Journal of Human Evolution 75 (2014) 90–109

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

# The pattern of hominin postcranial evolution reconsidered in light of size-related shape variation of the distal humerus

Michael R. Lague

*School of Natural Sciences and Mathematics, The Richard Stockton College of New Jersey, 101 Vera King Farris Drive, Galloway, NJ 08205, USA*

ARTICLE INFO

*Article history:*
Received 27 August 2013
Accepted 14 July 2014
Available online 13 August 2014

*Keywords:*
Allometry
Multivariate regression
Geometric morphometrics
*Australopithecus*
*Paranthropus*
Early *Homo*

ABSTRACT

Previous research suggests that some hominin postcranial features do not follow a linear path of increasing modernization through geological time. With respect to the distal humerus, in particular, the earliest known hominin specimens are reportedly among the most modern in morphology, while some later humeri appear further removed from the average modern human shape. Although Plio-Pleistocene humeri vary widely in size, previous studies have failed to account for size-related shape variation when making morphometric comparisons. This study reexamines hominin postcranial evolution in light of distal humeral allometry. Using two-dimensional landmark data, the relationship between specimen size and shape among modern humans is quantified using multivariate regression and principal components analysis of size-shape space. Fossils are compared with modern human shapes expected at a given size, as well as with the overall average human shape. The null hypothesis of humeral isometry in modern humans is rejected. Subsequently, if one takes allometry into account, the apparent pattern of hominin humeral evolution does not resemble the pattern described above. All 14 of the Plio-Pleistocene hominin fossils examined here share a similar pattern of shape differences from equivalently-sized modern humans, though they vary in the extent to which these differences are expressed. The oldest specimen in the sample (KNM-KP 271; *Australopithecus anamensis*) exhibits the least human-like elbow morphology. Similarly primitive morphology characterizes all younger species of *Australopithecus* as well as *Paranthropus robustus*. After 2 Ma, a subtly more human-like elbow morphology is apparent among specimens attributed to early *Homo*, as well as among isolated specimens that may represent either *Homo* or *Paranthropus boisei*. This study emphasizes the need to consider size-related shape variation when individual fossil specimens are compared with the average shape of a comparative group, particularly when specimens fall near an extreme of the comparative size distribution.



## Introduction

### *Humeral change through time*

Owing to its common preservation in the Plio-Pleistocene hominin fossil record, the distal humerus has been the subject of much attention (Straus, 1948; Patterson and Howells, 1967; McHenry, 1973, 1976; Kay, 1973; McHenry and Corruccini, 1975; Senut, 1979, 1981a,b, 1986; Feldesman, 1982; Senut and Tardieu, 1985; Rockwell, 1994; Lague and Jungers, 1996; Bacon, 2000; Yokley and Churchill, 2006). Taking advantage of the relative ubiquity of this element, McHenry and Brown (2008) used the distal humerus to support their observation that the hominin postcranial skeleton does not follow a linear path of increasing hominization through geological time. That is, many aspects of the postcranial skeleton (e.g., fore-to-hindlimb joint size proportions, ulnar morphology, pelvic architecture) reportedly have a more modern appearance in earlier hominins than in later hominins. For the distal humerus, in particular, McHenry and Brown (2008) demonstrated a pattern whereby the earliest known hominin distal humeri are among the most modern in morphology, while a number of humeri from later in time appear further removed from the average modern human shape.

The McHenry and Brown (2008) study is one of the few to examine hominin postcranial variation in an explicitly temporal framework using a relatively large sample of spatiotemporally and taxonomically diverse fossil hominin specimens. Feldesman (1982) conducted a larger-scale study of catarrhine humeral evolution that included hominoid fossils from the Oligocene and Miocene, as well as eight of the 14 Plio-Pleistocene hominin specimens used by McHenry and Brown (2008). In direct contrast to the McHenry and

*E-mail address:* Michael.Lague@stockton.edu.

http://dx.doi.org/10.1016/j.jhevol.2014.07.003
0047-2484/

Brown (2008) study, Feldesman (1982) concluded that earlier hominin distal humeri appear the most primitive and ape-like, whereas later specimens are more similar to modern *Homo*. Richmond and Jungers (2008) came to similar conclusions with respect to the proximal femur, noting a stable pattern of archaic morphology shared among australopiths, followed by a more human-like morphology among specimens attributed to early *Homo* (a pattern later corroborated by Harmon, 2009).

The conclusions of McHenry and Brown (2008) also conflict with previous studies indicating that the morphological variation observed among most of the Plio-Pleistocene hominin humeral fossils is not of sufficient magnitude to merit any taxonomic or functional distinctions among them (Hill and Ward, 1988; Lague and Jungers, 1996; Bacon, 2000). Based on comparisons with multiple extant hominoid taxa, it has been observed that early hominins are remarkably homogeneous with respect to distal humeral morphology and tend to differ from modern humans in similar ways (Lague and Jungers, 1996; Bacon, 2000). On this basis, one could argue that any descriptions of specific fossils as more or less 'human-like' are biologically superfluous, since the degree to which a particular fossil specimen is comparatively more similar to modern humans may simply represent random variation around a common fossil morphology.

