Neanderthal-Denisovan Ancestors Interbred with a Distantly-Related Hominin

Alan R. Rogers Nathan S. Harris Alan A. Achenbach

April 2, 2020

Early to middle Pleistocene of Eurasia

~1.8 mya: *Homo erectus* evolves in Africa, spreads into Eurasia

~550 kya: Late Acheulean appears in Europe.

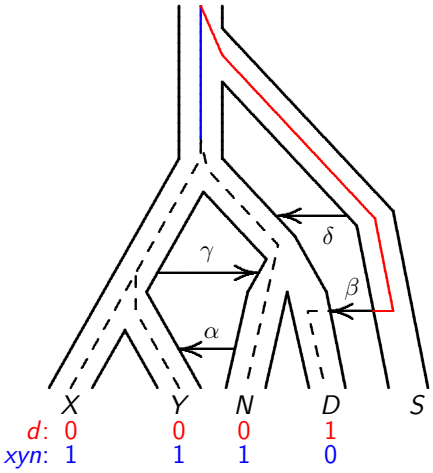
~430 kya: large-brained hominins at Sima de los Huesos

Similar fossils and tools occur earlier in Africa.

⇒ African invasion of Europe early in Middle Pleistocene.

What can genetics tell us about this period?

Gene genealogies and nucleotide site patterns



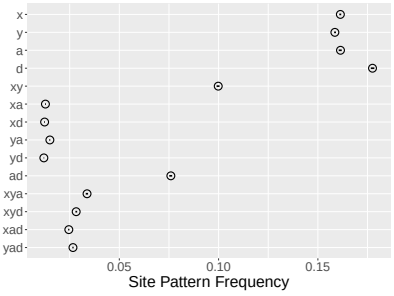
X, Africa; Y, Europe; N, Neanderthal; D, Denisovan; S, superarchaic.

XY is the ancestor of X and Y, etc.

Mutation on red branch → *site pattern* d. Blue branch → *xyn*.

0, ancestral; 1, derived.

Observed Site Pattern Frequencies

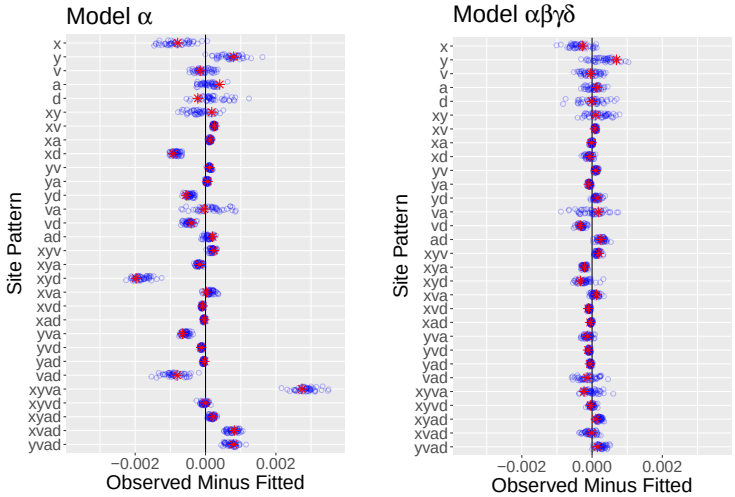


X, Africa; Y, Europe; A, Altai; D, Denisovan.

xy: random nucleotides from X and Y are derived; others are ancestral.

"Dots": 95% CIs.

Data: SGDP & Max Planck.



Key: *, real data; ○, bootstrap replicates.

Model selection and model averaging

Model selection by **bepe**, the bootstrap estimate of predictive error (Efron & Tibshirani 1993). Prefer model with smallest bepe value. Avoids overfitting.

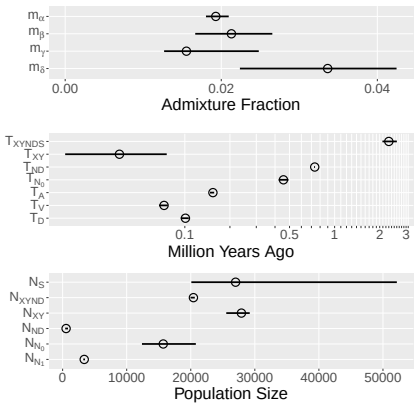
Model averaging by **booma**, bootstrap model averaging (Buckland, Burnham, and Augustin, 1997). Weight of ith model is fraction of bootstrap replicates in which it is best. Parameter estimates are weighted averages of per-model estimates. Addresses identifiability problems.

Bepe values and booma weights

Model	bepe	weight
α	1.16×10^{-6}	0
$\alpha\delta$	0.87×10^{-6}	0
$\alpha\gamma$	0.62×10^{-6}	0
$\alpha\gamma\delta$	0.44×10^{-6}	0
$\alpha\beta$	0.18×10^{-6}	0
$\alpha\beta\gamma$	0.17×10^{-6}	0
$\alpha\beta\delta$	0.15×10^{-6}	0.16
$\alpha\beta\gamma\delta$	0.13×10^{-6}	0.84

Reject models with weight zero: their disadvantage is large compared with variation in repeated sampling.

Strong support for two episodes of superarchaic admixture (β and δ); qualified support for admixture (γ) from early moderns into Neanderthals.



Superarchaic population separated ∼2 mya. It was large—between 20,000 and 50,000—or deeply subdivided.

neandersovan population (N_{ND}) was tiny, and split early ($T_{ND} > 700$ kya) to form Neanderthals and Denisovans.

∼3% admixture into neandersovans from superarchaics.

Interpretation

Superarchaics separated from other hominins ∼2 mya. They may represent the earliest Eurasians. Their population was either large or deeply subdivided.

∼750 kya, neandersovans separated from an African population, expanded into Eurasia, endured a bottleneck, interbred with superarchaics, and then (∼730 kya) split into eastern and western subpopulations (Denisovans & Neanderthals).

Acknowledgements

Daniel Tabin helped develop software for bepe and booma.

This project was supported by:

- National Science Foundation: BCS 1638840
- Center for High Performance Computing, U. of Utah.