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Beyond Shovel-Shaped Incisors: Neandertal Dental Morphology in a Comparative Context

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Abstract

Most research on Neandertal teeth has focused on shovel shaped incisors and/or taurodont molars. In the past 15 years there has been a renewed interested in Neandertal dental morphology, especially with regard to how they compare to recent and fossil modern humans. However, no complete description of Neandertal dental morphology has been published since the mid-1950s. Many more Neandertals and other fossil hominins have been discovered since then and are available for a comparative study. This paper provides a description of Neandertal dental morphology and places that morphology in a comparative fossil hominin context. It differs from previous work by focusing on fossil hominin variation (as opposed to contemporary modern human variation) and provides a comparative baseline in which Neandertal dental morphology can be assessed. The four comparative samples include European and West Asian Neandertals, European non-Neandertal archaics, South African/West Asian early modern humans and European early modern humans (e.g., Upper Paleolithic). A mean measure of divergence analysis shows that Neandertals are significantly different from early modern human groups, being four times more divergent from Afro-Asian and European early modern human samples than the early modern human samples are from each other. Moreover, Neandertals are more divergent from early modern Europeans than they are from the early modern Afro-Asians. Contrary to the results of a previous study they are significantly divergent from non-Neandertal archaics. The implications for these results are discussed.

INTRODUCTION

The first fossils identified as Neandertal (from the Neander Valley) were discovered in 1856, the same year of Gorjanovic-Kramberger's birth. Perhaps it is only fitting that 43 years later he would be involved in the discovery of the largest collection of Neandertal fossils of his time, consisting of more than 870 single fossils representing up to 80 individuals and including a collection of 279 teeth representing 12 to 28 individuals *(1, 2)*. Aside from the sheer number of teeth represented, the Krapina dental collection is especially impressive because many of the permanent teeth are unerupted or only minimally worn. As such, they comprise an ideal study collection for anthropologists interested in external crown morphology. In fact, the Krapina sample makes up a significant portion of the total number of Neandertal teeth currently available for study.

When Gorjanović-Kramberger discovered 'Krapina Man' on Hušnjak hill near the town of Krapina Croatia *(3, 4)* one of the things he took special note of was the unusual morphology of the upper incisors *(4)*. One aspect of this morphology was the presence of marked lingual marginal ridges. While shovel-shaped incisors (as they were known) had been observed in recent humans for decades (e.g., *5, 6–8*), Gorjanović-Kramberger *(4)* was the first to document their presence in the fossil record. However, Gorjanovič-Kramberger recognized that the distinctiveness of the Krapina incisors went beyond shovel shaping, citing the presence of unusually marked lingual tubercles extending from the cingulum in both central and lateral incisors.

While Gorjanović-Kramberger found the incisors to be the most interesting of the teeth *(4)*, his observations did not end there. He also noted that the posterior teeth, especially the molars, exhibited odd, prismatic roots. Radiographs of the teeth have shown that they possess large pulp chambers or taurodont (»bull-toothed«) roots.

For decades, few other dental traits in fossil hominins have received as much attention as shovel-shaped incisors and taurodont roots. During the middle part of the last century descriptive studies of Neandertal teeth alluded to additional unusual dental characters in Neandertals *(*e.g. *9, 10)*; and more recently, Zubov *(11, 12)* made special note of the epicristid, or mid-trigonid crest, on lower molars. However, until recently *(13–15)* little has been done to systematically follow-up on these potentially diagnostic traits.

Perhaps it was because the implicit goals of early studies of Neandertal morphology were to report new information and to ascertain their phylogenetic position vis-à--vis apes and modern humans (i.e., are they more ape like or more human like?) that little attention was paid to some of the more minor variants of Neandertal dental morphology. As a result, the general impression today is similar to that espoused by Boule and Vallois *(16)* nearly half a century ago. That is, except for a few characters, Neandertal teeth are much like our own.

In the latter part of the 20th century Neandertal incisor morphology was revisited by Crummet *(17)*. The eventual publication of the a standardized method for scoring dental morphology (e.g., the Arizona State University dental anthropology system –ASUDAS) *(18)* led to studies of their dental trait frequency pattern as well *(13, 19, 20)*. The latter studies showed that Neandertals exhibit a unique dental pattern relative to all living human groups. In addition to this unique pattern, additional morphological traits that are rare in contemporary humans have been identified *(15, 21, 22)*; for some of these their high frequency may be derived in Neandertals.

Because the number of Neandertal specimens has increased in the past 50 years, we are now in a better position to provide a systematic description of Neandertal dental morphology, much as Patte *(10)* did when the sample was much smaller. In addition, because the past several decades have led to the discovery of many new early modern human (European and African) fossils, we can provide a comparative context in which to assess the distinctiveness of their dentition relative to that of other fossil hominins.

This paper presents a summary of Neandertal dental morphology and places it in the context of other Middle-Late Pleistocene fossils currently available for study. The format of this paper consists of a description of the typical morphology observed on teeth in each of the four functional areas of the dentition (incisors, canines, premolars, molars). Each description is followed by a discussion of how these trait frequencies compare with those of other Middle-Late Pleistocene hominins. A multivariate analysis of biological distance is undertaken, testing the null hypothesis that the Neandertal dental pattern is not significantly different from that of other fossil hominins. Finally, a discussion of the utility of using dental morphology to identify Neandertals and to assess relationships among fossil hominins follows. The study presented here is similar in structure to an earlier one *(13)*, but it differs in its list of traits and in its sample composition, it which focuses on fossil hominins instead of recent modern humans for comparative study.

METHODS AND MATERIALS

The number of Neandertals available for study has increased substantially since the time of Krapina's discovery. The number of fossil hominins relevant for comparison (e.g., early modern humans from Europe, Africa and West Asia and non-Neandertal archaic[1] humans) has also increased, providing a reasonable sample size on which to base an assessment of Neandertal dental morphology. Table 1 provides a list of fossil hominins used in this study.

The Arizona State University Dental Anthropology System is used as a baseline for this study. This system currently consists of more than 36 tooth crown and root traits that are scored with the aid of 23 reference plaques *(18)*. A written description of each trait is used in conjunction with the reference plaques to facilitate accurate assessment of variation. Turner *(23)* indicated that of these traits, 29 best characterize genetic affinity. These 29 traits are least likely to be strongly influenced by environment when scored on »key« teeth as defined by the morphogenetic field concept *(24)*. While the ASUDAS serves as a good starting point for any dental morphological analysis, Bailey *(13, 15, 21, 22)* has shown that it does not encompass all important fossil hominin dental variation.

[1] Throughout this paper the term 'early modern Afro-Asian' refers to early (~100 kya – 70 kya) anatomically modern humans from Africa and West Asia and the term 'early modern European' refers to Upper Paleolithic anatomically modern humans from Europe (~34 kya – 15 kya). Non-Neandertal archaic(s) refers to European fossils also known as *H. heidelbergensis*.

TABLE 1

List of fossil hominin samples and teeth used in this study.

