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Tooth wear, Neanderthal facial morphology and the anterior dental loading hypothesis

Anna F. Clement [a,*], Simon W. Hillson [a], Leslie C. Aiello [b]

[a] *Institute of Archaeology, University College London, 31-34 Gordon Square, London WC1H 0PY, UK*
[b] *Wenner-Gren Foundation for Anthropological Research, Inc., 470 Park Avenue South, 8th Floor, New York, NY 10016, USA*

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ABSTRACT

The Anterior Dental Loading Hypothesis states that the unique Neanderthal facial and dental anatomy was an adaptive response to the regular application of heavy forces resulting from both the masticatory and cultural use of the anterior teeth. Heavy anterior tooth wear frequently observed in Neanderthal specimens is cited as a main source of evidence for heavy forces being applied to these teeth. From this, it might be predicted that the wear shown on the anterior teeth of Neanderthals would greatly exceed that of the posterior teeth and that this differential would be greater than in other hominins with different facial morphologies.

In this paper, a new method of examining tooth wear patterns is used to test these predictions in a large assemblage of Late Pleistocene hominins and a group of recent hunter–gatherers from Igloolik, Canada. The results show that all Late Pleistocene hominins, including Neanderthals, had heavily worn anterior teeth relative to their posterior teeth but, contrary to expectations, this was more pronounced in the modern humans than in the Neanderthals. The Igloolik Inuit showed heavier anterior tooth wear relative to their posterior teeth than any Late Pleistocene hominins. There was, however, a characteristic Neanderthal pattern in which wear was more evenly spread between anterior teeth than in modern humans. Overall, the evidence presented here suggests that all Late Pleistocene hominins habitually applied heavy forces between their anterior teeth and that Neanderthals were not exceptional in this regard. These results therefore does not support the Anterior Dental Loading Hypothesis.

Introduction

Despite the long history of research into Neanderthal craniofacial morphology, much debate still remains about its evolution. The main hypotheses include adaptation to cold climates, adaptation to high masticatory and paramasticatory forces, and genetic drift. Much attention has focused on the biomechanics of the Neanderthal face and in particular the way in which different features of its morphology might have evolved to resist strong bite forces.

These ideas can together be called the 'Anterior Dental Loading Hypothesis', which proposes that the unique Neanderthal facial anatomy was largely an adaptive response to the high magnitude of forces applied between the upper and lower anterior teeth. It has been proposed that this was the result of heavy use of the incisors and canines both for food preparation/mastication and as part of the toolkit in processing materials and/or producing artefacts and manipulating them (Smith, 1983; Rak, 1986; Demes, 1987; Trinkaus, 1987; Spencer and Demes, 1993; Brace, 1995). In comparison with those of modern humans, Neanderthal anterior teeth are large relative to their posterior teeth (Wolpoff, 1971; Trinkaus, 1978). In addition, they have a distinctive morphology with bulging, robust crowns and strongly marked shovelling in the maxillary incisors with unusually pronounced marginal ridges on the lingual side of the crowns. The incisors also have enlarged lingual tubercles and a strong curvature to the labial side of the maxillary incisors (Crummett, 1995; Ungar et al., 1997; Bailey, 2000, 2002, 2006). These features are seen as an adaptation to powerful forces acting on the teeth – the enlarged ridges and bulging sides would provide buttressing for the crown. They would also supply a larger volume of tooth that might confer a greater resistance to wear, and it is often observed that Neanderthal anterior teeth are heavily worn (Wallace, 1975; Puech, 1981; Trinkaus, 1983; Clement, 2000, 2008). This anterior tooth wear is cited as one of the main sources of evidence for the habitual application of heavy forces between these

* Corresponding author.
E-mail addresses: a.clement@ucl.ac.uk (A.F. Clement), simon.hillson@ucl.ac.uk (S.W. Hillson), laiello@wennergren.org (L.C. Aiello).

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teeth (Smith 1983; Rak, 1986; Demes, 1987; Trinkaus, 1987; Smith and Paquette, 1989; Brace, 1995), but until the late Holocene all hominin dentitions display high levels of wear.

Neanderthal cranio-facial morphology

Although many of the key features of the Neanderthal face are not unique, their combination is, defining Neanderthals as a distinct group within the genus *Homo*. This has led to an intense debate about the mechanisms that led to the evolution of the Neanderthal face (e.g. Howell, 1952; Rak, 1986; Trinkaus, 1987; Smith and Green, 1991; Spencer and Demes, 1993; Antón, 1994; Brace, 1995; Hublin, 2000; Ponce de León and Zollikofer, 2001; Franciscus, 2003; O'Connor et al., 2005; Rosas et al., 2006; Weaver et al., 2007; Weaver, 2009). The distinguishing features of Neanderthal cranio-facial morphology (in comparison with other Late Pleistocene and Holocene hominins) include: rounded and laterally projecting parietal bones; a posteriorly projecting occipital bone with a suprainiac fossa; sloping squamous portion of the frontal bone with double-arched brow ridges and a projecting glabella; posteriorly and inferiorly orientated temporomandibular joint; reduced mastoid processes; receding zygomatic arches; elongated upper facial height; total facial and particularly mid-facial prognathism; inflated infra-orbital regions of the maxilla; broad palate and alveolar processes (relative to length); absence of a canine fossa in the maxilla; wide nasal apertures; elevated pneumatization in the frontal, nasal and maxillary sinuses; robust mandibles with a receding symphysis, a rounder gonial area, a posteriorly positioned mental foramen, high coronoid and/or low condylar processes, large retromolar spaces, and large anterior tooth crowns relative to posterior tooth crowns (Smith, 1983; Stringer et al., 1984; Rak, 1986; Demes, 1987; Trinkaus, 1987; Smith and Paquette, 1989; Tattersall and Schwartz, 1998; Franciscus, 2003; Nicholson and Harvati, 2006; Rosas et al., 2006).

During the 1950s and 1960s, cold adaptation was identified as the main factor in the evolution of the unique Neanderthal facial morphology (Howell, 1952; Coon, 1962; Carey and Steegman, 1981). This hypothesis focused on the Neanderthal nasal region and became known as the 'nasal radiator hypothesis', suggesting their mid-facial prognathism and wide nasal cavity evolved in order to warm inspired air, preventing the effects of cold air on the brain. Later studies, such as those by Franciscus and Trinkaus (1988) and Laitman et al. (1996), further developed this hypothesis viewing the large dimensions of the external Neanderthal nose, the depressed nasal floor, the presence of an internal nasal margin and large paranasal sinuses as an adaptation for moisture retention and heat dissapation in cold and dry climates. More recent studies suggest that the Neanderthal's depressed internal nasal floor configuration and wide aperture are primarily the result of stochastic events, such as random genetic drift and local selection in isolated Neanderthal populations, rather than climatic adaptations (Franciscus, 2003; Holton and Franciscus, 2008).

