

REPLY TO ALMÉCIJA:

A new direction for reconstructing our last common ancestor with chimpanzees

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We welcome Almécija's critique (1), but his claims of "bias" in our conclusions are unfounded. All available evidence continues to support an African ape-like shoulder and pattern of forelimb use in our last common ancestor (LCA) with chimpanzees and bonobos (*Pan*). First, controlling for within-group size variation is uncontroversial (2), and neither biases our results nor obscures their biological meaning. *Gorilla* and *Pan* shape differences may still be size-related. Specifically, *Gorilla*'s expansive supraspinous fossa is plausibly associated with increased body mass and functional demands to stabilize the joint during knuckle-walking (3). Second, although we note that a "*Pan*-like" LCA may be favored based on total evidence, a more "*Gorilla*-like" condition is also plausible; hence, our title states support for an "African ape-like" LCA (4). That panin and hominin lineages may have subsequently evolved in different directions along the major axis of variation has no bearing on this conclusion; rather, it suggests joint orientation is highly evolvable. Indeed, although our analyses support homologies between African-ape and human shoulder shape, we also identify evidence for homoplasy in spine orientation among apes, including surprising data suggesting that orangutans retain primitive characteristics of the ancestral hominoid morphotype, consistent with parallelism. Third, the Dikika juvenile (not "baby") preserves the most complete evidence of *Australopithecus afarensis* shoulder anatomy known. Estimates of adult shape do not substantially differ from the juvenile because growth has only a weak effect on overall scapular shape. As we previously noted (5), Woranso-Mille may differ somewhat

from Dikika in joint lateralization, but this does not change our interpretation. Moreover, *Australopithecus sediba*, which is better preserved, is similarly intermediate, consistent with our interpretation. The proximity of australopithecines to *Nasalis* is more parsimoniously reconstructed as hominin convergence as a result of lateralization of the shoulder joint rather than independent evolution of a similar blade shape in chimpanzees, gorillas, and hominins. Fourth, there are multiple ways to test alternative hypotheses. Ours was not based on comparing tree lengths but rather on the congruence of the fossils with the model predictions and the number of evolutionary events required to explain them. Fifth, use of equal branch lengths does not force a punctuated model of evolution, while branch lengths based on genetic distances do not alter either our results or conclusions.

Finally, the most relevant message of our study is that because fossil evidence for the LCA will always be rare and difficult to identify (6), novel multidisciplinary approaches are needed to reconstruct its phenotype. Our work demonstrates how alternative models of the LCA make explicit and testable predictions about evolutionary trajectories and phenotypic transformations in the shoulder, which in turn point to differences in the underlying morphogenetic programs that may be directly testable in genomic datasets and model species. More importantly, this approach can be applied to other regions of the skeleton to predict more balanced and objective histories of selection. This is the focus of our current research, and we hope Almécija and others will join us in exploring this promising new direction.

1 Almécija S (2016) Pitfalls reconstructing the last common ancestor of chimpanzees and humans. *Proc Natl Acad Sci USA* 10.1073/pnas.1524165113.

2 Zelditch M, Swiderski DL, Sheets HD (2012) *Geometric Morphometrics for Biologists: A Primer* (Elsevier, New York), 2nd Ed.

3 Larson SG (2015) Rotator cuff muscle size and the interpretation of scapular shape in primates. *J Hum Evol* 80:96–106.

4 Young NM, Capellini TD, Roach NT, Alemseged Z (2015) Fossil hominin shoulders support an African ape-like last common ancestor of humans and chimpanzees. *Proc Natl Acad Sci USA* 112(38):11829–11834.

5 Young NM, Capellini TD, Roach NT, Alemseged Z (2015) Reply to Melillo: Woranso-Mille is consistent with an australopithecine shoulder intermediate between African apes and Homo. *Proc Natl Acad Sci USA* 112(52):E7160.

6 Steiper ME, Young NM (2008) Timing primate evolution: Lessons from the discordance between molecular and paleontological estimates. *Evol Anthro* 17(4):179–188.

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