Site	No. Teeth
Non-Neandertal archaic (European)	
Arago	22
Atapuerca	8
Fontana Ranuccio	2
Petralona	6
Steinheim	4
Mauer	5
Melpigano	1
Montmaurin	3
Total Non-Neandertal archaic (European) teeth	52
Neandertals	
Amud	6
Arcy-sur-Cure (Mousterian levels)	4
Chateauneuf	3
Ciota Ciara (Monte Fenera)	3
Combe Grenal	5
Eringsdorf	6
Devil's Tower, Gibraltar	1
Grotte Taddeo	5
Guattari	4
Hortus	19
Kebara	7
Krapina	151
Külna	4
La Fate	4
La Ferrassie	2
La Quina	10
Malarnaud	1
Monsempron	12
Montgaudier	1
Ochoz	5
Petit-puymoyen	15
Pontnewyedd	14
Regourdou	5
Saccopastore	9
Shanidar	9
Spy	9
Tabun	20
Taubach	1
Vindija	12
Total Neandertal teeth	347
Fossil anatomically modern humans	
Abeilles	3
Abri Blanchard	1
Abri Labatut	2
Abri Pataud	9
Arcy-sur-Cure Upper Paleolithic level	2
Dolní Věstonice	38
Farincourt	5
Fourneau du Diable	7
Fontechevade	2
Grotte des Rois	29
Gough's Cave	17
Grotte des Abeilles	3
Isturitz	6
La Chaud	11
La Ferrassie	3
La Gravette	1
La Madeleine	2
Laugerie Basse	10
Les Vachons	4
Miesslingtal	1
Mladeč	9
Oase	5
Oberkassel	12
Pavlov	7
Peche de la Boissiere	2
Roc de Combe	1
Solutre	1
St Germain la Rivière	35
Total early modern European teeth	229
Early modern Afro-Asians	
Die Kelders	9
Equus Cave	10
Klasies River Mouth	8
Hoedijes Punt	2
Sea Harvest	1
Qafzeh	56
Skhul	19
Total early modern Afro-Asian teeth	117

Therefore, a selection of supplemental traits that have been demonstrated to be useful in assessing fossil hominin variation have also been included *(see 13)*. Table 2 presents a list and description of the traits used in this study together with their presence/absence breakpoints.

Expression of each trait was scored on all relevant teeth in the morphological field and this information is used in the descriptive portion of the study. However, only the expression on the key tooth (or assumed key tooth for supplemental traits) for any given trait was used in the multivariate statistical analysis. Certain traits that are typically used in dental morphological studies were left out of this analysis because they were not present in any of the fossil hominins examined (e.g., enamel extension, P^3 distosagittal crest) or because they cannot be assessed from isolated teeth (e.g., incisor rotation or »winging«). Others were excluded (e.g., protostylid and parastyle) because it is unclear to the author whether or not certain morphologies observed in the fossil hominins are homologous to those observed in recent humans.

TABLE 2

Description of non-metric traits used in this study with their presence/absence breakpoints.

LABIAL CONVEXITY (I^1):
The extent to which the labial surface of the incisor is curved when viewed from an occlusal aspect. Presence = Grades 2–4.

SHOVELING I^1, I^2:
The presence of lingual marginal ridges. Presence = Grades 2–7.

DOUBLE SHOVELING I^1:
The presence of labial marginal ridges. Presence = 2–6.

LINGUAL TUBERCLES (*TUBERCULUM DENTALE*) I^1, I^2, C':
Tubercle occurring emanating from the cingular region of the lingual surface. Can range from the form of ridges to a cusp with a free apex. Presence = Grades 2–6.

INTERUPTION GROOVE I^2:
A groove that crosses the cingulum on the lingual tooth surface, often reaching the root. Presence = all expressions.

CANINE DISTAL ACCESSORY RIDGE C:
A ridge occurring in the distolingual fossa between the tooth apex and the distal marginal ridge. Presence = 1–5.

MESIAL CANINE RIDGE (BUSHMAN CANINE) C':
Mesiolingual ridge is larger than the distolingual ridge and is attached to the lingual tubercle. Presence = 2–3.

PREMOLAR ACCESSORY RIDGES OR MaxPAR (P^3, P^4):
The presence of accessory ridges on the buccal and lingual cusps of upper premolars. Degree of expression and location (buccal/lingual and mesial/distal) is scored. Presence = Grades 1–3.

ESSENTIAL CREST PRESENCE AND FORM (P^3, P^4):
Presence of the essential crest on the buccal or lingual cusp. Presence = Grades 1–3. Form may be a single ridge (Grade 1) or a bifurcated ridge (Grade 2).

ACCESSORY CUSPS (P^3, P^4):
The presence of a mesial or distal accessory marginal tubercle in which the sagittal sulcus is strongly bifurcated at the mesial and/or distal marginal ridge resulting in a bulge or free-standing accessory tubercle on the marginal ridge. Presence = any expression of an accessory marginal tubercle. Position – mesial or distal – is noted.

LINGUAL CUSP NUMBER (P_3, P_4):
Number and relative size of the lingual cusps. Presence = Grades 2–9.

MESIAL ACCESSORY RIDGE (P_3, P_4):
Presence of an accessory ridge on the mesiolingual border of the tooth. Presence = Grades 1–3.

DISTAL ACCESSORY RIDGE (P_3, P_4):
Presence of an accessory ridge on the distolingual border of the tooth. Presence = Grades 1–3.

TRANSVERSE CREST (P_3, P_4):
Presence of a crest or ridge connecting the buccal and lingual cusps. Also called the central occlusal ridge. Presence = Grades 1–3.

MESIAL LINGUAL GROOVE (P_3, P_4):
Degree of expression of a groove on the mesial lingual aspect of the tooth. Presence = Grades 1–3.

METACONID POSITION (P_3, P_4):
Position of the metaconid relative to mesial and distal crests of protoconid and position of protoconid apex. The metaconid may be mesial, medial or distal. Presence = Grade 1 (Mesially placed).

CROWN ASYMMETRY (P_3, P_4):
Shape of the lower premolars in occlusal view. Presence = Grades 1–2 (slight and marked asymmetry, respectively).

HYPOCONE (M^1, M^2, M^3):
The presence of the distolingual cusp (Cusp 4). Presence = Grades 3–5. Grades of 2 or less are considered 'reduced' here.

CUSP 5 (C5: M^1, M^2, M^3):
The presence of a fifth cusp (metaconule) that occurs between the metacone (Cusp 3) and hypocone (Cusp 4). Presence = Grades 1–5.

CARABELLI'S CUSP (M^1, M^2, M^3):
A cingulum derivative that occurs on the lingual surface of the protocone (Cusp 1). Expression ranges from a faint ridge/groove to a large cusp with a free apex. Presence = Grades 3–7.

GROOVE PATTERN (M_1, M_2, M_3):
A »Y« pattern occurs when Cusps 2 and 3 are in contact, a »+« pattern when Cusps 1 through 4 are in contact, and an »X« pattern when Cusps 1 and 4 are in contact.

ANTERIOR FOVEA (M_1, M_2, M_3):
Presence of a triangular depression distal to the mesial marginal ridge. The mesial accessory ridges of the protoconid and metaconid form the distal boundary of the depression. Presence = Grades 2–4.

4-CUSPED MOLAR (M_1, M_2, M_3):
The condition of possessing only four cusps, lacking the hypoconulid (the distalmost cusp situated between the entoconid and hypoconid).

DEFLECTING WRINKLE (M_1, M_2, M_3):
The presence of a distally deflected (instead of straight) medial ridge on Cusp 2. Presence = Grades 1–3.

DISTAL TRIGONID CREST (M_1, M_2, M_3):
A ridge or crest that connects the distal aspect of Cusps 1 and 2. Presence = Grade 1.

CUSP 6 (M_1, M_2, M_3):
The entoconulid or *tuberculum sextum* is a supernumerary cusp on the distal aspect of the tooth between the hypoconulid and entoconid. Presence = Grades 1–4.

CUSP 7 (M_1, M_2, M_3):
The *tuberculum intermedium* or metaconulid occurs on the lingual aspect of the tooth between the metaconid (Cusp 2) and entoconid (Cusp 4). Presence = Grades 1–4.

MESIAL MARGINAL ACCESSORY TUBERCLES (M^1, M^2, M^3):
Presence of a accessory tubercles of the mesial marginal ridge complex. (Scott and Turner, 1997). Expression ranges from absence (Grade 0) to marked (Grade 3). Presence = Grades 1–3.

