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On manual proportions and pad-to-pad precision grasping in *Australopithecus afarensis*

Sergio Almécija [a,b,*], David M. Alba [b,c]

[a] Department of Anatomical Sciences, Stony Brook University School of Medicine, Stony Brook, NY 11794-8081, USA
[b] Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICP, Campus de la UAB s/n, 08193 Barcelona, Spain
[c] Dipartimento di Scienze della Terra, Università di Torino, Via Valperga Caluso 35, 10125 Torino, Italy

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Background

In a recent contribution, Rolian and Gordon (2013) provided new randomization analyses to test whether *Australopithecus afarensis* possessed human-like manual proportions (particularly a long thumb/finger relationship), as previously argued by Alba et al. (2003). The latter authors had previously concluded that "thumb/hand proportions in *A. afarensis* are higher than in chimpanzees" and "not intermediate between apes and humans, but much closer (if not equal) to the modern human condition" (Alba et al., 2003: 241), thereby being suitable for human-like 'pad-to-pad' precision grasping. In contrast, Rolian and Gordon (2013: 393) claimed that their analyses provide "the most conservative estimates of manual proportions" in *A. afarensis*, leading them to conclude that manual proportions in this taxon "are more accurately described as in between those of *Gorilla* and *Homo*, and in some cases indistinguishable between these two taxa" (Rolian and Gordon, 2013: 401). Rolian and Gordon (2013: 393) therefore inferred that *A. afarensis* "could not produce precision grips with the same efficiency as modern humans, which may in part account for the absence of lithic technology in this fossil taxon." While we applaud Rolian and Gordon's (2013) efforts to rigorously assess the manual proportions of *A. afarensis*, we have several concerns about their methodology, their conclusions with regard to precision grasping in *A. afarensis*, and especially their somewhat misleading picture that the interdigital proportions (thumb to ray III) of modern humans overlap with those of western gorillas and even chimpanzees.

What is actually tested in each analysis

Alba et al. (2003) based their analysis on a composite hand of *A. afarensis* including selected bones from locality A.L. 333/333w that, based on provenance, size, and articular congruence, might belong to a single individual. They therefore discarded other bones that most likely belonged to other individual(s), and further assumed a ray attribution for non-pollical proximal and intermediate phalanges. Rolian and Gordon (2013) criticized such an approach, by arguing that none of these phalanges can be reliably allocated to ray. These authors rightly pointed out that Alba et al.'s (2003) conclusions relied on the hypothesis that the bones in their composite hand are correctly attributed to manual rays. Such a reconstruction might be wrong, but Rolian and Gordon (2013) did not provide any anatomical argument to disprove Alba et al. (2003)'s ray assignments. Moreover, Rolian and Gordon (2013) did not provide any statistical argument to contradict Alba et al. (2003)'s results, according to which (if their hand reconstruction was correct) the manual proportions of *A. afarensis* would be human-like even if the bones employed came from more than a single individual.

Instead, to circumvent the problem of ray attribution, Rolian and Gordon (2013) pooled together all of the non-pollical phalanges from all Hadar localities. This is why Rolian and Gordon (2013: 402) claimed that their analysis is more conservative than that of Alba et al. (2003), purportedly providing "the most stringent conditions for assessing manual proportions in *A. afarensis*." It might be alternatively argued that Rolian and Gordon's (2013) approach is rather unrealistic, since they are mixing fossil bones that, based on locality and size differences, must belong to more than one individual. Moreover, from an anatomical viewpoint, it does not seem like a

* Corresponding author.
E-mail addresses: sergio.almecija@stonybrook.edu, sergi.almecija@icp.cat (S. Almécija).

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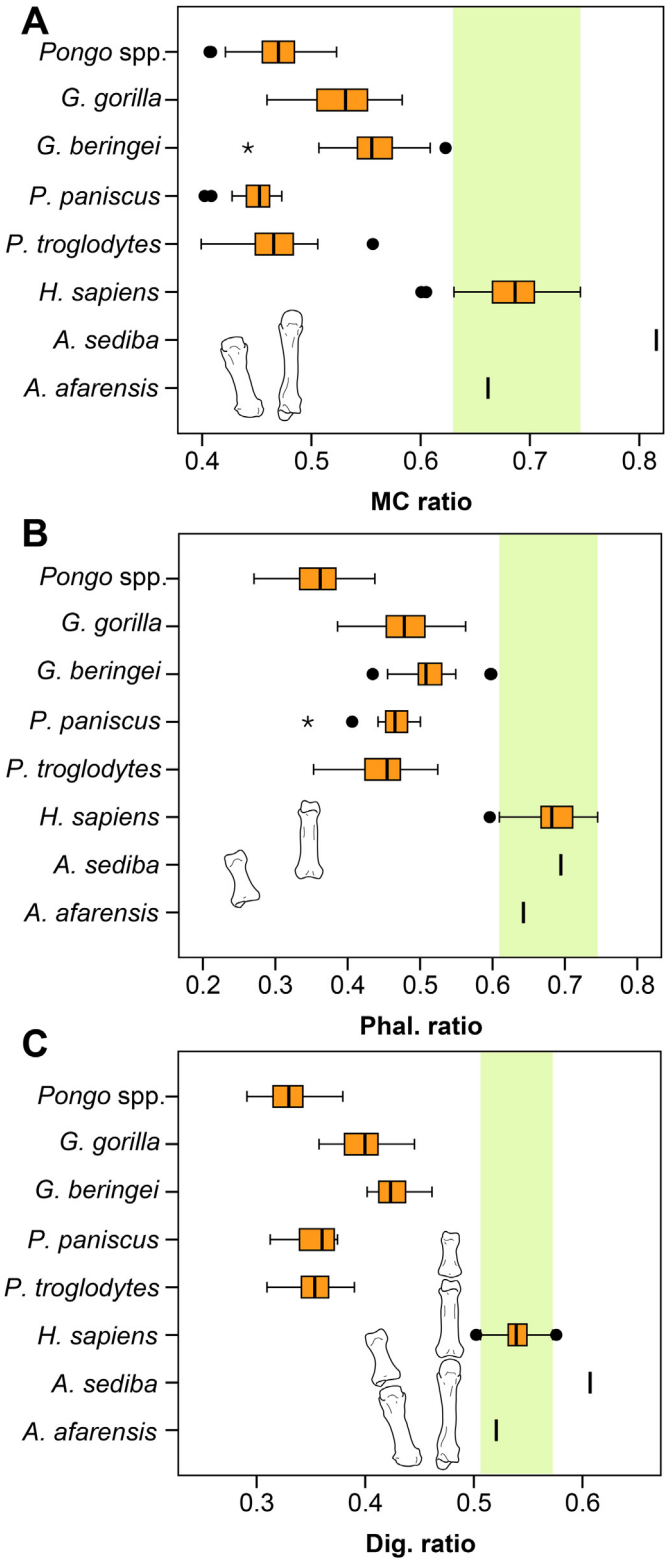

