smith and Paquette 1989; Spencer and Demes 1993; Brace 1995; Le Cabec et al. 2013). A variety of qualitative descriptions of Neandertal anterior dental morphology and wear patterns have been used to support the behavioral basis for the ADLH, including: labially worn, rounded, and non-occluding anterior teeth in some Neandertal fossils; frequent documentation of stone tool-induced cutmarks on the labial enamel; large anterior relative to posterior dental dimensions of Neandertals compared to modern humans; and large anterior tooth roots (Brace 1962b, 1964; Coon 1962; Smith 1983b; Trinkaus 1983).

While Neandertal dental morphology is suggestive of functional adaptation to repetitive and/or heavy loading of the anterior dentition in both mastication and the use of the teeth-as-tools, evidence for craniofacial skeletal functional adaptation to non-masticatory behavior is less clear. Although historically the focus has been largely qualitative (O’Connor et al. 2005), the modelling of bite force magnitude and/or efficiency of bite force production among Neandertals and modern humans have become more common in recent years (Antón 1990, 1994; Couture 1993; Spencer and Demes 1993; O'Connor et al. 2005; Holton 2009; Wroe et al. 2010; Eng et al. 2013). Qualitative descriptions of morphology postulated as functionally linked to non-masticatory behavior (although not ignoring the importance of resisting masticatory forces as well) include the well-defined nuchal and cervical muscle attachments necessary for stabilizing the head against repetitive gripping and pulling of objects held between the teeth like a vise (Brose and Wolpoff 1971; Smith 1983b; Trinkaus 1986; Smith and Paquette 1989), a vertically long face (Smith 1976, 1983; Rak 1986), and the orientation of the infraorbital region for efficient load dissipation (Smith 1983b; Rak 1986; Demes 1987; Trinkaus 1987). While the nuchal and cervical musculature attachments are likely reflective of muscular hypertrophy and can be linked to head stabilization, there is little support to date that facial height or the orientation of the infraorbital region in Neandertals is functionally linked to resisting loads placed on the craniofacial system during masticatory and/or non-masticatory activity.

Quantitative analyses repeatedly show that Neandertals are unlikely to have produced higher magnitude bite forces or have more efficient anterior bite force production than modern humans despite the seemingly elevated levels of anterior dental wear among Neandertals (Antón 1990, 1994, 1996; Couture 1993; Dobson and Trinkaus 2002; O'Connor et al. 2005; Clement et al. 2012). Furthermore, neutral evolutionary processes and climatic adaptation better explain many aspects of Late Pleistocene craniofacial evolution than functional adaptation to non-masticatory behaviors (Antón 1994; Maureille and Houêt 1998; Hublin 2002, 2009; Franciscus 2003; O'Connor et al. 2005; Weaver et al. 2007; Holton and Franciscus 2008; Weaver 2009; Holton et al. 2011). Finally, none of these studies of craniofacial morphology address whether the *potential* to produce high magnitude loads *actually* translates to the production of high loads in life. However, the direct analysis of dental chipping, fracture, and catastrophic crown failure can assess the differential loading of the anterior dentition among Neandertals and modern humans (e.g., Constantino et al. 2010; discussed futher below).

Craniofacial morphology does not provide definitive evidence for Neandertals engaging in more non-masticatory activity or producing higher magnitude loads with the anterior dentition relative to modern humans. However, the robust size and morphology of Neandertal anterior dental morphology, their heavy anterior relative to posterior occlusal attrition, the presence of labial cutmarks, and frequent chipping do support the behavioral inference for the use of teeth-as-tools (Cartmill and Smith 2009). Furthermore, differences in craniofacial form between Late Pleistocene human groups should not have any effect on the presence or patterning of specific dental wear features.

Anterior tooth dimensions and discrete morphology

In addition to the large metric dimensions of Middle and Late Pleistocene archaic human anterior teeth, the perception of robust anterior dental crowns is reinforced by a series of discrete morphological characteristics that are seen in high frequency among archaic humans but less frequently among Middle Paleolithic modern humans, Upper Paleolithic modern humans, and recent human groups (**Figure 3.1)**. Generally, the ASUDAS scoring procedures for discrete dental traits are used for modern human groups (Turner et al. 1991), but the system is typically modified for the study of archaic *Homo* given their propensity to exhibit “mass-additive” (as defined by Irish 1998) traits (e.g., labial convexity, shovel shaping, and lingual tubercles **Figure 3.2**) beyond the typical range of variation observed in modern humans (Crummett 1995; Bailey 2002, 2006; Bailey and Hublin 2006; Martinón-Torres et al. 2012).

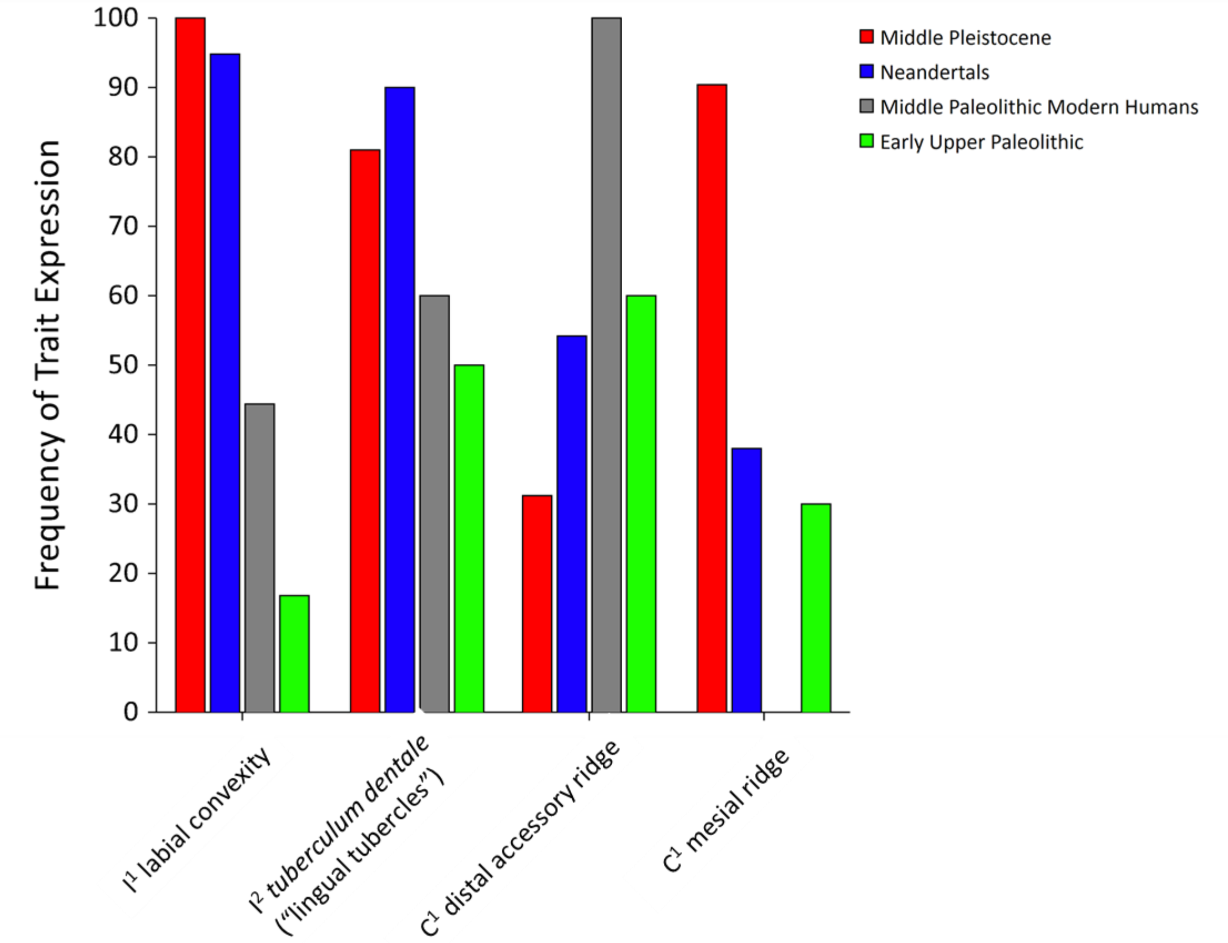


Figure 3.1 Maxillary anterior tooth discrete dental morphology.
Data on mass-additive traits available in the literature. Middle Pleistocene data is from Martinón-Torres et al. (2012). See Zapata et al. (2017) for remaining sources of data.

Like enamel thickness, tooth form and size are strongly tied to both fracture resistance (Lucas et al. 2008b; Lawn et al. 2009, 2013; Constantino et al. 2010, 2011) and the capacity to withstand lifelong wear (Lucas 2004). Larger teeth have the added benefit of providing more surface area, and therefore more microcontacts, for the efficient breakdown of exogenous substances (Lucas 2004) or increased surface area for non-masticatory manipulative behavior. With respect to Late Pleistocene humans, there is little overall difference between groups in mean postcanine buccolingual crown breadths; whereas, there is a marked reduction in labiolingual breadths of the anterior teeth between archaic and early modern (and recent) humans (Frayer 1978; Trinkaus 1978, 2004; Stefan and Trinkaus 1998; Hillson 2006; Trinkaus et al. 2014) – a difference established by the middle of the Middle Pleistocene in Europe (Trinkaus 2004).

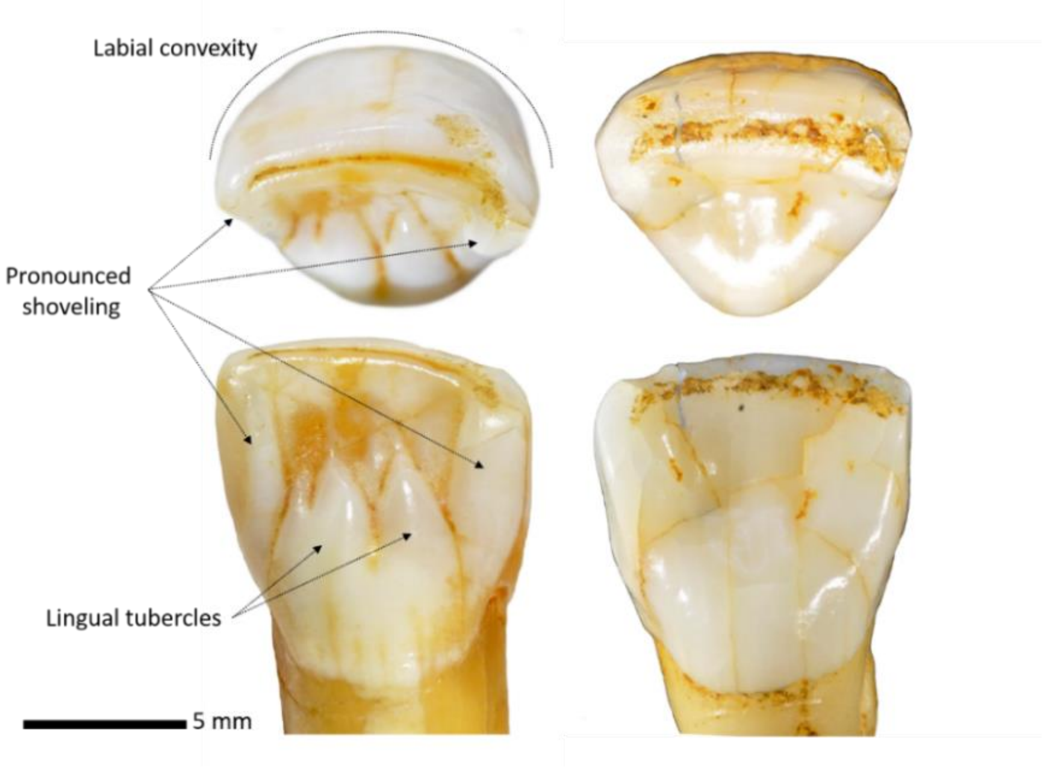


Figure 3.2 An example of mass-additive dental traits in archaic humans.
The complex and "robust" morphology of a Neandertal LI^1 (left: Saint-Brais) is contrasted with the relatively simple morphology an early modern human LI^1 (right: Brassempouy 2206). Note the antemortem enamel chipping on both incisors. The irregular labial surface of the Brassempouy incisor is due to a large calculus deposit.

In addition to the large, buttressed dental crowns Neandertals exhibit large anterior tooth roots when compared to modern humans in terms of length, cross-sectional properties, and total volume (Smith and Paquette 1989; Le Cabec et al. 2013). The long length of anterior tooth roots of Neandertals occurs independently of their large jaws (Le Cabec et al. 2012). Large anterior tooth roots are also found among Lower and Middle Pleistocene *Homo* suggesting that large roots are the ancestral condition (Smith and Paquette 1989; Le Cabec et al. 2013). While not common, some early modern humans do overlap with archaic humans in root dimensions (Le Cabec 2013; Trinkaus et al. 2013b, 2014).

Large roots have several benefits in high attrition environments. First, when the crown is fully worn away the tooth root functions as an occlusal surface and large roots remain functional longer than smaller roots. Second, the greater surface area of large roots provide more attachment area for the periodontal ligament fibers (Hylander 1977a). Lastly, long and broad roots provide an efficient means of dissipating occlusal forces into the surrounding alveolar bone (Smith 1983b; Smith and Paquette 1989), and the labiolingually broad root morphology efficiently resists compressive forces and fracture (Kloehn 1938; Trinkaus 1978; Le Cabec et al. 2013).

The morphologically robust and relatively large teeth of Archaic *Homo*, and particularly the Neandertals, are therefore generally interpreted as a buffer against a high levels of anterior tooth use in incisal preparation of food and especially for the use of teeth-as-tools (Smith 1976a, 1983b; Rak 1986; Demes 1987; Trinkaus 1987; Smith et al. 1989; Spencer and Demes 1993; Antón 1994).

Dental tissue proportions

Over the last decade there have been great advances in the use of 2D and 3D computed and microcomputed tomography for the quantification of dental tissue proportions (i.e., enamel, dentin, and pulp) and morphology (Macchiarelli et al. 2013). Neandertal dental tissue proportions are among the most widely published taxon using these newly available methodologies (Olejniczak et al. 2008; Bayle et al. 2009b, 2017; Smith et al. 2009, 2012; Crevecoeur et al. 2010b; Benazzi et al. 2011b; Willman et al. 2012; Le Cabec et al. 2013; Le Cabec et al. 2014). Other studies of dental tissue proportions include some specimens of Middle Pleistocene *Homo* (Raynal et al. 2010; Zanolli et al. 2010; Smith et al. 2012; Le Cabec et al. 2013; Liu et al. 2013; Zanolli and Mazurier 2013; Xing et al. 2014) and various Middle Paleolithic/Middle Stone Age humans from across Africa and southwest Asia (Smith et al. 2006, 2012; Hublin et al. 2012; Le Cabec et al. 2013), but few Upper Paleolithic/Later Stone Age early modern humans (Bayle et al. 2009a, 2010; Le Cabec et al. 2013). Overall trends in dental tissue proportions between Late Pleistocene human groups remain difficult to elucidate due to small sample sizes (Smith et al. 2012), and may be further conflated by grouping African Middle Paleolithic/Middle Stone Age regional samples (particularly those of North and South Africa) that have a complex mix of archaic and derived features (Trinkaus 2013). However, some interesting distinctions between Neandertals and (primarily recent) modern human dental tissue proportions have been outlined.

Smith and colleagues (2012) show that two-dimensional (2D) average enamel thickness and relative enamel thickness (a unitless measurement scaled to tooth size for intertaxon comparisons) is lower on average for Neandertal maxillary and mandibular canine, premolar, and molar teeth when compared to their fossil modern human and recent human sample. Incisor average enamel thickness values are similar between Neandertals and the fossil modern human sample but thinner in comparison to recent modern humans (Smith et al. 2012). These differences are largely due to the greatly expanded dentin volume in Neandertal dentitions relative to the modern human samples (Bayle et al. 2010, 2017; Smith et al. 2012). However, Bayle et al. (2017) show that 2D and 3D average enamel thickness values are similar to slightly higher among the Sima de las Palomas Neandertal maxillary incisors, but also emphasize that the chronological and geographic patterning of dental tissue proportions among Neandertals is poorly understood.

Interestingly, the mixed dentition of the Lagar Velho 1 child has intermediate enamel thickness values to the Roc de Marsal 1 Neandertal child and the Late Upper Paleolithic child La Madeleine 4 (Bayle et al. 2009a, b, 2010). Furthermore, the La Madeleine 4 child is similar to recent human enamel thickness values (Bayle et al. 2009a). The trends seen in the European Upper Paleolithic mixed dentitions are a case in point that more European adult dentitions must be studied in order to elucidate overall trends in archaic versus early modern human dental tissue proportions – trends that the largely African Middle Paleolithic/Middle Stone Age sample of the largest study to date (Smith et al. 2012) cannot fully remark upon.

As discussed in Chapter 2, dental wear is a result of dietary and environmental factors. Trends in dental tissue proportions do have an effect on rates of dental wear, but there is a complex interplay between enamel thickness and dental size, diet, and environment. This has led some researchers to critique the use of dental wear aging techniques for demographic and life history studies (Smith et al. 2012); but as discussed above with regard to differences in timing and sequence of dental development, most studies use ordinal scales and time-averaged samples by compressing the scale into fewer categories (e.g., Trinkaus 1995, 2011; Caspari and Lee 2004). The present study is less affected by the issue of differential enamel thickness between archaic and early modern humans given the focus on the anterior dentition. While it has been shown that the enamel of Neandertal canines exhibits lower average and relative enamel thickness values compared to the sample of fossil modern humans, the values for incisors are quite similar (Smith et al. 2012).

Postcanine enamel thickness is often used to infer dietary strategies of extinct human and non-human primates. Many researchers have suggested that thick enamel provides resistance to crack propagation and catastrophic crown failure related to hard-object feeding and its attendant production of high bite forces (Kay 1981; Dumont 1995; Lucas et al. 2008b, b; Vogel et al. 2008; Constantino et al. 2010, 2012). Similarly, thickly enameled anterior teeth would be more resistant to catastrophic failure. Thick enamel also provides a defense against the lifetime accumulation of dental wear in the presence of dietary abrasives and erosion in the postcanine teeth (Molnar and Gantt 1977; King et al. 2005; Rabenold and Pearson 2011, 2014; Pampush et al. 2013), and increases the longevity of anterior tooth use for incisal food preparation and use of the teeth in manipulative tasks. Typically, researchers frame the hard-object feeding versus lifetime resistance to wear in opposition, but the hypotheses need not be mutually exclusive (Pampush et al. 2013).

Reconciling dietary and manipulative use of the anterior teeth

The study and interpretation of wear (microwear especially) as an indication of ingestive behaviors among nonhuman primates has had a long history of study (e.g., Walker 1976; Ungar 1994; Krueger and Ungar 2009; Krueger 2011, 2014, 2015), but the advent of technocultural solutions that can make ingestion an exosomatic exercise complicates the issue among tool-using hominins. Fork and knife as well as cooking and other culinary traditions involving pre-ingestive preparation of food are intuitive examples of how culture or traditions among recent humans reduce the use of the incisors for ingestion. In deeper time, simpler behaviors such as the cutting, pounding, or grinding of foods could also relegate the incisors unnecessary as food bypasses the anterior dentition and is moved directly to the postcanine dentition for mastication. An example of exosomatic food breakdown, documented ethnographically in many disparate groups, that receives ample attention in Middle and Late Pleistocene contexts is the "stuff-and-cut" behavior (**Figure 2.6**). This technique involves gripping an object, often meat, between one hand and the anterior teeth while using the free hand to cut the food item close to the mouth with a stone tool or metal blade which breaks down food into smaller, chewable portions (Koby 1956; Brace 1962b, 1964, 1975; Uomini 2008).

Incisor and canine dental wear also complicates the issue of linking form and function to ingestion alone. The spatulate incisors of the anthropoid primates, including hominins, are generally thickest near the cervix and taper toward the occlusal surface. The canines are conical but are similarly thickened at the cervix and taper toward the occlusal surface. Relatively unworn incisors would therefore be most efficient at cutting and slicing food, while increasingly worn and blunted anterior teeth would be sufficient for the gripping, grinding, and fracture of food, but not cutting. Wallace (1975) noted the difficulties of cutting food with heavily worn anterior teeth and made specific reference to the heavily worn, rounded, and non-occluding teeth of La Ferrassie I and several recent human examples. Furthermore, the occlusal to cervical tapering of incisors and canines results in increasingly large occlusal surface area with progressive wear (until it diminishes when wear progresses to root surfaces). Increased surface area provides a greater number of microcontacts for simple fracture and gripping behaviors and would be more greatly accentuated in groups expressing more mass-additive anterior dental characteristics (e.g., labial convexity, shovel shaping, and lingual tubercles). Given the propensity of elevated anterior relative to posterior dental wear in many hunter-gatherers and most pre-industrial peoples (Molnar 1971; Kaifu 1999; Deter 2009; Clement et al. 2012), it is interesting to note that the use-life of the anterior teeth as a functional and efficient cutting and slicing edge aiding with ingestion is relatively short compared to its use-life as a blunt, but more expansive, occlusal surface. The use of cutting implements in stuff-and-cut behaviors is often used instead of incisor partitioning of foodstuffs – i.e., blunt, worn teeth are better for gripping and holding than cutting.

It has been suggested that wear in the form of dietary microstriations can be isolated from other forms of non-masticatory dental wear on the labial and occlusal surfaces of incisors using an SEM on the basis of size (Lozano et al. 2008), or through the use of comparative ethnographic framework and microwear texture analysis (Krueger and Ungar 2009; Krueger 2015). However, these methods may not be as straightforward as thought. For instance, objects manipulated with the anterior dentition in non-dietary contexts can have small grit or other exogenous particles adherent to them. These particles could induce the same size striations and pits expected to form through normal ingestive behavior. It is clear that other dental wear features should be taken into account to assist in understanding manipulative versus dietary influences on overall patterns of dental wear.

In summary, anterior tooth use for dietary purposes is a difficult process to detect in technologically inclined hominins as much of incisal preparation of foods can be exosomatic. Many of the behaviors that use the anterior teeth for preparing food for mastication can be viewed as non-masticatory behaviors. A final example illustrating this point can be found in a critique of Wallace's (1975) assertion that the rounding of the anterior dentition is entirely due to dietary behaviors. Wallace (1975:395) asserted that:

> *"Because of the open bite, with consequent loss of effective incision, La Ferrassie I grasped the grit-laden piece of meat or fibrous vegetable in hand and in a raking, stripping movement pulled it over the incisor stumps to shred or tear off a mouthful of food. Alternately and habitually pulled outwards, upwards, and downwards, grit-laden food [sic]."*

While the above scenario is related to incisor processing for food, the forceful behaviors are manipulative in the same sense that many uses of the dentition are non-masticatory, tool-using behaviors. In this sense, we can view the manipulation of foodstuffs with the anterior teeth as a form of manipulative behavior (Hylander 1977a; Cartmill and Smith 2009).

Anterior dental wear can be considered a palimpsest of dietary/ingestive and non-masticatory, manipulative behaviors. Careful consideration of multiple dental wear features and total occlusal wear can help determine relative differences in degree and use of the anterior dentition in chewing and as a tool.

Historical recognition of non-masticatory behavior among archaic humans

The use of “teeth-as-tools” for non-masticatory, manipulative behaviors is a central theme in reconstructions of Neandertal and archaic *Homo* behavioral repertoires. These non-masticatory behaviors are largely inferred from the degree and patterning of anterior dental wear and interpreted using ethnographic analogy and actualistic studies of human non-masticatory behaviors. Extensive anterior tooth wear was first acknowledged among the Neandertals specimens from Spy (Fraipont and Lohest 1887), and was followed by Martin’s (1923) description of wear-related striations on the labial surfaces of the maxillary anterior teeth of La Quina 5, but neither case was initially attributed to non-masticatory behaviors. Koby (1956) was the first to identify and attribute extensive labial striations on the Saint-Brais maxillary central incisor, and by extension the striations on the teeth of La Quina 5, to non-masticatory behaviors. Koby (1956) specifically identified the striations as cutmarks caused by accidental contact between a stone tool and the labial enamel when cutting materials held between the front teeth. He based this interpretation on non-masticatory behaviors documented ethnographically among the high-latitude hunter-gatherers.

Other researchers began to acknowledge that the use of teeth-as-tools was a likely contributor to the pattern of heavily worn, rounded, and non-occluding anterior teeth of some older adult Neandertals and archaic *Homo* fossils (e.g., La Ferrassie 1, Gibraltar 1, Shanidar 1, and Broken Hill 1). Eventually the large and morphologically robust anterior teeth of Neandertals and archaic *Homo* were considered alongside the dental wear evidence for non-masticatory behaviors (Brace 1962b, 1964; Coon 1962), and views stressing functional adaptation to non-masticatory behaviors and/or structural reduction through cultural innovation permeated the literature (Rak 1986; Demes 1987; Trinkaus 1987; Smith and Paquette 1989; Spencer and Demes 1993; Brace 1995; Le Cabec et al. 2013).

Direct analyses of non-masticatory dental wear on Pleistocene fossils

Instrumental striations on the anterior teeth caused by "stuff-and-cut" behaviors (Brace 1975) are the most frequently documented dental wear feature in the Pleistocene. Cutmarks are documented for the Early Pleistocene from one individual at Gran Dolina (Lozano et al. 2015) and at Dmanisi (Margvelashvili et al. 2016). Although no detailed analyses have been done on the striations, there is an intriguing case attributed to the central incisors of the OH 65 maxilla (*Homo habilis*) (Clarke 2012). However, instrumental striations are noted in abundance on Middle and Late Pleistocene human teeth: Boxgrove (Hillson et al. 2010), Broken Hill (Lalueza-Fox and Pérez-Pérez 1994), Mauer (Puech et al. 1987), Pontnewydd (Compton and Stringer 2012), Qesem (Sarig et al. 2016), Sima de los Huesos (Bermúdez de Castro et al. 1988; Lozano et al. 2004; Lozano et al. 2008; Lozano et al. 2009), Angles sur l'Anglin (Patte 1960), Cova Negra (Bermúdez de Castro et al. 1988; Arsuaga et al. 1989; Arsuaga et al. 2001), Hortus (de Lumley 1973; Estalrrich and Rosas 2015), Krapina (Lalueza-Fox and Frayer 1997; Fiore et al. 2015), Sima de las Palomas (Willman 2017), Regourdou 1 (Volpato et al. 2012), Shanidar (Trinkaus 1983), El Sidrón (Estalrrich and Rosas 2013, 2015), Spy (Estalrrich and Rosas 2015), Tabun C1 (Lalueza-Fox and Pérez-Pérez 1994), and Vindija (Frayer et al. 2010). To date, only a few examples exist among modern humans and all but one (Willman 2016) are from the Holocene (Lalueza-Fox and Pérez-Pérez 1994; Lozano et al. 2008; Molnar 2008; Dinnis et al. 2014). Striations have been examined in other studies using light-microscopy (Bax and Ungar

1999), but methods used in the study make it difficult to interpret and compare these striations to the work of other researchers. Other striations that have not been studied in the same ways but could be related to instruments contacting enamel are found elsewhere (Lukacs and Pastor 1988), but the striations are quite fine and etiology is uncertain. Finally, the Paleoindian Buhl burial has been cited numerous times as having cutmarked anterior teeth (Lozano et al. 2008, nd; Estalrrich and Rosas 2013, 2015; Bruner and Lozano 2014b; Spinapolice 2015; Bruner et al. 2016), but there is absolutely no reference to this form of dental wear anywhere in the original publication (Green et al. 1998).

Particular dental wear features (i.e., enamel flaking, pits and gouges, and occlusal striations) were documented using scanning electron microscopy (SEM) at low-level magnification for a small sample of Neandertals and Middle Paleolithic modern humans, and the total number of dental wear features was highest among the Neandertals (Ryan 1980b). Enamel chipping has been extensively documented in bioarchaeological research (see Chapter 2), but similar documentation in the form of inter- or intra-site comparisons is largely absent for Late Pleistocene fossils. It is not uncommon for chipping to be noted on individual teeth when present (Arsuaga et al. 1989; Formicola and Repetto 1989; Garralda and Vandermeersch 2000; Rougier 2003; Maureille et al. 2008; Doboş et al. 2010; Frayer et al. 2010; Liu et al. 2010; Janković et al. 2012); however, researchers will rarely note an absence of antemortem enamel chipping. Therefore, enamel chipping prevalence remains poorly understood for Middle to Late Pleistocene contexts aside from a few case studies for the Sima de los Huesos hominins (Lozano et al. 2008), some earlier (Rougier 2003) and later Neandertals (Estalrrich and Rosas 2015; Willman 2017), and the Late Upper Paleolithic humans from Taforalt (Bonfiglioli et al. 2004).

Incisor beveling angles reflect dentoalveolar compensation to progressive wear due to the cumulative effects of ingestive and non-masticatory anterior tooth-use. Compensatory mechanisms maintain functional occlusion as wear changes occlusal relationships during life (see Chapter 2), and beveling angles can document the shift from scissors occlusion to edge-to-edge occlusion of incisors. In older individuals with exceptional wear, the incisors may no longer occlude and often appear heavily rounded. An analysis of incisor beveling angles among Neandertals and recent human groups from the Holocene show more pronounced beveling among Neandertals (Ungar et al. 1997). The Holocene samples included Ipiutak hunter-gatherers from Point Hope, Alaska and food-producing Puebloan individuals from the southwestern United States (Ungar et al. 1997), but no fossils of Late Pleistocene early modern humans. Nonetheless, the study indicates that the mechanisms of anterior dentoalveolar compensation are similar across archaic and modern human groups despite differences in tooth size and morphology.

Additional studies looking at differences in the degree of wear between archaic and early modern humans is provided by analyses of macrowear gradients. Trinkaus (1992) observed macrowear and scaled it to buccolingual crown breadth (see Chapter 5) for a sample of Middle Paleolithic modern humans and Neandertals from southwest Asia to understand differences in the relative rates of wear between morphologically defined groups while accounting for the greater size of archaic relative to Middle Paleolithic modern human anterior teeth. His analysis showed similar degrees of wear but a clear separation of samples on the basis of large anterior tooth dimensions in the Neandertals. This implies that Neandertals exhibit higher rates of anterior relative to posterior tooth wear than Middle Paleolithic modern humans because their anterior teeth exhibit higher rates of wear despite their absolutely larger dimensions (i.e., larger teeth are expected to were more slowly than smaller teeth if all behavioral and environmental factors are equal). This study has been replicated with more inclusive samples of Neandertals and early modern humans (Doboş et al. 2010; Willman 2016, 2017). The results are largely the same, albeit there is some overlap between samples, and the large size of the anterior teeth in archaic *Homo* indicates an advantage in terms of resistance to cumulative wear.

Clement and colleagues (2012) examined occlusal wear gradients (ratio of dentine to enamel) in addition to controlling for eruption sequences. Their results showed considerable overlap between recent humans, early modern humans, and Neandertal samples. Some of the Holocene and early modern human fossils were even found to have more severe wear than Neandertals, in addition to a propensity for uneven wear across the anterior teeth compared to the evenly distributed wear across Neandertal anterior teeth (Clement et al. 2012). They conclude that there is no support for the ADLH and that all Late Pleistocene humans used their dentitions in similar ways. However, the use of occlusal wear ratios removes a biologically relevant factor in dental wear: tooth size. Even if dentin exposure is similar for each tooth type, there are differences in occlusal area between the groups. Thus, there is still some indication that the large anterior teeth of archaic *Homo* were under stabilizing selection given their establishment by the middle of the Middle Pleistocene and maintenance among later Neandertals (Trinkaus 2004) – possible related to maintaining functional dentitions for manipulative purposes throughout the lifetime.

Another macroscopic perspective on the use of teeth as tools uses data from Occlusal Fingerprint Analysis (OFA) (Fiorenza et al. 2011a; Fiorenza and Kullmer 2013, 2015; Fiorenza 2015). OFA (Kullmer et al. 2009) uses digital models of molar crowns to examine the patterning of occlusal wear facets related to contact between maxillary and mandibular teeth. Fiorenza and Kullmer (2011a) identified wear facets that are not thought to form under normal masticatory regimes and they coined the term “para-facets” to describe them. Para-facets were predominantly found on teeth of hunter-gatherers that are ethnohistorically known to have used their teeth-as-tools, but samples were limited to 35 maxillary molars from six different groups with nearly half the teeth (N=17) belonging to one group (Fiorenza et al. 2011a). The presence of para-facets was interpreted as forming through the use of teeth-as-tools – perhaps through clenching an object between the teeth and manipulated it with the hands. Para-facets have since been documented in Neandertals and Middle Paleolithic modern humans from Skhul and Qafzeh suggesting similar forms of non-masticatory behaviors (Fiorenza and Kullmer 2013; Fiorenza 2015). However, there is some debate as to whether para-facets are markers of non-masticatory behaviors. A main critique concerns the presence of malocclusion in many of the Middle Paleolithic modern humans examined (Sarig and Tillier 2014, 2016; Fiorenza and Kullmer 2015). However, the method is promising and expanded sampling of ethnohistoric groups may help refine interpretations as seen in microwear texture analyses (Krueger and Ungar 2009; Krueger 2015).

SEM-based approaches to labial microwear and non-masticatory behavior among Neandertals and early modern humans have provided mixed results as only one study has been attempted (Henry et al. 2006). An SEM microwear analysis suggested that the patterning of microwear on the labial surface of incisors among Neandertals and early modern humans co-varies with ecogeography rather than taxonomic or technocultural distinctions (Henry et al. 2006). The authors also discussed the difficulties in distinguishing the role of exogenous environmental grit, diet, and/or non-masticatory behaviors in the production of microwear (Henry et al. 2006) – conflicting factors that are also stressed in bioarchaeological contexts (Teaford et al. 2001). While not examining Pleistocene fossils, bioarchaeological research has shown that labial microwear can discriminate between groups on the basis of diet (Ungar and Spencer 1999; Romero and De Juan 2003, 2004), or that differences could relate to differences in the loading of the incisors (Spencer and Ungar 2000) – conclusions that are not necessarily mutually exclusive. Thus, SEM-based analyses of microwear have yielded conflicting results.

Krueger (2015; Krueger and Ungar 2009) has used a comparative database of bioarchaeological samples with well-documented information on diet, environmental abrasive loads, non-masticatory behaviors, and climate from ethnohistorical documents and/or archaeological inferences. Microwear texture variables for anisotropy, textural fill volume, heterogeneity, and complexity were shown to differentiate bioarchaeological groups (Krueger 2015). However, the differences must then be interpreted through the contextual data (i.e., diet, non-masticatory behaviors, abrasive loads, etc.) available for each bioarchaeological group. The assumptions made with comparative samples are then compounded with the additional of fossil taxa for which all behavioral and environmental contexts are inferred through human paleobiology and Pleistocene archaeology – contexts which are far less assured than in recent bioarchaeological samples.

Krueger and Ungar (2012) examined microwear textures for 17 Krapina individuals and determined that they were probably engaging in non-masticatory behaviors to a moderate degree based on textural fill volume and heterogeneity variable similarity to a Coast Tsimshian bioarchaeological sample, but Krapina had an environmental abrasive load more similar to that of a Puye Pueblo sample based on microwear texture complexity. Interestingly, the lack of similarity with the Nunavut sample was used suggested to the authors that the Krapina Neandertals were less actively using intensive clamping/grasping non-masticatory behaviors. However, it is interesting to note that the extensive documentation of labial cutmarks and chipping in the Krapina sample suggests they were engaged in intensive anterior tooth-use (Lalueza-Fox and Frayer 1997; Fiore et al. 2015). Another microwear texture study showed that Neandertal non-masticatory behavior varies between groups categorized “warm, woodland” and “cold, open steppe” (Krueger 2016). The “cold, open steppe” Neandertals were similar to the Ipiutak bioarchaeological sample (high textural fill volume and low anisotropy) suggesting extensive clamping and grasping non-masticatory behaviors – perhaps related to the production of cold weather necessities like hide (Krueger 2016). The “warm, woodland” sample was more similar to a Tigara sample that also engaged in non-masticatory behaviors but did not process the same types of materials as the Ipiutak (Krueger 2016). The ecogeographic difference between warm and cold Neandertal groups is a particularly novel finding especially when one considers the extent to which Neandertals have been viewed as behaviorally inflexible.

The above examples were not done with the most recently published comparative sample (11 bioarchaeological groups: Krueger 2015), so it is likely these conclusions will be refined in the future. While labial microwear textures in Neandertals co-vary with ecogeography (Krueger and Ungar 2012; Krueger 2016), Krueger (2011) suggests that early modern humans did not engage in much non-dietary tooth-use irrespective of climate, region, or chronology. Technology differences between Neandertals and early modern humans was proposed as an explanation for the relatively low and invariable signal for non-masticatory behaviors in her early modern human sample (Krueger 2011). In contrast, Willman (2016) has shown that the early modern humans from Dolní Věstonice II engaged in extensive non-masticatory behaviors, but that these behaviors produced different forms of dental wear features than are typically recognized among Neandertals (i.e., LSAMAT and vertical instrumental striations).

Interestingly, the results of incisor microwear texture analyses reached extremely similar conclusions to studies of molar microwear textures among early modern humans and Neandertals. The molar analyses show Neandertals varied their diets in different ecogeographic and climatic conditions whereas early modern humans did not (El Zaatari et al. 2011; El Zaatari and Hublin 2014; El Zaatari et al. 2016). In additional postcanine buccal microwear (Pinilla and Trinkaus 2017b), molar macrowear (Fiorenza et al. 2011b; Fiorenza 2015), and SEM microwear on labial incisor surfaces (Henry et al. 2006) all show strong patterning of wear by ecogeography among Neandertals and some early modern humans. As a whole, this may suggest that diet and ecogeography have a predominant signal in many forms of wear analysis. If this is the case, it is less clear how well microwear texture is characterizing non-masticatory versus dietary behaviors from incisor labial surface microwear textures. The contrasts in incisor microwear and dental wear feature analyses (e.g., cutmarks, chipping, etc.) outlined above also suggests that the non-masticatory signal from microwear texture analysis may not correlate strongly with the larger wear features documented using low-level microscopy and SEM. Some cross-validation of methodologies between microwear texture analysis and dental wear feature analyses would aid future interpretations.

Interproximal grooves are perhaps the only wear feature regularly published for archaic and modern human groups but their etiology is often debated (Formicola 1988b, 1991; Brown 1991; Frayer 1991; Lalueza-Fox et al. 1993; Bermúdez de Castro et al. 1997; Lebel et al. 2001; Trinkaus et al. 2003; Durband et al. 2012; Lozano et al. 2013; Sun et al. 2014). Interproximal grooves are generally found on the posterior teeth except for a few, rare cases featuring interproximal grooves between the anterior teeth of Upper Paleolithic and Holocene (Formicola and Repetto 1989; Molnar 2008; Willman, personal observation).

A final note on the documentation of wear features concerns prevalence. It is common for descriptions of fossils to include data on a dental feature *when they are present*. However, the focus on presence creates a natural overrepresentation of particular wear features (cutmarks, chipping, interproximal grooving, etc.). This dissertation attempts to rectify this bias by providing data on absence whenever possible. However, the concentration on prevalence in the literature will naturally lead to inflated prevalence in this research as well.

Conclusions

Detailed analyses of anterior dental wear are frequently neglected in analyses concerned with non-masticatory behaviors. The tendency is to cite evidence of extreme wear among Neandertals to support the ADLH or non-masticatory behavior in general, but systematic studies of wear are still relatively rare. The non-masticatory dental wear in Middle and Late Pleistocene humans is more fully documented than in early modern humans, and few studies or descriptions are comparable. Newer analyses that include modern human samples are methodologically driven, which makes the data difficult to compare – especially with analyses that focus on more traditional wear feature descriptions (cutmarks, chipping, macrowear, etc.). Cross-validation of methods and expanded sampling of early modern humans have been proposed as two ways forward in the study of Neandertal and early modern human non-masticatory behavior. Unfortunately, cross-validating other methods is outside of the scope of this dissertation. However, expanded sampling is possible and dental wear feature analysis for instrumental striations and enamel chipping will provide comparative data that will contribute to future studies aimed at cross-validation of newer methodologies.

Chapter 4. Materials

Introduction

The methods used in this dissertation differ for each individual analysis. Therefore, independent methods are presented with each analysis chapter. Here, a brief introduction to the samples studied, a description of dental molding and casting is provided, and a rationalization for sample sub-groupings. The chapter concludes with a table presented fossil samples studied and an indication of what analyses they were included in.

Sample descriptions

The macroscopic and microscopic methods used in this thesis require very different forms of data which means that sampling strategies differ greatly between analyses. A brief description of each sampling strategy is therefore warranted before detailed protocols are presented in individual analysis chapters.

Scaled occlusal macrowear gradients require no molding or casting of dentitions – only occlusal wear scores (Smith 1984) and buccolingual crown breadths were needed. All data was acquired from visual and metric investigations of the original specimens, or from published literature and photographs when the original specimens were not available. The completeness of fossils (number of observable teeth), and the presence of both wear and metric data when using data obtained from sources other than direct observation (e.g., literature and/or photographs) are the primary factors limiting sample size. Sampling strategies in each type of analysis address this issue.

A limiting factor for macrowear analyses is the presence of both anterior and posterior teeth in the same jaw. Data obtained from full arcades (I1-M2, see Chapter 5) are most limited in this regard given the relative rarity of complete dentitions in the Pleistocene fossil record. A second analysis of individual anterior teeth (I1, I2, or C) versus a first molars from the same jaw allowed more inclusive sampling of fragmentary dentitions. Finally, the use of data culled from the literature does not always provide paired metric and wear score data. Therefore, a final analysis observing differential occlusal wear of each anterior tooth (I1, I2, or C) versus a first molar of the same jaw, without corresponding metric data, was also performed.

Antemortem anterior dental chipping analyses sampled any anterior tooth that was available for study (also see Chapter 6 for taphonomic issues) with a limited number of observations obtained from comparable published analyses. Most observations could be made macroscopically or with low magnification. Thus, chipping could be assessed (in most cases) even if molding and casting was not possible due to the fragility of a specimen or prohibition by curators. Occasionally, an ante- or postmortem origin of an enamel chip could not be conclusively determined with macroscopic of low magnification observations. If the specimen was molded and cast it was observed with SEM to confirm the nature of the chip. If casts were not available, inconclusive specimens was removed from analyses.

Instrumental striations on labial enamel surfaces concentrated on a single tooth type (maxillary central incisors) – a sampling strategy intended to reduce error when calculating frequency by individual (see Chapter 7). The use of high-resolution epoxy-resin casts was necessary for each specimen with few exceptions. Light microscopy also works well for identifying some striations, but is less reliable when there are few striations and/or additional postmortem taphonomic modification of a surface. Therefore, the analysis of instrumental striations strongly emphasized analysis of high quality I^1 casts obtained from the original fossils by the author, or ones that were loaned to the author for this study.

Dental molding and casting for SEM analysis

Cotton-tipped applicators and 70% alcohol were used to gently clean tooth surfaces. After specimens air-dried, Colténe President Plus Jet light body polyvinylsiloxine (Coltène Whaledent) was used to generate dental molds. This material was chosen for its accurate replication properties (Beynon 1987; Hillson 1992; Pérez-Pérez et al. 2003; Galbany et al. 2004; Fiorenza et al. 2009; Goodall et al. 2015). Dust-free, plastic bags were used to store the molds immediately after their removal from the crowns.

Positive casts were made with Epo-tek 301 epoxy-resin. Casts were mounted on aluminum pin stubs and sputter-coated with ~ 20 nm of gold to guarantee conductivity for SEM analysis. Taphonomic surface alterations and antemortem dental wear features were documented on each dental cast using an accelerating voltage of 15 kV and working distance of 10-30 mm. Both high vacuum with secondary electron emission and low vacuum modes were used as needed. Analyses began with a field of view that encompassed a large portion of the labial enamel and magnification was increased to examine features in greater detail (Lozano et al. 2008). JEOL Neoscope JCM-5000 SEM (Monsanto Center Research Facility of the Missouri Botanical Garden, Saint Louis, MO, USA) was used for the majority of analyses, but a subset of the sample was analyzed using a Hitachi S3000N (SSTT-IUA) (Universitat de Barcelona, Spain).

Rationale for fossil sample sub-grouping

Chronological subdivisions are used to account for broad changes in behavior and technology throughout the Middle and Late Pleistocene. This is not to say that this study adopts any notion of "linear evolution", but acknowledges that there are vastly different technological strategies that were adopted by human groups during the Pleistocene. The chronological sub-grouping is based upon Marine Isotope Stages (MIS). Many of the fossils in this study have been directly or relatively dated with widely agreed upon results; however, there are fewer data available for some fossils (especially those from older excavations with less refined excavation techniques) which makes the use of broad chronological categories useful. The Neandertal sample is split into "earlier Middle Paleolithic Neandertals" (MIS 7-5) and "later Middle Paleolithic Neandertals" (MIS 4-3) – acknowledging both morphological and behavioral changes through time. However, the sample was condensed into a single group for macrowear gradient analyses due to small sample size. Likewise, early modern humans are divided into "Early Upper Paleolithic" (> 20 ka B.P.) and "Late Upper Paleolithic" (< 20 ka B.P. and > 10 ka B.P.) samples. The Early Upper Paleolithic corresponds largely to fossils with Aurignacian, Gravettian, and early Epigravettian chronologies and technocomplexes, but also includes fossils from non-Western Eurasian sites with morphological and chronological similarities (e.g., Tianyuan, Nazlet Khater, and Wadjak). The Late Upper Paleolithic sample designation corresponds with the onset of the Last Glacial Maximum and ends with the beginning of the Holocene. The 10 ka B.P. boundary used here is not the precise end of the Pleistocene, or beginning of the Holocene, but all samples close to this boundary are hunter-gatherers continuing the socioeconomic trends observed during the Late Upper Paleolithic. A few Mesolithic fossils were included in the macrowear gradient chapter as well. These groupings are chronologically broad enough to provide adequate sample sizes for analyses while not being too broad to completely mask behavioral variation across the assigned temporal boundaries (should meaningful variation exist).

In addition to the widely accepted Neandertal and Upper Paleolithic modern human groups described above are the Southwest Asian, MIS 5b, Middle Paleolithic modern humans from Skhul and Qafzeh. Again, this is a category based on both techno-chronological and morphological distinctions – acknowledging morphological distinctions from late archaic humans as well as chronological and technological differentiation from Early Upper Paleolithic modern humans. There are also a number of fossils from the Middle Paleolithic of North Africa (“Aterian” contexts) included in the macrowear gradient analysis. The samples from North Africa have a suite of derived and ancestral morphological characteristics and are described as “anatomically modern” humans by some researchers (e.g., Le Cabec et al. 2012, 2013; Smith et al. 2012) but “late archaic” humans by others (e.g., Trinkaus 2013). Therefore, the Aterian fossils were treated as a distinct sample based upon their technological, chronological, and geographic distinctions from the Neandertal and early modern human samples. Aterian data was only used in Chapter 5.

A small sample of Middle Pleistocene archaic *Homo* (including a few specimens attributed to the late Early Pleistocene) are discussed in relation to labial cutmarks, but are not a focus of this dissertation. These samples are largely for comparative purposes as the sample size is exceptionally meager, the chronology is rather broad, and consequently paleoenvironmental reconstructions are difficult. However, the Sima de los Huesos sample is well-documented with respect to specific dental wear features (Lozano et al. 2008, 2009); and it will provide a broader comparative perspective for some, predominantly microscopic, analyses.

Finally, not all fossils can be used for each analysis due to differences in completeness and preservation of individual dentitions. In addition, both macroscopic and microscopic methods are employed, but microscopic methods are only possible if high resolution casts were available for study or curators allowed the molding and casting of specimens. Therefore, **Table 4.1** notes which specimens were used for each analysis. Specific sources taken from the literature are listed in tables in the **Appendix** and are referenced in the analyses chapters.

Table 4.1 Fossil sites with specimens examined for each analysis.

