Journal of Human Evolution 111 (2017) 119–138

Contents lists available at ScienceDirect

Journal of Human Evolution

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

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

Heather M. Garvin [a, b, c, *], Marina C. Elliott [c], Lucas K. Delezene [c, d], John Hawks [c, e], Steven E. Churchill [c, f], Lee R. Berger [c], Trenton W. Holliday [c, g]

[a] *Department of Anthropology/Archaeology, Mercyhurst University, 501 East 38th Street, Erie, PA 16546, USA*
[b] *Department of Applied Forensic Sciences, Mercyhurst University, 501 East 38th Street, Erie, PA 16546, USA*
[c] *Evolutionary Studies Institute, University of the Witwatersrand, 1 Jan Smuts Avenue, Braamfontein, 2000, Johannesburg, South Africa*
[d] *Department of Anthropology, University of Arkansas, 330 Old Main, Fayetteville, AR 72701, USA*
[e] *Department of Anthropology, University of Wisconsin, 1180 Observatory Dr, Madison, WI 53706, USA*
[f] *Department of Evolutionary Anthropology, Duke University, Campus Box 90383, Durham, NC 27708, USA*
[g] *Department of Anthropology, Tulane University, 6823 St. Charles Ave, New Orleans, LA 70118, USA*

ARTICLE INFO

Article history:
Received 12 June 2016
Accepted 23 June 2017

Keywords:
Hominin
Sexual dimorphism
Body mass
Stature
Encephalization
Canine size dimorphism

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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* Corresponding author.
E-mail address: HMGarvin@gmail.com (H.M. Garvin).

http://dx.doi.org/10.1016/j.jhevol.2017.06.010
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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 postcrania is not certain (e.g., Trinkaus and Long, 1990). Further, the postcranial fossil record for Middle Pleistocene African *Homo* is especially lean (e.g., Grine et al., 1995; Pearson and Grine, 1997; Trinkaus et al., 1999; Trinkaus, 2009) when compared to the same time interval in Europe (e.g., Arsuaga et al., 2015). Thus, with the exception of the post 1.7 Ma Kenyan *H. erectus* material, little is known about body size, body size variation, limb proportions, and relative encephalization in non-modern species of African *Homo*.

Given the above, the discovery and analysis of fossil assemblages with definitive associations of crania and postcrania are critical to determining if *Homo* represents an adaptively uniform clade of hominins. This paper evaluates body size, body and tooth size variation, absolute and relative cranial capacity, and limb proportions in the recently described Dinaledi assemblage of *Homo naledi* fossils. During the 2013 and 2014 excavations, approximately 1550 *H. naledi* specimens were recovered from the Dinaledi Chamber, site U.W. 101, of the Rising Star cave system, located within the Cradle of Humankind, South Africa (Berger et al., 2015). These fossils include cranial, dental, and postcranial elements from multiple individuals; thus, they provide a rare opportunity to investigate these variables in a large sample of fossils from a single site that unequivocally represent a single species (Berger et al., 2015).[1]

The Dinaledi fossils have been dated to between 335 and 236 kya, which places them in the late Middle Pleistocene (Dirks et al., 2017). Thus, this date would slightly antedate the earliest anatomically modern humans in Africa (e.g., White et al., 2003), overlap with early Eurasian *Homo neanderthalensis* (*Homo heidelbergensis* to some) in age (e.g., Arsuaga et al., 2015), and place *H. naledi* more recently in time than specimens like Kabwe and Bodo that bridge the anatomical gap between *H. erectus* and *Homo sapiens* in Africa and that are variously referred to as *Homo rhodesiensis* or *H. heidelbergensis* (e.g., Rightmire, 1988). Despite the recent dates for the Dinaledi material, and many clearly expressed derived traits in the skull and postcranium that align it with the genus *Homo*, *H. naledi* also exhibits a number of primitive, *Australopithecus*-like traits (Berger et al., 2015; Harcourt-Smith et al., 2015; Kivell et al., 2015; Dembo et al., 2016; Feuerriegel et al., 2017; Laird et al., 2017; Marchi et al., 2017; Schroeder et al., 2017; Williams et al., 2017). Therefore, the Dinaledi assemblage is critical for examining potential diversity in *Homo* body plans during the late Middle Pleistocene.

The main objectives of this paper are to: 1) publish raw data derived from the Dinaledi Chamber *H. naledi* specimens, 2) compare the range of *H. naledi* body size and absolute and relative brain size (as represented in the Dinaledi assemblage) to other hominins, 3) describe and compare craniodental and body size variation within the Dinaledi specimens to other extant hominins, and 4) compare the *H. naledi* bauplan to that of *Australopithecus* and *Homo*.

2. Material and methods

2.1. Body mass

Berger et al. (2015) and Dirks et al. (2015) report that the current assemblage of fossils from the Dinaledi chamber represent a minimum of 15 individuals that span an age range from infant to elderly adult. The Dinaledi fossils are, however, derived from a commingled assemblage of multiple individuals of overlapping ontogenetic stages (Berger et al., 2015; Dirks et al., 2015). Thus, it is not yet possible to assemble confidently the majority of the remains into biological individuals. To estimate body mass in this sample, we focused on 20 well preserved adult postcranial elements. The postcranial minimum number of individuals in this sample was determined by evaluating material for duplicate elements and antimeres. When raw measurements failed to separate individuals, morphological features were visually compared between specimens. Based on the femoral subtrochanteric sample, a minimum of eight individuals are present in the sample (Fig. 1). None of these subtrochanteric specimens appears to be antimeres and their size, morphology, and lack of any evidence of fusion lines suggest they are all adults.

The minimum number of individuals represented by the other skeletal elements included in this study was fewer than that of the subtrochanteric sample. Nine femoral midshafts were available for analysis, of which seven were rights. The two left femoral midshafts, however, could not be ruled out as antimeres of the recovered right femora. In addition, associations between different skeletal regions (e.g., tali versus femoral specimens, etc.) could not be determined. As a result, it is likely that some individuals are represented more than once in this study. Body mass analyses were therefore carried out using all possible specimens, as well as using the more conservative subtrochanteric subsample ($n = 8$) to reduce duplication.

Articular dimensions and diaphyseal breadths were collected from the 20 *H. naledi* postcranial limb bones for body mass estimation (Table 1). Specimens displaying significant erosion or damage were excluded from the study. Using digital calipers, the following standard osteometric measures were recorded: femoral head superoinferior diameter, femoral subtrochanteric anteroposterior and mediolateral breadths, femoral anteroposterior and mediolateral breadths at approximately midshaft, radial head anteroposterior and mediolateral breadths, humeral head superoinferior diameter, and talar trochlear breadth and length. All measurements were collected by HMG and confirmed by TWH (Table 1). The U.W. 101-484 tibia, which is nearly complete in length and used for stature estimation, was not used for body mass estimation because the articular surfaces, which are the most common regions used for body mass estimation from the tibia, were too poorly preserved to estimate dimensions.

Body masses were estimated using the univariate regression equations (inverse calibration approach) provided by Grabowski et al. (2015). These equations were derived from a sample of 220 modern humans (116 males and 104 females) with documented cadaveric body masses from two U.S. skeletal collections, the Hamann-Todd Osteological Collection curated at the Cleveland Museum of Natural History and the Terry Collection curated at the Smithsonian National Museum of Natural History. They included individuals of both European and African ancestries and focused on collecting data from shorter-statured individuals in the Terry Collection, given that many fossil hominin species are presumed to be smaller bodied. The use of modern humans as a comparative

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[1] At the time of publication, Hawks et al. (2017) had recently announced the discovery of additional fossil remains attributed to *H. naledi* in a second chamber, the Lesedi Chamber, of the Rising Star Cave System, a distance of 145 m from the Dinaledi Chamber. The remains described in Hawks et al. (2017) reportedly represent a minimum of two adults, although the MNI and associations between the commingled remains are provisional. Hawks et al. (2017) indicate that only a small percentage of the Lesedi Chamber has been sampled and that additional remains will likely be uncovered with further excavation. Given the preliminary nature of the Lesedi Chamber material and unknown association with the Dinaledi Chamber, this study focuses only on the Dinaledi Chamber *H. naledi* material. However, preliminary analyses, including the recently published Lesedi Chamber subtrochanteric measurements (Hawks et al., 2017), do not substantially change the *H. naledi* body size averages or ISD calculations. As more remains are recovered from the Lesedi Chamber and associations between elements can be worked out, the *H. naledi* material from this second chamber may be used to test certain hypotheses put forth in this study (e.g., limb proportions) and can provide assemblage comparisons to the Dinaledi Chamber, as well as additional information on the species as a whole.

Figure 1. Dinaledi femoral specimens used for subtrochanteric body mass estimations in *Homo naledi*. A) U.W. 101-1136, B) U.W. 101-018, C) U.W. 101-002, D) U.W. 101-1391, E) U.W. 101-398, F) U.W. 101-1475, G) U.W. 101-1482, H) U.W. 101-003. Specimens arranged by cross-sectional area (ML*AP), from smallest (A) to largest (H). Note that specimen H has been cropped at the midshaft for visualization purposes.

Table 1
Homo naledi Dinaledi raw measurements (mm) collected for body size (stature and body mass) estimation.[a]

Specimen ID	Side	FHD	FSTap	FSTml	FMSap	FMSml	RHml	RH ap	HML	HH si	TTB[b]	TTL	TML[c]
U.W. 101-002	R		18.5	23.6	21.0	19.5							
U.W. 101-003	R		21.6	31.4	24.0	23.5							
U.W. 101-012	R				22.8	19.5							
U.W. 101-018	R		18.1	23.8									
U.W. 101-148	L										20.6	26.4	
U.W. 101-268	L				23.4	22.9							
U.W. 101-271	U	35.8											
U.W. 101-283	R								258.0	30.3			
U.W. 101-398	L		19.1	24.0									
U.W. 101-484	L												325.0
U.W. 101-520	L										17.1	26.2	
U.W. 101-545	R				22.2	20.2							
U.W. 101-935	L							19.3					
U.W. 101-1136	R		16.9	25.5	17.0	17.0							
U.W. 101-1284	R				22.8	20.0							
U.W. 101-1300	U	35.2											
U.W. 101-1346	R						17.4						
U.W. 101-1391	R		18.8	23.9	21.4	19.6							
U.W. 101-1417	R										18.4	21.5	
U.W. 101-1475	L		18.8	29.0									
U.W. 101-1482	L		20.7	28.9	23.0	24.7							

[a] FHD = femoral head superoinferior diameter, FSTap = femoral subtrochanteric anteroposterior breadth, FSTml = femoral subtrochanteric mediolateral breadth, FMSap = femoral anteroposterior breadth taken at approximately midshaft, FMSml = femoral mediolateral breadth taken at approximately midshaft, RHml = radial head mediolateral breadth, RHap = radial head anteroposterior breadth, HML = humeral maximum length, HHsi = humeral head superoinferior diameter, TTB = talar trochlear breadth, TTL = talar trochlear length, TML = tibial maximum length, including the malleolus but excluding the intercondylar eminence.

[b] Talar trochlear breadth measurements were taken at the distal end of the trochlea to be consistent with the comparative data. This is different from the measurement defined in McHenry (1992).

[c] Note that the tibia specimen U.W. 101-484 is almost complete, but is missing the tibial plateau proximal to the tibial tuberosity. Maximum tibial length was thus estimated using a regression formula, as well as comparisons with small bodied modern human tibiae (see Marchi et al., [2017] for details).

model is appropriate, as the Dinaledi specimens are morphologically and functionally more similar to modern humans than other extant hominoids, especially with regard to the weight bearing lower limb (Harcourt-Smith et al., 2015; Marchi et al., 2017). Further, the Grabowski et al. (2015) equations were derived from individuals with documented body masses, included some smaller bodied individuals, and have been used to estimate body mass in a wide range of fossil hominins. Grabowski et al. (2015) only supply equations for lower limb variables, as they are expected to have the highest correlation with body mass given that the lower limb bears the full weight of the body during bipedalism. Thus, the Grabowski et al. (2015) equations were only applicable to 14 specimens in the U.W. 101 assemblage.