Howell (1951, 1952) highlights the link between the evolution of Neanderthal facial morphology and random genetic drift, arguing their geographic isolation in glacial Europe provided optimum conditions for genetic drift to occur. Hublin (1990, 1998, 2000) further suggests that periodic climatic crises would have dramatically reduced the available territories in the European subcontinent, leading to demographic bottlenecks and subsequent genetic drift. A statistical analysis based on 37 standard cranial measurements from Neanderthal and modern human skulls tests predictions made from quantitative and population genetic history and shows that genetic drift could explain differences in their cranial morphology (Weaver et al., 2007).

Brothwell (1975) attributes the differences between modern human and Neanderthal facial morphology to differential growth rates, linking many features of the Neanderthal cranial and postcranial skeleton to early maturation (such as fusion of epiphyses in long bones and different components of the cranial base) followed by a long period of post-pubertal growth. More recently, Green and Smith (1990), Smith and Green (1991), and Smith (1991) associate accelerated *in utero* growth rates of the chondrocranium (the embryonic cartilaginous cranium) with the distinctive Neanderthal facial morphology. This work is supported by the findings of Maureille and Bar (1999), Ponce de León and Zollikofer (2001) and Franciscus (2003), that characteristic differences in cranial and mandibular shape between Neanderthals and modern humans arose very early in their development, possibly prenatally.

The evolution of the Neanderthal cranio-facial morphology has also been explained biomechanically as an adaptation to strong forces habitually applied to the anterior dentition (Brace, 1964; Smith, 1983; Rak, 1986; Demes, 1987; Trinkaus, 1987; Smith and Paquette, 1989; Spencer and Demes, 1993). This Anterior Dental Loading Hypothesis focuses particularly on the mid-facial prognathism, greater upper facial height and infra-orbital morphology (Smith, 1983; Rak, 1986; Demes, 1987; Trinkaus, 1987). Rak (1986) suggests that the unique facial morphology of Neanderthals stems from a change in the infra-orbital region from the coronal orientation of the generalised face (as seen in modern humans and other species within the genus *Homo*) to a more sagittal orientation, resulting in a prognathic mid-facial region and cheekbones (zygoma) that appear swept back. This together with a more anterior positioning of the tooth row with respect to the mandibular ramus would have rendered the infra-orbital plates more efficient in opposing the forces resulting from anterior dental loading, which would tend to rotate the anterior part of the face superiorly in the sagittal plane.

Trinkaus (1987) also argues that paramasticatory loading (that is, forces due to tasks outside the normal range required for feeding) of the Neanderthal anterior dentition resulted in elevated levels of mechanical stress in the facial skeleton. He agrees with Rak that several features of the zygomatico-maxillary region were an adaptation to this elevated level of stress. However, Trinkaus (1987) views the orientation of the infra-orbital plates as a secondary consequence of the relative antero-posterior positioning of the dental and masticatory muscle regions.

The ability of the Neanderthal musculo-skeletal system to generate exceptionally heavy anterior dental loads has also been widely debated (Demes, 1987; Antón, 1990, 1994; Couture, 1993; Spencer and Demes, 1993; O'Connor et al., 2005). Initial research by Demes (1987) into the biomechanics of the Neanderthal face supports the mechanical explanation for its unique morphology, finding that the inflated mid-facial profile of the Neanderthals would have offered more resistance against high torsional moments, resulting from heavy anterior tooth loading, than the concave mid-facial profile of most other hominins. In addition, Demes (1987) suggests that the smooth curvature of the infra-orbital plate in Neanderthals had a distinct mechanical advantage over the profile of the 'generalised' face, by reducing local stress concentrations.

Further research by Spencer and Demes (1993) also supports the idea that the Neanderthal cranio-facial morphology was at least in part specialised for anterior tooth use. In particular, they view the anterior migration of the masticatory muscles (masseter, temporalis and medial pterygoid) in Neanderthals, relative to the temporomandibular joint, combined with the shortening of the dental arcade through the more posteriorly positioned incisors and anterior migration of the molar teeth as mechanically advantageous in producing bite forces between their anterior teeth.

Antón (1994) uses a vector analysis model to assess whether the Neanderthal cranio-facial morphology was able to produce absolutely high dental loads. Unlike the previous studies of Demes (1987) and Spencer and Demes (1993), Antón (1994) finds that bite force production at both incisal and molar bite points were 20–22% smaller in Neanderthals than modern humans. She suggests this discrepancy between studies arises from estimations of muscle positions relative to the temporomandibular joint and criticises Demes (1987) and Spencer and Demes (1993) for using only muscle attachments on the cranium to estimate position and not those on the mandible, thus exaggerating the anterior migration of muscle force direction. Antón (1994) further suggests that the high level of dental wear seen in Neanderthal anterior teeth, rather than being caused by high levels of anterior dental loading, is most likely due to repetitive chewing in food preparation or other behaviours.

More recently, O'Connor et al. (2005) test the Anterior Dental Loading Hypothesis by assessing both force-production capability and force-production efficiency of the Neanderthal face using the entire masticatory system. They calculate measures of force-production capability and force-production efficiency using points taken with a 3-D digitiser on the cranium and associated mandibles of four Neanderthals and 29 early and recent modern humans. They find that Neanderthal's bite force capability is neither considerably more nor less efficient at generating anterior dental loads compared with early modern and recent modern humans. O'Connor et al. (2005) also find that force-production efficiency is maintained across a considerable range of facial size and robusticity, challenging the idea of a direct association between a high-magnitude anterior dental loads and Neanderthal facial morphology. They also conclude that if Neanderthals were not generating exceptionally heavy anterior dental load then the increased dental wear on their anterior teeth could only be the result of repetitive use.

The Neanderthal dentition

The morphology of the Neanderthal's anterior teeth has been seen as an adaptation to either masticatory or paramasticatory behaviours – that is, uniquely heavy use of incisors and canines in processing and chewing of food or heavy use of these teeth for activities not directly related to feeding (Stewart, 1959; Brace, 1962; Coon, 1962; Brace et al., 1981; Smith, 1983; Trinkaus, 1983; Demes, 1987; Antón, 1994; O'Connor et al., 2005). As noted above, the anterior tooth crowns are large compared with the posterior crowns, relative to modern human dentitions, and possess enlarged lingual tubercles, pronounced shovelling in the maxillary incisors, and strong labial curvature (Molnar, 1972; Puech, 1981; Ungar et al., 1997; Bailey, 2000, 2006). As for the morphology of the Neanderthal skull, these features of the dentition are not unique to Neanderthals but, in combination with each other and with the skull, they define a distinctive morphological complex.