Geographic Area	Site	MIS	Age	Cutmarks	Chipping	Macrowear	Dating & Context
Late Early Pleistocene to Middle Pleistocene							
Africa – Morocco	Rabat (Thomas Quarry)	12-11	470-360 ka BP			+	(Raynal et al. 2010)
Africa – Zambia	Broken Hill (Kabwe)	9 or 8	>300 ka BP	+	+	+	(Trinkaus 2009)
East Asia – China	Chaoxian	7-6	200-160 ka BP			+	(Chen et al. 1987; Bailey and Liu 2010)
East Asia – China	Jinnushan		>220 ka BP			+	(Chen and Yuan 1988)
Europe – Germany	Mauer	15	~600 ka BP	+	+	+	(Wagner et al. 2011)
Europe – Italy	Fontana Ranuccio	11	~400 ka BP		+	+	(Rubini et al. 2014)
Europe – Spain	Atapuerca – Sima del Elefante		1.3 to 1.2 ma BP	+			(Bermúdez de Castro et al. 2011)
Europe – Spain	Atapuerca – Gran Dolina	25	936 ka BP	+			(Parés et al. 2013)
Europe – Spain	Atapuerca – Sima del los Huesos	12	~430 ka BP	+	+	+	(Arsuaga et al. 2014)
Europe – United Kingdom	Boxgrove	13	~500 ka BP		+		(Roberts et al. 1997)
Earlier Neandertals (MIS 7-5)							
Europe – Belgium	Scladina I-4A	5e	127 +46/-32 ka BP			+	(Pirson et al. 2014)
Europe – Croatia	Krapina	6/5e	130 ± 10 ka BP	+	+	+	(Rink et al. 1995)
Europe – France	Bau de l'Aubesier 4	7 or 6	191 ± 15 – 169 ± 17 ka BP		+		(Lebel and Trinkaus 2002)
Europe – France	Biache-Saint-Vaast	7		+	+	+	(Rougier 2003)
Europe – France	La Chaise (Abri Bourgeois-Delaunay)	6/5	150-120 ka BP		+	+	(Blackwell et al. 1983; Condemi 2001)
Europe – France	Montgaudier	5e	~130 ka BP		+	+	(Mann and Vandermeersch 1997)
Europe – France	Montmaurin Coupe-Gorge	~7			+	+	(Billy 1982)
Europe – France	Payre	8/7			+	+	(Moncel and Condemi 2007; Moncel et al. 2008)

Table 4.1 Continued

***Earlier Neandertals (MIS 7-5)* Continued**

Geographic Area	Site	MIS	Age	Cutmarks	Chipping	Macrowear	Dating & Context
Europe – Germany	Erhingsdorf	7	~230 ka BP		+	+	(Blackwell and Schwarcz 1986)
Europe – Italy	Fate	5a				+	(de Lumley and Giacobini 2013a, b)
Europe – Italy	Saccopastore	7 or 5e	~250 ka BP or ~130-100 ka BP		+	+	(MIS 5e: Bruner and Manzi 2006; MIS 7: Marra et al. 2015)
Europe – United Kingdom	Pontnewydd	7	~220 ka BP	+	+	+	(Aldhouse-Green 1995; Aldhouse-Green et al. 2012)
West Asia – Israel	Tabun C2	6		+	+	+	(Grün and Stringer 2000; Mercier and Valladas 2003)
West Asia – Israel	Tabun C1, B-series, BC7	5	90 +30/-16 ka BP (BC7)	+	+	+	(Grün and Stringer 2000; Coppa et al. 2005)

Later Neandertals (MIS 4-3)

Geographic Area	Site	MIS	Age	Cutmarks	Chipping	Macrowear	Dating & Context
Europe – Belgium	Goyet	3		+	+	+	(Rougier et al. 2012)
Europe – Belgium	Spy	3	~36 ka BP	+	+	+	(Semal et al. 2009)
Europe – Croatia	Vindija	3	33-32 ka BP	+	+	+	(Karavanić 1995; Higham et al. 2006; Janković et al. 2006)
Europe – Czech Republic	Kůlna	3	50 ± 5 ka BP	+	+	+	(Rink et al. 1996; Svoboda et al. 1996; Svoboda 2005)
Europe – Czech Republic	Švédův stůl	4			+	+	(Svoboda et al. 1996; Svoboda 2005)
Europe – France	Angles Sur l'Anglin		"Mousterian"	+			(Patte 1960; Oakley et al. 1971; de Lumley 1976)
Europe – France	Arcy-sur-Cure (Grotte du Bison)	4				+	(David et al. 2009; Enloe 2011)
Europe – France	Arcy-sur-Cure (Grotte de l'Hyène)	4		+	+	+	(Oakley et al. 1971)
Europe – France	Bau de l'Aubesier	late MIS 5, MIS 4, or early MIS 3			+		(Trinkaus et al. 2000)
Europe – France	Grotte Boccard	4	Mousterian		+		(Maureille et al. 2008)

Table 4.1 Continued

Later Neandertals (MIS 4-3) Continued

Geographic Area	Site	MIS	Age	Cutmarks	Chipping	Macrowear	Dating & Context
Europe – France	Combe Grenal	4	~70 ka BP	+	+		(Garralda and Vandermeersch 2000)
Europe – France	La Ferrassie	3	~43–45 ka BP	+	+	+	(Heim 1976; Guérin et al. 2015)
Europe – France	Hortus	4		+	+	+	(de Lumley 1973; Condemi et al. 2010)
Europe – France	Genay	4				+	(de Lumley 1987; Yokoyama 1987; Garralda et al. 2008)
Europe – France	Monsempron	4		+	+	+	(Coulonges et al. 1952; Oakley et al. 1971)
Europe – France	Le Moustier	3		+	+	+	(Laville et al. 1980; Valladas et al. 1986; Mellars and Grün 1991)
Europe – France	Petit-Puymoyen	3		+	+	+	(Guillien 1961)
Europe – France	Les Pradelles (Marillac)	3	~45-40 ka BP			+	(Maureille et al. 2007; Mussini 2011)
Europe – France	La Quina	4		+	+	+	(Delpech 1996; Mellars 1996)
Europe – France	Regourdou	4		+	+	+	(Delpech 1996; Bonifay et al. 2007)
Europe – France	Saint-Césaire	3		+	+	+	(Lévêque and Backer 1993; Morin et al. 2005)
Europe – Germany	Neandertal	3	~40 ka BP	+	+	+	(Schmitz et al. 2002; Feine et al. 2006)
Europe – Hungary	Subalyuk	4	~70-60 ka BP			+	(Pap et al. 1996; Schwartz and Tattersall 2002)
Europe – Italy	Guattari	4	74-60 ka BP		+	+	(Schwarcz et al. 1991)
Europe – Spain	Banyoles	4	~66 ± 7 ka BP		+	+	(Grün et al. 2006)
Europe – Spain	Cova Foradá	4 or 3			+	+	(Campillo et al. 2002; Lozano et al. 2013)
Europe – Spain	Cova Negra	3		+	+		(Arsuaga et al. 2007)
Europe – Spain	El Sidrón	3	~49 ka BP	+	+		(Torres Pérez-Hidalgo et al. 2010; Wood et al. 2013b)
Europe – Spain	Sima de las Palomas	3	≤43–40 ka cal. BP and ~40-50 ka cal. BP	+	+	+	(Walker et al. 2008)

Table 4.1 Continued

Geographic Area	Site	MIS	Age	Cutmarks	Chipping	Macrowear	Dating & Context
Later Neandertals (MIS 4-3) Continued							
Europe – Spain	Valdegoba	6 to 3	180-31 ka BP (probably Würm)			+	(Quam et al. 2001)
Europe – Spain	Zafarraya		>46.7 ka BP	+	+	+	(Wood et al. 2013a)
Europe – Switzerland	Saint-Brais	3	“final Mousterian”; ~40 ka BP	+	+		(Koby 1956; Oakley et al. 1971; Becker and Rauber 2007)
Europe – United Kingdom	La Cotte de Saint Brelade	4-3				+	(Stringer and Currant 1986; Bates et al. 2013)
West Asia – Iraq	Shanidar	4-3	46.0 ± 1.5 ka to 70-60 ka BP for the middle of level D	+	+	+	(Trinkaus 1983)
West Asia – Israel	Amud	4-3	70-55 ka BP	+	+	+	(Suzuki and Takai 1970; Valladas et al. 1999; Rink et al. 2001)
West Asia – Israel	Kebara	4	~60 ka BP	+	+	+	(Valladas et al. 1987; Schwarcz et al. 1989; Bar-Yosef et al. 1992)
West Asia – Republic of Georgia	Sakijia	4 or 3	>45.7 ka BP (Würm I)			+	(Pinhasi et al. 2012; Moncel et al. 2015)
West Asia – Uzbekistan	Teshik-Tash	4 or 3				+	(Glantz et al. 2009)
Middle Paleolithic Modern Humans							
West Asia - Israel	Skhul	5	135-100 ka BP	+	+	+	(Grün et al. 2005)
West Asia - Israel	Qafzeh	5	MIS 5; 92 ± 5 ka BP	+	+	+	(Vandermeersch 1981; Schwarcz et al. 1988; Valladas et al. 1988)
North African Aterian							
Africa – Morocco	Dar es Soltane II	3				+	(Debénath et al. 1982; Hublin et al. 2012)
Africa – Morocco	Grotte des Contrebandiers	5b-5d	107 – 96 ± 4 ka BP			+	(Jacobs et al. 2011; Hublin et al. 2012)

Table 4.1 Continued

Early Upper Paleolithic

Geographic Area	Site	MIS	Age	Cutmarks	Chipping	Macrowear	Dating & Context
Africa – Democratic Republic of Congo	Ishango	3/2	~25-20 ka BP	+	+	+	(Boaz et al. 1990; Crevecoeur et al. 2010a)
Africa – Egypt	Nazlet Khater	3	37,570 ± 350/310 B.P.		+	+	(Crevecoeur 2008; Crevecoeur 2012)
Africa – Egypt	Wadi Kubbaniya	3/2	~25-20 ka BP			+	(Wendorf et al. 1986)
East Asia – China	Liujiang	3	~60-30 ka BP			+	(Wu 1982)
East Asia – China	Tianyuan	3	34,430 ± 510 BP		+	+	(Shang et al. 2007; Shang and Trinkaus 2010)
East Asia – China	Zhoukoudian Upper Cave	3	34-29 ka BP			+	(Wu and Poirier 1995)
Europe – Austria	Miesslingtal	3	"late Aurignacian"		+	+	(Szombathy 1950; Ahern et al. 2013)
Europe – Czech Republic	Brno II (Francouzská)	3	23,680 ± 200 BP		+	+	(Jelínek et al. 1959; Pettitt and Trinkaus 2000)
Europe – Czech Republic	Brno III	3				+	(Absolon 1929; Matiegka 1929)
Europe – Czech Republic	Dolní Věstonice	3	25,570 ± 280 to 26,640 ± 110 BP	+	+	+	(Trinkaus and Svoboda 2006)
Europe – Czech Republic	Mladeč	3	31,190 ± 400/390 B.P. (Mladeč 1); 31,320 ± 410/390 B.P. (Mladeč 2)		+	+	(Wild et al. 2005; Teschler-Nicola 2006)
Europe – Czech Republic	Pavlov	3	26-25 ka BP	+	+	+	(Trinkaus and Svoboda 2006)
Europe – Czech Republic	Předmostí	3	29-27 ka BP			+	(Svoboda 2008; Velemínská and Brůžek 2008)
Europe – France	Brassempouy	3	34-30 ka BP	+	+		(Henry-Gambier et al. 2004)
Europe – France	Isturitz			+	+		(Gambier 1990)
Europe – France	Abri Pataud	2	~22 ka BP	+	+	+	(Chiotti et al. 2015)
Europe – France	Les Rois	3	30.4-27.3 ka BP	+	+	+	(Ramirez Rozzi et al. 2009)
Europe – Italy	Arene Candide IP		23,440 ± 190 BP	+	+	+	(Pettitt et al. 2003)
Europe – Italy	Barma Grande 2-4			+	+	+	(Formicola 1988a; Formicola et al. 2004)

Table 4.1 Continued

Geographic Area	Site	MIS	Age	Cutmarks	Chipping	Macrowear	Dating & Context
Early Upper Paleolithic Continued							
Europe – Italy	Ostuni		24,410 ± 320 BP	+	+	+	(Vacca and Coppola 1993; Coppola 2012)
Europe – Romania	Muierii 1	3	~30 ka BP		+	+	(Soficaru et al. 2006; Doboş et al. 2010)
Europe – Russia	Kostenki 14 (Markina Gora)		~29 ka BP (minimum)			+	(Sinitsyn 1996; Sinitsyn et al. 1996; Sinitsyn 2004)
Europe – Russia	Sunghir	3	27,050 ± 210 BP (Cy1); 23,830 ± 220 BP (Cy2); 26,000 ± 410 BP (Cy3)		+	+	(Dobrovolskaya et al. 2012; Trinkaus et al. 2014)
Europe – Ukraine	Buran Kaya III, Layer 6-1	3	31,900 ± 240/220 BP	+	+		(Prat et al. 2011; Péan et al. 2013)
Europe – United Kingdom	Kent’s Cavern	3	~36 ka BP or 30,900 ± 900 ka BP		+	+	(Hedges et al. 1989; Higham et al. 2011; White and Pettitt 2012)
Southeast Asia – Indonesia	Wajak	3	37.4-28.5 ka BP (minimum age)		+	+	(Storm et al. 2013)
Southeast Asia – Laos	Tam Pa Ling	3	~46 ka BP			+	(Demeter et al. 2012)
West Asia – Israel	Nahal Ein Gev		25-22 ka BP			+	(Arensburg 1977; Hershkovitz et al. 1995)
Late Upper Paleolithic							
Africa – Algeria	Afalou Bou Rhummel	2	11,450 ± 230 to 13,120 ± 370 BP			+	(Hachi 1996; Hachi et al. 2002)
Africa – Morocco	Taforalt	2	12-11 ka BP			+	(Mariotti et al. 2009)
Africa – Sudan	Jebel Sahaba	2	14-12 ka BP			+	(Wendorf 1968)
East Asia – Japan	Minatogawa	2	18,250 ± 650 to 13,460 ± 110 BP			+	(Suzuki and Hanihara 1982; Kaifu et al. 2011; Matsu’ura and Kondo 2011)
Europe – Croatia	Šandalja II	2	12,320 ± 100 BP		+	+	(Janković et al. 2012)
Europe – Croatia	Vindija (Level D)	2		+	+	+	(Malez and Ullrich 1982; Janković et al. 2006)
Europe – Czech Republic	Koněprusy (Zlatý Kůň)	2	12,870 ± 70 BP		+	+	(Svoboda et al. 2002)

Table 4.1 Continued

Late Upper Paleolithic Continued							
Geographic Area	**Site**	**MIS**	**Age**	**Cutmarks**	**Chipping**	**Macrowear**	**Dating & Context**
Europe – France	Bruniquel (Abri Lafaye)	2	15,290 ± 150 BP			+	(Gambier et al. 2000)
Europe – France	Cap Blanc	2	Upper Magdalenian			+	(Dahlberg and Carbonell 1961; Oakley et al. 1971)
Europe – France	Farincourt	2	Upper Magdalenian		+	+	(Joffroy and Mouton 1946; Sauter 1957; Oakley et al. 1971)
Europe – France	Lafaye	2	Middle Magdalenian		+	+	Henry-Gambier, personal communication
Europe – France	Laugerie-Basse		Magdalenian			+	(Oakley et al. 1971)
Europe – France	Roc-de-Cave		11,210 ± 140 BP			+	(Gambier et al. 2000)
Europe – France	Rocher de la Peine	2	Late Magdalenian		+	+	(Ehrhardt 1992; Gambier and Houët 1993)
Europe – France	Rond-du-Barry 8	2	17,100 ± 450			+	(Gambier and Houët 1993)
Europe – France	Saint-Germaine-la-Rivière	2	15,780 ± 200 BP		+	+	(Gambier et al. 2000)
Europe – Germany	Bonn-Obercassel	2	11,570 ± 100 BP (OBK 1); 12,180 ± 100 BP (OBK 2)		+	+	(Street et al. 2006)
Europe – Germany	Brillenhöhle	2	12,470 ± 65 BP		+	+	(Orschiedt 2002)
Europe – Italy	Arene Candide	2/1	11-10 ka BP (AC 2, 3, & 4); 9,925 ± 50 BP (AC 5)			+	(Paoli et al. 1980; Formicola et al. 2005)
Europe – Italy	Grotta Giovanna	2	12,840 ± 100 BP (layer B)		+		(Cardini 1971; Bietti 1990; Naldini Segre 1992)
Europe – Italy	Maritza	2	Between 13.5 and 10.5 ka BP		+	+	(Mallegni 2005c)
Europe – Italy	Ortucchio	2	12,619 ± 410 BP		+	+	(Mallegni 2005d)
Europe – Italy	La Punta	2/1	10,581 ± 100		+	+	(Mallegni 2005b)
Europe – Italy	Riparo Fredian	2/1	9458 ± 91 BP (Level 4); 10,870 ± 119 BP (Level 5)	+	+	+	(Boschian et al. 1995; Mallegni 2005a; Vierin 2012)
Europe – Italy	Romanelli	2/1	~12-10 ka BP		+	+	(Fabbri 1987; Bietti 1990)
Europe – Italy	Romito		11,150 ± 150			+	(Mallegni and Fabbri 1995)
Europe – Italy	San Teodoro	2	14-10 ka BP			+	(Fabbri 1995; D'Amore et al. 2009)
Europe – Italy	Villabruna	2	12,140 ± 70 BP			+	(Vercellotti et al. 2008)

Table 4.1 Continued

Late Upper Paleolithic Continued

Geographic Area	Site	MIS	Age	Cutmarks	Chipping	Macrowear	Dating & Context
Europe – Portugal	Cisterna (Almonda)	2	~13 ka BP		+	+	(Trinkaus et al. 2011)
Europe – Romania	Climente II	2	12,565 ± 37 BP		+	+	(Bonsall et al. 2012)
Europe – Spain	Balma Guilanyà	1	11,095 ± 195			+	(Garcia-Guixé et al. 2009)
Europe – Spain	El-Mirón	2	15,460 ± 40 BP			+	(Carretero et al. 2015)
Europe – Spain	Nerja	2	Solutrean			+	(Lalueza-Fox 1995; Jordá Pardo and Aura 2008)
Europe – Switzerland	Le Bichon	2	11,760 ± 110 (tibia); 11,610 ± 110 (femur)		+	+	(Morel 1993)
Europe – United Kingdom	Gough's Cave	2	12,590 ± 50; 12,485 ± 50 BP	+	+	+	(Stevens et al. 2010)
Europe – United Kingdom	Tornewton	2	~15-10 ka BP		+		(Stringer and Powers 1978)
Southeast Australia	Cohuna	2/1	~13-9 ka BP			+	(Brown 1987)
Southeast Australia	Coobool Creek	2	12,500 ± 400 BP			+	(Brown 1987)
Southeast Australia	Kow Swamp	2/1	13,000 ± 280 to 9590 ± 130 BP			+	(Thorne 1975)
Southeast Australia	Talgai	2	11,650 ± 100 BP (soil horizon)			+	(Oakley et al. 1975)
Southeast Asia – Indonesia	Liang Lemdubu	2	19 ka BP			+	(O'Connor et al. 2005)
Southeast Asia – Laos	Tam Hang	2	13,740 ± 80 BP			+	(Shackelford and Demeter 2012; Kuzmin and Keates 2014)
Southeast Asia – Malaysia	Perak Man (Gua Gunung Ruhtuh)	2/1	10,120 ± 110 BP			+	(Majid 1994)
Southeast Asia – Papua New Guinea	Watinglo	2/1	10,000 BP			+	(Bulbeck and O'Connor 2011)
Southeast Asia – Vietnam	Hang Cho	1	9259 ± 206 BP			+	(Matsumura et al. 2008)

Table 4.1 Continued

***Late Upper Paleolithic* Continued**

Geographic Area	Site	MIS	Age	Cutmarks	Chipping	Macrowear	Dating & Context
West Asia – Israel	Ein Mallaha (Eynan)	2/1	Early, Late, and Final Natufian			+	(Bocquentin 2007)
West Asia – Israel	Erq El-Ahmar	2/1	Natufian			+	(Oakley et al. 1975)
West Asia – Israel	Hayonim	2	Early and Late Natufian; 12,360 ± 160 and 12,010 ± 180 BP			+	(Hopf and Bar-Yosef 1987; Belfer-Cohen 1988)
West Asia – Israel	Nahal Oren	2/1	Late Natufian			+	(Noy et al. 1973; Crognier and Dupouy-Madre 1974)
West Asia – Israel	Ohalo II	2	~19 ka BP	+	+	+	(Hershkovitz et al. 1995)
West Asia – Jordan	Wadi Hammeh	2	~12 ka BP			+	(Webb and Edwards 2002)
Mesolithic							
Europe – France	Baume de Montclus	1	~7-6.5 ka BP			+	(Ferembach 1974b; Meiklejohn et al. 2010)
Europe – France	Combe Capelle	1	8561 ± 27 BP			+	(Hoffmann et al. 2011)
Europe – France	Hoëdic	1	5750 ± 35 to 7165 ± 60 BP			+	(Meiklejohn et al. 2010)
Europe – France	Rochereil	1	Azilian			+	(Ferembach 1974a)
Europe – France	Téviec	1	6322 ± 40 to 6740 ± 60 BP			+	(Meiklejohn et al. 2010)
Europe – Italy	Mondeval de Sora	1	7,330 ± 59 BP				(Alciati et al. 1995)
Europe – Romania	Schela Cladovei	1	Late Mesolithic; ~7.2-6.3 ka cal. BP			+	(Bonsall 2008)
Europe – Spain	Braña-Arintero	1	6980±50 BP (Braña 1) 7030±50 BP (Braña 2)			+	(Vidal Encinas et al. 2010)
Europe – United Kingdom	Gough’s Cave	1	9,080 ± 150; 9,100 ± 100 BP			+	(Hedges et al. 1991)

Chapter 5. Scaled occlusal macrowear gradients

Hypotheses and Predictions

H_0: There will be no observable differences in scaled occlusal macrowear gradients between chronologically and morphologically-defined human groups.

This null hypothesis will be rejected if significant differences in the patterning of scaled occlusal wear gradients between groups are found between chronologically and morphologically-defined groups. If rejected, the magnitude and direction of the behavioral shifts among Middle and Late Pleistocene groups will be assessed.

Brief rationale for analysis

Extensive tooth wear, disproportionately concentrated on the anterior relative to posterior teeth is nearly universal among hunting and gathering peoples from the Pleistocene to the present day (Molnar 1972; Hinton 1981; Smith 1983a; Kaifu 2000b; Bermúdez de Castro et al. 2003; Deter 2009; Berbesque et al. 2012; Clement and Hillson 2012; Clement et al. 2012; Littleton et al. 2013; Botha and Steyn 2015). However, gross differences in dental dimensions between archaic and modern human groups make comparisons of occlusal wear gradients less straight forward than studies of more recent human groups. This is primarily due to the high frequencies of mass-additive dental traits found among archaic humans – particularly in the anterior dentition (see Chapter 3). There are several ways in which researchers have attempted to account for potential bias from between group dental size differences when examining macrowear gradients among Late Pleistocene humans.

One method is to restrict comparisons to groups with similarly sized dentitions. For instance, despite having additional comparative data on chimpanzees, Smith (1983) restricted comparisons to Late Pleistocene humans and Holocene foragers and agriculturalists when she examined I^1 versus M^1 wear gradients (ordinal wear scores were used [Smith 1983, 1984]). This was due to the massive size difference between human and chimpanzee central incisors: "*In chimpanzees, the heavily worn, greatly expanded maxillary central incisors attest to their use in stripping and husking foods. Since I^1 wear for chimpanzees and humans cannot reflect equal use due to the size difference, they are omitted from this comparison* (Smith 1983:119)." The reasoning behind the exclusion of non-human primate data is sound, but the same reasoning can be applied to comparisons of archaic and modern human group central incisors (or anterior teeth in general) – the larger anterior teeth of the former would require more wear per unit area to attain the same wear score as a smaller tooth crown from a modern human.

In a similar study, Kaifu (2000b) examined the antiquity of extensive dental wear in genus *Homo* and used Smith's (1984) occlusal wear scores to investigate patterns of wear across a relatively large sample of fossil *Homo.* The use of ordinal wear scores allowed Kaifu (2000a) to note that many hominin taxa exhibited high rates of wear. However, the interspecific differences in tooth size will inevitably effect the rate of dental wear, and these differences would be quite meaningful considering the range of crown size variation found across both time and space in genus *Homo*.

Clement and colleagues (2012) examined Neandertal and modern human occlusal wear gradients using ratios of dentin exposure while controlling for dental eruption sequence. They found that in many cases Pleistocene and recent human groups exhibited more extensive anterior dental wear than the Neandertals (Clement et al. 2012). Again, this study did not consider the differences in anterior tooth size between archaic and modern human groups.

The above examples illustrate a problem in assessing Pleistocene dental wear gradients: overlapping in occlusal wear (whether an ordinal scoring of ratio approach) does not account for differences in total crown volume lost when comparing groups that differ in some aspect of dental metrics. For example, if we examine a Neandertal I^1 and an Epipaleolithic modern human I^1 that exhibit the same ratio of dentin exposure (or even have same ordinal wear score) the Neandertal tooth would have lost more total crown volume given the larger tooth dimensions. Furthermore, the functional area of the occlusal surface changes drastically with increasing dental wear due to the changing convexity of a given crown. Incisors provide the most drastic example whereby the occlusal surface initially enlarges with increasing wear before diminishing again as wear approaches the root (see Figure 2 in Bermúdez de Castro et al. 2003).

The relatively thin enamel and expanded dentin in Neandertal teeth compared to those of modern humans poses a problem when using dentin exposure ratios. For instance, if one takes similarly sized Neandertal and early modern humans molars, each worn to a Smith stage 6 (i.e., the enamel rim is complete), the Neandertal would exhibit a higher percentage of exposed dentin, because Neandertals exhibit thinner overall enamel (see Chapter 2). Therefore, ordinal scales may be a more appropriate, albeit a less precise scale, because of enamel thickness differences between archaic and early modern humans (see Trinkaus 2011 for a similar argument). While no system accounts for differences in tissue proportions, wear, and crown size perfectly at the level of interspecific variation, it seems that some proxy for occlusal area relative to crown wear is both a biologically and functionally important consideration.

The introduction of crown size into analyses of occlusal macrowear helps parse out any influence differential tooth dimensions may have on macrowear variation at the individual and group-level (Trinkaus 1992; Doboş et al. 2010; Willman 2016, 2017). Trinkaus (1992) first employed a relatively simply means of controlling for tooth size when examining occlusal wear gradients by multiplying the occlusal wear score of a given tooth by its buccolingual crown breadth, the assumption is that similarly sized tooth surfaces wear at similar rates. Trinkaus (1992) summed anterior and posterior tooth scores separately and examined the results in bivariate plots. This approach introduces dental size, and ensures that similarly worn teeth are compared to each other through the use of the same multiplier (i.e., their wear score).

Graphically, the y-axis represents the scaled macrowear scores of the summed anterior teeth and the x-axis represents the scores for the posterior dentition. Slopes will be positive due to a greater number (and larger average breadth by tooth type) of the summed posterior teeth compared to summed anterior teeth with an additional influence from the multiplicative effect of occlusal wear scores. Due to the nature of the variables, values at the extremes of a distribution for any group will be highly influential on the slope of the line. At the level of the individual, anterior teeth are expected to wear more quickly than posterior teeth due to their smaller size. Thus, a difference in grade between groups is expected when teeth (particularly anterior ones) of different dimensions, but the same or similar wear scores, are compared.

Methods

Anterior relative to posterior occlusal macrowear was scaled to buccolingual crown dimensions by multiplying the occlusal wear score (Smith 1984) of a tooth by the buccolingual (BL) crown dimension of the same tooth. Right and left side Smith scores and BL widths were averaged for an individual if an antimere was present. Summed anterior (I1, I2, and C) scaled wear scores and summed posterior (P3-M2) scaled wear scores were then calculated for each individual with a complete hemi-arcade series. Calculations were done separately for maxillary and mandibular dentitions. The summed anterior scaled wear scores were plotted against the summed posterior scaled wear scores using bivariate plots. This method follows Trinkaus (1992) with several notable exceptions:

1. Teeth worn beyond their maximum buccolingual crown diameters were measured and included in the present study.
2. Smith's (1984) system of categorizing occlusal wear scores was substituted for the scale used by Molnar (1971).
3. Data obtained from the literature were also included in this analysis.
4. Third molars were excluded from the analysis.
5. Entire dentitions and partial dentitions were analyzed. Difference combinations of anterior and posterior teeth were included or dropped from analyses.

These exceptions to the methods employed previously (Trinkaus 1992) were made to increase fossil sample sizes beyond comparisons between the few relatively complete Middle and Late Pleistocene dentitions. The exceptions are explored more below.

1. Dental metrics

Buccolingual crown dimensions measured from original fossils were measured in a way that reflected occlusal wear rather than correcting for it. For instance, if a crown is worn to such a degree that the maximum buccolingual crown breadth is no longer preserved, a researcher may estimate tooth within a few fractions of a millimeter. However, this study only considers measurements that reflect the *functional* dimension of the tooth crown. That is to say that any tooth worn beyond its maximum dimensions is still providing a functional occlusal surface. Thus, the buccolingual dimensions measured will *reflect* occlusal wear instead of correcting for wear.

Measurements of worn teeth were made with calipers perpendicular to the cementoenamel junction (sometimes using the alveolar plane as an additional reference in cases of extreme or atypical wear) regardless of the degree of occlusal surface slanting. Lingual tilting of molars (Reinhardt 1983b; Taylor 1991) can create an occlusal surface that is equal to or even greater than the original crown dimensions due to the formation of strongly slanted wear and commensurate dislocation of root tips on one side of the tooth (typically the buccal roots in the mandible and lingual roots in the maxilla). This occurrence was more common and accentuated in the Late Upper Paleolithic samples, but was not common (Willman, personal observation). Nevertheless, attritional facets on the roots delimit the functional occlusal surface and the buccolingual dimension measured in these rare cases.

Smith (1984) scores of 6, 7, 8 and sometimes 5 are often accompanied by a substantial loss of crown height, buccolingual, and/or mesiodistal dimensions. Dental metrics are commonly sought for studies of biological distance or functional morphology; therefore, teeth worn to such an extent are of less utility for these purposes unless the original crown size can be reasonably estimated at the discretion of the researcher. Estimated maximum buccolingual dimensions are of no use in the present study and worn crown dimensions are infrequently reported in the literature. When using buccolingual dimensions from the literature, care was taken to determine whether the dimensions reflect actual, worn, or estimated buccolingual dimensions. If occlusal wear was severe, and there is no indication of whether a tooth was measured worn or if maximum diameters were estimated, that tooth/specimen was not included in the present study unless it could be re-measured firsthand or from high-quality casts. Furthermore, published dimensions were only used if they were rounded to the nearest 0.1 mm, since some studies (particularly older publications) only provide dimensions to the nearest 0.5 mm which are not accurate enough for the present study.

When antimeres were present, an average value for used. Buccolingual dimensions provided by B. H. Smith (personal communication) reflect wear and present no problems for the present study. The source of all buccolingual metrics are provided for each specimen in **Appendix Table 2**.

In addition to scaled occlusal wear gradients, differential wear of anterior teeth versus first molars wear also analyzed. These scores are the raw, unscaled Smith scores for individual anterior teeth minus the value of the first molar from the same jaw. Zero would indicate no difference between anterior and posterior wear scores, a positive score indicates higher anterior relative to posterior wear scores, and a negative score indicates molar wear was higher than anterior wear scores. Box and whisker plots using standard interquartile range scores are provided with complimentary density plots for each tooth type. The density plots help illustrate the overlap in values given the high frequency of overlapping scores in each sample.

2. Occlusal Wear

Trinkaus (1992) employed Molnar's (1971) occlusal wear recording system but all of the individuals included in that analysis have been re-coded for the present study using Smith's (1984) system. The Smith system is more commonly, but not universally, used by researchers in large part for its clear graphic and written description as well as its suggested use for standard osteological data collection (Buikstra and Ubelaker 1994). Molnar's system persists in the paleoanthropological literature, but it is largely synonymous with the Smith system in terms of intent and outcome (**Table 5.1**). One difference is the attention paid to secondary dentin formation by Molnar (1971), but secondary dentin is not always a useful characteristic when dentin is altered by postmortem processes (e.g., root etching, desert varnish, enamel/dentin spalling). One area of possible error is a Smith (1984) and Molnar (1971) scores of "1" are not entirely complimentary. Molnar concludes that a "1" is "unworn" but for the Smith system it can be unworn or "polished".

Table 5.1 Molar dental macrowear scoring systems.

	Smith	Molnar	Skinner
1	Unworn to polished or small facets (no dentin exposure).	Unworn	Enamel faceting (trace). On individual cusps of the primary molars and permanent molars this earliest stage of attrition is visible as tiny planes or facets which reflect light from their flat surfaces. [T]here is no reduction in crown height at this attrition stage.
2	Moderate cusp removal (blunting). Permanent molars show no more than one or two pinpoint exposures.	Wear facets, no observable dentin.	Enamel rounding (mid). Cusp tips are slightly smoothed and rounded with loss of angulated faceting. Main fissures and crenulations are largely pristine. There is only minimal loss of crown height.
3	Full cusp removal and/or some dentin exposure, pinpoint to moderate.	Cusp pattern partially or completely obliterated. Small dentin patches	Enamel flattening (advanced). There is appreciable reduction in crown height resulting in broad, flattish, low occlusal elevation. On cheek teeth the majority of the occlusal surface is involved although deeper fissures may be little affected. Cusp tips are obviously rounded. There is trace, or typically no, dentin exposure but dentin may be discernible through a thin enamel layer.
4	Several large dentin exposures, still discrete.	Three or more small dentin patches.	Slight dentin exposure. On molariform teeth, this stage is differentiated from the next by the fact that attrition tends to be angled such that dentin is exposed first on one side of the tooth and only later on the other as well. At this stage, one or two (rarely more) islands of dentin are exposed on one side of the tooth (buccal in lowers, lingual in uppers).
5	Two dentinal areas coalesced.	Three or more large dentin patches, secondary dentin, none to slight.	Dentin advanced. Dentin islands show on both sides of molariform teeth of a size exceeding that of the previous stage. There is no coalescence of dentin islands.
6	Three dentinal areas coalesced, or four coalesced with enamel island.	Secondary dentin moderate to extensive, entire tooth completely surrounded by enamel.	Strong dentin exposure. On molariform teeth there is coalescence of two or more islands of dentin even to the point where enamel remnants may only remain on the central occlusal surface. There is marked crown height reduction.
7	Dentin exposed on entire surface, enamel rim largely intact.	Crown, enamel worn away on at least one side, extensive secondary dentin.	Enamel ring. All occlusal enamel is worn away on molariform teeth leaving only an enamel ring of fairly uniform width circumferentially. There may be darkly stained islands of secondary dentin.
8	Severe loss of crown height, breakdown of enamel rim; crown surface takes on shape of roots.	Roots functioning in occlusal surface.	Root involvement. While self-explanatory, this occurs on the labial and buccal side of mandibular teeth and on the lingual side of maxillary teeth.

[1] Descriptions are from Smith (1984:45), Molnar (1971:178), and Skinner (1997:681-682).

Table 5.1 (Continued) Premolar dental macrowear scoring systems.

	Smith	Molnar	Skinner
1	Unworn to polished or small facets (no dentin exposure).	Unworn.	Enamel faceting (trace). [T]here is no reduction in crown height at this attrition stage.
2	Moderate cusp removal (blunting).	Wear facets, no observable dentin.	Enamel rounding (mid). Cusp tips are slightly smoothed and rounded with loss of angulated faceting. Main fissures and crenulations are largely pristine. There is only minimal loss of crown height.
3	Full cusp removal and/or moderate dentin patches.	Cusp pattern partially or completely obliterated. Small dentin patches.	Enamel flattening (advanced). There is appreciable reduction in crown height resulting in broad, flattish, low occlusal elevation. On cheek teeth the majority of the occlusal surface is involved although deeper fissures may be little affected. Cusp tips are obviously rounded. There is trace, or typically no, dentin exposure but dentin may be discernible through a thin enamel layer.
4	At least one large dentin exposure on one cusp.	Two or more dentin patches, one of large size.	Slight dentin exposure. On premolars one cusp, as opposed to both, shows slight dentin exposure.
5	Two large dentin areas (may be slight coalescence).	Two or more dentin patches, secondary dentin may be slight.	Dentin advanced. Dentin islands show on both sides of molariform teeth of a size exceeding that of the previous stage. There is no coalescence of dentin islands.
6	Dentinal areas coalesced, enamel rim still complete.	Entire tooth still surrounded by enamel, secondary dentin moderate to heavy.	Strong dentin exposure. On molariform teeth there is coalescence of two or more islands of dentin even to the point where enamel remnants may only remain on the central occlusal surface. There is marked crown height reduction.
7	Full dentin exposure, loss of rim on at least one side.	Crown (enamel) worn away on at least one side, extensive secondary dentin.	Enamel ring. All occlusal enamel is worn away on molariform teeth leaving only an enamel ring of fairly uniform width circumferentially. There may be darkly stained islands of secondary dentin.
8	Severe loss of crown height; crown surface takes on shape of roots.	Roots functioning in occlusal surface.	Root involvement. While self-explanatory, this occurs on the labial and buccal side of mandibular teeth and on the lingual side of maxillary teeth.

[1] Descriptions are from Smith (1984:45), Molnar (1971:178), and Skinner (1997:681-682).

Table 5.1 (Continued) Incisor and canine dental macrowear scoring systems.

	Smith	Molnar	Skinner
1	Unworn to polished or small facets (no dentin exposure).	Unworn.	Enamel faceting (trace). On canine teeth, faceting can be seen on the side or tip of the crown while incisors show initial reduction of mammelons. Otherwise there is no reduction in crown height at this attrition stage.
2	Point or hairline of dentin.	Wear facets minimal in size.	Enamel rounding (mid). On incisors, the mammelons are worn away while the incisal edge is still narrow and unflattened. There is only minimal loss of crown height.
3	Dentin line of distinct thickness.	Cusp pattern obliterated, small dentin patches may be present.	Enamel flattening (advanced). There is appreciable reduction in crown height resulting in broad, flattish, low occlusal elevation. Incisors exhibit a broad, flat incisal edge with crown reduction and often darkly staining dentin visible through a thin enamel veneer. Canines may tend to show relatively more dentin than the other teeth at this stage.
4	Moderate dentin exposure no longer resembling a line.	Dentine patch (minimal).	Slight dentin exposure. For canines, only a small spot of dentin is exposed—about the size of a pencil dot. Incisors show a thin strip of dentin, tapering mesially and distally—about the width of a thin pencil line.
5	Large dentin area with enamel rim complete.	Dentine patch (extensive).	Dentin advanced. Larger spots and strips of dentin may be seen on canines and incisors, respectively.
6	Large dentin area with enamel rim lost on one side or very thin enamel only.	Secondary dentin (moderate to extensive).	Strong dentin exposure. There is marked crown height reduction. Canine teeth show large dentin exposure with crowns about half original height. Incisors now resemble canine teeth with an expanding circle of dentin within the dentin strip, due to encroachment of attrition on the deep pulp chamber.
7	Enamel rim lost on two sides or remnants of enamel remain.	Crown (enamel) worn away on at least one side, extensive secondary dentin.	Enamel ring. There may be darkly stained islands of secondary dentin. Canines are judged to be at this stage by having circumferential enamel of a width similar to that of posterior teeth. Incisors show very strong height reduction with loss of interproximal contact and round or oval dentin exposure to a marked degree.
8	Complete loss of crown, no enamel remaining; crown surface takes on shapes of roots.	Roots functioning in occlusal surface.	Root involvement. While self-explanatory, this occurs on the labial and buccal side of mandibular teeth and on the lingual side of maxillary teeth.

[1] Descriptions are from Smith (1984:45), Molnar (1971:178), and Skinner (1997:681-682).

A third scoring system, that of Skinner (1997) is also still used on occasion. Again, this system is largely synonymous with the Smith and Molnar systems, differing in the specificity of its directions but not in how teeth were scored. The Skinner system was only used for the El Sidrón materials used in Chapters 8 and 9 but is included here for completeness. Nonetheless, and importantly, all three systems use eight categories and present similar diagrammatic and/or written examples of each wear stage. Thus, little translation error exists between the systems and in most cases error would not deviate by more than one stage in either direction – error that is within inter-observer error rates (Kimmerle et al. 2008). Other scoring systems found in the paleoanthropological literature focus on more precise details of molar wear (Scott 1979), use fewer categories (Broca 1879; Turner et al. 1991), or are close to the 8-stage systems (Brothwell 1989) but require some degree of guesswork (and therefore the introduction of potential error) to translate scores to Smith scales. Thus, descriptions using these systems were only used as supporting criteria for assigning Smith scores to fossils in the literature that were accompanied by accurate image documentation (occlusal photos and/or line drawings).

3. Data from other sources

Photographs and line drawings can provide accurate depictions of occlusal wear, especially when combined with multiple views and/or written descriptions of dental wear. The scoring of wear from images is most difficult in the slightly worn teeth (scores 1-2) and more heavily worn dentitions (scores 6-8). These stages most often differ between observers when examining skeletal material in person (Kimmerle et al. 2008), so it is no surprise that they are difficult to score from images. When examining highly worn dentitions it can be difficult to discern between an extremely thin ring or section of enamel and the loss of enamel on one, two, or all sides of a crown in some images (particularly black and white images or images on non-glossy paper). Similarly, young individuals with faint faceting or the slightest dentin exposure (scores 1 and 2) are also difficult to identity from photographs unless resolution is particular high.

The presence of antimeres allows two chances to score a given tooth type from an image. Right-left occlusal asymmetry rarely deviates by more than 1 wear category in Late Pleistocene samples (Willman, personal observation). Thus, if one antimere can be scored but the other cannot the risk of error is small and likely to be off by no more than a half category (0.5) after averaging. Due to these difficulties of documenting certain wear scores using images, the least worn and most worn teeth/dentitions are less represented than individuals with easily scored dentin exposure – particularly scores 3-6 across all tooth types. Scores 1 and 8 are most difficult to score from images (Willman, personal observation). In all cases, a conservative approach is taken when using images to obtain wear scores. Any tooth proving too difficult to document using photographs is omitted.

4. Exclusion of third molars

Third molars were eliminated because of their highly variable dimensions (Hillson 1996; Scott and Turner 2000; Barrett et al. 2012; Willman 2014) in addition to the common occurrence of third molar agenesis among recent (Carter and Worthington 2015) and Late Pleistocene humans (Hillson 2006; Willman, personal observation). Furthermore, maxillary and mandibular M3’s were not considered because they erupt and obtain functional occlusion in early adulthood which would exclude many younger-aged individuals from most comparisons of full arcades. The use of photographs to increase sample size would also be fruitless if third molars were included given the difficulties in discerning wear scores affecting only enamel (scores 1 or 2).

5. Entire dentitions and partial dentitions were analyzed.

The use of partial dentitions for macrowear gradient analysis is not common despite the rare occurrence of complete dentitions in the Pleistocene fossils record. However, anterior relative to posterior dental wear is possible for any number of teeth as long as at least one anterior tooth and one posterior tooth is present. Here, first molars were chosen as the posterior tooth and the comparisons with each anterior tooth of the same jaw were performed. Three recent studies have made use of this strategy when describing anterior dental wear for partial fossil dentitions (Doboş et al. 2010; Willman 2016, 2017).

Exploratory data analysis with bivariate plots

Bivariate plots of all anterior versus all posterior teeth (except third molars) are presented for each jaw. When examining complete dentitions, third premolars were considered anterior teeth in one analysis and posterior in another. Third premolars often co-vary in size and morphology with incisors and canines while fourth premolars co-vary with molars (see discussion in: Martinón-Torres and Bermúdez de Castro 2016), and meaningful variation in occlusal gradients may be masked by categorizing premolars strictly as posterior teeth. The 95% confidence intervals (CI) of both *y*-intercept and slope are provided in tables accompanying each plot. *P*-values for slope are presented for whether the slope is significantly different from zero. Although presented, these *P*-values are expected to be highly significant but generally uninformative due to small sample size. Furthermore, Regression lines are shown but are only meant to be used for exploratory, heuristic purposes and not as a means of prediction. The general trends are discussed below.

Results

I1-C versus P3-M2 scaled occlusal wear gradients

Figure 5.1 shows the results of maxillary (I^1-C versus P^3-M^2 and I^1-P^3 versus P^4-M^2) scaled macrowear gradients. The steep slope for the Middle Pleistocene humans is driven by the low values for Rabat 1 and a single individual from Sima de los Huesos – the 95% CI of slope and y-intercept overlap completely with the other samples. The predominant pattern in the maxillary dentition is one of similarity in rates of wear (occlusal wear scores are similar), but the difference in intercept indicates more tooth volume loss per unit of occlusal wear in archaic groups relative to modern humans, albeit with substantial overlap. The Middle Pleistocene and Neandertal samples are separated along a size gradient, as would be expected given the presence of large dental size and frequency of mass-additive dental traits in those groups. Likewise, the intermediate position of the Middle Paleolithic modern human is a product of similar rates of dental wear to the other samples and presence of intermediate dental size (and frequencies of mass-additive traits) when compared to archaic humans and their Upper Paleolithic successors. The Early Upper Paleolithic, Late Upper Paleolithic, and Mesolithic groups are largely indistinguishable in overall trends but the Late Upper Paleolithic and

Mesolithic groups tend to have a wide range of variability. This fact may be due in part to the broad geographic sampling of these groups, but also to the presence of the cultural modification on the dentition (i.e., incisor ablation – the intentional removal of healthy teeth) in several of the Late Upper Paleolithic groups. There is little difference in overall patterning when P^3's are considered anterior teeth – the relative position of each group is unchanged.

Figure 5.2 provides mandibular (I_1-C versus P_3-M_2 and I_1-P_3 versus P_4-M_2) scaled macrowear gradients. Scaled macrowear gradients in the mandibular dentition exhibit more overlap between samples than seen in the maxillary dentition. The Neandertals stand out again as having large dentitions relative to other groups which implies the removal of a greater volume of tooth mass per unit of occlusal wear compared to other groups. The Middle Paleolithic modern human and Early Upper Paleolithic groups are nearly indistinguishable and the one North African Aterian specimen (i.e., Grotte des Contrebandiers) falls on the Middle Paleolithic modern human line. Again, there is considerable variation in the Late Upper Paleolithic and Mesolithic samples. The lowest rate of anterior versus posterior wear is found in the Late Upper Paleolithic sample. This is most likely an artifact of combining samples with maxillary incisor ablation – and therefore, less wear on occluding mandibular incisors – with Late Upper Paleolithic samples that do not exhibit ablation. Again, including P_3's with the anterior dentition does little to disrupt the patterning already documented in incisors and canines.

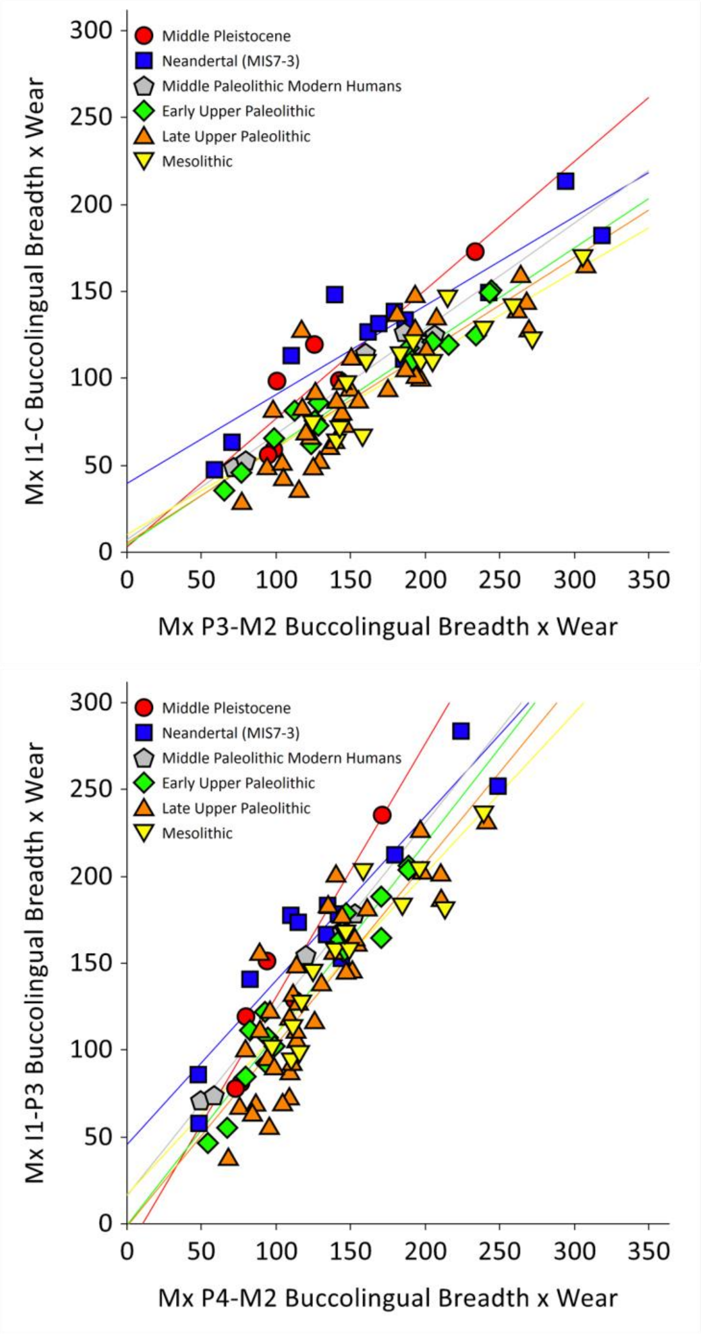
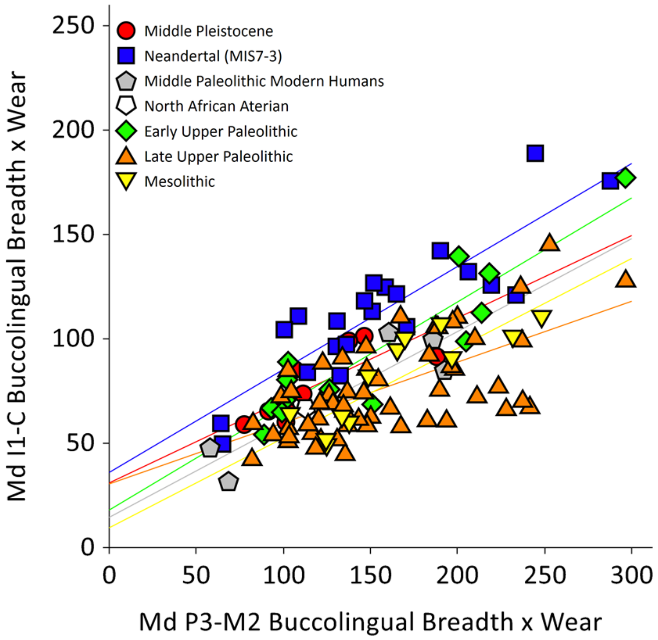


Figure 5.1 Maxillary scaled macrowear gradients of full dentitions.
Top: Anterior (I^1-C) versus posterior (P^3-M^2) dentition. Bottom: Anterior (I^1-P^3) versus posterior (P^4-M^2). Regression statistics in **Table 5.2**.



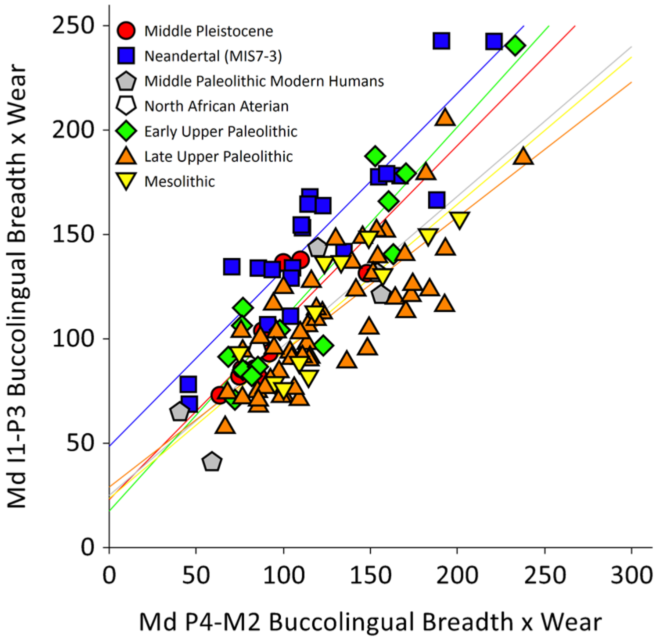


Figure 5.2 Mandibular scaled macrowear gradients of full dentitions.
Top: Anterior (I_1-C) versus posterior (P_3-M_2) dentition. Bottom: Anterior (I^1-P^3) versus posterior (P_4-M_2). Regression statistics in Table 5.2.

Table 5.2 Regression statistics for scaled occlusal wear gradient analyses of full dentitions.

Group	*N*	*y-int*	*95% CI*	*Slope*	*95% CI*	*r*	R^2	*P*
I^1-C vs P^3-M^2 (Fig. 5.1 top)								
Middle Pleistocene	6	2.77	-64.86 – 70.41	0.74	0.26 – 1.22	0.9061	0.8209	0.0128
Neandertals	12	39.71	19.00 – 60.42	0.51	0.40 – 0.62	0.9027	0.8148	<0.0000
MPMH[a]	6	7.33	-1.08 – 15.73	0.61	0.55 – 0.66	0.9811	0.9626	<0.0000
EUP[b]	15	4.16	-0.39 – 8.70	0.57	0.54 – 0.60	0.9761	0.9528	<0.0000
LUP[c]	37	5.41	-1.94 – 12.76	0.55	0.50 – 0.59	0.8451	0.7141	<0.0000
Mesolithic	15	10.49	0.05 – 20.92	0.50	0.45 – 0.56	0.8725	0.7612	<0.0000
I^1-P^3 vs P^4-M^2 (Fig. 5.1 bottom)								
Middle Pleistocene	6	-14.89	-94.01 – 64.24	1.46	0.71 – 2.20	0.9388	0.8813	0.0055
Neandertals	12	45.31	22.69 – 67.93	0.94	0.79 – 1.10	0.9381	0.8800	<0.0000
MPMH	6	16.34	10.31 – 22.37	1.07	1.02 – 1.12	0.9944	0.9888	<0.0000
EUP	15	-0.99	-8.81 – 6.83	1.10	1.04 – 1.16	0.9677	0.9365	<0.0000
LUP	37	-1.14	-11.31 – 9.02	1.04	0.97 – 1.12	0.8601	0.7398	<0.0000
Mesolithic	15	16.98	4.38 – 29.58	0.92	0.84 – 1.00	0.9007	0.8113	<0.0000
I_1-C vs P_3-M_2 (Fig. 5.2 top)								
Middle Pleistocene	10	30.86	1.23 – 60.50	0.40	0.15 – 0.64	0.7944	0.6311	0.0060
Neandertals	21	35.98	21.31 – 50.64	0.49	0.41 – 0.58	0.8739	0.7637	<0.0000
MPMH	5	14.53	-0.75 – 29.82	0.44	0.34 – 0.55	0.9022	0.8139	<0.0000
EUP	14	18.01	10.52 – 25.50	0.50	0.45 – 0.55	0.9216	0.8493	<0.0000
LUP	55	30.38	24.56 – 36.21	0.29	0.26 – 0.33	0.6421	0.4123	<0.0000
Mesolithic	12	9.32	0.39 – 18.24	0.43	0.38 – 0.48	0.8597	0.7391	<0.0000
I_1-P_3 vs P_4-M_2 (Fig. 5.2 bottom)								
Middle Pleistocene	10	22.87	-25.60 – 71.35	0.85	0.34 – 1.36	0.8045	0.6472	0.0050
Neandertals	21	48.47	31.60 – 65.34	0.85	0.71 – 0.98	0.8999	0.8098	<0.0000
MPMH	5	25.01	0.16 – 49.85	0.72	0.50 – 0.93	0.8566	0.7338	<0.0000
EUP	14	14.58	7.47 – 27.70	0.92	0.84 – 1.00	0.9301	0.8651	<0.0000
LUP	55	29.08	22.46 – 35.70	0.65	0.60 – 0.70	0.7891	0.6227	<0.0000
Mesolithic	12	23.49	11.28 – 35.70	0.70	0.61 – 0.80	0.8468	0.7170	<0.0000

[a] MPMH (Middle Paleolithic Modern Humans), [b] EUP (Early Upper Paleolithic), and [c] LUP (Late Upper Paleolithic)

Individual anterior teeth versus first molars scaled occlusal wear gradients

When considered individually, each maxillary anterior tooth exhibits a trend similar to that seen among the summed anterior and posterior maxillary teeth (**Figure 5.3**). Slopes are higher among Middle Pleistocene and Neandertal groups as compared to the modern human groups. However, the greatest difference can be attributed to the relatively larger anterior tooth dimensions among the archaic groups compared to modern human groups. Thus, there is a greater loss of anterior tooth volume per unit of occlusal wear in archaic groups versus modern human groups, but the variation among Early Upper Paleolithic, Late Upper Paleolithic, and Mesolithic samples is quite extensive with modest overlap across the range of archaic human variation.

Neandertal mandibular first and second incisor wear is higher with respect to all other groups, though mandibular canines differ more in terms of size than rate of wear (**Figure 5.3**). The trends among the Aterian specimens are unclear given the miniscule sample size (N = 2-3). Again, the trend among Late Upper Paleolithic I_1 and I_2 wear shows extremely low rates of attrition with respect to M_1 wear – a result of pooling samples of individuals with and without avulsion.

Rates of wear among individuals with the greatest degree of anterior occlusal wear are quite similar for several Early Upper Paleolithic and Neandertal individuals. The subtle differences in the slope of the exploratory regression lines may indicate a greater degree of anterior crown volume loss in archaic humans than early modern humans in most instances, but the regression lines are fitted to small samples with variably overlapping 95% CI's. Nonetheless, the rates of wear between groups for individual anterior teeth are quite similar to that seen in the analyses of the entire arcade. It seems that regardless of initial crown size these specimens all continued to actively engage in anterior tooth use until the functional occlusal surfaces of crowns were worn to root stubs. Root stubs are absolutely larger in archaic humans and the contrast is obvious when examining the relative difference between archaic and Late Upper Paleolithic individuals (with comparable small root breaths) toward the right ends of the distribution. Notice also that Early Upper Paleolithic and Neandertal specimens toward the right sides of the distributions also tend to have similar values – this indicates some overlap in root dimensions per unit of wear as would be expected based on the overlap in root morphology described in the literature (Le Cabec et al. 2013; Trinkaus et al. 2013a, 2014).

Differential occlusal wear scores: Individual anterior teeth versus first molars

The range of variation for the differential wear of individual maxillary and mandibular anterior teeth (**Figure 5.4** and **Table 5.4**) versus first molars from the same jaw shows substantial overlap between samples. In contrast to the analyses above, these figures express differential occlusal wear scores *without* accounting for crown size – thus, they are similar to analyses (Smith 1983a; Kaifu 2000b) outlined at the beginning of this chapter. Both maxillary and mandibular I1's show positive median differential wear values for Middle Pleistocene, Neandertal, Middle Paleolithic modern humans, and Early Upper Paleolithic groups. However, the second incisor and canine values median values tend to tend to be highest in Middle Pleistocene and Neandertal groups and negative or around zero in the Middle Paleolithic and Early Upper Paleolithic modern humans.

The widest range of variation is seen in values of Late Upper Paleolithic humans. The Late Upper Paleolithic samples are extremely geographically widespread, and many of the groups in the sample practice forms of incisor ablation (i.e., the culturally motivated removal of teeth: Chapter 2). It has been suggested that ablation results in increased reliance on the postcanine teeth for both non-masticatory, manipulative behaviors in addition to normal postcanine mastication of food (Bonfiglioli et al. 2004), which would explain the greater range of negative values (lower anterior wear and higher molar wear) in the Late Upper Paleolithic sample.

