Neanderthals Revisited: New Approaches and Perspectives

Edited by

Katerina Harvati
Max-Planck-Institute for Evolutionary Anthropology
Leipzig, Germany

Terry Harrison
Department of Anthropology, New York University
New York, USA

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Cover image by Philipp Gunz, adapted from a CT scan image
of La Ferrassie 1 by Jean-Jacques Hublin.

This volume is dedicated to the memory of W.W. Howells (1908–2005) for his remarkable and pioneering contributions to the study of human evolution, especially his role in the greater understanding and appreciation of the Neanderthals. He was mentor and source of inspiration to generations of anthropologists, and his work continues to be a tremendous resource for research in human variation and evolution.

14. Non-metric variation in recent humans as a model for understanding Neanderthal-early modern human differences: just how "unique" are Neanderthal unique traits?

J.C.M. AHERN

Department of Anthropology, University of Wyoming
Dept. 3431, 1000 E. University Ave,
Laramie, WY 82071, USA
jahern@uwyo.edu

Abstract

Using living humans as an extant referent, this paper examines the probability that the frequency differences in Neanderthal "unique" non-metric traits observed between Neanderthals and Upper Paleolithic modern humans could be sampled from two major populations of the same species. Neanderthal-like features occur in very low frequencies in living humans, if present at all. Rather, other features distinguish major human populations. The population frequency differences of these features are used as a model by which the Neanderthal – Upper Paleolithic frequency differences are assessed using a resampling simulation. This methodological approach tests the null hypothesis that the observed Neanderthal – Upper Paleolithic differences are not greater than what can be sampled from between two major human populations (Amerindians and Euroamericans). Results of the analysis fail to falsify this null hypothesis. Implications of these results for Neanderthal taxonomy are examined.

Introduction

The taxonomic position of Neanderthals has been the longest ongoing debate in paleoanthropology (cf., Trinkaus and Shipman, 1993). Since the late 1980s, this debate has been framed within the contemporary controversy surrounding modern human origins. In many respects, the taxonomy of Neanderthals has become the lynchpin of the modern human origins debate (Wolpoff et al., 2000). If Neanderthals were not one of us and were rather "*Homo neanderthalensis*," Multiregional Evolution could be regarded as incorrect, at least for Europe, while if Neanderthals were *Homo sapiens*, Recent African Evolution could be regarded as incorrect.

Greater morphometric difference between Neanderthals and modern humans than among living human populations and non-human

primate species and subspecies has been inter-preted as evidence that Neanderthals were a separate species (e.g., Harvati et al., 2004). Such an argument is based upon the assumption that fossil species should be comparable to extant species in their range of variation. Although there is good reason to doubt that such an extant referent "yardstick" can ever effectively *falsify* a single species hypothesis in fossil contexts (Kimbel and Rak, 1993; Ahern et al., 2005), the degree of variation in extant referents could potentially be used to *support* either a single or multiple species interpretation. Rigid hypothesis testing is preferable to such a probabilistic approach (i.e., where hypotheses are "supported" or not "supported" rather than "falsified" or "tenta-tively accepted"), yet it is clear that many multiple species controversies in the hominid fossil record lack the evidentiary resolution to effectively falsify a single species hypothesis (i.e., Frayer et al., 1993; Kramer et al., 2001; Henneberg and De Miguel, 2004; Wolpoff et al., 2004; Hawks, this volume; but see Ponce de León and Zollikofer, this volume; Rosas et al., this volume; Tattersall and Schwartz, this volume; Zollikofer and Ponce de León, this volume; for assumption of the

contrary). Despite a relatively extensive late hominid fossil record, sufficient evidence has not yet accumulated to falsify a hypothesis of Neanderthal and modern human conspecificity. Thus, we are faced with either ignoring the issue and assuming a single species, or attempting to assess the probability that Neanderthals and modern humans represent more than one species.

