



Why are there no persisting hybrids of humans with Denisovans, Neanderthals, or anyone else?

Ajit Varkia,1

The tour-de-force report of Sawyer et al. (1) on genomes of two Denisovans and the accompanying editorial and figure (2) support the notion of "a web of now-extinct populations linked by limited, but intermittent...gene flow" (3): involving multiple hominin lineages for thousands of years, before the mysterious disappearance of all taxa other than us "behaviorally modern humans" (BMHs). Although attention focuses on rare introgressions of non-BMH alleles facilitating adaptation of invading BMHs to ecological challenges, there is a bigger elephant in the room.

Current genomic and archaeological data indicate that BMHs arose in Africa ~100,000-200,000 y ago and spread across the planet (including the rest of Africa), encountering other extant hominins like Neanderthals, Denisovans, archaic African hominins, and possibly other lineages from earlier diasporas of Homo erectus. Although genomic evidence indicates interbreeding, the number of functional genes incorporated is limited, resulting in a "leaky replacement" (3), without persistence of true hybrids. Thus, our single BMH (sub)species was the "winner" in every contact/replacement event, spanning tens of thousands of years. I cannot find any other example wherein a single (sub)species from one geographic origin completely replaced all extant cross-fertile (sub)species in every planetary location, with limited introgression of functional genetic material from replaced taxa, and leaving no hybrid species. Typically, one instead finds multiple crossfertile (sub)species, with hybrid zones in between.

Although this apparent one-of-a-kind phenomenon could have occurred by chance, the singularity allows one to posit a uniquely complex genetic/biological/cultural transition of BMHs. As Pääbo suggested (3), adaptive accumulation of an "explosive constellation" of genetic variants (alleles) could have endowed BMHs with an unparalleled combination of

cognitive features, guaranteeing success at every subsequent encounter with other hominins.

Why did hybrid species not persist, at least at the geographical extremes of BMH expansion? Assuming that hundreds of new alleles comprised the BMH genotype, F₁ hybrids with other hominins would likely lack the complete cognitive package required to compete for mating within BMH groups. Tellingly, 10 of 10 non-BMH mitochondrial sequences are outside the current BMH range (1), suggesting that mating of BMH males with non-BMH females generated progeny that were not included within BMH groups. In contrast, progeny of female BMHs and non-BMH males may have had the opportunity to survive within BMH groups, with sufficient mating success rates to allow transmissions of a few alleles valuable to the newcomers, but related to ecological adaptation, not cognition.

Such "human exceptionalism" is currently frowned upon, as are extraordinary explanations of evolutionary events. However, unless there are other clear examples of such complete replacement of all related taxa by one single (sub)species, BMHs may indeed be a rare exception. Although environmental factors such as climate or infectious disease (4) could have generated the initial African bottleneck, the critical BMH phenotype was likely cognitive. This fits ecocultural models predicting Neanderthal extinction through competition with modern humans (5) and suggests an improbable BMH transition through a long-standing "psychological evolutionary barrier" possibly involving initially maladaptive features such as reality denial and mortality salience, which conspired to generate the winning combination (6).

Acknowledgments

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^aUniversity of California, San Diego/Salk Institute Center for Academic Research and Training in Anthropogeny (CARTA), La Jolla, CA 92093 Author contributions: A.V. wrote the paper.

The author declares no conflict of interest.

¹Email: a1varki@ucsd.edu