MID-TRIGONID CREST (M_1, M_2, M_3):
The presence of a low enamel ridge that connects the mesial portions of the protoconid (Cusp 1) and metaconid (Cusp 2). This trait was added to the ASUDAS in 1993 , however the scoring system used here is different than the one used there. Presence=Grades 1–3

A mean measure of distance analysis or MMD is used to assess phenetic similarity among the samples. As a multivariate statistic, it calculates group distances based on the entire suite of dental traits. Distances between two samples are considered significant ($p<0.025$) when the MMD is greater than twice the standard deviation . Studies of contemporary humans have shown general agreement between distances based on dental morphology using the MMD and biological relationships using other biological data *(*e.g., *27, 28)*. Thus, it seems reasonable to assume that relationships based on dental morphology are true biological relationships.

In MMD analyses, one should use avoid using traits that are inter-correlated. Data on dental inter-trait correlation (different traits on the same or different teeth) suggest that only two inter-trait correlations are significant in contemporary populations *(29)*. These occur between M^1 Carabelli's trait and M^1, M^2 hypocone and between M^1, M^2 Carabelli's trait and M_1, M_2 protostylid. While the protostylid was not included in this study, both M^1 Carabelli's trait and M^2 hypocone were. This could have a slight affect on the results, although no studies have been undertaken to ascertain whether these traits are inter--correlated in fossil hominins. My observations indicate that traits that are correlated in one fossil group (e.g., anterior fovea and mid-trigonid crest on lower molars in Neandertals) may not be correlated in another (e.g., early modern humans). In addition, whether any of the supplemental traits are significantly correlated with one another or other traits awaits further study with larger sample sizes.

DESCRIPTION OF THE NEANDERTAL DENTITION

Patte *(10)* was the first to provide a description of Neandertal dental morphology. Since that publication many more fossils have been discovered and more is known about the variability within the Neandertal sample. What follows is a review of the current state of knowledge about Neandertal permanent dental morphology and how it compares to that of other Middle-Late Pleistocene hominins. Trait frequencies are provided in Table 3 and details of trait expression (where relevant) are provided below. The primary focus, in terms of presenting trait frequencies, is on the key teeth that are most often used in comparative analyses (upper incisors, upper canines, upper and lower premolars and upper and lower molars).

Incisors (Fig 1)

The 'shovel-shaped' morphology of Neandertal incisors is well known. Turner *et al. (18)* focus only on marginal ridge development, while Mizoguchi *(30)* and Crummett *(17, 31)* have attempted to define shovel-shaping in terms of the whole tooth. Mizoguchi *(30)* included expression of lingual tubercles in his definition(s), while Crummett *(31)* proposed that shovel shaping is best expressed in three dimensions: marginal ridge development, lingual tubercles and labial crown convexity.

In Neandertals, marginal ridge development on the I^1 is ubiquitous and often quite marked in its expression. Using the ASUDAS standard breakpoint of presence (grade 2 or above), shoveling is present in 100% of the specimens. In addition, more than half (54%) of I^1 express very marked ridge development (grade 4 and above). On I^2 shoveling of grade 2 or more is also present in 100% and expression of grade 4 and above is present in 81% of the sample. Incisor lingual tubercles are also ubiquitous, and take the form of well-developed single or multiple ridges on the I^1 and often (62%) cusp-like tubercles on the I^2. Labial convexity on I^1 (grade 2 or above) is present in 96% of the Neandertal sample. In 71% of the sample it

TABLE 3

Non-metric traits, frequencies, samples sizes used in descriptive and multivariate analysis.

Traits	Non-Neandertal Archaic		Neandertal		Early Modern Afro-Asian		Early Modern European	
I^1	% presence	No.	% presence	No.	% presence	No.	% presence	No.
Labial convexity +	*	*	95.8	23/24	50.0	4/8	18.8	3/16
Shoveling +	*	*	91.7	22/24	33.3	2/6	50.0	6/12
Double shoveling +	*	*	4.3	1/23	0.0	0/7	0.0	0/16
Lingual tubercles	*	*	100	24/24	50.0	3/6	58.3	7/12
I^2								
Shoveling	100	1/1	100	31/31	83.3	5/6	42.9	3/7
Double shoveling	100	1/1	3.7	1/27	0.0	0/7	12.5	1/8
Lingual tubercles +	100	1/1	96.0	24/25	66.7	4/6	0.0	0/7
C^1								
Shoveling	100	1/1	95.8	23/24	100	5/5	50.0	4/8
Double shoveling	0.0	0/1	0.0	0/24	12.5	1/8	12.5	1/8
Distal accessory ridge	*	*	66.7	10/15	100	2/2	100	4/4
Lingual tubercles	100.0	1/1	84.0	21/25	20.0	1/5	50.0	4/8
Canine mesial ridge +	*	*	42.9	9/21	0.0	0/5	14.3	1/7
P^3								
Mesial/distal accessory ridges	100	2/2	63.2	12/19	33.3	1/3	25.0	1/4
Buccal essential crest form (bifurcated)	33.3	1/3	57.9	11/19	66.7	2/3	20.0	1/5
Accessory cusps +	50.0	1/2	66.7	14/21	50.0	3/6	42.9	3/7
P^4								
Mesial/distal accessory ridges	50.0	1/2	77.8	14/18	40.0	2/5	33.3	1/3
Buccal essential crest form (bifurcated)	50.0	2/4	70.0	14/20	0.0	0/4	0.0	0/3
Accessory cusps	50.0	1/2	47.6	10/21	12.5	1/8	33.3	1/3
M^1								
Cusp 5 +, *	25.0	1/4	63.6	14/22	40.0	2/5	52.9	9/17
Carabelli's trait +, *	75.0	3/4	68.0	17/25	33.3	2/6	40.0	8/20
Mesial acc cusps	0.0	0/1	40.0	4/10	0.0	0/1	22.2	2/9
Hypocone reduction	0.0	0/6	0.0	0/39	0.0	0/10	0.0	0/25
M^2								
Cusp 5	100	3/3	68.2	15/22	50.0	2/4	38.9	7/18
Carabelli's trait	66.7	2/3	50.0	11/22	14.3	1/7	15.8	3/19
Mesial acc cusps	100	1/1	100	10/10	50.0	1/2	12.5	1/8
Hypocone reduction +, *	0.0	0/4	6.1	2/33	0.0	0/7	15.0	3/20
M^3								
Cusp 5	100	1/1	35.3	6/17	33.3	1/3	28.6	4/14
Carabelli's trait	0.0	0/2	14.3	2/14	0.0	0/4	25.0	3/12
Mesial acc cusps	*	*	70.0	7/10	100	1/1	27.5	3/11
Hypocone reduction	0.0	0/1	68.4	13/19	25.0	2/8	57.1	8/14
Peg/Reduced/Absent	0.0	0/1	7.1	1/14	16.7	1/6	0.0	0/5
C_1								
Distal accessory ridge	50.0	1/2	84.6	11/13	100	3/3	28.6	2/7
P_3								
Mesial accessory ridge	0.0	0/4	23.5	4/17	0.0	0/2	12.5	1/8
Distal accessory ridge	75.0	3/4	90.0	18/20	50.0	1/2	100	9/9
Lingual cusp no. +, *	25.0	1/4	20.6	7/34	16.7	1/6	7.1	1/14
Metaconid position	25.0	1/4	6.3	2/32	50.0	2/4	20.0	3/15
Transverse crest	50.0	2/4	96.7	29/30	75.0	3/4	81.3	13/16
Asymmetry	66.7	2/3	94.4	17/18	75.0	3/4	56.3	9/16
Mesial lingual groove +, *	66.7	2/3	64.0	16/25	25.0	1/4	50.0	7/14