Extreme patterns of wear have been frequently documented in the Neanderthal dentition (Molnar, 1972; Wallace, 1975; Puech, 1981; Bermúdez de Castro et al., 1988; Lalueza et al., 1996; Ungar et al., 1997; Bax and Ungar, 1999), as well as a high incidence of chipping, fracturing and *ante-mortem* tooth loss (Puech, 1981; Tappen, 1985; Tillier et al., 1995; Fox and Frayer, 1997). The Neanderthal pattern of heavy wear has been compared with that of modern hunter–gatherer groups, such as the Greenland Inuit who use their teeth as tools for tasks such as softening raw seal-hide (Bax and Ungar, 1999). Molnar (1972) notes that Neanderthal incisors and canines exhibit heavier wear than their molars, which are, in contrast, relatively unworn. This is similar to the pattern reported in Inuit, and it has therefore been proposed that Neanderthals used their teeth in very similar ways (Ungar et al., 1997).

An early study of the Neanderthal dentition by Boule and Vallois (1957), which examines the teeth of La Ferrassie, concludes that there were stronger anterior movements of the mandible than in modern humans corroborated by the relatively large shallow glenoid fossa. Supporting evidence is provided by Smith (1976) who finds that the severity of Neanderthal tooth wear, evaluated through dentine exposure and presence of wear related pathologies, is greater than that seen in Upper Paleolithic modern humans, especially in regards to the anterior teeth. She suggests that this difference is caused by an increase in functional demands on the dentition and concomitant dental reduction. Puech's (1981) detailed examination of La Ferrassie 1's dentition suggests that the mastication of meat, plants and accompanying grit was responsible for the heavy anterior wear observed in this Neanderthal specimen, not the use of the teeth as tools. He also states that the very unusual and severe wear on the anterior teeth was accentuated by the anterior migration of masticatory pressures towards the end of this specimen's life. Others, such as Brace (1975), however, consider this wear to have resulted from paramasticatory activity.

One difficulty with these approaches lies in assessing the rate of tooth wear in groups of fossils which contain individuals of widely varying age-at-death and therefore overall level of tooth wear. As anterior teeth are at the centre of the discussion, it seems logical to make the comparison in terms of anterior tooth wear expressed as a ratio of posterior tooth wear in each individual. If the anterior dentition was indeed more heavily and/or more frequently loaded than the posterior dentition in Neanderthals, it is to be expected that these ratios would show consistently high values in Neanderthals of all ages-at-death, relative to other Late Pleistocene hominins. This is what the project described here is designed to do.

Materials

Tooth wear is measured in a sample of 2378 teeth from the dentitions of 139 specimens. These individuals are divided into the following groups; Neanderthals, Middle Palaeolithic modern humans, Upper Palaeolithic/Early Epi-Palaeolithic modern humans and modern day Inuit (Tables 1 and 2). The Neanderthal sample comes from sites in both Europe and Western Asia, including Amud, Kebara, Krapina, La Ferrassie, La Quina, Régourdou, Saccopastore, Shanidar, Spy, Tabun and Vindija. Specimens from the sites of Qafzeh and Skhul in modern day Israel make up the Middle Palaeolithic modern human group. The Upper Palaeolithic and Early Epi-Palaeolithic modern human groups contain individuals from sites in Europe, such as Abri Pataud, Dolní Věstonice, Farincourt, Isturitz, Lachaud, La Madelaine, Le Placard and Pavlov; Western Asia including, Ein Gev and Ohalo, and Afalou-bou-Rhummel in North Africa.

The sample of modern day Inuit comes from the island community of Igloolik, located in the north-eastern corner of the Melville Peninsula, Northwestern Territories, Canada. Dental research was conducted here as part of the International Biological Programme Human Adaptability Project between 1968 and 1973.

Table 1
Sample sizes.

Group	No. of specimens	No. of teeth measured		
		Upper	Lower	Total
Neanderthals	21	109	194	303
Middle Palaeolithic MHs	5	53	45	98
Upper Palaeolithic/Early Epi-Palaeolithic MHs	27	132	159	291
Inuit of Igloolik	86	764	922	1686
Total	139	1058	1320	2378

MHs = Modern *Homo sapiens*.

Table 2
Specimens.

Group	Source of image	Specimens
Neanderthals	Original specimens	Amud 1, La Ferrassie 1
		Kebara 2, Krapina 54, 55, 57, 58 & 59, Spy 1 & 2, Tabun II and CI Vindija 206 & 231
	Casts	Quina 5, Régourdou 1 and Saccopastore 2
	Published photographs	La Ferrassie 2 and Shanidar 1, 2 & 5
Middle Palaeolithic MHs	Original specimens	Skhul V and Qafzeh 5, 7, 9 &11.
Upper Palaeolithic/Early Epi-Palaeolithic MHs	Original specimens	Abri Pataud 1, Afalou-bou-Rhummel 1, 3, 10, 13 & 28, Dolní Věstonice 13, 14 15 & 16, Ein Gev 1, Farincourt, Isturitz series 7B & 71, Lachaud 3 & 5, La Madeleine 1, Le Placard 26, 28, 32, 42 & 43, Ohalo II-H1 & II-H2 and Pavlov 1, 2 & 3.
Inuit of Igloolik	Casts	All

MHs = Modern *Homo sapiens*.

The stone dental casts used in this study were made from alginate impressions collected from the local population between 1969 and 1971 (Mayhall, 1972). The relative isolation of this population at the start of the Adaptability Project meant that most individuals were still practicing a traditional lifestyle, which is reflected in their heavy tooth wear. The Inuit of Igloolik had access to a wide variety of abundant wildlife, including walrus, ringed seals, bearded seals, narwhal, caribou, artic wolf, hare, fox, and char and lake trout (Crowe, 1969). Sea mammal hunting was the major form of subsistence and caribou hunting was secondary to this. The uses of the teeth, for purposes other than mastication, were determined through extensive informal interviews, and both males and females were noted as using their teeth in activities such as softening rawhide for clothes (Mayhall, 1972). The dental morphology of the Igloolik sample fell within the normal range of Inuit populations with a high prevalence of incisor shovelling (Mayhall, 1976).

Methods

This study measures the area of exposed occlusal dentine using digital photographs of original specimens and casts or scans of published images. Our method maximises the number of dentitions that could be included by allowing the use of low-resolution casts, photographs and published images. The method also has the added advantage of providing a continuous measurement, which records fine variations in dentine exposure.

For directly examined specimens (casts and actual teeth), digital photographs are taken of the occlusal surface of the mandibular and maxillary teeth, using a Casio z40 camera and tripod. The teeth are positioned in the centre of the photograph with the lens of the camera perpendicular to their occlusal surfaces. In the case of published photographs, these are scanned at 300 dpi using a conventional flatbed scanner. Tooth wear is measured from the photograph or scanned image using image analysis software (Sigma Scan Pro). The margin of the occlusal surface of each tooth is outlined using a graphics tablet. The program determines the area by counting the number of pixels enclosed within this perimeter. The darker area of dentine, often stained brown in fossil and archaeological specimens, is then measured using the same method. If isolated patches of dentine are present on the occlusal surface of a tooth, they are measured individually and added together to calculate the total area. The summed area of dentine is then divided by the area of the occlusal surface to create a *dentine proportion*. Pixels are used instead of calibrated measurements to calculate the area of the occlusal surface and dentine, so it is not necessary to include a scale in each picture. Calibrated measurements are not needed because the method uses the ratio of areas. This also minimises the effect of variations in tilt of the occlusal surface relative to the camera. Occlusal surfaces that are damaged from heavy chipping, cracking or dental disease are excluded from the analysis.