NEANDERTHAL "AUTAPOMORPHIES"

A variety of non-metric traits have been posited as uniquely-derived (autapomorphic) for Neanderthals (see Table 1; Santa Luca, 1978; Stringer et al., 1984). Applying either the Phylogenetic Species Concept (Cracraft, 1989; cf. Rak, 1993) or the Morphospecies Concept (Cronquist, 1978; cf., Tattersall and Schwartz, 1998), the presence of unique derived features would be consistent with a separate species designation for Neanderthals. Yet, recent studies (e.g., Frayer, 1992a, b; Franciscus and Trinkaus, 1995; Quam and Smith, 1998; Stefan and Trinkaus, 1998; Jabbour et al., 2002; Trinkaus et al., 2003; Wolpoff and Frayer, 2005; Cartmill and Smith, in prep.) have reported that many of

Table 1. A list of purported Neanderthal non-metric cranial autapomorphies[1]

Trait	Reference[2]
Mandibular	
Asymmetrical Mandibular Notch	Rak, 1998; Rak et al., 2002
Horizontal-Oval Mandibular Foramen	Stringer et al.,1984
Medial Crest of the Mandibular Notch	Rak, 1998
Retromolar Space	Stringer et al., 1984
Cranial	
Anterior Mastoid Tubercle	Santa Luca, 1978; Stringer et al., 1984
Occipital Bun	Stringer et al., 1984
Suprainiac Fossa	Santa Luca, 1978
Large Occipitomastoid Crest	Stringer et al., 1984

[1] Other non-metric Neanderthal craniomandibular traits, that have been called autapomorphic, were excluded from the present analysis because of limited published data and/or unclear and contentious definitions. See Materials and Methods.
[2] References for the data used in this study are given in Table 2.

Table 2. Samples and summary counts and percentages: Neanderthals and Upper Paleolithic moderns

| | The Replaced | | | | D_{NUP} |
| | Neanderthals | | Upper Paleolithic | | |
Trait	Present (%)	n	Present (%)	n	Percentage difference
Anterior Mastoid Tubercle[1]	8 (34.8)	23	4 (11.4)[1]	44	23.4
Asymmetrical Mandibular Notch[2]	10 (71.4)	14	2 (11.8)	17	59.6
H-O Mandibular Foramen[3]	10 (52.6)	19	6 (11.5)	52	41.1
Medial CMN	11 (84.6)	13	1 (50)	2	34.6
Occipital Bun (liberal)[3, 4]	9 (81.8)	11	9 (60)	15	21.8
Occipital Bun (conservative)[4, 5]	9 (81.8)	11	0 (0)	15	81.8
Retromolar Space[6]	22 (78.6)	28	4.5 (28.1)	16	50.5
Suprainiac Fossa (liberal)[7]	23 (100)	23	19 (29.7)	64	70.3
Suprainiac Fossa (conservative)[8]	23 (100)	23	1 (1.6)	64	98.4
Occipitomastoid (liberal)[9]	11 (78.6)	14	1 (5.3)	19	73.3
Occipitomastoid (conservative)[10]	11 (100)	11	0 (0.0)	19	100

[1] Frayer (1992a).

[2] Cartmill & Smith (in prep.).

[3] Trinkaus & LeMay (1982). Assumes that the Upper Paleolithic "occipital buns" are homologous to those of Neanderthals, albeit different in form.

[4] Count excludes Stetten and Zlatý Kůn, which were included by Trinkaus & LeMay (1982) but have since been shown to be very recent.

[5] From Trinkaus & LeMay (1982) but assumes that the Upper Paleolithic "occipital buns" are not homologous to those of Neanderthals, albeit different in form.

[6] Franciscus & Trinkaus, 1995.

[7] After Frayer (1992a, b). The typical Upper Paleolithic suprainiac depression is scored as a suprainiac fossa.

[8] Hublin (1978, 1980) contends that the Neanderthal suprainiac fossa is not homologous to that seen in the Upper Paleolithic. Wolpoff et al. (2004) report that one Upper Paleolithic specimen, Mladeč 6, exhibits a Neanderthal-pattern suprainiac fossa.

[9] Assumes that the Upper Paleolithic specimen Mladeč 5 exhibits one (Wolpoff et al., 2004) and the Neanderthal specimens Saccopastore 1, Saccopastore 2, and La Quina 5 lack them.

[10] Assumes that no Upper Paleolithic specimens exhibit one. Also, the two Saccopastore specimens are eliminated from the Neanderthal sample, leaving only one Neanderthal that lacks a larger occipitomastoid crest, La Quina 5.

these traits are either not ubiquitous among Neanderthals or are also found in other populations. Especially interesting is the presence of many of these traits among Upper Paleolithic modern humans in Europe, since they were the immediate successors to Neanderthals (see Table 2). Frayer (1992a, b), Trinkaus and Zilhão (2002), Wolpoff et al. (2004) and others (e.g., Hawks, this volume) have argued that such persistence of Neanderthal features in post-Neanderthals indicates some level of genetic contribution of the former to the latter and, thus, Neanderthals and modern humans should be regarded as the same species. Yet, the frequencies of these traits can differ dramatically between Neanderthals and modern humans. The *pattern* of traits seems to indicate conspecificity,

but is the *degree* of trait frequency difference between Neanderthals and early modern humans greater than what we would expect to see between populations of the same species? Are the features in question species markers or population markers?