P_4								
Mesial accessory ridge	20.0	1/5	12.5	2/16	66.7	2/3	0.0	0/7
Distal accessory ridge	100	3/3	87.5	14/16	66.7	2/3	25.0	2/8
Lingual cusp no. +, *	80.0	4/5	90.6	29/31	66.7	4/6	50.0	8/16
Metaconid position	100	6/6	96.9	31/32	50.0	3/6	73.3	11/15
Transverse crest +, *	33.3	3/6	93.5	29/31	16.7	1/6	23.5	4/17
Asymmetry +, *	16.7	1/6	93.5	29/31	33.3	2/6	33.3	4/12
Mesial lingual groove	0.0	0/6	8.0	2/25	0.0	0/6	0.0	0/12
M_1								
Fissure pattern (Y)	100	6/6	97.3	36/37	100	8/8	92.9	26/28
Cusp number (4)	0.0	0/7	2.0	1/49	0.0	0/12	2.9	1/35
Deflecting wrinkle +, *	0.0	0/4	3.8	1/26	75.0	3/4	15.8	3/19
Distal-trigonid crest	0.0	0/5	3.0	1/33	0.0	0/6	4.0	1/25
Mid-trigonid crest	71.4	5/7	93.5	29/31	20.0	1/5	0.0	0/24
Cusp 6 +, *	0.0	0/3	36.4	8/22	0.0	0/7	18.2	4/22
Cusp 7 +, *	0.0	0/6	36.1	13/36	50.0	6/12	6.9	2/29
Anterior fovea +, *	83.3	5/6	88.6	31/35	83.3	5/6	52.6	10/19
M_2								
Y pattern +, *	70.0	7/10	75.0	27/36	100	6/6	44.4	12/27
Cusp number (4) +, *	0.0	0/10	0.0	0/39	10.0	1/10	35.0	7/20
Deflecting wrinkle	0.0	0/4	0.0	0/22	0.0	0/2	0.0	0/18
Distal-trigonid crest	0.0	0/7	13.8	4/29	0.0	0/6	0.0	0/24
Mid-trigonid crest	71.4	5/7	96.2	25/26	0.0	0/6	4.2	1/24
Cusp 6	0.0	0/5	50.0	11/22	0.0	0/3	23.5	4/17
Cusp 7	12.5	1/8	20.0	7/35	10.0	1/10	8.3	2/24
Anterior fovea	75.0	6/8	88.5	23/26	20.0	1/5	50.0	10/20
M_3								
Y pattern	0.0	0/1	41.2	7/17	50.0	3/6	55.6	10/18
Cusp number (4)	0.0	0/3	0.0	0/23	28.6	2/7	31.6	6/19
Deflecting wrinkle	0.0	0/4	6.7	1/15	0.0	0/4	0.0	0/14
Distal-trigonid crest	0.0	0/4	10.5	2/19	0.0	0/5	0.0	0/16
Mid-trigonid crest +, *	50.0	2/4	93.3	14/15	0.0	0/5	0.0	0/16
Cusp 6	66.7	2/3	50.0	5/10	40.0	2/5	41.2	7/17
Cusp 7	0.0	0/3	40.0	6/15	0.0	0/7	16.7	3/18
Anterior fovea	75.0	3/4	92.9	13/14	0.0	0/4	46.7	7/15

Note: +, traits used in 21-trait analysis, *, traits used in 15-trait analysis

is at or above the highest expression recorded by the ASUDAS (grade 4). The frequency of double shoveling is very low in Neandertals with only one tooth presenting the weakest of expressions (grade 1).

Shoveling is often considered the primitive hominin condition and it can be observed in Australopithecines, early and later *Homo*. Not surprisingly it is present in moderate frequencies in early modern Afro-Asians and Europeans I^1s (33% and 50%, respectively), although the marked expression observed in Neandertals is absent. Incisor lingual tubercles are less frequent and more weakly expressed in both early modern Afro-Asian and European I^1s (50 and 58%, respectively). The cusp form so frequent on Neandertal I^2s is absent in both Afro-Asian and European early modern samples. Finally, like the other two characters, labial convexity occurs in moderate frequencies in early modern Afro-Asians (50%) and in much lower frequencies in early modern Europeans (19%). However, expression of this trait higher than grade 3 is not observed in either group. None of the early modern Afro--Asian or European upper incisors exhibit double shoveling. Indeed, it appears to be a character that is unique to certain contemporary modern human groups *(32)*.

In sum, although incisor shoveling, labial convexity and lingual tubercles can be found in mild to moderate degrees in other hominids. Neandertals stand out in their high frequency and marked expression of these traits. In particular, it is the frequency with which they exhibit the combination of all three characters (96% in I^1) that makes them distinctive among fossil and recent hominins (only one of the early modern Afro-Asians and none of the early modern Europeans show this combination of characters).

Lower Incisors

Lower incisor morphology is not typically used in analyses of biological distance or taxonomy. This is pri-

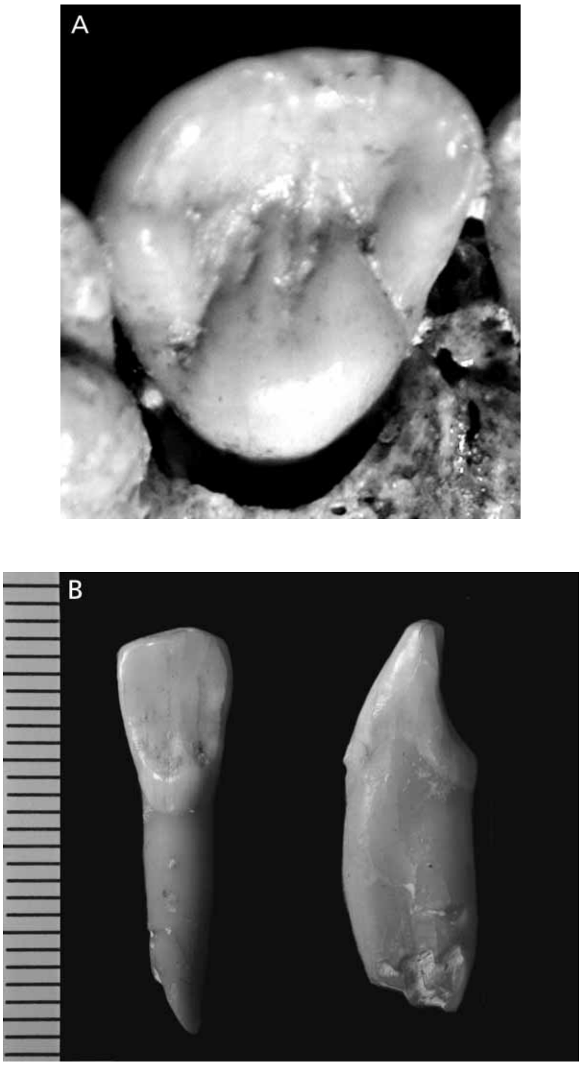

Figure 1. *(A) Neandertal I^1 with marked shovel shape, labial convexity and lingual tubercles and (B) I_2 with simplified morphology.*

marily because they are quite simple compared to other teeth. In contemporary and fossil humans both lingual and labial surfaces tend to be unremarkable. Shoveling and lingual tubercles development, when present, is only weakly expressed. Therefore, in terms of crown morphology the lower incisors are not particularly useful in sorting out taxonomy or biological relationships among Middle-Late Pleistocene hominins. However, Neandertal lower incisor crowns do appear to be distinctive in their relative size, being significantly larger relative to the posterior teeth than those of early modern humans *(33)*. In addition, a recent study suggests that the significantly longer lower incisor roots of Neandertals relative to early modern Europeans may also be diagnostic *(34)*.

Canines (Fig 2)

Upper canines

Neandertal canines tend to be robust. Morphologically, the lingual morphology of the upper canines, in particular, tends to reflect the incisor morphology. The tooth tends to be moderately to strongly convex in both labiolingual and inferiosuperior directions. Nearly all (96%) the Neandertal upper canines show at least slight (grade 2) shoveling and 42% exhibit a higher expression (grade 3). The frequency of lingual tubercles is also high (84%), with 32% exhbiting the tubercle form (> grade 4). Neandertals also present moderately high frequencies of the distal accessory ridge (67%), which can be quite large (20% exceed grade 3) and the canine mesial ridge or Bushman Canine (43%). While the canines show a higher frequency of double shoveling (33%) than the I^1, the expression is typically weak (grade 1).