Hominin body size estimates in Grabowski et al. (2015) typically yielded smaller point estimates than many previous studies. Grabowski et al. (2015) suggest that other studies may have overestimated masses because their reference samples contained larger bodied humans. To ensure that our results are comparable with studies of hominin mass that did not use Grabowski et al.'s (2015) equations, we also estimated body masses using a traditional approach that derived ordinary least squares (OLS) equations from multiple recent human comparative samples (data collected by the authors). These comparative samples include two large global samples: TWH ($n = 1281$; 21 population groups including smaller bodied African “Pygmies” and Andaman Islanders) and HMG ($n = 695$; six population groups, including smaller bodied Kulubnarti medieval Nubians). When possible, equations derived only from the Kulubnarti individuals ($n = 96$) were also applied for comparison since they represent a sufficient sample of smaller bodied African individuals from a single population. Because documented body masses were not available for all individuals, body mass was estimated for the modern reference samples using an average of results obtained from Grine et al. (1995) and Ruff et al. (1997), the latter of which was derived from the raw published data of McHenry (1992). Auerbach and Ruff (2004) found that the Ruff et al. (1997) equation tends to underestimate body mass, while the Grine et al. (1995) equation overestimates body mass, and thus suggest averaging values when applied to modern humans to reduce directional bias. Use of the femoral head to estimate body mass in these reference samples introduces an additional source of error (although see Steudel [1980] and Komar and Grivas [2008] for a discussion regarding errors in documented cadaveric body masses). In addition, global samples have been suggested to overestimate body mass in smaller bodied populations (Grabowski et al., 2015; Jungers et al., 2016). Use of the global samples, however, allowed body mass estimates from variables not included in Grabowski et al. (2015; e.g., upper limb elements). A modern human Swiss sample with documented cadaveric body masses, obtained from CT scans at the Institute of Forensic Medicine in Zurich (MCE), was also used in the subtrochanteric analyses ($n = 253$) for comparison with the global samples.

Given the aforementioned advantages of the Grabowski et al. (2015) approach, results derived from their equations are presented in detail in the main text, while the OLS results from the authors' modern human comparative data (TWH, HMG, and MCE) are briefly summarized in the text and presented in detail in the Supplementary Online Material (SOM).

2.2. Sexual dimorphism and size variation

For the Dinaledi assemblage, an index of sexual dimorphism (ISD) was calculated separately using the body mass estimates for all specimens and eight subtrochanteric mass estimates, with the mean body mass of each sample designated as a sectioning point and the ratio of the average value of those above the sectioning point to the average value of those below the sectioning point serving as the ISD. These results must be interpreted cautiously, as the true sexes of these fossil specimens are unknown. This “mean method” used to calculate the ISD provides a measure of relative size variation, and when used as an estimate of dimorphism, it effectively assumes that the larger bodied individuals are male and the smaller bodied individuals are females, and that there is no overlap in size between the sexes. As a result, the ISD may be affected by small or sex-biased samples and can overestimate dimorphism; however, this is the most commonly employed method of dimorphism calculation for assemblages of unknown sex and is preferred over the use of maximum/minimum ratios, which has been shown to grossly overestimate dimorphism (Plavcan, 1994).

The coefficient of variation (CV) has been shown to correlate with the ISD among species (e.g., Plavcan, 1994; Lockwood et al., 1996) and does not require sex designations to the *H. naledi* specimens. Therefore, we compared the estimated mass CV in the Dinaledi sample with ape and human mass CVs as a test of the hypothesis that sexual size dimorphism is greater or lesser than that observed in extant reference groups. CVs were calculated from the 14 Dinaledi body mass estimates obtained using Grabowski et al. (2015) and subtrochanteric femoral sizes (product of AP and ML measurements) and compared to CVs for extant reference samples of apes and humans. Chimpanzees, gorillas, and humans differ in observed body mass dimorphism; thus, these samples were chosen to capture a range of variation, from marked dimorphism (gorillas) to low dimorphism (humans). An equal number of males and females for each taxon were included in the CV analyses. Body masses for *Pan troglodytes* ($n = 90$) and *Gorilla* spp. ($n = 80$) were estimated using the species-specific equations provided in Almécija et al. (2015). *Gorilla* and *Pan* femoral head diameters and subtrochanteric femoral measurements were collected by TWH. The Swiss sample ($n = 250$) was used for the comparative CV analyses of *H. sapiens*. This sample was chosen because it contained a large number of individuals from a single population with documented cadaveric body masses and allowed equal numbers of males and females to be selected for analysis (see Elliott et al., 2014, 2016 for sample details). Because skeletal estimates of body mass may be less variable than cadaveric body masses, body masses for the Swiss sample were estimated from femoral head diameters (as described above), and the CV analyses were conducted on both the Swiss cadaveric and skeletally estimated body masses.

To compare magnitudes of variation in estimated *H. naledi* body masses to extant reference samples, we employed the “resampled extinct distribution method” described in Gordon et al. (2008). Briefly, both the *H. naledi* and reference sample masses were resampled, with replacement, at the sample size matching that of the Dinaledi assemblage ($n = 14$ for the Grabowski et al. [2015] based body mass estimates, $n = 20$ for OLS based mass estimates, and $n = 8$ for the subtrochanteric femoral measurements). Then, the difference between the CV of a random *H. naledi* iteration and that of a reference sample are calculated. A value of zero indicates that the CVs of the two samples are equal, a value greater than zero indicates that the reference sample has a larger CV, and a value less than zero indicates that *H. naledi* has a larger CV. This process is repeated to generate a distribution of CV differences from which confidence intervals (CI) can be constructed to test the hypothesis that the CV of *H. naledi* equals that of the reference sample. Given the large sample size for mass estimates for *H. naledi* using the Grabowski et al. (2015) formulae ($n = 14$) and the OLS formulae ($n = 20$), the distribution of differences was based on 10,000 iterations. For the smaller subtrochanteric sample ($n = 8$), the distributions are based upon 5000 iterations.

2.3. Stature and limb proportions

Only two adult limb bones were sufficiently preserved to accurately measure their lengths: the U.W. 101-283 humerus and the U.W. 101-484 tibia. Stature was estimated separately for these two elements using pooled-sex, OLS regression equations derived from three recent human comparative samples: 1) U.S. African- and European-Americans ($n = 192$), 2) Kulubnarti medieval Nubians ($n = 95$), and 3) Dart South African Blacks ($n = 76$). All samples were approximately sex balanced. The U.S. and Dart stature estimates are based on documented cadaveric statures, while the Kulubnarti estimates are based on revised Fully (1956) living stature estimates (Raxter et al., 2006). The equivalence of cadaveric statures versus living or skeletal statures has been debated (Bidmos, 2005; Komar and Grivas, 2008). Stature estimates also depend on the body size and proportions of the comparative samples. Instead of making assumptions regarding which comparative sample would most accurately reflect the body proportions of the Dinaledi hominins, the results of all three equations are presented. Finally, stature was estimated using the equation presented in Jungers et al. (2016), which was derived from a sample of human pygmies. The Jungers et al. (2016) equation requires both tibial and femoral lengths. Femoral length was estimated for the U.W. 101-484 tibia specimen based on the average crural index (and ±2SD) of a sample of 569 modern humans (HMG sample). Note that the HMG sample included 40 individuals with tibia length equal to or smaller than the U.W. 101-484 specimen (see SOM for reference sample details).

Relative limb lengths have important implications when estimating stature as well as assessing locomotor behaviors. Unfortunately, as the Dinaledi assemblage is commingled and contains numerous adults (Berger et al., 2015; Dirks et al., 2015), there are, as yet, no definitively associated adult upper and lower limb elements. We calculated a humero-tibial index in an exploratory comparison with modern humans using two specimens conservatively inferred to represent different individuals based on differences in size and robusticity (U.W.101-484 tibia and U.W. 101-283 humerus). To account for the uncertainty in the association between them, the humero-tibial index was compared to *P. troglodytes* ($n = 61$), *Gorilla* spp. ($n = 43$), and the smaller-bodied Kulubnarti sample of *H. sapiens* ($n = 90$) using a bootstrapping procedure. In brief, a bootstrap distribution was created for each extant taxon by randomly drawing, with replacement, a humerus and tibia from the reference sample and then calculating the index. In such a manner, a humerus and a tibia from different individuals could be randomly paired. The resampling procedure was repeated 10,000 times to generate the distribution of humero-tibial indices to which the *H. naledi* index was then compared.

Sexual dimorphism in stature was not estimated because 1) only two elements were sufficiently preserved for stature estimation, and 2) one was from the upper limb and the other the lower limb, and at present the inter-limb proportions of this species are unknown.

2.4. Endocranial volumes and encephalization quotients

Four partial calvariae recovered from the Dinaledi assemblage preserved sufficient portions of the neurocranium to assist with endocranial reconstructions and volume estimations. The two larger calvariae (DH1 and DH2) display more robust muscle markings and greater pneumatization of the mastoid region, suggesting that they are males (Berger et al., 2015; Laird et al., 2017). The DH1 specimen, in particular, displays a large, protruding external occipital protuberance. In comparison, the two smaller calvariae (DH3 and DH4) are more gracile and are presumed to be females. Two endocranial volumes were calculated virtually from three-dimensional (3D) surface scan models for the smaller DH3/DH4 and larger DH1/DH2 composites, resulting in estimates of 465 cc and 560 cc, respectively (see Berger et al., [2015] and SOM for details).

The endocranial volumes were used to estimate encephalization quotients (EQs) for *H. naledi*. The recently published EQ equation presented in Grabowski et al. (2016) was used along with the *H. naledi* body mass estimates obtained using Grabowski et al. (2015). Again, because both these EQ and body mass estimation equations were only recently published and result in notable differences from previously published methods and estimates, a more traditional approach using the OLS body mass estimates obtained from the authors' comparative samples and EQ equation derived from Martin (1981) and presented in Ruff et al. (1997) were implemented. Details regarding the traditional analyses are presented in the SOM.

Given that the calvariae have not been directly associated with any of the postcranial elements used for body size estimation, a range of body mass estimates were used to evaluate possible EQ values. The average Dinaledi endocranial volume and body mass estimates were used. In addition, for the smaller endocranial volume, the EQ was calculated using the average Dinaledi body mass, the lowest body mass estimate, and the average body mass from the smaller bodied subset (as determined by the "mean-method" sectioning point). For the larger endocranial volume, the EQ was calculated using the average Dinaledi body mass, the highest body mass estimate, and the average body mass from the larger bodied subset.

For exploratory purposes only, variation and potential sexual dimorphism in endocranial volumes were compared in *H. naledi* to extant reference samples. Endocranial volumes for *P. troglodytes*, *Gorilla gorilla*, and *Hylobates lar* were derived from wild-collected specimens with known collection localities and published in Isler et al. (2008). For *H. sapiens*, a large sample of Danish endocranial volumes ($n = 1050$) was provided by Dr. Ralph Holloway (pers. comm.). For each taxon, except gorillas, we chose sex balanced samples of 20 adult males and 20 adult females for comparison. A smaller sample of wild-collected gorillas fitting these criteria was available; for this taxon, the reference sample was 14 males and 14 females. As with the body size analyses, the reference data were resampled with replacement 10,000 times at a sample size matching that of the Dinaledi samples. The observed Dinaledi CV was compared to these bootstrap distributions to determine if it lies within the 95% confidence. The Dinaledi values were also compared to single-sex extant samples using the same resampling procedure. Finally, we compared indices of sexual dimorphism and max/min ratios in *H. naledi* to extant samples using the same bootstrapping procedure.