A MODEL OF INTRASPECIFIC REPLACEMENT

An ideal extant referent model for assessing the difference between Neanderthals and the modern humans who succeeded them would be one that compares a replaced population with the population that replaced it. During the past 500 years, North American Amerindian populations have been largely replaced and/or assimilated by European colonists, as well as by African and

Asian immigrants. Recent estimates for the 1492 AD Amerindian population size north of Mexico, range from 1,894,280 (Ubelaker, 1988) to 18,000,000 (Dobyns, 1983) with a reasonable estimate of 7,000,000 given by Thornton (1987, 1997). By 1900 AD, the Amerindian population of this region had dwindled to 375,000 (Thornton, 1997). Depending on the estimated population size at contact, the annual rate of decline was -0.28% to -0.97% (Thornton, 1997). While the Amerindian percentage of the total population was 100% prior to contact, it was only 0.5% of the total north-of-Mexico population by 1900. Of course, Amerindians have not been fully replaced by any means. However, although Amerindian numbers have increased during the 20th century, self-identified Amerindians (including people who identified themselves as only part Amerindian) made up only 0.9% of the total 2000 U.S. census (Oswalt, 2006). Like other contemporary American population classifications, the biological meaning of "Amerindian" has already significantly lessened. Only 9.5% of the North American Amerindian samples surveyed by Post et al. (1968) showed no European admixture, while 65% of the samples exhibited 5% or higher admixture (see also Szathmary and Auger, 1983; Crawford, 1998; Williams et al., 2000). Admixture rates for some eastern North American groups are as high as 50% (Pollitzer et al., 1967; Szathmary and Auger, 1983). Thus, North American Amerindians, as a biological population, have been largely assimilated and replaced by immigrant populations. Although the mechanisms and processes of Amerindian replacement and assimilation are certainly different from those by which Upper Paleolithic modern humans replaced Neanderthals (cf., Diamond, 1997), the North American analogy can potentially be used as a model of intraspecific human population replacement. For example, a scenario of intraspecific population replacement in Pleistocene Europe would be supported if the differences between Upper Paleolithic moderns and Neanderthals were found to be less than the differences between Euroamericans and Amerindians.

The null hypothesis tested is: the differences, between Neanderthals and Upper Paleolithic moderns in terms of Neanderthal non-metric cranial traits, are not significantly greater than those seen between Amerindians and Euroamericans for traits that characterize Amerindians. If the null hypothesis is falsified, the results of this study would lend support to a morphospecies designation for Neanderthals. If the null hypothesis is tentatively accepted, the results of this study would lend tentative support to classifying Neanderthals as *Homo sapiens*, since it would mean that the differences between Neanderthals and Upper Paleolithic modern humans are no greater than what is seen between two populations of living humans. The use of the Amerindian-Euroamerican model reinforces the null hypothesis compared to the use of many other possible examples of recent human population replacements, since it is not a complete replacement and there has been considerable admixture between Amerindians and Euroamericans. Yet, it is still useful since most of the population that has largely succeeded Amerindians in North America lacks significant Amerindian ancestry.

Materials and Methods

Data for frequencies and counts of Neanderthal traits among Neanderthals and Upper Paleolithic moderns were drawn from the sources cited in the footnotes of Table 2. Neanderthal traits were chosen if: (1) they were non-metric, (2) appropriate sources of data were available, and (3) they had been identified as autapomorphic for Neanderthals. Some cranial traits that have been reported as non-metric Neanderthal autapomorphies were not included since their frequency among Upper Paleolithic moderns has not been

Table 3. Samples and summary counts and percentages: Amerindians and Euroamericans

