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News and Views

Variation in Neandertals: a response to Harvati (2003)

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Scientists who study the past work within a uniformitarianist paradigm, so that our interpretations of patterns seen in the past are informed by our understanding of patterns in the present. In biological disciplines, for which systemic change, feedback mechanisms, and organismal adaptation are the norm, such an assumption of constancy through time is necessarily problematic. Therefore, we need to be careful about how we frame questions and design our methods for understanding the past, and clear about their weaknesses. This is especially true when our questions consider morphological variation over evolutionary time, as by definition neither is constant; without variation there is no evolution, while evolutionary change implies change in variation.

As one example of this, paleoanthropologists necessarily assume constancy of morphological variation through time, especially when trying to evaluate the relationships among important fossils, such as fossil hominins. This is largely because the meager human fossil record rarely records meaningful population variation, forcing us to use surrogate variational models derived predomi-

nantly from living species. This means that we are making the assumption that variation in the present adequately represents variation in the past, or that species in the present adequately represent species in the past, neither of which are likely to be true. Even recent studies of morphological variation in living primates show that closely related species can vary in different ways (e.g., Ackermann and Cheverud, 2000; Marroig and Cheverud, 2001; Ackermann, 2002), and that we can say important things about evolutionary processes by studying these differences in variation patterns (Ackermann and Cheverud, 2002, 2004; Marroig and Cheverud, 2004). This means that, when we do use variation in living species to interpret past taxonomic relationships, our methods and our interpretations of the past must be adjusted to take into account the fact that the assumption of constancy of variation throughout human evolution is likely false.

Recently, Harvati (2003) analyzed the taxonomic position of Neandertals relative to the inter- and intrapopulation variation seen in modern humans, including a small sample of Late Paleolithic and earlier anatomical moderns, as well as chimps and bonobos (Harvati, 2003). Her separation at the specific level of Neandertals from *Homo sapiens* was based largely on the fact that, for most

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analyses, the Mahalanobis' distances between Neandertals and the other *Homo* populations exceeded that seen among living human populations, among chimp subspecies, and between chimp and bonobo groups. This seems a fair conclusion, as the results suggest that the Neandertals are more different than what we generally see at an intraspecific (chimp subspecies; human populations) or interspecific (chimps vs. bonobos) level.

However, there are other possible explanations for these results, which necessarily arise from the methodology and, in particular, the assumptions about constancy of variation that underlie it. Mahalanobis' distance (D^2) is a statistic that measures dissimilarity using information on population variances and covariances. As was done by Harvati (2003), it can be used to calculate the morphological distance between two samples (i and j) as follows:

$$D_{ij}^2 = (\mu_i - \mu_j)' V^{-1} (\mu_i - \mu_j)$$

where μ_i is the vector of means for the i^{th} sample, μ_j is the vector of means for the j^{th} sample, and V is the variance/covariance (V/CV) matrix of the population. Implicit in the use of this statistic is an assumption that the variation of the population (as represented by the V/CV matrix) accurately represents the variation in the samples being compared.

For the two analyses (Step 1 and Step 2) performed by Harvati, fossil individuals would make little if any contribution to the population patterning of variance/covariance matrices, as Neandertals, the Late Paleolithic specimens, and early anatomically modern humans make up a tiny fraction of the total sample in all analyses (1.5%, 0.9%, and 0.3%, respectively, in Step 1, and 2.2%, 1.6%, and 0.6%, in Step 2, for the lumped human + *Pan* sample). Therefore, the V/CV matrices used to evaluate the Neandertal positioning relative to other samples essentially represent either a pooled human + *Pan* pattern of variation or a human variation pattern alone. If the Neandertals varied differently (either more or in different ways) from the extant samples, *this fact alone would inflate the D^2 values*. To illustrate, let's start with a hypothetical variance/covariance

matrix (V) and a vector (d) representing the difference in means between samples, (i.e., $\mu_i - \mu_j$):

$$V = \begin{bmatrix} .5 & .1 & .1 & .1 \\ .1 & .5 & .1 & .1 \\ .1 & .1 & .5 & .1 \\ .1 & .1 & .1 & .5 \end{bmatrix}$$

$$d = [2, 2, 2, 2]$$

The Mahalanobis' distance (D^2) is then:

$$D^2 = dV^{-1}d = 20.0$$

Increasing the distance between the two samples:

$$d = [3, 3, 3, 3]$$

$$D^2 = 45.0$$

Therefore, a larger distance value represents an increase in morphological distance—as represented by the larger distance vector—between the two samples being compared. This is how Harvati interpreted the higher distance values seen between Neandertals and humans relative to those between human samples. *But this is only one possible explanation for increased Mahalanobis' distances*. Increases in D^2 values can also result from having an estimate of variation that does not adequately represent the variation in the population from which one or both of the samples being compared were drawn. Differences in magnitude of variation will cause distances to be overestimated when samples from a more variable population are judged against a less variable V/CV matrix. Similarly, differences in pattern of variation will cause an inflation of distances when regions of low variation in one population are high in another and vice versa. For example, if one fossil population had a large amount of variation in head length (to take one arbitrary measurement), the perceived distances between samples drawn from that population would be magnified if the extant population V/CV matrix was relatively invariable in head length (perhaps because they went through a bottleneck or were a relict population).

