Dental Morphological Affinities Among Late Pleistocene and Recent Humans

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ABSTRACT This study uses analyses of Mean Measure of Divergence (MMD) to assess the affinities of ten populations representing early anatomically modern humans, Upper Paleolithic Europeans, recent modern humans, and Neandertals. The 18-trait MMD analysis demonstrates that, dentally, Neandertals are quite divergent from all modern humans. The results of cluster analyses based on MMD values suggest two major clusters: Neandertals and modern humans. The data also suggest two sub-clusters within the modern human cluster. One links Upper Paleolithic Europeans with recent North Africans and Europeans. The other links early anatomically modern humans with Late Pleistocene Africans and recent Sub-Saharan Africans. These results do not support a close relationship between Neandertals and any modern human groups sampled. They also tentatively suggest that, if the two populations were interbreeding, it is not reflected in their dental morphology. The results showing a close affinity between early anatomically modern humans and Sub-Saharan Africans are consistent with the Recent African Origin model for modern human origins.

INTRODUCTION

Over the past two decades research on modern human origins has focused on interpreting fossil remains within the framework of either of two competing models. These are the Multi-Regional Evolution model (MRE): modern humans evolved from archaic predecessors in many parts of the world (Wolpoff et al., 1984; Frayer et al., 1993) and the Recent African Origin model (RAO): modern humans have a single origin, from which they spread replacing existing "archaic" hominids in the rest of the world (Stringer et al., 1984; Cann, 1987; Stringer and Andrews, 1988). While most paleoanthropologists who study late Pleistocene human evolution no longer view these models as mutually exclusive and, therefore, accept some form of "out of Africa with admixture" hypothesis, most new research remains focused on testing either of the two more extreme models (Holliday, 1999; Kidder, 1999, Wolpoff et al., 1999).

Although early researchers gave considerable weight to certain morphological dental traits in classifying Neandertals and other hominids (Keith, 1924; 1925; Weidenreich, 1937), cranial and postcranial morphology and metrics have figured relatively more prominently in testing hypotheses for modern human origins (Stringer, 1992; Trinkaus, 1992; Holliday, 1997; Wolpoff et al., 1999). Studies that have emphasized the dentition have focused primarily on metric trends (Brace et al., 1987). Descriptive studies of dental morphology have dominated the literature on later Pleistocene hominid teeth (Genet-Varcin, 1966; 1972; Smith, 1976; Trinkaus, 1978; Tillier, 1979; Wolpoff, 1979; Tillier et al., 1989; Trinkaus et al., 1999) and systematic studies of tooth crown characteristics have only recently been brought to bear on the issue of modern human origins (Crummett, 1994; Stringer et al., 1997; Irish, 1998; Tyrell and Chamberlain, 1998).

Building on these studies that relied on samples of very recent modern humans and a single Neandertal sample (e.g., the one from Krapina), Bailey and Turner (1999) compared the dental morphology of three geographically distinct Neandertal samples to that of (geographically and temporally distinct) early anatomically modern humans (Qafzeh/Skūhl) and recent Europeans. The results of Mean Measure of Divergence analysis indicated that, dentally, all Neandertal groups are more similar to each other than they are to either modern human sample. The analysis also indicated that Neandertals from one region are no more similar to modern humans from the same region (in this case, Europe and Western Asia) than they are to other modern humans, as might be expected if they contributed significantly to later human evolution in these regions.

TABLE 1. Fossil and recent samples used in this study.

Site	Fossils, Casts	Maximum Individuals	Maximum Scorable Teeth
Neandertals, Central Europe			
Krapina	casts	34	203
Neandertals, Western Europe			
Petit Puymoyen	fossils	5	12
Monsempron	fossils	4	11
Devil's Tower	casts	1	2
Arcy-sur-cure	casts	3	10
La Quina	casts	2	23
Spy	casts	2	32
Montgoudier	casts	1	3
Combe Grenal	casts	1	6
Châteaueneuf	casts	1	4
Marillac	casts	1	3
La Ferrassie	casts	3	4
Régourdou	casts	1	16
Neandertals, Near East			
Amud	fossils, casts	2	33
Tabūn	casts	5	30
Kebara	fossils, casts	1	17
Shanidar	casts	5	36
Early Anatomically Modern Humans			
Quafzeh	fossils, casts	8	116
Skhūl	fossils, casts	6	55
Upper Paleolithic, Western Europe			
Abri Blanchard	fossils	1	1
Abri Labatut	fossils	2	5
Isturitz	fossils	5	16
La Chaud	fossils	3	34
Fontéchevade	fossils	2	2
Grotte des Rois	fossils	3	44
Gruta da Caldierao	fossils	6	7
Galeria da Cisterna	fossils	2	9
Upper Paleolithic, Central Europe			
USSR	published[4]		
Late Pleistocene Africa			
Late Pleiscocene Africa	published[2]		
Recent Modern Humans			
Sub-Saharan Africans	published[1,2,3]	772	
North Africa	published[1,2,3]	545	
Northwest Europe	published[4]	162	
Poundbury	published[1,2,3]	131	