Trait	The Replaced		The Replacer		Percentage difference
	Amerindians		Euroamericans		
	Present (%)	n	Present (%)	n	
Angled Zygomaticomax. Suture	97 (74)	131[1]	42 (35)	120[2]	39
Elliptic Palate	32 (42.7)	75[3]	2 (2.9)	68[4]	39.8
Not Sharp Nasal Sill[3]	46 (97.9)	47[5]	20 (31.2)	64[6]	66.7
Shoveled Incisors[4]	1180 (85)	1388[7]	168 (8.4)	2000[8]	76.6
Straight Palatine Suture[5]	37 (49.3)	75[3]	15 (12.6)	119[4]	36.7

[1] Holborow, 2002. Plains (n = 61), Southwest (n = 27), Peru (n = 43).
[2] Holborow, 2002. Northwest Plains frontier and forensic (n = 9), Terry Collection (n = 107).
[3] Rawlings, 2002. Northwest Plains and Smithsonian North American.
[4] Rawlings, 2002. Northwest Plains frontier and forensic, Terry Collection, and Maxwell Museum.
[5] Willson, 2004. Northwest Plains.
[6] Willson, 2004. Northwest Plains frontier and forensic (n = 12), Terry Collection (n = 52).
[7] Wissler, 1931. Southwest.
[8] Hrdlička, 1920. U.S. Whites.

established (e.g., the medial pterygoid tubercle, Rak et al., 1994; Quam and Smith, 1998) or whose anatomical variation has been shown to be more complex than previously thought (e.g., internal nasal specializations, Schwartz and Tattersall, 1996; Franciscus, 1999; and the medial pterygoid tubercle, Richards and Plourde, 1995; Antón, 1996). Two features that were used, mandibular notch form and position of the crest of the mandibular notch (Rak et al., 1994; Rak, 1998) were used despite work that has posited different interpretations of these features' variations (Quam and Smith, 1998; Stefan and Trinkaus, 1998; Jabbour et al., 2002; Wolpoff and Frayer, 2005). Frequency data for the Amerindian traits were drawn from the literature cited in the footnotes of Table 3. These traits have been documented as particularly useful in the assessment of ancestry from skeletal remains (Gill and Rhine, 1990) and help define Amerindian and Euroamerican populations. Frequencies and counts for these traits among Amerindian and Euroamerican samples are given in Table 3. As with most of the anatomy that comprises direct data from prehistoric populations, the genetic basis to all of the traits used in this study, Amerindian and Neanderthal, is far from clear. There is no reason to think that any of the Amerindian traits are any less heritable than the Neanderthal traits and vice versa.

A basic assumption of this analysis is that characteristics that distinguish one pair of intraspecific populations can be compared with non-homologous characteristics that distinguish another pair of populations. For testing the null hypothesis, there would be little utility in comparing the frequencies of Neanderthal traits among recent Amerindians and Euroamericans, or any other pair of extant human populations. Neanderthal traits purportedly distinguish Neanderthals from other human groups, and only some of these traits (e.g., midfacial projection, Wolpoff et al., 2004) still vary significantly between human populations. What characterizes population differences has changed over time and space, not to mention the fact that both Neanderthals *and* Upper Paleolithic moderns are extinct as definable populations. Thus, this analysis focuses upon comparing the past distribution of traits that characterized Neanderthals with the recent distribution of traits that characterize a recent human population, Amerindians.

Another assumption of this analysis is that "Amerindians," "Euroamericans," "Neanderthals," and "Upper Paleolithic modern humans" are roughly comparable types of populations. In terms of the samples that are used to represent these populations (see footnotes to Table 3 for details about the Amerindian and Euroamerican samples), the population groups have significant differences. The Amerindian population, as used in this study, is largely North American, although data for one trait (angled zygomaticomaxillary suture) include specimens from Peru. As far as can be gleamed from the literature, most, if not all, of the Amerindian samples used are from the past 2,000 years (see references cited in Table 3). Thus, the Amerindian "population" is represented by mostly recent North American samples. Nevertheless, such samples might be expected to exhibit regional subpopulation differences. Thus, if only one subpopulation of Amerindians is sampled, then the actual variation for a trait for Amerindians as a whole might be greatly underestimated. The samples that comprise the Euroamerican dataset suffer from the same limitations: they likely do not sample the full European colonizing population adequately, both in terms of subpopulations and time. Thus, how useful are these "Amerindian" and "Euroamerican" "populations?" Also, how do the limitations of these recent "populations" differ from those of the fossil populations "Neanderthals" and "Upper Paleolithic modern humans?" Both of the fossil samples have been greatly affected by discovery and preservation bias. For example, most of the well-preserved Neanderthal specimens are male and from Western Europe (cf. Wolpoff, 1999). Does such sampling adequately reflect a larger "Neanderthal" population? The unfortunate reality is that none of the "populations" that are usually used in comparative skeletal studies are adequately sampled. The present study is far from alone in this respect

(e.g., Frayer, 1992a, b; Schwartz and Tattersall, 1996; Antón, 1996; Harvati et al., 2004). It is the unfortunate reality of skeletal studies, and it is a reality that must be recognized as one of the potential pit-falls of any such work.