Shoveling on the upper canine occurs in high frequencies in both early modern Afro-Asian (100%) and

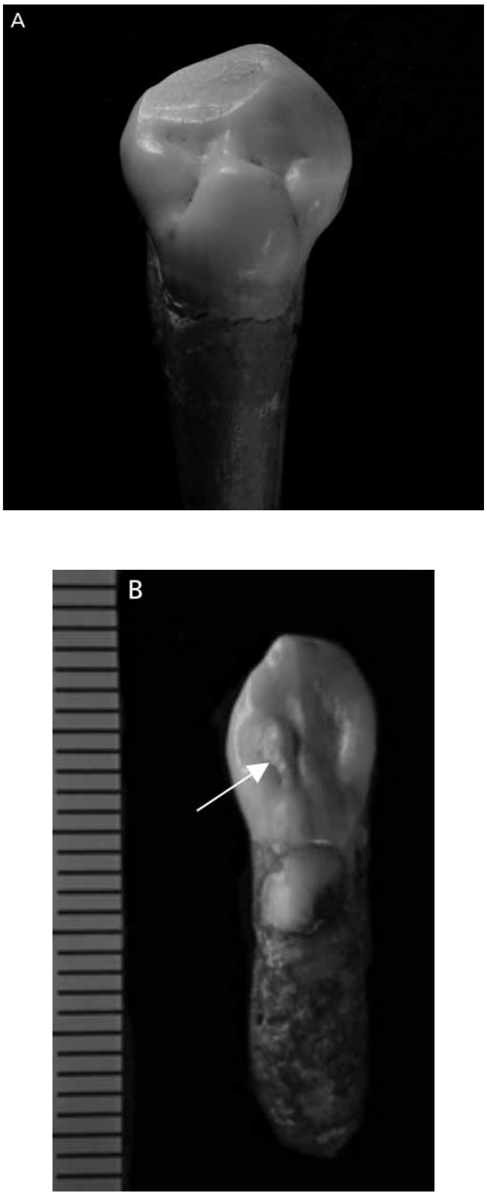

Figure 2. *(A) Neandertal C^1 with marked lingual tubercle development and (B) C_1 with marked distal accessory ridge (arrow).*

early modern European (50%) samples, although the expression does not exceed grade 2 in either group. Lingual tubercles are less common in the early modern groups than they are in Neandertals (20% in early modern Afro-Asian and 50% in early modern European samples). While they may be well developed, they do not attain the tubercle form observed in many Neandertals (>grade 4). The canine mesial ridge, which is a trait most frequently observed in contemporary Sub-Saharan Africans *(29)*, is absent in the early modern Afro-Asian sample but present in low frequencies (14%) in the early modern European sample. The distal accessory ridge is more frequent in early modern samples, being always present. In addition, the expression exceeds grade 3 in half the specimens of each group. Double shoveling is rare (12.5%) in early modern Afro-Asians and absent in early modern Europeans. Like that observed in Neandertals, expression, when present, is weak (grade 1).

Lower Canines

Like the lower incisors, the lower canines are rarely used in studies of biological distance or taxonomy. Their morphology tends to mirror that of the upper canine, with frequencies of the distal accessory ridge being more-or-less the same for the lower canines as it is for the upper canines in Neandertals and early modern Afro-Asians. However, the frequency for this trait in the lower canines in early modern Europeans is much lower than it is for the upper canines. Like the lower incisors, Neandertal lower canines tend to have large crowns relative to the posterior dentition. The difference between Neandertals and early modern humans is less significant than it is for the lower incisors, however *(33)*. The same distinction applies to the tooth root lengths *(34)*.

Premolars (Fig 3)

The occlusal morphology of Neandertal P^3 and P^4s is fairly similar. Both tend to present somewhat complex surfaces. In addition to their two primary cusps they also often present mesial and distal accessory cusplets (67% P^3 and 48% P^4), which tend to occur more frequently distally than mesially. The essential (medial) crest on both cusps is well developed in nearly every specimen and is often bifurcated in form (58% P^3 and 70% P^4). In addition, mesial and distal accessory ridges *(35)* are not uncommon (63% P^3 and 70% P^4), and occur more often buccally than lingually. Traits such as the distosagittal ridge, tricuspid premolars and odontomes that are rare in contemporary humans *(36)* are not observed in any of the Neandertal upper premolars.

The occlusal morphology of other fossil hominin upper premolars can also be complex. Frequencies do not differ very much among groups for traits on the P^3. The P^4 appears to be more simplified in early modern humans relative to Neandertals. In early modern humans they lack the bifurcated essential crest, present low frequencies of accessory crests (40% and 33% in early modern Afro-Asian European samples, respectively) and lower frequencies of mesial and distal accessory cusps (12.5% and 33% in early modern Afro-Asian and European samples, respectively). Of the early modern human samples, the European sample appears more simplified.

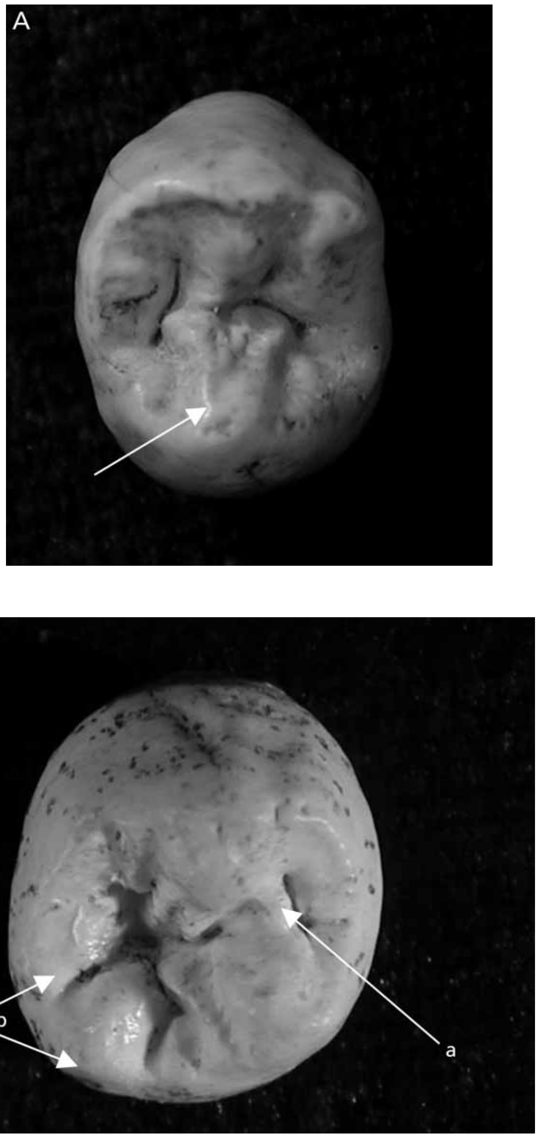

Figure 3. *(A) Neandertal P^4 with bifurcated essential crest (arrow) and (B) P_4 with slight crown asymmetry, marked transverse crest (a) and multiple lingual cusps (b) (arrows).*

Lower Premolars

Like the upper premolars the occlusal morphology of Neandertal lower premolars tend to be complex, exhibiting accessory fissure and crests. On the P_3 this is manifest by the nearly ubiquitous presence of a transverse crest connecting the buccal and lingual cusps, high frequencies of accessory ridges (distal: 90% and mesial: 24%) and a low frequency of accessory lingual cusps (20%). The metaconid tends to be about half the height of the protoconid and it is only rarely mesially oriented. In addition, a lingual groove that crosscuts the cingulum is not uncommon and occurs more frequently mesially (64%) than distally (33%). The occlusal crown outline tends to be somewhat asymmetrical (94%) and it is sometimes (39%) markedly so.