To illustrate, let's consider two hypothetical populations A and B, with the following

covariance matrices and distance vectors (although for clarity these values are hypothetical, the magnitudes of the variances and covariances are informed by data that I have collected from living apes and humans):

$$\begin{array}{l}
 \text{Population A} \\
 V_A = \begin{bmatrix} .5 & .1 & .1 & .1 \\ .1 & .5 & .1 & .1 \\ .1 & .1 & .1 & .05 \\ .1 & .1 & .05 & .1 \end{bmatrix} \\
 d_A = [2, 2, 1, 1] \\
 D_A^2 = 16.0
 \end{array}
 \qquad
 \begin{array}{l}
 \text{Population B} \\
 V_B = \begin{bmatrix} .1 & .05 & .1 & .1 \\ .05 & .1 & .1 & .1 \\ .1 & .1 & .5 & .1 \\ .1 & .1 & .1 & .5 \end{bmatrix} \\
 d_B = [1, 1, 2, 2] \\
 D_B^2 = 16.0
 \end{array}$$

Both Population A and Population B have the same amount of population variance/covariance (for both, the determinant of the matrix equals 0.001), and the same morphological distances between samples drawn from the population ($D_A^2 = D_B^2$), although their variance/covariance patterns differ, being essentially reversed. However, when the difference between two samples from Population B (i.e., d_B) is assessed using the variation of Population A (V_A), or vice versa, then $D^2 = 70.0!$ While this “reversed V/CV matrix” example is obviously extreme, even very small differences in covariance structure across a much larger number of variables can have a similar effect. So in other words, when two samples are compared using a covariance matrix that does not adequately reflect the pattern of variation in the sample population from which one or both of the samples were drawn, this fact alone can serve to inflate the perceived distance between them (Ackermann, 2002, 2003). *This inflated value says nothing about the biological or taxonomic relationship between the two samples being compared.*

It is therefore quite possible that the large distances seen between Neandertals and modern humans are merely an artifact of the fact that the human + *Pan* sample does not adequately reflect the variation seen among Neandertals in the past. A number of the other patterns seen in this analysis might also be explained by this phenom-

enon. Harvati suggested that the large distances between Skhul and Qafzeh and modern populations may be attributed to the very small sample size (1 or 2 individuals depending on the analysis), as distances can become inflated in such instances. Alternatively, differences in variation patterning between Skhul and Qafzeh and modern populations may offer an alternative explanation for these large distances. Differences in variation patterning could also explain why the distances among chimp and bonobo taxa are often *overestimated* (and not underestimated, as was expected by Harvati [2003: 114]) when evaluated using a pooled human/chimp V/CV matrix, as the bulk of that matrix was determined by the human sample, and these populations undoubtedly vary in different ways. I have shown previously that when the V/CV matrices from different species are substituted for the actual covariance matrix in order to calculate Mahalanobis’ distances among intraspecific pairs of chimps, gorillas, and humans, the distances are on average doubled (Ackermann, 2002). While the latter analysis was not strictly analogous to Harvati’s, as she assessed distances between samples that are generally larger than $n=1$ rather than between individuals (although some of the sample sizes were quite small), certainly such effects need to be taken into account when evaluating fossil relationships (see also Ackermann, 2003).

Harvati (2003: 122) herself stated that the results of her analysis—including support for the specific separation of Neandertals from modern humans—are not unequivocal, especially given that the patterning of “intra- and inter-specific morphological differentiation in humans may follow a different pattern from that observed in *Pan*.” To that, I would add that the variation in Neandertals might also follow a different pattern from what is seen in extant populations—not surprising if variation patterns have changed through evolutionary time as we expect. This idea is not new, and in fact Corruccini (1978) made similar criticisms of Howells’ (1972) analysis of Neandertals more than two decades ago. The results of Harvati’s principal components analyses (PCA) themselves nicely illustrate this difference in patterning, showing two distinct variance structures in the samples—for humans and *Pan*—with

Neandertals at the edge or slightly outside of the human sample variance (PCA decomposes the total variance of the data as represented by the correlation/covariance structure, and hence the results are also dependent on variance composition and underlying assumptions, much like in D^2).

There are broader conceptual issues at stake here. We know that variation is not constant through time, and that using extant models of variation as “yardsticks” against which we judge fossil samples is problematic. Yet, because we all (myself and colleagues included) work within a uniformitarianist paradigm, we must carefully consider the biases and assumptions inherent in this system, and clearly account for them—either in discussion or, when possible, in methodological design. Here, when assumptions about constancy of morphological variation through time are carefully considered, the results of Harvati’s distance analysis are ambiguous, in fact irreconcilably so given the data and methods used. While the results may show that Neandertals are a distinct species from *H. sapiens*, it is equally possible that they may simply indicate that the Neandertals varied differently from living populations. Harvati (2003: 122) is correct in suggesting that we need to develop new models for assessing the modern human-Neandertal relationship. These models must carefully consider variation and its changing nature through time if they are to help us reach scientifically valid conclusions. In fact, given that Neandertals are one of the few fossil hominin taxa for which we have reasonable sample sizes, one resolution to the ambiguity demonstrated here might be a better understanding of the patterning of variation *within* Neandertals. Because variability is itself the stuff of evolution, and differences in patterns of variation can provide insight into the evolutionary processes that produce them, this is a rich avenue for future research.

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