2.5. Dental size variation

Using fine-pointed digital calipers, upper and lower permanent canine mesio-distal and labio-lingual base measurements were collected at the crown cervix by LKD. For several of the canines, probable antimeres can be identified within the assemblage; in these instances, the average of the values for each pair of antimeres was used in subsequent analyses. Canine sample sizes ranged from five to six individuals, depending on the measurement. For comparison with levels of variance observed for the canines, buccolingual measurements were also collected from the upper and lower first and second molars (sample sizes ranged from five to nine, depending on the tooth and measurement).

Dinaledi dental size CVs were compared to geographically restricted samples of *H. lar*, *P. troglodytes*, *G. gorilla*, and *H. sapiens*. Thus, two samples with strongly dimorphic canines (chimpanzees and gorillas) and two samples with low levels of canine size dimorphism (humans and gibbons) were included. The comparative extant primate data were obtained from a variety of natural history collections (see supplemental information in Delezene [2015] for a list of collection localities). The human data were provided by Joel Irish (pers. comm.) and were derived from northern Sotho (also known as Pedi) individuals housed in the Dart Collection at the University of the Witwatersrand (Haeussler et al., 1989). For each extant taxon, sex balanced samples of 20 males and 20 females were utilized in the CV analyses. As with the body size and endocranial volume analyses, the dental reference data were resampled with replacement 10,000 times at a sample size matching that of the Dinaledi samples. The observed Dinaledi dental CVs were then compared to these bootstrap distributions to determine if they lie within the 95% CI for the various taxa.

3. Results

3.1. Body mass

Using the Grabowski et al. (2015) equations, the subtrochanteric diaphyseal breadths of the eight Dinaledi femora yield body mass estimates ranging from 34 to 44 kg, with a mean of 37.4 kg (95% CI of mean: 34.0–40.5 kg). When Grabowski et al.'s (2015) equations are applied to the 14 lower limb specimens (i.e., including midshaft and femoral head specimens), the results are similar (individual range = 33.1–43.4 kg, mean = 37.4 kg, 95% CI of mean = 35.5–39.4 kg; Table 2). Unfortunately, there is not enough information about the training sample utilized by Grabowski et al. (2015) within the main text or supplementary materials to be able to calculate prediction intervals for each estimate.

When equations derived from the authors' modern human comparative data are used, estimates are higher. The body mass estimates for the subtrochanteric specimens range from 42.1 to

Table 2
Homo naledi body mass estimates obtained using Grabowski et al. (2015) equations and OLS equations derived from authors' modern human comparative data.

Specimen ID	Side	Results using Grabowski et al. (2015)						Results using authors' modern human data[a]							
		FHD	FSTap	FSTml	FMSap	FMSml	AVE	FHD	FSTpr	FMSpr	RHml	RHap	HHsi	TT pr	AVE
U.W. 101-002	R		35.5	33.4	40.3	33.7	**35.7**		42.4	43.4					**42.9**
U.W. 101-003	R		40.1	48.2	43.9	41.4	**43.4**		55.2	50.6					**52.9**
U.W. 101-012	R				42.4	33.7	**38.1**			45.1					**45.1**
U.W. 101-018	R		34.9	33.7			**34.3**		42.1						**42.1**
U.W. 101-148	L													42.5	**42.5**
U.W. 101-268	L				43.2	40.2	**41.7**			49.3					**49.3**
U.W. 101-271	U	34.0					**34.0**	42.5							**42.5**
U.W. 101-283	R												35.9		**35.9**
U.W. 101-398	L		36.4	34.1			**35.3**		43.5						**43.5**
U.W. 101-520	L													37.8	**37.8**
U.W. 101-545	R				41.7	35.0	**38.4**			45.2					**45.2**
U.W. 101-935	L											52.4			**52.4**
U.W. 101-1136	R		33.1	36.9	35.2	29.0	**33.5**		42.1	37.7					**39.9**
U.W. 101-1284	R				42.4	34.7	**38.6**			45.5					**45.5**
U.W. 101-1300	U	33.1					**33.1**	41.1							**41.1**
U.W. 101-1346	R										47.5				**47.5**
U.W. 101-1391	R		36.0	33.9	40.8	33.9	**36.1**		43.1	43.9					**43.5**
U.W. 101-1417	R													35.2	**35.2**
U.W. 101-1475	L		36.0	43.5			**39.7**		48.1						**48.1**
U.W. 101-1482	L		38.8	43.3	42.7	43.7	**42.1**		50.9	50.8					**50.9**
Element averages		33.6	36.3	38.4	41.4	36.2	**37.4**	41.8	45.9	45.7	47.5	52.4	35.9	38.5	**44.2**

Measurement Abbreviations: FHD = femoral head superoinferior diameter; FSTap = femoral subtrochanteric anteroposterior breadth; FSTml = femoral subtrochanteric mediolateral breadth; FSTpr = product of anteroposterior and mediolateral femoral subtrochanteric breadths; FMSap = femoral anteroposterior breadth taken at approximately mid-shaft; FMSml = femoral mediolateral breadth taken at approximately mid-shaft; FMSpr = product of anteroposterior and mediolateral femoral midshaft breadths; RHml = radial head mediolateral breadth; RHap = radial head anteroposterior breadth; HHsi = humeral head superoinferior diameter; TTpr = product of talar trochlear breadth and length; AVE = Average body mass estimate per specimen.

[a] See Supplementary Materials for details regarding comparative modern human data and analyses.

55.2 kg, with a mean of 45.9 kg (95% CI of mean: 41.8–50.0 kg). The combined sample of 20 postcranial specimens (including upper limb specimens) yields a mean body mass of 44.2 kg (95% CI of mean: 41.9–46.5 kg) and a specimen range of 35.2–52.9 kg (Table 2). Ninety-five percent prediction intervals for each body mass estimate are presented in the SOM and are an average of 21.8 kg wide, spanning a cumulative range of 25.7 kg–68.2 kg.

Using the “mean method” (Plavcan, 1994) to estimate size dimorphism from the 14 Grabowski et al. (2015) derived Dinaledi body mass estimates results in an ISD of 1.16. For the eight subtrochanteric specimens, an ISD of 1.20 is obtained when body mass estimates from the anteroposterior and mediolateral measurements are averaged (Grabowski et al., [2015] provides separate equations for each). Individually, the subtrochanteric anteroposterior and mediolateral body mass estimates return an ISD of 1.09 and 1.31, respectively, reflecting greater size variation in mediolateral width of the subtrochanteric region. Using the 20 body mass estimates obtained from the authors' comparative human data (including upper limb estimates), an ISD of 1.19 is obtained. Using only the eight subtrochanteric body mass estimates, the ISD is 1.17 (see SOM for more details).

The Dinaledi body mass CV calculated from the 14 Grabowski et al. (2015) body masses falls entirely below the 95% CI for *Gorilla* spp, *P. troglodytes*, and the documented cadaveric *H. sapiens* body masses, but within the 95% CI for the *H. sapiens* body masses estimated from femoral head diameter (FHD; Table 3). Likewise, using the “resampled extinct distribution method” (Gordon et al., 2008), the *H. naledi* CV is significantly lower than all comparative samples except for that of the estimated *H. sapiens* distribution (Table 4). The cadaveric *H. sapiens* masses have a higher variance than the skeletally estimated masses for the same sample, though the ISD is similar (Table 3). Given that all other masses analyzed in the study (*P. troglodytes*, *Gorilla* spp., and *H. naledi*) were inferred from skeletal dimensions, the appropriate comparison is with the skeletally inferred masses for humans and not the cadaveric data. Similar results are obtained when using the 20 OLS estimates, except that the CI for the chimpanzee vs. *H. naledi* comparison barely overlap zero (SOM). Using the more conservative subtrochanteric area data ($n = 8$), the Dinaledi subtrochanteric CV (18.6) falls within the 95% CI for *Gorilla* spp. and *H. sapiens* and above the 95% CI for *P. troglodytes* (Table 5). Using the “resampled extinct distribution method”, the Dinaledi subtrochanteric CV cannot be distinguished statistically from any of the extant reference samples (Table 6).

3.2. Stature and limb proportions

Stature estimates from the humerus and tibia range from 139 to 156 cm (Table 7). If the estimates derived from the larger bodied U.S. sample are removed, stature estimates range from 139 to

Table 3
Body mass variation in extant apes, humans, and Dinaledi *Homo naledi* derived from a bootstrapped distribution of 10,000 iterations.

Samples	Males	Females	Total sample	ISD	Observed CV	Bootstrapped mean CV ($n = 14$)	95% CI
Gorilla spp.	40	40	80	1.94	36.5	36.2	24.6–47.7
Pan troglodytes	45	45	90	1.25	16.0	15.6	10.3–22.2
Homo sapiens (documented cadaveric)	125	125	250	1.17	25.1	24.4	15.3–35.2
Homo sapiens (estimated from FHD)	125	125	250	1.19	11.9	11.7	8.0–15.4
Homo naledi			14		9.0	8.6	6.1–10.7

Table 4
Comparisons of estimated Dinaledi *Homo naledi* body mass CV ($n = 14$) to extant apes and humans.[a]

Samples	Observed CV difference	Bootstrapped mean CV difference	95% CI	Probability that *H. naledi* CV is higher	Probability that *H. naledi* CV is lower
Gorilla vs. *H. naledi*.	27.5	27.5	16.1–30.1	$p < 0.0001$	$p > 0.9999$
P. troglodytes vs. *H. naledi*	7.0	7.0	1.2–13.6	$p = 0.0067$	$p = 0.9933$
H. sapiens (cadaveric) vs. *H. naledi*	16.1	15.7	6.4–26.9	$p < 0.0001$	$p > 0.9999$
H. sapiens (estimated) vs. *H. naledi*	2.9	3.1	−1.2–7.4	$p = 0.0832$	$p = 0.9168$

[a] Mass estimates for *H. naledi* were derived from the Grabowski et al. (2015) formulae.

Table 5
Subtrochanteric femoral size variation in extant apes, humans, and Dinaledi *Homo naledi* derived from bootstrapped distribution of 5000 iterations.

Samples	Males	Females	Total sample	ISD	Observed CV	Bootstrapped mean CV ($n = 8$)	95% CI
Gorilla spp.	13	13	26	1.43	20.3	19.8	14.3–25.0
Pan troglodytes	17	17	34	1.16	11.7	11.4	7.5–15.1
Homo sapiens	125	125	250	1.19	15.3	14.8	9.8–20.7
Homo naledi			8		18.6		

Table 6
Comparisons of Dinaledi *Homo naledi* subtrochanteric area CV ($n = 8$) to extant apes and humans based upon 5000 iterations.[a]

Samples	Observed CV difference	Bootstrapped mean CV difference	95% CI	Probability that *H. naledi* CV is higher	Probability that *H. naledi* CV is lower
Gorilla vs. *H. naledi*	1.7	3.1	−7.0–15.2	$p = 0.2982$	$p = 0.7018$
P. troglodytes vs. *H. naledi*	−6.9	−5.3	−11.5–1.6	$p = 0.8684$	$p = 0.1316$
H. sapiens vs. *H. naledi*	−3.3	−1.0	−11.6–11.1	$p = 0.6548$	$p = 0.3452$

[a] Negative values indicate that *H. naledi* has a larger CV.

Table 7
Dinaledi stature estimates and 95% prediction intervals obtained from comparative modern human data.