Many specimens lack a complete dentition, so it is sometimes necessary to substitute an antimere for a missing tooth. The possible effect of wear asymmetry was tested on a sample of 30 specimens from this study using a Mann–Whitney *U* test, and no significant differences between the dentine proportions of any teeth from the left and right sides of the maxilla and mandible were found ($P > 0.05$) (Clement, 2008 see SOM). Dentine proportions for the left and right teeth of the maxilla or mandible are, therefore, combined. When only one side is preserved, this dentine proportion is used and when both antimeres are present the average of the two scores is taken.

In addition, the repeatability of this method was tested by calculating the inter- and intra-observer measurement error for ten relatively complete specimens from a medieval sample; the effect of the angle of the camera in relation to the occlusal surface of teeth, and the measurement variation between digital photographs of the original, casts and scans of published images from the same specimens. These errors were addressed and found not to exceed 2%, and a full presentation of the analysis and data can be found in the SOM that accompany the paper.

Tooth wear and the eruption sequence

The dental eruption sequence is an important consideration when interpreting tooth wear patterns because it dictates the amount of time each tooth is exposed to wear. The first molar, for example, is normally the first permanent tooth to erupt, between six and eight years of age, whereas the third molar erupts significantly later in an individual's life, during the late teens and early twenties (Schour and Massler, 1941; Gustafson and Koch, 1974; Hillson, 1996). Thus, the first molar is exposed to considerably more wear (10–16 years) than the third molar. If we assume a constant rate of wear for all teeth then at any age it follows that earlier erupting teeth will exhibit the most advanced wear. If the rate of tooth wear is not constant for all teeth, then the degree of wear will not reflect the expected eruption sequence. This is the fundamental principle of the interpretations of wear patterns in this study.

Mean eruption times, such as those provided by Garn et al. (1972), can be used to suggest the expected wear pattern for an individual.[1] Figure 1 illustrates the differences in years between the eruption of the first molar and the other teeth within the maxilla and mandible. The first molar is normally the first permanent tooth to erupt in both the maxilla and mandible, and all other teeth fall below this dashed line, which represents the first molar. This expected wear pattern graph can be used to suggest the relative exposure to wear of different teeth. Due to its early eruption, the first molar is expected to be the most heavily worn tooth, closely

[1] Despite some individuals departing from the standard sequence (Smith and Garn, 1987), most modern humans follow a basic pattern for the eruption of teeth into the mouth (Hillson, 1996). It is also important to note that Neanderthals generally possessed the same eruption sequence as modern humans, so direct comparisons are possible, even though much less is known about the eruption timings of their teeth (Dean et al., 2001; Smith et al. 2007).

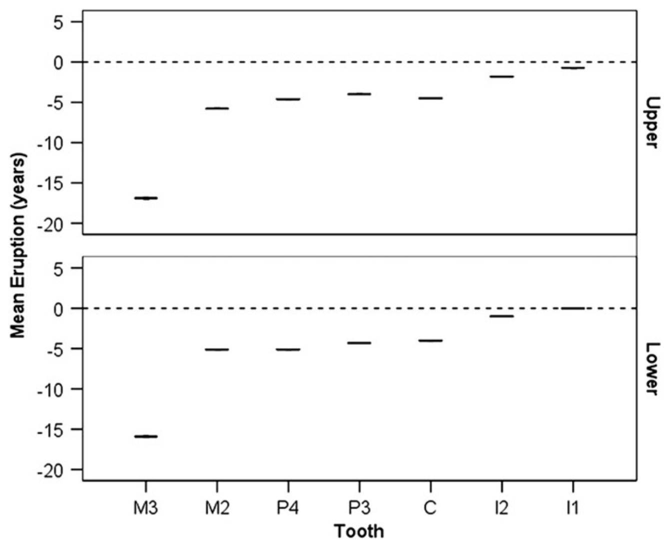

Figure 1. Mean eruption timings for all of the teeth within the maxilla and mandible, relative to the first molar. The vertical axis represents the average eruption timings and the horizontal axis represents the tooth type. The first molar is not shown as it is being used as the reference tooth, but is represented by a horizontal dashed line passing through 0 on the vertical axis. As the pattern of wear through the dentition strongly reflects relative eruption timing, this represents the expected pattern of wear. Mean eruption times from Garn et al. (1972).

followed by the first and second incisors. The canine, premolars and second molars, all demonstrate slightly later eruption times and would therefore be expected to be less worn. Finally, the third molar erupts much later than the others and is expected to show the least wear.

A complicating factor is that the pattern will tend to become obscured with age; that is, older individuals will have more wear (e.g. Lovejoy, 1985, Buikstra et al., 1994). To remove age as a factor, we present the wear measure of each tooth as a ratio of the wear measure for one particular reference tooth in the dentition. The first molar is selected as it is usually the first tooth to erupt, but any tooth can be used. The dentine proportions of each tooth are therefore divided by the dentine proportion of the first molar from the same jaw. In this study, the resulting figure for each tooth in each individual is known as the *wear ratio*. Those teeth with a similar wear state to the first molar should therefore have a wear ratio near 1. Those with more wear should have a wear ratio greater than 1, and those with less wear should have a wear ratio of less than 1. This method has been tested in two archaeological collections of medieval monks from London, whose wear patterns closely follow that illustrated in the expected wear pattern, as determined from the eruption sequence (Clement, 2007).

Results

Neanderthals

For Neanderthal maxillary anterior teeth, the wear ratios (relative to the first molar) are high (Figure 2). In fact, in no individual is a maxillary incisor or canine less worn than the first molar from the same jaw. The median ratios of both incisors and the canines cluster around 1.6 and their inter-quartile ranges overlap one another extensively. This is not what would be expected if the wear merely reflects the eruption sequence, where the first molars and first incisors should show a similar level of wear, the second incisor slightly less, and the canines even less. The anterior teeth also differ from the maxillary posterior teeth in their greater variation of wear