Figure 1. Boxplots showing intrinsic manual proportions in actual great ape and human samples, as well as in *A. afarensis* and *A. sediba*. A: 'metacarpal ratio'; B: 'phalangeal ratio'; and C: 'digit ratio.' Ratios computed following Rolian and Gordon (2013), but using maximum instead of interarticular lengths. Comparable results are obtained when using natural log-transformed data (as in Rolian and Gordon, 2013; see SOM Fig. S1). The long thumb of *A. sediba* might be partially caused by a relatively short third metacarpal in combination with the lack of styloid process. Boxes represent 25th and 75th percentiles, centerline is the median, whiskers represent non-outlier range, dots are outliers, and asterisks are extreme outliers. The non-outlier ranges of humans (shaded area on the plot, projected on the remaining taxa) do not overlap in any case (even including outliers for the digit ratio). Sample sizes for each ratio (A, B and C, respectively) are: *Pongo* (59, 52, 51); *G. gorilla* (100, 74, 67); *G. beringei* (65, 22, 20); *P. paniscus* (17, 21, 12); *P. troglodytes* (82, 65, 60); and *H. sapiens* (74, 55, 46). Data for *A. sediba* (MH2 individual) taken from Kivell et al. (2011); data for *A. afarensis* taken from Bush et al. (1982) and ray assignments from Alba et al. (2003).

good idea to pool phalanges from all non-pollical rays when computing indices of intrinsic manual proportions based on the third ray. In hominoids, proximal and intermediate phalanges of the non-median rays (i.e., digits II/V) are always shorter than those of the median rays (III/IV), and at the very least, phalanges from the fifth digit can be discriminated by using simple anatomical features, such as unilateral muscle insertions and trochlea orientation towards the median hand axis (e.g., Susman, 1979). As a result of pooling phalanges, the extant ranges of randomized ratios of Rolian and Gordon (2013) are increased so that humans and apes overlap (and we believe this is an artifact). It is therefore not surprising that Rolian and Gordon (2013) were often unable to discern whether *A. afarensis* is more human-like than gorilla-like (the fossil overlapped with the 95% confidence interval of both taxa). This fact reflects the methodological limitations of the authors' approach rather than manual proportions actually being intermediate in *A. afarensis*.

Actual intrinsic manual proportions in great apes and humans

When the intrinsic hand ratios performed by Rolian and Gordon (2013) are computed from associated hands of extant taxa (i.e., in actual instead of randomized individuals with pooled phalanges from all digits), the non-outlier ranges of humans never overlap with those of extant great apes (Fig. 1; Supplementary Online Material [SOM] S1). Only outliers of *Gorilla beringei* (not included in Rolian and Gordon's analyses) and *Homo sapiens* overlap for the 'metacarpal ratio' and the 'phalangeal ratio', but not for the 'digit ratio', which is the one that most properly depicts thumb-to-hand length proportions. It may be expected that the same ratios based on Rolian and Gordon's raw data (i.e., not randomized data, not reported by them), based on interarticular instead of maximum lengths, and including a larger sample of humans, would provide similar results. Comparing the randomized with the actual ratios might help to determine the extent to which Rolian and Gordon (2013)'s approach is 'stringent' (as they argue) instead of rather unrealistic (as it seems to us). The maximum length measurements employed in our Fig. 1 are in fact more conservative than their interarticular lengths, because by including the styloid process in third metacarpal length our results depict humans as having relatively shorter thumbs. Therefore, we predict that ratios based on Rolian and Gordon's associated specimens (i.e., actual individuals representing real sample distributions) would result in an even more clear-cut separation between humans and gorillas for both the metacarpal and digit ratios. When these ratios are computed for the composite hand of *A. afarensis* employed by Alba et al. (2003), this taxon clearly displays human-like proportions (Fig. 1). This fully agrees with the similar proportions preliminarily reported for an articulated skeleton of *Australopithecus africanus* (Clarke, 1999), as well as for the associated hand bones of *Australopithecus sediba* (Kivell et al., 2011; see Fig. 1). Evidence from these other taxa therefore strengthens the contention that australopiths as a whole displayed intrinsic manual length proportions allowing for human-like pad-to-pad precision grasping.

'Pad-to-pad' precision grasping

With regard to Rolian and Gordon's (2013) inferences on grasping behavior, it is most surprising that they refer to "tip-to-tip