Certain aspects of Neandertal P_4 shape and occlusal morphology have been described previously *(15, 21)*. Like the P_3, the P_4 tends to exhibit a strong and continuous transverse crest connecting the protoconid and metaconid (77%). The crest comprises the distal border of the anterior fovea, which is often quite large. The metaconid is more strongly developed in the P_4 and is usually subequal in height with the protoconid. Neandertals exhibit a moderate frequency of the distal accessory ridge (25%), but unlike the P_3 the mesial accessory ridge is absent. Very frequently the P_4 possesses accessory lingual cusps (91%), which may take the form of single (40%) or multiple (50%) distolingual cusps. In addition, like the P_3 the occlusal outline is nearly always asymmetrical (93.5%) and often strongly so (79%). In contrast to the P_3, the metaconid of P_4 is almost always mesially placed (97%) and is never distally placed. The combination of a strong transverse crest (grade 2), marked asymmetrical outline (grade 2) and multiple lingual cusps occurs in 61% of the Neandertal P_4s. In an additional 28%, two of these characters occur in combination.

Relative to the other fossil hominins examined here the occlusal surface of the Neandertal P_3 is not particularly distinctive. Each of the fossil groups exhibits high frequencies of P_3 crown asymmetry, although it is highest in Neandertals. While both non-Neandertal archaics and early modern Afro-Asians occasionally show marked asymmetry (33% and 25%, respectively) the early modern Europeans do not. A strong transverse crest is common in all fossil hominin P_3s. It is completely absent in only one Neandertals P_3 (3%), none of the non-Neandertal archaics, one of the four early modern Afro-Asians (25%) and three (18%) of the early modern Europeans. The mesial lingual groove is equally present in Neandertals and non-Neandertal archaics and less frequent in both early modern human samples. The distal accessory ridge is present in high frequencies in all fossil hominins, although it is highest in Neandertals and early modern Europeans, while the mesial accessory ridge is absent from all but the Neandertal samples. Aside from the presence and frequencies of mesial and distal accessory ridges, the P_3s do not appear to be particularly diagnostic. However, a morphometric analysis of the occlusal outline and cusp and groove relationships may prove otherwise *(37)*.

Most of the P_4 traits described above occur in some frequency in the fossil hominins studied. The high frequency of a marked transverse crest, asymmetry and multiple lingual cusps distinguish Neandertals from early modern samples, but less so from non-Neandertal archaics. It is the combination of traits that is very characteristic of Neandertals (see above), rather than any one trait alone. Interestingly, non-Neandertal archaics also show an incipient Neandertal pattern: the transverse crest is present in half the specimens, strong asymmetry in 17%, and multiple lingual cusps in 80%. One specimen exhibits the combination of all three traits while three (50%) show the combination of two traits. In contrast, while the early modern Afro-Asian sample exhibits relatively high frequencies of two lingual cusps (67%), three lingual cusps are not observed. The transverse crest occurs in one of the specimens and none possesses a marked asymmetrical outline. In early modern European P_4s the transverse crest is absent. Asymmetry occurs in 30% of the specimens but is never marked. Multiple lingual cusps occur frequently (43%) although only one of the P_4s possesses more than two lingual cusps. Unlike Neandertals, neither of the early modern groups possesses two or three traits in combination. It appears, therefore, that the combination of all three premolar traits is diagnostic of Neandertals (and their probable immediate ancestors).

Molars (Fig 4)

Upper molars

The four main cusps (protocone, paracone, metacone and hypocone) of the Neandertal M^1 tend to be well developed. The hypocone is never reduced or absent. In addition, a fifth cusp – the hypoconule – is not uncommon (64%). Carabelli's trait occurs frequently (68%) and is often well developed (33% > grade 5). Accessory cusps deriving from the mesial marginal ridge are common (40%). In addition to occlusal morphology, the distinctive skewed rhomboidal shape, relative cusp areas and cusp relationships have been described previously *(13, 22)*. These include the exceptionally large hypocone, relatively reduced and internally oriented metacone, and internally compressed cusp tips.

The M^2 also possesses four well-developed main cusps. The hypocone is rarely reduced and never absent. As in the M^1 the hypoconule is common (68%), as is Carabelli's trait (50%), although it is less often strongly developed (9% exceed grade 5). Accessory cusps deriving from the mesial marginal ridge are ubiquitous (100%). The morphometric distinctions (relative cusp areas, etc.) found in the M^1 are less pronounced in the M^2 and do not differ significantly from that of other fossil or even contemporary modern humans *(13)*.

The Neandertal M^3 often presents a hypocone that is reduced (68%) or essentially absent (37% <grade 2), but also may present a hypoconule (35%). In one case (7%) an individual's M^3s are much-reduced in size and morphology. Carabelli's trait occurs much less frequently on M^3 (14%) than it does on M^1 or M^2 and is rarely (7%) strongly developed. Accessory cusps deriving from the mesial marginal ridge are occur in 70% of the Neandertal specimens.

In terms of the key morphological traits observed in this study, non-Neandertal fossil hominins M^1s are broadly similar to that of Neandertals. The hypoconule is present although in lower frequency in non-Neandertal archaics (25%), early modern Afro-Asian (40%) and early modern European (53%) samples. Carabelli's trait is not infrequent in non-Neandertal fossil samples, and in 50% of the non-Neandertal archaic, 25% of the early modern

European and 33% of the early modern Afro-Asian samples it is well developed (grade 5 or higher). Hypocone reduction is absent in all fossil hominin M^1s. Mesial accessory cuspules occur in 22% of the early modern European sample, and are absent from each of the single non-Neandertal archaic and early modern Afro-Asian M^1 that could be scored for the trait. A morphometric analysis of M^1 shape showed a clear distinction between Neandertal and non-Neandertal groups. The relative occlusal polygon area is significantly smaller in Neandertals than it is in early modern Europeans *(13)*. It is also much smaller than that observed in the non-Neandertal archaics and early modern West Asians (no early Africans could be measured), although small sample sizes preclude significance testing. In terms of relative cusp areas, the Neandertals are distinct from early modern Europeans, possessing a relatively large hypocone and relatively small metacone. However, in these features they are similar to the early modern West Asian sample.

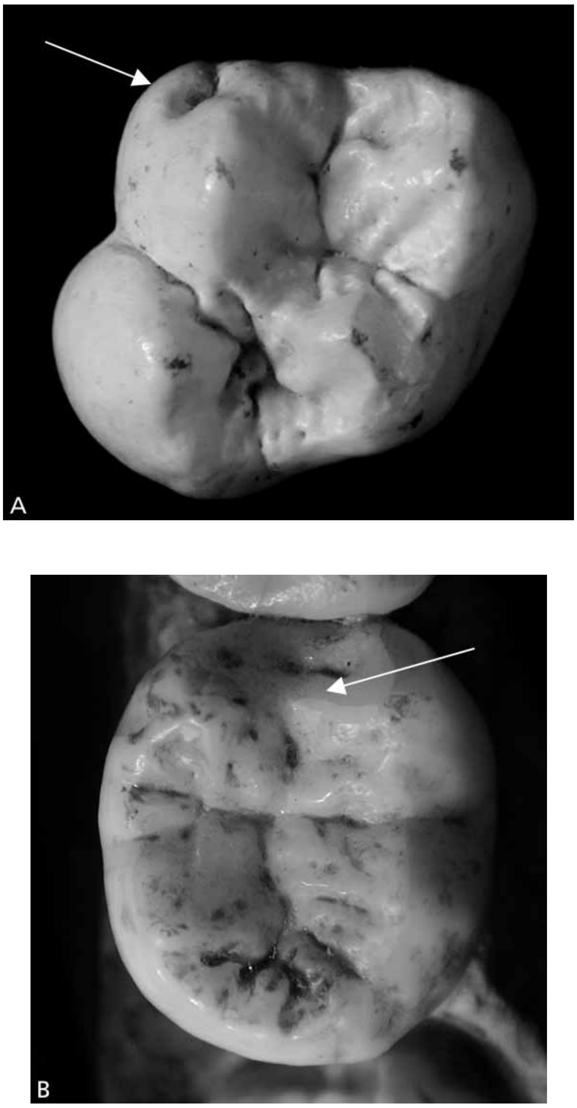

Figure 4. *(A) Neandertal M^1 with large Carabelli's cusp (arrow), large hypocone, reduced metacone, internally placed cusp tips and skewed shape and (B) M_1 with mid-trigonid crest (arrow).*

Neandertals and non-Neandertal archaics are broadly similar in their M^2 morphology, although Neandertal M^2s show slightly lower frequencies of the hypoconule and Carabelli's trait and slightly higher frequency of hypocone reduction (keeping in mind the small non-Neandertal archaic sample). In contrast, Neandertal M^2 are distinguished from that of early modern humans in the latter group's simplification of the tooth crown. The frequency for the hypoconule and Carabelli's trait – both mass-additive traits – is lower in both of the anatomically modern groups than it is in Neandertals, although frequency for higher expressions (5 or greater) is more-or-less the same for the three groups (9–14%). The frequency of hypocone reduction is low in all groups.

