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**Reply to Almécija et al. “Comment on inferences of hand use in  
Australopithecus africanus”**

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Almécija and colleagues (1) challenge our conclusions about evidence for human-like hand use in *Australopithecus africanus* on three points: 1) we do not give sufficient credence to published studies on the external morphology of australopith hand bones that are consistent with precision grip capabilities; 2) we overstate the evidence for a form-function signal in trabecular bone; and 3) our comparative sample and analyses do not support our reported differences in trabecular patterning between humans and extant apes. As we outline below, their critique suffers from a lack of recognition that 1) our study provides evidence for hand postures actually adopted by australopiths, rather than simply being potentially capable of doing so; 2) we base our conclusions on the 3D distribution of trabecular bone throughout the whole epiphysis rather than from particular measures of trabecular structure; and 3) our

comparative sample, which includes stone tool-using Tai chimpanzees, clearly indicates that humans have a distinctive trabecular pattern that is shared with Neandertals and *Au. africanus* (2).

Almécija et al. (1) suggest that our results fail “to refute the previously-existing hypothesis that human-like manipulation preceded systematized stone tool manufacture” (1: pg. 1). We do not make this claim and, to the contrary, state that our results are also consistent with the use of “forceful hand grips for any number of manipulative behaviours” (2: pg. 399). Almécija et al. (1) refer to previous studies (mainly their own) (3-5) based on the relative lengths and external morphology (i.e., tendon attachments) of hand bones that “have provided compelling evidence for pad-to-pad precision grasping well before the earliest-documented flaked stone tools” (1: pg. 2) and that australopiths and earlier hominins “were likely capable of human-like manipulation” (1: pg. 6; italics added). We do not disagree with these assertions or previous work. However, Almécija et al. (1) fail to acknowledge two key aspects of our study. First, what separates the advanced manual dexterity of humans from other primates, is not just “pad-to-pad precision grasping” (1: pg. 2), but forceful pad-to-pad precision grasping (6). Forceful precision grasping, due partly to the hypertrophied muscles to the human thumb compared with other primates, is demonstrated experimentally to be important during tool-use and tool-making behaviours (7-9), as well as many other day-to-day manipulative tasks that humans engage in (10). Well-developed muscle attachments on fossil hominin first metacarpals suggest the capability for forceful grasping (11), but it has not been previously shown that forceful grips were used or what kind of grips were used (e.g. forceful gripping of branch during locomotion vs. forceful precision gripping during manipulation).

This leads us to the second point that Almécija et al. (1) fail to recognise: our results are novel because they demonstrate actual behaviour, rather than the capability for particular

behaviours. The asymmetric distribution of trabecular bone within the base of the thumb and metacarpal heads in humans, Neandertals and *Au. africanus* (and the absence of this pattern in other 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. is not “unprecedented nor unexpected” (1:pg. 3). We argue simply that the inferences we can now make, based on the trabecular bone distribution and the well-accepted concept that trabecular bone remodels in response to habitual load during an individual’s lifetime (12-14, and references therein), are much stronger than they and others have been able to make based on external measurements and morphology of hand bones (3-5).

Almécija et al. (1) also take particular issue with our critique of external bone features for inferring actual loading; “external morphology can be ambiguous, as some features can be retentions from the ancestral condition and may not be functionally important” (2: pg. 395). This is not a novel critique; it is a fundamental assertion and common problem of any researcher trying to reconstruct behaviour in the past in palaeoanthropology (15) and beyond (16). We stand by this assertion. The author’s claim that we suggest that “trabecular organization will enable an individual to attain human-like grips” (1: pg. 3) is simply incorrect. We agree that the range of motion of each finger and thumb and the possibilities for their relative positions during manipulative activities is largely dictated by the size and shape of the bones themselves, as well as soft tissue morphology, and not by the trabecular bone found within their epiphyses. We do not suggest, as stated by Almécija et al., that trabecular structure dictates the “capacity to achieve human-like hand grips” (1: pg. 3), but rather that it 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* 17).

