

## TECHNICAL COMMENT

## HUMAN EVOLUTION

# Comment on “Human-like hand use in *Australopithecus africanus*”

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Skinner and colleagues (Research Article, 23 January 2015, p. 395), based on metacarpal trabecular bone structure, argue that *Australopithecus africanus* employed human-like dexterity for stone tool making and use 3 million years ago. However, their evolutionary and biological assumptions are misinformed, failing to refute the previously existing hypothesis that human-like manipulation preceded systematized stone tool manufacture, as indicated by the fossil record.

Skinner *et al.* (1) analyze metacarpal trabecular bone structure in the 3-million-year-old hominin *Australopithecus africanus* and infer based on these data that this taxon “was capable of habitual and forceful human-like opposition of the thumb and fingers during [...] tool-related behaviors, providing morphological evidence of committed tool use in a hominin hitherto considered not to be capable of these behaviors” (1). Specifically, they found that the trabecular organization of the pollical metacarpal of *A. africanus* is, in some respects, more human-like than chimpanzee-like, which they interpret as “morphological evidence...that can be linked to behavior and hand use during life” (1), with clear allusions to stone tool making and use throughout the article. Although we appreciate their effort to investigate a novel aspect of fossil morphology like trabecular structure, we note here limitations in the proposed evolutionary importance of their findings, which together with misinformed assumptions about bone mechanobiology make many of their conclusions unwarranted. We hope that the concerns that we raise will help promote a constructive discussion dealing with the complex topic of the relationships between form and function and redirect future research studies in human evolution.

It is well known that, like humans, all living great apes make and use tools, and some chimpanzees and capuchin monkeys even engage in

regular stone tool use (2). Humans, however, display especially advanced manual dexterity facilitated by a unique (among modern hominoids) type of interaction between the proximal pulps of our thumb and fingers (3). The primary anatomical requirement for this pad-to-pad precision grasping is having a long thumb relative to finger lengths (3–5). Previous analyses of hand bone morphology in australopiths (4, 6–8) and the Miocene hominin *Orrorin* (5) have provided compelling evidence for pad-to-pad precision grasping before the widespread occurrence of flaked stone tools, which indicates that a basic human-like hand structure is plesiomorphic for modern humans (Fig. 1). The emerging evolutionary picture is that increased reliance on bipedalism and enhanced manipulation were very early apomorphies of the hominin lineage, as a part of our original adaptive shift from apes in relation to new foraging strategies (5, 7). Thus, the eventual application of human-like hand structure to stone tool flaking and use was almost certainly an exaptation, not an adaptation (4). In this light, the inference by Skinner *et al.* of human-like hand use among australopiths is neither unprecedented nor unexpected.

Skinner *et al.* downplay previous evidence for human-like hand use among australopiths by arguing that because earlier studies were focused exclusively on external (cortical) bone features, they do not necessarily provide insight into how hominins were actually using their hands during life. As they see it, “external morphology can be ambiguous, as some features can be retentions from the ancestral condition and may not be functionally important” (1). The structure of internal trabecular bone, they argue, is a truer reflection of in vivo loading than cortical structure and less influenced by nonmechanical factors such as phylogeny. This claim is based on a simplified account of bone functional adaptation that trabecular remodeling throughout life is optimized to add and preserve bone where loading occurs and resorb bone where it does not. However, it is important to recognize that trabecular structure alone has little bearing on individual capacity to

achieve human-like hand grips. In fact, no type of trabecular organization will enable an individual to attain human-like grips if the external morphology of their hand bones does not permit it. Therefore, Skinner and colleagues’ conclusions rely on the circular reasoning that the external morphology of australopith hands actually allowed human-like grips, which weakens the basic premise of their study that trabecular structure is a more informative signal than external features.

Furthermore, Skinner *et al.*’s interpretation of trabecular bone functional adaptation is problematic for at least three reasons. First, while trabecular bone clearly can respond to mechanical signals, loads must be dynamic to be osteogenic (9). Relatively static loads associated with tool grasping [like those shown for the pollical metacarpal in figure 1 in (1)] have not been associated with enhanced trabecular morphology, independent of the magnitude of the applied force. Second, there is little evidence that trabecular bone is less influenced by genetics, or more influenced by loading, than cortical bone. Heritability estimates for trabecular density in humans range between 59 and 73%, whereas estimates for cortical density are between 17 and 42% [see references in (10)]. Moreover, human studies have shown that cortical morphology of weight-bearing elements scales far better with body mass (a proxy for mechanical loading) than trabecular architecture [e.g., (11)]. Third, if trabecular organization indeed correlates strongly with predicted loading conditions, then this should be evident throughout the skeleton, especially in weight-bearing elements. However, numerous previous attempts to identify functional loading signals in the trabecular structure of weight-bearing elements in humans and other primates have most often been unsuccessful (12). Thus, why mechanical signals induced by object manipulation should be uniquely discernible in hominin pollical metacarpals is unclear. Skinner *et al.* base their conclusions on their previous comparative analysis of trabecular structure in the hominoid third metacarpal (13). However, this analysis was unable to separate humans from gibbons or orangutans [figure 4 in (13)], and it failed to provide any direct evidence that observed differences between taxa were actually due to variation in lifetime mechanical loading. Inherently, extrapolating from this potentially phylogenetically dependent correlation in the third metacarpal to all metacarpals renders the conclusions of Skinner *et al.* even more speculative.

