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The thigh and leg of *Homo naledi*

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ABSTRACT

This paper describes the 108 femoral, patellar, tibial, and fibular elements of a new species of *Homo* (*Homo naledi*) discovered in the Dinaledi chamber of the Rising Star cave system in South Africa. *Homo naledi* possesses a mosaic of primitive, derived, and unique traits functionally indicative of a bipedal hominin adapted for long distance walking and possibly running. Traits shared with australopiths include an anteroposteriorly compressed femoral neck, a mediolaterally compressed tibia, and a relatively circular fibular neck. Traits shared with *Homo* include a well-marked linea aspera, anteroposteriorly thick patellae, relatively long tibiae, and gracile fibulae with laterally oriented lateral malleoli. Unique features include the presence of two pillars on the superior aspect of the femoral neck and a tubercular distal insertion of the pes anserinus on the tibia. The mosaic morphology of the *H. naledi* thigh and leg appears most consistent with a species intermediate between *Australopithecus* spp. and *Homo erectus* and, accordingly, may offer insight into the nature of the earliest members of genus *Homo*. These fossils also expand the morphological diversity of the *Homo* lower limb, perhaps indicative of locomotor diversity in our genus.

1. Introduction

The transition from *Australopithecus* to *Homo* probably involved changes to the postcranial skeleton (Bramble and Lieberman, 2004; Antón et al., 2014), but the limited number of postcranial remains assigned to early *Homo* has limited efforts to clarify the transition between the genera. There are isolated remains, such as KNM-ER 1472 (Leakey, 1973), KNM-ER 1481 (Kennedy, 1983), KNM-ER 5881 (Ward et al., 2015), and others (Wood and Leakey, 2011) that likely belong to *Homo*, however, given both the taxonomic diversity in early *Homo* (Leakey et al., 2012; Spoor et al., 2015; but see Van Arsdale and Wolpoff, 2012; Lordkipanidze et al., 2013) and the spatial and temporal overlap between early *Homo* and the robust australopiths, attribution of isolated fossils to a species of early *Homo* remains speculative and controversial (e.g., Moyà-Solà et al., 2008). South African localities, in particular, have yielded very little postcranial material confidently attributed to *Homo* (but see McHenry, 1994; Susman et al., 2001).

The most complete specimens attributed to early *Homo*, which preserve both craniodental and lower limb remains, include OH 62 (Johanson et al., 1987; although the attribution of this specimen to *Homo* has been questioned; see Berger et al., 2010), KNM-ER 3735 (Leakey and Walker, 1985), and the *Homo erectus* fossils from Dmanisi, Georgia (Lordkipanidze et al., 2007). It has been suggested that the OH 62 femur is relatively short (Johanson et al., 1987; but see Haeusler and McHenry, 2004), with a long, anteroposteriorly compressed neck. Yet, both OH 62 and KNM-ER 3735 have well-developed femoral pilasters and levels of femoral diaphyseal

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robusticity that are more human-like than those of australopiths, such as the *Australopithecus afarensis* partial skeleton A.L. 288-1 (Haeusler and McHenry, 2004, 2007). The diaphysis of the OH 62 femur, however, is not as mediolaterally expanded at the level below the lesser trochanter as is the A.L. 288-1 femur (Johanson et al., 1987). Limb proportions and general morphology of the Dmanisi lower limb are more human-like, although the Dmanisi remains also exhibit some primitive features in the foot and upper limb (Lordkipanidze et al., 2007; Pontzer et al., 2010). No other early *Homo* specimens are complete enough to provide an unambiguous attribution, making it difficult to characterize the lower limb of early members of our own genus.

Here, we describe the femora, patellae, tibiae, and fibulae of *Homo naledi* (Berger et al., 2015). Although the Dinaledi deposit is not yet dated, the overall cranial and postcranial morphology of *H. naledi* is most similar to Pleistocene fossils attributed to members of the genus *Homo* (Berger et al., 2015; Dembo et al., 2016).

2. Materials and methods

2.1. The Dinaledi and comparative sample

The thigh and leg remains of the Dinaledi assemblage consist of 108 femoral, patellar, tibial, and fibular elements (Table 1). Elements are defined as identifiable fossils (regardless of size or completeness) that do not clearly conjoin with any other known elements in the assemblage as it currently stands. The minimum number of individuals (MNI) and the maturity of the elements in the present sample were assessed using size, side, morphology, and epiphyseal fusion. Bone siding and anatomical overlap were the primary methods by which individuals in the postcranial assemblage were differentiated. Though the assemblage is remarkably homogenous morphologically, variation between bones of comparable size and from opposite sides was used in rare cases to distinguish unique individuals. State of epiphyseal fusion was used preferentially, wherever possible, in grouping elements into two broad developmental categories: mature (fused epiphyses) or immature (unfused epiphyses; no elements in the thigh and leg assemblage recovered to date have partially fused epiphyses). Size was used secondarily to estimate the maturity of fragmentary, isolated elements (not preserving epiphyses or metaphyses) and as a factor in differentiating individuals. Specimens that fell within or over the size range of elements determined to be mature by epiphyseal fusion were deemed mature. Elements markedly smaller than comparative mature specimens were designated immature. Maturity was not estimated for specimens of intermediate size. Overall, specimens sorted by size alone do not feature prominently in this work and are used primarily for classification purposes, whereas the most complete (typically preserving epiphyses or metaphyses) and thereby diagnostic elements of the assemblage are featured disproportionately in the present descriptions and analyses.