Almécija et al. (1) highlight three reasons that our interpretation of trabecular bone functional adaptation is problematic. First, they note that trabecular bone remodels under dynamic loads and not static loads, such as when one is “simply holding an object” (1: pg. 4). Not only does experimental evidence show that gripping force varies during static holding and thus load experienced by the hand is dynamic (18), but when one uses an object, gripping force (and the joint reaction force) will change throughout the duration of the task (8,9). Second, Almécija et al. claim that “there is little evidence that trabecular bone is less influenced by genetics, or more influenced by loading, than cortical bone” (1: pg. 4). They cite two studies; one which found little response in mouse trabecular bone to load incurred over just a short two-week period (18) and the other (19) which uses a highly problematic methodology (20). In contrast, the authors ignore the wealth of literature over the last two decades that demonstrates experimentally that trabecular bone structure can adapt to longer-term (i.e. minimum 8-10 weeks) cyclic loading (e.g., 12-14) and appears to do so better than cortical bone (21, but see 22). Although we acknowledge, as we did in our original paper (2: pg. 399), that the functional adaptation of bone is complex and there is still much to be learned, we accept this literature as strong evidence that one can reliably infer predominant joint loading from trabecular bone structure.

Third, regarding the debate about the relative contributions of genetics and loading to trabecular density, we emphasize that the key finding of our study is not about “density” of trabecular bone, but its relative distribution throughout the epiphyses. The claim that the failure of previous studies to find a strong link between trabecular structure and inferred patterns of loading weakens our argument is not substantiated. These previous studies examine a volume of interest within the epiphysis (usually in the humeral or femoral head) and quantify characteristics of trabecular structure such as bone volume/total volume (BV/TV), trabecular spacing, or degree of anisotropy. Our analysis differs from these studies

in that we quantify the distribution of BV/TV throughout the entire 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 significant 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 and does not support our conclusions. 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 the shared high BV/TV values between Pan and Au. africanus, suggesting that this may reflect that “the hands of these early hominins may still be used for arboreal locomotion” (2: pg. 399). It is important to note, since Almécija and colleagues refer specifically to stone tool use by the Tai chimpanzees (their Fig. 1) and their importance as part of the comparative sample, that Tai chimpanzee individuals were indeed included in our comparative sample [n=8 Mc1s and n=5 Mc3 and Mc5 each; see original Table S1 (2)] and do not show any similarity in distribution in the base of the thumb found in humans, Neandertals and Au. africanus. We agree that examining other non-human primates is likely to elucidate links between hand use and trabecular bone structure, but note that the limited trabecular bone structure in the epiphyses of smaller bodied hominoids (23) and monkeys (24) suggest caution in applying either our method or traditional volume-of-interest approaches to broad comparative samples. For example, gibbons, and siamangs 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) point out, even though the trabecular structure itself is very different between the two taxa.

Based on our understanding of the critiques of Almécija and colleagues (1), we see no reason to alter the conclusions of our original study (2). There is sufficient experimental evidence to indicate that the distribution of trabecular bone within an epiphysis can be used to reliably infer joint position during predominant loading. Comparisons of human and ape hand bones indicate different patterns of trabecular bone distribution in the thumb and fingers that correlate with inferred hand postures during loading. Both Neandertals and *Au africanus* share a distinctive, human-like pattern in the distribution of trabecular bone in the metacarpals consistent with forceful opposition of the thumb to the fingers in precision and power squeeze grips. The trabecular pattern provides novel evidence that *Au. africanus* was actually adopting these human-like grips as opposed to potentially being capable of doing so (but with no evidence that they actually did so on a regular basis) (3-5). Although we think it is quite likely that such forceful human-like grips were used for any number of manipulative behaviours, experimental evidence suggests tool-use and tool-production (albeit current studies are biased towards these behaviours; 8, 9) induce some of the highest non-locomotor loading on the hands. Thus, it is parsimonious, based on current evidence, to conclude that these hand grips (forceful precision and power squeeze ) were being adopted during tool use (be it of wood, bone, or stone) and this derived, human-like pattern is consistent with published evidence for the use of stone flakes by *Au. afarensis* (25). 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, 3-5), but until then, such gripping behaviours can only be considered a potential capability.

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