The M^3 of the non-Neandertal fossil groups are quite similar in trait frequencies. All show moderate frequencies of the hypoconule and Carabelli's trait. The early modern Afro-Asian sample has a lower frequency of hypocone reduction than either the Neandertal or early modern European group, but like Neandertals it shows a relatively high frequency of mesial accessory cusps. A single reduced M^3 can be found in each of the Neandertal and early modern Afro-Asian samples but not in any of the five early modern European individuals.

Lower molars

The Neandertal M_1 tends to be occlusally complex, possessing extra fissures and crests – many of which are not currently assessed by the ASUDAS. In terms of key morphological traits, the M_1 nearly always possesses at least five cusps (98%) and a Y fissure pattern (97%). Cusp 6 is also moderately frequent (36%) and Cusp 7 occurs in low frequencies (36%). The deflecting wrinkle is present in one of the specimens and the distal trigonid ridge is absent. The most remarkable features observed on this tooth are a wide and deep anterior fovea bordered distally by a continuous mid-trigonid crest. A well-developed anterior fovea occurs in 89% of the Neandertal M_1s sampled and a well-developed mid-trigonid crest occurs in 94%.

The Neandertal M_2 is similar to the M_1 in its morphology. None of the M_2s possess fewer than five cusps and 75% maintain the Y-pattern. Cusp 6 occurs in moderately high frequency (50%), while the frequency for Cusp 7 is lower (20%). The distal trigonid crest occurs infrequently (14%) and the deflecting wrinkle was not observed. As with M_1, the anterior fovea and mid-trigonid crest occur in high frequencies on M_2 (89% and 96% respectively).

The Neandertal M_3 presents five or more cusps and not infrequently Cusp 6 (50%) and/or Cusp 7 (40%). The fissure pattern may take a Y or X form, with the latter being more common (59%). The deflecting wrinkle and distal trigonid crest are occasionally present (7% and 10.5%, respectively). Like the other lower molars, the M_3 is notable for its high frequency of the mid-trigonid crest and associated large anterior fovea (93%, both traits).

The Neandertal M_1 is superficially similar to the M_1 of other fossil hominins. All fossil hominins show high frequencies for the primitive Y-5 pattern and low to absent frequencies of 4-cusped M_1. Frequencies for the distal trigonid crest and deflecting wrinkle are generally low in all groups, with the exception of the high frequency (75%) of the latter in the early modern Afro-Asian group. With the exception of the early modern European sample the non-Neandertal samples lack Cusp 6, whereas the early modern Afro-Asian sample is more like Neandertals than the other groups in its frequency for Cusp 7. The most notable way in which Neandertals differ from early modern humans (but not from non-Neandertal archaics) is in its high frequency of the mid-trigonid crest. Although most groups show high frequencies of the anterior fovea (early modern Europeans excepted), this does not co-occur with a mid-trigonid crest.

The high frequencies of Y-pattern together with the low frequency of 4-cusped M_2 align Neandertals with non-Neandertal archaics and early modern Afro-Asians. The early modern European sample, on the other hand, shows a considerably lower frequency for the Y-pattern (46%) and a considerably higher frequency for 4-cusped M_2 (35%). Not unlike Neandertals the distal-trigonid crest and deflecting wrinkle are absent in the non-Neandertal samples in this study and Cusp 7 occurs infrequently. The frequency for Cusp 6, however, is much lower in non-Neandertal fossil hominins. As was the case for M_1, the primary difference between Neandertal and early modern human M_2s is their high frequency of expression of both the mid-trigonid crest and anterior fovea.

Of the lower molars the M_3 is probably the most informative in distinguishing Neandertal from early modern humans. Unlike, Neandertals, the early modern humans M_3s are often four-cusped and have much lower frequencies of the anterior fovea and Cusp 7. In addition, neither of the early modern human samples show the mid-trigonid crest on the M_3, whereas in Neandertals it is present in 93% of the individuals. Interestingly, the anterior fovea is fairly common in early modern Europeans (47%) but in this case it does not co-occur with the mid-trigonid crest.

MULTIVARIATE ANALYSIS

The following analysis uses trait frequencies to obtain measures of dissimilarity (distances) among Neandertals and other Middle-Late Pleistocene fossil hominins (see Table 3 for traits used). The sample sizes varied from trait to trait. In order to maximize the number of traits all samples containing three or more individuals were used in the multivariate analysis. The Neandertal sample ranged from 14 to 40, while the early early modern Afro-Asian sample ranged from 6 to 12 and the early modern European sample ranged from 5 to 40. The non-Neandertal archaic sample was the smallest and ranged from 3 to 10 (one sample had an n of 3). Certain issues arise when using small sample sizes in MMD analyses *(see 38)*. Even though the MMD program utilizes the Freeman and Tukey angular transformation to correct for small sample sizes *(25, 26, 39)*, for certain traits the sample sizes are likely too small even for this correction. Therefore, some caution should be used in interpreting the significance of the MMD results.

The multivariate analysis consisted of two separate data sets. Because of its small sample size, in order for the non-Neandertal archaic group to be included in the MMD analysis several traits had to be excluded. Therefore the analysis was performed once including non-Neandertal archaic sample using 15 dental traits and a second time excluding the non-Neandertal archaic sample and using 21 dental traits. Tables 4 and 5 present the results of the MMD analysis.

TABLE 4

MMD values in a 15 trait comparison of Non-Neandertal archaics (AHS), Neandertals (N), early modern Afro-Asians (EAFAS) and early modern Europeans (EEUR)

	AHS	N	EAFAS	EEUR
AHS	0	0.175*	0.081	0.116
N		0	0.780*	0.849*
EAFAS			0	0.153*
EEUR				0

* = significant $p<0.025$

TABLE 5

MMD values in a 21 trait comparison of Neanderthals (N), early modern Afro-Asians (EAFAS) and early modern Europeans (EEUR)

	N	EAFAS	EEUR
N	0	0.714*	1.026*
EAFAS		0	0.180
EEUR			0

* = significant $p<0.025$

In the 15-trait analysis, the closest affinity with non-Neandertal archaics is with the early modern Afro-Asians group and the most distant affinity is with Neandertals. This is unexpected, given that a much closer (and non-significant) distance was previously found between Neandertals and non-Neandertal archaics using a somewhat different set of postcanine traits *(13)*. This could be attributable to different break points used in the two analyses (the previous study used a higher break point for P_4 asymmetry and P_4 transverse crest) or different sample compositions. It is worth noting that no anterior tooth traits were included in this analysis. Based on observations of non-Neandertal archaics (a.k.a. *H. heidelbergensis*) from Sima de los Huesos, Spain *(37)*, including incisor traits in the analysis (e.g., I^1 shoveling, I^1 labial convexity and I^2 lingual tubercles) would have very likely decreased the distance between the non-Neandertal archaic and Neandertal samples and increased the distance between the former and the early modern samples. The latter samples show low to moderate frequencies of I^1 shoveling I^1 labial convexity and I^2 lingual tubercles.