Specimen ID	Element	U.S.	Kulubnarti	Dart Africans	Jungers et al. (2016)[a]
U.W. 101-484	Tibia	156.0 (146.4–165.6)	144.5 (138.1–150.9)	147.8 (134.4–161.2)	143.2 (139.0–147.9)
U.W. 101-283	Humerus	149.4 (136.6–162.2)	139.4 (131.5–147.3)	142.7 (129.8–155.6)	–

[a] Note that femoral length is not available from the Dinaledi specimens. Thus, it was estimated based on the average crural index from a sample of 569 modern humans (HMG). Range in parentheses is based on crural index ± two standard deviations. See SOM for additional stature estimation details.

148 cm. The statures estimated from the U.W. 101-283 humerus are approximately 5 cm smaller than those of the U.W. 101-484 tibia. Using the authors' OLS equations, the humeral head measurement from U.W. 101-283 gives rise to the second smallest body mass estimate in our sample (36 kg, Table 2). This, along with the difference in length between these specimens (67 mm), suggests that they are not associated and represent different individuals (see SOM for further details). If the U.S. estimates are excluded, the average stature estimate is 143.6 cm. This is consistent with the results obtained using the Jungers et al. (2016) formula (143.2 cm). Prediction intervals cumulatively range from 129.8 to 165.6 cm (129.8–161.2 cm if the estimates derived from the U.S. samples are excluded; Table 7).

The results of the bootstrap analysis indicate that the *H. naledi* humero-tibial index (79.4) lies below the 95% confidence interval for both *P. troglodytes* and *G. gorilla*, but well within the confidence interval for Kulubnarti *H. sapiens* (Table 8, Fig. 2).

3.3. Absolute and relative brain size

The endocranial volumes for the Dinaledi calvariae are 465 cc (DH3/DH4) and 560 cc (DH1/DH2); thus the DH1/DH2 endocranial volume is approximately 20 percent larger than the smaller DH3/DH4 estimate. These calculations were derived from composite crania; thus, as an exploratory exercise only, we calculated the CVs for volumes treating these as four separate measurements. The *H. naledi* endocranial volume CV (10.1) never exceeds that of a mixed-sex sample of apes or humans and, in fact, only exceeds that of a single sex sample in two out of eight comparisons (*H. sapiens* males and *P. troglodytes* females, Table 9). When two males and two females are randomly drawn for the extant reference samples, the proposed *H. naledi* ISD (1.20) is significantly higher than the bootstrapped ISDs for the Danish modern humans, but within the 95% CIs of *G. gorilla*, *P. troglodytes*, and *H. lar* (Table 10). In reality, the *H. naledi* measurements were

Table 8
Comparison of humerus/tibia length index in extant apes, humans, and Dinaledi *Homo naledi*.

Taxon	Sample size	Observed HL/TL index	Bootstrapped mean HL/TL index	95% CI
Gorilla spp.	43	145.9	147.9	111.0–194.8
Pan troglodytes	61	122.3	122.8	103.9–146.5
Homo sapiens (Kulubnarti)	90	84.5	84.6	71.9–98.5
Homo naledi		79.4		

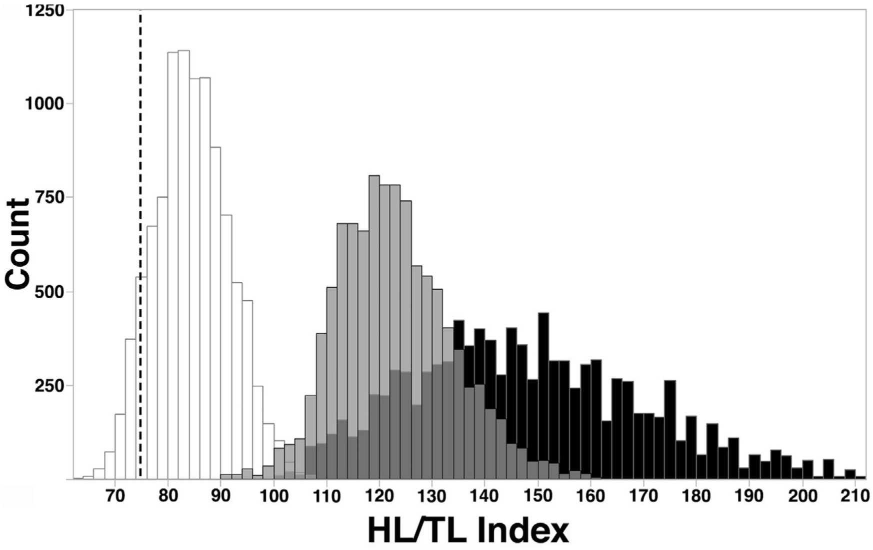

Figure 2. Bootstrapped distributions of humerus length/tibia length index. Dinaledi *Homo naledi* = dotted line, modern *Homo sapiens* = white, chimpanzees = gray, gorillas = black.

Table 9
Endocranial volume variation in extant apes, humans, and Dinaledi *Homo naledi*.

Samples	Males	Females	Total sample	Observed CV	Bootstrapped mean CV	95% CI
Gorilla gorilla	14	14	28	11.1	10.1	2.8–18.1
Gorilla gorilla	14		14	7.8	7.1	2.2–11.3
Gorilla gorilla		14	14	7.9	7.0	0.7–12.9
Pan troglodytes	20	20	40	9.5	8.6	2.3–15.4
Pan troglodytes	20		20	8.5	7.8	2.0–13.4
Pan troglodytes		20	20	6.1	5.5	1.4–10.0
Homo sapiens	20	20	40	7.4	6.8	1.9–12.6
Homo sapiens	20		20	5.9	5.4	1.5–9.2
Homo sapiens		20	20	7.5	6.3	1.7–14.4
Hylobates lar	20	20	40	8.2	6.9	2.2–11.3
Hylobates lar	20		20	7.7	7.5	2.0–11.6
Hylobates lar		20	20	7.6	6.9	1.8–11.8
Homo naledi			4	10.1		

Table 10
Endocranial volume ISD in extant apes, humans, and Dinaledi *Homo naledi*, assuming four *H. naledi* volumes.

Samples	Males	Females	Total sample	Observed ISD	Bootstrapped mean ISD	95% CI
Gorilla gorilla	14	14	28	1.17	1.17	1.01–1.36
Pan troglodytes	20	20	40	1.12	1.12	0.97–1.29
Homo sapiens	20	20	40	1.07	1.07	0.93–1.20
Hylobates lar	20	20	40	1.06	1.08	0.93–1.24
Homo naledi	2	2	4	1.20		

derived from composite reconstructions and should not be treated as independent measures. When the analysis is reduced to two observations for *H. naledi* (the smaller composite value of 465 cc and the larger composite value of 560 cc) and compared to bootstrapped ISDs, drawing one male and one female for the extant sample (Table 11), we find that, not surprisingly, the CIs for the extant samples are broader and the hypothesized *H. naledi* ISD falls within the distribution of all extant reference samples. In fact, drawing two individuals from single-sex samples and creating a distribution of max/min ratios shows that a max/min ratio of 1.20 falls within the distribution of all extant reference samples except that of Danish males (Table 12).

Table 11
Endocranial volume ISD in extant apes, humans, and Dinaledi *Homo naledi*, assuming two *H. naledi* volumes.

Samples	Males	Females	Total sample	Observed ISD	Bootstrapped mean ISD	95% CI
Gorilla gorilla	14	14	28	1.17	1.18	0.95–1.47
Pan troglodytes	20	20	40	1.12	1.13	0.92–1.38
Homo sapiens	20	20	40	1.07	1.08	0.87–1.25
Hylobates lar	20	20	40	1.06	1.08	0.88–1.30
Homo naledi	1	1	2	1.20		

Table 12
Endocranial volume max/min ratios in single sex samples of extant apes, humans, and Dinaledi *Homo naledi*.

Samples	Males	Females	Total sample	Observed max/min	Bootstrapped mean max/min	95% CI
Gorilla gorilla	14		14	1.27	1.09	1.00–1.26
Gorilla gorilla		14	14	1.34	1.09	1.00–1.28
Pan troglodytes	20		20	1.36	1.10	1.00–1.30
Pan troglodytes		20	20	1.26	1.07	1.00–1.23
Homo sapiens	20		20	1.23	1.07	1.00–1.20
Homo sapiens		20	20	1.36	1.08	1.00–1.30
Hylobates lar	20		20	1.27	1.10	1.00–1.26
Hylobates lar		20	20	1.31	1.09	1.00–1.25
Homo naledi			2	1.20		

Table 13
Dinaledi *Homo naledi* encephalization quotients.

Specimens	ECV	Estimates using Grabowski et al. (2015); Grabowski (2016)			Estimates using Ruff et al. (1997)[a]		
		Ave EQ	Min EQ	Max EQ	Ave EQ	Min EQ	Max EQ
DH3/DH4	465.0	3.57	3.41	3.67	2.46	2.30	2.74
DH1/DH2	560.0	3.93	3.76	4.10	2.61	2.52	2.76
Average	512.5	3.75			2.53		

[a] EQ equation in Ruff et al. (1997) derived from Martin (1981).

Using the Grabowski et al. (2015, 2016) equations and average endocranial and body mass estimates, an EQ of 3.75 is obtained. Using the minimum and maximum body masses for the larger and smaller bodied subsamples (based on sectioning points from the "mean method"), calculated EQs range from 3.41 to 4.10 (Table 13). When using the Ruff et al. (1997) EQ equation (derived from Martin's [1981] ¾ scaling equations) and the OLS body mass estimates derived from the authors' comparative samples, EQs range from 2.30 to 2.76, with an average of 2.53. Note that because these EQ equations (Ruff et al., 1997; Grabowski et al., 2016) assume different scaling relationships between brain and body size, the resultant estimates should only be compared to other published estimates using the same equations.

3.4. Dental size variation

Canine and molar size variation is low in the Dinaledi sample (Table 14, Fig. 3). For all four canine dimensions analyzed, the Dinaledi CV lies within the bootstrap distributions of humans and gibbons. Further, the Dinaledi CVs lie below the 95% CIs of gorillas, with the exception of the mandibular canine mesiodistal measurement. For three of four measures, the Dinaledi CVs lie within the 95% CIs of chimpanzees; however, they always fall in the lower end of the bootstrapped distribution.

The Dinaledi molar CVs generally lie below, or just at the lower end of, the distribution of *G. gorilla*, but within the distributions for humans, chimpanzees, and gibbons (Table 15). The higher CV for gorillas is consistent with a higher molar size ISD than for the other comparative samples.

4. Discussion

4.1. Body size and shape

The average *H. naledi* body mass (37.4 kg) obtained using the Grabowski et al. (2015) equations is most similar to the species average they report for *A. afarensis* (39.1 kg). The *H. naledi* average falls above the species averages for *A. africanus* (30.5 kg), *A. sediba* (25.8 kg), *H. habilis* (32.6 kg), and *H. floresiensis* (27.5 kg), and below their reported averages for early *Homo* (43.8 kg), Asian *H. erectus* (51.4 kg), and the combined group of African and Georgian *H. erectus* (50.0–51.0 kg; Table 16, Fig. 4). When taking into account the confidence intervals associated with the species averages presented in Grabowski et al. (2015), the *H. naledi* average body mass (and CI) lies above the CIs reported for *A. sediba* and below the CIs reported for Asian *H. erectus* and African and Georgian *H. erectus* (when all possible specimens are included). Overall, however, there is a large degree of variation among individual specimens resulting in high degree of overlap between taxa (Fig. 4).

Table 14
Canine size variation and dimorphism in extant apes, humans, and Dinaledi *Homo naledi*.