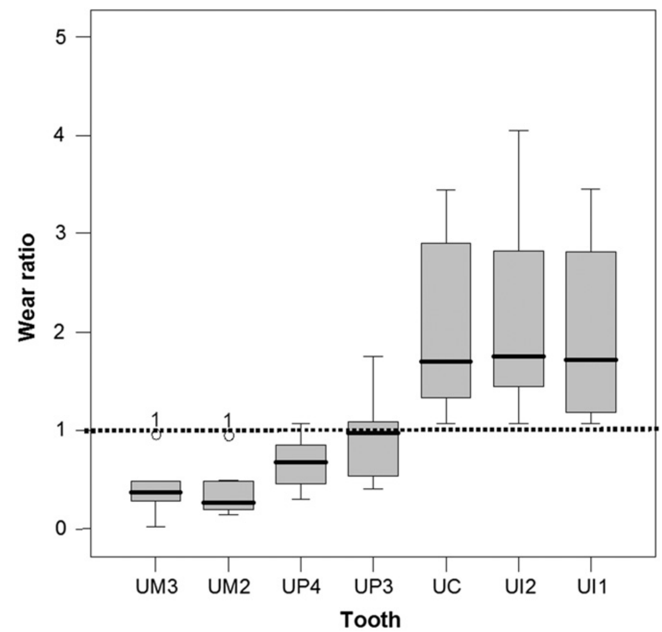

Figure 2. Maxillary Dentition – Neanderthal wear ratios (percent of occlusal surface area occupied by dentine), relative to the first molar. For a list of specimens included, see Table 2. This box plot (and the following ones) represents each individual tooth, starting with the back of the mouth (third molars) following through to the front (first incisors) – the first molar is not included as it is the reference tooth for these ratios. The top and bottom of each box represent the upper and lower quartile values, and so the height of the box represents the inter-quartile range. The bar inside each box represents the median, and the 'whiskers' represent the overall range of values. Outliers are represented by 'O' and '*' symbols: 'O' indicates values which are separated from the upper or lower quartile by more than 1.5 times the inter-quartile range; '*' indicates values separated by more than three times the inter-quartile range. The outlier labelled "1" represents La Ferrassie 1.

ratio values. Their inter-quartile ranges are three or even four times those of the posterior teeth. The differences in wear ratios between the maxillary anterior and posterior teeth are all statistically significant (Mann–Whitney U, $P < 0.05$).

The maxillary third premolar is at the crossover point of the graph, showing a median wear ratio between that of the anterior and posterior teeth. Its median wear ratio is about 1, whereas the other maxillary posterior teeth all have median wear ratios of less than 1. Although the third premolar's inter-quartile range overlaps 1, the majority of the range is less than 1 and its wear ratios are not statistically significantly different from any of the other posterior teeth (Mann–Whitney U, $P > 0.05$). This tooth clearly belongs with the other posterior teeth in terms of its wear state. Together, the maxillary premolars have slightly higher median wear ratios and inter-quartile ranges than do the second and third molars. In terms of eruption sequence, the maxillary premolars would be expected to be similar to the second molars. The third molars have a median wear ratio slightly higher than the second molars and this is again in contrast to the eruption sequence, which would predict the opposite pattern.

The mandibular anterior teeth show strikingly higher median wear ratios (relative to the mandibular first molar), and much larger inter-quartile ranges, than the maxillary anterior teeth and for this reason they are plotted on a different scale to the maxillary teeth (Figure 3). The mandibular incisor median values are three times those of the first molar, and in some individuals incisor wear is more than six times that of the first molars from the same jaw. Even the canine median value is twice that of the first molar, but has a much smaller inter-quartile range than those of the incisors. All of the mandibular anterior teeth show statistically significant

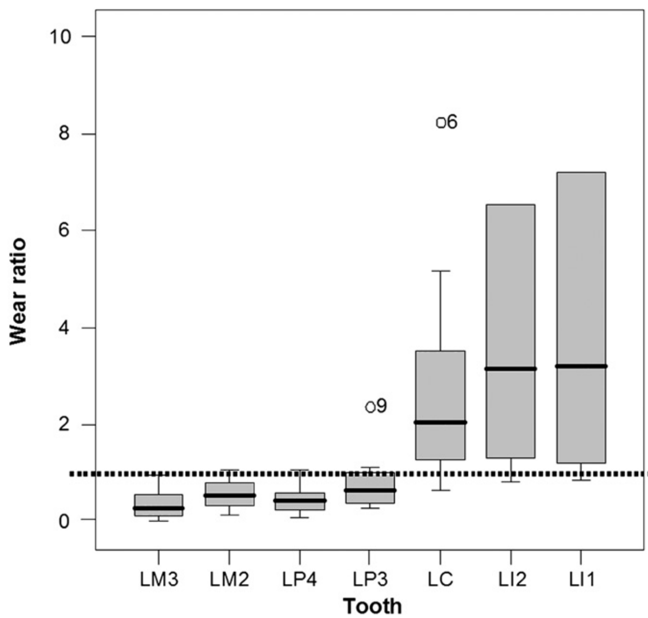

Figure 3. Mandibular Dentition – Neanderthal wear ratios, relative to the first molar (the vertical scale has been changed relative to Figure 2 to include the much greater variability). For a list of specimens included, see Table 2. For explanation of plot symbols, see Figure 2. Outliers labelled "9" and "6" represent Krapina 58 and Krapina 59, respectively.

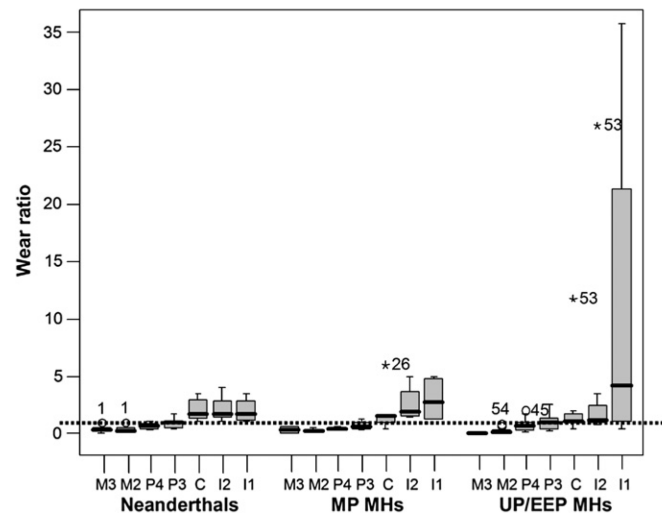

Figure 4. Maxillary Dentition – Neanderthal, Middle Palaeolithic modern human and Upper Palaeolithic/Early Epi-Palaeolithic modern humans wear ratios plotted separately, relative to the first molar (the vertical scale has been changed relative to Figures 2 and 3 because of the even greater variability). For a list of specimens included, see Table 2. For explanation of plot symbols, see Figure 2. Outlier labels: "1" La Ferrassie; "26" Qafzeh 5; "45" Le Placard 32; "53" Dolní Věstonice 15; and "54" Dolní Věstonice 16.

differences in their wear ratios compared to each of the posterior teeth (Mann–Whitney *U*, $P < 0.01$).