The Neanderthal – Upper Paleolithic trait frequency differences given in Table 2 can readily be compared to those given for Amerindians and Euroamericans given in Table 3. Yet, the small fossil samples confound the interpretation of such a comparison. In order to statistically assess the probability of finding as much percentage difference between Amerindians and Euroamericans as is observed in limited samples of Neanderthals and Upper Paleolithic moderns, a resampling procedure was employed. This procedure consisted of the following steps for each Neanderthal trait:

(1) Calculate:

$$P_n - P_{up} = D_{nup} \qquad (1)$$

where P_n is the observed frequency of the trait in the Neanderthal sample and P_{up} the frequency of the trait in the Upper Paleolithic sample.

(2) For each Amerindian trait:

(a) Draw a sample, X_{ai}, from the Amerindian sample with $n = n_n$, where n_n is the Neanderthal sample size.

(b) Draw a sample, X_{ea}, from the Euroamerican sample with $n = n_{up}$, where n_{up} is the Upper Paleolithic sample size.

(c) Calculate:

$$P_{ai} - P_{ea} = D_x \qquad (2)$$

where P_{ai} is the frequency of the Amerindian trait in X_{ai} and P_{ea} is the frequency of the trait in X_{ea}.

(d) Store D_x in a bin, Z.

(e) Repeat steps 2a – 2d until Z contains 10,000 D_x values.

(f) Calculate:

$$P_x = n_{Dx} \div 10{,}000 \qquad (3)$$

where n_{Dx} is the total number of D_x values in Z that are larger than D_{nup}, the frequency difference between the Neanderthal and Upper Paleolithic samples.

One problem with using frequency difference (i.e., D_{nup} and D_x) is that it emphasizes difference when a trait frequency is high. For example, if one sample has a frequency for a trait of 0.90 and the other sample has a frequency of 0.45, the frequency difference is 0.45. However, another trait could be in lower frequencies in the two samples: 0.20 versus 0.10 yielding a difference of 0.10. In both cases the ratio between the samples' frequencies is 0.50. Using the ratio would be a possible alternative, yet it is more problematic precisely because it would equate a 45% difference with a 10% difference. A run of simulated data demonstrates that the ratio approach results in a higher rate of Type II error than the frequency difference approach. Thus, frequency difference is used as the primary statistic in the resampling procedure.

The end result for each Neanderthal trait is a set of P_x values, each based upon an Amerindian- Euroamerican trait frequency difference model. P_x values are deemed significant if they are <0.05. A lower level of significance (i.e., as determined from Bonferroni correction [Hochberg, 1988]) might be preferable in different contexts because the many univariate tests will likely result in higher Type I error by chance alone. However, as noted below, a weak null hypothesis is preferable to an overly strong one in this analysis. If all of the P_x values for a Neanderthal trait are less than 0.05, the null hypothesis is deemed falsified for that trait. In other words, it is highly improbable that one would find as much difference between Amerindians and Euroamericans as one would between Neanderthals and Upper Paleolithic modern humans.

The assumptions and methodologies of this analysis increase the probability of incorrectly rejecting the null hypothesis that the Neanderthal – Upper Paleolithic difference is no greater than the Amerindian – Euroamerican difference (Type I error). This study assumes that if Neanderthals and Upper Paleolithic moderns are not different morphospecies we should not find any greater differences between them than found between two extant human populations for population characterizing traits. The selection of characteristic Amerindian traits that do not differ greatly between Amerindians and Euroamericans will weaken the null hypothesis while the selection of traits that show great difference still should not be greater than what would be expected between two morphospecies. The selection of Neanderthal traits is much more critical, since selecting traits that do not reportedly characterize Neanderthals from Upper Paleolithic moderns will increase the chance of Type II error. Thus, only Neanderthal traits that have been described as "autapomorphies" have been included in this study.