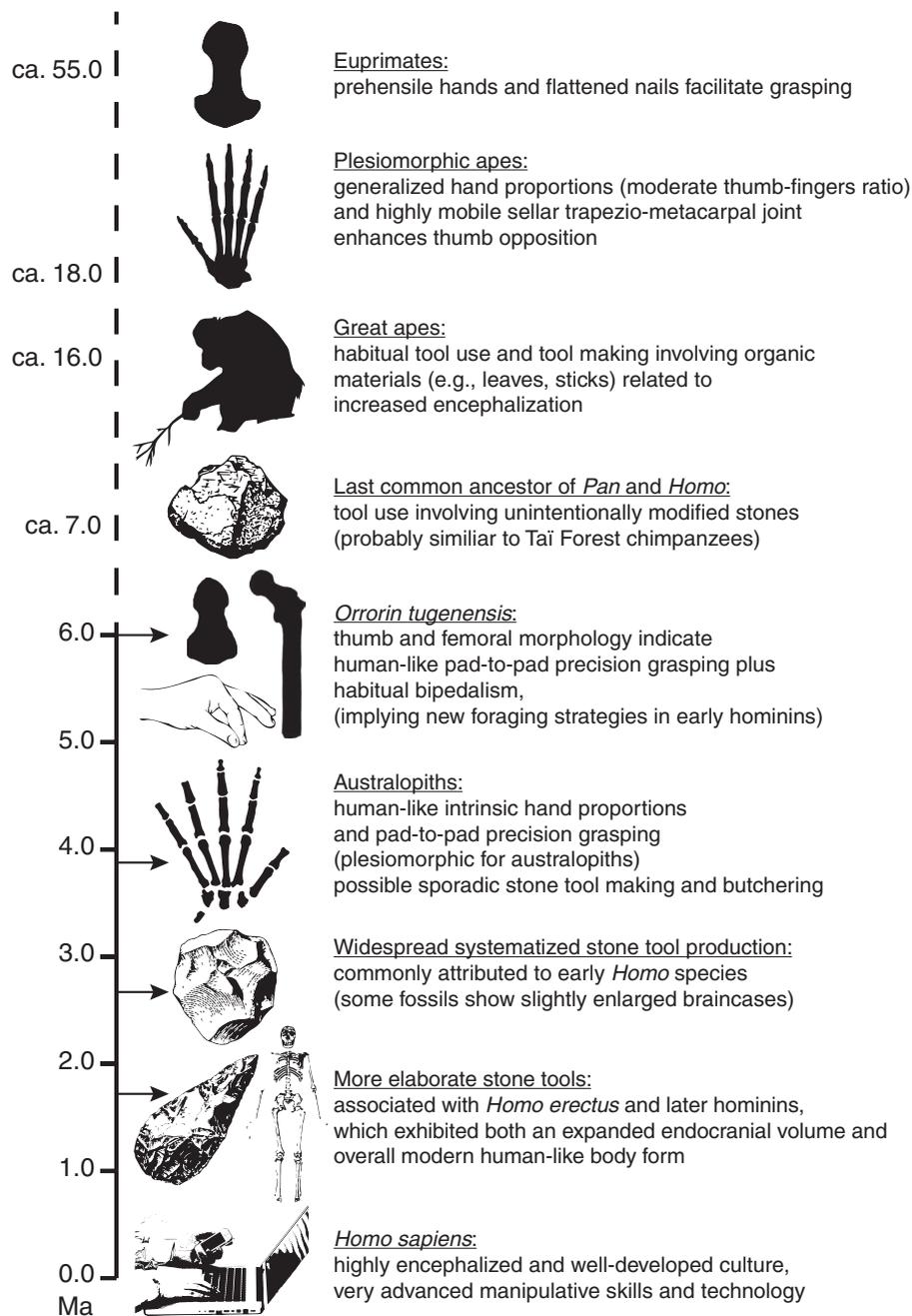
Nevertheless, even if one assumes that metacarpal trabecular structure closely reflects lifetime loading, Skinner *et al.*’s comparative evidence linking form to function is limited. Although the authors found that “[d]ifferences in the distribution of trabecular bone across apes and humans were also found in Mc3 and Mc5” (1), their pairwise comparisons [table S3 in (1)] indicate that this is only true for the fifth metacarpal head, for which no australopiths were sampled [table 1 in (1)]. For the third metacarpal head, differences in trabecular organization were only found between humans and African apes [table S3 in

