

## Metacarpal proportions in *Australopithecus africanus*

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### Abstract

Recent work has shown that, despite being craniodentally more derived, *Australopithecus africanus* had more apelike limb-size proportions than *A. afarensis*. Here, we test whether the *A. africanus* hand, as judged by metacarpal shaft and articular proportions, was similarly apelike. More specifically, did *A. africanus* have a short and narrow first metacarpal (MC1) relative to the other metacarpals? Proportions of both MC breadth and length were considered: the geometric mean (GM) of articular and midshaft measurements of MC1 breadth was compared to those of MC2–4, and MC1 length was compared to MC3 length individually and also to the GM of MC2 and 3 lengths. To compare the extant hominoid sample with an incomplete *A. africanus* fossil record (11 attributed metacarpals), a resampling procedure imposed sampling constraints on the comparative groups that produced composite intrahand ratios. Resampled ratios in the extant sample are not significantly different from actual ratios based on associated elements, demonstrating the methodological appropriateness of this technique. *Australopithecus africanus* metacarpals do not differ significantly from the great apes in the comparison of breadth ratios but are significantly greater than chimpanzees and orangutans in both measures of relative length. Conversely, *A. africanus* has a significantly smaller breadth ratio than modern humans, but does not significantly differ from this group in either measure of relative length. We conclude that the first metacarpals of *A. africanus* are more apelike in relative breadth while also being more humanlike in relative length, a finding consistent with previous work on *A. afarensis* hand proportions. This configuration would have likely promoted a high degree of manipulative dexterity, but the relatively slender, apelike first metacarpal suggests that *A. africanus* did not place the same mechanical demands on the thumb as more recent, stone-tool-producing hominins. © 2007 Elsevier Ltd. All rights reserved.

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### Introduction

A major debate in the study of early hominin evolution centers on how to interpret the locomotor implications of australopithecine postcranial anatomy, with one group of researchers holding that certain apelike features should be viewed as modifications for a semiarboreal lifestyle (Stern and Susman, 1983; Susman et al., 1984; Susman and Stern, 1991), while other researchers reject the assertion that climbing formed

a significant part of the australopithecine locomotor repertoire (Lovejoy, 1988; Latimer and Lovejoy, 1990; Latimer, 1991). Interpreting the evolutionary history in *Australopithecus afarensis* and *A. africanus* is further complicated by the fact that the older and more craniodentally primitive *A. afarensis* is hypothesized to have possessed more humanlike limb-size proportions, while the proportions of the younger *A. africanus* are more apelike (McHenry and Berger, 1998; Green et al., 2007). The contention that *A. africanus* may have possessed more apelike limb proportions than *A. afarensis* was the motivation for analyzing the relative hand proportions of *A. africanus*. Following with the nature of their overall limb proportions, we predict that the hands of *A. africanus* are more similar to those of the great apes; however, given that

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*A. afarensis* has been shown by others to be remarkably humanlike in its manual proportions (Watkins et al., 1993; Alba et al., 2003), we also test the possibility that *A. africanus* is more similar to modern humans in this regard. With at least one well-preserved metacarpal (MC) for digits one through four, we tested these possibilities with resampling techniques to examine thumb:finger MC ratios for 11 unassociated *A. africanus* metacarpals.

The modern human hand reflects the complex evolutionary history of a structure that was released from its locomotor burdens while undergoing positive selection for manual dexterity (Susman, 1979, 1998; Marzke, 1997). Napier (1956, 1960) argued that the long, broad thumb and relatively short fingers of the modern human hand facilitate a wide array of precision grips incorporating more distal opposition of both the pad and tip of the thumb to those of the other four digits. This relationship is evident when comparing the MC1 with the other four. While the human MC1 does not differ markedly in absolute length from those of great apes (especially chimpanzees), the second through fifth metacarpals are relatively much shorter (Schultz, 1930; Midlo, 1934). To further assess the relative contribution of metacarpal and phalangeal length to overall digit length in great apes and humans, Schultz (1930) examined the third digit and found that phalangeal length constituted a nearly identical proportion of the total finger length (MC plus total length of each phalanx) in these taxa. Thus, while hand length significantly differentiates, for example, humans from orangutans, “the evolutionary shortening as well as the lengthening of the hand has affected the metacarpal portion to practically the same extent as the phalangeal portion, since these portions maintained nearly the same relation to each other regardless of the relative total length of the hand” (Schultz, 1930: 383). To this end, differences in hand length can be ascertained by considering relative MC length as a proxy of overall digit length among these taxa. In addition, the modern human MC1 is noticeably broad in articular and midshaft dimensions, modifications that support significantly enlarged thenar musculature and the unique loading regimes imposed by tool production and use (Tuttle, 1969; Susman, 1994, 1998; Marzke, 1997). Similarly, human distal phalanges have broad apical tufts consistent with larger, fleshier finger pads that provide more surface area and sensation for stabilizing and orienting objects firmly with precision grips (Susman, 1979, 1998; Shrewsbury and Sonek, 1986; Marzke, 1997; but for a cautionary note on quantifying the relative size of apical tufts, see Smith, 2000). All of these features promote opposition of the thumb and fingers, often acknowledged as a hallmark of stone-tool manufacture and human manual dexterity.