Sample	Males	Females	Total sample	Measurement	ISD	Observed CV	Bootstrapped mean CV	95% CI
Gorilla gorilla	20	20	40	C_1MD	1.37	18.8	16.2	4.5–22.7
				C_1LL	1.41	18.8	17.9	6.5–25.2
				C^1MD	1.44	19.7	19.0	6.3–29.2
				C^1LL	1.40	19.4	17.3	7.4–24.4
Pan troglodytes	20	20	40	C_1MD	1.20	11.3	10.4	4.0–17.0
				C_1LL	1.21	12.4	11.4	4.3–20.0
				C^1MD	1.28	15.3	13.8	5.1–24.4
				C^1LL	1.20	12.2	10.9	4.4–21.4
Homo sapiens	20	20	40	C_1MD	1.04	7.6	7.1	2.6–11.7
				C_1LL	1.02	7.6	7.0	2.1–12.1
				C^1MD	1.03	6.6	6.2	2.3–10.7
				C^1LL	1.00	7.5	7.1	3.0–11.4
Hylobates lar	20	20	40	C_1MD	1.12	8.5	8.2	2.9–13.8
				C_1LL	1.07	7.4	7.0	2.7–11.1
				C^1MD	1.08	7.9	6.9	2.0–12.1
				C^1LL	1.09	9.6	8.2	3.8–12.6
Homo naledi			5	C_1MD		6.2		
			5	C_1LL		2.8		
			5	C^1MD		5.5		
			6	C^1LL		7.4		

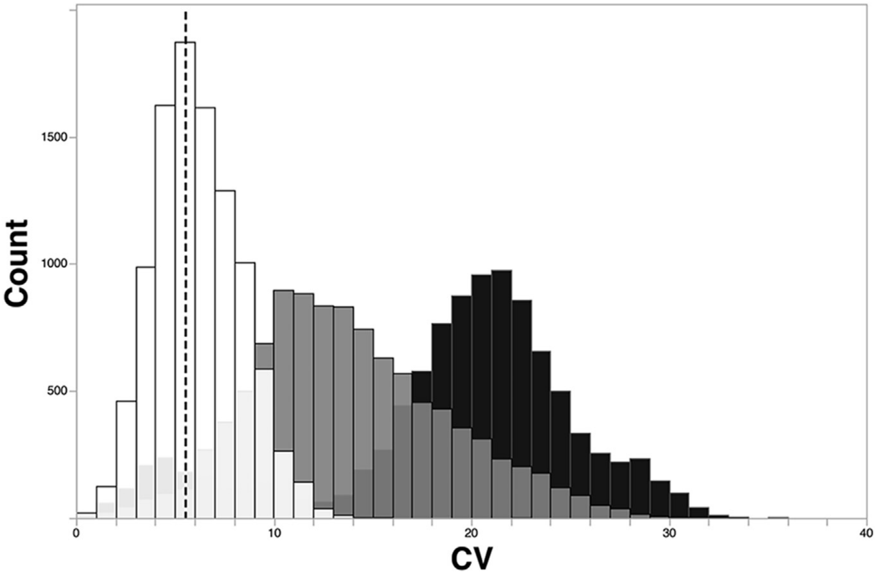

Figure 3. Bootstrapped comparison of Dinaledi maxillary canine mesiodistal length coefficient of variation (CV) to extant reference samples. Dinaledi *Homo naledi* = dotted line, modern *Homo sapiens* = white, chimpanzees = gray, gorillas = black.

Table 15
Molar breadth variation and dimorphism in extant apes, humans, and Dinaledi *Homo naledi*.

Sample	Males	Females	Total sample	Measurement	ISD	Observed CV	Bootstrapped mean CV	95% CI
Gorilla gorilla	20	20	40	M_1BL	1.09	7.0	6.8	3.4–10.2
				M_2BL	1.11	7.6	7.3	3.8–11.0
				M^1BL	1.09	6.6	6.4	3.7–8.7
				M^2BL	1.10	7.0	6.6	2.6–10.9
Pan troglodytes	20	20	40	M_1BL	1.02	4.9	4.6	2.2–7.1
				M_2BL	1.00	4.6	4.4	2.2–6.4
				M^1BL	1.01	4.4	4.2	2.0–6.7
				M^2BL	1.00	5.5	5.1	1.9–8.7
Homo sapiens	20	20	40	M_1BL	1.03	5.1	4.9	2.3–7.2
				M_2BL	1.07	5.9	5.9	2.8–8.7
				M^1BL	1.05	4.9	4.7	2.7–6.8
				M^2BL	1.03	7.9	7.4	2.7–13.3
Hylobates lar	20	20	40	M_1BL	1.06	5.4	5.0	2.0–7.6
				M_2BL	1.02	4.9	4.7	2.5–6.8
				M^1BL	1.06	5.6	5.4	3.0–7.7
				M^2BL	1.06	5.5	5.2	2.1–8.3
Homo naledi			7	M_1BL		3.2		
			8	M_2BL		3.8		
			9	M^1BL		2.0		
			5	M^2BL		3.8		

Table 16
Dinaledi *Homo naledi* body mass and brain size compared to fossil hominin estimates derived from Grabowski et al. (2015, 2016).[a]

Species[b]	Jungers et al. (2016)		Grabowski et al. (2015)		Grabowski et al. (2016)	
	BM	Range	BM	ISD	ECV	EQ
Homo naledi	37.4	33.1–43.4	37.4	1.16	465/560	3.75
Australopithecus afarensis	41.0	24.5–63.6	39.1	1.59	446.0	3.18
Australopithecus africanus	30.7	22.8–43.3	30.5	1.51	460.0	3.81
Australopithecus sediba	25.9	22.7–29.1	25.8		420.0	3.85
African *Homo* sp.	40.6	35.5–45.4				
Early *Homo*			43.8	1.42		
Homo habilis	33.7	27.3–38.4	32.6	1.41	624.3	4.97
Dmanisi *Homo erectus*	40.7					
African *Homo erectus*	48.9	29.4–64.4				
Asian *Homo erectus*	51.9	49.3–54.8	51.4	1.17	999.1	4.55
African and Georgian *Homo erectus*			50.0	1.53	747.8	6.00
Possible African and Georgian *Homo erectus*			51.0	1.46		
Homo floresiensis	27.5		27.5		425.7	3.75
Paranthropus boisei	46.4		35.3	1.46		
Paranthropus robustus	31.7	24.0–42.6	30.1	1.35		

[a] Comparisons between author's OLS body mass estimates, dimorphism, and EQ values are presented in the SOM.

[b] Jungers et al. (2016) uses the data in Grabowski et al. (2015), but takes a more conservative approach leaving out questionable taxonomic assignments and separating Dmanisi and African *Homo erectus*; thus, both interpretations are presented.

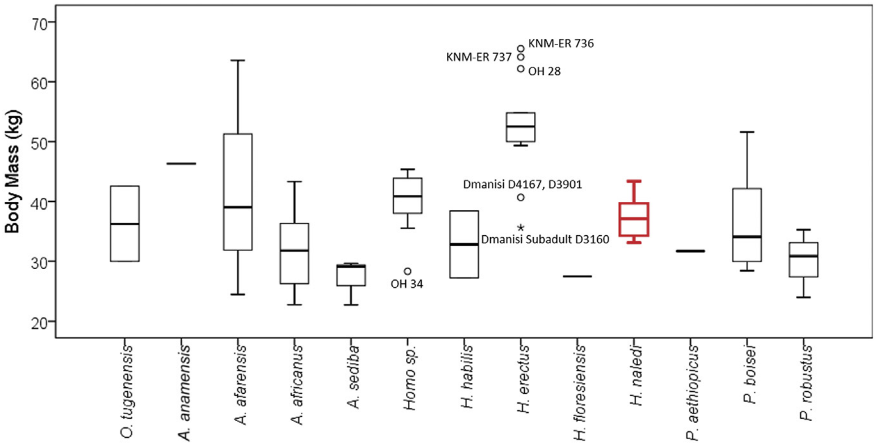

Figure 4. Estimated hominin body masses by species as presented by Grabowski et al. (2015). Plots show median (solid line), upper, and lower quartiles (box) and minimum/maximum values (whiskers). Dinaledi *Homo naledi* body masses (n = 14) estimated using Grabowski et al. (2015) equations. Comparative hominin body masses taken from multivariate estimates provided in Grabowski et al. (2015).

The body mass estimates obtained using the OLS equations derived from the authors' modern comparative data present larger point estimates (approximately 7.5 kg higher). As suggested by Grabowski et al. (2015) and Jungers et al. (2016), these values may be inflated due to the use of larger bodied individuals in the global reference samples used to derive the equations. If these values are compared to published hominin values from studies using similar methods and global reference samples, the range of *H. naledi* body masses overlaps with those for *A. afarensis, A. africanus, H. habilis*, and *Homo* sp. (e.g., KNM-ER 1472, KNM-ER 1482, KNM-ER 5881, KNM-ER 3882; McHenry, 1992; Skinner and Wood, 2006; Will and Stock, 2015). The Dinaledi values are below estimates for early African *H. erectus* (62.2 kg) and well below those estimated for Sima de los Huesos *H. heidelbergensis* (69.1 kg), Neandertals (75.4 kg), the individual represented by the Middle Pleistocene Kabwe tibia E 691 (>70 kg), and the undated, but presumably Middle Pleistocene, Berg Aukas individual (93 kg; Grine et al., 1995; Trinkaus et al., 1999; Arsuaga et al., 2015). The *H. naledi* body masses, however, overlap with Dmanisi *H. erectus* estimates (47–50 kg; Lordkipanidze et al., 2007, 2013).

Every method of body mass estimation comes with potential errors and limitations. For this reason, when considering the body size of *H. naledi*, it is useful to compare the raw skeletal dimensions for *H. naledi* to those published in Grabowski et al. (2015; see SOM for details). The *H. naledi* femoral head measurements (35.2 and 35.8 mm) fall at the high end of the *Australopithecus* range and below all reported *Homo* fossil specimens, with the exception of *H. floresiensis* (LB1 = 31.0 mm) and one *H. erectus* specimen (BSN49/P27 = 32.6 mm; see SOM). *H. naledi* femoral subtrochanteric products (ap*ml) overlap with *Australopithecus*, but fall below all *H. erectus* values, with the exception of the KNM-ER 1809 and Dmanisi D3160 subadult individuals (Fig. 5). When subtrochanteric measurements are evaluated individually, there is a larger range of variation among all taxa, although the *H. naledi* specimens generally fall below *H. erectus* specimens. This pattern is also true for the femoral midshaft measurements (see SOM for data). As suggested by the Grabowski et al. (2015) body mass results, however, there does appear to be a good degree of overlap between the various taxa, with some *Australopithecus* individuals appearing larger than certain *Homo* individuals, though there appears to be a significant size increase with *H. erectus*.

Regardless of whether the raw measurements, Grabowski estimates, or authors' OLS estimates are used, all results suggest that *H. naledi* body masses were lower on average than African and

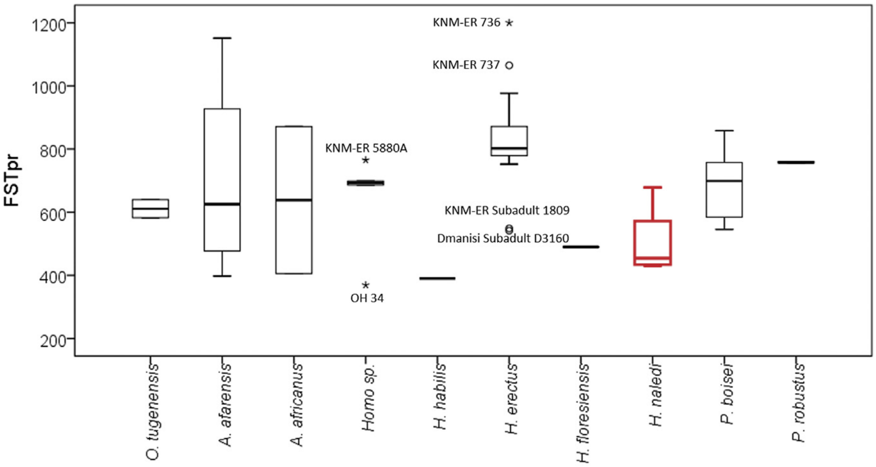

Figure 5. Hominin femoral subtrochanteric size (product of anteroposterior and mediolateral measurements) by species. Plots show median (solid line), upper, and lower quartiles (box) and minimum/maximum values (whiskers). Comparative hominin data taken from Grabowski et al. (2015). Specimens and data presented in SOM.