The mandibular premolars and second and third molars show less wear than the first molars in almost all individuals, with just a few individuals exceeding the first molar wear ratio. Of these teeth, the third premolars have a slightly higher wear ratio than do the fourth premolars, which would be expected from the eruption sequence. The second molar overlaps in its inter-quartile range with both premolars, and the third molar has a mandibular wear ratio lower than any of the other posterior teeth, again as expected from the eruption sequence.

Upper Palaeolithic/Early Epi-palaeolithic modern humans, Neanderthals and Middle Palaeolithic modern humans compared

In the maxillary dentition the Neanderthals contrast strongly with the Upper Palaeolithic/Early Epi-Palaeolithic modern humans, whilst the Middle Palaeolithic modern humans fit somewhere in between (Figure 4). Most noticeable are the high and extremely variable wear ratios in the Upper Palaeolithic and Early Epi-Palaeolithic modern human maxillary first incisors, but these are not statistically significantly different from the wear ratios of the Neanderthals first incisors (Mann–Whitney *U*, $P > 0.05$). By contrast, the wear ratios of the second incisors and canines are much less variable and their median values are not far from 1. The Middle Palaeolithic modern humans also show a higher median wear ratio for their maxillary first incisors than the Neanderthals, together with a larger inter-quartile range, but this is not nearly so marked as in the Upper Palaeolithic and Early Epi-Palaeolithic modern humans and also not statistically significantly different (Mann–Whitney *U*, $P > 0.05$). The median wear ratio value for Middle Palaeolithic modern human maxillary second incisors is about the same as for the Neanderthals, although they show somewhat more variation, and their canines show considerably lower wear ratios with the inter-quartile range overlapping 1. The Neanderthal canines and incisors are clearly distinguished from the other two groups by their similar medians and inter-quartile ranges, and by the fact that for all teeth the wear ratios are above 1. However, only the wear ratios of the Upper Palaeolithic/Early Epi-Palaeolithic modern human's maxillary canines show a statistically significant difference from those of the Neanderthals (Mann–Whitney *U*, $P < 0.05$).

The posterior teeth show more similar patterns of wear that quite closely resemble the eruption sequence in all groups. No statistically significant differences are found in these wear ratios between the three groups (Mann–Whitney *U*, $P > 0.05$). The premolars show higher wear ratios for both the Neanderthals and Middle Palaeolithic modern humans, with a median wear ratio of about 1 for their third premolars, which represent the crossover point of the graph. In the Upper Palaeolithic/Epi-Palaeolithic modern humans, the crossover point lies between the third premolar and canine. The third molars have somewhat higher wear ratios than expected from the eruption sequence in both the Neanderthal and Middle Palaeolithic modern humans groups.

In the mandibular dentition, the Upper Palaeolithic/Early Epi-Palaeolithic modern humans again stand out, but in a rather different way to the maxillary dentition (Figure 5). In the Neanderthal and Middle Palaeolithic groups, all anterior teeth have median wear ratios above 1, whereas the Upper Palaeolithic/Early Epi-palaeolithic modern humans have lower median values, with mandibular second incisors and canines near 1. The inter-quartile ranges for Upper Palaeolithic/Early Epi-Palaeolithic modern humans are also smaller and all overlap 1. In the Middle Palaeolithic mandibular anterior teeth, there is a strong gradient, with the lowest median and smallest inter-quartile range in the canines, followed by second incisors and then first incisors which show considerably higher median wear scores and inter-quartile ranges than the Neanderthals. In the Neanderthals, the mandibular incisors are similar in both median and inter-quartile range, whereas the canines have lower median and inter-quartile range values. Only the Neanderthal's mandibular canines show statistically significant differences in their wear ratios to Upper Palaeolithic/Early Epi-Palaeolithic modern human's (Mann–Whitney *U*, $P < 0.05$).

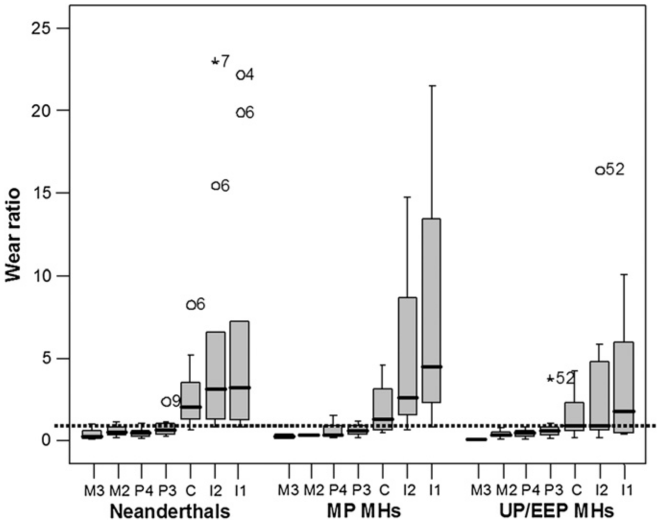

Figure 5. Mandibular Dentition – Neanderthal, Middle Palaeolithic modern human and Upper Palaeolithic/Early Epi-Palaeolithic modern humans wear ratios plotted separately, relative to the first molar (the vertical scale has been changed relative to Figure 4 because of the even greater variability). For a list of specimens included, see Table 2. For explanation of plot symbols, see Figure 2. Outlier labels: "4" Krapina 55; "6" Krapina 59; "7" Krapina 54; "9" Krapina 58; and Dolní Věstonice 14.

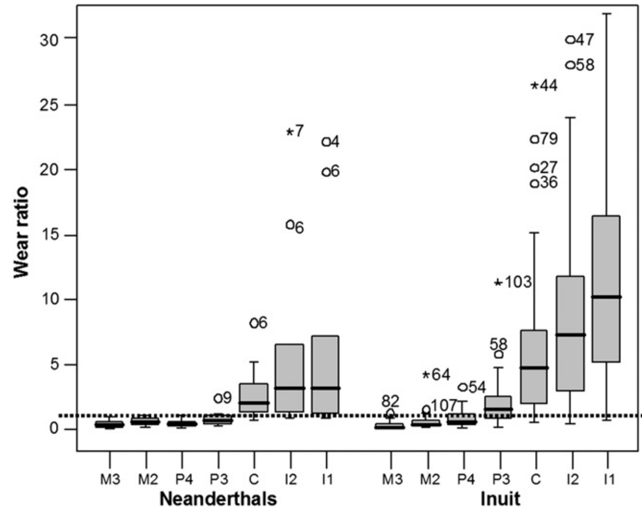

Figure 7. Mandibular Dentition – Neanderthal and Inuit wear ratios plotted separately, relative to the first molar (the vertical scale is the same as for Figure 6). For a list of specimens included, see Table 2. For explanation of plot symbols, see Figure 2. Outlier labels: "4" Krapina 55; "6" Krapina 59; and "7" Krapina 54. Inuit outliers not separately labelled because they all come from the same community.

