



Reply to Melillo: Woranso-Mille is consistent with an australopithecine shoulder intermediate between African apes and *Homo*

In reference to our recent paper (1), Melillo (2) makes three claims: (i) the adult Woranso-Mille (KSD-VP-1/1) scapula, which we did not consider in our analyses, suggests *Australopithecus afarensis* shoulders may be more derived than we report; (ii) our reconstructions indicate homoplasy, consistent with an “ape convergence” model; and (iii) *Australopithecus* shoulder shape is best explained by “committed terrestriality” and tool use and not a trade-off with arboreal efficiency. None of these claims alter the findings of our paper (1), that the australopithecine shoulder is intermediate between African apes and *Homo*, and that the hominin shoulder underwent a slow, sustained evolutionary transformation from an African ape-like last common ancestor to modern humans.

First, the Dikika juvenile is currently the best-preserved example of *A. afarensis* shoulder blade anatomy (3), and its adult shape can be modeled using conservative assumptions about growth (1, 4). As Melillo notes (2), blade shape has a strong phylogenetic signal (4), yet the Woranso-Mille scapula is missing critical portions of the inferior angle and supraspinous fossa (5), limiting its utility for ancestral state reconstruction. Although difficult to discern from the two published pictures, spine orientation in Woranso-Mille may be somewhat more lateralized than Dikika, but it also overlaps with African apes in a number of other metrics (5). Such differences between Dikika and Woranso-Mille are not surprising, because hominoid scapulae are known to be significantly more variable in shape compared with other primates (6). That

said, Melillo offers that “. . . the magnitude of shape difference between the two fossils does not exceed the level observable in living species” (2). Consequently, whereas including a more complete Woranso-Mille would inevitably increase the morphospace occupied by Dikika, the australopithecine shoulder is still less derived than *Homo* and modern humans.

Second, support for an African ape model is not contingent upon the absence of homoplasy. As we discuss in our paper, both models predict that chimpanzee/gibbon and human/orangutan similarities in spine orientation convergently evolved (1). Instead, we based our conclusion on the well-established principle that the simplest explanation is preferred. Because the ape convergence model posits living hominoids evolved from a more primitive shared ancestral morphotype, similar blade shapes would have had to independently evolve five times: once each between gorillas, chimpanzees/bonobos, and humans, and twice between gibbons and orangutans. In contrast, the African ape model predicts one event to evolve the African ape blade shape from a more primitive one shared by Asian apes, a much more parsimonious explanation.

Finally, we explicitly argue for a scenario in which both reduced reliance on arboreality and selection on more lateralized activities, such as tool-use in australopithecines and throwing in later *Homo*, served as sustained selective forces acting on shoulder shape (1). We do not dispute the importance of terrestrial bipedality, but simply note that the slow pace of scapular evolution supports

the continued, but diminished, importance of arboreality in australopithecines.

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1 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.

2 Melillo SM (2015) An alternative interpretation of the *Australopithecus* scapula. *Proc Natl Acad Sci USA*, 10.1073/pnas.1520902112.

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The authors declare no conflict of interest.

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