Another problem facing this study is the definition of the characters and how they are scored. The suprainiac fossa is a perfect example of this. Both Neanderthals and many modern humans, especially those in the European Upper Paleolithic, exhibit depressions just superior to inion (Bräuer and Brög, 1998). Frayer (1992a) scores both such structures as suprainiac fossae, while Hublin (1978, 1980, pers. comm.) contends that they are not homologous. Further clouding the definition of the suprainiac fossa as a Neanderthal autapomorphy is the presence of broad suprainiac fossae that meet all of Santa Luca's (1978) and Hublin's (1978) definitions of the Neanderthal form on the later Middle Pleistocene African specimen, Eyasi 1 (Trinkaus, 2004) and the Late Pleistocene African specimen, ADU-VP-1/3 (Haile-Selassie et al., 2004). For traits, like the suprainiac fossa, whose anatomy and distribution are

controversial, both liberal (e.g., Frayer, 1992a, b) and conservative (e.g., Hublin, 1980; Bräuer and Brög, 1998) data were used. The best approach to dealing with such variation in character scoring would be to provide extensive character descriptions accompanied by ontogenetic and functional analyses of each trait. Although this is highly recommended, it is beyond the scope of this paper to resolve such character scoring controversies. By including both liberal and conservative data, it is hoped that this study will provide more than just a one-sided story.

suprainiac fossa while all of the Neanderthals were scored as exhibiting them. If this is the accurate interpretation of suprainiac fossa anatomy, then the frequency difference between Neanderthals and their immediate modern successors for at least one Neanderthal "autapomorphy" is significantly greater than what we would see between Amerindians and Euroamericans. Yet, all of the Neanderthal – Upper Paleolithic differences for all of the other Neanderthal traits, whether scored liberally or conservatively, could potentially be sampled from two intraspecific populations.

Results

The results of the resampling procedure are given in Table 4. The null hypothesis was falsified for only one of the cranial traits, the conservative data set for the suprainiac fossa. In this data, only one Upper Paleolithic specimen (Mladeč 6) was scored as possessing a

Discussion

The results of this study fail to refute the null hypothesis in all instances but one. Whether or not the Upper Paleolithic anatomy is homologous to the Neanderthal anatomy is a significant issue, as demonstrated by the results for the occipital bun, occipitomastoid crest, and

Table 4. Resampling Procedure Results[1]

	Referent Model: Amerindian – Euroamerican Differences				
	Elliptic Palate	Curved ZM Sut.	Sharp Nas. Sill	Shovel. Incisors	Straight Pal. Sut.
Mandible					
H-O Mand. For.	0.452	0.410	0.999	>0.999	0.385
Asym. Mand. Notch	0.063	0.098	0.692	0.932	0.071
Medial CNM	0.999	0.996	0.923	0.999	>0.999
Retromolar Space	0.125	0.202	0.891	0.992	0.139
Cranial[2]					
Ant. Mastoid Tub.	0.946	0.903	>0.999	>0.999	0.874
Suprainiac Fossa 1	**0.002**	**0.001**	0.333	0.797	**0.002**
Suprainiac Fossa 2	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Occipital Bun 1	0.856	0.821	>0.999	>0.999	0.807
Occipital Bun 2	**0.006**	**0.003**	0.093	0.427	**0.006**
Occipitomastoid 1	**0.006**	**0.009**	0.343	0.670	**0.010**
Occipitomastoid 2	**0.001**	**0.000**	**0.006**	0.123	**0.001**

[1] The values given are the proportions of Amerindian – Euroamerican resampling distribution that exhibited greater percentage difference than observed between the Neanderthal and Upper Paleolithic samples (see Methods for full description). Values in **bold** are $P < 0.05$ and are considered significant.

[2] The results for Suprainiac Fossa 1, Occipital Bun 1, and Occipitomastoid 1 are based upon liberal estimates of the frequency of Neanderthal traits in the Upper Paleolithic (e.g., Frayer, 1992), while Suprainianc Fossa 2, Occipital Bun 2, and Occipitomastoid 2 are based upon conservative estimates (see Table 2).

suprainiac fossa. When the Upper Paleolithic anatomy is assumed to not be homologous, the probabilities of sampling the Neanderthal – Upper Paleolithic difference from the referent model becomes much lower (although still possible with the exception of the suprainiac fossa). Although more explicit definitions and scorings are needed for these traits, the fact that only one of the conservative datasets falsified the null hypothesis, means that the Neanderthal – Upper Paleolithic difference in terms of Neanderthal characteristic non-metrics traits is not great.