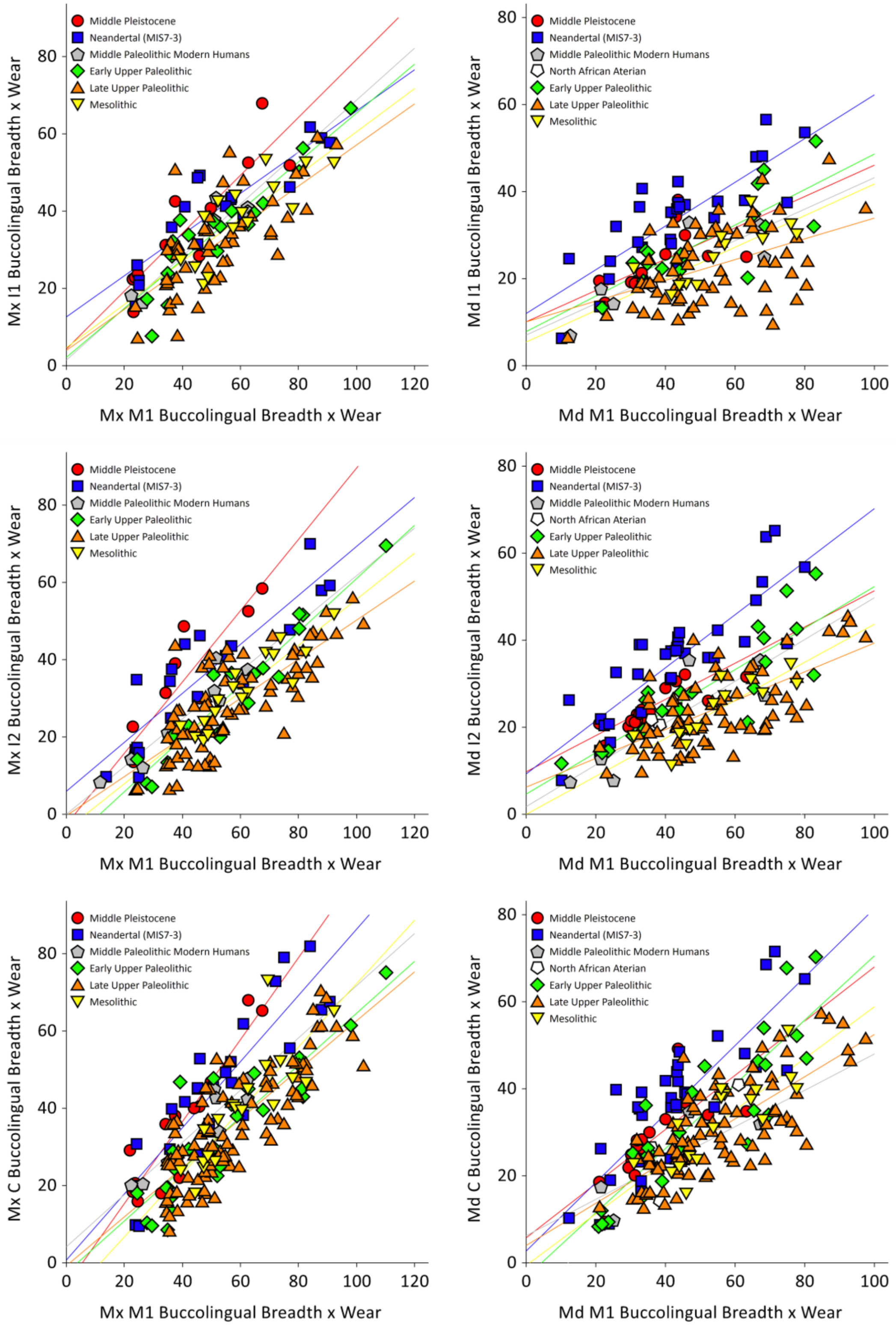


Figure 5.3 Maxillary (left side) and mandibular (right side) scaled macrowear gradients. Individual I1 versus M1 (top), I2 versus M1 (middle), and C versus M1 (bottom). Descriptive statistics are found in **Table 5.3**.

Table 5.3 Regression statistics for scaled occlusal wear gradient analyses of individual anterior teeth (I1, I2, or C) against first molar of same jaw.

Group	*N*	*y-int*	*95% CI*	*Slope*	*95% CI*	*r*	*R^2*	*P*
***I^1 vs M^1* (Fig. 5.3 top left)**								
Middle Pleistocene	11	4.26	-8.99 – 17.50	0.75	0.46 – 1.03	0.7970	0.7484	0.0002
Neandertals	17	12.55	6.92 – 18.18	0.53	0.43 – 0.63	0.8862	0.7853	<0.0000
MPMH[a]	7	1.36	-3.23 – 5.95	0.67	0.57 – 0.77	0.9408	0.8852	<0.0000
EUP[b]	20	2.22	-0.66 – 5.10	0.63	0.58 – 0.68	0.9087	0.8258	<0.0000
LUP[c]	54	3.99	1.16 – 6.82	0.53	0.48 – 0.58	0.7152	0.5115	<0.0000
Mesolithic	15	4.74	-0.02 – 9.51	0.56	0.48 – 0.63	0.8001	0.6402	<0.0000
***I^2 vs M^1* (Fig. 5.3 middle left)**								
Middle Pleistocene	11	-2.73	-15.02 – 9.56	0.92	0.61 – 1.23	0.9146	0.8365	0.0001
Neandertals	20	6.02	0.26 – 11.79	0.63	0.52 – 0.74	0.8837	0.7809	<0.0000
MPMH	9	-0.03	-3.21 – 3.15	0.62	0.55 – 0.69	0.9505	0.9035	<0.0000
EUP	21	-7.87	-10.12 – -5.61	0.69	0.65 – 0.73	0.9536	0.9093	<0.0000
LUP	78	-0.30	-2.40 – 1.79	0.51	0.47 – 0.54	0.7717	0.5955	<0.0000
Mesolithic	17	-4.02	-1.09 – 1.48	0.60	0.55 – 0.64	0.9085	0.8254	<0.0000
***C vs M^1* (Fig. 5.3 bottom left)**								
Middle Pleistocene	14	-5.96	-17.26 – 5.34	1.06	0.78 – 1.34	0.9222	0.8504	<0.0000
Neandertals	25	0.68	-6.35 – 7.71	0.85	0.73 – 0.98	0.8909	0.7937	<0.0000
MPMH	8	4.16	-0.39 – 8.71	0.67	0.58 – 0.77	0.9352	0.8745	<0.0000
EUP	27	-2.64	-5.87 – 0.59	0.67	0.62 – 0.73	0.8847	0.7827	<0.0000
LUP	99	-0.78	-2.81 – 1.27	0.63	0.60 – 0.67	0.8104	0.6568	<0.0000
Mesolithic	19	-9.73	-15.29 – -4.19	0.82	0.73 – 0.91	0.8298	0.6885	<0.0000
***I_1 vs M_1* (Fig. 5.3 top right)**								
Middle Pleistocene	15	10.02	-0.36 – 20.40	0.36	0.09 – 0.63	0.6240	0.3894	0.0129
Neandertals	27	12.03	7.40 – 16.67	0.50	0.40 – 0.60	0.8161	0.6659	<0.0000
MPMH	6	7.01	2.22 – 11.80	0.36	0.26 – 0.47	0.8375	0.7015	<0.0000
EUP	17	7.78	4.35 – 11.21	0.41	0.35 – 0.47	0.7870	0.6194	<0.0000
LUP	66	10.16	7.85 – 12.47	0.24	0.20 – 0.28	0.4618	0.2132	<0.0000
Mesolithic	12	5.37	1.83 – 8.90	0.36	0.30 – 0.43	0.7693	0.5918	<0.0000
***I_2 vs M_1* (Fig. 5.3 middle right)**								
Middle Pleistocene	19	9.76	2.82 – 16.69	0.42	0.23 – 0.60	0.7518	0.5652	0.0002
Neandertals	33	9.31	4.94 – 13.68	0.61	0.52 – 0.70	0.8511	0.7245	<0.0000
MPMH	6	1.75	-3.81 – 7.31	0.48	0.36 – 0.60	0.8685	0.7543	<0.0000
EUP	22	4.65	1.90 – 7.40	0.48	0.43 – 0.53	0.8513	0.7246	<0.0000
LUP	79	6.19	4.44 – 7.95	0.33	0.30 – 0.36	0.6652	0.4425	<0.0000
Mesolithic	13	0.0305	-3.08 – 3.14	0.44	0.38 – 0.49	0.8407	0.7068	<0.0000
***C vs M_1* (Fig. 5.3 bottom right)**								
Middle Pleistocene	19	5.69	-4.86 – 16.25	0.62	0.34 – 0.91	0.7464	0.5570	0.0002
Neandertals	35	2.78	-3.13 – 8.69	0.79	0.66 – 0.92	0.8241	0.6792	<0.0000
MPMH	5	6.24	-0.40 – 12.87	0.42	0.29 – 0.55	0.8418	0.7086	<0.0000
EUP	25	-3.28	-6.82 – 0.26	0.74	0.67 – 0.80	0.8750	0.7657	<0.0000
LUP	93	4.06	2.22 – 5.90	0.48	0.45 – 0.52	0.7517	0.5651	<0.0000
Mesolithic	17	-0.61	-4.76 – 3.53	0.59	0.52 – 0.67	0.8154	0.6649	<0.0000

[a] MPMH (Middle Paleolithic Modern Humans), [b] EUP (Early Upper Paleolithic), and [c] LUP (Late Upper Paleolithic)

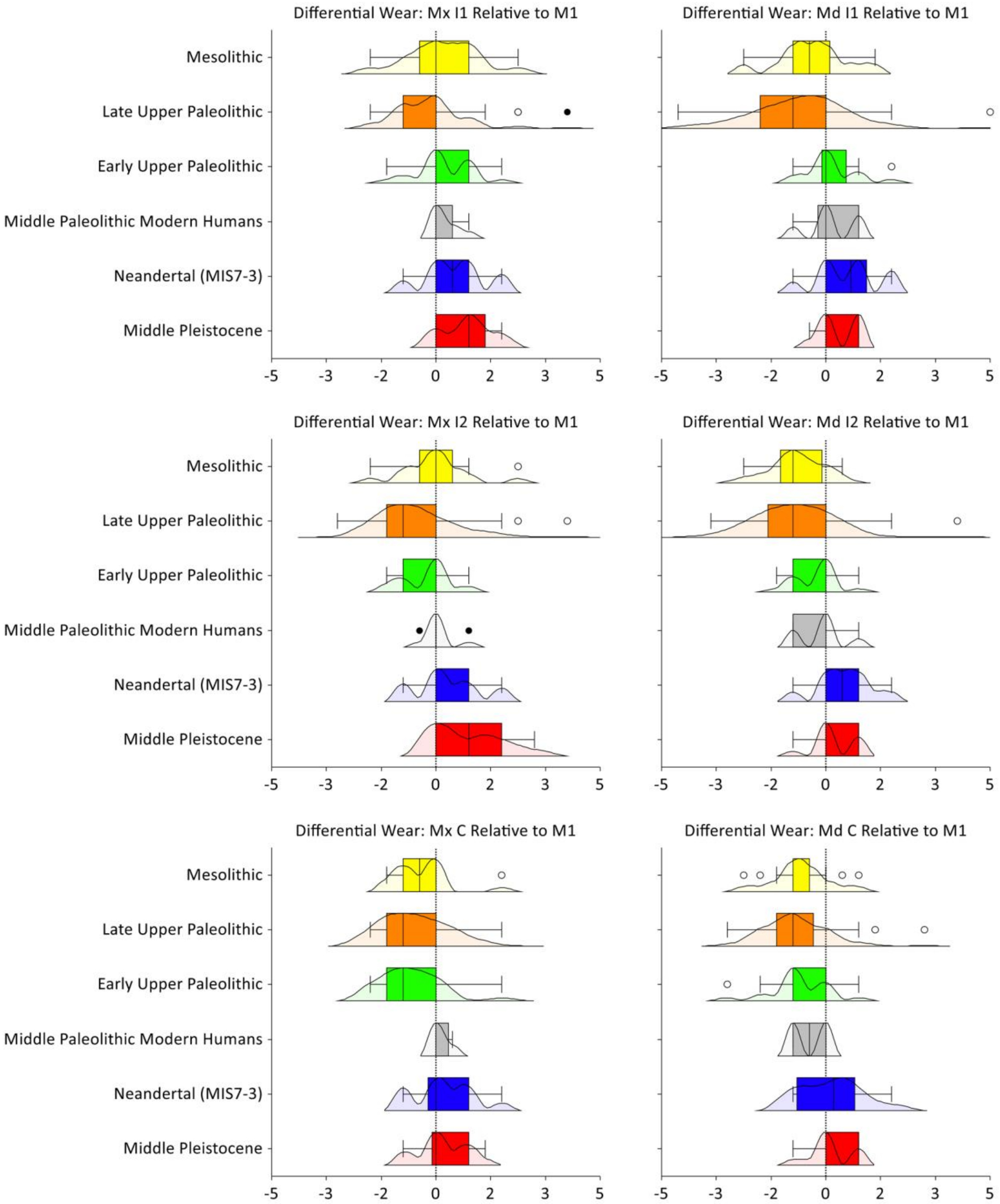


Figure 5.4 Maxillary (left side) and mandibular (right side) differential wear scores. I1's (top), I2's (middle), and C's (bottom) occlusal wear scores minus M1's wear score. Box and whisker plots show interquartile range. Density plots are transparent. Positive scores indicate greater anterior relative to first molar occlusal wear.

The range of values in the Late Upper Paleolithic also encompasses several outliers with high anterior relative to first molar wear values. These extreme anterior tooth-biased differential wear scores for some Late Upper Paleolithic specimens were also evident in the scaled occlusal wear analyses, but the much lower values along the x-axis were indicative of the small roots functioning as occlusal surfaces in the Late Upper Paleolithic specimens versus similarly worn teeth in other groups. Molar size does not vary substantially across groups of Late Pleistocene humans (Trinkaus 2004), so it is clear that the main difference in the previous analyses are a result of crown and root dimensions. However, the unscaled differential wear scores shown here indicate that there is extensive anterior tooth use across all samples, but when contrasted with the scaled analyses we can see that there is a meaningful difference in the "utility" or "functionality" of a heavily worn archaic (and to some extent Middle Paleolithic modern human or Early Upper Paleolithic human) dentition than that of later early modern humans – especially those from the Late Upper Paleolithic. Consider the outliers from the Late Upper Paleolithic – these individuals have relative low wear scores on their molars indicating that the anterior teeth are relegated non-functional early in life compared to archaic and some Early Upper Paleolithic humans. Taken as a whole, this indicates a high frequency of anterior tooth use among some Late Upper Paleolithic specimens without the benefit of large, wear resistant anterior teeth. Put another way, the use-life of anterior teeth among early modern humans engaging in substantial non-masticatory behaviors would be considerably shorter than that of archaic humans.

Table 5.4 Descriptive statistics for maxillary and mandibular differential wear scores.

I^1 relative to M^1 wear	**N**	**Median**	**Mode**	**Min**	**Max**	**Range**
Middle Pleistocene	11	1.0	1.0	0	2.0	2.0
Neandertals (MIS 7-3)	18	0.5	0, 1.0	-1.0	2.0	3.0
Middle Paleolithic Modern Humans	8	0	0	0	1.0	1.0
Early Upper Paleolithic	24	0	0	-1.5	2.0	3.5
Late Upper Paleolithic	84	0	0	-2.0	4.0	6.0
Mesolithic	17	0	0, 1.0	-2.0	2.5	4.5
I^2 relative to M^1 wear	**N**	**Median**	**Mode**	**Min**	**Max**	**Range**
Middle Pleistocene	11	1.0	0	0	3.0	3.0
Neandertals (MIS 7-3)	21	0	0	-1.0	2.0	3.0
Middle Paleolithic Modern Humans	9	0	0	-0.5	1.0	1.5
Early Upper Paleolithic	24	0	0	-1.5	1.0	2.5
Late Upper Paleolithic	109	-1.0	-1.0	-3.0	4.0	7.0
Mesolithic	20	0	0	-2.0	2.5	4.5
C^1 relative to M^1 wear	**N**	**Median**	**Mode**	**Min**	**Max**	**Range**
Middle Pleistocene	14	0	0	-1.0	1.5	2.5
Neandertals (MIS 7-3)	26	0	0	-1.0	2.0	3.0
Middle Paleolithic Modern Humans	8	0	0	0	0.5	0.5
Early Upper Paleolithic	31	-1.0	-1.0	-2.0	2.0	4.0
Late Upper Paleolithic	132	-1.0	-1.0	-2.0	2.0	4.0
Mesolithic	21	-0.5	0	-1.5	2.0	3.5
I_1 relative to M_1 wear	**N**	**Median**	**Mode**	**Min**	**Max**	**Range**
Middle Pleistocene	9	0	0, 0.5	-0.5	1.0	1.5
Neandertals (MIS 7-3)	10	0.75	0, 1.0	-1.0	2.0	3.0
Middle Paleolithic Modern Humans	6	0	0	-1.0	1.0	2.0
Early Upper Paleolithic	18	0	0	-1.0	2.0	3.0
Late Upper Paleolithic	79	-1.0	0	-4.5	5.0	9.5
Mesolithic	14	-0.5	-1.0, -0.5, 0	-2.5	1.5	4.0
I_2 relative to M_1 wear	**N**	**Median**	**Mode**	**Min**	**Max**	**Range**
Middle Pleistocene	12	0	0	-1.0	1.0	2.0
Neandertals (MIS 7-3)	12	0.5	0, 0.5, 1.0	-1.0	2.0	3.0
Middle Paleolithic Modern Humans	7	0	0	-1.0	1.0	2.0
Early Upper Paleolithic	19	0	0	-1.5	1.0	2.5
Late Upper Paleolithic	89	-1.0	-1.0	-3.5	4.0	7.5
Mesolithic	16	-1.0	-1.0	-2.5	0.5	3.0
C_1 relative to M_1 wear	**N**	**Median**	**Mode**	**Min**	**Max**	**Range**
Middle Pleistocene	11	0	0	-1.0	1.0	2.0
Neandertals (MIS 7-3)	12	0.25	-1.0, 0.5	-1.0	2.0	3.0
Middle Paleolithic Modern Humans	6	-0.5	-1.0, 0	-1.0	0	1.0
Early Upper Paleolithic	24	-1.0	-1.0	-3.0	1.0	4.0
Late Upper Paleolithic	99	-1.0	-1.0	-3.0	3.0	6.0
Mesolithic	19	-1.0	-1.0	-2.5	1.0	3.5

Summary

The macrowear analyses presented here broadly support conclusions from other studies that emphasize a high degree of anterior relative to posterior occlusal wear among hunter-gatherers (compared to non-foraging peoples) generally (Molnar 1972; Hinton 1981; Smith 1983a; Kaifu 2000b; Bermúdez de Castro et al. 2003; Deter 2009; Berbesque et al. 2012; Clement and Hillson 2012; Clement et al. 2012; Littleton et al. 2013; Botha and Steyn 2015). This pattern suggests that the use of teeth-as-tools for manipulative behaviors is a consistent trend among hunting and gathering peoples throughout much of human evolution. Exceptions to the rule seem only to exist when cultural factors, such as incisor ablation, shift dietary *and* non-masticatory behaviors to the posterior dentition in some groups.

The reduction in anterior tooth size across the archaic to modern human morphological transition in the Late Pleistocene is well documented, but seemingly at odds with occlusal macrowear trends. One benefit of having large anterior teeth is that more volume can be lost per unit of occlusal wear (as measured via ordinal or ratio methods), which greatly increases the use-life and functionality of anterior teeth late into the lifetime of a given individual. However, anterior tooth reduction leads to higher differential wear values in some modern humans – thus anterior teeth become largely non-functional earlier in life among hunter-gatherers with smaller anterior crown dimensions than those with larger anterior teeth. However, differential wear is difficult to study due to the postmortem and antemortem loss of heavily worn anterior teeth (Willman, personal observation). Even though exceptionally worn, many older Neandertals and early modern humans retained their full dentitions until death (Trinkaus 2013). By the Late Upper Paleolithic, anterior crown and root dimensions have further reduced and there is a trend toward higher anterior versus posterior wear differentials. Higher rates of antemortem tooth loss occur in the Late Upper Paleolithic compared with any other preceding period (Lacy 2014), and rates of anterior tooth loss and wear-associated dental pathology appear more frequently (Willman, personal observation). Ordinal dental wear scores as well as buccolingual dimensions are unaccounted for in cases of antemortem tooth loss. Therefore, any antemortem tooth loss related to wear-induced pathology will skew results in any macrowear gradient analysis. Future research is planned to integrate pathological loss into a wear-scoring system to account for this discrepancy. Given the high rates of oral pathology in terminal Pleistocene compared to preceding periods it is likely that these analyses have underestimated the degree to which small anterior teeth have been lost due to wear and associated pathology.

These results suggest that anterior dental wear is high across Middle and Late Pleistocene groups but that large anterior dentitions are beneficial in maintaining a functional dentition throughout the life-course. Reduced dentitions do not necessarily mean less anterior tooth-use for manipulative behaviors, but do correspond with decreased functionality of the anterior dentition later in life among individuals with smaller dentitions.

Thus, it is difficult to claim that a shift toward less habitual use of the anterior dentition for manipulative purposes leads to anterior dental size reduction among early modern humans through some form of relaxed selection on anterior tooth size. If anything, large anterior teeth should have been under stabilizing selection among early modern humans as well as archaic humans given their similarly heavy reliance on the anterior dentition for manipulative purposes. In sum, it does not appear that tooth-use, or lack thereof, was a significant factor influencing the reduction in anterior tooth morphology among early modern humans, and other mechanisms are needed to explain tooth reduction in the Late Pleistocene. This will be discussed further in Chapter 8.

Chapter 6. Antemortem enamel chipping of the anterior teeth

Hypotheses and Predictions

H_0: There will be no observable differences in the frequency of enamel chipping between chronologically and morphologically-defined human groups.

This null hypothesis will be rejected if significant differences in the patterning of enamel chipping between groups are found between chronologically and morphologically-defined groups. If rejected, the magnitude and direction of the behavioral shifts among Middle and Late Pleistocene groups will be assessed.

A brief rationale for analysis

The maintenance of morphologically and absolutely larger anterior dentitions among archaic humans versus a reduction in anterior tooth dimensions and lower frequency of mass-additive dental traits among early modern humans has been attributed to many causes. The massive character of archaic human anterior dentitions has been discussed in terms of functional adaptations to heavy attrition, high peak loads, repetitive loading, or some combination of these factors. In contrast, socioeconomic and technocultural evolution is thought to release early modern humans from the selective pressures that maintained the robust anterior dentitions of their archaic predecessors and contemporaries. Occlusal macrowear gradients were examined to address the correlation between anterior dental size on the degree of cumulative dental wear incurred throughout the lifetime of an individual, and the relative importance of anterior versus posterior tooth-use across fossils groups.

Instrumental striations, or “cutmarks”, on labial enamel will be examined to document a particular forms of manipulative behavior (e.g., “stuff-and-cut” behaviors – Chapter 7). While these analyses comment on the repetition of non-masticatory behaviors and resultant accumulation of wear, they do little to comment on the magnitude of loads placed on the anterior dentition.

Enamel chipping comments directly on the loads that the anterior teeth are subjected to. Occasionally, non-masticatory behaviors involve bite forces that are high enough to induce fracture or chipping of enamel. Dental fracture, or catastrophic crown failure in extreme cases, poses a serious threat to individual fitness, therefore, it stands to reason that it may be an important selective pressure in hominin dental evolution (Chai et al. 2009; Constantino et al. 2010; Lee et al. 2011; Strait et al. 2013).

Recent experimental research documents a close relationship between the size of an enamel chip dimension on bunodont tooth crowns and the forces required to propagate chipping/fracture. Experiments initially relied on ideal glass dome models but were later replicated through experiments on extracted human teeth and observations across mammalian taxa that share bunodont postcanine dental morphology (e.g., peccaries, sea otters, monkeys, apes, and humans) (Chai and Lawn 2007b, a; Lawn and Lee 2009; Lawn et al. 2009; Lee et al. 2009; Myoung et al. 2009; Chai et al. 2010, 2011; Constantino et al. 2011; Ziscovici et al. 2014). These analyses have generated equations to calculate the bite forces necessary to produce an individual enamel chip or fracture observed on the postcanine teeth of earlier hominins and non-human primates (Constantino et al. 2010, 2012). These equations are specific to bunodont crowns, but have shown that bite forces can be reliably predicted from the absolute dimensions of enamel chips. While specific equations for calculating bite forces from chipping on the anterior dentition are not available[8], the relationship between chip size and the force required to propagate enamel fracture in the postcanine dentition is still informative. In this sense, the size of an enamel chip on an anterior tooth can provide some evidence of the forces the tooth was subjected to in vivo – i.e., larger chips require higher bite forces to propagate.

Despite the great extent to which anterior bite force production among Neandertals relative to early modern humans as inferred from craniofacial moment arms and hypertrophy has been discussed in the literature (see Chapter 3), there are obvious limitations to addressing bite force production from analyses of cranial fossils. Most obvious is the dearth of complete cranial fossils from the Pleistocene. Therefore, a direct analysis of estimated bite forces from enamel chipping fracture using abundant dental fossils provides a welcome alternative to address relative bite force production across Middle and Late Pleistocene human groups. However, bite force production is not the sole interest in collecting data on enamel chipping and fracture. For instance, bioarchaeological studies have illustrated the utility of recording dental chipping to understand variation in prehistoric human non-masticatory behaviors and diet across different samples (Turner and Cadien 1969; Belcastro et al. 2007; P. Molnar 2008; Scott and Jolie 2008; Scott and Winn 2011). The chipping and fracture of teeth is occasionally commented upon with regard to Pleistocene dental fossils (e.g., Matiegka 1929; Brace et al. 1981; Puech 1981; Formicola and Repetto 1989; Liu et al. 2010; Janković et al. 2012), but this data does not immediately lend itself to quantitative analyses because the *absence* of

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[8] The equations for calculated bite force estimates have only been established for bunodont premolar and molar teeth. New equations would have to be generated for incisors and canines.

chipping/fracture is not explicitly noted in many of these studies. However, the systematic documentation of both the presence and absence of dental chipping has become more common and allows comparisons of frequency between some studies (Ryan 1980b; Bonfiglioli et al. 2004; Lozano et al. 2008, nd; Estalrrich and Rosas 2015).

In short, dental chipping records past behaviors that involved high enough anterior bite force production to cause enamel fracture. As such, dental chipping allows one to comment on the degree to which different fossil groups engaged in manipulative behaviors that had the potential to damage or destroy a tooth in addition to influencing craniofacial growth and remodeling through dental loading. Therefore, variation in enamel chipping, together with the scaled macrowear gradient analyses presented previously, has important implications for understanding behavioral factors involved in the transition from archaic to modern human morphology during the Late Pleistocene.

Materials

Materials examined include original fossils, high quality epoxy-resin casts, and a subset of data derived from the literature (see Chapter 4). Enamel chipping data for the Sima de los Huesos archaic humans was published as "present or absent", and divided into two categories: the labial-occlusal edge and the remaining occlusal surface (Lozano 2005; Lozano et al. 2008). The Sima de los Huesos data for both categories were combined since the location of chipping was not considered in the present study (see below). Sima de los Huesos tooth associations by individual are listed in **Appendix Table 1**. Data from El Sidrón, Hortus, and Spy (Estalrrich and Rosas 2015) was published using the ordinal scoring system employed here (see below).

Data will also be presented on postcanine enamel chipping for comparative purposes. The data has been presented in part elsewhere (Azar et al. 2015), but is elaborated upon here. The samples closely correspond to the categories and fossils used throughout the entirety of this dissertation, but there are subtle differences nonetheless. The “Earlier Neandertal” sample is limited to the Krapina (MIS 6/5e) Neandertals. The “Later Neandertal (MIS 4-3)” sample overlaps with the sample used for anterior dental wear analyses with the exception of a few specimens that are unique to postcanine analyses (they do not have anterior teeth so were not analyzed in other analyses). The Late Neandertals are: Amud, Goyet, Kůlna, Malarnaud, Monsempron, Le Moustier, Oliviera, Shanidar, Shovakh, Spy, Švédův stůl, and Vindija. The “Early Modern Human” sample includes individuals from Barma Grande, Dolní Věstonice, Miesslingtal, Mladeč, Muierii, Oase, Ohalo II, Ostuni, Abri Pataud, Předmostí, Sunghir, and Tianyuan. The two specimens from Ohalo II were considered Late Upper Paleolithic specimens in the anterior tooth analyses. However, they are dated to 19,000 BP (Hershkovitz et al. 1995), and are frequently included in analyses of pre-Late Glacial Maximum humans.

Methods

Antemortem versus postmortem chipping

Antemortem versus postmortem enamel chipping is often readily discernable when studying original fossils on the basis of chip color and morphology of the chip edges (Scott and Winn 2011). For instance, postmortem chips – which occur after deposition, excavation, and while curated – typically differ in color from the rest of a tooth surface. Specifically, the edge of a postmortem chip may exhibit a “fresher” appearance such that the fractured surface color differs from the rest of the enamel surface. If dentin is exposed through occlusal wear it often differs in color from dentin exposed through postmortem fracture. In addition, the edge of a postmortem chip or fracture is often sharp or jagged whereas the edges of a chip sustained in vivo are generally rounded and worn unless they occurred close to the time an individual died. Handheld magnification (~10x) and a portable light microscope were used to examine all original fossils studied to ensure accurate diagnosis of antemortem versus postmortem chipping.

When dental casts were observed in lieu of original fossils the chip color criteria are no longer useful unless color photographs were also available. Instead, edge characteristics of each chip were examined under low magnification to confirm natural edge rounding and wear for each chip. Chips that were difficult to diagnose on dental casts were examined using SEM which allowed higher magnification and depth of field. Antemortem chipping was distinguished from other postmortem taphonomic factors based on microscopic surface alterations established in the literature (King et al. 1999; Pérez-Pérez et al. 2003; Martínez and Pérez-Pérez 2004). When SEM was used, the methods for molding, casting, and preparation of specimens followed the methods outlined in Chapter 6. In all cases, a conservative approach was taken and any instance of enamel chipping that could not be definitively ascribed to ante- or postmortem processes was not considered in the analyses.

Frequencies of chipping for the sample from Sima de los Huesos could not be calculated in the same manner described above, because only the teeth affected by antemortem chipping were listed by tooth type and individual in publications (Lozano 2005; Lozano et al. 2008). The frequency of postmortem chipping was presented but this was not broken down by tooth type or individual. While individual teeth with significant postmortem damage were removed from the calculations of chipping frequencies for the fossils examined directly in this study, this was not possible for the Sima de los Huesos fossils. Therefore, the chipping frequencies for the Middle Pleistocene archaic human sample in the present study should be viewed with caution, since the frequency would be higher if the individuals with postmortem damage could be removed from calculations.

Ordinal scoring of enamel chipping

Chipping was first scored as present or absent based on the criteria mentioned previously. Scoring presence or absence allowed the broadest possible comparisons with previously published literature. As with labial cutmarks (see Chapter 6) the frequency of teeth with chipping counted as “present” may be slightly inflated. This is because a tooth with postmortem damage to the occlusal surface, particularly the circumference of the occlusal margin where chipping occurs, but no clear evidence of antemortem chipping on undamaged areas was not included in frequency counts. However, if a tooth has evidence of antemortem chipping, as well as postmortem damage, it was still counted having a chip “present”. While this may slightly inflate the number of chips counted as present in this study, the bias is uniform across the samples studied here.

When present, antemortem chips were also scored using an ordinal system for each tooth affected. Bonfiglioli and colleagues (2004:449) provided the following criteria for grading enamel chipping (**Figure 6.1** and **Figure 6.2**):

- Grade 1 – slight crack or fracture (0.5 mm), or larger but superficial enamel flake loss.
- Grade 2 – square irregular lesion (1 mm) with the enamel more deeply involved.
- Grade 3 – crack bigger than 1 mm involving enamel and dentin or a large, very irregular fracture that could destroy the tooth.

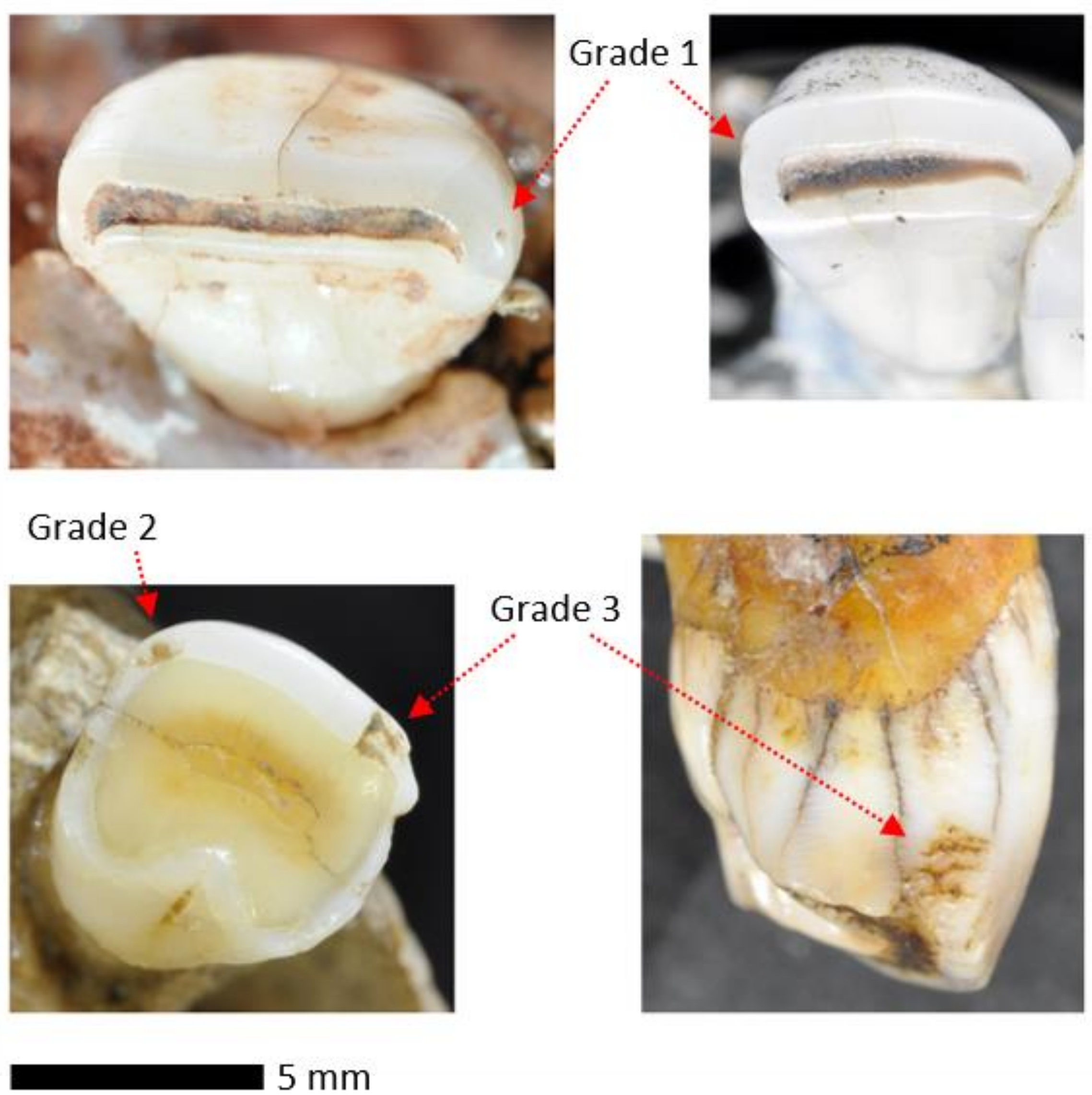

Figure 6.1 Examples of ordinal chipping scores on anterior teeth.

When assessing ordinal scores, size was considered the most important grading criteria for this study. Constantino et al. (2010) employ a minimum cutoff of 0.1 mm when measuring enamel chipping in molars and the same cutoff is followed here. If a possible chip of small size was uncertain, it was not counted.

Small chips are extremely frequent along interproximal contact areas on the occlusal surface. For this reason, chips were only graded as “present” at an interproximal contact if they were on the “large end” of a grade 1 chips (i.e., approaching grade 2 in size). The ubiquity of small interproximal chips is one reason to exclude them, but the primary reason to exclude them when studying Pleistocene human teeth is due to the high prevalence of subvertical grooves on the interproximal facets of archaic human teeth (see **Figure 2.3**). The furrows of subvertical grooves are often visible on the interproximal edge of the occlusal surface (Kaidonis et al. 1992) and can be mistaken for small, grade 1 chips (Willman, personal observation). Subvertical grooves are particular common in the Pleistocene, and especially among archaic humans (Villa and Giacobini 1995a; Villa and Giacobini 1995b; Egocheaga et al. 2004; Estalrrich et al. 2011; Brink et al. 2012; Compton and Stringer 2012; Sarig et al. 2016). While not absent, they are less commonly found in modern humans (Kaidonis et al. 1992; Ramirez Rozzi et al. 2009; Willman, personal observation). Thus, counting only larger antemortem chips at interproximal surfaces in all fossil groups ensures that no bias from supposedly greater degree of subvertical grooves, and by extension misattributed grade 1 chips, in the archaic human samples.

Figure 6.2 Examples of ordinal chipping scores on molars and measurements taken to determine bite force.
Chipping scores are 1, 2, and 3 from left to right. Chip size (“*h*”) and tooth diameter (“*D*”).

The relatively thin enamel of Neandertals versus modern humans could also yield a higher degree of dentin involvement when chips are large, and less dentin involvement in the more thickly enameled teeth of modern humans. For example, a 1 mm irregular chip (grade 2) in a modern human is unlikely to penetrate to dentin, but a similarly sized enamel chip on an Neandertal tooth with thinner enamel may actually penetrate through to dentin – this would make the Neandertal chip a grade 3 chip despite the similarity in size to the hypothetical grade 2 chip in a thickly enameled modern human. Therefore, chip dimensions were considered more important when assigning an ordinal score to chips that had some dentin involvement. Furthermore, chips on relatively unworn teeth are common but rarely penetrate to the level of dentin even when they are quite large (grade 2 or 3) due to the relatively thicker enamel of cusp tips versus the progressively thinner enamel toward the cementoenamel junction. Using chip size, rather than relying on a dentin involvement for chips graded as 2 and 3, ensures that the closest approximation of the maximum dimension of a chip is being recorded – size being the biomechanically relevant data for calculating proxies for bite forces.

Occlusal wear (Smith 1984) was recorded in addition to enamel chipping on specimens directly examined for this study as a means of assessing bias between samples containing skewed numbers of teeth in higher of lower wear categories. Chipping on dentin (teeth worn to the roots – Smith scores of 8) was given special consideration, because the author had observed dentin chipping in pilot studies on Holocene materials. However, other researchers choose to record enamel chipping only if two-thirds of the crown remains and/or there is a complete occlusal rim (Scott and Winn 2011). Thus some data screening was necessary. **Table 6.1** shows the number of teeth from each sample that had Smith scores of 8. Only 4.0% of the total number of teeth with adequate preservation for inclusion in this study were worn to roots. However, these teeth were disproportionately observed in Later Neandertal (MIS 4-3) maxilla and mandibles, Early Upper Paleolithic mandibles, and Late Upper Paleolithic maxillae. Further examination revealed that of all the teeth with Smith scores of 8 (n=31), only one had dentin chipping (3.2%). However, chipping was observed on teeth with wear scores up to grade 7 in the present study and in a previous study of the Sima de los Huesos sample (chipping: Lozano 2005; wear scores: Martinón-Torres, et al. 2012; see **Appendix Table 1** for tooth associations) which further supports the minimum inclusion criteria for the present study. From these data screening observations, it was decided that teeth having some enamel remaining to be considered in analyses (Smith Scores 1-7). Furthermore, biomechanical analyses of chipping are intended for enamel chipping and fracture only (Constantino et al. 2010). Therefore, all 31 root-worn teeth, initially fitting criteria for inclusion on the basis of preservation, are eliminated from further analyses. The results of this study may not be completely comparable to previously published bioarchaeological studies that use lesser worn teeth as a minimum requirement for inclusion, but is comparable with concern to the chipping literature concerning Pleistocene fossils.

Table 6.1 Counts and frequencies of anterior teeth with Smith score of "8" before removal*.

	Middle Pleistocene	Earlier Neandertals (MIS 7-5)	Later Neandertals (MIS 4-3)	Middle Paleolithic Modern Humans	Early Upper Paleolithic	Late Upper Paleolithic
Maxilla	0/80	0/59	7/103	0/40	1/69	6/42
	0.0%	0.0%	6.8%	0.0%	1.4%	14.3%
Mandible	0/102	0/57	7/74	0/15	10/72	0/59
	0.0%	0.0%	9.5%	0.0%	13.9%	0.0%
Smith score of "8" across all samples			31/772 4.0%			
Chipped teeth with Smith score of "8" across all samples			1/31 3.2%			

* Frequency = count/total observations.

The choice of grading chipping by tooth type rather than by individual is used here, since using an "individual" can be a major source of bias in comparative analyses (Scott and Winn 2011). This is also a concern in the analysis of labial cutmarks and will be discussed in more detail subsequently (Chapter 7), but the basic premise is that an "individual" represented by 12 anterior teeth and with a single chipped tooth (1/12 or 8.3% of their anterior teeth) would be counted as an "individual" with chipping in a prevalence count by individuals. However, this is different from an individual with 12 chipped anterior teeth when issues of chipping severity is of interest, and different from counting a single tooth (with or without chipping) as a single "individual" (Scott and Winn 2011). This obviously makes for many separate comparisons but it is nevertheless an honest way of presenting comparable data when dealing with fragmentary fossil dentitions.

The location of a chip on chip tooth was not considered here despite being considered elsewhere (Scott and Winn 2011; Estalrrich and Rosas 2015). If more than one chip was present on the same tooth, the grade for the largest chip was recorded for severity analyses. The presence of multiple chips was not considered separately in this study.

Binomial, one proportion confidence limits (95% CL) for presence/absence data were calculated in NCSS (Hintze 2012). Cross tabulation and Chi-square tests were used to compare frequency differences between groups for the presence/absence data for anterior tooth chipping. Exact *P*-values and Chi-square values were calculated in NCSS (Hintze 2012) using count data. Tests yielding $P \leq 0.05$ are considered significant. However, more emphasis will be placed on tests yielding $P \leq 0.01$ in the results and discussion, since it more reliably reduces the probability of Type I errors (Chandler 1995; see also Lozano et al. 2008).

Comparisons with posterior dental chipping

Presence, absence, and ordinal scores were collected for posterior dental chipping using the same criteria as detailed for the anterior dentition. Additional data were collected to calculate relative chip size, actual bite force (P_F) maximum potential bite force (P_{max}) from premolar and molar chip and crown dimensions (Constantino et al. 2010). **Figure 6.2** illustrates the measurement of chip size ("h") and tooth diameter ("D") from scaled occlusal photographs that are then used in calculations to determine bite force estimates (Constantino et al. 2010). All measurements were made from scaled photographs using tpsDig11 (Rohlf 2006). As with documentation of chips on the anterior teeth, when more than one chip was present on a single tooth, the largest chip was measured.

Actual bite force (PF) and maximum, potential bite force (Pmax) were calculated from the following equations (Constantino et al. 2010):

$$\text{Equation 1: } P_F = T'h3/2$$

$$\text{Equation 2: } P_{max} = 0.16T'h3/2$$

Actual bite force (P_F) is a product of chip dimensions and is therefore an accurate reflection of the bite forces produced *in vivo* on hard foods, dietary (grit) inclusions, or other hard objects worked with the postcanine dentition (which on occasion, may be non-masticatory but this is not readily apparent from chipping only in most cases). Maximum, potential bite force (P_{max}) is similar to the bite force estimates generated in biomechanics studies of the craniofacial skeleton in that they are an estimate of the maximum bite forces that *could* be produced. Relative chip size was also calculated as h/D. The practical limit of chip size (the ratio, 0.3) is indicated in resultant plots as a reference point (Constantino et al. 2010). Skewness, Kurtosis, and Omnibus tests indicated that P_F, P_{max}, and relative chip size (h/D) are not normally distributed. Significant differences were assessed with ANOVA (Kruskal-Wallis).

Results

Figure 6.3 displays percentage and cumulative frequencies of all anterior teeth analyzed in the present analysis corresponding to each Smith (1984) wear score (after removing teeth with wear scores of 8). Corresponding tooth counts by wear category are found in **Table 6.2** and **Table 6.3**. The Early Upper Paleolithic maxillary and mandibular samples have high numbers of less worn (scores 1-3) teeth compared to other groups. The earlier Neandertal sample approaches the Early Upper Paleolithic sample in cumulative total of maxillary teeth worn to stage 1, 2, and 3. The earlier Neandertal sample is dominated by teeth from Krapina – a site known for its young age profile (Bocquet-Appel and Arsuaga 1999). Similarly, the Sima de los Huesos sample comprises the majority of the Middle Pleistocene sample and also has a relatively young age profile (Bocquet-Appel and Arsuaga 1999) – which is reflected in the large number of teeth with stage 3 wear (especially in the mandible). The Middle Paleolithic modern humans have low sample sizes making any overall trends relatively meaningless. In general, there are few less worn (stage 1 and to some degree stage 2) and few heavily worn (stage 6-7) across all samples. The majority of anterior teeth sampled are categorized by wear stages 3, 4, and 5.

Table 6.2 Maxillary anterior tooth sample composition (pooled sides and tooth types).

	Tooth Count by Smith Wear Scores							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**Total**
Middle Pleistocene	1	13	18	17	14	10	7	80
Earlier Neandertals (MIS 7-5)	6	11	16	16	5	5	0	59
Later Neandertal (MIS 4-3)	5	10	14	24	28	10	5	96
Middle Paleolithic Modern Human	0	8	3	6	16	7	0	40
Early Upper Paleolithic	14	12	17	10	8	3	4	68
Late Upper Paleolithic	1	7	7	8	5	2	6	36

Table 6.3 Mandibular anterior tooth sample composition (pooled sides and tooth types).

	Tooth Count by Smith Wear Scores							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**Total**
Middle Pleistocene	0	3	60	28	3	7	1	102
Earlier Neandertals (MIS 7-5)	2	5	14	12	19	5	0	57
Later Neandertal (MIS 4-3)	0	8	12	14	22	6	5	67
Middle Paleolithic Modern Human	1	5	1	5	3	0	0	15
Early Upper Paleolithic	9	10	20	9	6	6	2	62
Late Upper Paleolithic	4	8	11	22	11	3	0	59

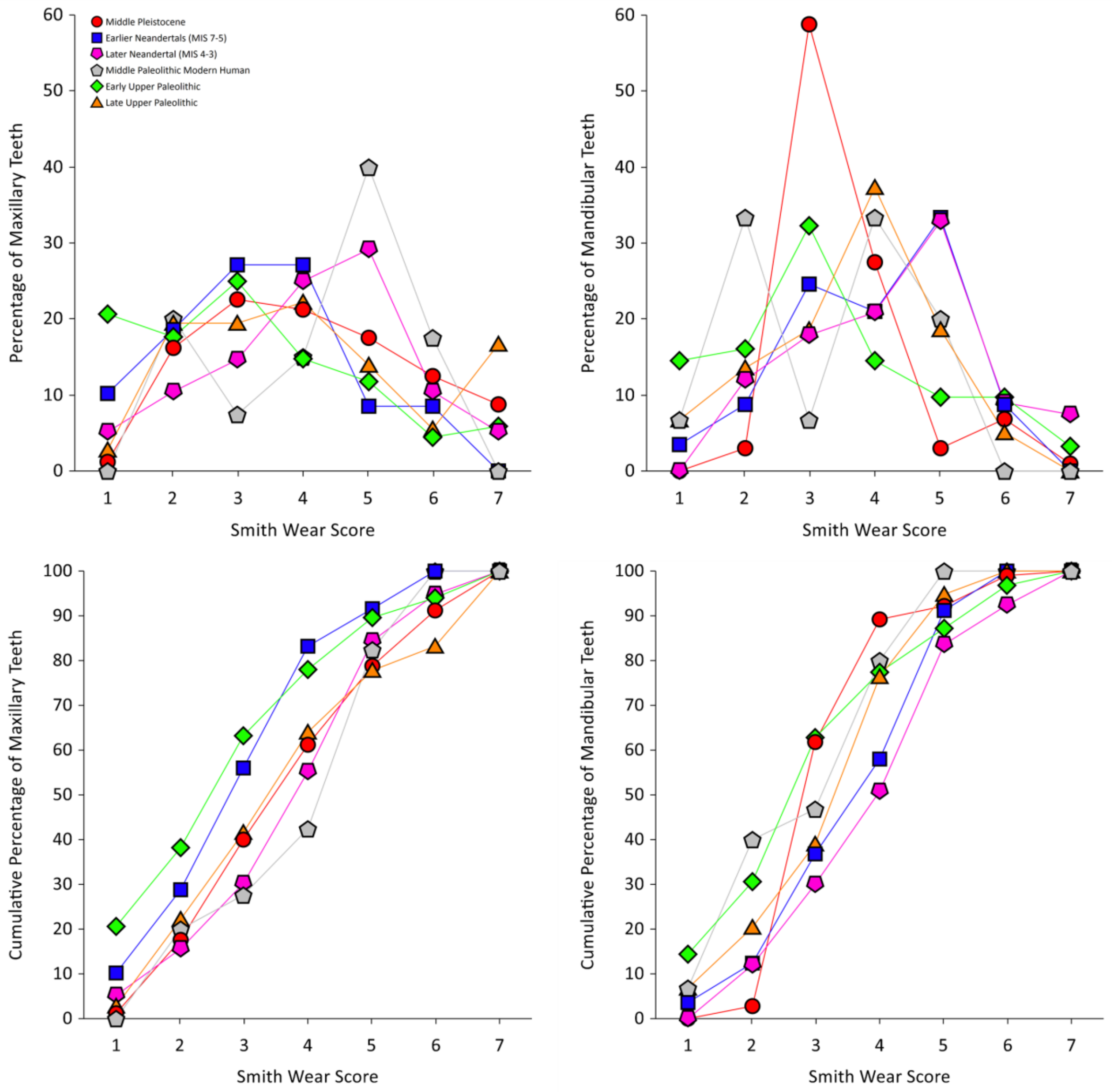

Figure 6.3 Sample composition by Smith (1984) wear scores.
Tooth types (first and second incisors and canines) and sides (left and right) are pooled for each sample. Top graphs: percentage of teeth in each wear category. Bottom graphs: cumulative percentage of teeth in each wear category.

Chipping frequencies by tooth type and jaw are presented graphically in **Figure 6.4**, but the raw data on counts should be referenced in **Table 6.4** and **Table 6.5** since sample size varies dramatically between some samples. This is particularly telling when examining the binomial, one proportion 95% confidence limits (95% CL) presented for each tooth type. The 95% CL's are broad with extensive overlapping across groups at each tooth type (**Table 6.4** and **Table 6.5**)

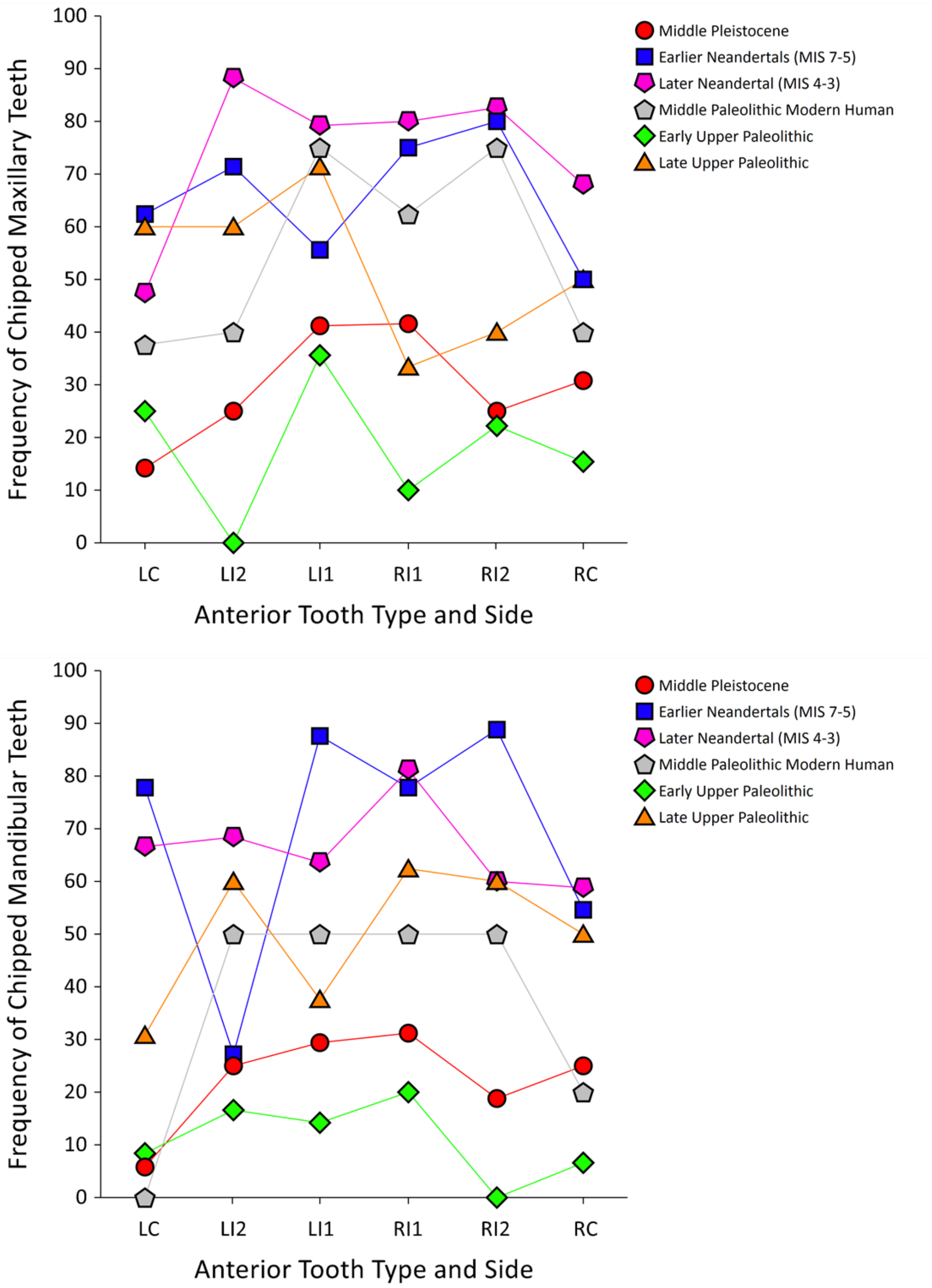

Figure 6.4 Percentage of chipped teeth by tooth, jaw, and side. Maxillary teeth (top) and mandibular teeth (bottom).

Table 6.4 Anterior dental chipping frequency by maxillary tooth, side, and jaw.