The mandibular posterior teeth more closely resemble the expected wear pattern from the eruption sequence in all groups, with wear ratios falling below 1 and a strong downward gradient from mandibular third premolars, to fourth premolars, to second molars and third molars. No statistically significant differences are found between the wear ratios of the posterior teeth between the three groups (Mann–Whitney U, $P > 0.05$).

Inuit and Neanderthals compared

In the maxillary dentition, there is a strong contrast between the wear patterns (relative to the first molar) of the Neanderthals and Inuit of Igloolik (Figure 6). The Inuit maxillary anterior teeth show much higher median wear ratios and much larger inter-quartile ranges than those of the Neanderthals (or indeed any of the Late Pleistocene hominins, apart from the Upper Palaeolithic/Early Epi-Palaeolithic maxillary first incisors). This is particularly apparent in the incisors, which show statistically significant differences in their ratios compared with the Neanderthals (Mann–Whitney U, $P < 0.01$). In the Neanderthals, the median wear ratios for the anterior teeth all cluster around 1.6 with similar inter-quartile ranges. In the Inuit, the incisor median wear ratios are three to four times those of the Neanderthals. There is a strong gradient in both medians and inter-quartile ranges going from canines to second incisors to first incisors. This is entirely lacking in the Neanderthals. Contrastingly, the posterior teeth from both groups all possess median wear ratios of less than 1. While the inter-quartile ranges are slightly larger for the Inuit posterior teeth, the median ratios for the premolars and third molars are slightly higher for the Neanderthals. No statistically significant differences are found between the Neanderthal and Inuit wear ratios for their posterior teeth (Mann–Whitney U, $P > 0.05$).

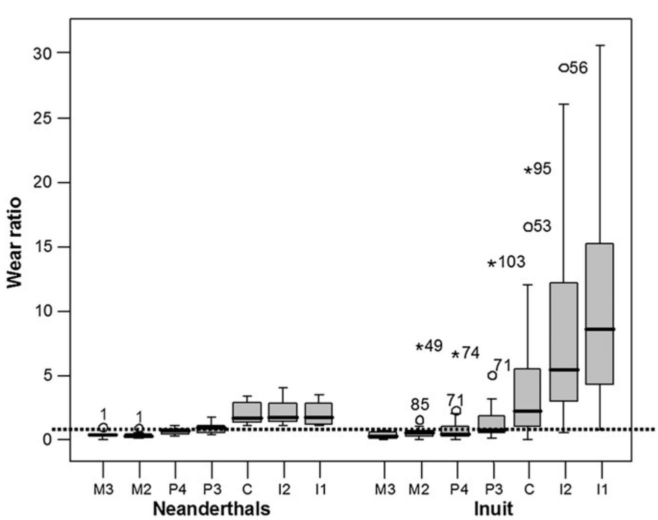

Figure 6. Maxillary Dentition – Neanderthal and Inuit wear ratios plotted separately, relative to the first molar (the vertical scale is the same as for Figure 7). For a list of specimens included, see Table 2. For explanation of plot symbols, see Figure 2. Outlier labelled "1" represents La Ferrassie 1. Inuit outliers not separately labelled because they all come from the same community.

In the mandibular dentition, there is still a contrast between Neanderthal and Inuit anterior tooth wear patterns but it is less marked, due to the somewhat higher medians and inter-quartile ranges in the Neanderthals' mandibular incisors. For the mandibular anterior teeth statistically significant differences are only found in the first incisor and canine between the Neanderthals and Inuit (Mann–Whitney U, $P < 0.01$). Again, there is a strong gradient in both medians and inter-quartile ranges for the Inuit group, going from mandibular third premolars, to canines, second incisors and first incisors, which is lacking in the Neanderthals. All of the mandibular posterior teeth from both groups possess wear ratio medians of less than 1 and small inter-quartile ranges, relative to the mandibular anterior teeth, apart from the third premolar in the Inuit group, which rises above 1. The mandibular third premolar shows a statistically significant difference in its wear ratios between the Neanderthals and Inuit (Mann–Whitney U, $P < 0.01$).

We also compared the overall tooth wear present in the maxillary and mandibular first molars in all four groups. Each group showed a large range of wear values for their maxillary and mandibular first molars, with the Inuit from Igloolik exhibiting slightly lower mean dentine proportions for both their maxillary and mandibular first molars. The Upper Palaeolithic/Early Epi-

Palaeolithic group possessed the highest mean dentine proportion for their maxillary and mandibular first molars. By comparing the wear ratios between and within the different groups rather than the dentine proportions the relative degree of anterior wear can be assessed independently of the overall level of wear for any individual dentition.

Discussion

The Anterior Dental Loading Hypothesis states that the high magnitude of forces, resulting from masticatory and cultural use of the anterior teeth, was an important factor in the evolution of the Neanderthals' unique facial anatomy (Smith, 1983; Rak, 1986; Demes, 1987; Brace, 1995). One of the main sources of evidence for this high magnitude of forces is the heavy tooth wear that has frequently been observed on Neanderthal anterior teeth. The amount of wear present on these anterior teeth was therefore predicted to exceed that present on the first molars and indeed on all of the other posterior teeth. In addition, it was suggested that if the Anterior Dental Loading Hypothesis was correct then other groups of hominins with different facial morphologies from the Neanderthals would exhibit lower levels of anterior tooth wear.

Almost all of the Neanderthal specimens included in this study possess heavier anterior tooth wear than recent archaeological populations eating an agriculturally-based diet (Clement, 2007, 2008). In general, the mandibular anterior teeth display higher wear ratios than the maxillary anterior teeth, and the maxillary third premolars higher wear ratio values than the other posterior teeth. If the pattern of wear reflects the magnitude of forces applied by the dentition, then it seems reasonable to suggest that the heaviest forces were applied by Neanderthals in the anterior part of their dentition, including incisors, canines and third premolars. The wear ratios are greater in the mandibular anterior dentition, the part that would have been moving in life (Hylander 1977).

In contrast to the pattern of wear predicted from the eruption sequence of the teeth (Figure 1), these results confirm that Neanderthals were exerting strong forces on their anterior teeth. Discussion of the Anterior Dental Loading Hypothesis further predicts that only Neanderthals would show this pattern of heavy anterior wear, or at least that it would be markedly heavier than that observed in any other hominin. However, the results of this study show that the Neanderthal specimens are neither unique, nor do they have extreme anterior tooth wear, when compared with a sample of Late Pleistocene hominins and recent hunter–gatherers from Igloolik, Canada. Middle Palaeolithic modern human specimens from Qafzeh and Skhul show higher median wear ratios than the Neanderthals in the maxillary incisors and mandibular first incisors, with larger inter-quartile ranges. It would seem reasonable to suggest that these hominins were also habitually applying forces between their anterior teeth that were at least as high as those applied by Neanderthals, or were repeated as frequently.