INDIVIDUAL TRAITS OR COMBINATION OF TRAITS?

This study examined the likelihood of sampling as much Amerindian-Euroamerican difference as observed between Neanderthals and Upper Paleolithic moderns. In doing so, traits were examined univariately. It is possible that the most significant way that Neanderthals differed from Upper Paleolithic moderns was in their *combination* of traits, as opposed to the presence or frequency of individual traits. A probabilistic assessment of such trait combination differences was not made in this study, although this would be an interesting avenue for future work. A fundamental, practical problem with this approach would be the lack of specimens, both fossil and contemporary, that preserve multiple features. In a survey of forty Amerindian crania in the University of Wyoming Skeletal Repository, only fourteen preserved four of four traits examined (nasal sill, zygomatico-maxillary suture, palate shape, and transverse palatine suture). The forty crania were selected since they preserved at least one of the traits surveyed. Of thirteen Neanderthal specimens for which individual data was either available from the literature or could be scored directly from originals or casts, nine (Biache 1, Forbes' Quarry, Guattari 1, La Chapelle, La Ferrassie 1, La Quina 5,

Saccopastore 1, Spy 1, Spy 2) preserved four of the four traits surveyed (occipital bun, occipitomastoid crest, anterior mastoid tubercle, and suprainiac fossa). Yet, unlike the survey of the Amerindian collection, there is a bias in which Neanderthal specimens are reported on in the literature or are available as casts. Well-preserved specimens tend to be better represented both in individual observations and in availability of casts. The reality of the human skeletal record, either fossil or recent, is that very few specimens are well preserved. Furthermore, this preservation is not random, especially in the case of Neanderthals. Far more well-preserved Neanderthals are known from Western Europe, than from Central or Eastern Europe. Of the nine that preserve four of the four traits surveyed, all were from Western Europe. Since Western Europe would have been the portion of the Neanderthal range farthest from other human populations, it would be expected that Western European Neanderthals would be the most different from other humans (including Upper Paleolithic invaders from the East) if Neanderthals were a population of a larger human species.

When only Neanderthal and Amerindian individuals that preserved four of the four traits are examined, six of nine (66.7%) Neanderthals exhibit the Neanderthal variant for all four traits and six of fourteen (42.9%) Amerindians exhibit the Amerindian variant for all four traits. Given how small these samples are, it is not surprising that the frequency of "all-Neanderthal" Neanderthals is not significantly different from the frequency of "all-Amerindian" Amerindians ($p = 0.40$, Fisher's Exact Test). Fundamentally, a meaningful assessment of just how common Neanderthals with a combination of multiple Neanderthal traits are will have to wait until sufficient comparative samples are acquired. Of course, more well-preserved Neanderthals from across their range would be useful (Stefan and Trinkaus, 1998), although sample sizes may never be

sufficient to know how homogeneous Neanderthals were in terms of trait combinations except in comparison with extant referents. Even if sufficient samples were available, would a significantly greater frequency of Neanderthals with multiple Neanderthal traits than Upper Paleolithic specimens with multiple traits demonstrate Neanderthal specificity? Such a degree of difference could perhaps justify their classification as a different morphospecies. Yet, would such a classification even be evolutionarily meaningful?

SPECIES

The issue of how past variation compares with extant variation, although relevant, is not necessarily the same as whether or not Neanderthals and Upper Paleolithic moderns were the same species. In their morphometric analysis of distance between Neanderthals and modern humans, Harvati et al. (2004; see also Harvati, 2003) use the morphospecies concept in the form of yardsticks developed from extant species variation, although they overstate its acceptance in the field (cf. Kimbel and Martin, 1993). They state: "Species in paleontology should be equivalent to living ones in the variation that they accommodate" (Harvati et al., 2004: 1147). Harvati et al. (2004) conclude that, since the Mahalanobis Distance (D^2) between their Neanderthal and Upper Paleolithic samples was statistically greater than almost all of their intraspecific and most of their interspecific comparisons of cercopithecoids and African great apes, Neanderthals likely represented a different species from modern humans. The Harvati et al. (2004) study and the current analyses are applicable to a test of a single morphospecies, yet are morphospecies evolutionarily meaningful units? The morphospecies concept is pragmatically strong but ontologically weak, since it potentially constructs species units that do not have evolutionary meaning (Kimbel and Rak, 1993; Mayden, 1997). Temporal variation within a

phyletic lineage, whether directional or stochastic, has the potential to be misinterpreted as multiple species when the morphospecies approach is taken (Ahern et al., 2005; but see Harvati et al., 2005).