Group	LC^1	LI^2	LI^1	RI^1	RI^2	RC^1	X^2	P
Middle Pleistocene	14.3 2/14 17.8 – 42.8	25.0 3/12 5.49 – 57.2	41.2 7/17 18.4 – 67.1	41.7 5/12 15.2 – 72.3	25.0 3/12 5.5 – 57.2	30.8 4/13 9.1 – 61.4	3.72	0.5897
Earlier Neandertal (MIS 7-5)	62.5 5/8 24.5 – 91.5	71.4 5/7 29.0 – 96.3	55.6 5/9 21.2 – 86.3	75.0 9/12 42.8 – 94.5	80.0 12/15 51.9 – 95.7	50.0 7/14 23.0 – 77.0	3.92	0.5608
Later Neandertal (MIS 4-3)	47.4 9/19 24.5 – 71.1	88.2 15/17 63.6 – 98.5	79.2 19/24 57.9 – 92.9	80.0 16/20 56.3 – 94.3	82.6 19/23 61.2 – 95.1	68.0 17/25 46.5 – 85.1	10.91	**0.0532**
Middle Paleolithic Modern Humans	37.5 3/8 8.5 – 75.5	40.0 2/5 5.3 – 85.3	75.0 3/4 19.4 – 99.4	62.5 5/8 24.5 – 91.5	75.0 3/4 19.4 – 99.4	40.0 2/5 5.3 – 85.3	3.29	0.6548
Early Upper Paleolithic	25.0 3/12 5.49 – 57.2	0.0 0/11 0.0 – 28.5	35.7 5/14 12.7 – 64.8	10.0 1/10 2.5 – 44.5	22.2 2/9 2.8 – 60.0	15.4 2/13 1.9 – 45.5	6.14	0.2930
European Late Upper Paleolithic	60.0 6/10 26.2 – 87.8	60.0 3/5 14.6 – 94.7	71.4 5/7 29.4 – 96.3	33.3 1/3 8.4 – 90.6	40.0 4/10 12.2 – 73.8	50.0 4/8 15.7 – 84.3	2.42	0.7883

Each group and tooth type has three row values. Top: percent chipped teeth; middle: chipped teeth/total; bottom: binomial, one proportion confidence limits (95% CL) for percentage calculation.

X^2 and *P*-values for the H_0 of equal proportions of chipping across tooth types within each group. **Bold** value indicate rejection of H_0 for equivalent proportions at $P \leq 0.05$. df = 5.

Table 6.5 Anterior dental chipping frequency by mandibular tooth type.

Group	LC$_1$	LI$_2$	LI$_1$	RI$_1$	RI$_2$	RC$_1$	X^2	*P*
Middle Pleistocene	5.9	25.0	29.4	31.3	18.8	25.0	4.11	0.5334
	1/17	5/20	5/17	5/16	3/16	4/16		
	1.5 – 28.7	8.7 – 49.1	10.3 – 56.0	11.0 – 58.7	4.1 – 45.7	7.3 – 52.4		
Earlier Neandertal (MIS 7-5)	77.8	27.3	87.5	77.8	88.9	54.5	12.97	**0.0365**
	7/9	3/11	7/8	7/9	8/9	6/11		
	40.0 – 97.2	6.0 – 61.0	47.4 – 99.7	40.0 – 97.2	51.8 – 99.7	23.4 – 83.3		
Later Neandertal (MIS 4-3)	66.7	68.4	63.6	81.3	60.0	58.8	2.46	0.7829
	14/21	13/19	7/11	13/16	12/20	10/17		
	43.0 – 85.4	43.5 – 87.4	30.8 – 89.1	54.4 – 96.0	36.1 – 80.9	32.9 – 81.6		
Middle Paleolithic Modern Humans	0.0	50.0	50.0	50.0	50.0	20.0	2.40	0.7915
	0/2	1/2	1/2	1/2	1/2	1/5		
	0.0 – 84.2	1.3 – 98.7	1.3 – 98.7	1.3 – 98.7	1.3 – 98.7	0.5 – 71.6		
Early Upper Paleolithic	8.3	16.7	14.3	20.0	0.0	6.7	3.31	0.6524
	1/12	2/12	1/7	2/10	0/12	1/15		
	2.1 – 38.5	2.1 – 48.4	3.6 – 57.9	2.5 – 55.6	0.0 – 26.5	1.7 – 32.0		
European Late Upper Paleolithic	30.8	60.0	37.5	62.5	60.0	50.0	3.71	0.5923
	4/13	6/10	3/8	5/8	6/10	5/10		
	9.1 – 61.4	26.2 – 87.8	8.5 – 75.5	24.5 – 91.5	26.2 – 87.8	18.7 – 81.3		

Each group and tooth type has three row values. Top: percent chipped teeth; middle: chipped teeth/total; bottom: binomial, one proportion confidence limits (95% CL) for percentage calculation.

X^2 and *P*-values for the H_0 of equal proportions of chipping across tooth types within each group. **Bold** value indicate rejection of H_0 for equivalent proportions at $P \leq 0.05$. df = 5.

The null hypothesis that there are no differences in the proportion of chipping across maxillary anterior tooth types is rejected only for Later Neandertals, but the result is barely significant (*P* = 0.0532) and would not be considered significant if a more conservative significance level ($P \leq 0.01$) is used (**Table 6.4** and **Figure 6.4**). The null hypothesis that there are no differences in the proportion of chipping across mandibular anterior tooth types is rejected only for Earlier Neandertals, but the result (*P* = 0.0365) would not be considered significant if a more conservative significance level ($P \leq 0.01$) is used. The low number of left I_2 chipping is the strongest influence on a lack of equivalence between maxillary tooth types among the Earlier Neandertals (**Figure 6.4** and **Table 6.5**).

When tooth types (I1, I2, and C) are pooled by right or left side some groups exhibit more than 20% right-left asymmetry (**Table 6.6** and **Figure 6.5**). However, there is extensive overlap in 95% CL's and the null hypothesis of equivalent proportion of chipping across left and right sides was not rejected for any group regardless of whether maxillary or mandibular teeth wear examined (**Table 6.6**).

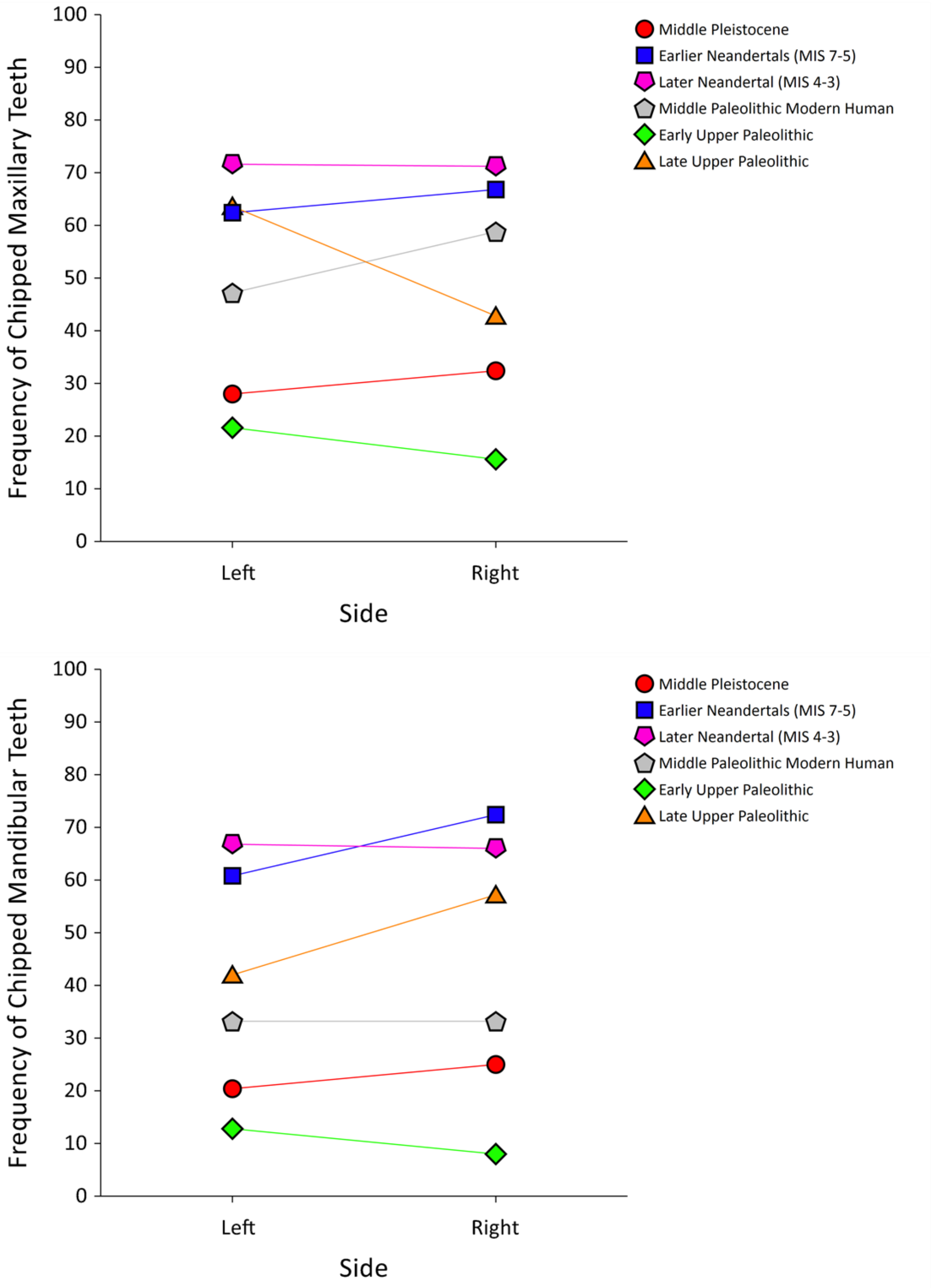

Figure 6.5 Percentage of chipped anterior teeth by side.
I1, I2, and C teeth are pooled for each side.

Table 6.6 Percentage of chipped teeth by side.

	Maxilla				***Mandible***			
	Left	**Right**	X^2	***P***	**Left**	**Right**	X^2	***P***
Middle Pleistocene	27.9	32.4	0.19	0.6597	20.4	25.0	0.31	0.5765
	12/43	12/37			11/54	12/48		
	15.3 – 43.7	18.0 – 49.8			10.6 – 33.5	13.6 – 39.6		
Earlier Neandertal (MIS 7-5)	62.5	68.3	0.23	0.6339	60.7	72.4	0.88	0.3489
	15/24	28/41			17/28	21/29		
	40.6 – 81.2	51.9 – 81.9			40.6 – 78.5	52.8 – 87.3		
Later Neandertal (MIS 4-3)	71.7	76.4	0.38	0.5352	66.7	66.0	0.00	0.9459
	43/60	52/68			34/51	35/53		
	58.6 – 82.6	64.6 – 85.9			66.7 – 79.2	51.7 – 78.48		
Middle Paleolithic Modern Humans	47.1	58.8	0.47	0.4920	33.3	33.3	0.00	1.0000
	8/17	10/17			2/6	3/9		
	23.0 – 72.2	32.9 – 81.6			4.3 – 77.7	7.5 – 70.1		
Early Upper Paleolithic	21.6	15.6	0.40	0.5253	12.9	8.1	0.42	0.5169
	8/37	5/32			4/31	3/37		
	9.8 – 38.2	5.3 – 32.8			3.6 – 29.8	1.7 – 21.9		
European Late Upper Paleolithic	63.6	42.9	1.86	0.1721	41.9	57.1	1.36	0.2433
	14/22	9/21			13/31	16/28		
	40.7 – 82.8	21.8 – 66.0			24.6 – 60.9	37.2 – 75.5		

Each group and tooth type has three row values. Top: percent chipped teeth; middle: chipped teeth/total; bottom: binomial, one proportion confidence limits (95% CL) for percentage calculation.

X^2 and *P*-values for the H_0 of equal proportions of chipping across left and right sides of a given jaw by group. **Bold** value indicate rejection of H_0 for equivalent proportions at $P \leq 0.05$. df = 2.

When all teeth are pooled by jaw significant differences between samples are found (**Figure 6.6** and **Table 6.7**). There is a risk of over counting individuals represented by more than one (and up to 6 total) anterior teeth by jaw – i.e., it is more likely for an individual with a chip on one tooth to have a chip on another tooth. Nonetheless, the Middle Pleistocene sample has relatively low chipping frequencies as does the Early Upper Paleolithic sample (albeit the Early Upper Paleolithic sample has a wide 95% CL). Both of these samples are also characterized by low occlusal wear scores (**Figure 6.3**, **Table 6.2**, and **Table 6.3**). However, the low Middle Pleistocene values may also be due to interobserver error, since the sample is overwhelmingly from Sima de los Huesos individuals and that data was taken from the literature.

The null hypothesis of equivalent proportions between groups is rejected for both maxilla and mandible (**Table 6.7**). The relative Chi-square contribution of each group shows that Middle Pleistocene, Later Neandertal, and Early Upper Paleolithic proportions were the strongest contributors to the total Chi-square result ($X^2 = 76.41$, $P \leq 0.000$, df = 5: **Table 6.7**). Assuming independence, chipping was lower than expected for the Middle Pleistocene and Early Upper Paleolithic groups but higher than expected for the Later Neandertals (**Table 6.7**). For the mandible, there were large relative Chi-square contributions from the Middle Pleistocene, Earlier and Later Neandertals, and Early Upper Paleolithic human groups to the overall Chi-square result ($X^2 = 84.79$, $P \leq 0.000$, df = 5: **Table 6.7**). Again, chipping in the Middle Pleistocene and Early Upper Paleolithic groups was lower than expected under an assumption of independence, whereas it was higher than expected in the Earlier and Later Neandertal groups (**Table 6.7**).

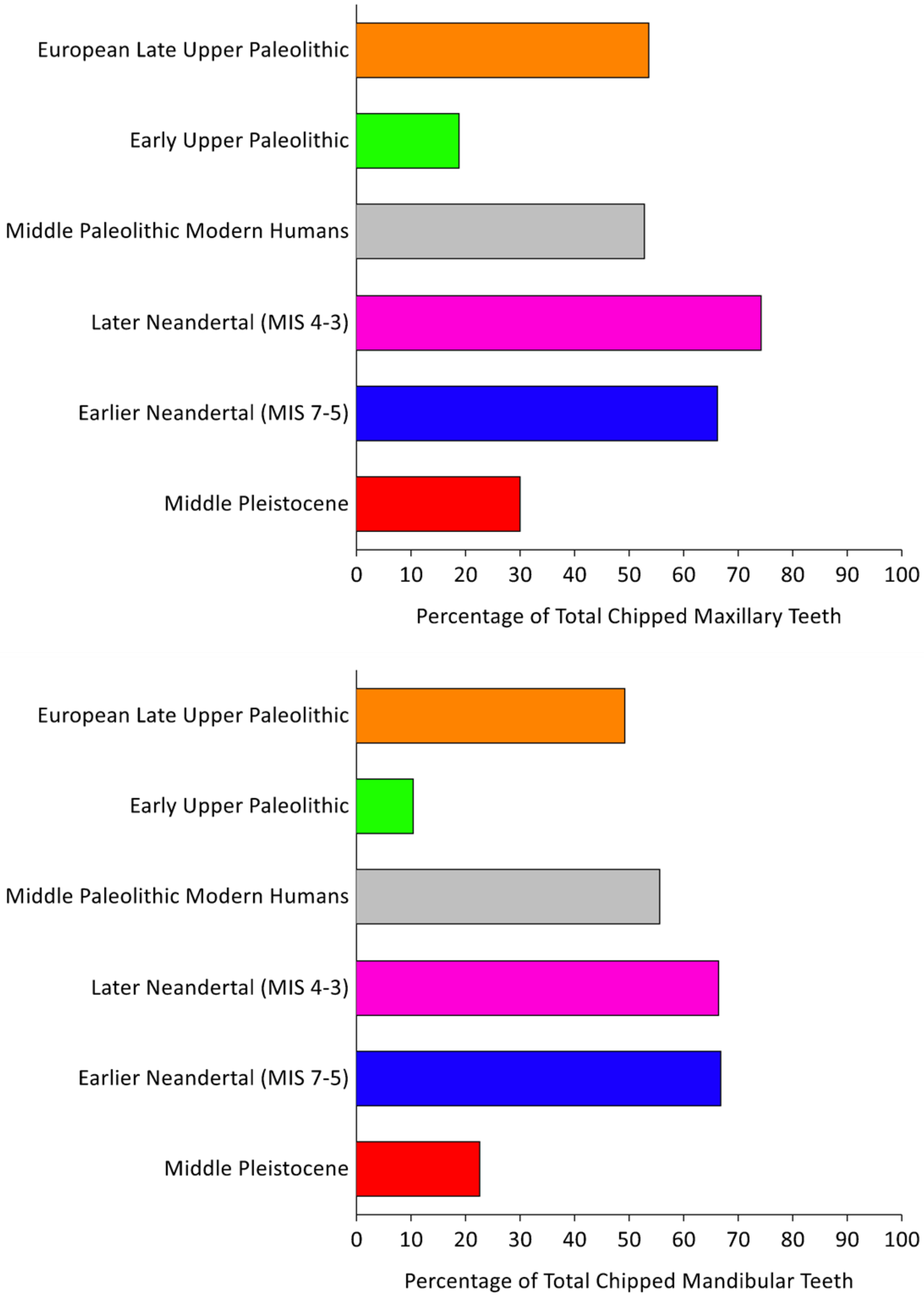

Figure 6.6 Percentage of total chipped teeth by jaw.
Samples are composed of pooled left and right I1, I2, and C for each group. Maxilla: top; mandible: bottom.

Table 6.7 Percentage and cross tabulation results for anterior enamel chipping by jaw.

	Maxilla				Mandible			
	Percent	Present	Absent	Total X^2	Percent	Present	Absent	Total X^2
Middle Pleistocene	30.0	24 (-)	56		22.6	23 (-)	79	
	20.3 – 41.3	7.21	7.67	14.88	14.9 – 31.9	9.82	7.36	17.18
Earlier Neandertal (MIS 7-5)	66.2	43 (+)	22		66.7	38 (+)	19	
	53.4 – 77.4	2.69	2.86	5.55	52.9 – 78.6	7.54	5.65	13.19
Later Neandertal (MIS 4-3)	74.2	95 (+)	33		66.4	69 (+)	35	
	65.7 – 81.5	12.76	13.57	26.33	56.4 – 66.4	13.39	10.04	23.43
Middle Paleolithic Modern Humans	52.9	18 (+)	16		55.6	5 (+)	4	
	35.1 – 70.2	0.01	0.01	0.02	21.2 – 86.3	0.34	0.25	0.59
Early Upper Paleolithic	18.8	13 (-)	56		10.3	7 (-)	61	
	10.4 – 30.1	14.32	15.24	29.56	4.2 – 20.1	16.82	12.62	29.44
European Late Upper Paleolithic	53.5	23 (-)	20		49.2	29 (+)	30	
	37.7 – 68.8	0.03	0.03	0.06	35.9 – 62.5	0.55	0.41	0.96
Total	51.6	216	203	76.41*	42.9	171	228	84.79*
	46.7 – 56.4				37.9 – 47.9			

Percent columns for maxilla and mandible have two rows for each group. Top: percent chipped teeth. Bottom: binomial, one proportion confidence limits (95% CL) for percentage calculation.

Present/Absent columns for maxilla and mandible have two rows for each group. Top: number of teeth. Bottom: X^2 contribution of present or absent counts to total X^2. Expected counts assuming independence: (-) = less than expected; (+) = more than expected.

Total X^2 column: each group's contribution to "Total" row at bottom of table.

***** Significant at $P \leq 0.0000$. Reject H_0 of equal proportions of chipping across groups in maxilla or mandible across groups. df = 5.

The calculation of relative chip size (*h*/*D*), actual bite force (P_F) and maximum potential bite force (P_{max}) for postcanine teeth are provided in **Figure 6.7** and **Table 6.8**. Overall, these values show extensive overlap between modern and archaic human groups, and the values are considerably lower than those calculated for early fossil hominins and non-human primates using the same methods (e.g., Constantino et al. 2010, 2012). Relative chip size is particularly informative given how short the values for each fossil sample fall in relation to the practical chip limit (dashed line with 0.3 value in **Figure 6.7**). Similarly, the actual bite force values measured from chip dimensions (P_F) do not overlap at all with the values produced for the maximum potential bite force (P_{max}). These values only calculate posterior bite forces in the sample but chip size is a good indicator of bite force. Variation in postcanine chipping variables was not normally distributed so Kruskal-Wallis one-way ANOVA was used to determine whether significant differences in medians exist between groups. No significant differences were found between groups for relative chip size (*h*/*D*), actual bite force (P_F) and maximum potential bite force (P_{max}) (**Table 6.8**).

Table 6.8 Values for relative chip size (*h/D*) actual bite force (P_F) and maximum, potential bite force (P_{max}) for postcanine teeth by fossil sample.

						Kruskal-Wallis[a]	
	Group	***N***	**Mean**	**SD**	**95% CI**	**X^2**	***P***
h/D	Early Modern Human	40	0.060	0.028	0.056 – 0.064	1.86	0.3941
	Neandertal (MIS 4-3)	73	0.056	0.029	0.052 – 0.060		
	Krapina (MIS 6/5e)	15	0.071	0.038	0.057 – 0.085		
P_F	Early Modern Human	31	130.40	94.90	117.17 – 143.63	1.59	0.4522
	Neandertal (MIS 4-3)	54	131.60	108.86	117.10 – 146.10		
	Krapina (MIS 6/5e)	15	169.50	140.62	116.99 – 222.00		
P_{max}	Early Modern Human	40	1435.66	419.68	1377.14 – 1494.18	1.06	0.5874
	Neandertal (MIS 4-3)	70	1472.61	421.11	1416.52 – 1528.69		
	Krapina (MIS 6/5e)	15	1353.53	335.16	1228.38 – 1478.68		

[a] df = 2

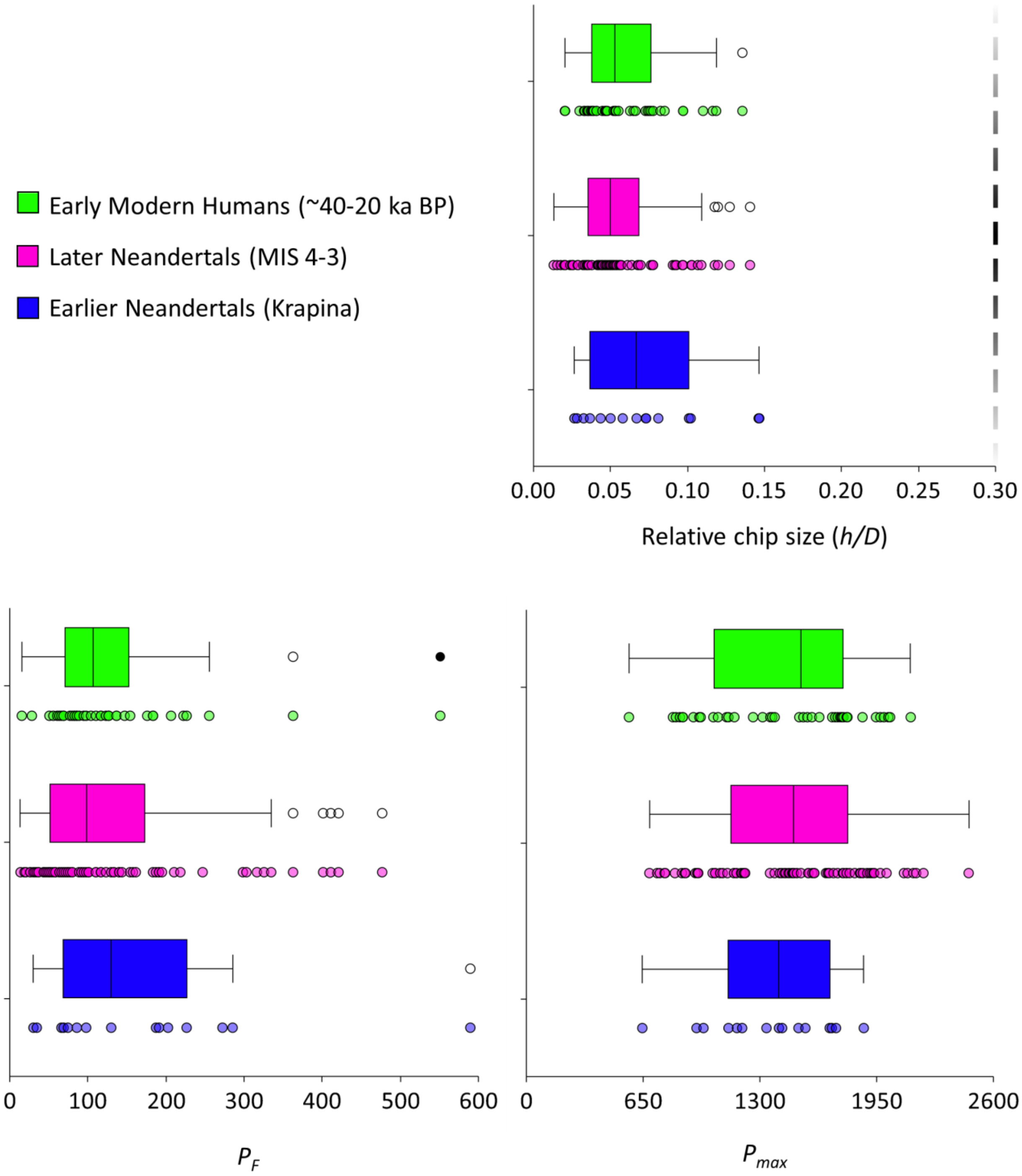

Figure 6.7 Graphs of relative chip size (*h*/*D*), P_F, and P_{masx} for the postcanine dentition. Note: the samples used for posterior dental chipping differ slightly from those of other analyses in this thesis. See Chapter 6 Methods.

Comparisons of ordinal chipping score frequencies for anterior and posterior chipping gives a relative indicator of actual bite force production for the anterior teeth (**Figure 6.8** and **Table 6.9**) despite the inability to directly calculate bite force estimates for anterior teeth. Chipping scores are numerous but small (score 1) across the anterior dentition (**Figure 6.8** and **Table 6.9**). Larger chips are found in the maxillary anterior teeth more frequently than the mandibular teeth. There are few large (grade 3) chips across the samples in the anterior teeth. Larger chips (grades 2 and 3) are found in relatively equal amounts across the posterior teeth as is to be expected from the calculations of bite force based on chip size. Samples sizes are rather small and 95% CL's overlap considerably across anterior and posterior teeth in both jaws. The number of chipped teeth is small and when categorized by ordinal score the samples are smaller yet. Therefore, some caution in interpreting the frequency plots (**Figure 6.8**) is advised.

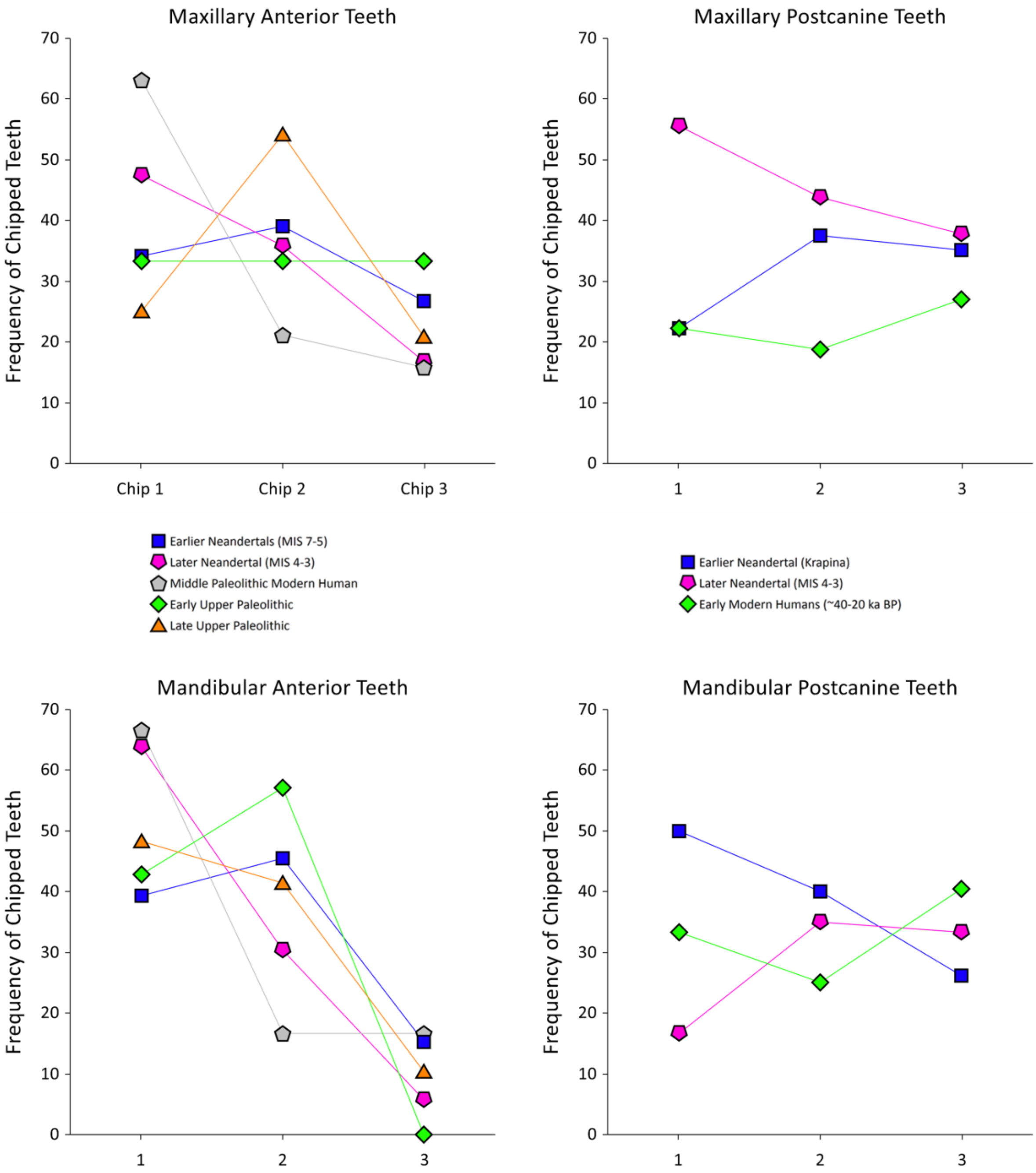

Figure 6.8 Frequency of enamel chips in each ordinal size category for anterior and posterior dentitions. Frequencies are based on the total number of chips across all tooth types and sides. Some bias is expected. Note: anterior and postcanine teeth consist of slightly different sample groupings.

Table 6.9 Comparison of ordinal score frequencies for each chipped anterior and posterior tooth.

	Earlier Neandertal (MIS 7-5 or Krapina MIS6/5e)				Later Neandertal (MIS 4-3)				Middle Paleolithic Modern Human		Early Upper Paleolithic ("Early Modern Human")				Late Upper Paleolithic	
Maxillary Teeth																
Chip Score	*Anterior*	*N*	*Posterior*	*N*	*Anterior*	*N*	*Posterior*	*N*	*Anterior*	*N*	*Anterior*	*N*	*Posterior*	*N*	*Anterior*	*N*
1	34.1	14	22.2	2	47.4	45	37.5	6	63.2	12	33.3	4	35.1	13	25.0	6
2	39.0	16	55.6	5	35.8	34	43.8	7	21.1	4	33.3	4	37.8	14	54.2	13
3	26.8	11	22.2	2	16.8	16	18.8	3	15.8	3	33.3	4	27.0	10	20.8	5
Mandibular Teeth																
Chip Score	*Anterior*	*N*	*Posterior*	*N*	*Anterior*	*N*	*Posterior*	*N*	*Anterior*	*N*	*Anterior*	*N*	*Posterior*	*N*	*Anterior*	*N*
1	39.4	13	50.0	3	63.8	44	40.0	8	66.7	4	42.9	3	26.2	11	48.3	14
2	45.5	15	16.7	1	30.4	21	35.0	7	16.7	1	57.1	4	33.3	14	41.4	12
3	15.2	5	33.3	2	5.8	4	25.0	5	16.7	1	0.0	0	40.5	17	10.3	3

Conclusions

Some significant differences in chipping frequencies were found, but differences between archaic and early modern humans are not as starkly contrasted as might be expected given the propensity to emphasis anterior tooth-use among archaic humans in the literature. For instance, the cross-tabulation results do show significant differences in the total chipping by jaw across samples. Earlier and Later Neandertals tend to have a higher proportion of anterior dental chipping in both jaws, but it is interesting that Middle Pleistocene anterior dental chipping is lower than expected in both jaws (as was the Early Upper Paleolithic). The contrast is particular interesting because both Middle Pleistocene and Neandertal groups are characterized by large anterior teeth, but the former exhibits less evidence of engaging in behaviors that chip enamel. Part of the low frequency among the Middle Pleistocene and Early Upper Paleolithic samples may be due to the younger age (inferred through the relatively low degree of occlusal wear) in the samples. In contrast, the frequency of anterior dental chipping is quite high among the Middle Paleolithic and Late Upper Paleolithic modern humans. The latter group also exhibits the smallest anterior tooth size on average among the samples examined. Thus, anterior dental chipping does not exhibit a clear chronological or morphological trend across the human groups examined here.

Posterior dental chipping shows that archaic and modern human groups do not differ significantly in estimates of maximum potential posterior bite force or in terms of actual bite forces produced. This result coincides well with data on postcanine dental size trends in the Middle and Late Pleistocene – there is relatively little change in overall dimensions across the Late Pleistocene archaic to modern human morphological transition (Trinkaus 2004).

Furthermore, enamel chipping of small, medium, and large sizes are found among the teeth of each fossil group examined in the present study. This indicates that individuals in each group engaged in anterior tooth-using behaviors that required a range of bite forces.

Chipping cannot account for all manipulative behaviors (especially those involving biting down on more pliant materials), but enamel chipping does provide another insight into non-masticatory behavior that analyses of degree (wear gradients) or type (cutmark analysis) cannot provide in isolation. Some biases have been pointed out in terms of sample composition (e.g., young age of Middle Pleistocene and Early Upper Paleolithic samples; and the very small sample of Middle Paleolithic modern humans). However, the biases inherent in the analysis of small fossil samples helps to an illustrate an important point: we cannot make sweeping generalizations about archaic versus modern human anterior tooth-use in fossil human groups on the basis a single variable. Results do not follow clear chronological trends or have clearly delineated patterns across morphologically defined groups.

Chapter 7. Instrumental cutmarks on the labial enamel surfaces of anterior teeth

Hypotheses and Predictions

H_0: There will be no difference in the frequency of central maxillary incisors with labial surface instrumental striations between chronologically and morphologically-defined human groups.

This null hypothesis will be rejected if significant differences in the frequency of instrumental striations are found between chronologically and morphologically-defined groups. If rejected, the magnitude and direction of the behavioral shifts among Middle and Late Pleistocene groups will be assessed.

A brief rationale for analysis

The methods used to identify instrumental striations (**Figure 7.1**) on the labial surfaces of anterior teeth vary greatly between studies. Many researchers have noted obvious cutmarks on anterior teeth (most commonly maxillary central incisors) that are often visible macroscopically or with low magnification such as the Neandertals from Angles sur l'Anglin, Cova Negra, Hortus, La Quina, Saint-Brais, and Shanidar (Martin 1923; Koby 1956; Patte 1960; de Lumley 1973; Trinkaus 1983; Arsuaga et al. 1989). Other studies rely on higher magnification through the use of standard light microscopy, stereomicroscopy, SEM, or a combination of microscopic methods to identity and/or quantify labial cutmark frequency, metric variation, and orientation (Koby 1956; Bermúdez de Castro et al. 1988; Arsuaga et al. 1989; Lalueza-Fox 1992; Lalueza-Fox et al. 1993; Lalueza-Fox and Pérez-Pérez 1994; Lalueza-Fox and Frayer 1997; Lozano et al. 2004, 2008, 2009, nd; Frayer et al. 2010, 2012; Hillson et al. 2010; Volpato et al. 2012; Estalrrich and Rosas 2013, 2015; Fiore et al. 2015; Sarig et al. 2016; Willman 2017). A new method using 3D microscopy produces incredibly high-resolution metric data (Hillson et al. 2010), but access to this technology is not widespread. However, it is difficult to compare metric data on striations when using different microscopic techniques (but see Estalrrich and Rosas 2015 for an example of combined SEM and light microscopy), and it is even more difficult to rely on published metric data without knowing the taphonomic status of each tooth analyzed.

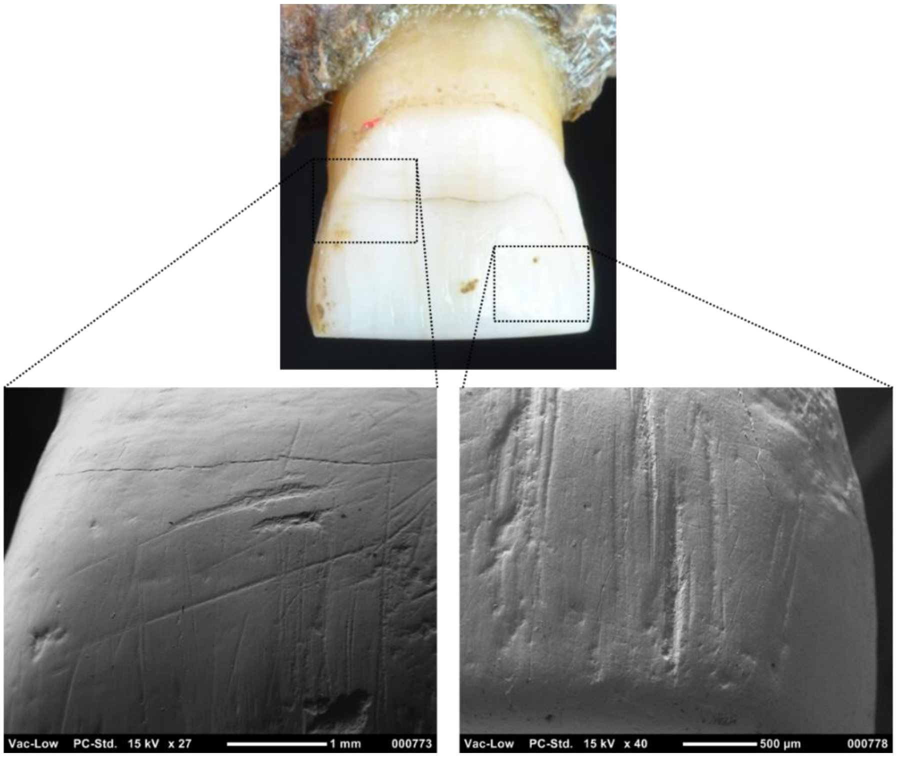

Figure 7.1 SEM micrographs of cutmarks of the left I^1 of Dolní Věstonice 13.

Labial cutmarks are frequently studied to determine handedness of fossil hominins as an indirect assessment of hemispheric dominance given the apparent association between handedness, hemispheric dominance, and a capacity for language (Frayer et al. 2010, 2012;

Volpato et al. 2012; Fiore et al. 2015). Other studies are more concerned with frequency, metric variation, and orientation of labial cutmarks as a source of information on a non-masticatory behavior (Lalueza-Fox 1992; Lalueza-Fox and Pérez-Pérez 1994; Lalueza-Fox and Frayer 1997; Lozano et al. 2008, 2015; Hillson et al. 2010; Estalrrich and Rosas 2013, 2015; Willman 2016, 2017). The different interpretive goals of each type of study are often accompanied by different data presentation (e.g., comparisons by tooth type, pooling data for all teeth in the dentition of a single individual, or pooling all data for all individuals in an entire sample or "population"). Thus, a lack of standardized data presentation, in addition to methodological differences, creates major discrepancies in the presentation of continuous cutmark data in the literature. This makes it particularly difficult to compare the results of different studies, irrespective of what methods are used to obtain continuous data (Willman 2016, 2017).

In contrast to studies concerned with cutmark frequency, metric variation, and orientation much can be gained from studies that only consider cutmark prevalence. It is relatively easy to identify instrumental striations that originate from non-masticatory, "stuff-and-cut" behaviors (see Methods) regardless of the microscopic technique used. However, some behavioral resolution is lost when continuous data are abandoned for larger sample size and more control over data when using cutmark prevalence. For instance, detailed data on cutmark metric variation and striation orientation may specify some degree of skill, dexterity, type of tool used for stuff-and-cut behaviors, or the type of processing behavior habitually engaged in. However, postmortem modification of enamel surfaces already prevents the collection of continuous data in many cases. For instance, the Sima de las Palomas Neandertal dental sample is replete with postmortem taphonomic damage (e.g., glue, enamel spalling, brecciated surfaces, etc.) that lead to the publication of data on a tooth-by-tooth basis (Willman 2017). Some teeth could not be scored at all, the collection of presence/absence data for some wear features was possible for some, and the collection of partial or complete continuous data was possible for the remainder of the sample. While the degree of data salvaged from collections with extensive postmortem modification can still reveal a great deal of information regarding manipulative behavior, there is no guarantee that the studies from the literature, that provide some form of comparative data, used the same or similar taphonomic criteria to determine which specimens were included or excluded from each type of analysis.

The identification of cutmarks (and other dental wear features) as present or absent is far more standardized than the measurement of continuous variables between studies despite some loss of behavioral resolution. Thus, one can have far greater confidence in using presence and absence data culled from the literature. This approach has proved particularly useful when comparing different fossil or taxonomic groups. An example is provided by Bruner, Lozano, and colleagues (Bruner and Lozano 2014b, 2015; Bruner and Iriki 2016; Bruner et al. 2016) where they provide prevalence data on labial cutmarks for groups of "*Homo antecessor", "Homo heidelbergensis",* Neandertals, and recent modern humans to comment on possible cognitive differences and similarities across the sample groups. The primary critique of such approaches is in how the frequency of presence or absence is calculated. In the above cases, prevalence is calculated for each individual regardless of how many teeth were present for that individual. For example, an individual with only two mandibular canines (or any other combination of missing and present teeth) would be considered equivalent to an individual with all 12 maxillary and mandibular anterior teeth.

Tooth type is also an important consideration since central and lateral incisors are more frequently cutmarked than canines (Lalueza-Fox and Frayer 1997; Lozano et al. 2008), and wear patterns tend to differ between maxillary and mandibular dentitions (Volpato et al. 2012; Fiore et al. 2015). One must also ask whether it is appropriate to compare individuals with deciduous incisors and canines with samples of permanent teeth. Even better, if sample size permits, would be to compare by tooth type and occlusal wear scores to have a coarse control over age and the amount of crown remaining.

Another problem with prevalence data is that cutmarks are typically noted in fossil descriptions when present, but the *absence* of cutmarks is not typically noted in fossil descriptions. However, the absence of cutmarks by tooth or individual is noted when the focus of a particular study is on the patterning of instrumental striations within or between samples (e.g., Lalueza-Fox and Pérez-Pérez 1994; Lalueza-Fox and Frayer 1997; Lozano et al. 2008; Bruner and Lozano 2014b). This situation may contribute toward an inflated frequency of cutmarks in the literature for archaic humans. Interestingly, there is now only one publication on instrumental striations on early modern human teeth (Willman, 2016). Holocene samples, although not explicitly stated as such, are used as a proxy for early modern humans (Bruner and Lozano 2014b, 2015; Bruner and Iriki 2016; Bruner et al. 2016) for comparisons with archaic humans. However, very few samples of recent (Holocene) humans have been studied and the methods used vary (Lalueza-Fox and Pérez-Pérez 1994; Bax and Ungar 1999; Lozano et al. 2008, 2015; Dinnis et al. 2014).

This analysis therefore identifies and quantifies the frequencies of labial cutmarks among archaic and early modern humans using standardized sample selection criteria. Thus, there is no assumption of equivalence between individuals with variably complete dentitions. This is accomplished by considering only teeth of the same type. In this case, data will only be considered for maxillary central incisors. Idiosyncratic variation related to the ways in which tools contacted the dentition (i.e., the width and length of the striations, and orientation of striations indicative of the motion of hand and tool) are not considered here, but have been presented for two new samples elsewhere (Willman 2016, 2017). The criteria and methods of analysis are explored further below.

Materials

Scanning electron microscopy (SEM) was used to identify cutmarks on labial surfaces of most specimens described in this chapter. A smaller subset of the sample was examined using a portable light microscope when molding and casting of the original fossils was not possible. Materials include original fossils examined and/or molded and cast by the author, high-resolution dental casts provided by colleagues, and data obtained from the literature.

Methods

Taphonomic considerations

Taphonomic alterations of enamel surfaces (e.g., chemical erosion, root-etching, abrasion, adhering breccia or glue, etc.) are distinguished from in vivo wear processes using criteria based on microscopic surface attributes (King et al. 1999; Pérez-Pérez et al. 2003; Martínez and Pérez-Pérez 2004; Willman 2017). Teeth with enamel surfaces heavily altered by postmortem taphonomic processes would not be considered in quantitative analyses concerned with cutmark length, width, and orientation. However, this analysis is concerned only with presence or absence of cutmarks so certain exceptions are made. If an area of a labial surface is partially obscured by any number of localized, postmortem features (e.g., glue, enamel spalls, breccia, etc.) the tooth could still be counted as having cutmarks “present” if there are undisputable, antemortem cutmarks present on another area of the same tooth. In contrast, it is much more difficult to make an argument that a tooth with extensive postmortem damage has an absence of cutmarks if all of the enamel is not clearly visible. Therefore, heavily damaged teeth with no cutmark data do not contribute to frequency calculations.

It is acknowledged here that the above sampling practice may introduce potential for error, but the criteria for inclusion or exclusion of a tooth is consistent across fossils samples analyzed here which suggests that any bias would be evenly distributed across samples. Fossil descriptions frequently discuss the presence of labial cutmarks when obvious, but there is no trend in noting their absence. Thus, any sample inflation that the taphonomic inclusion/exclusion criteria introduces to this study are merely contributing to a bias already present in the literature – i.e., the frequency of individuals with cutmarked teeth is artificially inflated.

Identifying cutmarks of cultural origin

Following taphonomic assessments, striations were categorized as cutmarks of cultural/instrumental origin or as dietary striations. The width and morphology of striations caused by in vivo behaviors are particularly useful for elucidating dietary or non-masticatory behavioral origins for each feature. Dietary striations are usually less than 5 µm wide, whereas cutmarks are as small as ~10 µm, commonly range between 20-40 µm, and can occasionally exceed 100 µm (Bermúdez de Castro et al. 1988; Lalueza-Fox and Pérez-Pérez 1994; Lalueza-Fox and Frayer 1997). Enamel cutmarks can also be identified from their characteristic micromorphology that includes microstriations within the borders of a cutmark, hertzian cone fractures along the striation edge, and V-shaped cross-sections – all of which are seen in experimental replications of cutmarks on bone and enamel (Bromage and Boyde 1984; Bermúdez de Castro et al. 1988; Bromage et al. 1991; Lozano et al. 2004; Frayer et al. 2010; Estalrrich and Rosas 2013). However, as Frayer and colleagues (2010) noted, cutmark micromorphology is often worn away in-vivo through dietary abrasion as well as through the repetition of non-masticatory behaviors. Thus, striation depth, width, and length are often needed to distinguish relatively worn (i.e., earlier occurring) instrumental striations from other wear features. In any case, a conservative approach is adopted, and the presence of labial cutmarks is not assigned to a tooth unless it is highly consistent with an instrumental origin.

The use of data from the literature

Labial cutmark data for several samples was culled from the literature. The permanent teeth from Sima de los Huesos required more extensive preparation for inclusion. Presence or absence of cutmarks for each tooth was compiled using data from Lozano and colleagues (Lozano 2005; Lozano et al. 2008), and occlusal wear scores as well as individual tooth associations for each Sima de los Huesos individual were obtained from the supplemental material published by Martinón-Torres et al. (2012). The teeth associated with each individual (Martinón-Torres, et al. 2012) were double-checked against previously published attributions (Lozano 2005; Lozano et al. 2008) for discrepancies between studies. A few teeth that were “not assigned” to a Sima de los Huesos individual in earlier studies (Lozano 2005; Lozano et al. 2008) have since been associated with an individual dentition in the more recent morphological description (Martinón-Torres et al. 2012). These more recent associations are used in the present analysis. Specific points of departure between the assignment of each tooth to an individual dentition in the non-masticatory dental wear studies (Lozano 2005; Lozano et al. 2008) and the morphological study (Martinón-Torres et al. 2012) are addressed in the footnotes of **Appendix Table 1**.

Results

All maxillary central incisors analyzed in the present study exhibit labial cutmarks irrespective of the group being analyzed (**Table 7.1**). Furthermore, the current analysis is an understatement of the number of individual archaic humans exhibiting labial cutmarks, since a large number of teeth other than I^1’s were documented in previous analyses. However, the goal was to compare equivalent data by only using the most frequently cutmarked tooth type.

The most important consideration to come from this analysis is that Middle and Upper Paleolithic early modern human groups (**Figure 7.2**) also exhibit cutmarks on permanent teeth to the same extent as archaic humans. Therefore, a high prevalence of cutmarked teeth is not a unique feature of archaic humans. Instead it provides a physical manifestation of a habitual, manipulative behavior that is shared across Middle and Late Pleistocene human groups regardless of morphologically defined group affiliations.

Implications for differential archaic and modern visuospatial integration

A final note on anterior tooth use relates to the opening comments in this dissertation with respect to making broad generalizations about prehistoric behavior, cognition, and competitive advantage (among other topics) between Nenadertals and early modern humans. The major issue being the use of Holocene or ethnohistoric comparative collections as proxies for early modern humans (Chapter 1).

Table 7.1 Comparison of curtmark counts and frequencies on I^{1}'s across samples.

Group	Individuals with cutmarks on right and/or left I^1	present/total	Frequency
Sima de los Huesos	SH I, SH II, SH V, SH VII, SH XVI, SH XVIII, SH XX, SH XXI, SH XXXI, AT-8, AT-54, AT-280, AT-1943, AT-1958, AT-3885, AT-198/199	16/16	100%
Earlier Neandertal (MIS 7-5)	KDP 4, 5, 6, 17, 18, 29, 30, 35, Q; Tabun C1, B-Series III	11/11	100%
Later Neandertals (MIS 4-3)	Spy I; Vindija 290; Combe Grenal Vl Angles Sur l'Anglin; Arcy Hyène B7IV66/D4IV66; Hortus VII, VIII, IX, X; La Quina 5; Saint-Césaire; Neandertal N66; Cova Negra 7856; Sidrón Adult 1, 2, 3, 4, 5, 6, Adolescent 2, 3, and Juvenile 1; Palomas 19/73/79, 59/90; Zafarraya 23; Saint-Brais; Shanidar 2	28/28	100%
Middle Paleolithic Modern Humans	Skhul 2, 4; Qafzeh 5, 6, 7, 9, 11	7/7	100%
Early Upper Paleolithic	Ishango 22295-24; Brassempouy 1046, 2206; Buran Kaya 135, 136, 137; Les Rois w/#, 5, 45; Dolní Věstonice 3, 13; Pavlov 1; Arene Candide IP; Barma Grande 3, 4; Ostuni 1	16/16	100%
Late Upper Paleolithic	Riparo Fredian 6, Gough's Cave,	2/2	100%

Instrumental cutmarks on the labial surfaces of anterior teeth were recently used to support a hypothesis of differential, or mismatched, visuospatial integration and extended cognition among archaic humans compared to *Homo sapiens* (Bruner and Lozano 2014b, 2015; Bruner et al. 2016). This hypothesis requires one to accept that parietal lobe expansion is characteristic of Neandertals and that the morphological differences in the brain correspond to functional/cognitive differences between morphologically differentiated groups (Bruner 2010, 2014; Bruner and Lozano 2014b, 2015; Bruner and Iriki 2016; Bruner et al. 2016). The frequency of instrumental striations on the anterior teeth by individual was thought to be a representative behavioral signal for refined (*Homo sapiens:* low frequency of instrumental striations) or impaired (Archaic *Homo* including the Neandertals: high frequency of instrumental striations) visuospatial integration among fossil groups.

Using previously publishing data on instrumental cutmarks from Sima de los Huesos fossils, a collection of Australian Aborigines (Lozano et al. 2008), and data on Neandertals available in the literature; Bruner and Lozano (Bruner and Lozano 2014b) suggest that cutmarks on archaic human teeth occur among 100% of archaic humans, but occur to a lesser degree (46%) in a comparative sample of Australian Aboriginal individuals. Furthermore, the low frequency of cutmarks among the Gran Dolina hominins is used to suggest that Middle Pleistocene archaic *Homo* and the Neandertals are behaviorally derived (and this behavior is assumed to be phylogenetically controlled through neurological function) with respect to their extensive use of the mouth for manipulative behavior compared to the ancestral condition and that of later *Homo sapiens* (Bruner and Lozano 2014b, 2015; Bruner et al. 2016). Unfortunately, the Gran Dolina sample was not addressed here as the criteria for inclusion in the present study required the presence of maxillary central incisors for which Gran Dolina has none (Bermúdez de Castro et al. 1999, 2006, 2008).

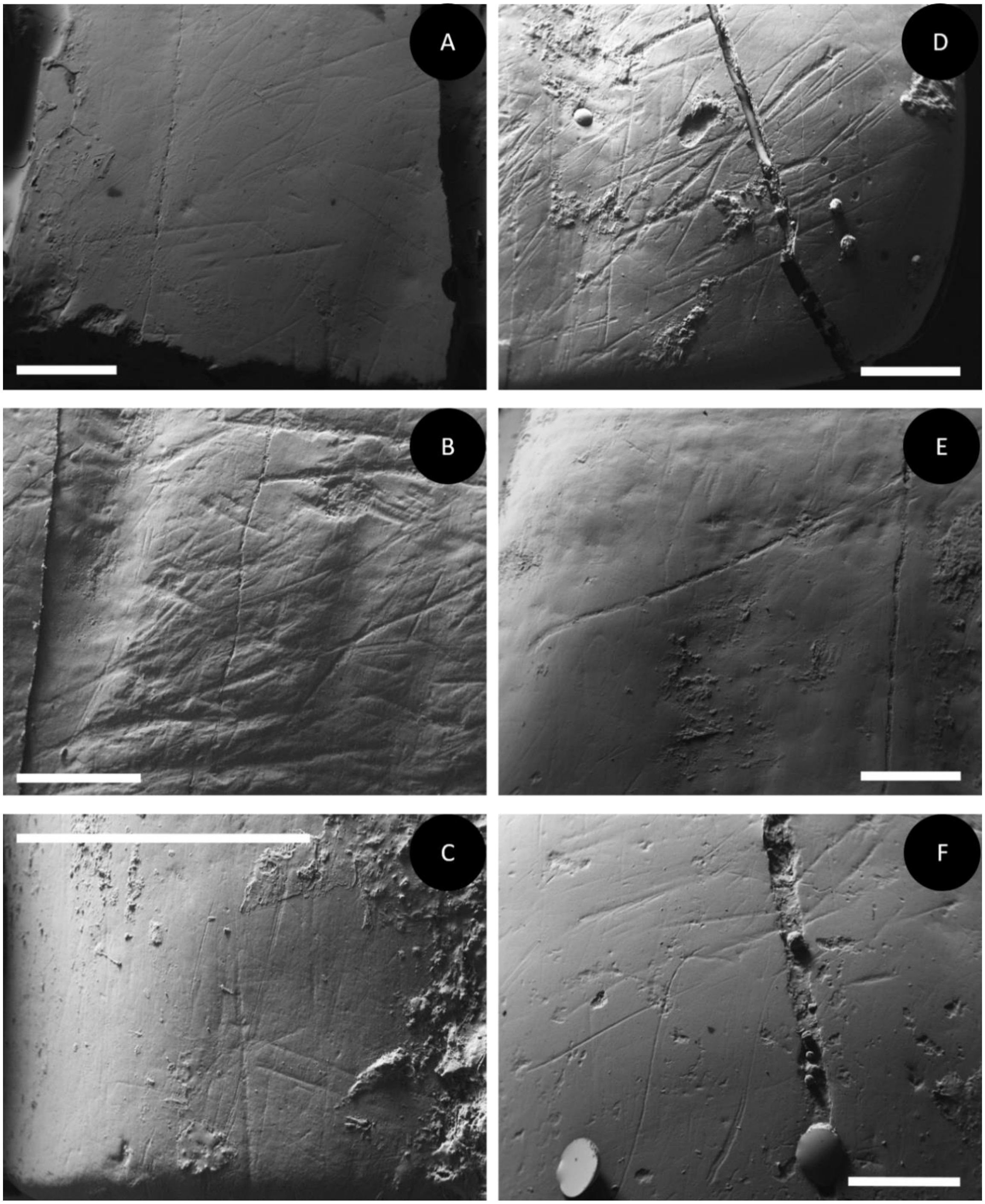

Figure 7.2 Examples of cutmarks on various early modern human maxillary central incisors. (A) Les Rois w/# right I^1, (B) Les Rois 45 left I^1 (C) Ostuni left I^1, (D) Buran Kaya left I^1, (E) Barma Grande 3 left I^1, (F) Qafzeh 6 left I^1. Scale bar = 1 mm.

