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Body size, brain size, and sexual dimorphism in *Homo naledi* from the Dinaledi Chamber

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ABSTRACT

Homo erectus and later humans have enlarged body sizes, reduced sexual dimorphism, elongated lower limbs, and increased encephalization compared to *Australopithecus*, together suggesting a distinct ecological pattern. The mosaic expression of such features in early *Homo*, including *Homo habilis*, *Homo rudolfensis*, and some early *H. erectus*, suggests that these traits do not constitute an integrated package. We examined the evidence for body mass, stature, limb proportions, body size and dental size dimorphism, and absolute and relative brain size in *Homo naledi* as represented in the Dinaledi Chamber sample. *H. naledi* stature and body mass are low compared to reported values for *H. erectus*, with the exception of some of the smaller bodied Dmanisi *H. erectus* specimens, and overlap with larger *Australopithecus* and early *Homo* estimates. *H. naledi* endocranial volumes (465–560 cc) and estimates of encephalization quotient are also similar to *Australopithecus* and low compared to all *Homo* specimens, with the exception of *Homo floresiensis* (LB1) and the smallest Dmanisi *H. erectus* specimen (D4500). Unlike *Australopithecus*, but similar to derived members of genus *Homo*, the *Dinaledi* assemblage of *H. naledi* exhibits both low levels of body mass and dental size variation, with an estimated body mass index of sexual dimorphism less than 20%, and appears to have an elongated lower limb. Thus, the *H. naledi* bauplan combines features not typically seen in *Homo* species (e.g., small brains and bodies) with those characteristic of *H. erectus* and more recent *Homo* species (e.g., reduced mass dimorphism, elongated lower limb).

1. Introduction

The appearance of large bodies and brains, long legs, and low magnitudes of sexual dimorphism has long been considered an important milestone in the evolution of *Homo*. These traits are often linked to changes in cognition, behavior, and ecology that signal a shift in adaptive niche relative to *Australopithecus*. Human-like body masses, statures, and lower limb elongation have generally been first attributed to early African *Homo erectus* (Ruff, 2002; Lieberman et al., 2008; Jungers, 2009; Antón, 2012; Holliday, 2012; Antón et al., 2014; Will and Stock, 2015; but see Grabowski et al., 2015), which has also been characterized by a substantially larger brain size and lower magnitude of sexual size dimorphism when compared to *Australopithecus*. These human-like traits appear to persist among many hominin species throughout the Middle and Late Pleistocene, with the exception of *Homo floresiensis* (Brown et al., 2004; Morwood et al., 2005; Tocheri et al., 2007; Jungers et al., 2009). However, the interdependency of these anatomical features, so important to our understanding of the evolution of life history and the adaptive niche(s) of *Homo* species, remains obscure for a few reasons.

For one, the origin of *Homo* and the early diversification of the species assigned to the genus are not well documented. The first

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species of *Homo* likely appeared between two and three million years ago (e.g., Villmoare et al., 2015); however, only a handful of potential *Homo* fossils have been recovered from this period (reviewed in Kimbel, 2009). During this interval, and just after 2.0 Ma, several species of late-surviving *Australopithecus* (e.g., *Australopithecus africanus, Australopithecus garhi*, and *Australopithecus sediba*) are synchronic with both definitive (i.e., *Homo habilis*, *Homo rudolfensis*, and early *H. erectus*) and purported *Homo* populations (e.g., LD 350, A.L. 666, Stw 53, UR 501, isolated Omo specimens; Suwa, 1990; Kimbel et al., 1996, 1997; Suwa et al., 1996; Asfaw et al., 1999; Schrenk et al., 2007; Berger et al., 2010; Villmoare et al., 2015). To varying extents, these *Australopithecus* species, or at least individuals within the species (e.g., Sts 19), may share derived craniodental and/or postcranial features with *Homo*, leading some to argue for their possible inclusion within, or ancestry to, *Homo* (e.g., Asfaw et al., 1999; Berger et al., 2010). Phylogenetic relationships among the multiple species of late *Australopithecus* and early *Homo*, which are mostly inferred from characters of the skull and teeth, are not well resolved and are a topic of enduring debate (e.g., Lieberman et al., 1996; Wood and Collard, 1999; Strait and Grine, 2004; Collard and Wood, 2007; Pickering et al., 2011; Antón, 2012; Holliday, 2012; Kimbel, 2013; Antón et al., 2014; Dembo et al., 2015, 2016; Hawks et al., 2015; Villmoare et al., 2015). Further, given the patchy evidence for early *Homo* and the wide range of body plans present in taxa attributed to *Homo*, identifying which species belong in the genus is not straightforward. In fact, some (e.g., Wood and Collard, 1999; Wood, 2014) have argued that early *Homo* species, particularly *H. habilis* and *H. rudolfensis*, as well as the later *H. floresiensis*, should be removed from the genus and placed within *Australopithecus* or their own genus because they generally lack the derived features characteristic of *Homo* species that are thought to reflect a significant adaptive shift from *Australopithecus*.