Asian *H. erectus* and Middle and Late Pleistocene *H. heidelbergensis/rhodesiensis*, and higher than values for *A. sediba* and *H. floresiensis*. Overall, body mass estimates for *A. afarensis, A. africanus*, and early *Homo* depend on specimens included and methods employed (i.e., statistical methods and reference samples), with the more recent Grabowski et al. (2015) estimates suggesting a large degree of body size variation within these taxa. This is further complicated by limited samples, highly fragmented specimens, and the fact that many of the specimens used to create these species averages come from a range of geographic locations and temporal spans, which may introduce additional variation. The discovery of additional specimens and continued advances in methods of body mass estimation will help reconcile current debates surrounding body mass estimation in small bodied species; regardless, it seems abundantly clear that *H. naledi* was smaller bodied than contemporaneous Eurasian and African *Homo* species.

The stature estimates obtained from the two most complete elements within the Dinaledi specimens (U.W. 101-484 tibia and U.W. 101-283 humerus) suggest that these individuals stood approximately 143.5 cm tall. This average value excludes the slightly higher estimates obtained using the U.S. reference sample (156.0 cm and 149.4 cm), as the larger U.S. body sizes in the reference sample likely results in overestimates for the smaller bodied *H. naledi* individuals. The Dinaledi stature estimates fall at the high end of the *Australopithecus* range (about 100 cm for *A. afarensis* females and 150 cm for *A. afarensis* males) and are greater than estimates for *H. habilis* (about 100 cm for females and 130 cm for males). They fall slightly below estimates for *Homo* sp. specimens KNM-ER 1472 and KNM-ER 1481 (ca. 150–155 cm) that may represent *H. rudolfensis* (McHenry, 1991, 1992; Ruff and Walker, 1993; McHenry and Coffing, 2000; Will and Stock, 2015), as well as the average estimates for stature in the Dmanisi *H. erectus* specimens (ca. 149 cm according to Lordkipanidze et al., [2007] or slightly greater than 150 cm according to Will and Stock [2015]) and within the broad range of stature estimates for South African early *Homo* (135–159 cm; Will and Stock, 2015). The Dinaledi estimates are, however, short relative to average heights for the Sima de los Huesos *H. heidelbergensis* (164 cm), Neandertals (161 cm), early modern humans (177 cm; Arsuaga et al., 2015), and that estimated from the Kabwe E 691 tibia (~170 cm; Trinkaus et al., 1999). The Dinaledi statures are also shorter than early eastern African *H. erectus*, which has estimated statures greater than 160 cm and as extreme as 185 cm (Antón et al., 2007; Antón, 2012; Dingwall et al., 2013; Will and Stock, 2015). It is important to note that the *H. naledi* stature was estimated from only two elements in an assemblage that represents a minimum of 15 individuals and, thus, may not represent an accurate species average. If more material is recovered or associations between postcranial elements can be determined, stature estimates should be revised to reflect the correct body proportions and size variation within the species. Further, the current Dinaledi assemblage does not allow us to examine dimorphism in height, though, it would be surprising to find much evidence for height dimorphism given the relatively low estimates for body mass dimorphism described above.

To date, the only adult Dinaledi limb bones that are complete enough to estimate their lengths are a humerus and a tibia. As stated above, there is no definitive evidence that these bones represent a single individual. If a humero-tibial index is calculated from these specimens, the resultant index (79.4) is much lower than indices calculated from associated elements from other fossil specimens. For example, Lordkipanidze et al. (2007) suggest that D3901, a tibia, and D4507, a humerus, represent a single individual. The Dmanisi humeral head is damaged along its proximal end and some subjectivity is required to estimate its length. However, using data they report, this individual has a humero-tibial index of 98.3. The Dmanisi index is more similar to that of *A. afarensis* specimen A.L. 288-1 (99.5 or 104.3, depending on the estimate of tibia length) and *H. floresiensis* specimen LB 1 (102.3) than it is to its supposed conspecific KNM-WT 15000 (84.0) or to Neanderthals (average = 92.6, range = 90.0–97.7, $n = 4$) and Paleolithic modern humans (average = 84.5, range = 82.5–86.7, $n = 3$; TWH, unpublished data). The D3901/D4507 value appears to indicate an individual that lacks the lower limb elongation seen in KNM-WT 15000 (Pontzer et al., 2010). Humero-femoral indices reported in Jungers et al. (2016) similarly suggest that the Dmanisi D4507 individual had a relatively short hindlimb in comparison to modern human pygmy groups, but had a humero-femoral index much lower than values for LB1 (*H. floresiensis*), A.L. 288-1 (*A. afarensis*), and ARA-VP-6/500 (*Ardipithecus ramidus*). In contrast, although the Dinaledi humerus and tibia may be unassociated, the resampling analysis indicates that the 79.4 value falls within the modern human bootstrapped distribution and outside those of African apes (Table 8), which supports the interpretation of an elongated lower limb in *H. naledi* relative to *Australopithecus* (see also Marchi et al., 2017). With single observations for most early hominin species, the distribution of values representative of their species or populations is currently unknowable (e.g., Jungers, 2009). Until future discoveries increase the sample size of complete limb bones or reveal associated postcranial remains, caution is urged in interpreting the biomechanical and evolutionary implications of relative limb length in *H. naledi* and other hominins.

4.2. Body size and craniodental variation

With the exception of the four more complete calvaria (DH1, DH2, DH3, and DH4), of which DH1/DH2 are presumed to be male and DH3/DH4 female based on expression of craniofacial features, sex is not hypothesized for any other specimens included in this study. In order to estimate the degree of sexual size dimorphism in the sample, the mean body mass estimate was used as a sectioning point to create a larger bodied subsample (potentially male) and smaller bodied subsample (potentially female). By taking a ratio of the means of the larger and smaller subsamples, an index of sexual dimorphism (ISD) was calculated. This was done using all samples, as well as only the subtrochanteric samples using both the Grabowski equations and the OLS equations derived from the authors' data. The results suggest that *H. naledi* males were no more than 20% heavier than females. Since sexes are unknown and were estimated based on size, this estimate should be interpreted cautiously. In addition, because the body mass estimates are roughly unimodal and the mean method assumes no overlap between the sexes, this is likely an overestimation of the actual magnitude of dimorphism (Plavcan, 1994).

The modern human reference data provide a good example of the effect of using the mean method to estimate dimorphism. If the mean method is used to calculate a body mass ISD from the HMG global modern human sample ($n = 695$), an estimate of 1.22 is obtained for the pooled sample and population specific ISDs range from 1.17 to 1.22 (average ISD = 1.20). The actual sexual dimorphism in the modern human sample, however, is lower: 1.15 for the pooled sample and 1.10 to 1.16 in the population specific subsamples. Overall, average body mass dimorphism in modern human populations is reported to be approximately 1.15, and is documented to range between 1.07 and 1.28 (Stini, 1972, 1976; Ruff, 1994, 2002; Smith and Jungers, 1997). For comparison, reported average body mass dimorphism in *P. troglodytes* is approximately 1.30 and in *G. gorilla* is 1.68 (Plavcan and van Schaik, 1997); although the chimpanzee and gorilla samples utilized in this study have an estimated body mass ISD of 1.27 and 1.99, respectively. Resampling analyses comparing the Dinaledi body mass CVs to chimpanzees, gorillas, and modern humans also suggest that the level of body size variation observed in the Dinaledi Chamber *H. naledi* individuals is relatively low compared to these extant taxa and most similar to modern humans. It should be noted, however, that the Dinaledi CV point estimate may underestimate the true variation in the species if the sex composition of the *H. naledi* samples used in these analyses are unbalanced. Further, it is noted that using subtrochanteric size alone does not distinguish *H. naledi* variation from any of the extant reference samples (Tables 5 and 6). This reflects both the fact that chimpanzee skeletal dimorphism tends to be less than in human samples (Gordon et al., 2008; Plavcan, 2012b), the opposite of the mass dimorphism pattern, and that the sample size is smaller for this comparison, and thus the CIs are wide. These results do not invalidate the conclusion that *H. naledi* mass dimorphism is human-like, but it does serve as a reminder that some of the low variance observed in the mass estimates may reflect the fact that *H. naledi* individuals are represented more than once in mass estimates.

Australopithecus has been argued to be highly mass dimorphic, while *H. erectus* is argued to have mass dimorphism on par with modern humans (McHenry, 1992; McHenry and Coffing, 2000). Not all researchers, however, agree that *Australopithecus* was highly mass dimorphic (e.g., Reno et al., 2003, 2005, but see Plavcan et al., 2005; Gordon et al., 2008) and there are hints from fossils assigned to *H. erectus* that size dimorphism may be more pronounced than traditionally appreciated (Simpson et al., 2008). *H. habilis* sensu lato mass dimorphism estimates range from 1.64 (McHenry, 1992; McHenry and Coffing, 2000) to 1.27 (Skinner and Wood, 2006), while sexual dimorphism in *H. habilis* sensu stricto and *H. rudolfensis* is generally estimated to be lower (1.16 and 1.18, respectively, according to Skinner and Wood [2006]), which illustrates the problematic nature of body size estimation in early *Homo* using taxonomically ambiguous samples. Overall, *H. naledi* size variation, both in skeletal dimensions and estimated mass, falls within the range of *H. sapiens* (McHenry and Coffing, 2000; Ruff, 2002; Plavcan, 2012a), suggesting that it was not characterized by the high magnitude of dimorphism inferred for *Australopithecus* or *H. habilis* sensu lato.

Although body size variation in excess of that observed in modern human populations is observed in many hominin species (e.g., *A. afarensis*), such body size estimates include fossil specimens from varying sites and dates, which introduces temporal and geographic variation (reviewed for *A. afarensis* in Kimbel and Delezene [2009]). This is an issue not only with *Australopithecus* samples, but also for *H. erectus*, which in its broadest configuration includes specimens from across Africa, Europe, and Asia that range in age from ca. 1.9 Ma to less than 1.0 Ma in Africa and much more recent in Asia (e.g., Antón et al., 2007, 2014). Further, caution must be exercised when interpreting the *H. habilis* and *H. rudolfensis* estimates, as many incorporate isolated postcranial elements that have no secure taxonomic affinities, and the dimorphism values can vary greatly depending on the specimens and body mass estimates included in the analysis. By contrast, the number of elements used to estimate Dinaledi body mass dimorphism is larger than most fossil hominin samples, and samples a geographically and temporally confined assemblage (Dirks et al., 2015). Thus, the estimate of body mass dimorphism in the Dinaledi sample is robust compared to most other African hominin assemblages.