In his recent review and analysis of species and species concepts in human evolution, Holliday (2003, this volume) offers a refreshing take on the issue of whether or not Neanderthals should be designated their own species. He notes that many closely related, yet readily distinguished, "species" mate and produce fertile offspring. Although a liberal application of the biological species concept would necessitate assigning these "species" to the same species, Templeton (1989), as Holliday (2003) notes, argues that they should be identified as separate species because they maintain separation through cohesion. Such a view lessens the importance of autapomorphies for species identification, since some "autapomorphic" traits can become homoplasies (or at least homoplasy-like) through introgression (Holliday, 2003). Holliday (2003) thus labels Neanderthals as their own species, *Homo neanderthalensis*, but allows for the sharing of traits through introgression. In order for this explanation to be valid, within Holliday's framework, Neanderthals and modern humans should retain separate cohesiveness. How this cohesiveness should be defined is difficult, however. This is especially the case when we compare one group, Neanderthals, with the group that succeeded them, Upper Paleolithic moderns. This is a very different situation than the papionin (Jolly, 2001), deer (Cathey et al., 1998), and canid examples cited by Holliday (2003) to illustrate interspecific gene flow. The main lines of evidence for these cases are the presence of hybrids, hybrid zones and evidence of genetic introgression. Neanderthals are usually compared to a potentially post-hybridization population: Upper Paleolithic modern humans. We lack any F1 (or F10, for that matter) Neanderthal – modern human hybrids and probably always will because of

the limitations of the fossil record. What we do seem to have, in the case of the Upper Paleolithic moderns, is evidence of genetic admixture, since many "uniquely" Neanderthal features persist into the Upper Paleolithic. That the present study indicates that the frequency in these traits does not differ between Neanderthals and the Upper Paleolithic moderns more than we would expect for two populations of the same species is a further demonstration of some degree, perhaps significant, admixture.

While extreme viewpoints on the fate of the Neanderthals, such as overall regional continuity (Coon, 1962) or complete replacement (Stringer and Andrews, 1988) are explicit regarding Neanderthal specificity, the well-occupied intermediate ground (e.g., Bräuer, 1989; Smith et al., 1989; Stringer, 1992; Stringer and Gamble, 1993; Hawks and Wolpoff, 2001; Trinkaus and Zilhão, 2002) is far from unified regarding the issue. Although seemingly more true to the intermediate ground and the amorphous reality of species boundaries, Holliday's (2003) and others' (e.g., Jolly, 2001) interpretations have not resulted in consensus on the issue of Neanderthal systematics. Both Holliday (2003) and Wolpoff (1999) adhere to the evolutionary species concept (Wiley, 1981), yet Holliday sees a unique origin and fate and evolutionary tendency for Neanderthals (thus, *Homo neanderthalensis*), while Wolpoff does not. Wolpoff contends that the only identifiable evolutionary lineage is the human one that appears approximately 2 million years ago and is still alive today (thus, Neanderthals represent an extinct population). The question, whether or not the degree of admixture and the degree of "cohesiveness" of the Neanderthals are sufficient to falsify a single species hypothesis for Neanderthals and modern humans, remains unanswered. Even more fundamentally, any measure of species boundaries is dependent upon the species concept being employed.

Summary

This study failed to refute the hypothesis that the Neanderthal trait frequency differences between Neanderthals and Upper Paleolithic moderns are not significantly greater than the Amerindian trait frequency differences between Amerindians and Euroamericans. Although the statistical results are not unanimous, their overall pattern is consistent with a tentative acceptance of the single morphospecies hypothesis based upon the data examined. Additional trait data and/or an analysis of trait combinations could potentially falsify the single morphospecies hypothesis. A better understanding of the variation, ontogeny, and function of Neanderthal non-metric traits will be important for future work. Although this study's results are relevant to whether or not Neanderthals and Upper Paleolithic moderns were different morphospecies, morphospecies are not necessarily evolutionarily meaningful units.

Acknowledgements

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