Thus, archaic humans are suggested to rely on their bodies, and more specifically their mouths, for manipulative behaviors than modern humans: *"Our hypothesis is based on a naïve* *but reasonable assumption: mouth is to eat, hand is to handle* (Bruner and Lozano 2014a:303)." This is attributed this to a "*mismatch between cultural and neural complexity*" (Bruner and Lozano 2014b:276) among archaic humans compared to *Homo sapiens.* However, the study makes a comparison between a group of hunter-gatherers (Australian Aboriginals) that are over 40,000 years removed from the early modern human groups of biological relevance to the hypothesis. An examination of maxillary central incisors from Middle and Upper Paleolithic modern humans in the present study shows that 100% of individuals had labial cutmarks on their anterior dentitions. Thus, any inferiority in visuospatial integration that is present among archaic humans is also present in early modern humans on the basis of this instrumental striation data.

Furthermore, there is rich ethnographic documentation of the use of teeth-as-tools in the form of both literature and film that documents the use of teeth-as-tools among Australian Aboriginal hunter-gatherers (Gould 1968, 1969; Barrett 1977; Hayden 1979; Brown and Molnar 1990; Dunlop and Martin-Jones 2011 [1967]). Thus, even if Australian Aboriginal hunter-gatherers did not engage in stuff-and-cut behaviors as frequently as archaic humans (or early modern humans) it is evidence that they still relied on a suite of other non-masticatory behaviors for manipulative behaviors. The cutting instruments used by ethnohistoric Australian aborigines may also have played a role in the low instrumental striation frequency. Glass and metal was quickly adopted by Australian Aboriginals following European colonization of Australia (Head and Fullagar 1997; Cooper and Bowdler 1998; Harrison 2002; Dunlop and Martin-Jones 2011 [1967]). Metal cutting edges are highly efficient but metal is also softer than stone. It can be hypothesized that the less efficient cutting edges of Pleistocene lithic implements compared to glass or metal instruments used by Australian Aboriginals could account for some of the discrepancies in frequencies of individuals with instrumental striations between groups.

Thus, there is no support from instrumental striations for deficient visuospatial integration and impoverished extended cognition among archaic humans based on the presence or absence of instrumental striations. This analysis urges caution in sampling strategies for comparative studies assessing the role of particular behaviors to explain the demise of Neandertals. It is of the utmost necessity to look at temporospatially relevant groups (i.e., early modern humans) rather than using one or a few comparative samples from the Holocene or ethnographic present as proxies for the behavioral repertoire of all *Homo sapiens*.

Chapter 8. Discussion

H_0: There are no significant differences in anterior tooth-use between archaic Homo and Neandertals compared to early modern humans.

And three main sets of questions will be addressed in relation to the null hypothesis:

1. *Are differences in anterior tooth use for manipulative behavior evident across morphologically defined or temporally partitioned groups of Middle and Late Pleistocene humans? If so, what is the magnitude or degree of change in the behavioral shift?*
2. *To what degree can anterior dental morphology be attributed to functional adaptations to the high magnitude and/or repetitive loading of the dentition through non-masticatory behaviors?*
3. *To what extant does the presence of labial cutmarks on the anterior dentition differ across morphologically defined and temporally partitioned groups of Middle and Late Pleistocene humans?*

Introduction

The results of this dissertation largely highlight similarities rather than differences in the use of the anterior dentition for manipulative behaviors among Middle and Late Pleistocene humans. The overall trend is largely a hunter-gatherer trend: the anterior dentition is disproportionately worn when compared to the posterior dentition. This trend is related to a palimpsest of dietary and manipulative behaviors. Since, some non-masticatory behaviors (e.g., "stuff-and-cut", peeling of tubers, etc.) are also related to the preparation of foodstuffs the line between dietary and non-masticatory behaviors are further blurred. Thus, the use of the anterior dentition for manipulative behavior is common in degree (scaled occlusal wear gradients), magnitude (anterior dental chipping), and type of behavior (labial cutmarks on the anterior dentition) across the human groups considered in the present study. The main difference relates to structural reduction in both mass-additive traits and overall dimensions of the anterior dentition among early modern humans – an apparent paradox if one accepts that morphology reflects adaptation to function (i.e., habitual use). In terms of these results one might ask: *How is it that modern human anterior teeth underwent structural reduction without a clear reduction in anterior tooth-use for dietary and manipulative behaviors?*

Scaled occlusal macrowear gradients

Macrowear analyses show substantial overlap between archaic and early modern human groups. A high degree of anterior dental wear is commonly associated with hunter-gatherers from Pleistocene, Holocene, and ethnographic contexts (Molnar 1972; Hinton 1981; Smith 1983a; Kaifu 2000b; Bermúdez de Castro et al. 2003; Deter 2009; Berbesque et al. 2012; Clement and Hillson 2012; Clement et al. 2012; Littleton et al. 2013; Botha and Steyn 2015; Willman 2016, 2017), and the results shown here are in agreement. However, there is a particularly meaningful distinction in the degree of anterior dental wear when archaic and modern human anterior tooth crown dimensions are considered in conjunction with occlusal wear.

Clement and colleagues (2012) used an innovative technique to examine occlusal macrowear across Neandertal, early modern, and recent human groups that took into account biologically meaningful differences in the timing of dental eruption and tooth size. However, their use of dentin to enamel exposure ratios may not be an appropriate method when comparing human groups with grossly different tooth sizes (Willman 2016). The present study shows that the most meaningful variable related to dental wear gradients is in fact, anterior tooth size. The unscaled occlusal wear differentials scores were similar across archaic and modern human groups (particularly for maxillary and mandibular central incisors). On the other hand, macrowear gradients scaled to tooth size consistently show a grade shift between archaic humans from modern human variability, albeit with modest overlap. The use of “scale free” dentin exposure ratios removes the biologically relevant variable (crown size) that contrasts archaic and modern human groups. In fact, Clement et al. (2012) show extensive overlap between archaic and modern human samples (in some cases more so than the unscaled differential wear used here), including some modern human outliers that have occlusal wear well above the range found in their Neandertal sample. However, the use of occlusal wear scores as a scaling factor in the present study ensures that variation in dental size is being compared between individuals exhibiting similar degrees of occlusal wear. In this respect, the functional occlusal surface area is emphasized – a larger tooth is more resistant to cumulative dental wear. Scale-free analyses largely treat all teeth as if they are the same size, eliminating this important metric distinction.

A major exception to the general trend in high rates of anterior relative to postcanine dental wear was found in the Late Upper Paleolithic. Incisor ablation was present in many of the regional samples of Late Upper Paleolithic individuals. Ablation is well-documented among Late Upper Paleolithic hunter-gatherers and relates to aspects of individual and group-level social identity (Stojanowski et al. 2014, 2016; Willman et al. 2016). However, the removal of incisors through ablation promotes increased focus on the postcanine teeth for both dietary and non-masticatory behaviors (Bonfiglioli et al. 2004). Furthermore, in cases of maxillary incisor ablation, the mandibular teeth have no opposition, and little occlusal wear as a result. Thus, anterior dental wear can be low, whereas postcanine wear is elevated – the opposite of what typically characterizes hunter-gatherer dental macrowear. These factors help explain the wide range of variation in Late Upper Paleolithic macrowear gradients.

The tempo and mode of dental reduction from the Middle to the Late Pleistocene has been substantially refined in recent years, and the once clear trends relating tooth-use and function are no longer valid (Trinkaus 2004). The large anterior teeth of Neandertals, regularly associated with functional adaptation to non-masticatory behaviors (Brace 1967; Brace and Mahler 1971; Wolpoff 1979; Stefan and Trinkaus 1998; Hillson and Trinkaus 2002), are now known to be the ancestral characteristics of earlier archaic *Homo* (Trinkaus 2004; Smith 2013). Thus, the Neandertals maintained large anterior dentitions which benefit non-masticatory behaviors by increasing the surface area available for manipulative behaviors and provide resistance in the face of cumulative wear. Large anterior tooth roots would provide many of the same functional benefits as large crowns in terms of wear resistance, and are also thought to be an ancestral trait of archaic *Homo* (Smith and Paquette 1989; Le Cabec 2013), albeit with some overlap with early modern humans (Le Cabec et al. 2013; Trinkaus et al. 2013a; Trinkaus et al. 2014). Long roots are especially significant when one considers the normal process of supereruption that teeth undergo with increasing occlusal wear, thus promoting use-life long after the root becomes the functional occlusal surface.

Given the apparent advantages of large and robust anterior dental crowns and roots among archaic *Homo* we are left with a paradox: why do anterior dental crown (and root) dimensions reduce among early modern humans without a correlated reduction in anterior dental wear? This question will be returned to at the end of this discussion.

Dental enamel chipping

It has been suggested that the large anterior teeth and faces of Neandertals, and archaic humans more generally, are related to the functional demands placed on the anterior dentition related to the use of teeth-as-tools. The anterior dental loading hypothesis (ADLH) posits that high and/or repeated loading of the anterior dentition provided a significant adaptive pressure on Middle and Late Pleistocene craniodental remains whereby high functional demands on the anterior teeth selected for robust morphology in archaic *Homo* while the reduced robusticity of craniodental traits among *Homo sapiens* is evidence of relaxed selection largely attributed to technological change (Smith 1983b; Rak 1986; Demes 1987; Trinkaus 1987; Smith and Paquette 1989; Spencer and Demes 1993; Brace 1995; Le Cabec et al. 2013). However, the production of high magnitude and efficient anterior bite forces is now thought to have been no more possible among Neandertals than early modern humans (Antón 1990, 1994, 1996; Couture 1993; Dobson and Trinkaus 2002; O'Connor et al. 2005; Clement et al. 2012). Data from dental enamel chipping also supports this conclusion.

Studies of bite force production on the posterior dentition across a wide variety of bunodont mammals and primates, including hominins, shows a strong relationship between the size of individual enamel fractures and chips with bite force production (Constantino et al. 2010, 2012; Lee et al. 2011; Lawn et al. 2013; Strait et al. 2013). The prerequisite for postcanine fracture is that bite forces are produced on hard-objects. It is clear from the prevalence of chipping in the anterior teeth considered in the present study that forceful biting on hard-objects with the anterior dentition occurred with regularity among Middle and Late Pleistocene humans. While some significant differences were found with respect to chipping frequencies across groups, the differences were not strictly contrasted across morphologically-defined (archaic versus anatomically modern) or by chronology. Furthermore, all three chip sizes were found on the anterior teeth of each chronologically and morphologically defined group. This suggests a general similarity in the frequency and magnitude of bite forces produced on hard-objects with the anterior teeth across archaic and early modern human groups in this study. Equations for the calculation of actual (P_F) and maximum potential (P_{max}) bite force are not available for the anterior teeth but the size and frequency of chips suggests a general similarity. Bite force from enamel chipping has been calculated for postcanine teeth from Krapina, a sample of later Neandertals (MIS 4-3), and early modern humans which shows complete overlap between premolar and molar bite force production between groups (previously noted by Azar et al. 2015). Enamel chipping results provide physical evidence for the production of bite forces capable of spalling enamel in vitro, which is a welcome addition to biomechanical analyses that provide evidence of potential maximum bite force production. Thus, the enamel chipping data presented here support the conclusions of biomechanical analyses of archaic and modern human craniofacial morphology both in that anterior (and posterior) bite force production was not likely to have been higher in magnitude among archaic *Homo* than among early modern humans.

Instrumental striations on the labial enamel of maxillary central incisors

Labial striation analyses showed that some striations were present on the maxillary central incisors of all groups examined in the present study. This is an important conclusion since only one other study using methods comparable to those used to study archaic humans has been completed to date that focused exclusively on early modern humans (Willman 2016). Other studies have documented instrumental striations on the anterior teeth of recent modern humans, notable Australian Aboriginal hunter-gatherers (e.g., Lozano et al. 2008), but the extent to which the use of ethnographic samples are representative proxies for the behaviors of Late Pleistocene early modern humans is greatly challenged by the instrumental striation data presented here. The universality of instrumental striations on archaic and early modern human teeth examined in this study refutes the hypothesis of differential visuospatial integration among archaic and modern humans (Bruner and Lozano 2014a, b, 2015; Bruner and Iriki 2016; Bruner et al. 2016).

In terms of non-masticatory behaviors, instrumental striations document the used of the anterior dentition in clamping and grasping behaviors while a tool is used close to the mouth to manipulate the materials being held between the teeth. The most common behavior attributed to the formation of instrumental striations in the literature is the “stuff-and-cut” behavior. However, Willman (2016) has shown that clamping materials between the teeth while performing scraping tasks may account for the predominant patterns of vertical striations on the anterior teeth of early modern humans from Dolní Věstonice II. However, oblique striations are far more frequently documented among archaic humans (reviewed in Willman 2016, 2017). One can therefore suggest that the documentation of presence/absence data on instrumental striations is greatly limiting our view of how tooth-using behaviors varied throughout the Pleistocene – especially among early modern humans for which much less is known. Meaning distinctions may still be found in terms of variation in striation length, width, orientation, frequency, and/or patterning across additional tooth types in future studies. Studies focusing on these details may be able to reveal behavioral differentiation that contrasts archaic and modern groups to a degree that presence/absence analyses do not reveal. The data from Dolní Věstonice II (Willman 2016) is a step in this direction.

However, the presence of these striations among both archaic and anatomically modern human groups, like enamel chipping, at the very least suggests that a similar range of anterior tooth-using behaviors were being used by Pleistocene humans regardless morphological distinctions or chronology. Again, given the range of similarity in behaviors, and a generalized "hunter-gatherer" trend in anterior versus posterior macrowear gradients, trends in anterior dental reduction among early modern humans are difficult to explain in terms of the changing patterns of use or disuse of the teeth-as-tools during the Pleistocene.

The paradox of dental structural reduction and tooth-use

Research on craniofacial biomechanics has been used to suggest that explanations for craniofacial evolution and differentiation among archaic and early modern humans are unlikely to be explained by the Anterior Dental Loading Hypothesis alone. Instead, neutral evolutionary processes (e.g., gene flow and genetic drift), climatic adaptation, energetic, developmental, or some combination of factors may better explain the evolution of the unique suite of craniofacial traits that differentiate archaic and modern human groups (Antón 1994; Maureille and Houêt 1998; Hublin 2002, 2009; Franciscus 2003; O'Connor et al. 2005; Weaver et al. 2007; Holton and Franciscus 2008; Cartmill and Smith 2009; Weaver 2009; Holton et al. 2011; Rae et al. 2011a; Smith 2015). However, the large and robust anterior dentitions of archaic *Homo* can still be viewed as an advantage when one considers the degree to which the hunter-gatherers engage in non-masticatory behaviors with their anterior dentitions. Thus, it remains interesting and paradoxical that the ancestral condition of large anterior dental crowns should be maintained among late archaic Neandertals, but reduced among early modern humans since it is clear that early modern humans also engaged in extensive use of their anterior teeth-as-tools. Thus, the primary contrast between archaic and modern humans appears to be one that would relate to the functionality of the anterior dentition for manipulative tasks in old-aged individuals. The difficulty remains as to how to explain this difference in terms of reproductive fitness advantages among archaic or early modern humans.

Dental reduction has long interested paleoanthropologists and bioarchaeologists and many hypotheses have been put forth in attempts to explain trends in crown reduction during human evolution (see review in: Pinhasi and Meiklejohn 2011). Particularly relevant hypothesis to the present discussion is that of the “Probable Mutation Effect” first put forth by Brace (1963) and expanded upon by Brace others (Brace 1964a, 1979, 1995, 2005; Wolpoff 1969, 1975; Brace and Mahler 1971; Brose and Wolpoff 1971). In short, the Probable Mutation Effect posits that under conditions of relaxed selection (usually associated with archaeological evidence for technocultural sophistication through time) there will be an accumulation of random mutations that would otherwise be removed through natural selection. The accumulation of mutations will ultimately result in the reduction of structural integrity – the relevant example here being the size or complexity of anterior dental crowns. However, Frayer (1977, 1978) has shown that dental reduction in the European Upper Paleolithic was not uniform through time – it was more marked between the Early and Late Upper Paleolithic than from the Late Upper Paleolithic to Mesolithic. In addition, variation in crown size decreased over time from Early to Late Upper Paleolithic to Mesolithic (Frayer 1977, 1978). Taken as a whole, Frayer (1977, 1978) suggests that the evidence better supports directional selection related to diachronic changes in technocultural complexes during the Upper Paleolithic and Early Holocene rather than neutral processes favored under the Probable Mutation Effect. Importantly, Frayer (1978) also acknowledges:

> *"[T]he rate of change in tooth dimensions is very low when measured in millennia or generations. Because of this, it is inherently difficult to demonstrate the precise factors conferring higher fitness on smaller-toothed individuals."* – Frayer 1978:134

The results of Frayer's (1977, 1978) research have been refined through greater chronological control in recent analyses (Trinkaus 2004; Pinhasi and Meiklejohn 2011), with the important conclusion gained is that:

> *"[T]he magnitude and nature of these changes need to be addressed on a case-to-case geographical basis, before it is possible to draw conclusions about universal evolutionary trends."* – Pinhasi and Meiklejohn 2011:471

Smith (1977a, b) challenged the views of Middle to Late Pleistocene shifts in functional demand on the dentition as a correlate of changing technological and behavioral strategies (see: Brace 1962a, b, 1964, 1967; Brose and Wolpoff 1971) by examining both dental size and attrition. Smith (1977a, b) concluded that:

> *"Similarly the observed reduction in tooth size was not associated with any concomitant reduction in functional demands made on the dentition, but appears to have outstripped them, as demonstrated by the increased severity of attrition found in the later smaller-toothed groups."* – Smith (1977b)

Despite the relatively small sample size and a lack of chronological refinement at the time of the study, Smith's (1977a, b) overall conclusions that dental reduction occurred without a concomitant shift in the dis/use of the dentition is largely supported by the work in this thesis. Thus, anterior dental reduction does not necessarily mean less anterior tooth-use for manipulative behaviors, but it would be associated with less functionality in old age for individuals with smaller dentitions. In this respect, the issue of anterior dental reduction despite high levels of anterior dental wear among early modern humans becomes even more complicated as a selective advantage of having small anterior teeth is not readily apparent among hunter-gatherer groups engaging in high levels of non-masticatory behaviors.
Thus, given little change in the use or function of anterior teeth in Paleolithic hunter-gatherers, how do demonstrably smaller anterior teeth become more frequent in early modern humans compared to Archaic *Homo?*

The literature on anterior tooth-use occasionally calls such behaviors maladaptive or "risky" because objects such as stone tools come into contact with enamel (e.g., Bruner and Lozano 2014b; Bruner et al. 2016), indeed cutmarks on the labial root surfaces of some archaic human teeth indicate a certain amount of oral health risk is involved (Hillson et al. 2010; Sarig et al. 2016), but the relationship between the use of teeth-as-tools and oral pathology is better documented in Holocene humans (Molnar 2008, 2011) than in Pleistocene contexts. However, Lalueza-Fox and Frayer (1997:148) provide a comment worth quoting at length:

> "*If cutting objects with stone tools was the activity which left these marks on the anterior teeth, the Neanderthals must have had sufficient dexterity and manual control to avoid oral tissue damage. Alternatively, Neanderthals had bloodied lips and gums from recklessly dragging knives across oral tissues. The precise action which produced these scratches is unknown, but any activity executed on the labial face of the incisors and canines must have required some skill and fine control of movement to avoid soft tissue damage.*"

It is also well established that chipping and fracture can destroy a tooth (Bonfiglioli et al. 2004; Lee et al. 2011; Scott and Winn 2011); but estimates of bite force production are similar across Pleistocene humans, and there is little evidence to suggest that the severity of chipping differed between groups (Chapter 6). Resistance to a lifetime accumulation of occlusal wear has generally been cited as an important factor for primate and mammalian longevity (Logan and Sanson 2002; Bermúdez de Castro et al. 2003; DeGusta et al. 2003; King et al. 2005, 2012; Cuozzo and Sauther 2006), and dental size would be an important characteristic of resistance to wear (as are enamel tissue mechanical properties – see Chapter 2). However, there is little evidence for differential mortality profiles among archaic and early modern humans (Trinkaus 2011), and both Neandertals and early modern humans (excluding the Late Upper Paleolithic) tend to maintain their full dentitions until death – and in many cases, crowns are completely worn away and roots are functioning as the occlusal surfaces (Trinkaus 2013; Willman 2016). Furthermore, pulp exposure through attrition (or fracture) can occur through extreme rates of attrition (Calcagno and Gibson 1991; Larsen 2015), and smaller teeth would be more susceptible to this factor. However, were rates of wear extreme enough to expose a pulp chamber early enough in life to affect individual reproductive fitness and therefore selection for anterior tooth size?

The extent to which anterior dental size confers a functional advantage that translates to increased reproductive fitness is difficult to prove. Similarly, any co-variation between tooth size, wear, and oral health would have obvious effects on physiological fitness (morbidity), but the extent to which these relationships contribute to differential reproductive fitness between archaic and early modern humans is questionable given that oral health decline has a clear relationship with aging. Furthermore, poor oral health is not widespread in the Pleistocene until the Late Upper Paleolithic/terminal Pleistocene (Da-Gloria and Larsen 2014; Humphrey et al. 2014; Lacy 2014; Willman et al. 2016). Smith (2013, 2015) has suggested that the large teeth and the structures supporting them are developmentally expensive tissues, and while maxillary growth trajectories are derived in modern humans relative to archaic *Homo* (Maureille and Bar 1999; Lacruz et al. 2015), it is unclear whether these aspects of growth have significantly different developmental "costs". However, evidence for a difference in the degree of developmental stress associated with Neandertals relative to early modern humans is not necessarily supportive of clear differences between the groups. Instead it appears that growing up in the Pleistocene was generally difficult regardless of group-level morphological affinity (Ogilvie et al. 1989; Trinkaus et al. 2001; Guatelli-Steinberg et al. 2004, 2013, 2014; Barrett et al. 2012; Willman 2014; Cowgill et al. 2015).

This review of issues surrounding anterior dental reduction in Neandertals versus early modern humans suggests that it is extremely difficult to pinpoint a causative relationship between anterior tooth-use and crown reduction among early modern humans. However, evolutionary models aimed at explaining dental reduction are often impossible or extremely difficult test (Pinhasi and Meiklejohn 2011). Furthermore, the view of Late Pleistocene human population dynamics being developed through recent advances in ancient DNA as well as traditional analyses of skeletal morphometrics are painting an increasingly complex scenario of human population dynamics (Crevecoeur 2008; Holt and Formicola 2008; Doboş et al. 2010; , 2014Trinkaus et al. 2013a; Brewster et al. 2014; Demeter et al. 2015; Fu et al. 2015, 2016; Jones et al. 2015; Liu et al. 2015; Tryon et al. 2015; Crevecoeur et al. 2016). The mosaic of archaic and derived dental morphology in some early modern human fossils may be illustrative of local archaic contributions to the gene pool through assimilation (Smith et al. 1989, 2005; Trinkaus and Zilhão 2002; Trinkaus 2005, 2013; see also: Ackermann et al. 2016). Explaining the continued trend toward decreasing crown size despite high levels of anterior dental wear in later early modern human groups is still difficult to explain. How small changes in crown size in earlier versus later early modern humans confers a reproductive fitness advantage in the latter group remains largely unknown (Frayer 1978).

An interesting comparison can be made with the shift to food producing economies in later prehistory. The transition to food production in many parts of the world is associated with poor physiological fitness – or high morbidity – among food producing peoples compared to their hunter-gatherer predecessors (for review see: Larsen 2015). However, these same groups also have higher reproductive fitness than the preceding populations of hunter-gatherers in the same region (Lambert 2009; Page et al. 2016). As Lambert (2009:607) suggests:

> *"Health decline could have been a costly by-product of an economic system that enhanced fertility and led to population growth. As long as it did not affect reproductive rate, declining health may have wielded little influence on how people chose to make a living."*

The widespread evidence for poor oral health among hunter-gatherers during the Terminal Pleistocene and Early Holocene compared to preceding periods (Frayer 1989; Brennan 1991; Holt and Formicola 2008; Da-Gloria and Larsen 2014; Humphrey et al. 2014; Lacy 2014; Willman et al. 2016) may also be interpreted through this scenario of trade-offs between physiological fitness and reproductive fitness. The archaeological record of the Upper Paleolithic is frequently viewed as a feedback loop between cultural factors promoting socioeconomic innovation and intensification and population growth:

> *"[T]he European [Upper Paleolithic] would show – with hiccups and setbacks caused by catastrophic events or adverse environmental change – the operation of an exponential process of population pressure: adaptive success, reflected in demographic expansion, triggered by and leading to technological innovation or economic intensification, in turn bringing about further population growth."* – Zilhão 2014:1778

Thus, Upper Paleolithic cultural shifts may have enhanced reproductive fitness in much the same way as regional transitions to food production did, and while diachronic changes in Upper Paleolithic morbidity occurred they did not seem to influence reproductive fitness greatly.

The above analogy offers a way to explain how anterior tooth reduction could occur despite little evidence for change in the use of the dentition as a tool among Late Pleistocene hunter-gatherers – and especially between the Early and Late Upper Paleolithic samples. As a whole, the data and discussion presented has indicated that large anterior teeth are advantageous to hunter-gatherers due to the intensive use of teeth for dietary and non-masticatory behaviors. This observation is not new and is especially evident when contrasting archaic human anterior dental dimensions with those of modern humans. However, a consistent trend showing high levels of anterior versus posterior dental wear and similar patterning of dental wear features (i.e., chipping and instrumental striations) persists among early modern humans despite diachronic shifts in crown size during the Late Pleistocene. At first glance, this may appear to support views of directional selection for smaller teeth (e.g., Frayer 1977, 1978), or relaxed selection on crown size others (e.g., Brace 1964a, 1979, 1995, 2005; Wolpoff 1969, 1975; Brace and Mahler 1971; Brose and Wolpoff 1971) through shifts in technocultural sophistication during the Pleistocene. But, and importantly, if anterior dental size in humans is indicative of the amount of anterior tooth-use for dietary and non-masticatory behaviors the expectation is that less anterior dental wear would be present in small-toothed hunter-gatherers. While wear is certainly less in terms of volume loss (scaled macrowear analyses: Chapter 6), the degree of anterior dental wear is still high (see differential wear analysis in Chapter 6 and Clement et al. 2012) in samples with smaller anterior tooth dimensions. Although not directly analyzed in the present study, antemortem anterior tooth loss is certainly higher in Late Upper Paleolithic samples than any preceding period (Willman, personal observation). Together, all of these trends highlight a co-occurrence between increasing morbidity – as evident through oral pathology – and anterior dental reduction. A morphological shift that results in higher morbidity is difficult to explain in terms of functional adaptation to a specific behavior like the use of teeth-as-tools. Thus, selection appears to be acting on cultural behaviors promoting an increase in fertility and/or fecundity among early modern humans, whereas the shift toward smaller anterior teeth and an associated increase in oral pathology/morbidity may have come about through stochastic evolutionary processes (e.g., gene flow and genetic drift). This scenario provides a possible mechanism whereby socioeconomic innovation and intensification is an indirect influence on spatiotemporal variation in dental size without invoking directional selection on crown size related to non-masticatory manipulative behavior.

To summarize, it is difficult to distinguish any clear causative relationship between the structural reduction of the anterior teeth and tooth-use among early modern humans. In fact, there is a paradoxical relationship between the high rate of anterior tooth-use and concomitant crown reduction among early modern humans. Neandertals maintained the ancestral condition of having large and robust anterior dentitions from their Middle Pleistocene predecessors, and it is obviously from this study and many others that Neandertals and their predecessors frequently engaged in non-masticatory behaviors with their anterior dentition. However, it is extremely difficult to establish a causative relationship between form (anterior tooth morphology/size) and function (non-masticatory behaviors) when evidence from early modern humans is also considered. It is proposed that selection (whether “relaxed” or directional) was not the most parsimonious causative explanation for dental reduction among early modern humans. Instead, small anterior teeth have shorter “use-lives” and a greater association with high morbidity in later life. Thus, we can view small anterior dentitions as a mismatch between morphology and behavior (non-masticatory behavior) among early modern humans as compared to their archaic neighbors. An explanation invoking stochastic evolutionary processes combined selection for cultural behaviors that enhanced reproductive fitness through shifts in fertility/fecundity may better explain the how small anterior teeth came to be the dominant form in the Upper Paleolithic. Finally, it is worth repeating here that the Neandertals and their archaic predecessors are less in need of explanation than the early modern humans are in terms of morphology. As stated by Trinkaus (2006a:607):

> *"When these data on probable trait polarities are combined and one appropriately uses the available data from the entire skeleton and dentition, it is not the Neandertals who appear unusual, special, derived, autapomorphous. It is we."*

Final conclusions

This thesis set out to bridge gaps in our understanding of non-masticatory uses of the anterior dentition among Middle and Late Pleistocene humans to illustrate how group-level similarities and differences in non-masticatory behaviors relate to broader patterns of biocultural change during the Pleistocene. In particular, this study addresses the degree to which the body or technocultural solutions to manipulative behavior are relied upon during a period of extensive technological and social change. Many of the research gaps that were addressed have persisted despite recent methodological advances in the study of non-masticatory dental wear. This is largely due to the nature of comparisons with early and recent modern humans or lack of comparisons altogether. We know a great deal about archaic human behaviors in the Pleistocene, especially that of the Neandertals. However, there has been remarkably little research on the paleobiology the earliest modern humans until quite recently. Thus, there was much to be gained by in-depth coverage of early modern human fossils using approaches that were broadly comparable with previously published data on archaic humans. Importantly, comparisons were made between the groups of greatest paleobiological relevance to the issues of interest in the Middle and Late Pleistocene and avoiding the frequent problems associated with the comparison of recent human skeletal and behavioral variation

Three complimentary analyses of anterior dental wear were used in this thesis. Analyses ranged from scale-sensitive analyses of anterior versus posterior dental wear gradients to analyses of individual dental wear features by tooth type using enamel chipping and instrumental striation analyses. This multifaceted approach allowed greater coverage of a fragmentary fossil records and use of previously published data for comparative purposes. Furthermore, each analysis was able to comment on different aspects of non-masticatory tooth-use. Anterior versus posterior scaled macrowear gradients were informative of degree of anterior tooth use and how crown size influenced graded differences across groups. Dental chipping comments on the magnitude of anterior tooth loading as well as the repetition of those loads. Finally, analyses of instrumental cutmarks gave insights into a form of non-masticatory behavior largely associated with archaic humans but unknown among early modern humans.

The results of analyses show that there is some difference in the degree to which archaic and modern humans used their anterior dentitions, but this is largely an artifact of tooth dimensions – the anterior teeth of many modern humans were worn down to similar a degree as that of Neandertals, but early modern humans anterior teeth became non-functional at a faster rate due to their smaller average size. Dental chipping revealed little difference in anterior tooth use between fossil groups and there was little evidence to indicate that anterior or posterior teeth were used to produce higher magnitude forces on average between archaic and modern human groups. Likewise, the evidence from central incisor labial cutmarks shows no differences between archaic and early modern humans in terms of presence or absence.

The historical use of recent human samples as a proxy for early modern human behavior have been somewhat misleading. A degree of difference between archaic and modern humans in terms of non-masticatory behavior does exist, but it is modest or absent depending on which behavior and corresponding paleobiological indicator is examined. The historical focus on the use of the anterior teeth-as-tools as a significant selective force in Late Pleistocene craniofacial evolution is probably overstated based on previous biomechanical approaches to the topic, rather than on the thorough documentation of the actual traces of non-masticatory behavior left behind as dental wear. Approaches addressing developmental or neutral evolutionary processes may yield insights into the evolution of Neandertal and early modern human craniodental morphology that functional and behavioral studies have not yet been able to ascertain.

Finally, future studies aimed at understanding the behavioral differences between Neandertals and early modern humans should focus on direct comparisons between fossil groups. Our understanding of regional variation in Neandertal non-masticatory behavior is far more complete than it is for early modern humans. Furthermore, only one study now shows that the early modern humans from Dolní Věstonice II exhibit the same types of non-masticatory wear features as seen in many groups of archaic *Homo,* but that the patterning of these features is quite distinct from those seen among archaic *Homo* (Willman 2016). High-resolution analyses of wear features that go beyond presence/absence documentation are likely to reveal meaningful variation across chronologically and morphologically-defined groups of Pleistocene humans.

References Cited

Absolon K. 1929. New finds of fossil human skeletons in Moravia. Anthropologie 7:79-89.

Ackermann RR. 2005. Variation in Neandertals: a response to. Journal of human evolution 48(6):643-646.

Ackermann RR, Mackay A, Arnold ML. 2016. The hybrid origin of “modern” humans. Evolutionary Biology 43:1-11.

Addy M, Shellis R. 2006. Interaction between attrition, abrasion and erosion in tooth wear.

Ahern JCM, Janković I, Voisin J-L, Smith FH. 2013. Modern human origins in Central Europe. In: Smith FH, Ahern JCM, editors. The Origins of Modern Humans: Biology Reconsidered. Hoboken: Wiley Blackwell. p 151-221.

Alcázar de Velasco A, Arsuaga JL, Martínez Mendizábal I, Bonmatí A. 2011. Revisión de la mandíbula humana de Bañolas, Gerona, España. Boletín de la Real Sociedad Española de Historia Natural Sección geológica 105(1-4):99-108.

Alciati G, Coppa A, Macchiarelli R. 1995. La dentizione del cacciatore mesolitico di Mondeval de Sora (S. Vito di Cadore, Belluno). Bullettino di Paletnologia Italiana 86:153-196.

Alciati G, Coppa A, Macchiarelli R, Pertile F. 1993. La dentizione del caccitore epigravettiano del riparo Villabruno A (valle del Cosmon, Belluno) Quaderni d'Anatomia Pratica 49:73-100.

Aldhouse-Green S. 1995. Pontnewydd Cave, Wales, a later Middle Pleistocene hominid and archaeological site: a review of stratigraphy, dating, taphonomy and interpretation. In: Bermúdez de Castro JM, Arsuaga JL, Carbonell E, editors. Human Evolution in Europe and the Atapuerca Evidence. Vallodolid: Junta de Castilla y Leon. p 37-55.

Aldhouse-Green S, Peterson R, Walker E. 2012. Neanderthals in Wales: Pontnewydd and the Elwy Valley Caves. Oxford: Oxbow Books.

Alexandersen V, editor. 1988. Description of the human dentitions from the Late Mesolithic grave-fields at Skateholm, Southern Sweden. Stockholm: Almqvist & Wiskell International. 106-163 p.

Alt KW, Pichler SL. 1998. Artificial modifications of human teeth. In: Alt KW, Rösing FW, Teschler-Nicola M, editors. Dental Anthropology: Fundamentals, Limits, and Prospects. Wien: Springer Verlag. p 387-415.

Anderson JE. 1968. Late Paleolithic skeletal remains from Nubia. In: Wendorf F, editor. The Prehistory of Nubia, Vol 2. Dallas: Fort Burgwin Research Center. p 996–1040.

Angel JL, Kelley JO. 1986. Description and comparison of the skeleton. In: Wendorf F, Schild R, editors. The Prehistory of Wadi Kubbaniya Volume I: The Wadi Kubbaniya Skeleton. Dallas: South Methodist University Press. p 53-70.

Antón S. 1990. Neandertals and the anterior dental loading hypothesis: a biomechanical evaluation of bite force production. Kroeber Anthropological Society Papers(71-72):67-76.

Antón SC. 1994. Mechanical and other perspectives on Neandertal craniofacial morphology. In: Corruccini RS, Ciochon RL, editors. Integrative Paths to the Past: Paleoanthropological Advances in Honor of F Clark Howell. New Jersey: Prentice Hall. p 677-695.

Antón SC. 1996. Tendon-associated bone features of the masticatory system in Neandertals. Journal of Human Evolution 31(5):391-408.

Arensburg B. 1977. New Upper Palaeolithic human remains from Israel. Eretz-Israel 13:208-215.

Arsuaga JL, Martínez I, Lorenzo C, Quam R, Carretero M, Gracia A. 2001. Las estrías del incisivo de Cova Negra. In: Villaverde V, editor. De Neandertales a Cromaones: El Inicio del Poblamiento Humano en las Tierras Valencianas. València: Universitat de València. p 327-328.

Arsuaga JL, Gracia A, Martínez I, Bermúdez de Castro JM, Rosas A, Villaverde V, Fumanal MP. 1989. The human remains from Cova Negra (Valencia, Spain) and their place in European Pleistocene human evolution. Journal of Human Evolution 18(1):55-92.

Arsuaga JL, Villaverde V, Quam R, Martínez I, Carretero JM, Lorenzo C, Gracia A. 2007. New Neandertal remains from Cova Negra (Valencia, Spain). Journal of Human Evolution 52(1):31-58.

Arsuaga JL, Martínez I, Arnold LJ, Aranburu A, Gracia-Téllez A, Sharp WD, Quam RM, Falguères C, Pantoja-Pérez A, Bischoff J. 2014. Neandertal roots: cranial and chronological evidence from Sima de los Huesos. Science 344(6190):1358-1363.

Azar MC, Johnson NA, Willman JC. 2015. Preliminary analysis of postcanine enamel chipping among Neandertals and early modern humans: Implications for diet and bite force production. AAPA Committee on Diversity Undergraduate Research Symposium, 84th Annual Meeting of the American Association of Physical Anthropologists, Saint Louis, Missouri:10.

Azaz B, Michaeli Y, Nitzan D. 1977. Aging of tissues of the roots of nonfunctional human teeth (impacted canines). Oral Surgery, Oral Medicine, Oral Pathology 43(4):572-578.

Azaz B, Ulmansky M, Moshev R, Sela J. 1974. Correlation between age and thickness of cementum in impacted teeth. Oral Surgery, Oral Medicine, Oral Pathology 38(5):691-694.

Bailey SE. 2002. Neandertal Dental Morphology: Implications for Modern Human Origins. Tempe: Arizona State University.

Bailey SE. 2006. Beyond shovel-shaped incisors: Neandertal dental morphology in a comparative context. Periodicum Biologorum 108(3):253-267.

Bailey SE, Hublin J-J. 2006. Dental remains from the Grotte du Renne at Arcy-sur-Cure (Yonne). Journal of Human Evolution 50(5):485-508.

Bailey SE, Liu W. 2010. A comparative dental metrical and morphological analysis of a Middle Pleistocene hominin maxilla from Chaoxian (Chaohu), China. Quaternary International 211(1-2):14-23.

Bar-Yosef O, Vandermeersch B, Arensburg B, Belfer-Cohen A, Goldberg P, Laville H, Meignen L, Rak Y, Speth JD, Tchernov E. 1992. The excavations in Kebara Cave, Mt. Carmel. Current Anthropology 33(5):497-550.

Barrett CK, Guatelli-Steinberg D, Sciulli PW. 2012. Revisiting dental fluctuating asymmetry in Neandertals and modern humans. American Journal of Physical Anthropology 149(2):193-204.

Barrett MJ. 1977. Masticatory and non-masticatory uses of teeth. In: Wright RVS, editor. Stone Tools as Cultural Markers: Change, Evolution and Complexity. Canberra: Australian Institute of Aboriginal Studies. p 18-23.

Barroso-Ruız C, de Lumley MA, Caparrós M, Verdú L. 2003. Los restos humanos Neandertalenses de la cueva del Boquete de Zafarraya. El pleistocene superior del la cueva del Boquete de Zafarraya. Seville: Consejerıa de Cultura de la Junta de Andalucıa. p 327-387.

Bates M, Pope M, Shaw A, Scott B, Schwenninger J-L. 2013. Late Neanderthal occupation in North-West Europe: rediscovery, investigation and dating of a last glacial sediment sequence at the site of La Cotte de Saint Brelade, Jersey. Journal of Quaternary Science 28(7):647-652.

Bax JS, Ungar PS. 1999. Incisor labial surface wear striations in modern humans and their implications for handedness in Middle and Late Pleistocene hominids. International Journal of Osteoarchaeology 9(3):189-198.

Bayle P, Le Luyer M, Robson Brown KA. 2017. The Palomas dental remains: enamel thickness and tissue proportions. In: Trinkaus E, Walker MJ, editors. The People of Palomas: Neandertals from the Sima de las Palomas, Cabezo Gordo, Southeastern Spain. College Station: Texas A&M University Press.

Bayle P, Braga J, Mazurier A, Macchiarelli R. 2009a. Brief communication: High-resolution assessment of the dental developmental pattern and characterization of tooth tissue proportions in the late Upper Paleolithic child from La Madeleine, France. American Journal of Physical Anthropology 138(4):493-498.

Bayle P, Braga J, Mazurier A, Macchiarelli R. 2009b. Dental developmental pattern of the Neanderthal child from Roc de Marsal: a high-resolution 3D analysis. Journal of Human Evolution 56(1):66-75.

Bayle P, Macchiarelli R, Trinkaus E, Duarte C, Mazurier A, Zilhao J. 2010. Dental maturational sequence and dental tissue proportions in the early Upper Paleolithic child from Abrigo do Lagar Velho, Portugal. Proceedings of the National Academy of Sciences of the United States of America 107(4):1338-1342.

Becker D, Rauber G. 2007. Esquisse de l'histoire des mammifères et gisements fossilifères de Suisse. Société Neuchâteloise des Sciences Naturelles 130:5-48.

Begg PR. 1954. Stone age man's dentition: with reference to anatomically correct occlusion, the etiology of malocclusion, and a technique for its treatment. American Journal of Orthodontics 40(4):298-312, 373-383, 462-475, 517-531.

Belcastro G, Rastelli E, Mariotti V, Consiglio C, Facchini F, Bonfiglioli B. 2007. Continuity or discontinuity of the life-style in central Italy during the Roman imperial age-early middle ages transition: Diet, health, and behavior. American Journal of Physical Anthropology 132(3):381-394.

Belfer-Cohen A. 1988. The Natufian Graveyard in Hayonim Cave. Paléorient 14(2):297-308.

Benazzi S, Fiorenza L, Katina S, Bruner E, Kullmer O. 2011a. Quantitative assessment of interproximal wear facet outlines for the association of isolated molars. American Journal of Physical Anthropology 144(2):309-316.

Benazzi S, Nguyen HN, Schulz D, Grosse IR, Gruppioni G, Hublin J-J, Kullmer O. 2013. The evolutionary paradox of tooth wear: simply destruction or inevitable adaptation? PLoS ONE 8(4):e62263.

Benazzi S, Viola B, Kullmer O, Fiorenza L, Harvati K, Paul T, Gruppioni G, Weber GW, Mallegni F. 2011b. A reassessment of the Neanderthal teeth from Taddeo cave (southern Italy). Journal of Human Evolution 61(4):377-388.

Berbesque JC, Marlowe FW, Pawn I, Thompson P, Johnson G, Mabulla A. 2012. Sex differences in Hadza dental wear patterns. Human Nature 23(3):270-282.

Bermúdez de Castro JM, Bromage TG, Jalvo YF. 1988. Buccal striations on fossil human anterior teeth: evidence of handedness in the middle and early Upper Pleistocene. Journal of Human Evolution 17(4):403-412.

Bermúdez de Castro JM, Arsuaga JL, Perez PJ. 1997. Interproximal grooving in the Atapuerca-SH hominid dentitions. American Journal of Physical Anthropology 102:369-376.

Bermúdez de Castro JM, Rosas A, Nicolás ME. 1999. Dental remains from Atapuerca-TD6 (Gran Dolina site, Burgos, Spain). Journal of Human Evolution 37(3-4):523-566.

Bermúdez de Castro JM, Martinón-Torres M, Sarmiento S, Lozano M, Arsuaga JL, Carbonell E. 2003. Rates of anterior tooth wear in Middle Pleistocene hominins from Sima de los Huesos (Sierra de Atapuerca, Spain). Proceedings of the National Academy of Sciences 100(21):11992-11996.

Bermúdez de Castro JM, Pérez-González A, Martinón-Torres M, Gómez-Robles A, Rosell J, Prado L, Sarmiento S, Carbonell E. 2008. A new early Pleistocene hominin mandible from Atapuerca-TD6, Spain. Journal of Human Evolution 55(4):729-735.

Bermúdez de Castro JM, Martinón-Torres M, Gómez-Robles A, Prado-Simón L, Martín-Francés L, Lapresa M, Olejniczak AJ, Carbonell E. 2011. Early Pleistocene human mandible from Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain): A comparative morphological study. Journal of Human Evolution 61(1):12-25.

Bermúdez de Castro JM, Carbonell E, Gómez A, Mateos A, Martinón-Torres M, Muela A, Rodríguez J, Sarmiento S, Varela S. 2006. Paleodemografía del hipodigma de fósiles de homininos del nivel TD6 de Gran Dolina (Sierra de Atapuerca, Burgos): estudio preliminar. Estudios Geológicos 62(1):145-154.

Berry D. 1976. Excessive attrition. The eruption and occlusion of teeth: proceedings of the 27th symposium of Colston Research Society London: Butterworths. p 146-155.

Beynon AD. 1987. Replication technique for studying microstructure in fossil enamel. Scanning Microscopy 1(2):663-669.

Beyron H. 1964. Occlusal relations and mastication in Australian aborigines. Acta Odontologica 22(6):597-678.

Bietti A. 1990. The late Upper Paleolithic in Italy: an overview. Journal of World Prehistory 4(1):95-155.

Billy. 1982. Les dents humaines de la grotte du Coupe-Gorge à Montmaurin. Bulletins et Mémoires de la Société d'Anthropologie de Paris:211-225.

Binford LR. 2001. Constructing Frames of Reference: An Analytical Method for Archaeological Theory. Berkeley: University of California Press.

Blackwell B, Schwarcz H. 1986. U-series analyses of the lower travertine at Ehringsdorf, DDR. Quaternary Research 25(2):215-222.

Blackwell B, Schwarcz HP, Debénath A. 1983. Absolute dating of hominids and palaeolithic artifacts of the cave of La Chaise-de-Vouthon (Charente), France. Journal of Archaeological Science 10(6):493-513.

Blanchard R, Peyrony D, Vallois HV. 1972. Le gisement et le squelette de Saint-Germain-la-Rivière. Paris: Masson.

Boaz NT, Pavlakis P, Brooks AS. 1990. Late Pleistocene-Holocene human remains from Ishango, Zaire. Evolution of Environments and Hominidae in the African Western Rift Valley, Virginia Museum of Natural History Memoir 1:273-299.

Bocquentin F. 2007. A Final Natufian population: health and burial status at Eynan-Mallaha. In: Faerman M, Horwitz LK, Kahana T, Zilberman U, editors. Faces from the Past: Diachronic Patterns in the Biology of Human Populations from the Eastern Mediterranean. Oxford: BAR International Series. p 66-81.

Bocquentin F, Sellier P, Murail P. 2005. Abrasion dentaire et travail spécialisé dans la population natoufienne de Mallaha (Israël). Comptes Rendus Palevol 4(4):351-357.

Bocquet-Appel J-P, Arsuaga J-L. 1999. Age Distributions of Hominid Samples at Atapuerca (SH) and Krapina Could Indicate Accumulation by Catastrophe. Journal of Archaeological Science 26(3):327-338.

Bonfiglioli B, Mariotti V, Facchini F, Belcastro MG, Condemi S. 2004. Masticatory and non-masticatory dental modifications in the Epipalaeolithic necropolis of Taforalt (Morocco). International Journal of Osteoarchaeology 14(6):448-456.

Bonifay E, Vandermeersch B, Couture C, Panattoni R. 2007. La Sépulture Néandertalienne du Regourdou. Imprimerie France, Quercy.

Bonsall C. 2008. The Mesolithic of the Iron Gates. In: Bailey G, Spikins P, editors. Mesolithic Europe. Cambridge: Cambridge University Press. p 238-279.

Bonsall C, Boroneanţ A, Soficaru A, McSweeney K, Higham T, Miriţoiu N, Pickard C, Cook G. 2012. Interrelationship of age and diet in Romania's oldest human burial. Naturwissenschaften 99(4):321-325.

Borrero-Lopez O, Pajares A, Constantino PJ, Lawn BR. 2014. A model for predicting wear rates in tooth enamel. Journal of the Mechanical Behavior of Biomedical Materials 37(0):226-234.

Borrero-Lopez O, Pajares A, Constantino PJ, Lawn BR. 2015. Mechanics of microwear traces in tooth enamel. Acta Biomaterialia 14(0):146-153.

Boschian G, Mallegni F, Tozzi C. 1995. The Epigravettian and Mesolithic site of Fredian Shelter (N Tuscany). Quaternaria Nova 5:45-80.

Boskey AL, Coleman R. 2010. Aging and bone. Journal of Dental Research 89(12):1333-1348.

Bosshardt DD, Selvig KA. 1997. Dental cementum: the dynamic tissue covering of the root. Periodontology 2000 13(1):41-75.

Botha D, Steyn M. 2015. Dental health of the late 19th and early 20th century Khoesan. HOMO 66(3):187-202.

Bouchneb L, Maureille B. 2004. Sillons d'usure interproximaux: reproduction expérimentale, analyse et application des résultats aux observations sur la lignée néandertalienne. Bulletins et mémoires de la Société d'Anthropologie de Paris 16(1-2):37-48.

Brace CL. 1962a. Refocusing on the Neanderthal problem. American Anthropologist:729-741.

Brace CL. 1962b. Cultural factors in the evolution of the human dentition. In: Montagu MFA, editor. Culture and the Evolution of Man. Oxford: Oxford University Press. p 343-354.

Brace CL. 1963. Structural reduction in human evolution. American Naturalist 97:39-49.

Brace CL. 1964a. The probable mutation effect. The American Naturalist 98(903):453-455.

Brace CL. 1964b. The fate of the "classic" Neanderthals: a consideration of hominid catastrophism. Current Anthropology 5(1):3-43.

Brace CL. 1967. Environment, tooth form and size in the Pleistocene. Journal of Dental Research 46:809-816.

Brace CL. 1975. Comment on ‘Did La Ferrassie I use his teeth as tools?’. Current Anthropology 16:396-397.

Brace CL. 1979. Krapina, "Classic" Neanderthals, and the evolution of the European face. Journal of Human Evolution 8(5):527-550.

Brace CL. 1995. Biocultural interaction and the mechanism of mosaic evolution in the emergence of "modern" morphology. American Anthropologist 97(4):711-721.

Brace CL. 2005. “Neutral theory” and the dynamics of the evolution of “Modern” human morphology. Human Evolution 20(1):19-38.

Brace CL, Mahler PE. 1971. Post-Pleistocene changes in the human dentition. American Journal of Physical Anthropology 34(2):191-203.

Brace CL, Ryan AS, Smith BH. 1981. Comment on: "tooth wear in La Ferrassie man". Current Anthropology 22:426-430.

Brennan MU. 1991. Health and Disease in the Middle and Upper Paleolithic of Southwestern France: A Bioarchaeological Study. New York: New York University.

Bresson F. 2000. Le squelette du Roc-de-Cave (Saint-Cirq-Madelon, Lot)/The Roc-de-Cave skeleton (Saint-Cirq-Madelon, Lot). Paleo 12(1):29-59.

Brewster C, Meiklejohn C, von Cramon-Taubadel N, Pinhasi R. 2014. Craniometric analysis of European Upper Palaeolithic and Mesolithic samples supports discontinuity at the Last Glacial Maximum. Nature Communications 5.

Brink JS, Herries AIR, Moggi-Cecchi J, Gowlett JAJ, Bousman CB, Hancox JP, Grün R, Eisenmann V, Adams JW, Rossouw L. 2012. First hominine remains from a ∼1.0 million year old bone bed at Cornelia-Uitzoek, Free State Province, South Africa. Journal of Human Evolution 63(3):527-535.

Broca P. 1879. Instructions relatives à l'étude anthropologique du système dentaire. Bulletins de la Société d'anthropologie de Paris 2(1):128-163.

Bromage TG, Boyde A. 1984. Microscopic criteria for the determination of directionality of cutmarks on bone. American Journal of Physical Anthropology 65(4):359-366.

Bromage TG, Bermúdez de Castro JM, Fernández-Jalvo Y. 1991. The SEM in taphonomic research and its application to studies of cutmarks generally and the determination of handedness specifically. Anthropologie 29:163-169.

Brose DS, Wolpoff MH. 1971. Early Upper Paleolithic man and Late Middle Paleolithic tools. American Anthropologist 73:1156-1194.

Brothwell DR. 1989. The relationship of tooth wear to ageing. In: Iscan MY, editor. Age Markers in the Human Skeleton. Springfield: Charles C. Thomas. p 303–316.

Brown P. 1987. Pleistocene homogeneity and Holocene size reduction: the Australian human skeletal evidence. Archaeology in Oceania 22(2):41-67.

Brown P. 1989. Coobool Creek: A Morphological and Metrical Analysis of the Crania, Mandibles and Dentitions of a Prehistoric Australian Human Population. Canberra: Australian National University.

Brown Q, Balikci A. 1967. At the Winter Sea Ice Camp. Watertown: Documentary Educational Resources. p 141 minutes.

Brown T. 1991. Interproximal grooving: different appearances, different etiologies, reply to Dr. Formicola. American Journal of Physical Anthropology 86:86-87.

Brown T, Molnar S. 1990. Interproximal grooving and task activity in Australia. American Journal of Physical Anthropology 81:545-553.

