



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

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