[1]Irish (1993), [2]Irish (1995), [3]Irish and Turner (1990), [4]Turner (1984). Upper Paleolithic Western Europe and Upper Paleolithic Central Europe samples were combined in the analysis. See text for explanation.

The primary objective of this study is to ascertain the dental relationships among fossil and recent human populations. This study differs from earlier ones by using a larger fossil sample (including Upper Paleolithic Europeans and early modern humans) and by using 18 tooth crown traits. MRE predicts that different geographic areas will show regional morphological differences that persist through time (Wolpoff, 1995:239). Therefore, as a test of MRE in Europe and Western Asia, I use Mean Measure of Divergence and cluster analyses to test the null hypothesis that Neandertal and AMH populations from one geographical region are (dentally) more similar to each other than either is to populations from other regions. The results of this study are discussed in terms of identifying a Neandertal dental morphological pattern and the significance it has for models of human origins.

MATERIALS and METHODS

MATERIALS

The samples include ten populations representing Neandertals and anatomically modern humans (AMH). The Neandertal, early AMH, and Upper Paleolithic Western European data were collected by me from both original fossils and high-definition casts that were produced and made available for study by Erik Trinkaus. The remaining data were taken from published sources (Table 1).

The Neandertal Sample

The Neandertal sample is divided into subsets based on their geographical sourcing. These subsets include Central European Neandertals, Western European Neandertals, and Near Eastern Neandertals (Table 1). Specimens included in the Central European subset are from the site of Krapina, Croatia. The 33 individuals used in this study are the result of Wolpoff's (1979) grouping of isolated and *in situ* teeth based on tooth morphology, wear and association, and also three composite individuals based on isolated teeth.

Data for specimens representing Western European Neandertals were collected from sites in France, Belgium and Spain. For some sites that consist largely of isolated teeth (e.g., Le Rois) composite individuals were created based on tooth status and morphology. Specimens representing Near East Neandertals are from Israel and Iraq.

The Modern Human Sample

The large modern human sample is divided into early AMH, Late Pleistocene African, Upper Paleolithic European and Recent human groups. The early AMH sample consists of individuals from sites of Qafzeh and Skhūl, Israel. The Upper Paleolithic European sample consists of data collected on fossils from sites in France and Portugal and published data on Upper Paleolithic fossils from Central Europe. The published data represent Late Pleistocene Africa, North African, Sub-Saharan Africa, England (Irish and Turner,1990; Irish, 1993; 1995) and Upper Paleolithic Northwest and Central Europe (Turner, 1984) (Tables 1, 2).

TABLE 2. Dental trait percentages and frequencies of ocurrence in samples used in this study.