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**Fig. 1. Simplified timeline showing major evolutionary advances in human manipulative capabilities.**

The fossil record indicates that the story of human advanced manipulation has very early origins, predating the widespread appearance of systematized flaked stone tool manufacture. Basic human-like hand proportions allowing for refined manipulation have been inferred in *Orrorin* and all australopith species and confirmed by the virtually complete hand of *Australopithecus sediba*. The morphological results of Skinner *et al.* merely support these previous findings. Ma, million years ago.

(7)], with *A. africanus* showing values closer to apes than humans. Ultimately, Skinner *et al.*'s numerical results support human-like hand use in *A. africanus* based only on certain similarities with the trabecular pattern of the pollical metacarpal base of humans as compared to chimpanzees. In our opinion, it is overly risky to draw profound conclusions about hominin paleobiol-

ogy based solely on a comparative sample of two taxa (*Pan* versus *Homo*). It is noteworthy that a previous inference (14) of australopith stone tool manufacture based on pollical metacarpal external morphology that relied on a comparative sample of only chimpanzees and humans was no longer supported once gorillas were included in the analysis [i.e., gorillas were

similar to hominins (15)]. A more credible test relating pollical metacarpal trabecular structure to manipulative behaviors would incorporate not only gorillas (as they did with rays three and five) but also other primates with dexterous hands like *Theropithecus* (specialized forager) or the Tai Forest chimpanzees and *Cebus* (stone tool users). Such a strategy would permit evaluation of whether the observed morphological signatures of Skinner *et al.* are ecophenotypic (as they argue) instead of merely representing a hominin phylogenetic signal.

Ultimately, the results of Skinner *et al.*, far from demonstrating strong evidence of stone tool manufacture and use among australopiths, support previous observations reached on the basis of external morphology that australopith hands were, in some ways, more similar to those of humans than to apes, and thus were likely capable of human-like manipulation (4–8). However, this does not mean that human hands evolved for the sole purpose of making and using stone tools, for which cognitive capabilities should be also considered, as Napier and others indicated before (3).

**Note added in proof:** The recently described lithic artifacts from Lomekwi 3, northwestern Kenya, are claimed to represent the earliest evidence of intentional stone tool production at 3.3 Ma [S. Harmand *et al.* (16)]. This discovery is consistent with human-like manual dexterity being an ancient adaptation among hominins. Even so, as Harmand *et al.* argue, and in agreement with our view, the decisive adaptation enabling “Lomekwian” stone knapping (to yet-identified hominins) was likely neurological.

#### REFERENCES AND NOTES

1. M. M. Skinner *et al.*, *Science* **347**, 395–399 (2015).
2. M. A. Panger, A. S. Brooks, B. G. Richmond, B. Wood, *Evol. Anthropol.* **11**, 235–245 (2002).
3. J. Napier, *Nature* **196**, 409–411 (1962).
4. D. M. Alba, S. Moyà-Solà, M. Köhler, *J. Hum. Evol.* **44**, 225–254 (2003).
5. S. Almécija, S. Moyà-Solà, D. M. Alba, *PLOS ONE* **5**, e11727 (2010).
6. D. J. Green, A. D. Gordon, *J. Hum. Evol.* **54**, 705–719 (2008).
7. S. Almécija, D. M. Alba, *J. Hum. Evol.* **73**, 88–92 (2014).
8. T. L. Kivell, J. M. Kibii, S. E. Churchill, P. Schmid, L. R. Berger, *Science* **333**, 1411–1417 (2011).
9. T. Sugiyama, J. S. Price, L. E. Lanyon, *Bone* **46**, 314–321 (2010).
10. L. M. Yerges *et al.*, *J. Bone Miner. Res.* **25**, 330–338 (2010).
11. J. D. Schipilow, H. M. Macdonald, A. M. Liphardt, M. Kan, S. K. Boyd, *Bone* **56**, 281–289 (2013).
12. C. N. Shaw, T. M. Ryan, *Am. J. Phys. Anthropol.* **147**, 187–200 (2012).
13. Z. J. Tsegai *et al.*, *PLOS ONE* **8**, e78781 (2013).
14. R. L. Susman, *Science* **265**, 1570–1573 (1994).
15. W. C. McGrew *et al.*, *Science* **268**, 586–589 (1995).
16. S. Harmand *et al.*, *Nature* **521**, 310–315 (2015).

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