Further, recent discoveries challenge the view that body and brain size increases are associated with the origin of *Homo* and the geographical spread of the genus. For example, the 1.8 million-year-old *H. erectus* specimens from Dmanisi, Georgia, which currently represent the oldest anatomical evidence for *Homo* outside of Africa, are smaller bodied and smaller brained than most early African *H. erectus* specimens (Rightmire et al., 2006; Lordkipanidze et al., 2007, 2013; Spoor et al., 2007; Grabowski et al., 2015; Will and Stock, 2015). In particular, Dmanisi cranium D4500 has an estimated cranial capacity of 546 cc, which when combined with body size estimates from likely associated postcranial bones yields an encephalization quotient similar to *Australopithecus* (Lieberman, 2007; Lordkipanidze et al., 2007, 2013; Lieberman et al., 2008; de Sousa and Cunha, 2012; see also Grabowski et al., 2015, 2016). These cranial capacity, body size, and encephalization values are lower than reported ranges for African *H. erectus* (Skinner and Wood, 2006; Spoor et al., 2007; de Sousa and Cunha, 2012; Grabowski et al., 2015, 2016), suggesting that the earliest migrants out of Africa lacked the large brains and bodies typical of early African *H. erectus*.

Recent fossil discoveries and geological re-dating of fossil deposits in Africa also point to a complex pattern of body and brain size evolution for genus *Homo* (Jungers et al., 2016). For example, the bulk of the early African *H. erectus* fossils postdate 1.7 Ma (Gathogo and Brown, 2006; Feibel et al., 2009; Joordens et al., 2013; Lepre and Kent, 2015) and are, thus, younger than the Dmanisi *H. erectus* material. Therefore, the perception that *H. erectus* had modern limb proportions, taller statures, and larger brains than earlier *Homo* species is largely influenced by the relatively complete 1.6 Ma KNM-WT 15000 juvenile partial skeleton and the ca. 1.5–1.6 Ma KNM-ER 3733 and 3883 crania, which have endocranial volumes in excess of 800 cc (Lepre and Kent, 2015). At the other end of the time scale, the geologically young *H. floresiensis* is *Australopithecus*-like in its absolute brain size, stature, lack of lower limb elongation, and expression of primitive traits in the wrist and pelvis (e.g., Brown et al., 2004; Morwood et al., 2005; Tocheri et al., 2007; Jungers et al., 2009). Thus, Kenyan and Dmanisi specimens may suggest that significant increases in brain and body size occurred within the evolving *H. erectus* lineage, and not necessarily at its origin. Further, the wide range of body and brain size variation evident in *H. erectus* and the expression of a primitive body plan in *H. floresiensis* raises questions regarding the role these traits played in the geographic dispersal of species of *Homo*, the phylogenetic relationships among early and later *Homo* species (e.g., Lordkipanidze et al., 2013), and the adaptive unity of the genus (e.g., Wood, 2011).

While new fossil discoveries indicate that some populations of *H. erectus*, like Dmanisi, have smaller bodies and brains, other fossil finds (e.g., KSD-VP-1/1; Haile-Selassie et al., 2010) and new approaches to body size estimation suggest that some *Australopithecus* individuals are larger than previously appreciated. In a comprehensive study of hominin body mass, Grabowski et al. (2015) found that human-like body masses characterize some, although not all, *Australopithecus afarensis* specimens. Further, they report that *H. habilis* had body masses equal to or smaller than *A. afarensis* (e.g., 38.4 kg for KNM-ER 3735 and 27.3 kg for OH 62) and that *H. erectus* body mass (51.4 kg) was significantly larger than all earlier hominins. Therefore, they suggest that there is no clear increase in body size from *Australopithecus* to *Homo*.

Body size estimates for African *Homo* species are problematic, further complicating the picture. Accurate estimates of body mass and stature require associated postcranial specimens that preserve the necessary features and linear dimensions for analysis. That evidence is sorely lacking for many *Homo* species. For early African *H. erectus*, associated postcranial and cranial remains are limited to KNM-ER 803, KNM-ER 1808, and KNM-WT 15000 (see Antón et al., [2007] and Ward et al., [2015] for reviews). For *H. habilis*, the postcranial record is even leaner. With the exception of the OH 7 skull fragments and hand, and the possibly associated OH 8 foot, only the highly fragmented OH 62 (Johanson et al., 1987) and KNM-ER 3735 (Leakey et al., 1989) partial skeletons have craniodental material directly associated with postcranial remains (Haeusler and McHenry, 2004; Antón et al., 2014). Body size, size variation, relative brain size, and limb proportions for *H. rudolfensis* are effectively unknown because no postcranial elements have been found in direct association with diagnostic skull fragments or teeth (Lieberman et al., 2008; Antón, 2012; Antón et al., 2014; Grabowski et al., 2015; Jungers et al., 2016). In the interval of 1.9–2.1 Ma, a few well preserved, but isolated, eastern African postcranial fossils share derived features with *Homo* (e.g., KNM-ER 737, KNM-ER 1472, KNM-ER 1475, KNM-ER 1481, KNM-ER 3228, and KNM-ER 5881), and these specimens, which may represent *H. rudolfensis*, are at times included in early *Homo* body and skeletal size analyses (e.g., Skinner and Wood, 2006; Ward et al., 2015). Combining these isolated specimens with *H. habilis* into the broader *H. habilis* sensu lato increases the mean body mass and degree of body size variation, which, in turn, affects the interpretation of body and relative brain size variation in early eastern African *Homo*. The picture in South Africa is equally unclear. Early *Homo* craniodental fossils are found at Sterkfontein (e.g., Stw 80 and Stw 53), Swartkrans (e.g., SK 15, SK 27, SK 45, SK 847), and Drimolen (Broom and Robinson, 1949; Robinson, 1953; Hughes and Tobias, 1977; Kuman and Clark, 2000; Moggi-Cecchi et al., 2010). Isolated postcranial fossils from Swartkrans have at one time or another been attributed to early *Homo* (Susman, 1989; Susman et al., 2001; Drapeau, 2015; Will and Stock, 2015); however, given the co-occurrence of *Homo* and *Paranthropus* at Swartkrans, the taxonomic attribution of the