	Labial Convexity UI1		Shovel UI1		Double Shovel UI1		*Tuberculum dentale* UI2		Mesial Ridge UC		Distal Acc. Ridge UC		Hypocone UM2		Cusp 5 UM1		Carabelli's Trait UM1	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
FOSSIL SAMPLES																		
Qafzeh/Skūhl	6	50.0	4	0.0	5	0.0	6	50.0	5	0.0	3	100.0	7	100.0	6	50.0	6	66.7
W. Europe Upper	3	0.0	3	66.7	3	0.0	1	0.0	1	0.0	1	100.0	4	100.0	5	60.0	4	50.0
Near East Neandertals	3	66.7	3	100.0	4	0.0	5	100.0	2	100.0	1	100.0	6	100.0	4	0.0	1	0.0
Central Europe	13	100.0	13	100.0	12	0.0	13	100.0	12	50.0	7	42.9	9	100.0	7	71.4	8	87.5
Western Europe Neandertals	6	83.3	6	100.0	4	0.0	6	50.0	4	50.0	3	66.7	8	100.0	4	75.0	5	80.0
PUBLISHED DATA																		
C. Europe Upper			6	16.7	6	16.7	3	66.7	3	0.0	3	33.3	5	60.0	6	0.0	7	57.1
Africa Late Pleistocene			22	59.1	20	0.0	18	38.9	18	22.2	7	71.4	27	92.6	14	28.6	13	46.2
Sub-Saharan Africa	425	55.5	413	28.1	437	1.1	454	61.2	586	18.1	483	71.8	772	99.0	618	32.8	683	51.2
North Africa	177	38.4	154	19.5	175	8.6	188	38.8	261	6.1	195	17.9	446	76.7	619	32.8	357	12.6
Northwest Europe	173	8.7	34	29.4	28	39.3	50	64.0	62	4.8	19	31.6	115	81.7	97	15.5	115	33.9
England			107	13.1	109	19.3	102	25.5	84	4.8	70	57.1	113	77.0	115	12.2	115	60.9
TRAIT PRESENCE	2-4		2-7		2-6		2-7		1-5		1-5		1-5		1-5		2-6	

	Parastyle UM3		Lingual Cusp No. LP2		Groove Pattern LM2		Cusp No. LM1		Cusp No LM2		Protostylid LM1		Cusp7 LM1		Anterior Fovea LM1		Peg/Red/ Absence UM3	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
FOSSIL SAMPLES																		
Qafzeh/Skūhl	7	14.3	3	66.7	5	40.0	7	0.0	7	33.6	7	0.0	7	0.0	2	50.0	5	20.0
W. Europe Upper	2	50.0	3	33.3	6	66.7	6	33.3	8	12.5	7	28.6	8	12.5			2	0.0
Near East Neandertals	1	0.0	4	100.0	4	75.0	5	0.0	6	33.3	6	0.0	7	14.3			4	50.0
Central Europe	8	12.5	14	85.7	14	78.6	10	40.0	12	0.0	14	0.0	12	58.3	12	91.7	6	0.0
Western Europe	5	0.0	10	70.0	11	100.0	13	53.8	14	0.0	15	20.0	15	26.7	10	90.0	5	0.0
PUBLISHED DATA																		
C. Europe Upper	1	0.0	4	25.0	6	16.7	7	0.0	5	80.0	7	14.3	8	0.0			4	0.0
Africa Late Pleistocene	34	0.0	39	0.0	15	93.3	27	59.3	30	30.0	33	6.1	21	28.6	28	3.6	39	0.0
Sub-Saharan Africa	550	2.0	530	68.5	617	52.4	561	16.6	585	24.1	556	21.0	598	38.5	418	67.5	708	5.4
North Africa	332	1.2	270	72.6	402	30.6	352	7.7	381	33.6	351	32.5	408	5.1	198	37.9	545	15.2
Northwest Europe	71	1.4	100	65.0	137	24.1	102	6.9	111	59.5	125	20.0	143	7.0			162	25.3
England	63	7.9	59	59.3	77	20.7	76	9.2	78	73.1	75	20.0	79	3.8			78	11.5
TRAIT PRESENCE	1-5		2-3		Y		1-5		4		1-8		1-5		2-5		P/R/A	

Upper Paleolithic Western European and Upper Paleolithic Central Europeans were combined into one sample in the analysis. W.Europe is Western Europe. C. Europe is Central Europe. Sources of data are given in Table 1. Empty cells indicate no data.

METHODS

Data were collected using the standardized Arizona State University dental anthropology system (ASUDAS) (Turner et al., 1991) on all teeth that were not heavily worn. Where dentitions were relatively complete (i.e., teeth were *in situ* or were known to belong to one individual) only the antimere showing the highest degree of trait expression (the individual count method) (Turner and Scott, 1977) was used in the analysis.

Although data were collected using the complete set of ASUDAS tooth crown and root traits (where possible) only 18 traits were used in the analysis (Table 2). This allowed for the largest number of comparisons with published data. For each of these traits, the variation was dichotomized at the standard breakpoint according to the ASU scoring system (Table 2). Analysis consisted of assessment of biological affinity, cluster analysis, and trait frequency comparisons. The Mean Measure of Divergence (MMD) (Smith in Berry and Berry, 1967) was used for assessing biological affinity. This method provides a measure of phenetic similarity based on the entire suite of dental traits. The greater the value of the MMD, the less is the likelihood that two groups being compared are closely related. Divergence between two samples was considered significant at the 0.025 level of probability when the MMD is greater than twice the standard deviation (Sjøvold, 1973). Cluster analyses were based on dissimilarity matrices derived from MMD values. Both complete linkage and Ward's methods were used to generate dendrograms depicting phenetic relationships among samples.