The remaining pair-wise comparisons (between Neandertals and early modern samples) are significant. The distances between Neandertal and early modern human samples are the highest and the distance between the two early modern human samples are the lowest. Neandertals are more than four times more distant from the early modern samples than the early modern samples are from each other. And they are more distant form early modern Europeans than they are from early modern Afro-Asians.

In the 21-trait analysis, from which non-Neandertal archaics are excluded, the results are very similar. The distance between Neandertal and early modern Afro-Asian samples is, in fact, very similar. The inclusion of the anterior tooth traits in the analysis substantially increases the distance between Neandertals and early modern Europeans. It also increases the distance between the two early modern human samples but to a lesser degree.

DISCUSSION: WHAT CAN TEETH TELL US ABOUT THE EVOLUTION OF NEANDERTALS?

Early in the 20th century tooth morphology made up an intergral part of interpreting Neandertal phylogeny. Some researchers concluded that the dental evidence excluded Neandertals from modern human ancestry *(40)*. Others felt that Neandertal teeth differed little from our own *(16, 41)* – the latter sentiment seems to be the one that has been retained. Aside from the high frequency of taurodont molars and exceptional tooth size Neandertals have been thought to possess »no features that cannot be found in modern man« *(42: 327)*. Traits that were differently expressed in Neandertals were considered by many to be primitive and of no phylogenetic significance *(4, 16)*. Subsequently, although not completely forgotten, the Neandertal dental morphology became less important with most studies focusing primarily on cranial and post-cranial morphology. Interestingly, dental morphology has played a more significant role in deciphering the taxonomy of and relationships among Plio-Pleistocene hominins *(43–48)*, than it has for later hominins. It has only been relatively recently that researchers have returned their attention to the teeth *(13, 15, 20, 22, 37, 49)*. Even so, some continue to claim that Neandertal teeth are morphologically 'undiagnostic' *(50)*, even in the face of evidence to the contrary *(15, 21, 22)*.

In a recent analysis comparing postcanine dental morphology of Neandertals, contemporary and fossil humans Neandertals were found to exhibit a unique pattern of dental trait frequencies *(13)*. In addition, among contemporary populations they were found to be most distant from South Asians (i.e., from India) and Europeans and least distant from Australians, although MMD values between Neandertals and all contemporary humans were found to be high and significant. Among the fossil hominins Neandertals were found to be significantly distant from Upper Paleolithic and early modern humans from Qafzeh and Skhul *(13)*.

The present study focuses on placing Neandertals in a comparative fossil hominin context and comprises a slightly different set of traits, including those on the anterior teeth. It is based on larger samples, which include several additional early modern humans from Europe and South Africa. While it is somewhat surprising that the non-Neandertal archaics in this study are most distant (and significantly so) from Neandertals, it is very likely that this is due to trait selection (e.g., no anterior tooth traits were used) that was necessitated by small sample sizes. The remaining results are similar to the previous study, in that the Neandertal – early modern European (»Upper Paleolithic« in the earlier study) pair-wise comparison produces the highest MMD value and that Neandertals are very distant from both early modern human samples. The distance between the Neandertal and early modern European samples is highly significant, although the two groups are slightly less distant than was found the earlier study (MMD=1.026 vs 1.159). The distance between Neandertals and the earliest modern humans (e.g., those from South Africa and the Near East) is higher in the present study (0.714) than it was in the previous study (0.653), which was based only on the West Asian specimens. In both cases the MMD values (distances) are significant. This could be interpreted to indicate that the Neandertal unique dental pattern (relative to contemporary modern humans) is not a primitive retention but is derived from the ancestral condition.

This study, like the previous one, also found that many traits observed in Neandertals can be found in varying frequencies in other fossil hominin groups. Based on their occurrence in Plio-Pleistocene hominins (e.g., *32, 51)*, most are likely to be primitive retentions. The primary difference between Neandertals and other fossil hominin groups is in (i) the exceptionally high frequency of certain traits, (ii) the marked expression of these and other traits and (iii) the combination of certain traits in individual teeth. Contrary to recent assertions *(50)*, it is inaccurate to conclude that Neandertal teeth are undiagnostic simply because some typically 'Neandertal' traits can be found in low frequencies in modern humans. A recent study that calculated the probability that a dental series belonged either to Neandertals or Upper Paleolithic modern humans showed that when all the data are considered, a secure diagnosis can be made *(52)*. Even more recently, Bailey and Weaver *(53)* have developed a computer program that calculates the posterior probability that any particular individual (sometimes consisting of only a single tooth) belongs to Neandertal vs. anatomically modern human groups. It has produced good classificatory results (83% correct) similar to that generally viewed as acceptable for sexing archaeologically derived specimens from the pelvis (e.g., 85%) *(54)*. Therefore, tooth crown morphology should be considered an important diagnostic tool, especially when the question is: »Is it Neandertal or is it anatomically modern?«

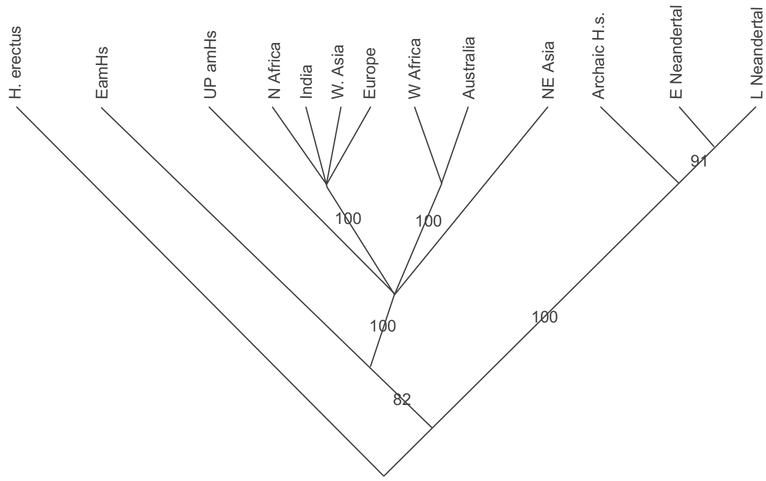

Figure . *The 75 ma ority consensus tree produced from the 11 most parsimonious cladograms based on an earlier study* (13).

Working out the phylogenetic relationships among Middle-Late Pleistocene hominins based on dental morphology is a more difficult task. First, cladistic analyses require that traits be coded into character states (e.g., present/absent, small/medium/large). Dental non-metric traits are neither 'present' nor 'absent' but rather continuously graded in their expression. Second, even if one categorizes variation into such character states, there is a great deal of variation within hominin groups (especially in contemporary humans) and it is inaccurate to provide a single character state for an operational taxonomic unit (OTU). One way around this is to use Thiele's gap weighting method *(55)*, in which trait frequencies can be broken up into character states preserving information on the size of gaps between the states. This kind of analysis has been undertaken previously *(13)* and for the most part, the cladistic results were very similar to the results of a phenetic analysis based on MMD distances. In that analysis Neandertals and non-Neandertal archaics (a.k.a. *H. heidelbergensis*) shared a more recent common ancestor with each other than either one did with early or contemporary anatomically modern humans (Figure 5).

The difference in phenetic similarity between Neandertals and non-Neandertal archaics in this and the previous study *(13)* should be explored with larger samples that would enable the use of anterior tooth crown traits. Although the number of non-Neandertal archaic humans is growing *(56)*, the number of teeth available for study is still small. Preliminary analyses by Martin n- Torres *et al. (37)* suggest that diagnostic Neandertal traits are already present in low frequencies in the Sima de los Huesos material. Forthcoming publications on these and other individuals from this time period from African and Europe will prove, no doubt, to be very interesting.

* Note: Portions of this manuscript were published previously in my dissertation (Bailey, 2002).

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