Bruner E. 2010. Morphological differences in the parietal lobes within the human genus. Current Anthropology 51(S1):S77-S88.

Bruner E. 2014. Functional craniology and brain evolution. In: Bruner E, editor. Human Paleoneurology. New York: Springer. p 57-94.

Bruner E, Manzi G. 2006. Saccopastore 1: the earliest Neanderthal? A new look at an old cranium. In: Harvati K, Harrison T, editors. Neanderthals revisited: new approaches and perspectives. Dordrecht: Springer. p 23-36.

Bruner E, Lozano M. 2014a. Three hands for the Neandertal lineage: reply to the comments. Journal of Anthropological Sciences 92:303-305.

Bruner E, Lozano M. 2014b. Extended mind and visuo-spatial integration: three hands for the Neandertal lineage. Journal of Anthropological Sciences 92:273-280.

Bruner E, Lozano M. 2015. Three hands: one year later. Journal of Anthropological Sciences 93:191-195.

Bruner E, Iriki A. 2016. Extending mind, visuospatial integration, and the evolution of the parietal lobes in the human genus. Quaternary International 405, Part A:98-110.

Bruner E, Lozano M, Lorenzo C. 2016. Visuospatial integration and human evolution: the fossil evidence Journal of Anthropological Sciences 94:1-18.

Buikstra JE, Ubelaker DH. 1994. Standards for Data Collection from Human Skeletal Remains. Fayetteville: Arkansas Archeological Survey Research Series.

Bulbeck D. 2006. The Last Glacial Maximum human burial from Liang Lemdubu in northern Sahulland. In: O'Connor S, Spriggs M, Veth P, editors. The Archaeology of the Aru Islands, Eastern Indonesia, Terra Australis 22. Canberra: Pandanus Press. p 255-294.

Bulbeck D, O'Connor S. 2011. The Watinglo mandible: a second terminal Pleistocene Homo sapiens fossil from tropical Sahul with a test on existing models for the human settlement of the region. HOMO 62(1):1-29.

Calcagno JM, Gibson KR. 1991. Selective compromise: evolutionary trends and mechanisms in hominid tooth size. In: Kelley MA, Larsen CS, editors. Advances in Dental Anthropology. New York: Wiley-Liss. p 59-76.

Campillo D, Subirà ME, Chimenos E, Aparicio A, José, Pérez-Pérez A, Vila S. 2002. Estudi de les restes humanes de la campanya 2000 de la Cova Foradâ (Oliva, València). Cypsela 14:143-150.

Caporale SS, Ungar PS. 2016. Rodent incisor microwear as a proxy for ecological reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 446:225-233.

Cardini L. 1971. Rinvenimenti paleolitici nella grotta Giovanna (Siracusa). Atti XIII Riunione Scientifica dell'Istituto Italiano di Preistoria e Protostoria:25-35.

Caron F, d'Errico F, Del Moral P, Santos F, Zilhão J. 2011. The reality of Neandertal symbolic behavior at the Grotte du Renne, Arcy-sur-Cure, France. PLoS One 6(6):e21545.

Carretero JM, Quam RM, Gómez-Olivencia A, Castilla M, Rodríguez L, García-González R. 2015. The Magdalenian human remains from El Mirón Cave, Cantabria (Spain). Journal of Archaeological Science 60(0):10-27.

Carter K, Worthington S. 2015. Morphologic and Demographic Predictors of Third Molar Agenesis: A Systematic Review and Meta-analysis. Journal of Dental Research 94(7):886-894.

Cartmill M, Smith FH. 2009. The Human Lineage. Hoboken: John Wiley & Sons.

Caspari R, Lee S-H. 2004. Older age becomes common late in human evolution. Proceedings of the National Academy of Sciences of the United States of America 101(30):10895-10900.

Chai H, Lawn BR. 2007a. Edge chipping of brittle materials: effect of side-wall inclination and loading angle. International Journal of Fracture 145(2):159-165.

Chai H, Lawn BR. 2007b. A universal relation for edge chipping from sharp contacts in brittle materials: a simple means of toughness evaluation. Acta Materialia 55(7):2555-2561.

Chai H, Lee JJW, Lawn BR. 2010. Fracture of tooth enamel from incipient microstructural defects. Journal of the Mechanical Behavior of Biomedical Materials 3:116-120.

Chai H, Lee JJW, Lawn BR. 2011. On the chipping and splitting of teeth. Journal of Mechanical Behavior of Biomedical Materials 4:315-321.

Chai H, Lee JJW, Constantino PJ, Lucas PW, Lawn BR. 2009. Remarkable resilience of teeth. Proceedings of the National Academy of Sciences of the United States of America 106(18):7289-7293.

Chandler RC. 1995. Practical considerations in the use of simultaneous inference for multiple tests. Animal Behaviour 49(2):524-527.

Chen T, Yuan S. 1988. Uranium-series dating of bones and teeth from Chinese Paleolithic sites Archaeometry 30(1):59-76.

Chen T, Yuan S, Guo S, Hu Y. 1987. Uranium series dating of fossil bones from the Hexian and Chaoxian human fossil sites. Acta Anthropologica Sinica 6:249–254.

Chiotti L, Nespoulet R, Henry-Gambier D. 2015. Occupations and status of the Abri Pataud (Dordogne, France) during the Final Gravettian. Quaternary International 359–360:406-422.

Churchill SE, Rhodes JA. 2006. How strong were the Neandertals? Leverage and muscularity at the shoulder and elbow in Mousterian foragers. Periodicum Biologorum 108(4):457-470.

Ciochon RL, Piperno DR, Thompson RG. 1990. Opal phytoliths found on the teeth of the extinct ape Gigantopithecus blacki: implications for paleodietary studies. Proceedings of the National Academy of Sciences 87(20):8120-8124.

Clarke RJ. 2012. A Homo habilis maxilla and other newly-discovered hominid fossils from Olduvai Gorge, Tanzania. Journal of Human Evolution 63(2):418-428.

Clement AF. 2007. A new method for recording tooth wear. In: Zakrzewski SR, White W, editors. Proceedings of the Seventh Annual Conference of the British Association for Biological Anthropology and Osteoarchaeology. Oxford: Archeopress. p 72-81.

Clement AF, Hillson SW. 2012. Intrapopulation variation in macro tooth wear patterns—a case study from Igloolik, Canada. American Journal of Physical Anthropology 149(4):517-524.

Clement AF, Hillson SW, de La Torre I. 2009a. Teeth: an integral part of the hominin tool kit. PaleoAnthropology 2009:A8.

Clement AF, Hillson SW, Aiello LC. 2012. Tooth wear, Neanderthal facial morphology and the anterior dental loading hypothesis. Journal of Human Evolution 62(3):367-376.

Clement AF, Hillson SW, de la Torre I, Townsend GC. 2009b. Tooth use in Aboriginal Australia. Archaeology International 11:37-40.

Compton T, Stringer C. 2012. The human remains. In: Aldhouse-Green S, Peterson R, Walker EA, editors. Neanderthals in Wales: Pontnewydd and the Elwy Valley Caves. Oxford: Oxbow Books. p 118-230.

Comuzzie AG, Steele DG. 1989. Enlarged occlusal surfaces on first molars due to severe attrition and hypercementosis: Examples from prehistoric coastal populations of Texas. American Journal of Physical Anthropology 78(1):9-15.

Condemi S. 1992. Les hommes fossiles de Saccopastore. Cahier de paleoanthropologie.

Condemi S. 2001. Les Néandertaliens de La Chaise: Abri Bourgeois-Delaunay: Comité des travaux historiques et scientifiques-CTHS.

Condemi S, Voisin J-L, Belmaker M, Moncel M-H. 2010. Revisiting the question of Neandertal regional variability: a view from the Rhône Valley Corridor. Collegium Antropologicum 34(3):787-796.

Constantino PJ, Markham K, Lucas PW. 2012. Tooth chipping as a tool to reconstruct diets of great apes (Pongo, Gorilla, Pan). International Journal of Primatology 33(3):661-672.

Constantino PJ, Borrero-Lopez O, Pajares A, Lawn BR. 2016. Simulation of enamel wear for reconstruction of diet and feeding behavior in fossil animals: A micromechanics approach. BioEssays 38(1):89-99.

Constantino PJ, Lee JJW, Chai H, Zipfel B, Ziscovici C, Lawn BR, Lucas PW. 2010. Tooth chipping can reveal the diet and bite forces of fossil hominins. Biology Letters 6:826-829.

Constantino PJ, Lee JJW, Morris D, Lucas PW, Hartstone-Rose A, Lee W-K, Dominy NJ, Cunningham A, Wagner M, Lawn BR. 2011. Adaptation to hard-object feeding in sea otters and hominins. Journal of Human Evolution 61(1):89-96.

Cook DC, Bastos MQR, Lopes C, Mendonça de Souza S, Santos RV. 2015. Pretos Novos: evidence for African oral hygiene practices in Brazil, 1769–1830. International Journal of Osteoarchaeology 25(2):238-244.

Coon CS. 1962. The Origin of Races. New York: Knopf.

Cooper Z, Bowdler S. 1998. Flaked glass tools from the Andaman Islands and Australia. Asian Perspectives:74-83.

Coppa A, Grün R, Stringer C, Eggins S, Vargiu R. 2005. Newly recognized Pleistocene human teeth from Tabun Cave, Israel. Journal of Human Evolution 49(3):301-315.

Coppola D, editor. 2012. Il Riparo di Agnano nel Paleolitico Superiore. La Sepoltura Ostuni 1 ed i Suoi Simboli. Martina Franca: Nuova Editrice Apuli.

Corruccini RS. 1990. Australian aboriginal tooth succession, interproximal attrition, and Begg's theory. American Journal of Orthodontics and Dentofacial Orthopedics 97(4):349-357.

Corruccini RS. 1991. Anthropological aspects of orofacial and occlusal variations and anomalies. In: Kelly MA, Larsen CS, editors. Advances in Dental Anthropology. New York: Wiley-Liss. p 295-323.

Corruccini RS. 1999. How anthropology informs the orthodontic diagnosis of malocclusion's causes: Edwin Mellen Press.

Corruccini RS, Handler JS, Mutaw RJ, Lange FW. 1982. Osteology of a slave burial population from Barbados, West Indies. American Journal of Physical Anthropology 59(4):443-459.

Corruccini RS, Jacobi KP, Handler JS, Aufderheide AC. 1987. Implications of tooth root hypercementosis in a Barbados slave skeletal collection. American Journal of Physical Anthropology 74(2):179-184.

Coulonges L, Lansac A, Piveteau J, Vallois HV. 1952. Le Gisement préhistorique de Monsempron Lot-et-Garonne. Annales de Paléontologie 38:83-120.

Couture C. 1993. Changements de position du massif facial et de l'articulation temporo-mandibulaire dans la ligneé néandertalienne. Organisation crânio-maxillo-faciale des néandertaliennes. Comptes Rendus De L Academie Des Sciences Serie II 316(11):1627-1633.

Cowgill LW, Mednikova MB, Buzhilova AP, Trinkaus E. 2015. The Sunghir 3 Upper Paleolithic Juvenile: Pathology versus Persistence in the Paleolithic. International Journal of Osteoarchaeology 25(2):176-187.

Crétot M. 1997. Modifications dento-céphalométriques spontanées après le stade adulte jeune. L'Orthodontie Français 68(1):41-55.

Crevecoeur I. 2008. Étude Anthropologique du Squelette du Paléolithique Supérieur de Nazlet Khater 2 (Égypte). Leuven: Leuven University Press.

Crevecoeur I. 2012. The Upper Paleolithic human remains of Nazlet Khater 2 (Egypt) and past modern human diversity. In: Hublin J-J, McPherron SP, editors. Modern Origins: A North African Perspective. Dordrecht: Springer. p 205-219.

Crevecoeur I, Semal P, Cornelissen E, Brooks AS. 2010a. The Late Stone Age human remains from Ishango (Democratic Republic of Congo). Contribution to the study of the African Late Pleistocene modern human diversity. American Journal of Physical Anthropology:87-87.

Crevecoeur I, Brooks A, Ribot I, Cornelissen E, Semal P. 2016. Late Stone Age human remains from Ishango (Democratic Republic of Congo): New insights on Late Pleistocene modern human diversity in Africa. Journal of Human Evolution 96:35-57.

Crevecoeur I, Bayle P, Rougier H, Maureille B, Higham T, Johannes van der P, De Clerck N, Semal P. 2010b. The Spy VI child: A newly discovered Neandertal infant. Journal of Human Evolution 59:641-656.

Crognier E, Dupouy-Madre M. 1974. Les Natoufiens du Nahal Oren, Israël. Etude anthropologique. Paléorient 2(1):103-121.

Crothers A, Sandham A. 1993. Vertical height differences in subjects with severe dental wear. The European Journal of Orthodontics 15(6):519-525.

Crummett TL. 1995. The three dimensions of shovel-shaping. In: Moggi-Cecchi J, editor. Aspects of Dental Biology: Paleontology, Anthropology and Evolution. Florence: International Institute for the Study of Man. p 305-313.

Cuozzo FP, Sauther ML. 2006. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): A function of feeding ecology, dental structure, and individual life history. Journal of Human Evolution 51(5):490-505.

Cybulski JS. 1974. Tooth wear and material culture: precontact patterns in the Tsimshian area, British Columbia. Syesis 7:31-35.

D'Amore G, Di Marco S, Tartarelli G, Bigazzi R, Sineo L. 2009. Late Pleistocene human evolution in Sicily: comparative morphometric analysis of Grotta di San Teodoro craniofacial remains. Journal of Human Evolution 56(6):537-550.

d'Errico F, Borgia V, Ronchitelli A. 2012. Uluzzian bone technology and its implications for the origin of behavioural modernity. Quaternary International 259:59-71.

d’Incau E, Saulue P. 2012. Understanding dental wear. Journal of Dentofacial Anomalies and Orthodontics 15(01):null-null.

d’Incau E, Couture C, Maureille B. 2012. Human tooth wear in the past and the present: Tribological mechanisms, scoring systems, dental and skeletal compensations. Archives of Oral Biology 57(3):214-229.

d’Incau E, Couture C, Crépeau N, Chenal F, Beauval C, Vanderstraete V, Maureille B. 2015. Determination and validation of criteria to define hypercementosis in two medieval samples from France (Sains-en-Gohelle, AD 7th–17th century; Jau-Dignac-et-Loirac, AD 7th–8th century). Archives of Oral Biology 60(2):293-303.

Da-Gloria P, Larsen CS. 2014. Oral health of the Paleoamericans of Lagoa Santa, central Brazil. American Journal of Physical Anthropology 154(1):11-26.

Dahlberg AA. 1963. Dental evolution and culture. Human Biology 35:237-249.

Dahlberg AA, Carbonell VM. 1961. The dentition of the Magdalenian female from Cap Blanc, France. Man 61:49-50.

Damuth J, Janis CM. 2014. A comparison of observed molar wear rates in extant herbivorous mammals. Annales Zoologici Fennici: BioOne. p 188-200.

Danenberg PJ, Hirsch RS, Clarke NG, Leppard PI, Richards LC. 1991. Continuous tooth eruption in Australian Aboriginal skulls. American Journal of Physical Anthropology 85(305-312).

Dastmalchi R, Poison A, Bouwsma O, Proskin H. 1990. Cementum thickness and mesial drift. Journal of Clinical Periodontology 17(10):709-713.

David F, D'Iatchenko V, Enloe JG, Girard M, Hardy M, Lhomme V, Roblin-Jouve A, Tillier A-m, Tolmie C. 2009. New Neandertal remains from the Grotte du Bison at Arcy-sur-Cure, France. Journal of Human Evolution 57(6):805-809.

De Luca Canto G, Torres de Freitas S, Schuldt Filho G, de Sousa Vieira R. 2013. Association between mandibular torus and parafunctional activity. international journal of stomatology & occlusion medicine 6(2):43-49.

de Lumley M-A. 1973. Anténéandertaliens et Néandertaliens du Bassin Meidterranéen Occidental Européen. Provence: Editions du Laboratoire de Paleontologie Humaine et de Prehistorie.

de Lumley M-A. 1976. Les Néandertaliens dans le Nord et le Centre. In: de Lumley H, editor. La Préhistoire Française Tome I: Les Civilisations Paléolithiques et Mésolithiques de la France. Paris: Éditions du CNRS. p 588-594.

de Lumley M-A, Giacobini G. 2013a. Les néandertaliens de la Caverna delle Fate (Finale Ligure, Italie). I - Chronostratigraphie, restes squelettiques. L'Anthropologie 117(3):273-304.

de Lumley M-A, Giacobini G. 2013b. Les néandertaliens de la Caverna delle Fate (Finale Ligure, Italie). II – Les dents. L'Anthropologie 117(3):305-344.

de Lumley MA. 1987. Les restes humains Néandertaliens de la Brèche de Genay, Côte-d'Or, France. Anthropologie 91(1):119-162.

Dean MC, Jones ME, Pilley JR. 1992. The natural history of tooth wear, continuous eruption and periodontal disease in wild shot great apes. Journal of Human Evolution 22(1):23-39.

Debénath A, Raynal J-P, Texier J-P. 1982. Position stratigraphique des restes humains paléolithiques marocains sur la base des travaux récents. Comptes Rendus de l'Académie des Sciences, Paris Série II 294(294):1247–1250.

DeGusta D, Everett MA, Milton K. 2003. Natural selection on molar size in a wild population of howler monkeys (Alouatta palliata). Proceedings: Biological Sciences 270(ArticleType: research-article / Issue Title: Supplement: Biology Letters / Full publication date: Aug. 7, 2003 / Copyright © 2003 The Royal Society):S15-S17.

Delpech F. 1996. L'environnement animal des Moustériens Quina du Périgord. Paleo 8(1):31-46.

Demes B. 1987. Another look at an old face: biomechanics of the Neandertal facial skeleton reconsidered. Journal of Human Evolution 16(297-303).

Demeter F, Shackelford LL, Bacon A-M, Duringer P, Westaway K, Sayavongkhamdy T, Braga J, Sichanthongtip P, Khamdalavong P, Ponche J-L. 2012. Anatomically modern human in Southeast Asia (Laos) by 46 ka. Proceedings of the National Academy of Sciences 109(36):14375-14380.

Demeter F, Shackelford L, Westaway KD, P., Bacon A-M, Ponche J-L, Wu X, Sayavongkhamdy T, Zhao J-X, Barnes L, Boyon M et al. . 2015. Early modern humans and morphological variation in Southeast Asia: fossil evidence from Tam Pa Ling, Laos. PLoS ONE 10(4):e0121193 doi:0121110.0121371/journal.pone.0121193.

Deter CA. 2009. Gradients of occlusal wear in hunter-gatherers and agriculturalists. American Journal of Physical Anthropology 138(3):247-254.

Deter CA. 2012. Correlation between dental occlusal wear and approximal facet length. International Journal of Osteoarchaeology 22(6):708-717.

Di Vincenzo F, Churchill SE, Manzi G. 2012. The Vindija Neanderthal scapular glenoid fossa: Comparative shape analysis suggests evo-devo changes among Neanderthals. Journal of Human Evolution 62(2):274-285.

Dinnis R, Bello SM, Chamberlain AT, Coleman C, Stringer C. 2014. A cut-marked Neolithic human tooth from Ash Tree Shelter, Derbyshire, UK. Cave and Karst Science 41(3):114-117.

Doboş A, Soficaru A, Trinkaus E. 2010. The Prehistory and Paleontology of the Peştera Muierii (Romania). Études et Recherches Archéologiques de l'Université de Liège 124:1-122.

Dobrovolskaya M, Richards M-P, Trinkaus E. 2012. Direct radiocarbon dates for the Mid Upper Paleolithic (eastern Gravettian) burials from Sunghir, Russia. Bulletins et Mémoires de la Société d'Anthropologie de Paris 24(1-2):96-102.

Dobson SD, Trinkaus E. 2002. Cross-sectional geometry and morphology of the mandibular symphysis in Middle and Late Pleistocene Homo. Journal of Human Evolution 43(1):67-87.

Dumont ER. 1995. Enamel thickness and dietary adaptation among extant primates and chiropterans. Journal of Mammalogy:1127-1136.

Dunlop I, Martin-Jones J. 2011 [1967]. People of the Australian Western Desert Pyrmont: National Film and Sound Archive of Australia. p 314 minutes.

Durband AC, Westaway MC, Rayner DR. 2012. Interproximal grooving of lower second molars in WLH 4. Australian Archaeology(75):118.

Egocheaga JE, Pérez-Pérez A, Rodríguez L, Galbana J, Martínez LM, Antunes MT. 2004. New evidence and interpretation of subvertical grooves in Neandertal teeth from Cueva de Sidron (Spain) and Figueira Brava (Portugal). Anthropologie 42:49-52.

Ehrhardt K. 1992. The bone, antler and ivory assemblage from Rocher de la Peine, commune des Eyzies (Dordogne). French Paleolithic Collections in the Logan Museum of Anthropology, Beloit College 1(2):203-244.

El Zaatari S. 2008. Occlusal molar microwear and the diets of the Ipiutak and Tigara populations (Point Hope) with comparisons to the Aleut and Arikara. Journal of Archaeological Science 35(9):2517-2522.

El Zaatari S. 2010. Occlusal microwear texture analysis and the diets of historical/prehistoric hunter-gatherers. International Journal of Osteoarchaeology 20(1):67-87.

El Zaatari S, Hublin J-J. 2014. Diet of Upper Paleolithic modern humans: evidence from microwear texture analysis. American Journal of Physical Anthropology 153(4):570-581.

El Zaatari S, Krueger KL, Hublin J-J. 2014. Dental microwear texture analysis and the diet of the Scladina I-4A Neandertal child. In: Toussaint M, Bonjean D, editors. The Scladina I-4A Juvenile Neandertal (Andenne, Belgium): Palaeoanthropology and Context. Liège: Études et Recherches Archéologiques de Université de Liège. p 363-378.

El Zaatari S, Grine FE, Ungar PS, Hublin J-J. 2011. Ecogeographic variation in Neandertal dietary habits: Evidence from occlusal molar microwear texture analysis. Journal of Human Evolution 61(4):411-424.

El Zaatari S, Grine FE, Ungar PS, Hublin J-J. 2016. Neandertal versus modern human dietary responses to climatic fluctuations. PLoS ONE 11(4):e0153277.

Enbom L, Magnusson T, Wall G. 1985. Occlusal wear in miners. Swedish Dental Journal 10(5):165-170.

Eng CM, Lieberman DE, Zink KD, Peters MA. 2013. Bite force and occlusal stress production in hominin evolution. American Journal of Physical Anthropology 151(4):544-557.

Enloe JG. 2011. Middle Palaeolithic Cave Taphonomy: Discerning Humans from Hyenas at Arcy-sur-Cure, France. International Journal of Osteoarchaeology:n/a-n/a.

Erdal YS. 2008. Occlusal grooves in anterior dentition among Kovuklukaya inhabitants (Sinop, northern Anatolia, 10th century AD). International Journal of Osteoarchaeology 18(2):152-166.

Eshed V, Gopher A, Hershkovitz I. 2006. Tooth wear and dental pathology at the advent of agriculture: new evidence from the Levant. American Journal of Physical Anthropology 130:145-159.

Estalrrich A, Rosas A. 2013. Handedness in Neandertals from the El Sidron (Asturias, Spain): Evidence from instrumental striations with ontogenetic inferences. PLoS ONE 8(5).

Estalrrich A, Rosas A. 2015. Division of labor by sex and age in Neandertals: an approach through the study of activity-related dental wear. Journal of Human Evolution 80(0):51-63.

Estalrrich A, Young MB, Teaford MF, Ungar PS. 2015. Environmental perturbations can be detected through microwear texture analysis in two platyrrhine species from Brazilian Amazonia. American Journal of Primatology 77(11):1230-1237.

Estalrrich A, Rosas A, Garcia-Vargas S, Garcia-Tabernero A, Santamaria D, de la Rasilla M. 2011. Subvertical Grooves on Interproximal Wear Facets From the El Sidron (Asturias, Spain) Neandertal Dental Sample. American Journal of Physical Anthropology 144(1):154-161.

Fabbri PF. 1987. Restes humains retrouvés dans la grotte Romanelli (Lecce, Italie) : Etude anthropologique. Bulletins et Mémoires de la Société d'Anthropologie de Paris:219-247.

Fabbri PF. 1995. Dental anthropology of the Upper Palaeolithic sample from San Teodoro and inference on the peopling of Sicily. Zeitschrift für Morphologie und Anthropologie 80(3):311-327.

Fabbri PF, Mallegni F. 1988. Dental anthropology of the Upper Palaeolithic remains from Romito cave at Papasidero (Cosenza, Italy). Bulletins et Mémoires de la Société d'anthropologie de Paris 5(3):163-177.

Feine SC, Hillgruber KF, Münzel S, Schmitz RW. 2006. Evidence for the use of faunal resources in the recovered materials from the rediscovered cave sediments in the Neander Valley. In: Schmitz RW, editor. Neanderthal 1956-2006. Mainz am Rhein: Philipp von Zabern Verlag. p 161-170.

Ferembach D. 1974a. Le squelette humain azilien de Rochereil (Dordogne). Bulletins et Mémoires de la Société d'anthropologie de Paris 1(2):271-291.

Ferembach D. 1974b. Le squelette épicastelnovien de la Baume de Montclus (Gard). Bulletins et Mémoires de la Société d'Anthropologie de Paris 1(1):109-127.

Fiore I, Bondioli L, Radovčić J, Frayer DW. 2015. Handedness in the Krapina Neandertals: a re-evaluation. PaleoAnthropology 2015:19-36.

Fiorenza L. 2015. Reconstructing diet and behaviour of Neanderthals from Central Italy through dental macrowear analysis. Journal of Anthropological Sciences 93:1-15.

Fiorenza L, Kullmer O. 2013. Dental wear and cultural behavior in Middle Paleolithic humans from the Near East. American Journal of Physical Anthropology 152(1):107-117.

Fiorenza L, Kullmer O. 2015. Dental wear patterns in early modern humans from Skhul and Qafzeh: A response to Sarig and Tillier. HOMO 66(5):414-419.

Fiorenza L, Benazzi S, Kullmer O. 2009. Morphology, wear and 3D digital surface models: materials and techniques to create high-resolution replicas of teeth. Journal of Anthropological Sciences 87:211-218.

Fiorenza L, Benazzi S, Kullmer O. 2011a. Para-masticatory wear facets and their functional significance in hunter-gatherer maxillary molars. Journal of Archaeological Science 38(9):2182-2189.

Fiorenza L, Benazzi S, Tausch J, Kullmer O, Bromage TG, Schrenk F. 2011b. Molar macrowear reveals Neanderthal eco-geographic dietary variation. PLoS ONE 6(3):e14769-e14769.

Fishman LS. 1976. Dental and skeletal relationships to attritional occlusion. The Angle Orthodontist 46(1):51-63.

Formicola V. 1988a. The triplex burial of Barma Grande (Grimaldi, Italy). HOMO 39(3-4):130-143.

Formicola V. 1988b. Interproximal grooving of teeth: additional evidence and interpretation. Current Anthropology 29(4):663-671.

Formicola V. 1991. Interproximal grooving: different appearances, different etiologies. American Journal of Physical Anthropology 86:85-86.

Formicola V, Repetto E. 1989. The dentition of the Cro-Magnon type, Grotte des Enfants 4 (Grimaldi, Italy). Bulletin du Musée d'Anthropologie Préhistorique de Monaco 32:51-62.

Formicola V, Pettitt PB, Del Lucchese A. 2004. A direct AMS radiocarbon date on the Barma Grande 6 Upper Paleolithic skeleton. Current Anthropology 45(1):114-118.

Formicola V, Pettitt PB, Maggi R, Hedges R. 2005. Tempo and mode of formation of the Late Epigravettian necropolis of Arene Candide cave (Italy): direct radiocarbon evidence. Journal of Archaeological Science 32(11):1598-1602.

Forsberg CM. 1979. Facial morphology and ageing: a longitudinal cephalometric investigation of young adults. The European Journal of Orthodontics 1(1):15-23.

Fraipont J, Lohest M. 1887. La race humaine de Néanderthal ou de Canstadt en Belgique. Archives de Biologie 7:587–757.

Franciscus RG. 2003. Internal nasal floor configuration in Homo with special reference to the evolution of Neandertal facial form. Journal of Human Evolution 44(6):701-729.

Frayer DW. 1977. Metric dental change in the European Upper Paleolithic and Mesolithic. American Journal of Physical Anthropology 46(1):109-120.

Frayer DW. 1978. Evolution of the Dentition in Upper Paleolithic and Mesolithic Europe. Lawrence: University of Kansas Publications in Anthropology.

Frayer DW. 1989. Oral pathologies in the European Upper Paleolithic and Mesolithic. BAR International Series(508):255-281.

Frayer DW. 1991. On the etiology of interproximal grooves. American Journal of Physical Anthropology 85:299-304.

Frayer DW, Russell MD. 1987. Artificial grooves on the Krapina Neanderthal teeth. American Journal of Physical Anthropology 74(3):393-405.

Frayer DW, Jelínek J, Oliva M, Wolpoff MH. 2006. Aurignacian male crania, jaws and teeth from the Mladeč Caves, Moravia, Czech Republic. In: Teschler-Nicola M, editor. Early Modern Humans at the Moravian Gate: The Mladeč Caves and their Remains. Vienna: Springer Verlag. p 185-272.

Frayer DW, Fiore I, Lalueza-Fox C, Radovčić J, Bondioli L. 2010. Right handed Neandertals: Vindija and beyond. Journal of Anthropological Sciences 88:113-127.

Frayer DW, Lozano M, Bermúdez de Castro JM, Carbonell E, Arsuaga JL, Radovčić J, Fiore I, Bondioli L. 2012. More than 500,000 years of right-handedness in Europe. Laterality: Asymmetries of Body, Brain and Cognition 17(1):51-69.

Fu Q, Hajdinjak M, Moldovan OT, Constantin S, Mallick S, Skoglund P, Patterson N, Rohland N, Lazaridis I, Nickel B et al. . 2015. An early modern human from Romania with a recent Neanderthal ancestor. Nature 524(7564):216-219.

Fu Q, Posth C, Hajdinjak M, Petr M, Mallick S, Fernandes D, Furtwängler A, Haak W, Meyer M, Mittnik A et al. . 2016. The genetic history of Ice Age Europe. Nature advance online publication.

Galbany J, Martínez LM, Pérez-Pérez A. 2004. Tooth replication techniques, SEM imaging and microwear analysis in primates: methodological obstacles. Anthropologie 42:5-12.

Galbany J, Altmann J, Pérez-Pérez A, Alberts SC. 2011. Age and individual foraging behavior predict tooth wear in Amboseli baboons. American Journal of Physical Anthropology 144(1):51-59.

Galbany J, Romero A, Mayo-Alesón M, Itsoma F, Gamarra B, Pérez-Pérez A, Willaume E, Kappeler PM, Charpentier MJ. 2014. Age-related tooth wear differs between forest and savanna primates. PLoS ONE 9(4):e94938.

Gambier D. 1990. Les vestiges humains du gisement d'Isturitz (Pyrénées-Atlantiques). Etude anthropologique et analyse des traces d'action humaine intentionnelle. Antiquités nationales(22-23):9-26.

Gambier D, Houët F. 1993. France Upper Palaeolithic. In: Orban R, Slachmuylder JL, Semal P, Roels D, editors. Hominid Remains: An Up-Date. Bruxelles: Université Libre de Bruxelles. p 1-120.

Gambier D, Valladas H, Tisnérat-Laborde N, Arnold M, Bresson F. 2000. Datation de vestiges humains présumés du Paléolithique supérieur par la méthode du Carbone 14 en spectrométrie de masse par accélérateur. Paleo 12(1):201-212.

García-Diez M, Garrido D, Hoffmann DL, Pettitt PB, Pike AW, Zilhão J. 2015. The chronology of hand stencils in European Palaeolithic rock art: Implications of new U-series results from El Castillo Cave (Cantabria, Spain)(advance online). Journal of Anthropological Sciences 93:1-18.

Garcia-Guixé E, Martínez-Moreno J, Mora R, Núñez M, Richards MP. 2009. Stable isotope analysis of human and animal remains from the Late Upper Palaeolithic site of Balma Guilanyà, southeastern Pre-Pyrenees, Spain. Journal of Archaeological Science 36(4):1018-1026.

Gardner B, Goldstein H. 1931. The significance of hypercementosis. Dental Cosmos 73(11):1065-1069.

Garralda MD, Vandermeersch B. 2000. Les Néandertaliens de la grotte de Combe-Grenal (Domme, Dordogne, France). Paléo 12:213-259.

Garralda MD, Maureille B, Pautrat Y, Vandermeersch B. 2008. La molaire d’enfant néandertalien de Genay (Côte-d’Or, France). Réflexions sur la variabilité dentaire des Néandertaliens. PALEO Revue d'archéologie préhistorique(20):89-100.

Gautney JR, Holliday TW. 2015. New estimations of habitable land area and human population size at the Last Glacial Maximum. Journal of Archaeological Science 58:103-112.

Genet-Varcin E, Miquel M. 1967. Contribution à l’étude du squelette magdalénien de l’abri Lafaye à Bruniquel (Tarn et Garonne). L'Anthropologie 71(5-6):467-478.

Gibbons A. 2012. An evolutionary theory of dentistry. Science 336(6084):973-975.

Gilmore CC, Grote MN. 2012. Estimating age from adult occlusal wear: a modification of the miles method. American Journal of Physical Anthropology 149(2):181-192.

Glantz MM, Athreya S, Ritzman T. 2009. Is Central Asia the eastern outpost of the Neandertal range? A reassessment of the Teshik-Tash child. American Journal of Physical Anthropology 138(1):45-61.

Glass G. 1991. Continuous eruption and periodontal status in pre-industrial dentitions. International Journal of Osteoarchaeology 1(3-4):265-271.

Goodall RH, Darras LP, Purnell MA. 2015. Accuracy and precision of silicon based impression media for quantitative areal texture analysis. Scientific reports 5.

Gottlieb B. 1927. The gingival margin. Proceedings of the Royal Society of Medicine 20:1671-1674.

Gould RA. 1968. Chipping stones in the Outback. Natural History 77(2):42-49.

Gould RA. 1969. Yiwara: Foragers of the Australian Desert. New York: Scribner.

Green TJ, Cochran B, Fenton T, Woods JC, Titmus G, Tieszen L, Davis MA, Miller SF. 1998. The Buhl burial: a paleoindian woman from southern Idaho. American Antiquity 63(437-456).

Grün R, Stringer C. 2000. Tabun revisited: revised ESR chronology and new ESR and U-series analyses of dental material from Tabun C1. Journal of Human Evolution 39(6):601-612.

Grün R, Maroto J, Eggins S, Stringer C, Robertson S, Taylor L, Mortimer G, McCulloch M. 2006. ESR and U-series analyses of enamel and dentine fragments of the Banyoles mandible. Journal of Human Evolution 50(3):347-358.

Grün R, Stringer C, McDermott F, Nathan R, Porat N, Robertson S, Taylor L, Mortimer G, Eggins S, McCulloch M. 2005. U-series and ESR analyses of bones and teeth relating to the human burials from Skhul. Journal of Human Evolution 49(3):316-334.

Guatelli-Steinberg D. 2009. Recent studies of dental development in Neandertals: implications for Neandertal life histories. Evolutionary Anthropology 18(1):9-20.

Guatelli-Steinberg D, Larsen CS, Hutchinson DL. 2004. Prevalence and the duration of linear enamel hypoplasia: a comparative study of Neandertals and Inuit foragers. Journal of Human Evolution 47(1-2):65-84.

Guatelli-Steinberg D, Buzhilova AP, Trinkaus E. 2013. Developmental stress and survival among the Mid Upper Paleolithic Sunghir children: Dental enamel hypoplasias of Sunghir 2 and 3. International Journal of Osteoarchaeology 23:421-431.

Guatelli-Steinberg D, Reid DJ, Bishop TA, Larsen CS. 2005. Anterior tooth growth periods in Neandertals were comparable to those of modern humans. Proceedings of the National Academy of Sciences of the United States of America 102(40):14197-14202.

Guatelli-Steinberg D, Reid DJ, Bishop TA, Larsen CS. 2007. Not so fast: A reply to Ramirez Rozzi and Sardi (2007). Journal of Human Evolution 53(1):114-118.

Guatelli-Steinberg D, Stinespring-Harris A, Reid DJ, Larsen CS, Hutchinson DL, Smith TM. 2014. Chronology of linear enamel hypoplasia formation in the Krapina Neanderthals. PaleoAnthropology 2014:431-445.

Guérin G, Frouin M, Talamo S, Aldeias V, Bruxelles L, Chiotti L, Dibble HL, Goldberg P, Hublin J-J, Jain M et al. . 2015. A multi-method luminescence dating of the Palaeolithic sequence of La Ferrassie based on new excavations adjacent to the La Ferrassie 1 and 2 skeletons. Journal of Archaeological Science 58:147-166.

Gügel IL, Grupe G, Kunzelmann K-H. 2001. Simulation of dental microwear: Characteristic traces by opal phytoliths give clues to ancient human dietary behavior. American Journal of Physical Anthropology 114(2):124-138.

Guillien Y. 1961. Le Petit-Puymoyen: préhistorie, géomorphologie, géochronologie. Bulletin de la Société préhistorique de France 58(11/12):787-795.

Hachi S. 1996. L'Ibéromaurusien, découvertes des fouilles d'Afalou. L'Anthropologie 100:55-76.

Hachi S, Fröhlich F, Gendron-Badou A, de Lumley H, Roubet C, Abdessadok S. 2002. Figurines du Paléolithique supérieur en matière minérale plastique cuite d'Afalou Bou Rhummel (Babors, Algérie). Premières analyses par spectroscopie d'absorption Infrarouge. L'Anthropologie 106(1):57-97.

Haeussler A. 1996. Dental Anthropology of Russia, Ukraine, Georgia, Central Asia: Evaluation of Five Hypotheses for Paleo-Indian Origins. Tempe: Arizona State University.

Haeussler AM. 1995. Upper Paleolithic teeth from the Kostenki sites on the Don River, Russia. In: Moggi-Cecchi J, editor. Aspects of Dental Biology: Palaeontology, Anthropology and Evolution. Florence: International Institute for the Study of Man. p 315-332.

Hanihara K, Ueda H. 1982. Dentition of the Minatogawa man. In: Suzuki H, Hanihara K, editors. The Minatogawa Man. Tokyo: University of Tokyo Press. p 51-59.

Hara AT, Livengood SV, Lippert F, Eckert GJ, Ungar PS. 2016. Dental surface texture characterization based on erosive tooth wear processes. Journal of Dental Research 95(5):537-542.

Hardy BL. 2010. Climatic variability and plant food distribution in Pleistocene Europe: Implications for Neanderthal diet and subsistence. Quaternary Science Reviews 29(5-6):662-679.

Harris EF, Corruccini E. 2008. Quantification of dental occlusal variation: a review of methods. Dental Anthropology 21:1-11.

Harrison R. 2002. Australia's iron age: aboriginal post-contact metal artefacts from old Lamboo Station, Southeast Kimberley, Western Australia. Australasian Historical Archaeology:67-76.

Hasund A. 1964. Attrition and dental arch space. Report of the congress European Orthodontic Society. p 121-131.

Hayden B. 1979. Palaeolithic Reflections: Lithic Technology and Ethnographic Excavation Among Austrailian Aborigines. Canberra: Austrailian Institute of Aboriginal Studies.

Head L, Fullagar R. 1997. Hunter-gatherer archaeology and pastoral contact: Perspectives from the northwest Northern Territory, Australia. World Archaeology 28(3):418-428.

Hedges R, Housley R, Law I, Bronk C. 1989. Radiocarbon dates from the Oxford AMS system: Archaeometry datelist 9. Archaeometry 31(2):207-234.

Hedges R, Housley R, Bronk C, van Klinken G. 1991. Radiocarbon dates from the AMS system: datelist 13. Archaeometry 33:282-283.

Heij Do, Opdebeeck H, van Steenberghe D, Kokich VG, Belser U, Quirynen M. 2005. Facial development, continuous tooth eruption, and mesial drift as compromising factors for implant placement. The International Journal of Oral & Maxillofacial Implants 21(6):867-878.

Heim JL. 1976. Les hommes fossiles de La Ferrassie I: Le gisement, les squelettes adultes (crâne et squelette du tronc). Archives de L'Institut de Paleontologie Humaine Mémoire 35:1-331.

Hellman M. 1934. The form of the Talgai palate. American Journal of Physical Anthropology 19(1):1-15.

Henry-Gambier D, Maureille B, White R. 2004. Vestiges humains des niveaux de l'Aurignacien ancien de sute de Brassempouy (Landes). Bulletins et mémoires de la Société d’Anthropologie de Paris 16(1-2):49-87.

Henry AG, Gordon KD, Trinkaus E, Brooks AS. 2006. Teeth as tools? A comparison of Neanderthal and early modern human incisor microwear. PaleoAnthropology.

Hershkovitz I, Speirs MS, Frayer D, Nadel D, Wish-Baratz S, Arensburg B. 1995. Ohalo II H2: A 19,000-year-old skeleton from a water-logged site at the Sea of Galilee, Israel. American Journal of Physical Anthropology 96(3):215-234.

Higham T, Ramsey CB, Karavanić I, Smith FH, Trinkaus E. 2006. Revised direct radiocarbon dating of the Vindija G(1) upper Paleolithic Neandertals. Proceedings of the National Academy of Sciences of the United States of America 103(3):553-557.

Higham T, Compton T, Stringer C, Jacobi RM, Shapiro B, Trinkaus E, Chandler B, Gröning F, Collins C, Hillson SW. 2011. The earliest evidence for anatomically modern humans in northwestern Europe. Nature 479(7374):521-524.

Hillson S. 1996. Dental Anthropology. Cambridge: Cambridge University Press.

Hillson SW. 1992. Impression and replica methods for studying hypoplasia and perikymata on human tooth crown surfaces from archaeological sites. International Journal of Osteoarchaeology 2:65-78.

Hillson SW. 2006. Dental morphology, proportions, and attrition. In: Trinkaus E, Svoboda J, editors. Early Modern Human Evolution in Central Europe: The People of Dolní Věstonice and Pavlov. New York: Oxford University Press. p 179-223.

Hillson SW, Trinkaus E. 2002. Comparative dental crown metrics. In: Zilhão J, Trinkaus E, editors. Portrait of the Artist as a Child: The Gravettian Human Skeleton from the Abrigo do Lagar Velho and its Archeological Context. Lisboa: Trabalhos de Arqueología, 22. p 356-364.

Hillson SW, Parfitt SA, Bello SM, Roberts MB, Stringer CB. 2010. Two hominin incisor teeth from the middle Pleistocene site of Boxgrove, Sussex, England. Journal of Human Evolution 59:493-503.

Hinton RJ. 1981. Form and patterning of anterior tooth wear among aboriginal human groups. American Journal of Physical Anthropology 54(4):555-564.

Hinton RJ. 1982. Differences in interproximal and occlusal tooth wear among prehistoric Tennessee indians: implications for masticatory function. American Journal of Physical Anthropology 57(1):103-115.

Hintze J. 2012. NCSS 8. Kaysville: NCSS, LLC. www.ncss.com.

Hlusko LJ. 2003. The oldest hominid habit? Experimental evidence for toothpicking with grass stalks. Current Anthropology 44(5):738-741.

Hlusko LJ, Carlson JP, Guatelli-Steinberg D, Krueger KL, Mersey B, Ungar PS, Defleur A. 2013. Neanderthal teeth from Moula-Guercy, Ardèche, France. American Journal of Physical Anthropology 151(3):477-491.

Hoffmann A, Hublin J-J, Hüls M, Terberger T. 2011. The *Homo aurignaciensis hauseri* from Combe-Capelle - a Mesolithic burial. Journal of Human Evolution 61(2):211-214.

Holliday TW, Gautney JR, Friedl L. 2014. Right for the wrong reasons: reflections on modern human origins in the post-Neanderthal genome era. Current Anthropology 55(6):696-724.

Holt BM, Formicola V. 2008. Hunters of the Ice Age: the biology of Upper Paleolithic people. American Journal of Physical Anthropology 137(S47):70-99.

Holton NE. 2009. Modeling of Masticatory Biomechanics in Living Humans as a Baseline for Testing Functional Hypotheses in Neandertals. Iowa City: The University of Iowa. 215 p.

Holton NE, Franciscus RG. 2008. The paradox of a wide nasal aperture in cold-adapted Neandertals: a causal assessment. Journal of Human Evolution 55(6):942-951.

Holton NE, Yokley TR, Franciscus RG. 2011. Climatic adaptation and Neandertal facial evolution: A comment on Rae et al. (2011). Journal of Human Evolution 61(5):624-627.

Hopewell-Smith A. 1920. Concerning human cementum. Journal of Dental Research 2(1):59-76.

Hopf M, Bar-Yosef O. 1987. Plant remains from Hayonim cave, western Galilee. Paléorient 13(1):117-120.

Hublin J-J. 2002. Climatic changes, paleogeography, and the evolution of the Neandertals. Neandertals and modern humans in Western Asia: Springer. p 295-310.

Hublin J-J, Verna C, Bailey S, Smith T, Olejniczak A, Sbihi-Alaoui FZ, Zouak M. 2012. Dental evidence from the Aterian human populations of Morocco. In: Hublin J-J, McPherron S, editors. Modern Origins. Dordrecht: Springer. p 189-204.

Hublin JJ. 2009. The origin of Neandertals. Proceedings of the National Academy of Sciences 106(38):16022-16027.

Humphrey LT, Bocaege E. 2008. Tooth evulsion in the Maghreb: chronological and geographical patterns. African Archaeological Review 25(1-2):109-123.

Humphrey LT, De Groote I, Morales J, Barton N, Collcutt S, Bronk Ramsey C, Bouzouggar A. 2014. Earliest evidence for caries and exploitation of starchy plant foods in Pleistocene hunter-gatherers from Morocco. Proceedings of the National Academy of Sciences 111(3):954-959.

Hylander WL. 1977a. The adaptive significance of Eskimo craniofacial morphology. In: Dahlberg AA, Graber TM, editors. Orofacial growth and development. Paris: Mouton Publishers. p 129-169.

Hylander WL. 1977b. Morphological changes in human teeth and jaws in a high-attrition environment. In: Dahlberg AA, Graber TM, editors. Orofacial growth and development. Paris: Mouton Publishers. p 301-333.

Irish JD. 1998. Ancestral dental traits in recent Sub-Saharan Africans and the origins of modern humans. Journal of Human Evolution 34(1):81-98.

Irish JD, Turner CG. 1987. More lingual surface attrition of the maxillary anterior teeth in American Indians: Prehistoric panamanians. American Journal of Physical Anthropology 73(2):209-213.

Jacobs Z, Meyer MC, Roberts RG, Aldeias V, Dibble H, El Hajraoui MA. 2011. Single-grain OSL dating at La Grotte des Contrebandiers (‘Smugglers’ Cave’), Morocco: improved age constraints for the Middle Paleolithic levels. Journal of Archaeological Science 38(12):3631-3643.

Janković I, Ahern JCM, Karavanić I, Stockton T, Smith FH. 2012. Epigravettian human remains and artifacts from Šandalja II, Istria, Croatia. PaleoAnthropology:87-122.

Janković I, Karavanić I, CM Ahern J, Brajković D, Mauch Lenardić J, Smith FH. 2006. Vindija cave and the modern human peopling of Europe. Collegium Antropologicum 30(3):457-466.

Jardine PE, Janis CM, Sahney S, Benton MJ. 2012. Grit not grass: Concordant patterns of early origin of hypsodonty in Great Plains ungulates and Glires. Palaeogeography, Palaeoclimatology, Palaeoecology 365–366(0):1-10.

Jelínek J, Pelíšěk J, Valoch K. 1959. Der fossile Mensch Brno II. Anthropos 9:5-30.

Joffroy R, Mouton lAP. 1946. La station magdalénienne de Farincourt (H.-M.). Bulletin de la Société préhistorique de France 43(3/4):91-100.

Johansson A-K, Omar R, Carlsson GE, Johansson A. 2012. Dental erosion and its growing importance in clinical practice: from past to present. International journal of dentistry 2012.

Johansson A, Kiliaridis S, Haraldson T, Omar R, Carlsson GE. 1993. Covariation of some factors associated with occlusal tooth wear in a selected high-wear sample. European Journal of Oral Sciences 101(6):398-406.

Jones ER, Gonzalez-Fortes G, Connell S, Siska V, Eriksson A, Martiniano R, McLaughlin RL, Gallego Llorente M, Cassidy LM, Gamba C et al. . 2015. Upper Palaeolithic genomes reveal deep roots of modern Eurasians. Nature Communications 6.

Jordá Pardo JF, Aura JET. 2008. 70 fechas para una cueva: revisión crítica de 70 dataciones C14 del Pleistoceno Superior y Holoceno de la Cueva de Nerja (Málaga, Andalucía, España). Espacio, Tiempo y Forma Serie I, Prehistoria y Arqueología 1:239-256.

Kaidonis J. 2008. Tooth wear: the view of the anthropologist. Clinical Oral Investigations 12(0):21-26.

Kaidonis JA, Townsend GC, Richards LC. 1992. Interproximal tooth wear: a new observation. American Journal of Physical Anthropology 88:105-107.

Kaidonis JA, Richards LC, Townsend GC. 1993. Nature and frequency of dental wear facets in an Australian aboriginal population. Journal of Oral Rehabilitation 20:333-340.

Kaidonis JA, Ranjitkar S, Lekkas D, Townsend GC. 2012. An anthropological perspective: another dimension to modern dental wear concepts. International journal of dentistry 2012.

Kaifu Y. 1996. Edge-to-edge bite and tooth wear. Bulletin of the National Science Museum Tokyo Series D 22:45-54.

Kaifu Y. 1999. Changes in the pattern of tooth wear from prehistoric to recent periods in Japan. American Journal of Physical Anthropology 109(4):485-499.

Kaifu Y. 2000a. Tooth wear and compensatory modification of the anterior dentoalveolar complex in humans. American Journal of Physical Anthropology 111(3):369-392.

Kaifu Y. 2000b. Was extensive tooth wear normal in our ancestors?: A preliminary examination in the genus *Homo*. Anthropological Science 108(4):371-385.

Kaifu Y, Kasai K, Townsend GC, Richards LC. 2003. Tooth wear and the "design" of the human dentition: A perspective from evolutionary medicine. American Journal of Physical Anthropology 122(S37):47-61.

Kaifu Y, Fujita M, Kono RT, Baba H. 2011. Late Pleistocene modern human mandibles from the Minatogawa Fissure site, Okinawa, Japan: morphological affinities and implications for modern human dispersals in East Asia. Anthropological Science 119(2):137-157.

Karavanić I. 1995. Upper Paleolithic occupation levels and late-occurring Neandertal at Vindija Cave (Croatia) in the context of Central Europe and the Balkans. Journal of Anthropological Research 51(1):9-35.

Kay RF. 1981. The nut-crackers–a new theory of the adaptations of the Ramapithecinae. American Journal of Physical Anthropology 55(2):141-151.

Kelly RL. 2013. The Lifeways of Hunter-Gatherers: The Foraging Spectrum. Cambridge: Cambridge University Press.

Kerr NW. 1991. Prevalence and natural history of periodontal disease in Scotland - The mediaeval period (900-1600 A.D.). Journal of Periodontal Research 26:346-354.

Khan F, Young WG. 2011. The multifactorial nature of toothwear. Toothwear, the ABC of the Worn Dentition:1-14.

Kieser JA, Dennison KJ, Kaidonis JA, Huang D, Herbison PGP, Tayles NG. 2001. Patterns of dental wear in the early Maori dentition. International Journal of Osteoarchaeology 11(3):206-217.

Kimmerle EH, Prince DA, Berg GE. 2008. Inter-observer variation in methodologies involving the pubic symphysis, sternal ribs, and teeth*. Journal of forensic sciences 53(3):594-600.

King SJ, Arrigo-Nelson SJ, Pochron ST, Semprebon GM, Godfrey LR, Wright PC, Jernvall J. 2005. Dental senescence in a long-lived primate links infant survival to rainfall. Proceedings of the National Academy of Sciences of the United States of America 102(46):16579-16583.

King SJ, Boyer DM, Tecot S, Strait SG, Zohdy S, Blanco MB, Wright PC, Jernvall J. 2012. Lemur habitat and dental senescence in Ranomafana National Park, Madagascar. American Journal of Physical Anthropology 148(2):228-237.

King T, Andrews P, Boz B. 1999. Effect of taphonomic processes on dental microwear. American Journal of Physical Anthropology 108(3):359-373.

Klein RG. 2008. Out of Africa and the evolution of human behavior. Evolutionary Anthropology: Issues, News, and Reviews 17(6):267-281.

Kloehn SJ. 1938. The Significance of Root Form as Determined by Occlusal Stress*. The Angle Orthodontist 8(3):213-230.

Koby FE. 1956. Une incisive néandertalienne trouvée en Suisse. Verhandenlungen der Nuturforschers Gesellschaft in Basal 67:1-15.

Kramar C. 2008. L'état de santé de l'homme du Bichon. In: Chauvière F-X, editor. La Grotte du Bichon: Un Site Préhistorique des Montagnes Neuchâteloises. Hauterive: Archéologie Neucâteloise. p Dossier 5:16.

Krogstad O, Dahl BL. 1985. Dento-facial morphology in patients with advanced attrition. The European Journal of Orthodontics 7(1):57-62.

Kronfeld R. 1938. The biology of cementum. J Am Dent Assoc 25(9):1451.

Krueger KL. 2011. Dietary and Behavioral Strategies of Neandertals and Anatomically Modern Humans: Evidence from Anterior Dental Microwear Texture Analysis. Fayetteville: University of Arkansas.

Krueger KL. 2014. Contrasting the Ipiutak and Tigara: Evidence from incisor microwear texture analysis. In: Hilton CE, Auerbach BM, Cowgill LW, editors. The Foragers of Point Hope: The Biology and Archaeology of Humans on the Edge of the Alaskan Arctic. Cambridge: Cambridge University Press. p 99-119.

Krueger KL. 2015. Reconstructing diet and behavior in bioarchaeological groups using incisor microwear texture analysis. Journal of Archaeological Science: Reports 1:29-37.

Krueger KL. 2016. Dentition, behavior, and diet determination. In: Irish JD, Scott GR, editors. A Companion to Dental Anthropology. Malden: John Wiley & Sons, Inc. p 396-411.

Krueger KL, Ungar PS. 2009. Incisor microwear textures of five bioarcheological groups. International Journal of Osteoarchaeology 20(5):549-560.

Krueger KL, Ungar PS. 2012. Anterior dental microwear texture analysis of the Krapina Neandertals. Central European Journal of Geosciences 4(4):651-662.