RESULTS

Mean Measure of Divergence

The MMDs calculated between samples are presented in Table 3. MMDs that are statistically significant ($p<.025$) have asterisks. The MMDs between each modern human sample and each Neandertal sample are very high and significant. In contrast, the MMDs between Neandertal samples are neither high nor significant. The average MMDs between Neandertals (combined sample) and modern humans is 0.605 (Table 3). This is in marked contrast to the average MMD values among Neandertal samples (0.126) and among modern human samples (0.158) given in Table 3. This difference is even larger than the one found by Tyrell and Chamberlain (1998) based on genetic diversity coefficients.

TABLE 3. Mean Measure of Divergence (MMD) values between groups analyzed in this study.

Modern Humans		NWE	PBY	SSA	NAF	QSK	LPA	EUP		WEN	CEN	NEN	
Northwest Europe	(NWE)		0.104*	0.294*	0.098*	0.195*	0.356*	0.061		0.589*	0881*	0.465*	
Poundbury	(PBY)	0.104*		0.328*	0.103*	0.066	0.345*	0.006		1.010*	1.090*	0.707*	
Sub-Saharan Africa	(SSA)	0.294*	0.328*		0.244*	0.020	0.098*	0.150		0.286*	0.421*	0.324*	
Northern Africa	(NAF)	0.098*	0.103*	0.244*		0.194*	0.225*	0.070		0.680*	0.883*	0.646*	
Qafzeh/Skhūl	(QSK)	0.195*	0.066	0.020	0.194*		0.179*	0.019		0.481*	0.718*	0.388*	
Late Pleistocene Africa	(LPA)	0.356*	0.345*	0.098*	0.225*	0.179*		0.154*		0.396*	0.392*	0.521*	
European Upper Paleolithic	(EUP)	0.061	0.006	0.150	0.070	0.019	0.154*		AVG	0.482*	0.810*	0.530*	AVG
Average Modern Human MMDs		0.185	0.159	0.189	0.156	0.112	0.226	0.077	0.158	0.572	0.747	0.515	0.605
Neandertals													
Western Europe	(NEW)	0.589*	1.010*	0.286*	0.680*	0.481*	0.396*	0.482*			0.009	0.106	
Central Europe	(CEN)	0.881*	1.090*	0.421*	0.883*	0.718*	0.392*	0.810*		0.009		0.272	
Near East	(NEN)	0.465*	0.707*	0.324*	0.646*	0.388*	0.521*	0.530*		0.106	0.272		AVG
Average Neandertal MMDs										0.053	0.136	0.189	0.126

* indicates a statistically significant MMD. AVG is the average of MMD's, discussed above in the section, " Results." An empty cell indicates the result, had a sample been compared with itself.

If modern humans evolved through the process of local evolution in Europe and the Near East we would predict phenetic analyses to show that Neandertals are (dentally) more similar to AMH from the same geographic region than they are to AMH and Neandertals from other geographic regions. Contrary to this prediction MMD values indicate that Neandertals are much more similar to each other than they are to any modern human population. Moreover, the modern population that is dentally most similar (although still quite divergent) to Neandertals is Sub-Saharan Africans (not Recent or Upper Paleolithic Europeans). This finding is in agreement with findings by Stringer et al (1997) and Tyrell and Chamberlain (1998) based on cladistic analyses and genetic distance coefficients, respectively.

