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An analysis of morphological evolution in the hominid lower limb using methods from quantitative genetics

Marianne J. Cooper¹, Mark A. Conaway^{1,2}, Noreen von Cramon-Taubadel¹

1 - Buffalo Human Evolutionary Morphology Lab, Department of Anthropology, University at Buffalo · 2 - Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa 50010

Morphological differences are a common line of evidence in studies of evolutionary processes, but it is difficult to distinguish evolutionarily significant traits among the measurable morphological features. Quantitative genetics, which focuses on the evolution of continuous traits, provides mathematical frameworks for estimating the evolutionary pressures on lineages and individual traits. The application of quantitative genetics methods to phenotypic data can therefore help researchers identify potential directional selection in morphological evolution [1,2]. Lande's generalized genetic distance (GGD) is one method that can provide insight into the strength and direction of selection over evolutionary transitions and allow us to estimate whether observed morphological change is the result of directional selection on the observed trait or an indirect change influenced by selection on other traits [1,2]. These applications are especially useful in the study of evolution in the *Homo* lineage where change is often assumed to be adaptive [3,4].

This study tests for directional selection in the morphological evolution of the hominid lower limb using 45 interlandmark distances (traits) on the os coxa, femur, tibia, and fibula of *Homo sapiens* (n=35), *Pan troglodytes* (n=34), *Gorilla gorilla* (n=35), and *Pongo pygmaeus* (n=30) using Lande's GGD. Estimates of ancestral traits were calculated for three ancestral nodes: the last common ancestor (LCA) of *Pan* and *Homo*, the LCA of African apes, and the LCA of hominids, using a rapid maximum likelihood algorithm [5]. Mean estimated ancestral traits and mean traits of extant taxa were then used to calculate Lande's GGD for each evolutionary transition. Genetic drift cannot be rejected as the primary evolutionary force in the branch from the LCA of African apes to *G. gorilla*. Strong directional selection was identified in two transitions: the branch from the LCA of *Homo* and *Pan* to *H. sapiens*, and in the branch from the LCA of *Homo* and *Pan* to *P. troglodytes*. Strong stabilizing selection was identified in all other branches.

Selection gradients (representing estimated magnitude and direction of selection pressure on each trait) and selection responses (representing estimated magnitude and direction of real morphological change in trait size from ancestor to descendant) were calculated for the two branches under strong directional selection. Large selection gradients were indicated in the os coxa, tibia, and femur in the branch leading to *H. sapiens*. Decreased height of the os coxa, increased diameter of the femoral head, and elongation of the tibia were under the strongest directional selection. Large selection gradients also were indicated in all four elements on the branch leading to *P. troglodytes*. Here, increased height of the os coxa, decreased anteroposterior breadth of the acetabulum, and decreased diameter of the femoral head were under the strongest selection.

The pattern and magnitude of selection gradients were different among the lineages, indicating that they experienced unique evolutionary pressures resulting in directional selection on different morphological traits. Both lineages also showed large estimated selection responses in traits that were not estimated to be under strong directional selection, or responses to selection opposing the selective pressures on the trait. This indicates that, for these traits, the morphology of the descendant branch was not the result of direct selection. These traits included morphological features that are often assumed to be adaptive, such as the relative size of the tibial plateau in *H. sapiens*. Overall, results indicate the morphology of lower limb elements is derived in both *P. troglodytes* and *H. sapiens*, and emphasize the need to separate observed morphological change from evolutionarily significant morphological change when investigating evolutionary morphology, particularly in the *Homo* lineage.

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References: [1] Lande, R., 1979. Quantitative Genetic Analysis of Multivariate Evolution, Applied to Brain: Body Size Allometry. *Evolution*. 33, 16. [2] Lande, R., Arnold, S.J., 1983. The measurement of selection on correlated characters. *Evolution*. 37, 1210–1226. [3] Schroeder, L., Ackermann, R.R., 2017. Evolutionary processes shaping diversity across the *Homo* lineage. *J. Hum. Evol.* 111, 1–17. [4] Schroeder, L., von Cramon-Taubadel, N., 2017. The evolution of hominoid cranial diversity: A quantitative genetic approach. *Evolution*. 71, 2634–2649. [5] Goolsby, E.W., Bruggeman, J., Ané, C., 2017. Rphylopars: fast multivariate phylogenetic comparative methods for missing data and within-species variation. *Methods in Ecology and Evolution*. 8, 22–27.