Assuming the sex assignments are correct, the Dinaledi male calvariae are approximately 20% larger in cranial capacity than the females. This is similar to *H. erectus* endocranial dimorphism values reported for eastern African (20%), Dmanisi (24%), and Sangiran (17%) samples (Lieberman, 2011). Although extant *H. sapiens* dimorphism in endocranial volume is generally estimated around 8% (Lieberman, 2011), sexual dimorphism values up to 19% have been reported for some modern human samples (Tobias, 1975; Lorenzo et al., 1998). Estimating dimorphism in endocranial volume is problematic for most hominin samples. For example, the inclusion of the small-brained KNM-ER 42700 in *H. erectus* led Spoor et al. (2007) to suggest that dimorphism in that taxon is pronounced, but not excessive when compared to extant apes. However, the smallest *H. erectus* cranial capacity, that of D4500, is attributed to a male. Thus, it is plausible that the size variance in *H. erectus* cranial capacity results not from sexual dimorphism alone but is also strongly influenced by pooling temporally and geographically disjunct populations (e.g., Antón et al., 2007; Kappelman et al., 2008).

Though four individuals contributed to the calculation of endocranial volumes for the Dinaledi hominins, we suggest caution when interpreting the results presented here. If the assignment of the two larger crania as males and the two smaller as females is correct, this indicates an ISD of 1.20 that is high relative to our modern human sample, but within the range of all extant ape comparative samples. However, when variance was compared to mixed-sex and single-sex extant samples, the Dinaledi CV rarely exceeded that of single sex samples (Table 8). Further, when we reduce the analysis to single female and single male composite values, the CIs for the reference samples become very broad and the Dinaledi ISD values can easily be sampled in all reference samples. Further, if max/min values are computed for single-sex reference samples, the Dinaledi value of 1.20 can be sampled in all reference samples, except Danish males, which again reflects the broad CIs for the reference samples at small sample sizes. Thus, the conclusion that the ISD of *H. naledi* exceeds that of humans hinges upon the correct sex allocation, as well as the assumption that each of these estimates represents the average value for their sex group. If the sex allocation is wrong or the individuals represent extremes within the sample, then, effectively, the current estimate for *H. naledi* endocranial volume ISD could be exaggerated beyond the true population-level dimorphism in the species. Alternatively, given that the variance in the four Dinaledi crania rarely exceeds that of single sex samples, it is also possible that the specimens do not reflect the entire size variation within the sample and that an ISD of 1.20 underestimates the true population dimorphism.

Resampling analyses also suggest that canine and molar size variation is relatively low. This low level of dental size variation does not hint at a high degree of size dimorphism and is consistent with observations from other hominin samples (e.g., Leutenegger and Shell, 1987; Suwa et al., 2009). This is unlike the pattern observed in *Australopithecus*, where low canine size dimorphism is coupled with high body size dimorphism (Plavcan and van Schaik, 1997; Kimbel and Delezene, 2009; Plavcan, 2012a). Although both the ISD and CV estimates calculated for *H. naledi* are influenced by small samples and the sex composition of the Dinaledi sample, their combined results conservatively indicate that there is no evidence for strong body size or dental size dimorphism in this assemblage of *H. naledi*. While a high level of sexual dimorphism is associated with polygynous mating systems and intense male-male competition, low levels of dimorphism, such as that exhibited by *H. naledi*, are not characteristic of any single mating strategy (Plavcan, 2012a). Thus, the ecological and behavioral implications of low dimorphism in *H. naledi* (and *Homo* broadly) are uncertain (see Plavcan, 2012a for further discussion).

As pointed out by Plavcan (2012b), to understand truly the behavioral implications of changes in sexual dimorphism in the fossil record, it is important to look at changes in male and female size independently. For example, a decrease in sexual dimorphism could result from a decrease in male size (while female size remains stable) or an increase in female size (while male size remains stable). A decrease in male size would possibly suggest relaxed levels of intra-male mate competition. On the other hand, an increase in female body size might suggest increased resources for females (Plavcan, 2012b). Though the geological date of the Dinaledi hominins is reported at 335–236 ka (Dirks et al., 2017), this does not help us resolve which scenario of body size change relative to *Australopithecus* or early *Homo* led to low levels of dimorphism in *Homo* broadly or *H. naledi* specifically. *H. naledi* is small for a species of *Homo* of that geological age; however, its ambiguous phylogenetic position relative to *H. erectus* (e.g., Dembo et al., 2016) makes it difficult to determine if *H. naledi* retains reduced dimorphism from a common ancestor with *H. erectus* or whether it evolved the condition independently.

4.3. Endocranial volume and encephalization

The smaller Dinaledi endocranial volume (465 cc) falls within the range of, and actually close to, reported mean values for *A. afarensis* and *A. africanus* and is below the reported minimum value for all other *Homo* specimens (approximately 510 cc for KNM-ER 1813), with the exception of *H. floresiensis* specimen LB1 (417 cc; Holloway et al., 2004; Skinner and Wood, 2006; de Sousa and Cunha, 2012; SOM). The larger Dinaledi cranial capacity (560 cc), however, falls at or just beyond reported maximum volumes for *Australopithecus*, within the range of *H. habilis* sensu stricto estimates (ca. 509–594 cc), below that of adult *H. rudolfensis* specimen KNM-ER 1470 (ca 750 cc) and subadult *H. rudolfensis* specimen KNM-ER 1590 (>800 cc), and is comparable to the smallest *H. erectus* specimen (D4500 = 546 cc; Holloway et al., 2004; Spoor et al., 2007; Lordkipanidze et al., 2013). Of note, with the exception of D4500, the other four well preserved Dmanisi crania all exceed estimates for capacities in the Dinaledi sample (D2280 = 730 cc, D2282/D11 < 650 cc, D2700/2735 = 601 cc, and D3444/3900 = 641 cc). Outside of the Dmanisi specimens, the next smallest cranial capacity for *H. erectus* is evinced by the KNM-ER 42700 late subadult specimen, which is estimated to have achieved its adult cranial capacity of 691 cc at death (Spoor et al., 2007). In South Africa, the ca. 1.9–2.1 Ma Swartkrans Member 1 (Herries et al., 2009) crushed SK 27 cranium, attributed to early *Homo*, has an estimated cranial capacity of 700 cc. This specimen has a mixed dentition; therefore, its adult brain size would have certainly exceeded its value at death (Clarke, 1977). The absolute endocranial volume of *H. naledi* is smaller than that typically seen in *Homo* and is matched by D4500, KNM-ER 1813, and LB1, three specimens attributed to different *Homo* species. Small brains appear to be a more common feature of *Homo* species than previously appreciated.

The *H. naledi* EQ obtained using Grabowski et al.'s (2016) best fit equation (~3.75) is the same as their reported value for *H. floresiensis* (3.75) and similar to values for *A. africanus* (3.81) and *A. sediba* (3.85). Besides *H. floresiensis*, the range of *H. naledi* EQ values estimated from the various body mass and endocranial volumes (3.41–4.10) fall below all other *Homo* species averages (Table 14). The next highest EQ for a *Homo* species is 4.55 for early *H. erectus* (Africa + Georgian). *H. habilis* sensu stricto has a reported EQ of 4.97, while *H. erectus* and Middle and Late Pleistocene *Homo* species have values of 6.0 and above (Grabowski et al., 2016).

Although absolute values change if the Ruff et al. (1997) EQ equation and OLS body mass estimates are utilized, the *H. naledi* EQ values (~2.53) are still low compared to similarly derived values for all *Homo* specimens (including *H. floresiensis*), with the exception of D4500 (EQ = 2.4), the smallest Dmanisi cranium (Rightmire et al., 2006; de Sousa and Cunha, 2012; Lordkipanidze et al., 2013; Arsuaga et al., 2015). Two other adult crania from Dmanisi yield EQs of 2.9 and 3.1, which, though low for *H. erectus*, exceed estimates for the Dinaledi hominins (Lordkipanidze et al., 2007). Thus, like the D4500 specimen and *H. floresiensis, H. naledi* extends relative encephalization for *Homo* into the range typical of *Australopithecus*.

4.4. Behavioral, ecological, and taxonomic implications

Wood and Collard (1999; Wood, 2014) outlined six criteria proposed to apply to the adaptive grade of *Homo*: body size, body shape, locomotion, mastication, growth and development, and relative brain size. Applying these criteria to fossil evidence attributed to *H. habilis* and *H. rudolfensis*, they and others (e.g., Wolpoff, 1999; Tattersall, 2016) have suggested that these species fall outside the adaptive grade of *Homo* and should be reassigned to *Australopithecus* or possibly a novel genus. In 1999, *H. habilis* and *H. rudolfensis* were outliers within *Homo* in many respects. Both had a smaller brain size than *H. erectus* as known at the time and both had relatively large postcanine dentitions. The postcranial specimens attributed to *H. habilis*, including the OH 62 and KNM-ER 3734 partial skeletons, the OH 8 foot, and the OH 35 tibia, all demonstrate a small body size. Some have suggested evidence that *H. habilis* had a relatively long upper limb and therefore different body shape than *H. erectus* and *H. sapiens*, likely indicative of some arboreality (Haeusler and McHenry, 2004). With a small body size, locomotion could not have the same energetic efficiency as in species with taller stature. Reviewing this evidence, Wood and Collard (1999) judged that *H. habilis* failed all six criteria for membership in *Homo*. *H. rudolfensis* presents no definitive fossil evidence pertaining to body size and shape, or locomotion, but it failed the remaining three criteria.

The fossil evidence pertaining to the definition and diagnosis of *Homo* has changed markedly since 1999. At that time, KNM-ER 1470 (holotype of *H. rudolfensis*), at 752 cc, was smaller than any known *H. erectus* cranium other than the very small OH 12. Now, many of the earliest specimens of *H. erectus* have endocranial volumes smaller than KNM-ER 1470 or OH 7 (holotype of *H. habilis*), including every one of the five crania in the Dmanisi sample (Lordkipanidze et al., 2007, 2013). The Dmanisi sample today also documents postcranial dimensions that are at the small end of those estimated for early African *H. erectus* (or *H. ergaster*). Moreover, several fossils of *A. afarensis* now document individuals inferred to have had body sizes that overlap with values observed for *Homo* (e.g., Grabowski et al., 2015). In addition, *H. floresiensis* was discovered. This species had strikingly short stature, well outside the range of normal individuals in even the smallest human populations (Jungers et al., 2016). Its holotype LB1 cranium has an endocranial volume smaller than all but a few known *Australopithecus* specimens (Brown et al., 2004). It had relatively long feet and short lower limbs, implying some aspects of its locomotion were very different from humans (e.g., Jungers et al., 2009). Yet this species had an absolutely small postcanine dentition and *Homo*-like facial reduction and canine fossae (e.g., Brown et al., 2004; Morwood et al., 2005; Kaifu et al., 2015) The species survived well into the Late Pleistocene, and while some authors have argued it may descend from an *Australopithecus* lineage (Brown and Maeda, 2009), phylogenetic analyses consistently place it either within or at the base of *Homo* (Argue et al., 2009; Dembo et al., 2015, 2016). Still, by Wood and Collard's (1999) criteria, *H. floresiensis* would not qualify as *Homo* (Collard and Wood, 2007).

In placing *H. naledi* within the genus *Homo*, Berger et al. (2015) emphasized the evidence for humanlike adaptations of the hand and wrist for manipulation, humanlike adaptations of the foot and hind limb for efficient long-distance bipedal locomotion, and absolutely small postcanine teeth, which may be associated with processing a diet with high energy density. These three sets of anatomical specializations of *Homo* define ways that humans and our fossil relatives interacted with their physical environments and ecologies. Thus, these derived features, many of which have been described and analyzed in more detail in subsequent publications (Harcourt-Smith et al., 2015; Kivell et al., 2015; Marchi et al., 2017), could be argued to support an adaptive *Homo* grade including *H. naledi*. Wood and Collard, however, would assuredly exclude *H. naledi* from the genus *Homo* based on initial reports of the relatively small brain and body sizes compared to traditional *H. erectus* specimens (Berger et al., 2015) and a number of more primitive *Australopithecus*-like traits, such as features of the upper limb and hand that suggest that *H. naledi* retained some climbing capabilities (Kivell et al., 2015; Feuerriegel et al., 2017). Berger et al. (2015) also emphasized that *H. naledi* shares much of the structural configuration of its cranium with species of *Homo*, noting similarities with *H. erectus*, *H. habilis*, and *H. rudolfensis*, as well as others (also see Laird et al., 2017; Schroeder et al., 2017). Phylogenetic analyses of craniodental traits, which do not obviously interact directly with ecology, combine to suggest that *H. naledi* belongs within the *Homo* clade (Dembo et al., 2016). This study aimed to further evaluate *H. naledi* body size and body size variation, absolute and relative brain size, and craniodental variation among the specimens recovered from the Dinaledi chamber in order to provide additional insight into the gradistic and cladistic positions of this new species.