CLUSTER ANALYSIS

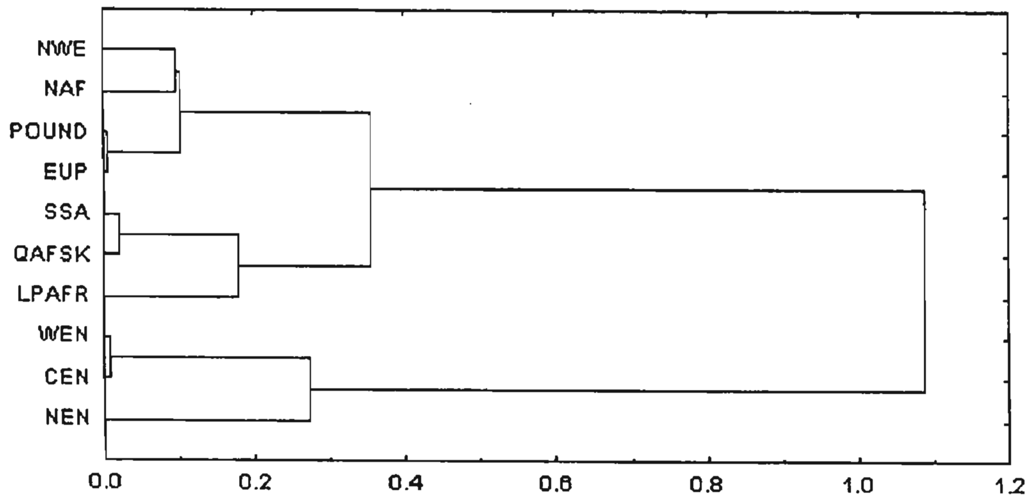

Fig. 1 Complete linkage method cluster dendrogram of MMD values of ten modern and Neandertal samples. Abbreviations given in Table 2.

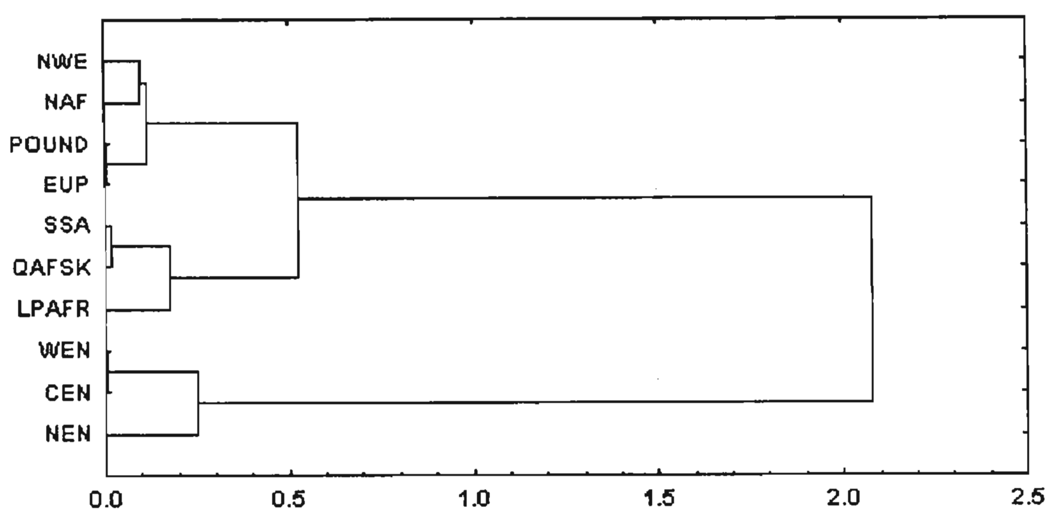

Fig. 2. Wards method cluster dendrogram of MMD values between ten modern human and Neandertal samples. Abbreviations given in Table 2.

Both cluster analyses resulted in identical dendrograms (Figures 1 and 2). Both suggest that Neandertals and modern humans fall into two distinct clusters, with modern human samples (regardless of their geographic or temporal sourcing) clustering with each other to the exclusion of Neandertals. Within the modern human cluster other sub-clusters are apparent. One links Upper Paleolithic Europeans with Recent Europeans and North Africans. The other links the early AMH (Qafzeh/Skhūl) sample with Recent Sub-Saharan Africans and (more distantly) Late Pleistocene Africans.

TRAIT FREQUENCY ANALYSIS

Both MMD and cluster analyses suggest that the Neandertal dental pattern is unique. A close inspection of trait frequencies can provide clues about which traits contribute to the distinctiveness of Neandertal teeth. Of the traits listed in Table 4, unusual incisor morphology that combines strong shoveling, labial convexity, and tubercle development is the most noteworthy of Neandertal dental traits. Neandertals show an average frequency of 100.0% for shoveling, 90.9% for labial convexity, and 87.5% for *tuberculum dentale*. Interestingly, what the frequencies in Table 4 do not show is that Neandertals also exhibit some of the highest expressions of these traits. For example, scores for labial convexity expression are often higher than the highest grade (grade 4) on the ASUDAS scale (Bailey, personal observation).