The Anterior Dental Loading Hypothesis could be taken to predict that there should therefore be some similarities in the morphology of their teeth, jaws and face. Whilst more robust than Upper Palaeolithic modern humans, the Qafzeh and Skhul specimens lack key Neanderthal features, such as a large nasal aperture, swept back zygomatic arches and a retromolar space in the mandible, along with a prominent mental eminence and somewhat reduced brow ridges. The morphology is still distinctive, however, with large teeth in robust jaws and a heavily buttressed face that differs markedly from later modern humans. It is possible that the morphology represents an adaptation of a different kind in supporting the teeth under the application of heavy loads. This is undermined by the observation in this study that Upper Palaeolithic and Early Epi-Palaeolithic modern humans also show evidence of heavy anterior tooth wear, relative to the posterior teeth. The pattern is slightly different to that of the Middle Palaeolithic modern humans, being mainly concentrated in the first incisors, which in the maxilla show not only a high median value, but also an extremely wide range in values. In fact, some specimens possess exposed dentine proportions up to 35 times that of the first molar, a level of wear that is only equalled by the Inuit of Igloolik. Investigation of this unusual wear pattern (Clement, 2008) shows that the specimens from the Central European sites of Dolní Věstonice and Pavlov are responsible for the higher dentine proportions in the maxillary first incisors, relative to the first molar. This pattern of wear also suggests that these Upper Palaeolithic/Early Epi-Palaeolithic modern humans were able to apply heavy forces with their anterior dentition without the facial morphologies that characterise either group of Middle Palaeolithic hominins.

The heavy anterior tooth wear of Inuit hunter–gatherers has been said to echo that of the Neanderthals (Leigh, 1925; Pedersen, 1947; Bang and Hasund, 1971; Hylander, 1977; Rak, 1986; Demes, 1987; Mayhall and Kanazawa, 1989; Ungar et al., 1997; Bailey, 2002). However, until now the relationship between Inuit and Neanderthal tooth wear has not been formally measured. Although we found both the Neanderthals and Inuit from Igloolik to exhibit a pattern of heavy anterior tooth wear, Inuit anterior wear is by far the greater of the two in both the maxillary and the mandibular dentition. The biggest difference occurs in the maxillary incisors, with the Inuit possessing median wear ratios that are three to four times those of the Neanderthals. The Igloolik Inuit also possess much larger inter-quartile ranges and overall ranges in wear ratios. However, the anterior wear is more evenly spread in the Neanderthals than in the Inuit. If tooth wear reflects the magnitude of forces being placed on the dentition, then the extremely high wear ratios displayed by the Inuit of Igloolik suggests that they were subjecting their anterior teeth to much stronger or more repetitive forces than the Neanderthals. This questions the assumption that their teeth were used to perform similar tasks.

The results of this study therefore suggest that the heavy wear frequently observed in Neanderthal specimens falls within the range of both Late Pleistocene hunter–gatherers and recent Inuit from Igloolik and can no longer be used as supporting evidence for the Anterior Dental Loading Hypothesis.

Tooth wear is, however, a complex process affected by a multitude of different factors, including biological, physical and cultural (Barrett and Brown, 1975; Kaifu et al., 2003). It could be argued that the dental morphology and size of the Neanderthal anterior teeth enabled them to better resist the process of wear than Late Pleistocene and more recent hunter–gatherers from Igloolik. While this possibility cannot currently be discounted, the Inuit, who possess similar dental morphologies in their anterior teeth to the Neanderthals such as incisor shovelling, show even higher tooth wear ratios for their anterior teeth compared to their posterior teeth. This suggests that the dental morphology of these teeth was insufficient in resisting the heavy forces being placed upon them.

Although Neanderthals possessed a similar eruption sequence to modern humans, much less is known about the eruption timings of the teeth (Dean et al., 2001; Smith et al., 2007). Whilst differences in eruption timings between Neanderthals and modern humans might have a small impact on their expected wear pattern, it would not affect the expected order of wear between individual teeth. Differences in eruption timing could therefore not explain the lack of extreme anterior tooth wear in Neanderthals compared with other groups of Late Pleistocene and the more recent modern humans from Igloolik.

It could also be argued that high magnitudes of force may not necessarily result in increased tooth wear and that the heavy anterior tooth wear frequently observed in groups of hunter–gatherers (e.g. Leigh, 1925; Pedersen, 1947; Smith, 1976; Hinton, 1981; Puech, 1981; Richards, 1985; Mayhall and Kanazawa, 1989; Clement, 2008) was rather the result of their repetitive use. Whilst repetitive use of the anterior teeth would have undoubtedly contributed to the tooth wear observed in these teeth, the relationship between heavy tooth wear and the magnitude of forces has previously been documented (Hylander, 1977; Hinton, 1981; Richards, 1985; Kiliaridis et al., 1995). The work of Hylander (1977) has shown that the Inuit of Canada, Alaska and Greenland placed a high magnitude of forces on their anterior teeth, more than any other group of modern humans. The wear pattern observed in this study for the Inuit of Igloolik strongly shows that the anterior teeth, which are subjected to the highest magnitude of forces, are also the most heavily worn teeth within their dentition.

The results of this study also support the work by Antón (1994) and O'Connor et al. (2005) by suggesting that Neanderthals were not generating considerably heavier anterior dental loads than early modern or recent modern humans. These studies further suggest that the increased dental wear on their anterior teeth could only be the result of repetitive use. The results of this study, however, do not demonstrate that Neanderthals actually possess an increased amount of wear on their anterior teeth, relative to their posterior teeth, compared to other a sample of both Late Pleistocene hominins and recent hunter–gatherers from Igloolik.

Conclusions

The new method used in this study to measure and assess the pattern of tooth wear, combined with availability of a large collection of digital images and published illustrations, make it possible to produce a large database of measurements for Neanderthals, Middle Palaeolithic modern humans, Upper Palaeolithic and Early Epi-Palaeolithic modern humans. Contrary to previous assumptions, the evidence provided by this analysis of Late Pleistocene tooth wear patterns does not directly support the Anterior Dental Loading Hypothesis as an explanation of the selective pressures driving the evolution of the Neanderthals' unique cranio-facial morphology. A simple prediction of this hypothesis is that Neanderthals should have a uniquely heavy concentration of wear in the anterior part of the dentition. While the degree of wear present on their anterior teeth relative to the posterior teeth is high, it is not exceptional when compared with that of Middle Palaeolithic modern humans or Upper Palaeolithic and Early Epi-Palaeolithic modern humans. Both these groups of modern humans possess very different cranio-facial morphologies to the Neanderthals. The Late Pleistocene hominins all have heavy anterior tooth wear, relative to the posterior teeth, but it is dwarfed by that of the modern Inuit hunter–gatherers from Igloolik.

The Neanderthals do however show a unique pattern of wear, with evenness in the wear across the anterior dentition that is not observed in any of the modern human groups. This evenness of wear is matched by a wider dental arcade accommodating large anterior teeth, relative to the rest of the dentition.

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Appendix. Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.jhevol.2011.11.014.

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