Our more in-depth analysis of *H. naledi* body and brain size indicates that *H. naledi* departs from most specimens attributed to *H. erectus* in Africa by having an absolutely and relatively smaller endocranial volume, smaller estimated body mass, and smaller estimated stature. *H. naledi* does, however, overlap in stature and mass estimates with the Dmanisi sample of *H. erectus*. It can even be argued that the *H. naledi* stature and body mass estimates fall within the normal values for small bodied modern human populations (Berger et al., 2015; Jungers et al., 2016); however, this is partly a reflection of the large range of body size variation in modern human populations. Although there is overlap in body size between *Australopithecus* and early *Homo* (McHenry, 1992, 1994; Ruff, 2002; Holliday, 2012; Pontzer, 2012; Antón et al., 2014; Grabowski et al., 2015), *H. naledi* is on average slightly larger in size than *Australopithecus* (especially true in comparison to *Australopithecus* females). Sexual dimorphism in the Dinaledi specimens also appears to be low and is most consistent with other *Homo* species, including modern humans. While the upper limb of *H. naledi* evinces features indicative of the capacity to exploit arboreal substrates and to make tools (Berger et al., 2015; Kivell et al., 2015; Feuerriegel et al., 2017), the results of this study suggest that *H. naledi* likely possessed an elongated lower limb (see also Marchi et al., 2017)—a feature argued by some to be related to increased ranging behavior and perhaps long-distance running (Bramble and Lieberman, 2004; Steudel-Numbers, 2006). This is combined with evidence of a derived foot indicative of efficient terrestrial bipedalism (Berger et al., 2015; Harcourt-Smith et al., 2015), suggesting *Homo*-like locomotion. Overall, this and previous studies reveal that *H. naledi* satisfies at least two (locomotion and mastication) of the six adaptive grade criteria put forth by Wood and Collard (1999; Collard and Wood, 2007; Wood, 2014), with potential arguments in favor of two more criteria (body size and body shape) given *H. naledi*'s intermediate body size and elongated lower limbs. Future studies analyzing the juvenile specimens recovered from the Dinaledi chamber will help delineate where *H. naledi* falls in terms Wood and Collard's (1999) growth and development criterion.

H. naledi is markedly not like archaic or modern humans in its small brain size and low encephalization. *H. naledi* endocranial volume estimates from the Dinaledi Chamber are smaller than the mean for *H. habilis*, smaller than every specimen attributed to *H. rudolfensis*, and smaller than any specimen of *H. erectus* except D4500 from Dmanisi (Lordkipanidze et al., 2013). No *H. naledi* specimen rises to the endocranial volume of the smallest *H. erectus* cranium from Africa, KNM-ER 42700 (Spoor et al., 2007). *H. floresiensis* LB1 has a smaller endocranial volume than *H. naledi* DH3/DH4 (Kubo et al., 2013), but the larger inferred body mass for *H. naledi* yields a smaller estimate of EQ. If brain size remains the deciding criterion for admitting species into the genus *Homo*, then *H. naledi* must fail to make the *Homo* grade.

But brain size is only a single character, which does not map consistently with other evidence of relationships within the genus *Homo* (e.g., Dembo et al., 2015, 2016). Few relationships within the genus can be said to be certain, because *Homo* is a clade with repeated evidence for parallelism and evolutionary reversals of many features. As a result, there are many possible trees that the present evidence cannot reject, including trees that place *H. naledi* near the very base of the genus (Dembo et al., 2016). Also, no recent phylogenetic analysis of hominins has incorporated postcranial evidence together with cranial and dental evidence, leaving uncertainty about how to interpret the mosaic of postcranial morphology in *H. naledi*. Many cranial and dental features of *H. naledi* point to a close relationship with other *Homo* species. As a result, no cladistic definition of *Homo* can exclude *H. naledi* at this time without making the remainder of the genus paraphyletic.

Models tend to relate an increased body size in *Homo* with increased home range size and a concomitant increase in carnivorous behavior associated with a need for higher quality diet to feed a bigger brain (Martin, 1981; McHenry, 1994; O'Connell et al., 1999; Aiello and Key, 2002; Antón et al., 2002; Bramble and Lieberman, 2004). Specifically, it is argued that larger bodies and larger brains are only made possible via a higher quality diet (Aiello and Wheeler, 1995; Bramble and Lieberman, 2004), and a high quality diet itself is only possible via an increase in both carnivory and home range size, since it has long been recognized that mammalian carnivores exploit greater home ranges and day ranges than similarly sized herbivorous or omnivorous mammals (Harestad and Bunnell, 1979; Gittleman and Harvey, 1982; Lindstedt et al., 1986; Carbone et al., 2005). Additionally, Antón et al. (2002) found that home range size in primates is positively correlated with both body mass and diet quality. With regard to *H. naledi*, if slightly larger female body sizes than typical of *Australopithecus* is a reflection of enhanced carnivory, diet quality, and larger ranges as suggested by evolutionary models (Martin, 1981; McHenry, 1994; O'Connell et al., 1999; Aiello and Key, 2002; Antón et al., 2002; Bramble and Lieberman, 2004), it is, however, not associated with a relatively larger brain. If there is a specific adaptive grade associated with *Homo*, it was either first attained or secondarily maintained by small brained species.

The combination of traits in *H. naledi* makes it apparent that body size, body size dimorphism, and brain size are not coupled evolutionarily, or that even in the presence of genetic constraints these traits are capable of evolving in directions not predicted by the pattern of within species covariance (e.g., Grabowski, 2016), and were likely under different selection regimes. The results of this study support others (e.g., Jungers et al., 2016) that have also highlighted the uncoupled nature of these traits and resultant difficulties of using the combination of these traits to define taxonomic thresholds. The expansion of the fossil record of *Homo* to include *H. naledi* makes it clear that we understand little about the ecological diversification of taxa within the genus or how body mass, limb proportions, and brain size influenced the geographical spread of *Homo* within and outside of Africa.

An inclusive view of *Homo*, with *H. habilis* and *H. rudolfensis* occupying basal positions, would include taxa with postcranial morphologies indicating arboreality (*H. naledi*, *H. habilis*), those with *Australopithecus*-like encephalization (*H. naledi, H. floresiensis*, some Dmanisi *H. erectus*), those with smaller bodies than typical of *H. erectus* (*H. habilis*, *H. floresiensis*, *H. naledi*, and Dmanisi *H. erectus*), and taxa with diverse craniodental configurations (e.g., Leakey et al., 2012; Antón et al., 2014; Berger et al., 2015). Such variation in *Homo* species, including the Dmanisi *H. erectus* specimens, suggests that creating an adaptively uniform genus defined by large bodies, large brains, and committed terrestrial bipedalism as presented by Wood and Collard (1999), may not accurately represent true evolutionary relationships. The variation within *Homo* as presently understood clearly shows the difficulty of a grade-based definition for the genus. A clade-based definition is also problematic because various attempts to work out the phylogenetic relations at the base of the genus have come to conflicting conclusions. In addition, how large or small of a clade to include within a genus is, of course, an arbitrary decision. It is presently impossible to exclude *H. naledi* from the clade including both *H. erectus* and *H. sapiens* (Dembo et al., 2016). Thus, even a very narrow cladistic definition of the genus would include *H. naledi*, meaning that a substantial diversity of brain size within *Homo* must therefore be recognized. As mentioned by Dembo et al. (2016), future phylogenetic analyses using a supermatrix that also includes postcranial characters may yield different tree topologies than the craniodental data alone. The absolute and relative body and brain size data, as well as the dimorphism and variation results, presented in this paper will be valuable variables in such analyses.

The Dinaledi Chamber assemblage of *H. naledi* dates to the later Middle Pleistocene, likely between 236 and 335 kya (Dirks et al., 2017). Phylogenetic analyses suggest that the ancestral lineage leading to *H. naledi* persisted throughout at least the entire Middle Pleistocene (Dembo et al., 2016) and, if *H. naledi* is derived from near the root of the genus *Homo* (e.g., Hawks and Berger, 2016; Berger et al., 2017), this would be indicative of a deep temporal history for this species. However, with the totality of the *H. naledi* hypodigm coming from the Rising Star cave system, the geographic and temporal range of *H. naledi* is not known. With a late Middle Pleistocene age, *H. naledi* may have been in competition for space and resources with other lineages of *Homo*, some of which had much larger brain and body sizes by the Middle Pleistocene. With *H. floresiensis*, many authors have hypothesized that its long isolation shielded the species from competition by larger brained human populations. The same cannot be true of *H. naledi*. Future studies of the diet of *H. naledi* that combine evidence from dental wear, stable isotopes, and dental calculus (e.g., Henry et al., 2012) and dental topographical analysis (e.g., Ungar, 2007; Berthaume et al., 2010) may provide insight into the diet and possible ecological position of *H. naledi*.

5. Conclusions

While morphologically distinct from all previously documented hominin species, the Dinaledi *H. naledi* body size estimates overlap with *Australopithecus*, *H. habilis*, and the smaller Dmanisi *H. erectus* specimens and appear smaller than African and Asian *H. erectus, H. neanderthalensis*, *H. heidelbergensis*, and *H. sapiens*. Sexual size dimorphism in *H. naledi* is relatively low and comparable to reported values for *H. erectus* and *H. sapiens*, and dental size dimorphism is very slight. Endocranial volume and relative encephalization for *H. naledi* overlaps with the range of *Australopithecus*, falling below all reported *Homo* values with the exception of *H. floresiensis* and the smallest Dmanisi *H. erectus* specimen (D4500). In these respects, *H. naledi* represents an extension of the range of variation of fossil *Homo* within Africa. The results of this study support the hypothesis that body size, sexual dimorphism, and relative encephalization do not represent a functionally integrated package of features. With its combination of intermediate body mass, intermediate stature, and small endocranial volume, *H. naledi* challenges the hypothesis that *Homo* and *Australopithecus*, as currently defined, belong to clearly distinct adaptive grades.

Acknowledgments

We thank the National Geographic Society (SP20-15), the National Research Foundation of South Africa (98839), the South African Centre for Excellence in Palaeosciences (Ref CoE2017-068), the Palaeontological Scientific Trust, the University of the Witwatersrand, and the Graduate School of the University of Wisconsin-Madison (JH) for providing funding for this research. Financial support for LKD was provided by Connor Family Faculty Fellowship and the Office of Research and Development at the University of Arkansas. Thanks to Dr. Michael Plavcan for his guidance in setting up the bootstrapping procedures for comparing relative humerus and tibia length in *H. naledi* to comparative samples. LKD also thanks Amelia Villaseñor for assistance with the R programs used to perform the bootstrapping analyses. Thanks also to Dr. Joel Irish for providing data on modern human canine size and Dr. Ralph Holloway for providing data on modern human endocranial volumes. We are grateful for the thoughtful and constructive comments provided by the editor, associate editor, and anonymous reviewers on this manuscript.

Supplementary Online Material

Supplementary online material related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2017.06.010.

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