When compared to world averages for trait frequencies (Table 4) Neandertals are at the extreme ends of the modern range for many traits (incisor shoveling, mandibular first molar cusp 7, absence of 4-cusped mandibular second molars, absence of maxillary incisor double shoveling). They are even outside the range of variation for some traits (mesial ridge, Carabelli's cusp, M^1 cusp 5, M^2 Y-groove). This pattern is not found in any recent or fossil population studied. Moreover, with the exception of double shoveling absence and Carabelli's cusp presence, Neandertals exhibit a pattern opposite that seen in living Europeans, who are characterized by trait absence more than trait presence (Mayhall and Saunders, 1986; Scott and Turner, 1997).

TABLE 4. Neandertal combined trait frequencies compared to world ranges in trait frequencies in modern humans.

Trait (tooth) presence	Low Frequency Groups	High Frequency Groups	World Range	Neandertal Frequency
Shoveling (I^1) 3+	Western Eurasia, Sub-Saharan Africa, Sahul-Pacific	North and East Asia, Americas	0.0%-91.0%	80.0%
Double Shoveling (I^1) 2+	Western Eurasia, Sub-Saharan Africa, Sahul-Pacific, Sunda-Pacific	Americas	0.0%-70.5%	0.0%
Mesial Ridge (C') 1+	Western Eurasia, Americas, Sahul-Pacific, Sunda-Pacific	Sub-Saharan Africa	0.0%-35.0%	55.6%
Hypocone Absence (M^1)	Sub-Saharan Africa. Australia, New Guinea	Europe, India, Northeast Siberia, American Arctic	3.3%-30.6%	0.0%
Carabelli's Cusp (M^1) 3+	North Asia, Americas, Jomon, Ainu	Western Europe	1.9%-36.0%	55.8%
Cusp 5 (M^1) 1+	Western Eurasia, Americas	Sub-Saharan-Africa, Sahul Pacific	10.4%-62.5%	72.7%
Cusp Number (M_2) 4	San, Americas	Western Eurasia	4.4%-84.4%	11.1%
Y Groove (M_2) Y	Western Eurasia, Americas, Sunda-Pacific, Australia	San	7.6%-71-9%	84.5%
Cusp 6 (M_1) 1+	Western Eurasia	Polynesia, Australia	4.7%-61.7%	31.3%
Cusp 7 (M_1) 1+	Western Eurasia, Americas, Sunda-Pacific, Sahul-Pacific	Sub-Saharan Africa	3.1%-43.7%	33.1%

Data and their sources for high and low frequency groups and world ranges of trait frequencies in Scott and Turner (1997).

SUMMARY AND CONCLUSIONS

This multivariate analysis of dental morphology supports the conclusions of previous studies suggesting that the Neandertal dental morphological pattern is unique among human groups. This is not surprising given the numerous cranial and postcranial differences observed between Neandertals and modern humans (Trinkaus, 1981; Rak, 1986; Stringer and Gamble, 1993; Holliday, 1997), In contrast, the dental morphological pattern of the earliest AMH (represented by Quafzeh/Skhūl) is quite similar to both Upper Paleolithic and recent modern humans.

This study also found that the dental morphology of European Neandertals was the most different from Upper Paleolithic and recent Europeans. Likewise, Near East Neandertals showed no particular affinity to early modern humans (Qafzeh/Skhūl) from the same region. These findings tentatively suggest that if genes were flowing between Neandertals and early modern humans in Europe and the Near East, it did not significantly impact their dental morphology.

As regards the competing models for modern human origins, these findings are consistent with the Recent African Origin model. But do they disprove MRE? While it is true that the MRE model predicts regional continuity between archaic and modern populations in multiple geographic regions, it does not predict that regional continuity between modern humans and their archaic predecessors will be found everywhere (Wolpoff, 1995). Wolpoff and Caspari (1997:277-268) have explicitly stated that:

> If Neandertals could be proved extinct in Europe, without any mixing or contribution to later Europeans, it would not prove Multiregional evolution wrong, but only that replacement was the mode of Multiregional evolution in Europe.

Therefore, while this study suggests dental discontinuity between Neandertals and modern humans in Europe and Western Asia, additional comparative studies among later Pleistocene and recent modern human groups are needed to test hypotheses for modern human origins in other Old World regions.

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