

VARIATION IN NASAL BREADTH AS A TEST OF GENETIC DRIFT IN EUROPEAN NEANDERTALS

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Abstract. — Metric variation in nasal breadth does not support the hypothesis that European Neandertals from the earlier Würm were isolated and lost their variation or intensified their features because of genetic drift.

Key words: Neandertal evolution, drift, nasal breadth.

VARIATION DE LA LARGEUR NASALE COMME TEST DE LA DÉRIVE GÉNÉTIQUE
DES NÉANDERTHALIENS EUROPÉENS

Résumé. – La variation métrique qui s'observe pour la largeur nasale des Néanderthaliens du Würm ancien ne conforte pas l'idée d'un isolat géographique pour ces derniers. L'hypothèse d'une dérive génétique qui aurait favorisé l'intensification de caractères propres à la lignée n'est pas confirmée.

Mots-clés : Evolution des Néanderthaliens, dérive génétique, largeur nasale.

INTRODUCTION

Neandertal nasal anatomy and metric variation have been a focus of anthropological interest for much of this century, perhaps beginning most dramatically with C.S. Coon's (1962) contention that, as we prefer to paraphrase it, a Neandertal face could be described as being similar to the result of what one could do to a rubber model of an archaic human face, by pulling the nose forward from a fixed point on the zygomatic arches and bringing along the attached midfacial structures. His comments were lucid and quite visual, and

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stimulated by them and the 1953 A.W. Proetz publication on nasal physiology, a series of papers addressing Neandertal nasal anatomy and metric variation in an adaptive context followed (Glennville, 1969; Wolpoff, 1969; Carey and Steegman, 1981; Trinkaus, 1987; Dean, 1988; Franciscus and Trinkaus, 1988; Franciscus and Long, 1991; Franciscus, 1999). There has recently been a resurgence of interest in the nasal morphology of European Neandertals, but one with a more taxonomic focus (Schwartz and Tattersall, 1996; Franciscus, 1999, but see Murphy and Monge, 1998). In particular, several researchers have attempted to demonstrate whether or not the Neandertal population was characterized by unique derived nasal traits that might reflect isolation of the Neandertal population from other contemporary humans.

One key paper (Maureille and Houët, 1998) uses nasal data in an innovative approach to test the degree of isolation of the Neandertal lineage. In this paper, Maureille and Houët examine the case for genetic drift in the Neandertal population by comparing the variation in nasal measurements from Neandertal and pre-Neandertal populations. As the basis for their study, they suggest that the level of metric variation in an isolated population should be lower compared to a non-isolated population because of the effect of genetic drift, a prediction never examined in the nasal data before. They write that the *"decrease of the variability of the Würmian Neandertals with respect to that of the pre-Neandertals ... could be interpreted as genetic drift ... it would have been favored by an isolation of the European population"* (p. 27).

This hypothesis is both interesting and intuitively attractive. Because genetic drift has a greater magnitude in smaller and more isolated populations, a population that does not receive gene flow from other populations should have a higher level of drift, and therefore less genetic variation, compared to an equal-sized population that receives many migrants from other populations. Many have argued that Würm Neandertals have a large number of distinctive features compared to other human populations because they underwent this kind of isolation. Therefore we might expect the level of metric variation in Neandertals also to reflect such isolation, if in fact Neandertal populations were isolated from other human groups. The results of the Maureille and Houët analysis conforms to this expectation and shows that their sample of European and West Asian Neandertals had less variation in nasal height and breadth, as measured by the standard deviation of these variables, than a Middle to Late Pleistocene sample of pre-Neandertals from these regions. The Neandertal sample also was less variable in these measures than recent human populations, according to their publication. They interpreted the low variability in Neandertals in these measurements to be additional evidence of genetic drift.

However, their study included both European and Asian individuals in its Neandertal and pre-Neandertal samples, which introduces a potential problem, since the groups have different proportions of Asian and European members. Moreover, it was the *European* Neandertals who presumably were isolated during the last glaciation, and not those from Western Asia. This could hinder our understanding of the pattern of possible isolation and genetic drift in the groups. We tried to replicate the approach of the Maureille and Houët study by repeating their analysis on a larger sample of Middle and Late Pleistocene

Würm Neandertals		Pre-Würm Europeans	
Vindija 259 *	26.2	Montmaurin 4 *	27.5
St. Césaire	27.7	Arago 21	29.2
Vindija 225 *	28.5	Krapina Maxilla E *	29.7
Kulna *	30.0	Krapina 3 *	30.0
La Chapelle-aux-Saints	33.2	Steinheim	31.6
Arcy-sur-Cure 9	33.3	Atapuerca 1199 *	32.0
La Ferrassie 1	34.0	Castel del Guido *	32.0
Gibraltar	34.1	Saccopastore 1	32.9
Mt Circeo	35.1	Saccopastore 2	33.7
		Petralona	36.4
		Atapuerca 767/963 *	37.0
		Atapuerca cranium 5	38.5
Mean	31.3	Mean	32.5
Standard Deviation	3.3	Standard Deviation	3.4
Coefficient of Variation	10.4	Coefficient of Variation	10.3

Table I. — Nasal breadths of European hominids (in mm). This sample includes a number of European specimens not included the Maureille and Houët study (as indicated). We know of no other European Neandertal or pre-Neandertal noses that are available for study.

(*: *Specimens not used by Maureille and Houët*)

hominids, but one limited to Europe alone (the additional specimens we used are indicated in Table I). Like these authors, we calculated the means and their standard deviations for our earlier and later samples, and compared these. However, by restricting the problem to a European one, we expect to more validly examine the possible isolation of Neandertals through its effect on these means and variations.

