Response to Comment on “Human-like hand use in Australopithecus africanus”

Matthew M. Skinner,1,2,3,4 Nicholas B. Stephens,3 Zewdi J. Tsegai,3 Alexandra C. Foote,2 N. Huynh Nguyen,3 Thomas Gross,4 Dieter H. Pahr,5 Jean-Jacques Hublin,5 Tracy L. Kivell1,3,4*

Almécija and colleagues claim that we apply a simplified understanding of bone functional adaptation and that our results of human-like hand use in Australopithecus africanus are not novel. We argue that our results speak to actual behavior, rather than potential behaviors, and our functional interpretation is well supported by our methodological approach, comparative sample, and previous experimental data.

A lmécija et al. (1) challenge our conclusions on three points: (i) we do not give sufficient credence to published studies on the external morphology of australopith hand bones that are consistent with precision grip capabilities; (ii) we overstate the evidence for a form-function signal in trabecular bone; and (iii) our comparative sample and analyses do not support differences in trabecular patterning between humans and extant apes. Their critique suffers from a lack of recognition that: (i) our study provides evidence for hand postures actually adopted by australopiths, rather than those they were potentially capable of; (ii) we base our conclusions on the three-dimensional distribution of trabecular bone throughout the epiphysis rather than on particular measures of subregions of trabecular structure; and (iii) our comparative sample, which includes stone tools using Tai chimpanzees, indicates that humans have a distinctive trabecular pattern that is shared with Neandertals and Australopithecus africanus (2).

We do not claim that our results “refute the previously existing hypothesis that human-like manipulation preceded systematized stone tool manufacture” (1); to the contrary, we state that our results are consistent with the use of “forceful hand grips for any number of manipulative behaviors” (2). Almécija et al. (1) refer to previous studies (mainly their own) based on the relative lengths and external morphology of hand bones that “have provided compelling evidence for pad-to-pad precision grasping before the widespread occurrence of flaked stone tools” (1) and that australopiths and earlier hominins “were likely capable of human-like manipulation” (1). We agree; however, Almécija et al. (1) fail to acknowledge that our results are novel because they reflect (i) actual behavior, rather than the capability for particular behaviors and (ii) forceful pad-to-pad precision grasping, which is what separates human dexterity from that of other primates (3). The asymmetric distribution of trabecular bone within the base of the thumb and metacarpal heads in humans, Neandertals, and A. africanaus (and the absence of this pattern in apes) provides evidence for habitual, forceful opposition of the thumb to the fingers. We agree that inferences for human-like hand use among australopiths referred to by Almécija et al. are neither “unprecedented nor unexpected” (1). However, the inferences we can now make, based on the trabecular bone distribution and the well-accepted concept that trabealae remodel in response to habitual load during an individual’s lifetime (4, 5), are much stronger than they and others have been able to make based on external morphology of hand bones alone.

Almécija et al. (1) also take issue with our statement that “external morphology can be ambiguous, as some features can be retentions from the ancestral condition and may not be functionally important” (2). This is an often-recognized, fundamental problem of any researcher trying to reconstruct behavior in the past in palaeoanthropology (6) and beyond (7), and we stand by this assertion. Their claim that we suggest that “trabecular organization will enable an individual to attain human-like grips” (1) is simply incorrect. Clearly, the range of motion of each finger and thumb and the possibilities for their relative positions during manipulation are largely dictated by the size and shape of the bones themselves, as well as soft tissues, and not by trabecular bone. We assert that the trabecular pattern indicates whether or not individual australopiths were actually adopting these grips with enough force to maintain an appropriate distribution of trabecular bone [i.e., a physiological adaptation, sensu (8)].

Almécija et al. (1) highlight three reasons that our interpretation of trabecular bone functional adaption is problematic. First, they note that trabecular bone remodels under dynamic loads and not static loads, such as when one is “tool grasping” (1). Not only does experimental evidence show that gripping force varies during static holding, and thus that loads experienced by the hand are dynamic (9), but when one uses an object, gripping force will fluctuate throughout the duration of the task (10, 11).

Second, they claim that “there is little evidence that trabecular bone is less influenced by genetics, or more influenced by loading, than cortical bone” (1). The authors ignore substantial experimental evidence that trabecular bone structure can adapt to longer-term (i.e., minimum 8 to 10 weeks) cyclic loading (e.g., (4, 5)) and appears to do so better than cortical bone (12). Indeed, one of the authors themselves has recently used trabecular bone to infer function in fossil hominins (13).

Third, they claim that the failure of previous studies to find a strong link between trabecular structure and inferred patterns of loading weakens our argument. These previous studies examine a volume of interest within the epiphysis and quantify characteristics of trabecular structure such as the ratio of bone volume to total volume (BV/TV), trabecular spacing, or trabecular number. Our analysis differs from these studies in that we quantify the distribution of BV/TV throughout the entire epiphysis, and the key finding of our study is based not on the “density” of trabecular bone but on its relative distribution throughout the epiphysis. This includes the distribution of trabeculae just beneath the articular joint surface, where joint reaction forces are initially incurred, which allows us to infer the joint position during predominant loading.

Finally, Almécija et al. (1) suggest that a lack of differences in pairwise comparisons in BV/TV in the third metacarpal (Mc3) between humans and Asian apes weakens our argument for a link between form and function. Unfortunately, they are conflating two sets of results: those for average BV/TV throughout the epiphysis and the distribution of trabecular bone throughout the epiphysis. Furthermore, we acknowledge that shared high BV/TV values between Pan and A. africanaus, suggesting that this may reflect that “the hands of these early hominins may still be used for arboreal locomotion” (2). Contrary to Almécija et al.’s (1) claim, our comparative sample does include tool-using Tai chimpanzees [Pan troglodytes verus; original table SI (2)], and their metacarpals do not show any similarity to the trabecular distribution found in humans, Neandertals, and A. africanaus. We agree that examining other nonhuman primates is likely to further elucidate links between hand use and trabecular structure, but the limited trabecular bone in the epiphyses of smaller-bodied hominoids and...
monkeys (14) suggests caution in applying either our method or traditional volume-of-interest approaches to broad comparative samples. For example, hylobatids have very few trabecular struts in their hand bone epiphyses. This yields similar average BV/TV values in hylobatids and humans, as Almécija et al. (1) highlight, even though the trabecular structure itself is very different between the two taxa. Based on our understanding of Almécija and colleagues’ (1) critique, we see no reason to alter the conclusions of our study (2).

Thus, it is parsimonious, based on current evidence that tool use and tool production [albeit current studies (10, 11) are biased toward these behaviors] induce some of the highest nonlocomotor loading on the hands. By this derived, human-like pattern is consistent with evidence for stone flake use by *A. afarensis* (15). Future analyses of trabecular structure in earlier hominins may indeed reveal that such forceful precision grips were actually used long before evidence of tool use, supporting the claims of Almécija et al. (1), but until then, such gripping behaviors can only be considered a potential capability.

Note added in proof: Recently described pre-Oldowan stone tools from Kenya, named the Lomekwian [S. Harmand et al. (16)], are relevant to this discussion and particularly interesting, as they occur at least 0.5 Ma before the appearance of the genus Homo. The large size of hammers, anvils, and flakes that characterize the Lomekwian are suggestive of considerable loading of the thumb and fingers during flake production, and this is consistent with our evidence for high BV/TV and the distribution of trabecular bone in the base of the thumb consistent with forceful precision grips in *Australopithecus*. Biomechanical analyses of hand loading during simulated Lomekwian tool production would shed light on potential links between this behavior and the patterns of trabecular bone distribution in the hands of pre-*Homo* hominins.

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