Lague and Jungers (1996) noted two exceptions to the apparent shape homogeneity observed among most Plio-Pleistocene humeri. KNM-ER 739 and 1504, both tentatively attributed to *Paranthropus boisei* (Leakey, 1971, 1973), were found to share a common morphology distinctly different from that of the other fossils. McHenry and Brown (2008) found the same two specimens to be among those most different in shape from an average modern human. In light of the conclusions of Lague and Jungers (1996), this would suggest that after a long period of relative stasis in early hominin elbow morphology, a different pattern evolved among some 2.0–1.5 Ma Turkana hominins that was even further removed from typical modern human shape. While this sequence of events is not unlikely given the diversity of hominins at this time period, the picture is also complicated by the fact that McHenry and Brown (2008) came to completely different conclusions with respect to the morphometric affinities of the two specimens noted above. In particular, they reported that KNM-ER 1504 is significantly different in morphology from the other 2.0–1.5 Ma Turkana humeri (including KNM-ER 739) based on variation observed within both modern humans and chimpanzees.

Another specimen of particular interest in this matter is the ancient specimen from Kanapoi, Kenya (KNM-KP 271). Originally described by Patterson and Howells (1967), the Kanapoi humerus was eventually attributed to *Australopithecus anamensis* (Leakey et al., 1995, 1998; Ward et al., 2001). Due to its reported age (4.12–4.07 Ma), KNM-KP 271 is central to the conclusions of McHenry and Brown (2008), who found it to be more modern-looking than all but two (SK 24600, SKX 10924) of the other 13 fossil humeri they examined. Although Patterson and Howells (1967) noted some similarity to modern humans in metric comparisons (compared with chimpanzees), they accurately predicted that the Kanapoi humerus would eventually be attributed to *Australopithecus*. Subsequent to its original description, however, a number of researchers emphasized its modern human-like qualities more strongly (e.g., McHenry and Corruccini, 1975; McHenry, 1976; Day, 1978), some to the point of suggesting its inclusion (despite its ancient age) in the genus *Homo* (Senut, 1979, 1980,1981a; Senut and Tardieu, 1985). Other authors concluded that its placement in the genus *Homo* was unjustified, and that its greatest morphometric affinities are with other australopith humeri (Feldesman, 1982; Lague and Jungers, 1996; Bacon, 2000). Of particular relevance to the present study is the observation by Bacon (2000) that the morphological features that generally formed the basis for the '*Homo*-like' characterization of KNM-KP 271 are not only highly variable in modern humans, but also significantly dependent upon size.

*Modern human allometry and the effect of specimen size*

Comparison of multiple fossil specimens to an average shape in an extant reference group, particularly when the fossils are highly variable in size, is based on the implicit assumption that shape variation in the extant group is isometric (i.e., that the size of the specimen being compared has no influence on the resulting distance metric). The potential importance of considering size-related shape variation of the distal humerus is apparent when one considers the wide range of sizes observed among the available fossils, from the tiny Lucy (AL 288-1) to the comparatively massive KNM-ER 6020. Given that Plio-Pleistocene humeri span the entire size range of modern humans (see below), comparisons of any individual fossil to an average modern human shape may be misleading, particularly at sizes well above or below the modern size average. For example, if some proportion of modern human shape variation is size-related (as suggested by Bacon, 2000), then a particularly small (or large) fossil may be much closer in shape to an average human of similar size than to the overall average human (Fig. 1). Given any degree of size-related shape variation, it would be more reasonable to compare fossil specimens with the average human shape at a similar size, rather than to the overall mean shape.

The potential effect of size on our understanding of fossil hominin distal humeral variation has hardly been explored. Although Lague and Jungers (1999) examined size-related shape variation of the distal humerus within various hominoid taxa, their study focused upon sexual dimorphism and did not address variation among fossil humeri. As noted above, Bacon (2000) suggested that the 'human-like' characterization of KNM-KP 271 is invalid when one considers modern human allometry. Nevertheless, she did not explicitly examine humeral allometry or its implications for a wider range of fossil specimens.

In this study, I reexamine the pattern of hominin postcranial change through time in light of scaling of distal humeral shape in

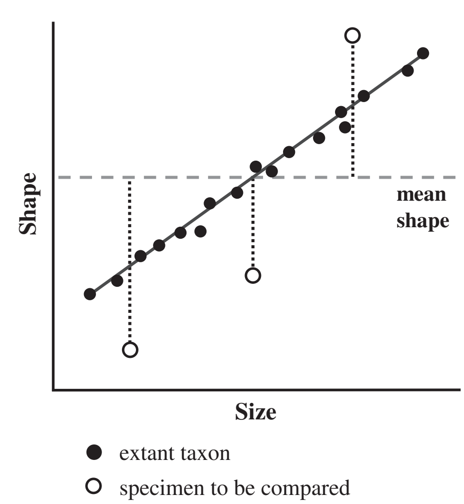


**Figure 1.** The potential effect of allometry in comparative morphometric analysis (simplified two-dimensional case). If the extant comparative group is characterized by size-related shape variation (as depicted here), then comparisons of relatively small and/or large fossil specimens to the overall mean shape (dotted line; line of isometry) might yield different results than comparisons made to the shape expected at a given size (solid line).