Kuhn SL, Stiner MC. 2001. The antiquity of hunter-gatherers. In: Panter-Brick C, Layton RH, Rowley-Conwy P, editors. Hunter-gatherers: Interdisciplinary perspectives. Cambridge: Cambridge University Press. p 99-142.

Kuhn Steven L, Stiner Mary C. 2006. What's a mother to do? The division of labor among Neandertals and modern humans in Eurasia. Current Anthropology 47(6):953-981.

Kullmer O, Benazzi S, Fiorenza L, Schulz D, Bacso S, Winzen O. 2009. Occlusal fingerprint analysis: Quantification of tooth wear pattern. American Journal of Physical Anthropology 139(4):600-605.

Kusimba S. 2005. What is a hunter-gatherer? Variation in the archaeological record of eastern and southern Africa. Journal of Archaeological Research 13(4):337-366.

Kuzmin YV, Keates SG. 2014. Direct radiocarbon dating of Late Pleistocene hominids in Eurasia: current status, problems, and perspectives. Radiocarbon 56(2):753-766.

Lacruz RS, Bromage TG, O'Higgins P, Arsuaga JL, Stringer CB, Godinho RM, Warshaw J, Martinez I, Gracia-Tellez A, Bermúdez de Castro JM et al. . 2015. Ontogeny of the maxilla in Neanderthals and their ancestors. Nat Commun 6.

Lacy SA. 2014. Oral Health and its Implications in Late Pleistocene Western Eurasian Humans. Saint Louis: Washington University in Saint Louis.

Lalueza-Fox C. 1992. Information obtained from the microscopic examination of cultural striations in human dentition. International Journal of Osteoarchaeology 2(2):155-169.

Lalueza-Fox C. 1995. Restos humanos del nivel solutrense de la Cueva de Nerja (Málaga). Zephyrvs 48:289-297.

Lalueza-Fox C. 1996. Les restes humanes del jaciment Epipaleolític da la Balma de Guilanyà (Navès, Solsonès). Pyrenae 27:279-285.

Lalueza-Fox C, Pérez-Pérez A. 1994. Cutmarks and post-mortem striations in fossil human teeth. Human Evolution 9:165-172.

Lalueza-Fox C, Frayer DW. 1997. Non-dietary marks in the anterior dentition of the Krapina Neanderthals. International Journal of Osteoarchaeology 7(2):133-149.

Lalueza-Fox C, Pérez-Pérez A, Turbón D. 1993. Microscopic study of the Banyoles mandible (Girona, Spain): diet, cultural activity and toothpick use. Journal of Human Evolution 24(4):281-300.

Lalueza-Fox C, Perez-Perez A, Juan J. 1994. Dietary information through the examination of plant phytoliths on the enamel surface of human dentition. Journal of Archaeological Science 21(1):29-34.

Lalueza-Fox C, Juan J, Albert RM. 1996. Phytolith analysis on dental calculus, enamel surface, and burial soil: information about diet and paleoenvironment. American Journal of Physical Anthropology 101(1):101-113.

Lalueza Fox C. 1992. Information obtained from the microscopic examination of cultural striations in human dentition. International Journal of Osteoarchaeology 2(2):155-169.

Lambert PM. 2009. Health versus fitness. Current Anthropology 50(5):603-608.

Langbroek M. 2012. Trees and ladders: A critique of the theory of human cognitive and behavioural evolution in Palaeolithic archaeology. Quaternary International 270:4-14.

Langbroek M. 2014. Ice age mentalists: debating neurological and behavioural perspectives on the Neandertal and modern mind. Journal of Anthropological Sciences 92:285-289.

Larsen CS. 1985. Dental modification and tool use in the western Great Basin. American Journal of Physical Anthropology 67:393-402.

Larsen CS. 1997. Bioarchaeology: Interpreting Behavior From the Human Skeleton. Cambridge: University of Cambridge Press.

Larsen CS. 2015. Bioarchaeology: Interpreting Behavior from the Human Skeleton, 2nd Edition. Cambridge: Cambridge University Press.

Larsen CS, Teaford MF, Sandford MK. 1998. Teeth as tools at Tutu: extramasticatory behavior in prehistoric St. Thomas, U.S. Virgin Islands. In: Alt KW, Rösing FW, Teschler-Nicola M, editors. Dental Anthropology: Fundamentals, Limits, and Prospects. Austria: Spinger-Verlag Wein New York. p 401-420.

Laville H, Rigaud J-P, Sackett J. 1980. Rock shelters of the Perigord: geological stratigraphy and archaeological succession. New York: Academic Press

Lawn BR, Lee JJW. 2009. Analysis of fracture and deformation modes in teeth subjected to occlusal loading. Acta Biomaterialia 5(6):2213-2221.

Lawn BR, Lee JJW, Chai H. 2010. Teeth: among nature's most durable biocomposites. Annual Review of Materials Research 40(1):55-75.

Lawn BR, Lee JJW, Constantino PJ, Lucas PW. 2009. Predicting failure in mammalian enamel. Journal of the Mechanical Behavior of Biomedical Materials 2:33-42.

Lawn BR, Bush MB, Barani A, Constantino PJ, Wroe S. 2013. Inferring biological evolution from fracture patterns in teeth. Journal of Theoretical Biology 338:59-65.

Le Cabec A. 2013. Anterior dental loading and root morphology in Neanderthals: Université de Toulouse, Université Toulouse III-Paul Sabatier.

Le Cabec A, Kupczik K, Gunz P, Braga J, Hublin J-J. 2012. Long anterior mandibular tooth roots in Neanderthals are not the result of their large jaws. Journal of Human Evolution 63(5):667-681.

Le Cabec A, Gunz P, Kupczik K, Braga J, Hublin J-J. 2013. Anterior tooth root morphology and size in Neanderthals: taxonomic and functional implications. Journal of Human Evolution 64(3):169-193.

Le Cabec A, Verna C, Toussaint M, Hublin J-J, Kupczik K. 2014. Micro-computed tomographic quantification of tooth size and tissue proportions in the Scladina juvenile, a shortrooted neandertal. In: Toussaint M, Bonjean D, editors. The Scladina I-4A Juvenile Neandertal (Andenne, Belgium): Palaeoanthropology and Context. Liège: Études et Recherches Archéologiques de Université de Liège. p 325-350.

Lebel S, Trinkaus E. 2002. Middle Pleistocene human remains from the Bau de l'Aubesier. Journal of Human Evolution 43(5):659-685.

Lebel S, Trinkaus E, Faure M, Fernandez P, Guerin C, Richter D, Mercier N, Valladas H, Wagner GA. 2001. Comparative morphology and paleobiology of Middle Pleistocene human remains from the Bau de l'Aubesier, Vaucluse, France. Proceedings of the National Academy of Sciences of the United States of America 98(20):11097-11102.

Lee JJW, Constantino PJ, Lucas PW, Lawn BR. 2011. Fracture in teeth—a diagnostic for inferring bite force and tooth function. Biological Reviews 86(4):959-974.

Lee JJW, Kwon JY, Chai H, Lucas PW, Thompson VP, Lawn BR. 2009. Fracture modes in human teeth. Journal of Dental Research 88:224-228.

Legoux P. 1975. Présentation des dents des restes humains de l'Abri Pataud. In: Movius HL, editor. Excavation of the Abri Pataud, Les Eyzies (Dordogne). Cambridge: Peabody Museum of Archaeology and Ethnology. p 27-68.

Leider AS, Garbarino VE. 1987. Generalized hypercementosis. Oral Surgery, Oral Medicine, Oral Pathology 63(3):375-380.

Leroi-Gourhan A. 1958. Etude des restes humains fossiles provenant des grottes d'Arcy-sur-Cure. Annales de Paléontologie 44:87-148.

Lévêque F, Backer AM. 1993. Context of a Late Neandertal: Implications of Multidisciplinary Research for the Transition to Upper Paleolithic Adaptations at Saint-Césaire, Charante-Maritime, France: Prehistory Press.

Levers BGH, Darling AI. 1983. Continuous eruption of some adult human teeth of ancient populations. Archives of Oral Biology 28(5):401-408.

Lieberman DE, Bramble DM, Raichlen DA, Shea JJ. 2007. The evolution of endurance running and the tyranny of ethnography: A reply to Pickering and Bunn (2007). Journal of Human Evolution 53(4):439-442.

Littleton J, Scott R, McFarlane G, Walshe K. 2013. Hunter-gatherer variability: dental wear in South Australia. American Journal of Physical Anthropology 152(2):273-286.

Liu W, Wu X, Pei S, Wu X, Norton CJ. 2010. Huanglong Cave: A Late Pleistocene human fossil site in Hubei Province, China. Quaternary International 211(1-2):29-41.

Liu W, Schepartz LA, Xing S, Miller-Antonio S, Wu X-J, Trinkaus E, Martinón-Torres M. 2013. Late Middle Pleistocene hominin teeth from Panxian Dadong, South China. Journal of Human Evolution 64(5):337-355.

Liu W, Martinón-Torres M, Cai Y-j, Xing S, Tong H-w, Pei S-w, Sier MJ, Wu X-h, Edwards RL, Cheng H et al. . 2015. The earliest unequivocally modern humans in southern China. Nature 526(7575):696-699.

Lobbezoo F, Ahlberg J, Glaros A, Kato T, Koyano K, Lavigne G, Leeuw R, Manfredini D, Svensson P, Winocur E. 2013. Bruxism defined and graded: an international consensus. Journal of Oral Rehabilitation 40(1):2-4.

Logan M, Sanson GD. 2002. The effect of tooth wear on the feeding behaviour of free-ranging koalas (Phascolarctos cinereus, Goldfuss). Journal of Zoology 256(1):63-69.

Lorkiewicz W. 2011. Nonalimentary tooth use in the Neolithic population of the Lengyel Culture in Central Poland (4600-4000 BC). American Journal of Physical Anthropology 144(4):538-551.

Lovejoy CO. 1985. Dental wear in the Libben population: its functional pattern and role in the determination of adult skeletal age at death. American Journal of Physical Anthropology 68:47-56.

Lozano M. 2005. Estudio del Desgaste a Nivel Microcópico de los dientes Anteriores de los Homínidos del Yacimiento Pleistocénico de Sima de los Huesos (Sierra de Atapuerca, Burgos). Tarragona: Universitat Rovira i Virgili Facultat de Lletres.

Lozano M, Bermúdez de Castro JM, Martinón-Torres M, Sarmiento S. 2004. Cutmarks on fossil human anterior teeth of the Sima de los Huesos Site (Atapuerca, Spain). Journal of Archaeological Science 31(8):1127-1135.

Lozano M, Bermúdez de Castro JM, Carbonell E, Arsuaga JL. 2008. Non-masticatory uses of anterior teeth of Sima de los Huesos individuals (Sierra de Atapuerca, Spain). Journal of Human Evolution 55(4):713-728.

Lozano M, Bermúdez de Castro JM, Arsuaga JL, Carbonell E. 2015. Diachronic analysis of cultural dental wear at the Atapuerca sites (Spain). Quaternary International:http://dx.doi.org/10.1016/j.quaint.2015.1008.1028.

Lozano M, Mosquera M, Bermúdez de Castro JM, Arsuaga JL, Carbonell E. 2009. Right handedness of *Homo heidelbergensis* from Sima de los Huesos (Atapuerca, Spain) 500,000 years ago. Evolution and Human Behavior 30(5):369-376.

Lozano M, Subirà ME, Aparicio J, Lorenzo C, Gómez-Merino G. 2013. Toothpicking and periodontal disease in a Neanderthal specimen from Cova Foradà site (Valencia, Spain). PLoS ONE 8(10):e76852.

Lucas PW. 2004. Dental Functional Morphology: How Teeth Work. New York: Cambridge University Press.

Lucas PW, Omar R. 2012. Damaged! A new overview of dental wear. Archives of Oral Biology 57(3):211-213.

Lucas PW, van Casteren A. 2015. The wear and tear of teeth. Medical Principles and Practice 24(Suppl. 1):3-13.

Lucas PW, Constantino PJ, Wood BA. 2008a. Inferences regarding the diet of extinct hominins: structural and functional trends in dental and mandibular morphology within the hominin clade. Journal of Anatomy 212(4):486-500.

Lucas PW, Constantino PJ, Wood BA, Lawn BR. 2008b. Dental enamel as a dietary indicator in mammals. BioEssays 30(4):374-385.

Lucas PW, Philip SM, Al-Qeoud D, Al-Draihim N, Saji S, van Casteren A. 2016. Structure and scale of the mechanics of mammalian dental enamel viewed from an evolutionary perspective. Evolution & Development 18(1):54-61.

Lucas PW, Omar R, Al-Fadhalah K, Almusallam AS, Henry AG, Michael S, Thai LA, Watzke J, Strait DS, Atkins AG. 2013. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. Journal of The Royal Society Interface 10(80):20120923.

Lucas PW, van Casteren A, Al-Fadhalah K, Almusallam AS, Henry AG, Michael S, Watzke J, Reed DA, Diekwisch TGH, Strait DS. 2014. The role of dust, grit and phytoliths in tooth wear. Annales Zoologici Fennici 51(1):143-152.

Lukacs J, Pastor R. 1988. Activity-induced patterns of dental abrasion in prehistoric Pakistan: evidence from Mehgarh and Harappa. American Journal of Physical Anthropology 76:377-398.

Lundström A, Lysell L. 1953. An anthropological examination of a group of medieval Danish skulls, with particular regard to the jaws and occlusal conditions. Acta Odontologica 11(2):111-128.

Lysell L, Filipsson R. 1958. A profile-roentgenologic study of a series of medieval skulls from northern Sweden. Odontologisk Tidskrift 66:161-174.

Macchiarelli R, Bayle P, Bondioli L, Mazurier A, Zanolli C. 2013. From outer to inner structural morphology in dental anthropology: integration of the third dimension in the visualization and quantitative analysis of fossil remains. In: Scott GR, Irish JD, editors. Anthropological Perspectives on Tooth Morphology: Genetics, Evolution, Variation. Cambridge: Cambridge University Press. p 250-295.

Macchiarelli R, Bondioli L, Debenath A, Mazurier A, Tournepiche J-F, Birch W, Dean MC. 2006. How Neanderthal molar teeth grew. Nature 444(7120):748-751.

Macias ME, Churchill SE. 2015. Functional morphology of the Neandertal scapular glenoid fossa. The Anatomical Record 298(1):168-179.

Macintosh NWG. 1952a. The Talgai teeth and dental arch: Remeasurement and reconstruction. Oceania 23(2):106-109.

Macintosh NWG. 1952b. The Cohuna cranium: teeth and palate. Oceania 23(2):95-105.

Madre-Dupouy M. 1992. L'enfant du Roc de Marsal: étude analytique et comparative: Editions du Centre National de la Recherche Scientifique.

Mair LH. 2000. Wear in the mouth: the tribological dimension. Tooth Wear and Sensitivity London, Martin Dunitz:181-188.

Mair LH, Padipatvuthikul P. 2010. Wear mechanisms in the mouth. Proceedings of the Institution of Mechanical Engineers, Part J: Journal of Engineering Tribology 224(6):569-575.

Majid Z. 1994. The Excavation of Gua Gunung Runtuh and the Discovery of the Perak Man in Malaysia. In: Majid Z, editor. The Perak Man and Other Prehistoric Skeletons of Malaysia. Pulau Pinang: Penerbit Universiti Sains Malaysia.

Maki J, Trinkaus E. 2011. Opponens pollicis mechanical effectiveness in Neandertals and early modern humans. PaleoAnthropology:62-71.

Malez M, Ullrich H. 1982. Neuere palaanthropologische untersuchungen am material aus der Hohle Vindija (Kroatien, Jugoslawein). Palaeontologia Jugoslavica 29:1-44.

Mallegni F. 1995. The teeth and the periodontal apparatus of the Neandertal mandibles from Guattari Cave (Monte Circeo, Lazio, Italy). Zeitshrift für Morphologie und Anthropologie 80(3):329-351.

Mallegni F. 2005a. Riparo Fredian. In: Alciati G, Pesce Delfino V, Vacca E, editors. Catalogo dei Resti Fossili Umani Italiani dal Paleolitico al Mesolitico. Roma: Istituto Italiano di Antropologia. p 64-65.

Mallegni F. 2005b. La Punta. In: Alciati G, Pesce Delfino V, Vacca E, editors. Catalogo dei Resti Fossili Umani Italiani dal Paleolitico al Mesolitico. Roma: Istituto Italiano di Antropologia. p 87.

Mallegni F. 2005c. Maritza. In: Alciati G, Pesce Delfino V, Vacca E, editors. Catalogo dei Resti Fossili Umani Italiani dal Paleolitico al Mesolitico. Roma: Istituto Italiano di Antropologia. p 92-93.

Mallegni F. 2005d. Ortucchio. In: Alciati G, Pesce Delfino V, Vacca E, editors. Catalogo dei Resti Fossili Umani Italiani dal Paleolitico al Mesolitico. Roma: Istituto Italiano di Antropologia. p 102-103.

Mallegni F, Fabbri PF. 1995. The human skeletal remains from the Upper Palaeolithic burials found in Romito cave (Papasidero, Cosenza, Italy). Bulletins et mémoires de la Société d'anthropologie de Paris 7(3):99-137.

Mann A, Vandermeersch B. 1997. An adolescent female Neanderthal mandible from Montgaudier Cave, Charente, France. American Journal of Physical Anthropology 103(4):507-527.

Marean CW. 2015. An evolutionary anthropological perspective on modern human origins. Annual Review of Anthropology 44(1):533-556.

Margvelashvili A, Zollikofer CPE, Lordkipanidze D, Peltomäki T, Ponce de León MS. 2013. Tooth wear and dentoalveolar remodeling are key factors of morphological variation in the Dmanisi mandibles. Proceedings of the National Academy of Sciences 110(43):17278-17283.

Margvelashvili A, Zollikofer CPE, Lordkipanidze D, Tafforeau P, Ponce de León MS. 2016. Comparative analysis of dentognathic pathologies in the Dmanisi mandibles. American Journal of Physical Anthropology 160(2):229-253.

Mariotti V, Bonfiglioli B, Facchini F, Condemi S, Belcastro MG. 2009. Funerary practices of the Iberomaurusian population of Taforalt (Tafoughalt; Morocco, 11-12,000 BP): new hypotheses based on a grave by grave skeletal inventory and evidence of deliberate human modification of the remains. Journal of Human Evolution 56(4):340-354.

Marlowe FW. 2005. Hunter-gatherers and human evolution. Evolutionary Anthropology 14(2):54-67.

Marlowe FW, Berbesque JC. 2009. Tubers as fallback foods and their impact on Hadza hunter-gatherers. American Journal of Physical Anthropology 140(4):751-758.

Marra F, Ceruleo P, Jicha B, Pandolfi L, Petronio C, Salari L. 2015. A new age within MIS 7 for the Homo neanderthalensis of Saccopastore in the glacio-eustatically forced sedimentary successions of the Aniene River Valley, Rome. Quaternary Science Reviews 129:260-274.

Marshall J. 1971. Bitter melons. Watertown: Documentary Educational Resources. p 30 minutes.

Marshall J, Gardner R. 1957. The Hunters. !Kung Series. Watertown: Documentary Educational Resources. p 72 minutes.

Martin H. 1923. L'Homme fossile de la Quina. Paris: Doin.

Martínez LM, Pérez-Pérez A. 2004. Post-mortem wear as indicator of taphonomic processes affecting enamel surfaces of hominin teeth from Laetoli and Olduvai (Tanzania): Implications to dietary interpretations. Anthropologie 42(1):37-42.

Martinón-Torres M, Bermúdez de Castro JM. 2016. The hominins 2: the genus *Homo*. In: Irish JD, Scott GR, editors. A Companion to Dental Anthropology. Malden: John Wiley & Sons, Inc. p 67-84.

Martinón-Torres M, Bermúdez de Castro JM, Gómez-Robles A, Prado-Simón L, Arsuaga JL. 2012. Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). Journal of Human Evolution 62(1):7-58.

Martinón-Torres M, Martín-Francés L, Gracia A, Olejniczak AJ, Prado-Simón L, Gómez-Robles A, Lapresa M, Carbonell E, Arsuaga JL, Bermúdez de Castro JM. 2011. Early Pleistocene human mandible from Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain): A palaeopathological study. Journal of Human Evolution 61(1):1-11.

Matiegka J. 1929. The skull of the fossil man Brno III, and the cast of its interior. Anthropologie 7:90-107.

Matiegka J. 1934. Homo předmostensis, fosilní člověk z Předmostí na Moravě, I, Lebky. Praha: České Akademie věd a umění.

Matsu'ura S, Kondo M. 2011. Relative chronology of the Minatogawa and the Upper Minatogawa series of human remains from Okinawa Island, Japan. Anthropological Science 119(2):173-182.

Matsumura H, Zuraina M. 1995. Metrical analysis of the dentition of Perak man from Gua Gunung Runtuh in Malaysia. Bulletin of the National Science Museum, Tokyo, Series D 21:1-10.

Matsumura H, Zuraina M. 2005. Bioanthropological significance of prehistoric human skeletal remains in Malaysia. The Perak Man and other prehistoric skeletons of Malaysia Penang (Malaysia): Penerbit Universiti Sains Malaysia:425-446.

Matsumura H, Yoneda M, Dodo Y, Oxenham MF, Cuong NL, Thuy NK, Dung LM, Long VT, Yamagata M, Sawada J. 2008. Terminal Pleistocene human skeleton from Hang Cho

Cave, northern Vietnam: implications for the biological affinities of Hoabinhian people. Anthropological Science 116(3):201-217.

Maureille B, Houêt F. 1998. La variabilité morpho-métrique du nez: dérive génique dans la lignée néandertalienne? Biométrie humaine et anthropologie 16(1-2):27-33.

Maureille B, Bar D. 1999. The premaxilla in Neandertal and early modern children: ontogeny and morphology. Journal of Human Evolution 37(2):137-152.

Maureille B, Rougier H, Houët F, Vandermeersch B. 2001. Les dents inférieures du néandertalien Regourdou 1 (site de Regourdou, commune de Montignac, Dordogne): analyses métriques et comparatives. PALEO Revue d'archéologie préhistorique(13):183-200.

Maureille B, Djindjian F, Garralda MD, Mann A, Vandermeersch B. 2008. Les dents moustériennes de la grotte Boccard, lieu-dit Bas-de-Morant (commune de Créancey, Côte-d'Or, Bourgogne). Bulletins et mémoires de la Société d’Anthropologie de Paris 20:1-2.

Maureille B, Mann A, Beauval C, Bordes JG, Bourguignon L, Costamagno S, Couchoud I, Lacrampe-Guyaubère F, Laroulandie V, Marquet J-C. 2007. Le gisement moustérien des Pradelles (Marillac-le-Franc, Charente): passé, présent, futur. Actes du XXVI° Congrès Préhistorique de France: Congrès du Centaire de la Société Préhistorique de France, Avignon-Bonnieux, 20-25 septembre 2004 In: Evin J(éd), Un siècle de construction du discours scientifique en Préhistoire 3:249-262.

Mays S. 2002. The Relationship Between Molar Wear and Age in an Early 19th Century AD Archaeological Human Skeletal Series of Documented Age at Death. Journal of Archaeological Science 29(8):861-871.

Mays S, de la Rua C, Molleson T. 1995. Molar crown height as a means of evaluating existing dental wear scales for estimating age at death in human skeletal remains. Journal of Archaeological Science 22(5):659-670.

Meiklejohn C, Bosset G, Valentin F. 2010. Radiocarbon dating of Mesolithic human remains in France. Mesolithic Miscellany 21(1):10-56.

Mellars P. 1996. The Neanderthal Legacy: An Archaeological Perspective from Western Europe. Princeton: Princeton University Press.

Mellars P. 2005. The impossible coincidence. A single-species model for the origins of modern human behavior in Europe. Evolutionary Anthropology: Issues, News, and Reviews 14(1):12-27.

Mellars P, Grün R. 1991. A comparison of the electron spin resonance and thermoluminescence dating methods: the results of ESR dating at Le Moustier (France). Cambridge Archaeological Journal 1(02):269-276.

Merbs C. 1968. Anterior tooth loss in Arctic populations. Southwestern Journal of Anthropology 28:20-32.

Merbs CF. 1983. Patterns of activity-induced pathology in a Canadian Inuit population. Ottawa: National Museums of Canada.

Mercier N, Valladas H. 2003. Reassessment of TL age estimates of burnt flints from the Paleolithic site of Tabun Cave, Israel. Journal of Human Evolution 45(5):401-409.

Miles AEW. 1963. Assessment of the ages of a population of Anglo-Saxons from their dentitions. Proceedings of the Royal Society of Medicine 55(10):881-886.

Milner GR, Larsen CS. 1991. Teeth as artifacts of human behavior: intentional mutilation and accidental modification. In: Kelley MA, Larsen CS, editors. Advances in Dental Anthropology. New York: Wiley-Liss. p 357-378.

Minozzi S, Manzi G, Ricci F, di Lernia S, Borgognini Tarli SM. 2003. Nonalimentary tooth use in prehistory: An example from early Holocene in Central Sahara (Uan Muhuggiag, Tadrart Acacus, Libya). American Journal of Physical Anthropology 120(3):225-232.

Molleson T. 2005. The third hand: Neolithic basket makers of Abu Hureyra. In: Żądzińska Eb, editor. Current trends in dental morphology research: refereed full papers from 13th International Symposium on Dental Morphology. Wydawnictwo: Uniwersytetu Łódzkiego.

Molnar P. 2008. Dental wear and oral pathology: Possible evidence and consequences of habitual use of teeth in a Swedish Neolithic sample. American Journal of Physical Anthropology 136(4):423-431.

Molnar P. 2011. Extramasticatory dental wear reflecting habitual behavior and health in past populations. Clinical Oral Investigations 15(5):681-689.

Molnar S. 1971. Human tooth wear, tooth function and cultural variability. American Journal of Physical Anthropology 34(2):175-189.

Molnar S. 1972. Tooth wear and culture: a survey of tooth functions among some prehistoric populations. Current Anthropology 13(5):511-526.

Molnar S, Gantt DG. 1977. Functional implications of primate enamel thickness. American Journal of Physical Anthropology 46(3):447-454.

Moncel M-H, Bahain J-J, Falguères C, Patou-Mathis M, Rousseau L, Valladas H, Auguste P, Ayliffe L, Bocherens H, Bouteaux A. 2008. Le site de Payre. Occupations humaines dans la vallée du Rhône à la fin du Pléistocène moyen et au début du Pléistocène supérieur.

Moncel MH, Condemi S. 2007. The humans remains of the site of Payre (S-E France, MIS 7-5). Remarks on stratigraphic position and interest. Anthropologie 45(1):19-29.

Moncel Mh, Pleurdeau D, Pinhasi R, Yeshurun R, Agapishvili T, Chevalier T, LeBourdonnec FX, Poupeau G, Nomade S, Jennings R et al. . 2015. The Middle Palaeolithic record of Georgia: a synthesis of the technological, economic and paleoanthropological aspects. Anthropologie 53(1-2):93-125.

Morel P. 1993. Une chasse à l'ours brun il y a 12000 ans: nouvelle découverte à la grotte du Bichon (La Chaux-de-Fonds). Archéologie Suisse 16(3):110-117.

Morin E, Tsanova T, Sirakov N, Rendu W, Mallye J-B, Lévêque F. 2005. Bone refits in stratified deposits: testing the chronological grain at Saint-Césaire. Journal of Archaeological Science 32(7):1083-1098.

Murphy T. 1959a. Compensatory mechanism in facial height adjustment to functional tooth attrition. Australian Dental Journal 4:312-323.

Murphy T. 1959b. Gradients of dentine exposure in human molar tooth attrition. American Journal of Physical Anthropology 17(3):179-186.

Murphy T. 1964. Reduction of the dental arch by approximal attrition. British Dental Journal 116:483-488.

Mussini C. 2011. Les Restes Humains Moustériens des Pradelles (Marillac-le-Franc, Charente, France): Étude Morphométrique et Réflexions Sur un Aspect Comportemental des Néandertaliens. Bourdeaux: Bordeaux 1.

Myoung S, Lee JJW, Constantino P, Lucas PW, Chai H, Lawn BR. 2009. Morphology and fracture of enamel. Journal of Biomechanics 42(12):1947-1951.

Naldini Segre E. 1992. Arte mobiliare della Grotta Giovanna (Siracusa). Atti della XXVIII Riunione Scientifica dell'Istituo Italiano di Preistoria e Protostoria, L'arte in Italia dal Paleolitico all'età del Bronzo, Firenze 20-22 Novembre 1989. Firenze: Istituto Italiano di Preistoria e Protostoria. p 347-354.

Nara T, Hanihara T, Dodo Y, Vandermeersch B. 1998. Influence of the interproximal attrition of teeth on the formation of Neanderthal retromolar space. Anthropological Science 106(4):297-309.

Newman HN, Levers BGH. 1979. Tooth eruption and function in an early Anglo-Saxon population. Journal of the Royal Society of Medicine 72:341-350.

Niewoehner W. 2006. Neanderthal hands in their proper perspective. Neanderthals Revisited: New Approaches and Perspectives. p 157-190.

Niewoehner WA. 2001. Behavioral inferences from the Skhul/Qafzeh early modern human hand remains. Proceedings of the National Academy of Sciences 98(6):2979-2984.

Noy T, Legge AJ, Higgs ES. 1973. Recent excavations at Nahal-Oren, Israel. Proceedings of the Prehistoric Society 39(DEC):75-&.

O'Connor CF, Franciscus RG, Holton NE. 2005. Bite force production capability and efficiency in Neandertals and modern humans. American Journal of Physical Anthropology 127(2):129-151.

O'Connor S, Aplin K, Szabó K, Pasveer J, Veth P, Spriggs M. 2005. Liang Lemdubu: a Pleistocene cave site in the Aru Islands. In: O'Connor S, Spriggs M, Veth P, editors. The Archaeology of the Aru Islands, Eastern Indonesia, Terra Australis 22 Canberra: Pandanus Press. p 171–204.

Oakley KP, Campbell BG, Molleson TI. 1971. Catalogue of Fossil Hominids. Part II: Europe. London: Trustees of the British Museum (Natural History).

Oakley KP, Campbell BG, Molleson TI. 1975. Catalogue of Fossil Hominids Part III: Americas, Asia, Australia. London: Trustees of The British Museum (Natural History).

Ogden A. 2008. Advances in the paleopathology of teeth and jaws. In: Pinhasi R, Mays S, editors. Advances in Human Paleopathology. Chichester: John Wiley and Sons, Ltd. p 293-307.

Ogilvie MD, Curran BK, Trinkaus E. 1989. Incidence and patterning of dental enamel hypoplasia among Neandertals. American Journal of Physical Anthropology 79:25-41.

Olejniczak AJ, Smith TM, Feeney RNM, Macchiarelli R, Mazurier A, Bondioli L, Rosas A, Fortea J, de la Rasilla M, Garcia-Tabernero A et al. . 2008. Dental tissue proportions and enamel thickness in Neandertal and modern human molars. Journal of Human Evolution 55(1):12-23.

Orschiedt J. 2002. Secondary burial in the Magdalenian: The Brillenhöhle (Blaubeuren, Southwest Germany). PALEO Revue d'archéologie préhistorique(14):241-256.

Osborn J. 1961. An investigation into the interdental forces occurring between the teeth of the same arch during clenching the jaws. Archives of Oral Biology 5(3):202-211.

Owen LR. 2005. Distorting the Past: Gender and the Division of Labor in the European Upper Paleolithic. Tübingen: Kerns Verlag.

Page AE, Viguier S, Dyble M, Smith D, Chaudhary N, Salali GD, Thompson J, Vinicius L, Mace R, Migliano AB. 2016. Reproductive trade-offs in extant hunter-gatherers suggest adaptive mechanism for the Neolithic expansion. Proceedings of the National Academy of Sciences 113(17):4694-4699.

Pampush JD, Duque AC, Burrows BR, Daegling DJ, Kenney WF, McGraw WS. 2013. Homoplasy and thick enamel in primates. Journal of Human Evolution 64(3):216-224.

Paoli G, Parenti R, Sergi S. 1980. Gli scheletri mesolitici della caverna delle Arene Candide (Liguria). Memorie dell'Istituto Italiano di Paleontologia Umana Roma 3:33-154.

Pap I, Tillier A, Arensburg B, Chech M. 1996. The Subalyuk Neanderthal remains (Hungary): a re-examination. Annales Historico-Naturales Musei Nationalis Hungaricus 88:233-270.

Parés JM, Arnold L, Duval M, Demuro M, Pérez-González A, Bermúdez de Castro JM, Carbonell E, Arsuaga JL. 2013. Reassessing the age of Atapuerca-TD6 (Spain): new paleomagnetic results. Journal of Archaeological Science 40(12):4586-4595.

Patte E. 1960. Découverte d’un Néandertalien dans la Vienne. L’Anthropologie 64:512-517.

Patte É. 1962. La Dentition des Néanderthaliens. Paris: Masson.

Péan S, Puaud S, Crépin L, Prat S, Quiles A, der Plicht Jv, Valladas H, Stuart AJ, Drucker DG, Patou-Mathis M. 2013. The Middle to Upper Paleolithic sequence of Buran-Kaya III (Crimea, Ukraine): New stratigraphic, paleoenvironmental, and chronological results. Radiocarbon 55(2).

Pedersen PO. 1947. Dental investigations of Greenland Eskimos. Proceedings of the Royal Society of Medicine 40(12):726-732.

Pedersen PO. 1949. The East Greenland Eskimo Dentition. Numerical Variations and Anatomy: A Contribution to Comparative Ethnic Odontography: Meddelelser Om Grønland 142: CA Reitzel.

Pedersen PO, Jakobsen J, editors. 1989. Teeth and jaws of Qilakisoq mummies: Meddelelser om Grønland, Man & Society. 112-130 p.

Péquart M, Péquart S-J, Boule M, Vallois HV. 1937. Téviec: Station-Nécropole Mésolithique du Morbihan. Paris: Bulletins et Mémoires de la Société d'Anthropologie de Paris 18. Masson.

Pérez-Pérez A, Espurz V, Bermúdez de Castro JM, de Lumley MA, Turbón D. 2003. Non-occlusal dental microwear variability in a sample of Middle and Late Pleistocene human populations from Europe and the Near East. Journal of Human Evolution 44(4):497-513.

Pettitt PB, Trinkaus E. 2000. Direct radiocarbon dating of the Brno 2 Gravettian human remains. Anthropologie 38(2):149-150.

Pettitt PB, Richards MP, Maggi R, Formicola V. 2003. The Gravettian burial known as the Prince (‘Il Principe’): new evidence for his age and diet. Antiquity 77(295):15-19.

Picton D. 1962. Tilting movements of teeth during biting. Archives of Oral Biology 7(2):151-159.

Pinhasi R, Meiklejohn C. 2011. Dental reduction and the transition to agriculture in Europe. In: Pinhasi R, Stock JT, editors. Human Bioarchaeology of the Transition to Agriculture. Malden: John Wiley & Sons, Ltd. p 451-474.

Pinhasi R, Nioradze M, Tushabramishvili N, Lordkipanidze D, Pleurdeau D, Moncel M-H, Adler D, Stringer C, Higham T. 2012. New chronology for the Middle Palaeolithic of the southern Caucasus suggests early demise of Neanderthals in this region. Journal of human evolution 63(6):770-780.

Pinheiro BC, Pinheiro TN, Capelozza ALA, Consolaro A. 2008. A scanning electron microscopic study of hypercementosis. Journal of Applied Oral Science 16(6):380-384.

Pinilla B, Trinkaus E. 2017a. The Palomas dental remains: size and proportions. In: Trinkaus E, Walker MJ, editors. The People of Palomas: Neandertals from the Sima de las Palomas, Cabezo Gordo, Southeastern Spain. College Station: Texas A&M University Press.

Pinilla B, Trinkaus E. 2017b. The Palomas dental remains: Postcanine wear. In: Trinkaus E, Walker MJ, editors. The People of Palomas: Neandertals from the Sima de las Palomas, Cabezo Gordo, Southeastern Spain. College Station: Texas A&M University Press.

Pirson S, Bonjean D, Toussaint M. 2014. Stratigraphic origin of the juvenile remains from Scladina cave: re-evaluation and consequences for their palaeoenvironmental and chronostratigraphic contexts. In: Toussaint M, Bonjean D, editors. The Scladina I-4A Juvenile Neandertal (Andenne, Belgium): Palaeoanthropology and Context. Liège: Études et Recherches Archéologiques de Université de Liège. p 93-124.

Ponce de León MS, Zollikofer CPE. 1999. New evidence from Le Moustier 1: Computer-assisted reconstruction and morphometry of the skull. The Anatomical Record 254(4):474-489.

Porr M, Alt KW. 2006. The burial of Bad Dürrenberg, central Germany: Osteopathology and osteoarchaeology of a Late Mesolithic shaman's grave. International Journal of Osteoarchaeology 16(5):395-406.

Porter CC, Marlowe FW. 2007. How marginal are forager habitats? Journal of Archaeological Science 34(1):59-68.

Prada Marcos ME. 2010. Los hombres Mesolíticos de la Cueva de la Braña-Arintero. Estudio antropológico. In: Vidal Encinas JM, Prada Marcos ME, editors. Los Hombres Mesolíticos de la Cueva de la Braña-Arintero (Valdelugueros, León). León: Junta de Castilla y León. p 92-118.

Prat S, Péan SC, Crépin L, Drucker DG, Puaud SJ, Valladas H, Lázničková-Galetová M, van der Plicht J, Yanevich A. 2011. The oldest anatomically modern humans from far southeast Europe: direct dating, culture and behavior. PLoS ONE 6(6):e20834.

Proffit WR, Fields Jr HW, Sarver DM. 2007. Contemporary Orthodontics, Fourth Edition. Saint Louis: Mosby Elsevier Health.

Prpié-Mehiéié G, Buntak-Kobler D. 1998. Occupational tooth-wear in clothing industry workers. Coll Antropol 22:241-249.

Puech P-F. 1981. Tooth wear in La Ferrassie man. Current Anthropology 22(4):424-430.

Puech P-F. 1982. L'usure dentaire de l'homme de Tautavel. L'Homo erectus et la place de l'homme de Tautavel parmi les hominidés fossiles. Colloque

International du CNRS, Nice:249-274.

Puech P, Puech S, Cianfarani F, Albertini H. 1987. Tooth wear and dexterity in *Homo erectus*. In: Giacobini G, editor. Hominidae. Milan: JACA. p 247-250.

Quam RM, Arsuaga JL, Bermúdez de Castro JM, Díez CJ, Lorenzo C, Carretero M, García N, Ortega AI. 2001. Human remains from Valdegoba Cave (Huérmeces, Burgos, Spain). Journal of Human Evolution 41(5):385-435.

Rabenold D, Pearson OM. 2011. Abrasive, silica phytoliths and the evolution of thick molar enamel in primates, with implications for the diet of Paranthropus boisei. PLoS ONE 6(12):e28379.

Rabenold D, Pearson OM. 2014. Scratching the surface: a critique of's conclusion that phytoliths do not abrade enamel. Journal of Human Evolution.

Rae TC, Koppe T, Stringer CB. 2011a. The Neanderthal face is not cold adapted. Journal of Human Evolution 60(2):234-239.

Rae TC, Koppe T, Stringer CB. 2011b. Hyperpneumatized Neanderthals? Reply to Holton et al. (2011). Journal of Human Evolution 61(5):628-629.

Rak Y. 1986. The Neanderthal: a new look at an old face. Journal of Human Evolution 15:151-164.

Ramirez Rozzi FV, Bermúdez de Castro JM. 2004. Surprisingly rapid growth in Neanderthals. Nature 428(6986):936-939.

Ramirez Rozzi FV, d'Errico F, Vanhaeren M, Grootes PM, Kerautret B, Dujardin V. 2009. Cutmarked human remains bearing Neandertal features and modern human remains associated with the Aurignacian at Les Rois. Journal of Anthropological Sciences 87:153-185.

Raynal J-P, Sbihi-Alaoui F-Z, Mohib A, El Graoui M, Lefèvre D, Texier J-P, Geraads D, Hublin J-J, Smith T, Tafforeau P et al. . 2010. Hominid Cave at Thomas Quarry I (Casablanca, Morocco): Recent findings and their context. Quaternary International 223-224(0):369-382.

Reinhard KJ, Danielson DR. 2005. Pervasiveness of phytoliths in prehistoric southwestern diet and implications for regional and temporal trends for dental microwear. Journal of Archaeological Science 32(7):981-988.

Reinhardt GA. 1983a. Attrition and the edge-to-edge bite: an anthropological study. The Angle Orthodontist 53(2):157-164.

Reinhardt GA. 1983b. Relationships between attrition and lingual tilting in human teeth. American Journal of Physical Anthropology 61:227-237.

Rhodes JA, Churchill SE. 2009. Throwing in the Middle and Upper Paleolithic: inferences from an analysis of humeral retroversion. Journal of Human Evolution 56(1):1-10.

Richards LC, Brown T. 1981. Dental attrition and age relationships in Australian Aboriginals. Archaeology in Oceania 16:94-98.

Rink WJ, Schwarcz HP, Smith FH, Radovĉiĉ J. 1995. ESR ages for Krapina hominids. Nature 378:24.

Rink WJ, Schwarcz HP, Valoch K, Seitl L, Stringer CB. 1996. ESR Dating of Micoquian Industry and Neanderthal Remains at Kůlna Cave, Czech Republic. Journal of Archaeological Science 23(6):889-901.

Rink WJ, Schwarcz H, Lee H, Rees-Jones J, Rabinovich R, Hovers E. 2001. Electron spin resonance (ESR) and thermal ionization mass spectrometric (TIMS) 230Th/234U dating of teeth in Middle Paleolithic layers at Amud Cave, Israel. Geoarchaeology 16(6):701-717.

Roberts MB, Parfitt SA, Pope MI, Wenban-Smith FF, Macphail RI, Locker A, Stewart JR. 1997. Boxgrove, West Sussex: rescue excavations of a Lower Palaeolithic landsurface (Boxgrove Project B, 1989–91). Proceedings of the Prehistoric Society 63:303-358.

Roebroeks W, Soressi M. 2016. Neandertals revised. Proceedings of the National Academy of Sciences 113(23):6372-6379.

Roebroeks W, Sier MJ, Nielsen TK, De Loecker D, Parés JM, Arps CES, Mücher HJ. 2012. Use of red ochre by early Neandertals. Proceedings of the National Academy of Sciences 109(6):1889-1894.

Rohlf FJ. 2006. tpsDig. 2.10 ed. New York: Department of Ecology and Evolution.

Romero A, De Juan J. 2003. Microscopic features on enamel incisor surfaces: implications as regards feeding behavior in bio-archaeological groups. International Journal of Dental Anthropology 4:1-9.

Romero A, De Juan J. 2004. Microdesgaste dental en incisivos humanos prehistóricos. In: Egocheaga JE, editor. Biología de poblaciones humanas: diversidad, tiempo, espacio Secretaría del XII Congreso de la SEAB y Sociedad Española de Antropología Biológica. p 241-246.

Romero A, De Juan J. 2012. SEM, teeth, and palaeoanthropology: the secret of ancient human diets. In: Schatten H, editor. Scanning Electron Microscopy for the Life Sciences. Cambridge: Cambridge University Press. p 236-256.

Romero A, Galbany J, De Juan J, Pérez-Pérez A. 2012. Short-and long-term in vivo human buccal–dental microwear turnover. American Journal of Physical Anthropology 148(3):467-472.

Rosas A, Estalrrich A, Garcia-Vargas S, Garcia-Tabernero A, Huguet R, Lalueza-Fox C, de la Rasilla M. 2013. Identification of Neandertal individuals in fragmentary fossil assemblages by means of tooth associations: The case of El Sidron (Asturias, Spain). Comptes Rendus Palevol 12(5):279-291.

Rose JC, Roblee RD. 2009. Origins of dental crowding and malocclusions: an anthropological perspective. Compendium of Continuing Education in Dentistry 30(5):292-300.

Rougier H. 2003. Étude Dectriptive et Comparative de Biache-Saint-Vaast 1 (Biache-Saint-Vaast, Pas-de-Calais, France) Bordeaux: L'Université Bordeaux 1.

Rougier H, Crevecoeur I, Wolpoff MH. 2006. Lower third premolar rotation in the Krapina dental sample. Periodicum Biologorum 108(3):269-278.

Rougier H, Crevecoeur I, Beauval C, Bocherens H, Flas D, Germonpré M, Semal P, van der Plicht J. 2012. New data from an old site: Neandertals at Goyet (Belgium) and their mortuary behaviour. American Journal of Physical Anthropology 147:252-253.

Rubini M, Cerroni V, Festa G, Sardella R, Zaio P. 2014. A revision of hominin fossil teeth from Fontana Ranuccio (Middle Pleistocene, Anagni, Frosinone, Italy). Journal of Human Evolution 77:204-216.

Ruiz J, Subirà ME, Prada Marcos ME. 2010. Caracterización morfomtrica dental de los individuos Mesolíticos de la Braña-Arintero. In: Vidal Encinas JM, Prada Marcos ME, editors. Los Hombres Mesolíticos de la Cueva de la Braña-Arintero (Valdelugueros, León). León: Junta de Castilla y León. p 138-145.

Ryan AS. 1980a. Anterior dental microwear in Neanderthals. American Journal of Physical Anthropology 52(2):274-274.

Ryan AS. 1980b. Anterior Dental Microwear in Hominid Evolution: Comparisons with Humans and Nonhuman Primates. Ann Arbor: University of Michigan.

Ryan AS. 1993. Anterior dental microwear in late Pleistocene human fossils. American Journal of Physical Anthropology Supplement 16:171.

Ryan AS, Johanson DC. 1989. Anterior dental microwear in Australopithecus afarensis: comparisons with human and nonhuman primates. Journal of Human Evolution 18(3):235-268.

Saffar JL, Lasfargues JJ, Cherruau M. 1997. Alveolar bone and the alveolar process: the socket that is never stable. Periodontology 2000 13(1):76-90.

Sai LH. 2004. Dentofacial features of the Perak Man. In: Majid Z, editor. The Perak Man and Other Prehistoric Skeletons of Malaysia. Pulau Pinang: Penerbit Universiti Sains Malaysia. p 73-90.

Sarchet P. 2015. Unveiling the Red Lady of El Mirón. New Scientist 225(3013):8-9.

Sarig R, Tillier A-m. 2014. Reconstructing cultural behavior from dental wear studies: Is para-facets analysis approach scientifically valid? HOMO 65(3):181-186.

Sarig R, Tillier A-m. 2016. Dental wear patterns in early modern humans from Skhul and Qafzeh: A response to Luca Fiorenza and Ottmar Kullmer. HOMO 67(1):85-87.

Sarig R, Slon V, Abbas J, May H, Shpack N, Vardimon AD, Hershkovitz I. 2013. Malocclusion in early anatomically modern human: a reflection on the etiology of modern dental misalignment. PLoS ONE 8(11):e80771.

Sarig R, Gopher A, Barkai R, Rosell J, Blasco R, Weber GW, Fornai C, Sella-Tunis T, Hershkovitz I. 2016. How did the Qesem Cave people use their teeth? Analysis of dental wear patterns. Quaternary International 398:136-147.

Sauter MR. 1957. Étude des vestiges osseux humains des grottes préhistoriques de Farincourt (Haute-Marne, France). Archives Suisses d'Anthropologie Générale 22:6-37.

Schmitz RW, Serre D, Bonani G, Feine S, Hillgruber F, Krainitzki H, Paabo S, Smith FH. 2002. The Neandertal type site revisited: Interdisciplinary investigations of skeletal remains from the Neander Valley, Germany. Proceedings of the National Academy of Sciences 99(20):13342-13347.

Schulz PD. 1977. Task activity and anterior tooth grooving in prehistoric California Indians. American Journal of Physical Anthropology 46(1):87-91.

Schwarcz H, Grün R, Vandermeersch B, Bar-Yosef O, Valladas H, Tchernov E. 1988. ESR dates for the hominid burial site of Qafzeh in Israel. Journal of Human Evolution 17(8):733-737.

Schwarcz H, Buhay W, Grün R, Valladas H, Tchernov E, Bar-Yosef O, Vandermeersch B. 1989. ESR dating of the Neanderthal site, Kebara Cave, Israel. Journal of Archaeological Science 16(6):653-659.

Schwarcz HP, Bietti A, Buhay W, Stiner M, Grun R, Segre A. 1991. On the reexamination of Grotta Guattari: uranium-series and electron-spin-resonance dates. Current Anthropology 32(3):313-316.

Schwartz JH, Tattersall I. 2002. The Human Fossil Record Volume One: Terminology and Craniodental Morphology of Genus *Homo* (Europe). New York: Wiley-Liss.

Scott EC. 1979. Dental wear scoring technique. American Journal of Physical Anthropology 51(2):213-217.

Scott GR, Turner CG. 2000. The Anthropology of Modern Human Teeth: Dental Morphology and its Variation in Recent Human Populations. Cambridge: Cambridge University Press.

Scott GR, Jolie RB. 2008. Tool-use and yarn production in Norse Greenland. Alaska Journal of Anthropology 6(1-2):253-264.

Scott GR, Winn JR. 2011. Dental chipping: Contrasting patterns of microtrauma in Inuit and European populations. International Journal of Osteoarchaeology 21(6):723-731.

Seddon RP. 1984. A cephalometric study of the Romano—British. The European Journal of Orthodontics 6(1):303-312.

Semal P, Rougier H, Crevecoeur I, Jungels C, Flas D, Hauzeur A, Maureille B, Germonpré M, Bocherens H, Pirson S et al. . 2009. New data on the late Neandertals: Direct dating of the Belgian Spy fossils. American Journal of Physical Anthropology 138(4):421-428.

Shackelford L, Demeter F. 2012. The place of Tam Hang in Southeast Asian human evolution. Comptes Rendus Palevol 11(2):97-115.

Shackelford LL. 2007. Regional variation in the postcranial robusticity of late Upper Paleolithic humans. American Journal of Physical Anthropology 133(1):655-668.

Shackelford LL, Harris AES, Konigsberg LW. 2012. Estimating the distribution of probable age-at-death from dental remains of immature human fossils. American Journal of Physical Anthropology 147(2):227-253.

Shang H, Trinkaus E. 2010. The Early Modern Human from Tianyuan Cave, China. College Station: Texas A&M University Press.

Shang H, Tong HW, Zhang SQ, Chen FY, Trinkaus E. 2007. An early modern human from Tianyuan Cave, Zhoukoudian, China. Proceedings of the National Academy of Sciences of the United States of America 104(16):6573-6578.

Shea JJ. 2011. *Homo sapiens* is as *Homo sapiens* was. Current Anthropology 52(1):1-35.

Shea JJ, Sisk ML. 2010. Complex projectile technology and *Homo sapiens* dispersal into Western Eurasia. PaleoAnthropology:100-122.

Shipman P, Rose J. 1984. Cutmark mimics on modern and fossil bones. Current Anthropology 2(1):116-117.

Sinitsyn A. 1996. Kostenki 14 (Markina gora): Data, problems, and perspectives. Préhistoire Européenne 9:273-313.

Sinitsyn A. 2004. Les sepultures de Kostenki: chronologie, attribution culturelle, rite funéraire. In: Otte M, editor. La Spiritualité: Actes du Colloque de la Commission 8 de l'UISPP. Liège: ERAUL. p 237-244.

Sinitsyn A, Allsworth-Jones P, Housley R. 1996. Kostenki 14 (Markina Gora): new AMS dates and their significance within the context of the site as a whole. Préhistoire Européenne 9:269-271.

Skinner M. 1997. Dental wear in immature Late Pleistocene European hominines. Journal of Archaeological Science 24(8):677-700.

Sládek V, Ruff CB, Berner M, Holt B, Niskanen M, Schuplerová E, Hora M. 2016. The impact of subsistence changes on humeral bilateral asymmetry in Terminal Pleistocene and Holocene Europe. Journal of Human Evolution 92:37-49.

Smith BH. 1983a. Dental Attrition in Hunter-Gatherers and Agriculturalists. Ann Arbor: The University of Michigan.

Smith BH. 1984. Patterns of molar wear in hunter-gatherers and agriculturalists. American Journal of Physical Anthropology 63(1):39-56.

Smith BH. 1991. Dental development and the evolution of life history in Hominidae. American Journal of Physical Anthropology 86(2):157-174.

Smith FH, editor. 1976a. The Neandertal Remains from Krapina: A Descriptive and Comparative Study. Knoxville, TN: University of Tennessee.

Smith FH. 1983b. Behavioral interpretations of changes in craniofacial morphology across the archaic/modern *Homo sapiens* transition. In: Trinkaus E, editor. The Mousterian Legacy: BAR. p 137-209.

Smith FH. 2013. The fate of the Neandertals. Journal of Anthropological Research 69(2):167-200.

Smith FH. 2015. Neanderthal adaptation: the biological costs of brawn. In: Sanz N, editor. Human Origin Sites and the World Heritage Convention in Eurasia, Volume I. Paris: UNESCO World Heritage Papers 41 p206-219.

Smith FH, Paquette SP. 1989. The adaptive basis of Neandertal facial form, with some thoughts on the nature of modern human origins. In: Trinkaus E, editor. The Emergence of Modern Humans: Biocultural Adaptations in the Later Pleistocene. Cambridge: Cambridge University Press. p 181-210.

Smith FH, Falsetti AB, Donnelly SM. 1989. Modern human origins. American Journal of Physical Anthropology 32:35-68.

Smith FH, Janković I, Karavanić I. 2005. The assimilation model, modern human origins in Europe, and the extinction of Neandertals. Quaternary International 137(1):7-19.

Smith P. 1976b. Dental pathology in fossil hominids: what did Neanderthals do with their teeth? Current Anthropology 17(1):149-151.

Smith P. 1977a. Selective pressures and dental evolution in hominids. American Journal of Physical Anthropology 47:453-458.

Smith P. 1977b. Regional variation in tooth size and pathology in fossil hominids. American Journal of Physical Anthropology 47(3):459-466.

Smith SA. 1918. The fossil human skull found at Talgai, Queensland. Philosophical Transactions of the Royal Society of London Series B, Containing Papers of a Biological Character:351-387.

Smith TM, Toussaint M, Reid DJ, Olejniczak AJ, Hublin JJ. 2007a. Rapid dental development in a Middle Paleolithic Belgian Neanderthal. Proceedings of the National Academy of Sciences of the United States of America 104(51):20220-20225.

Smith TM, Olejniczak AJ, Tafforeau P, Reid DJ, Grine FE, Hublin JJ. 2006. Molar crown thickness, volume, and development in South African Middle Stone Age humans. South African Journal of Science 102:513-517.

Smith TM, Harvati K, Olejniczak AJ, Reid DJ, Hublin J-J, Panagopoulou E. 2009. Dental development and enamel thickness in the Lakonis Neanderthal molar. American Journal of Physical Anthropology 138(1):112-118.