MATERIALS AND METHODS

We took two samples of European hominids, from before the Würm glaciation and during it, to test the hypothesis of isolation in Europe during the last glaciation through an examination of nasal variability. We incorporated measurements from 9 European Würm Neandertals and 12 pre-Würm Europeans. In order to maximize the sizes of the samples, we used only the measurement of maximum breadth of the nasal aperture because it is easy to replicate. The average reproducibility error for nasal breadth is under 0.1 mm. for MHW, who took measurements on the original specimens for all cases except Atapuerca crania 5, 1199, and 767/963, which were from published descriptions (Arsuaga *et al.*, 1997). The specimens and measurements are listed in Table 1, and the comparisons with the results reported by Maureille and Houët (1998) are in Table II.

	Maureille and Houet study	This study (Table I)
Pre-Würm Neandertal mean (mm)	33.0	32.5
Sample size	9	12
σ	4.4	3.4
Würm Neandertal mean	34.2	31.3
Sample size	8	9
σ	1.8	3.3

Table II. — Nasal breadth statistics in the samples of the two studies compared (in mm). Our study excludes Neandertals from Western Asia used in both samples by Maureille and Houet, while including some European specimens they did not, as indicated in Table 1.

Because the time span represented by the pre-Würm group is much longer than the span of the Würm group, we might expect that their variation would be higher. This makes our test conservative, in that several factors predict lowered variation in the later Neandertal group. We therefore can accept the absence of reduced variability as a valid refutation of the drift hypothesis.

RESULTS AND DISCUSSION

From comparing the variation in the groups of European hominids presented here, there is no basis for the suggestion that Neandertals are less variable in nasal breadth than earlier European hominids. Though the both the mean and standard deviation of the Würm group are smaller than all those of the pre-Würm group, they are not significantly so (means: $p = 0.702$, Mann-Whitney test; variance: $p = 0.734$, Levene's test). Since the means of the groups are different, a more appropriate comparison of the variation in the groups may be the coefficient of variation (CV). The CV of the Würm Neandertals (10.4%) is just about the same as that of the pre-Würm Europeans (10.3%). It is evident from these samples that the variation in nasal aperture breadth in Neandertals is not significantly smaller than that in earlier Europeans. Therefore, all these data cannot constitute evidence for isolation or genetic drift in European Neandertals.

We believe that these results are different from those presented in the Maureille and Houët (1998) study because the specimens from Western Asia are omitted, while more pre-Neandertals and Neandertals are included, in fact all of them that are available for examination. These samples more validly address the drift hypothesis for the same reasons.

We wondered whether *both* groups might exhibit low levels of variation compared to recent human populations. We therefore looked at data on nasal aperture breadth for equal numbers of males and females from two recent populations from different parts of the

world: 140 New Guinean (Hambly, 1940) and 56 Cowichan (Oettking, 1930) crania. Both the mean and variance of nasal aperture breadth in these recent populations are much smaller than the values observed in either of the Pleistocene European samples. The CV of nasal aperture breadth in the New Guinean sample is 7.0%, and the CV of the Cowichan sample is 7.2%. In each sample, the male-specific and female-specific CV's are similar to each other and are slightly lower than the total CV (New Guinean: male = 6.5%, female = 7.1%; Cowichan: male = 6.2%, female = 6.9%). For these reasons, we conclude that neither pre-Würm nor Würm Europeans have low variation in nasal aperture breadth compared to recent human populations, and that the level of variation exhibited in these samples is unlikely to be the result of any bias in the sex of individuals represented in the samples. The higher level of metric variation observed among these Pleistocene specimens relative to all the recent populations may be the result of sampling individuals separated by long spans of time, during which there may have been evolutionary changes.

However, it is important to note that while these results strongly suggest that drift in a small isolated population is not the best explanation for Neandertal nasal variation, they do not completely rule out the possibility that some degree of isolation or genetic drift in the European Neandertals may have occurred. Drift may occur in any population, and isolation may be accomplished by distance, and not just geographic barriers. The use of any morphological data, metric or non-metric, to address the issue of isolation presents a significant problem. For morphological data to provide a valid test of a hypothesis of isolation, the amount of variance in the morphological traits attributable to either selection or environmental factors must be the same among the populations being compared. This is a large problem because we have every reason to believe that different human populations have experienced different selective and environmental histories. Such differences in selection and the environment are potentially much more powerful than genetic drift in affecting the pattern of morphological variation.

In fact, there are several reasons to suppose that the breadth of the nasal aperture in Neandertals and other populations may have been affected by natural selection, along with other morphological traits related to the nose (Wolpoff, 1969; Franciscus and Long, 1991). Furthermore, populations in Europe during parts Middle and Late Pleistocene are likely to have experienced very different climatic patterns and environments. It is certainly credible that these factors may have affected the mean and variance of nasal aperture breadth among these populations. Selection and inconstant environmental factors may affect the mean and variance of this and other traits in ways that are not easily predictable.

For this reason, morphological data for individual traits may be unable to provide a fully convincing test of isolation among fossil populations. While low morphological variation may be the result of genetic drift, it may also be caused by selection or environmental factors. And while marked morphological variation may be unlikely if drift alone affects the genes underlying the observed traits, selection or variation in environmental factors may cause even a very small population to exhibit high variation. Analyses that do not account for these factors cannot provide valid tests of population parameters from morphological data.

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