While traits such as large thumbs have been linked to human manual dexterity, several authors have argued that differences in the hands of some great apes, especially *Pan*, do not preclude them from effectively manipulating objects in their environment (Goodall, 1986; Christel, 1993; McGrew, 1995; Boesch and Boesch-Achermann, 2000; Panger et al., 2002). Nonetheless, elongated fingers and musculature specialized for locomotor activities limits proficient tool production (Schick et al., 1999). A great deal of work, then, has been

devoted to understanding when (and in what archaeological context) the unique characteristics of human hands first appeared in the hominin lineage. Part of this effort has been the investigation of australopith hand morphology and the extent to which it reflects tool use and/or locomotion (Marzke, 1971, 1983; Marzke and Marzke, 1987; Susman, 1988, 1994, 2005; Marzke et al., 1992, 1998).

Studies of *A. africanus* and *A. afarensis* have found that, while these species are not known to be associated with stone tools, certain characteristics of their hands appear more similar to humans than those of apes (Ricklan, 1987, 1988, 1990; Marzke, 1997; Alba et al., 2003). In carefully analyzing the *A. africanus* hand material from Sterkfontein in South Africa, Ricklan (1990) argued that the increased relative length of the Stw 418 first metacarpal indicated an ability to perform precise pad-to-pad grips. Ricklan (1987, 1988, 1990) further proposed that the hand of *A. africanus* was more like that of modern humans than those of *A. afarensis* and *Homo habilis* (OH 7), based on features characteristic of strong yet precise gripping capabilities. Although he did not rule out the possibility that the *A. africanus* hand was adapted for “climbing activities” (Ricklan, 1987: 662), he argued that features such as (1) the broad apical tuft on the distal pollical phalanx of specimen Stw 294, with evidence for the attachment of the flexor pollicis longus (but see Susman [2005], who outlined uncertainty as to whether this fossil originated from Sterkfontein’s *A. africanus*-bearing Member 4 or the younger Member 5, which has yielded the remains of early *Homo* and associated stone tools), (2) a humanlike MC1 saddle joint capable of both flexion and abduction during opposition of the thumb and fingers (described as conjunct rotation after MacConaill [1946] or automatic axial rotation after Kapandji [1982]), (3) a well-developed insertion for the extensor carpi radialis muscle on the MC2 base, and (4) a mechanically advantageous MC3 styloid process (which may help to limit displacement at the third carpometacarpal joint during activities such as stone-tool hammering in which forces are directed at the MC head [Marzke and Marzke, 1987]) were consistent with a hand predominantly adapted for manual dexterity and tool use (Ricklan, 1987, 1988, 1990).

More recently, Alba et al. (2003) analyzed the manual proportions in *A. afarensis* by means of a randomization technique, which allowed for the possibility that the bones in their fossil assemblage represented multiple individuals. Using metacarpals and proximal and middle phalanges from the A.L. 333 assemblage, Alba et al. (2003) evaluated residuals from regressions of first digit length against (1) third digit length and (2) body mass and performed a randomization procedure to build composite hands from each of their comparative samples. They used this method to examine the probability that each hand would be correctly assigned to the species from which it was built, and to test if the results of their first analysis changed when composite hands were produced from bones belonging to several different individuals. This randomization technique was a conservative approach in that they eliminated much of the sampling or taphonomic factors (e.g., the winnowing of smaller individuals from the fossil

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