Smith TM, Tafforeau P, Reid DJ, GrÃ¼n R, Eggins S, Boutakiout M, Hublin J-J. 2007b. Earliest evidence of modern human life history in North African early Homo sapiens. Proceedings of the National Academy of Sciences 104(15):6128-6133.

Smith TM, Olejniczak AJ, Zermeno JP, Tafforeau P, Skinner MM, Hoffmann A, Radovčić J, Toussaint M, Kruszynski R, Menter C et al. . 2012. Variation in enamel thickness within the genus *Homo*. Journal of Human Evolution 62(3):395-411.

Soames JV, Southam JE. 2005. Oral Pathology. Oxford: Oxford University Press.

Soficaru A, Doboş A, Trinkaus E. 2006. Early modern humans from the Pestera Muierii, Baia de Fier, Romania. Proceedings of the National Academy of Sciences 103(46):17196-17201.

Spencer MA, Demes B. 1993. Biomechanical analysis of masticatory system configuration in Neandertals and Inuits. American Journal of Physical Anthropology 91(1):1-20.

Spencer MA, Ungar PS. 2000. Craniofacial morphology, diet and incisor use in three native American populations. International Journal of Osteoarchaeology 10(4):229-241.

Speth JD. 2010. Paleoanthropology and Archaeology of Big-Game Hunting: Protein, Fat, or Politics? New York: Springer.

Spinapolice EE. 2015. Third hand: a testable hypothesis. Journal of Anthropological Sciences 93:169-171.

Spradley JP, Glander KE, Kay RF. 2016. Dust in the wind: how climate variables and volcanic dust affect rates of tooth wear in central american howling monkeys. American Journal of Physical Anthropology 159(2):210-222.

Stefan VH, Trinkaus E. 1998. Discrete trait and dental morphometric affinities of the Tabun 2 mandible. Journal of Human Evolution 34(5):443-468.

Stevens RE, Jacobi RM, Higham TFG. 2010. Reassessing the diet of Upper Palaeolithic humans from Gough's Cave and Sun Hole, Cheddar Gorge, Somerset, UK. Journal of Archaeological Science 37(1):52-61.

Stojanowski CM, Carver CL, Miller KA. 2014. Incisor avulsion, social identity and Saharan population history: New data from the Early Holocene southern Sahara. Journal of Anthropological Archaeology 35(0):79-91.

Stojanowski CM, Johnson KM, Paul KS, Carver CL. 2016. Indicators of idiosyncratic behavior in the dentition. In: Irish JD, Scott GR, editors. A Companion to Dental Anthropology. Malden: John Wiley & Sons, Inc. p 377-395.

Storm P, Wood R, Stringer C, Bartsiokas A, de Vos J, Aubert M, Kinsley L, Grün R. 2013. U-series and radiocarbon analyses of human and faunal remains from Wajak, Indonesia. Journal of Human Evolution 64(5):356-365.

Strait DS, Constantino PJ, Lucas PW, Richmond BG, Spencer MA, Dechow PC, Ross CF, Grosse IR, Wright BW, Wood BA. 2013. Viewpoints: Diet and dietary adaptations in early hominins: The hard food perspective. American Journal of Physical Anthropology 151(3):339-355.

Street M, Terberger T, Orschiedt J. 2006. A critical review of the German Paleolithic hominin record. Journal of Human Evolution 51(6):551-579.

Stringer CB, Powers R. 1978. A late Pleistocene human tooth from Tornewton Cave, Devonshire, England. Transactions of the British Cave Research Association 5(4):221-224.

Stringer CB, Currant AP. 1986. Hominid specimens from La Cotte de St. Brelade. In: Callow P, Cornford J, editors. La Cotte de St Brelade. Norwich: Geo Books. p 155-158.

Sun C, Xing S, Martín-Francés L, Bae C, Liu L, Wei G, Liu W. 2014. Interproximal grooves on the Middle Pleistocene hominin teeth from Yiyuan, Shandong Province: New evidence for tooth-picking behavior from eastern China. Quaternary International 354(0):162-168.

Suzuki H, Takai F. 1970. The Amud Man and His Cave Site. Tokyo: Academic Press.

Suzuki H, Hanihara K. 1982. The Minatogawa man: the Upper Pleistocene man from the island of Okinawa: University of Tokyo Press.

Svoboda J, Ložek V, Vlček E. 1996. Hunters between east and west: The Paleolithic of Moravia: Plenum.

Svoboda JA. 2005. The Neandertal extinction in eastern Central Europe. Quaternary International 137(1):69-75.

Svoboda JA. 2008. The Upper Paleolithic burial area at Předmostí: ritual and taphonomy. Journal of Human Evolution 54(1):15-33.

Svoboda JA, van der Plicht J, Kuzelka V. 2002. Upper Palaeolithic and Mesolithic human fossils from Moravia and Bohemia (Czech Republic): some new ^{14}C dates Antiquity 76(294):957-962.

Szombathy J. 1950. Der menschliche Unterkiefer aus dem Miesslingtal bei Spitz, N-Ö. Archaeologia Austriaca 5:1-5.

Tanga C, Quintili V, Tinarelli R, D'Anastasio R, Viciano J. 2016. Non-masticatory dental lesions in the Samnite necropolis of Alfedena (V–III centuries BCE; central-southern Italy). Journal of Paleopathology 26(1):15-26.

Taylor RMS. 1991. Anatomy and Biology of Tooth Dislocation and Wear in the Pre-European and Australian Aborigine: Edge-to-Edge Bites, Crowded Anteriors, and Other Dental Features: Dept. of Anatomy, University of Auckland.

Teaford MF. 1988. A review of dental microwear and diet in modern mammals. Scanning Microscopy 2(2):1149-1166.

Teaford MF. 2007. Dental microwear and paleoanthropology: cautions and possibilities. In: Bailey SE, Hublin J-J, editors. Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Dordrecht: Springer. p 345-368.

Teaford MF, Oyen OJ. 1989. In vivo and in vitro turnover in dental microwear. American Journal of Physical Anthropology 80(4):447-460.

Teaford MF, Lytle JD. 1996. Diet-induced changes in rates of human tooth microwear: A case study involving stone-ground maize. American Journal of Physical Anthropology 100(1):143-147.

Teaford MF, Larsen CS, Pastor RF, Noble VE. 2001. Pits and scratches: microscopic evidence of tooth use and masticatory behavior in La Florida. In: Larsen CS, editor. Bioarchaeology of Spanish Florida. Gainsville: University Press of Florida. p 82-112.

Temple DH. 2016. Caries: the ancient scourge. In: Irish JD, Scott GR, editors. A Companion to Dental Anthropology. Malden: John Wiley & Sons, Inc. p 433-449.

Teschler-Nicola M. 2006. Early Modern Humans at the Moravian Gate: The Mladec Caves and their Remains. Vienna: Springer Verlag.

Teyssandier N. 2008. Revolution or evolution: the emergence of the Upper Paleolithic in Europe. World Archaeology 40(4):493-519.

Thomas NG. 1921. Formation of the apices of teeth. Journal of the American Dental Association 8(1):11-17.

Thompson JL, Illerhaus B. 1998. A new reconstruction of the Le Moustier 1 skull and investigation of internal structures using 3-D-µCT data. Journal of Human Evolution 35(6):647-665.

Thorne A, Macumber P. 1972. Discoveries of Late Pleistocene man at Kow Swamp, Australia. Nature 238:316-319.

Thorne AG. 1975. Kow Swamp and Lake Mungo: Towards an Osteology of Early Man in Australia. Sydney: University of Sydney.

Tillier A, Sansilbano-Collilieux M, David F, Enloe JG, Girard M, Hardy M, D'iatchenko V, Roblin-Jouve A, Tolmie C. 2013. Les vestiges néanderthaliens provenant des niveaux moustériens I et J de la Grotte du Bison à Arcy-sur-Cure (Yonne): bilan actuel. Bulletins et Mémoires de la Société d'Anthropologie de Paris 25(1-2):39-54.

Tompkins RL. 1996. Relative dental development of Upper Pleistocene hominids compared to human population variation. American Journal of Physical Anthropology 99(1):103-118.

Torres Pérez-Hidalgo TJd, Ortiz Menéndez JE, Grün RW, Martínez García E, Santamaría Álvarez D, Rasilla Vives Mdl, Fortea Pérez FJ. 2010. Dating of the hominid (Homo Neanderthalensis) remains accumulation from el Sidron Cave (Pilona, Asturias, north Spain): an example of a multi-methodological approach to the dating of upper pleistocene sites. Archaeometry 52:680–705.

Toussaint M. 2014. The dentition of the Scladina I-4A juvenile Neandertal. In: Toussaint M, Bonjean D, editors. The Scladina I-4A Juvenile Neandertal (Andenne, Belgium): Palaeoanthropology and Context. Liège: Études et Recherches Archéologiques de Université de Liège. p 233-306.

Trinkaus E. 1978. Dental remains from the Shanidar adult Neanderthals. Journal of Human Evolution 7:369-382.

Trinkaus E. 1983. The Shanidar Neandertals. New York: Academic Press.

Trinkaus E. 1986. The Neandertals and Modern Human Origins. Annual Review of Anthropology 15(1):193-218.

Trinkaus E. 1987. The Neandertal face: evolutionary and functional perspectives on a recent hominid face. Journal of Human Evolution 16(5):429-443.

Trinkaus E. 1992. Morphological contrasts between the Near Eastern Qafzeh-Skhul and late archaic human samples: Grounds for a behavioral difference? In: Akazawa T, Aoki K, Kimura T, editors. The Evolution and Dispersal of Modern Humans in Asia. Tokyo: Hokusen-Sha Publishing Company. p 277–294.

Trinkaus E. 1995. Neanderthal mortality patterns. Journal of Archaeological Science 22(1):121-142.

Trinkaus E. 2004. Dental crown dimensions of Middle and Late Pleistocene European humans. In: Rubio S, editor. Miscalánea en Homenaje a Emiliano Aguirre. Alcalá de Henares: Museo Arqueológico Regional.

Trinkaus E. 2005. Early modern humans. Annual Review of Anthropology 34(1):207-230.

Trinkaus E. 2006a. Modern human versus Neandertal evolutionary distinctiveness. Current Anthropology 47(4):597-620.

Trinkaus E. 2006b. The upper limb remains. In: Trinkaus E, Svoboda J, editors. Early Modern Human Evolution in Central Europe: The People of Dolní Věstonice and Pavlov. Oxford: Oxford University Press. p 327-372.

Trinkaus E. 2008. Behavioral implications of the Muierii 1 early modern human scapula. Annuaire Roumain d'Anthropologie 48(2008).

Trinkaus E. 2009. The human tibia from Broken Hill, Kabwe, Zambia. PaleoAnthropology 2009:145-165.

Trinkaus E. 2011. Late Pleistocene adult mortality patterns and modern human establishment. Proceedings of the National Academy of Sciences 108(4):1267-1271.

Trinkaus E. 2013. The paleobiology of modern human emergence. In: Smith FH, Ahern JCM, editors. The Origins of Modern Humans: Biology Reconsidered. Hoboken: Wiley. p 393-434.

Trinkaus E, Churchill SE. 1988. Neandertal radial tuberosity orientation. American Journal of Physical Anthropology 75(1):15-21.

Trinkaus E, Zilhão J. 2002. Phylogenetic implications. In: Zilhão J, Trinkaus E, editors. Portrait of the Artist as a Child: The Gravettian Human Skeleton from the Abrigo do Lagar Velho and Its Archaeological Context. Lisboa: Trabalhos de Arqueologia 22. p 497-518.

Trinkaus E, Svoboda J. 2006. Early Modern Human Evolution in Central Europe: The People of Dolní Věstonice and Pavlov. Oxford: Oxford University Press.

Trinkaus E, Lebel S, Bailey SE. 2000. Middle Paleolithic and recent human dental remains from the Bau de L'Aubesier, Monieux (Vaucluse). Bulletin de la Société d'Anthropologie de Paris 12(3-4):207-226.

Trinkaus E, Maley BC, Buzhilova AP. 2008. Brief communication: Paleopathology of the Kiik-Koba 1 Neandertal. American Journal of Physical Anthropology 9999(9999):NA.

Trinkaus E, Constantin S, Zilhão J. 2013a. Life and Death at the Peştera cu Oase: A Setting for Modern Human Emergence in Europe. Oxford: Oxford University Press.

Trinkaus E, Bailey S, Rougier H. 2013b. The dental and alveolar remains of Oase 1 and 2. In: Trinkaus E, Constantin S, Zilhão J, editors. Life and Death at the Peştera cu Oase: A Setting for Modern Human Emergence in Europe. Oxford: Oxford University Press.

Trinkaus E, Bailey SE, Davis SJM, Zilhão J. 2011. Magdalenian Human Remains from the Galeria da Cisterna, (Almonda karstic system, Torres Novas, Portugal). O Arqueólogo Português Série V(1):395-413.

Trinkaus E, Buzhilova AP, Mednikova MB, Dobrovolskaya MV. 2014. The People of Sunghir: Burials, Bodies, and Behavior in the Earlier Upper Paleolithic. Oxford: Oxford University Press.

Trinkaus E, Formicola V, Svoboda J, Hillson SW, Holliday TW. 2001. Volni Vestonice 15: Pathology and persistence in the Pavolovian. Journal of Archaeological Science 28(12):1291-1308.

Trinkaus E, Marks AE, Brugal J-P, Bailey SE, Rink WJ, Richter D. 2003. Later Middle Pleistocene human remains from the Almonda Karstic system, Torres Novas, Portugal. Journal of Human Evolution 45(3):219-226.

Tryon CA, Crevecoeur I, Faith JT, Ekshtain R, Nivens J, Patterson D, Mbua EN, Spoor F. 2015. Late Pleistocene age and archaeological context for the hominin calvaria from GvJm-22 (Lukenya Hill, Kenya). Proceedings of the National Academy of Sciences.

Turner CG, Cadien JD. 1969. Dental chipping in Aleuts, Eskimos and Indians. American Journal of Physical Anthropology 31(3):303-310.

Turner CG, Machado LMC. 1983. A new dental wear pattern and evidence for high carbohydrate consumption in a Brazilian archaic skeletal population. American Journal of Physical Anthropology 61:125-130.

Turner CG, Nichol CR, Scott GR. 1991. Scoring procedures for key morphological traits of the permanent dentition: the Arizona State University dental anthropology system. In: Kelley MA, Larsen CS, editors. Advances in Dental Anthropology. New York: Wiley-Liss. p 13-31.

Turner G, Anderson T. 2003. Marked occupational dental abrasion from medieval Kent. International Journal of Osteoarchaeology 13(3):168-172.

Ubelaker DH. 1989. Human Skeletal Remains. Washington D.C.: Taraxacum.

Ungar PS. 1994. Incisor microwear of Sumatran anthropoid primates. American Journal of Physical Anthropology 94(3):339-363.

Ungar PS. 2015. Mammalian dental function and wear: a review. Biosurface and Biotribology 1(1):25-41.

Ungar PS, Grine FE. 1991. Incisor size and wear in *Australopithecus africanus* and *Paranthropus robustus*. Journal of Human Evolution 20(4):313-340.

Ungar PS, Spencer MA. 1999. Incisor microwear, diet, and tooth use in three Amerindian populations. American Journal of Physical Anthropology 109(3):387-396.

Ungar PS, Sorrentino J, Rose JC. 2012. Evolution of human teeth and jaws: Implications for dentistry and orthodontics. Evolutionary Anthropology: Issues, News, and Reviews 21(3):94-95.

Ungar PS, Teaford MF, Glander KE, Pastor RF. 1995. Dust accumulation in the canopy: A potential cause of dental microwear in primates. American Journal of Physical Anthropology 97(2):93-99.

Ungar PS, Fennell KJ, Gordon K, Trinkaus E. 1997. Neandertal incisor beveling. Journal of Human Evolution 32(5):407-421.

Ungar PS, Grine FE, Teaford MF, Pérez-Pérez A. 2001. A review of interproximal wear grooves on fossil hominin teeth with new evidence from Olduvai Gorge. Archives of Oral Biology 46:285-292.

Ungar PS, Scott RS, Scott JR, Teaford M. 2008. Dental microwear analysis: historical perspectives and new approaches. In: Irish JD, Nelson GC, editors. Technique and application in dental anthropology. Cambridge: Cambridge University Press. p 389-425.

Uomini NT. 2008. In the knapper’s hands: identifying handedness from lithic production and use. In: Longo L, Skakun N, editors. "Prehistoric Technology’’ 40 Years Later: Functional Studies and the Russian Legacy. Oxford: B.A.R. International Series. p 51-62.

Uomini NT. 2011. Handedness in Neanderthals. In: Conard NJ, Richter J, editors. Neanderthal Lifeways, Subsistence and Technology: One Hundred Fifty Years of Neanderthal Study. New York: Springer. p 139-158.

Vacca E, Coppola D. 1993. The Upper Paleolithic burials at the cave of Santa Maria de Agnano (Ostuni, Brindisi): preliminary report. Rivista di Antropologia 71:275-284.

Valladas H, Geneste J-M, Joron J, Chadelle J. 1986. Thermoluminescence dating of Le Moustier (Dordogne, France).

Valladas H, Reyss JL, Joron JL, Valladas G, Bar-Yosef O, Vandermeersch B. 1988. Thermoluminescence dating of Mousterian Proto-Cro-Magnon' remains from Israel and the origin of modern man. Nature 331(6157):614-616.

Valladas H, Mercier N, Froget L, Hovers E, Joron J-L, Kimbel WH, Rak Y. 1999. TL dates for the Neanderthal site of the Amud Cave, Israel. Journal of Archaeological Science 26(3):259-268.

Valladas H, Joron J-L, Valladas G, Arensburg B, Bar-Yosef O, Belfer-Cohen A, Goldberg P, Laville H, Meignen L, Rak Y. 1987. Thermoluminescence dates for the Neanderthal burial site at Kebara in Israel.

Vallois HV, de Félice S. 1977. Les Mésolithiques de France. Archives de l'Institut de Paléontologie Humaine 37. Paris: Masson.

Vandermeersch B. 1981. Les Hommes Fossiles de Qafzeh (Israël). Paris: C.N.R.S.

Varrela J. 1990. Effects of attritive diet on craniofacial morphology: a cephalometric analysis of a Finnish skull sample. The European Journal of Orthodontics 12(2):219-223.

Varrela T, Paunio K, Wouters F, Tiekso J, Söder P-Ö. 1995. The relation between tooth eruption and alveolar crest height in a human skeletal sample. Archives of Oral Biology 40(3):175-180.

Varrela T, Paunio K, Wouters F, Söder P, Tiekso J, Möllerström A. 1989. Alveolar crest level in a population with advanced dental attrition. J Dent Res 68:954.

Velemínská J, Brůžek J. 2008. Early Modern Humans from Předmostí: A New Reading of Old Documentation. Prague: Academia.

Vercellotti G, Alciati G, Richards MP, Formicola V. 2008. The Late Upper Paleolithic skeleton Villabruna 1 (Italy): a source of data on biology and behavior of a 14.000 year-old hunter. Journal of Anthropological Sciences 86:143-163.

Vidal Encinas JM, Prada Marcos ME, Fernández Rodríguez C, Fuertes Prieto MN. 2010. Los hombres Mesolíticos de la cueva de la Braña-Arintero (Valdelugueros, León): el hallazgo, situación, aspectos arqueo-anthropológicos, cronología y contexto cultural. In: Vidal Encinas JM, Prada Marcos ME, editors. Los Hombres Mesolíticos de la Cueva de la Braña-Arintero (Valdelugueros, León). León: Junta de Castilla y León. p 16-61.

Vierin S. 2012. Revisione dei Reperti Umani Provenienti dal Sito Epigravettiano e Mesolitico 'Riparo Fredian', Molazzana, (LU). Firenze: Universita' Degli Studi di Firenze.

Villa G, Giacobini G. 1995a. Subvertical grooves of interproximal facets in neandertal posterior teeth. American Journal of Physical Anthropology 96(1):51-62.

Villa G, Giacobini G. 1995b. Interproximal wear of Neandertal posterior teeth. Characteristics of subvertical grooves. Aspects of Dental Biology: Paleontology, Anthropology and Evolution Int Inst for the Study of Man, Firenze:177-182.

Villa P, Roebroeks W. 2014. Neandertal demise: an archaeological analysis of the modern human superiority complex. PLoS ONE 9(4):e96424.

Villmoare B, Kuykendall K, Rae T, Brimacombe C. 2013. Continuous dental eruption identifies Sts 5 as the developmentally oldest fossil hominin and informs the taxonomy of *Australopithecus africanus*. Journal of Human Evolution 65(6):798-805.

Villotte S, Prada Marcos ME. 2010. Marcadores ocupacionales en los hombres Mesolíticos de la Braña-Arintero. In: Vidal Encinas JM, Prada Marcos ME, editors. Los Hombres Mesolíticos de la Cueva de la Braña-Arintero (Valdelugueros, León). León: Junta de Castilla y León. p 120-128.

Villotte S, Knüsel CJ. 2014. “I sing of arms and of a man…”: medial epicondylosis and the sexual division of labour in prehistoric Europe. Journal of Archaeological Science 43:168-174.

Villotte S, Churchill SE, Dutour OJ, Henry-Gambier D. 2010. Subsistence activities and the sexual division of labor in the European Upper Paleolithic and Mesolithic: Evidence from upper limb enthesopathies. Journal of Human Evolution 59(1):35-43.

Villotte S, Chiotti L, Nespoulet R, Henry-Gambier D. 2015. Étude anthropologique des vestiges humains récemment découverts issus de la couche 2 de l’abri Pataud (Les Eyzies-de-Tayac-Sireuil, Dordogne, France). BMSAP 27(3-4):158-188.

Vlček E. 1993. Fossile Menschenfunde von Weimar-Ehringsdorf. Stuttgart: Konrad Theiss Verlag.

Vogel ER, van Woerden JT, Lucas PW, Atmoko SSU, van Schaik CP, Dominy NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: Pan troglodytes schweinfurthii and Pongo pygmaeus wurmbii. Journal of Human Evolution 55(1):60-74.

Voisin J-L, Condemi S, Wolpoff MH, Frayer DW. 2012. A new online database (http://anthropologicaldata.free.fr) and a short reflection about the productive use of compiling internet data. PaleoAnthropology doi:10.4207/PA.2012.ART76:241-244.

Volpato V, Macchiarelli R, Guatelli-Steinberg D, Fiore I, Bondioli L, Frayer DW. 2012. Hand to mouth in a Neandertal: right-handedness in Regourdou 1. PLoS ONE 7(8):e43949.

von Bonin G. 1935. The Magdalenian skeleton from Cap-Blanc in the Field Museum of Natural History: University.

Wagner GA, Maul LC, Löscher M, Schreiber HD. 2011. Mauer – the type site of *Homo heidelbergensis*: palaeoenvironment and age. Quaternary Science Reviews 30(11):1464-1473.

Walker A, Hoeck HN, Perez L. 1978. Microwear of mammalian teeth as an indicator of diet. Science 201(4359):908-910.

Walker MJ, Gibert J, Lopez MV, Lombardi AV, Perez-Perez A, Zapata J, Ortega J, Higham T, Pike A, Schwenninger JL et al. . 2008. Late Neandertals in Southeastern Iberia: Sima de las Palomas del Cabezo Gordo, Murcia, Spain. Proceedings of the National Academy of Sciences of the United States of America 105(52):20631-20636.

Walker PL. 1976. Wear striations on the incisors of ceropithecid monkeys as an index of diet and habitat preference. American Journal of Physical Anthropology 45(2):299-307.

Wallace JA. 1975. Did La Ferrassie I use his teeth as a tool? Current Anthropology 16(3):393.

Wang Q, Wright BW, Smith A, Chalk J, Byron CD. 2010. Mechanical impact of incisor loading on the primate midfacial skeleton and its relevance to human evolution. The Anatomical Record 293(4):607-617.

Watanabe E, Demirjian A, Buschang PH. 1998. Longitudinal posteruptive mandibular tooth movements of males and females. Journal of Dental Research 77:3054.

Waters-Rist A, Bazaliiskii VI, Weber AW, Goriunova OI, Katzenberg MA. 2010. Activity-induced dental modification in Holocene Siberian hunter-fisher-gatherers. American Journal of Physical Anthropology 143(2):266-278.

Weaver TD. 2009. The meaning of Neandertal skeletal morphology. Proceedings of the National Academy of Sciences 106(38):16028-16033.

Weaver TD, Roseman CC, Stringer CB. 2007. Were neandertal and modern human cranial differences produced by natural selection or genetic drift? Journal of Human Evolution 53(2):135-145.

Webb SG, Edwards PC. 2002. The Natufian human skeletal remains from Wadi Hammeh 27 (Jordan). Paléorient 28(1):103-123.

Weidenreich F. 1945. The paleolithic child from the Teshik-Tash Cave in Southern Uzbekistan (Central Asia). American Journal of Physical Anthropology 3(2):151-163.

Wendorf F. 1968. Site 117: a Nubian final paleolithic graveyard near Jebel Sahaba, Sudan. In: Wendorf F, editor. The Prehistory of Nubia: Volume II. Dallas Southern Methodist University. p 954-995.

Wendorf F, Schild R, Close A. 1986. The Prehistory of Wadi Kubbaniya, v. 1, The Wadi Kubbaniya Skeleton: A Late Paleolithic Burial from Southern Egypt. Southern Methodist University Press Dallas.

White LA. 1959. The Evolution of Culture. New York: McGraw-Hill.

White M, Pettitt P. 2012. Ancient digs and modern myths: the age and context of the Kent's Cavern 4 maxilla and the earliest *Homo sapiens* specimens in Europe. European Journal of Archaeology 15(3):392-420.

Whittaker DK, Parker JH, Jenkins C. 1982. Tooth attrition and continuing eruption in a Romano-British population. Archives of Oral Biology 27:405-409.

Whittaker DK, Molleson T, Daniel AT, Williams JT, Rose P, Resteghini R. 1985. Quantitative assessment of tooth wear, alveolar-crest height and continuing eruption in a Romano-British population. Archives of Oral Biology 30(6):493-501.

Whittaker DK, Griffiths S, Robson A, Roger-Davies P, Thomas G, Molleson T. 1990. Continuing tooth eruption and alveolar crest height in an eighteenth-century population from Spitalfields, East London. Archives of Oral Biology 35(2):81-85.

Wild EM, Teschler-Nicola M, Kutschera W, Steier P, Trinkaus E, Wanek W. 2005. Direct dating of Early Upper Palaeolithic human remains from Mladec. Nature 435(7040):332-335.

Willman JC. 2014. Dental fluctuating asymmetry among early modern humans and Neandertals. Abstracts of the PaleoAnthropology Society Meetings 2014:A29.

Willman JC. 2016. Dental wear at Dolní Věstonice II: Habitual behaviors and social identities written on teeth. In: Svoboda J, editor. Dolní Věstonice II: Chronostratigraphy, Paleoethnology, Paleoanthropology Dolní Věstonice Studies 21. Brno: Archeologický ústav AV ČR. p 353-371.

Willman JC. 2017. The dental remains: non-masticatory wear In: Trinkaus E, Walker MJ, editors. The People of Palomas: Neandertals from the Sima de las Palomas, Cabezo Gordo, Southeastern Spain. College Station: Texas A&M University Press.

Willman JC, Shackelford L, Demeter F. 2016. Incisor ablation among the Late Upper Paleolithic people of Tam Hang (Northern Laos): Social identity, mortuary practice, and oral health. American Journal of Physical Anthropology 160(3):519-528.

Willman JC, Maki J, Bayle P, Trinkaus E, Zilhão J. 2012. Middle Paleolithic human remains from the Gruta da Oliveira (Torres Novas), Portugal. American Journal of Physical Anthropology 149(1):39-51.

Withnell CB, Ungar PS. 2014. A preliminary analysis of dental microwear as a proxy for diet and habitat in shrews. Mammalia 78(3):409-415.

Wobst HM. 1978. The archaeo-ethnology of hunter-gatherers or the tyranny of the ethnographic record in archaeology. American Antiquity 43(2):303-309.

Wolpoff MH. 1969. The effect of mutations under conditions of reduced selection. Social biology 16(1):11-23.

Wolpoff MH. 1971a. Metric Trends in Hominid Dental Evolution. Cleveland: Case Western Reserve University Studies in Anthropology.

Wolpoff MH. 1971b. Interstitial wear. American Journal of Physical Anthropology 34(2):205-227.

Wolpoff MH. 1975. Dental reduction and the probable mutation effect. American Journal of Physical Anthropology 43(2):307-308.

Wolpoff MH. 1979. The Krapina dental remains. American Journal of Physical Anthropology 50:67-113.

Wood B. 2013. Palaeontology: Gritting their teeth. Nature 493(7433):486-487.

Wood RE, Barroso-Ruíz C, Caparrós M, Jordá Pardo JF, Galván Santos B, Higham TFG. 2013a. Radiocarbon dating casts doubt on the late chronology of the Middle to Upper Palaeolithic transition in southern Iberia. Proceedings of the National Academy of Sciences 110(8):2781-2786.

Wood RE, Higham TFG, De Torres T, Tisnérat-Laborde N, Valladas H, Ortiz JE, Lalueza-Fox C, Sánchez-Moral S, Cañaveras JC, Rosas A. 2013b. A new date for the neanderthals from El Sidrón cave (Asturias, Northern Spain). Archaeometry 55(1):148-158.

Woodburn J, Hudson S. 1966. The Hadza: The Food Quest of a Hunting and Gathering Tribe of Tanzania (16 mm. film). London: London School of Economics.

Woodburn JC. 1970. Hunters and Gatherers: The Material Culture of the Nomadic Hadza. London: British Museum London.

Wroe S, Ferrara TL, McHenry CR, Curnoe D, Chamoli U. 2010. The craniomandibular mechanics of being human. Proceedings of the Royal Society B: Biological Sciences:rspb20100509.

Wu R. 1982. Paleoanthropology in China, 1949–1979. Current Anthropology 23:473–477.

Wu X, Poirier FE. 1995. Human Evolution in China. A Metric Description of the Fossils and a Review of the Sites. Oxford: Oxford University Press.

Xia J, Zheng J, Huang D, Tian ZR, Chen L, Zhou Z, Ungar PS, Qian L. 2015. New model to explain tooth wear with implications for microwear formation and diet reconstruction. PNAS 112(34):10669–10672.

Xing S, Martinón-Torres M, Bermúdez de Castro JM, Zhang Y, Fan X, Zheng L, Huang W, Liu W. 2014. Middle Pleistocene hominin teeth from Longtan Cave, Hexian, China. PLoS ONE 9(12):e114265.

Yokoyama Y. 1987. Datation absolue du site de Genay en Bourgogne, France, par les méthodes 230Th/234U et 231Pa/235U, utilisant la spectrométrie gamma. L'Anthropologie 91(1):109-112.

Zanolli C, Mazurier A. 2013. Endostructural characterization of the *H. heidelbergensis* dental remains from the early Middle Pleistocene site of Tighenif, Algeria. Comptes Rendus Palevol 12(5):293-304.

Zanolli C, Bayle P, Macchiarelli R. 2010. Tissue proportions and enamel thickness distribution in the early Middle Pleistocene human deciduous molars from Tighenif, Algeria. Comptes Rendus Palevol 9(6-7):341-348.

Zapata J, Bayle P, Lombardi AV, Pérez-Pérez A, Trinkaus E. 2017. The Palomas dental remains: preservation, wear and morphology In: Trinkaus E, Walker MJ, editors. The People of Palomas: Neandertals from the Sima de las Palomas, Cabezo Gordo, Southeastern Spain. College Station: Texas A&M University Press.

Zhou J, Zhao Y, Xia C, Jiang L. 2012. Periodontitis with hypercementosis: report of a case and discussion of possible aetiologic factors. Australian Dental Journal 57(4):511-514.

Zhou Z, Zheng J. 2006. Oral tribology. Proceedings of the Institution of Mechanical Engineers, Part J: Journal of Engineering Tribology 220(8):739-754.

Zilhão J. 2014. The Upper Palaeolithic of Europe. In: Renfrew C, Bahn P, editors. The Cambridge World Prehistory. Cambridge: Cambridge University Press. p 1753-1785.

Ziscovici C, Lucas PW, Constantino PJ, Bromage TG, van Casteren A. 2014. Sea otter dental enamel is highly resistant to chipping due to its microstructure.

Zuckerman MK, Armelagos GJ. 2011. The origins of biocultural dimensions in bioarchaeology. In: Agarwal SC, Glencross BA, editors. Social Bioarchaeology. Malden: Wiley-Blackwell. p 15-43.

Zum Gahr K-H. 1987. Microstructure and wear of materials: Elsevier.

Appendix

Appendix Table 1. Tooth associations by Sima de los Huesos individual used in analyses.

Specimen	LI^1	LI^2	LC^1	RI^1	RI^2	RC^1	LI$_1$	LI$_2$	LC$_1$	RI$_1$	RI$_2$	RC$_1$
SH I	AT-3194	AT-1754		AT-3193	AT-283		AT-1460	AT-1464	AT-276	AT-609	AT-275	AT-60
SH II	AT-27	AT-2279		AT-42			AT-1472	AT-597	AT-578	AT-162	AT-55	AT-2
SH III							AT-104	AT-103	AT-67		AT-1726	AT-1952
SH V	AT-2765	AT-3257				AT-2759						
SH VII	AT-554		AT-163	AT-553		AT-144	AT-555	AT-195	AT-145	AT-1469	AT-5	AT-591
SH X												AT-1951
SH XI								AT-167[a]	AT-161		AT-723[a]	
SH XII	AT-560[b]	AT-53[a]									AT-300	AT-300
SH XV							AT-1762	AT-1753	AT-1755		AT-1461	AT-2394
SH XVI	AT-2752	AT-2772	AT-2392	AT-2786	AT-2769		AT-3252		AT-2778		AT-3256	AT-2784
SH XVIII	AT-1143	AT-1124	AT-2151	AT-2395	AT-2280	AT-2207	AT-2390	AT-2066	AT-410	AT-2195	AT-957	AT-2165
SH XX	AT-953	AT-820	AT-955	AT-954	AT-962	AT-558	AT-2730		AT-808		AT-1123	AT-2783
SH XXI	AT-2773					AT-3192	AT-3258	AT-3251				
SH XXII		AT-961[a]			AT-3195	AT-3191	AT-3199	AT-3198		AT-3250	AT-2753	AT-2766
SH XXIII								AT-607	AT-607	AT-595	AT-594	AT-593
SH XXIV						AT-2388		AT-2391	AT-2438	AT-596	AT-281	
SH XXV							AT-3882	AT-3937	AT-3938	AT-3883	AT-3884	AT-3886
SH XXVII			AT-3075			AT-3255						
SH XXVIII[c]	AT-165	AT-3196	AT-818	AT-814		AT-219	AT-2775	AT-2776[d]	AT-2762	AT-3253		
Not assigned	AT-198			AT-199								
Not assigned				AT-54								
Not assigned	AT-1958											
Not assigned	AT-280											

Appendix Table 1. Continued

Specimen	LI^1	LI^2	LC^1	RI^1	RI^2	RC^1	LI$_1$	LI$_2$	LC$_1$	RI$_1$	RI$_2$	RC$_1$
Not assigned	AT-1943											
Not assigned	AT-3885											
Not assigned	AT-8											
Not assigned					AT-29							
Not assigned					AT-2274							
Not assigned					AT-1844							
Not assigned					AT-1444							
Not assigned		AT-1953			AT-1962							
Not assigned		AT-7										
Not assigned						AT-44						
Not assigned						AT-1475						
Not assigned						AT-1758						
Not assigned			AT-958									
Not assigned			AT-1757									
Not assigned			AT-6									
Not assigned			AT-1942									
Not assigned										AT-2397		
Not assigned										AT-956		
Not assigned							AT-1474			AT-166		
Not assigned							AT-3241			AT-4		
Not assigned							AT-3242			AT-2384		
Not assigned											AT-592	
Not assigned								AT-608			AT-282	
Not assigned								AT-2278				
Not assigned												AT-1960

Appendix Table 1. Continued

Specimen	LI^1	LI^2	LC^1	RI^1	RI^2	RC^1	LI$_1$	LI$_2$	LC$_1$	RI$_1$	RI$_2$	RC$_1$
Not assigned												AT-1144
Not assigned									AT-567			
Not assigned									AT-164			
Not assigned	AT-126[e]											

[a] Previously “not assigned” to an individual (Lozano 2005; Lozano et al. 2008). New assignment based on Martinón-Torres et al. (2012).

[b] Previously “not assigned” to an individual (Lozano 2005; Lozano et al. 2008). New assignment based on Martinón-Torres et al. (2012). No data on cutmarks but there is an antemortem enamel chip.

[c] Previously referred to as SH XXXI (Lozano 2005; Lozano et al. 2008), but now referred to as SH XXVIII following Martinón-Torres et al. (2012).

[d] Previously assigned to SH XXVII (Lozano 2005; Lozano et al. 2008), but now assigned to as SH XXVIII following Martinón-Torres et al. (2012).

[e] This tooth appears in Lozano (2005) where it is listed as having an antemortem chip on the labial-occlusal edge. However, the tooth is not listed in Lozano et al. (2008) or the supplement in Martinón-Torres et al. (2012). The absence of this tooth in the latter publications was cause for excluding it from analyses here.

Appendix Table 2. Sources of buccolingual metrics and macrowear for each fossil used in macrowear gradient analyses.

Geographic Area	Site	Buccolingual Metrics	Macrowear	Notes
Late Early Pleistocene to Middle Pleistocene				
Africa – Morocco	Rabat (Thomas Quarry)	Original fossils	Original fossils	
Africa – Zambia	Broken Hill	Original fossils	Original fossils	
East Asia – China	Chaoxian	(He 2000)	(He 2000)	
East Asia – China	Jinnushan	(He 2000)	(He 2000)	
Europe – Germany	Mauer	E. Trinkaus	High-resolution casts (A. Pérez-Pérez)	
Europe – Italy	Fontana Ranuccio	(Rubini et al. 2014)	(Rubini et al. 2014)	FR1R, FR1L, and FR2 are considered the same individual.
Europe – Spain	Atapuerca – Gran Dolina	(Bermúdez de Castro et al. 1999)	(Bermúdez de Castro et al. 1999)	
Europe – Spain	Atapuerca – Sima del los Huesos	(Martinón-Torres et al. 2012)	(Martinón-Torres et al. 2012)*	*Molnar (1971) scores which were assumed to be equivalent to Smith (1984)
Earlier Neandertals (MIS 7-5)				
Europe – Belgium	Scladina	(Toussaint 2014)	(Toussaint 2014)*	* Line drawings, photographs, and description.
Europe – Croatia	Krapina	(Wolpoff 1979)	High-resolution casts (E. Trinkaus)	
Europe – France	Biache-Saint-Vaast	(Rougier 2003)	(Rougier 2003)*	*Line drawings, photographs, and description.
Europe – France	La Chaise (Abri Bourgeois-Delaunay)	(Condemi 2001)	(Condemi 2001)*	*Line drawings and photographs
Europe – France	Montgaudier	(Mann and Vandermeersch 1997)	(Mann and Vandermeersch 1997)*	*Line drawings, photographs, and description.
Europe – Germany	Erhingsdorf	(Vlček 1993)	Original fossils	
Europe – Italy	Fate	(de Lumley and Giacobini 2013b)	(de Lumley and Giacobini 2013b)*	*Photographs
Europe – Italy	Saccopastore	(Condemi 1992)	(Condemi 1992)*, high-resolution casts (E. Trinkaus)	*Photographs

Appendix Table 2. Continued

Geographic Area	Site	Buccolingual Metrics	Macrowear	Notes
Earlier Neandertals (MIS 7-5) Continued				
Europe – United Kingdom	Pontnewydd	(Compton and Stringer 2012)	(Compton and Stringer 2012)	*Photographs, and description.
West Asia – Israel	Tabun C2	E. Trinkaus	High-resolution casts and photos (E. Trinkaus)	
West Asia – Israel	Tabun C1	Original fossils	Original fossils	
West Asia – Israel	Tabun B-series	E. Trinkaus	High-resolution casts and photos (E. Trinkaus)	
West Asia – Israel	Tabun BC7	(Coppa et al. 2005)	(Coppa et al. 2005)*	*Photographs
Later Neandertals (MIS 4-3)				
Europe – Belgium	Goyet	Original fossils	Original fossils	
Europe – Belgium	Spy	Original fossils	Original fossils	
Europe – Croatia	Vindija	Original fossils	Original fossils	
Europe – Czech Republic	Kůlna	Original fossils	Original fossils	
Europe – Czech Republic	Švédův stůl	Original fossils	Original fossils	
Europe – France	Arcy-sur-Cure (Grotte du Bison)	(David et al. 2009; Tillier et al. 2013)	(David et al. 2009; Tillier et al. 2013)*	*Photographs and description
Europe – France	Arcy-sur-Cure (Grotte de l'Hyène)	(E. Trinkaus)	Color photographs and high-resolutioncasts (E. Trinkaus); (Leroi-Gourhan 1958)*	*Line drawings
Europe – France	La Ferrassie	High-resolution epoxy-resin casts (E. Trinkaus);	Color photographs and high-resolution casts (E. Trinkaus);	
Europe – France	Hortus	(de Lumley 1973)	(de Lumley 1973)*	*Photographs and line drawings
Europe – France	Genay	(de Lumley 1987)	(de Lumley 1987)*	*Photographs
Europe – France	Monsempron	Original fossils	Original fossils	
Europe – France	Le Moustier	Original fossils	Original fossils	
Europe – France	Petit-Puymoyen	Original fossils	Original fossils	
Europe – France	Les Pradelles (Marillac)	(Mussini 2011)*	(Mussini 2011)**	*Literature (RP^3-M^3) and published photographs (RC^1). Measurement of the canine was attained using scaled photograph (Mussini 2011:137) and tpsDig (Rohlf 2006). An average of measurements taken in occlusal (10.0

				mm), mesial (9.8 mm), and distal (9.8 mm) view is the value used in this analysis. **Occlusal photographs and descriptions. Wear translated to Smith (1984) scores from Murphy (1959b) and Molnar (1971) scores.

Appendix Table 2. Continued

Geographic Area	Site	Buccolingual Metrics	Macrowear	Notes
Later Neandertals (MIS 4-3) Continued				
Europe – France	La Quina	E. Trinkaus	High-resolution casts and research grade casts (E. Trinkaus)	
Europe – France	Regourdou	(Maureille et al. 2001)	High-resolution casts and research grade casts (E. Trinkaus)	
Europe – France	Saint-Césaire	E. Trinkaus	High-resolution casts (A. Pérez-Pérez), photographs (E. Trinkaus)	
Europe – Germany	Neandertal	Original fossils	Original fossils	
Europe – Hungary	Subalyuk	(Pap et al. 1996)	Research grade cast (E. Trinkaus); (Pap et al. 1996)*	*Photographs
Europe – Italy	Guattari	(Mallegni 1995)	High resolution casts (E. Trinkaus; (Mallegni 1995)*	*Photographs
Europe – Spain	Banyoles	(de Lumley 1973)	(de Lumley 1973; Alcázar de Velasco et al. 2011)*	*Photographs and line drawings
Europe – Spain	Cova Foradá	(Campillo et al. 2002; Lozano et al. 2013)	High-resolution casts (A. Pérez-Pérez); (Campillo et al. 2002; Lozano et al. 2013)*	*Photographs
Europe – Spain	Sima de las Palomas	Original fossils	Original fossils	
Europe – Spain	Valdegoba	(Quam et al. 2001)	(Quam et al. 2001)*	*Photographs and description
Europe – Spain	Zafarraya	E. Trinkaus	high-resolution casts (A. Pérez-Pérez), research grade cast E. Trinkaus	(Barroso-Ruız et al. 2003)
Europe – United Kingdom	La Cotte de Saint Brelade	(Stringer and Currant 1986)	(Stringer and Currant 1986)*	*Photographs
West Asia – Iraq	Shanidar	(Trinkaus 1983)	Photographs and high-resolution casts (E. Trinkaus)	

Appendix Table 2. Continued

Geographic Area	Site	Buccolingual Metrics	Macrowear	Notes
Later Neandertals (MIS 4-3) Continued				
West Asia – Israel	Amud	Original fossils	Original fossils	
West Asia – Israel	Kebara	Original fossils	Original fossils	
West Asia – Republic of Georgia	Sakijia	No data	(Moncel et al. 2015)*	*Photographs
West Asia – Uzbekistan	Teshik-Tash	(Wolpoff 1971a)	(Schwartz and Tattersall 2002)*	*Photographs
Middle Paleolithic Modern Humans				
West Asia - Israel	Skhul	E. Trinkaus	High-resolution casts (E. Trinkaus)	
West Asia - Israel	Qafzeh	E. Trinkaus; original fossils	Original fossils; high-resolution casts (E. Trinkaus)	
North African Aterian/South African Middle Stone Age				
Africa – Morocco	Dar es Soltane II	(Hublin et al. 2012)	(Hublin et al. 2012)*	*Photographs
Africa – Morocco	Grotte des Contrebandiers	(Hublin et al. 2012)	(Hublin et al. 2012)*	*Photographs
Early Upper Paleolithic				
Africa – Democratic Republic of Congo	Ishango	Original fossils	Original fossils	
Africa – Egypt	Nazlet Khater	Original fossils	Original fossils	
Africa – Egypt	Wadi Kubbaniya	No data	(Angel and Kelley 1986)*	*Photographs
East Asia – China	Liujiang	F. Demeter*	Photographs**	*Personal communication **Photograph (http://www.chinapage.com/archeology/Liujiang.htm)
East Asia – China	Tianyuan 1	(Shang and Trinkaus 2010)*	(Shang and Trinkaus 2010)* and research grade cast**	*Photographs **provided by E. Trinkaus
East Asia – China	Zhoukoudian Upper Cave	E. Trinkaus	(Kaifu 2000b)	
Europe – Austria	Miesslingtal 1	Original fossils	Original fossils	
Europe – Czech Republic	Brno II (Francouzská)	Original fossils	Original fossils	

Appendix Table 2. Continued

Geographic Area	Site	Buccolingual Metrics	Macrowear	Notes
Early Upper Paleolithic Continued				
Europe – Czech Republic	Brno III	(Matiegka 1929)	(Matiegka 1929; Kaifu 2000b)*	*Photographs, descriptions, and published wear scores
Europe – Czech Republic	Dolní Věstonice 3, 13, 14, 15, & 16	Original fossils	Original fossils	
Europe – Czech Republic	Mladeč 8 & 9	Original fossils	Original fossils	
Europe – Czech Republic	Pavlov 1 & 3	Original fossils	Original fossils	
Europe – Czech Republic	Předmostí 1, 3, 4, 7, 9, 10, 14, & 18	(Matiegka 1934)	(Velemínská and Brůžek 2008)*	*Photographs
Europe – France	Abri Pataud	(Legoux 1975; Villotte et al. 2015)	(Legoux 1975; Villotte et al. 2015)*	*Photographs and wear scores
Europe – France	Les Rois	(Ramirez Rozzi et al. 2009)	Original fossils	
Europe – Italy	Arene Candide IP	High-resolution cast (A. Pérez-Pérez)	High-resolution cast (A. Pérez-Pérez)	
Europe – Italy	Barma Grande 2-4	Original fossils	Original fossils	
Europe – Italy	Ostuni 1	Original fossils	Original fossils	
Europe – Romania	Muierii 1	Original fossils; (Doboş et al. 2010)*	Original fossils; (Doboş et al. 2010)*	*Published measurements and photographs used for right M_1-M_2 only.
Europe – Russia	Kostenki 14 (Markina Gora)	E. Trinkaus	(Haeussler 1995; Haeussler 1996)*	*Photographs and descriptions
Europe – Russia	Sunghir 1, 2, & 3	(Trinkaus et al. 2014)	(Trinkaus et al. 2014)	
Europe – United Kingdom	Kent's Cavern KC4	(Higham et al. 2011)	Original fossils	
Southeast Asia – Indonesia	Wajak	Original fossils	Original fossils	
Southeast Asia – Laos	Tam Pa Ling 1	(Demeter et al. 2012)	Photograph (D. Demeter)	
West Asia – Israel	Nahal Ein Gev	Original fossils	Original fossils	
Late Upper Paleolithic				
Africa – Algeria	Afalou Bou Rhummel	(Voisin et al. 2012)	Original fossils	
Africa – Morocco	Taforalt	(Voisin et al. 2012)	Original fossils	
Africa – Sudan	Jebel Sahaba	No data	Original fossils	

Appendix Table 2. Continued

Geographic Area	Site	Buccolingual Metrics	Macrowear	Notes
Late Upper Paleolithic Continued				
East Asia – Japan	Minatogawa	(Hanihara and Ueda 1982)	(Hanihara and Ueda 1982; Kaifu et al. 2011)*	*Photographs
Europe – Czech Republic	Koněprusy (Zlatý Kůň)	(Voisin et al. 2012)	Original fossils	
Europe – France	Bruniquel (Abri Lafaye)	(Genet-Varcin and Miquel 1967)	(Genet-Varcin and Miquel 1967)*	*Photographs and descriptions
Europe – France	Cap Blanc	(Frayer 1978)	(von Bonin 1935; Dahlberg and Carbonell 1961)*	*Photographs and descriptions
Europe – France	Farincourt	Oringinal fossils	Original fossils	
Europe – France	Lafaye	Original fossils	Original fossils	
Europe – France	Laugerie-Basse	B. H. Smith*	B. H. Smith*	*personal communication
Europe – France	Roc-de-Cave	(Bresson 2000)	(Bresson 2000)	
Europe – France	Rocher de la Peine	Original fossils	Original fossils	
Europe – France	Rond-du-Barry 8	High-resolution cast (A. Pérez-Pérez)	High-resolution cast (A. Pérez-Pérez)	
Europe – France	Saint-Germaine-la-Rivière	(Blanchard et al. 1972)	(Blanchard et al. 1972)*	*Photographs
Europe – Germany	Bonn-Obercassel	Original fossils	Original fossils	
Europe – Germany	Brillenhöhle	Original fossils	Original fossils	
Europe – Italy	Arene Candide	(Frayer 1978)	(Paoli et al. 1980)*	*Photographs
Europe – Italy	Maritza	Original fossils	Original fossils	
Europe – Italy	Ortucchio	Original fossils	Original fossils	
Europe – Italy	La Punta	Original fossils	Original fossils	
Europe – Italy	Riparo Fredian	Original fossils	Original fossils	
Europe – Italy	Romanelli	Original fossils	Original fossils	
Europe – Italy	Romito	(Fabbri and Mallegni 1988)	(Fabbri and Mallegni 1988)*	*Molnar (1971) scores which were assumed to be equivalent to Smith (1984)
Europe – Italy	San Teodoro	(Fabbri 1995)	(Fabbri 1995)	*Molnar (1971) scores which were assumed to be equivalent to Smith (1984)
Europe – Italy	Villabruna	(Alciati et al. 1993)	(Alciati et al. 1993)	
Europe – Romania	Climente II	Original fossils	Original fossils	
Europe – Spain	Balma Guilanyà	(Lalueza-Fox 1996)	(Lalueza-Fox 1996)	
Europe – Spain	El-Miron	(Carretero et al. 2015)	(Carretero et al. 2015; Sarchet 2015)*	*Photographs, wear score for LC_1 from photo in Sarchet 2015

Appendix Table 2. Continued

Geographic Area	Site	Buccolingual Metrics	Macrowear	Notes
Late Upper Paleolithic Continued				
Europe – Spain	Nerja	(Lalueza-Fox 1995)	(Lalueza-Fox 1995)	
Europe – Switzerland	Le Bichon	Original fossils	Original fossils	
Europe – United Kingdom	Gough's Cave	Original fossils	Original fossils	
Southeast Australia	Cohuna	P. Brown*	(Macintosh 1952b)**	*Personal communication; **Photographs and line drawings
Southeast Australia	Coobool Creek	(Brown 1989)	P. Brown*	*Line drawings provided via personal communication
Southeast Australia	Kow Swamp	P. Brown*; (Thorne and Macumber 1972; Thorne 1975)	(Thorne and Macumber 1972; Thorne 1975)**	*Kow Swamp 2 and 15; **photographs
Southeast Australia	Talgai	P. Brown*	(Smith 1918; Hellman 1934; Macintosh 1952a)*	*Photographs and line drawings
Southeast Asia – Indonesia	Liang Lemdubu	(Bulbeck 2006)	(Bulbeck 2006; Bulbeck and O'Connor 2011)*	*Photographs, line drawings, and description
Southeast Asia – Laos	Tam Hang	Original fossils	Original fossils	
Southeast Asia – Malaysia	Perak Man (Gua Gunung Ruhtuh)	(Sai 2004)	(Matsumura and Zuraina 1995; Matsumura and Zuraina 2005)*	*Photographs and description
Southeast Asia – Papua New Guinea	Watinglo	(Bulbeck and O'Connor 2011)	(Bulbeck and O'Connor 2011)	
Southeast Asia – Vietnam	Hang Cho	(Matsumura et al. 2008)	(Matsumura et al. 2008)	
West Asia – Israel	Ein Mallaha (Eynan)	Original fossils	Original fossils	
West Asia – Israel	Erq El-Ahmar	Original fossils	Original fossils	
West Asia – Israel	Hayonim	Original fossils	Original fossils	
West Asia – Israel	Nahal Oren	Original fossils	Original fossils	
West Asia – Israel	Ohalo II	Original fossils	Original fossils	
West Asia – Jordan	Wadi Hammeh	(Webb and Edwards 2002)	(Webb and Edwards 2002)*	*Photographs

Appendix Table 2. Continued

Geographic Area	Site	Buccolingual Metrics	Macrowear	Notes
Mesolithic				
Europe – France	Baume de Montclus	Original fossils*; (Frayer 1978)**	Original fossils*; (Ferembach 1974b; Frayer 1978)***	*Mandible only; **maxilla; ***published photographs
Europe – France	Combe Capelle	Original fossils	Original fossils	
Europe – France	Hoëdic 1, 4, 6, 8, & 9	B. H. Smith*	B. H. Smith*	*Personal communication
Europe – France	Rochereil 1	(Frayer 1978)	(Ferembach 1974a; Vallois and de Félice 1977)*	*Photographs
Europe – France	Téviec 11 & 13	(Frayer 1978)	(Péquart et al. 1937)*	*Photographs
Europe – Italy	Mondeval de Sora 1	(Alciati et al. 1995)	(Alciati et al. 1995)*	*Molar wear scores were determined from written description and published photographs.
Europe – Romania	Schela Cladovei	Original fossils	Original fossils	
Europe – Spain	Braña-Arintero	No data	(Prada Marcos 2010; Ruiz et al. 2010; Villotte and Prada Marcos 2010)*	*Photographs
Europe – United Kingdom	Gough’s Cave	Original fossils	Original fossils	