The femoral sample represents a minimum of eight mature and three immature individuals, while three mature individuals have been identified from the patellae. Seven mature and two immature individuals are known from the tibiae, and eight mature, two immature, and one individual of unknown developmental state are represented by the fibulae (Table 2). Descriptions of the most complete specimens are included in the main text. Descriptions of less anatomically informative fragments are presented in the Supplementary Online Material (SOM). The immature sample is pictured and described: it is largely morphologically consistent with the mature sample, but these specimens are excluded from diagnoses and analyses due to the potential for ontogenetic variation that cannot be fully evaluated at this time and is the subject of

Table 1
List of *Homo naledi* thigh and leg remains.

Catalog number	Element	Superoinferior preserved length (mm)
Femur		
U.W. 101-002	Right proximal femur	136.3
U.W. 101-003	Right femoral shaft	219.2
U.W. 101-012	Right femoral shaft	210.7
U.W. 101-014[a]	Femoral shaft	65.3
U.W. 101-018	Right proximal femur	97.5
U.W. 101-143	Right proximal femoral shaft	66.0
U.W. 101-215	Left distal femur	101.0
U.W. 101-268	Left femoral shaft	227.2
U.W. 101-271	Femoral head	35.8
U.W. 101-341	Femoral fragment	86.7
U.W. 101-398	Left proximal femur	144.1
U.W. 101-421	Left proximal femur	55.3
U.W. 101-545	Right distal femoral shaft	106.0
U.W. 101-857	Left distal femoral shaft	78.5
U.W. 101-898	Femoral condyle fragment	21.5
U.W. 101-938[a]	Right proximal femur	272.9
U.W. 101-1000[a]	Right proximal femur	95.2
U.W. 101-1098[a]	Right epiphyseal head	25.7
U.W. 101-1120[a]	Left distal femur	21.7
U.W. 101-1136	Right proximal femur	115.3
U.W. 101-1284	Right distal femoral shaft	158.4
U.W. 101-1300	Femoral head	35.2
U.W. 101-1391	Right proximal femur	137.2
U.W. 101-1434	Left proximal femur	83.0
U.W. 101-1475	Left proximal femur	99.3
U.W. 101-1482	Left femoral shaft fragment	121.9
U.W. 101-1523[a]	Right distal femoral shaft	84.3
U.W. 101-1555[a]	Femoral neck fragment with attached partial head	24.5
U.W. 101-1694[a]	Right distal femoral condyle	18.3
Patella		
U.W. 101-852	Right patella	24.9
U.W. 101-1404	Right patella	26.0
U.W. 101-1512	Partial patella	23.7
U.W. 101-1639	Right patella	23.0
Tibia		
U.W. 101-013	Distal tibial shaft	85.5
U.W. 101-017	Right proximal tibial shaft	57.0
U.W. 101-042[a]	Tibial shaft fragment	51.2
U.W. 101-072	Left distal tibial shaft	119.9
U.W. 101-085	Tibia shaft fragment	53.5
U.W. 101-136	Right proximal tibial shaft	92.5
U.W. 101-213	Right proximal tibial shaft	159.0
U.W. 101-237	Left proximal tibial shaft	59.6
U.W. 101-239	Proximal tibial shaft	109.8
U.W. 101-313	Left proximal tibial shaft	59.0
U.W. 101-402	Right distal tibial shaft	67.0
U.W. 101-420	Left distal tibia	82.7
U.W. 101-484	Right tibia	293.0
U.W. 101-498[a]	Left proximal tibial shaft	138.8
U.W. 101-500	Left proximal tibial shaft	144.4
U.W. 101-567	Tibia shaft fragment	58.7
U.W. 101-571	Right proximal tibial shaft	120.7
U.W. 101-586	Tibial shaft fragment	45.7
U.W. 101-711	Left distal tibia	48.3
U.W. 101-848	Right tibial shaft	124.9
U.W. 101-973	Left proximal tibial shaft	114.4
U.W. 101-996[a]	Right tibia	249.7
U.W. 101-1070[a]	Left tibia	278.0
U.W. 101-1210	Right distal tibial shaft	56.9
U.W. 101-1214	Right tibial midshaft	35.6
U.W. 101-1241	Left distal tibial shaft	63.5
U.W. 101-1262	Right distal tibia	36.5
U.W. 101-1288	Right distal tibial shaft	142.4
U.W. 101-1295	Tibial shaft fragment	42.1
U.W. 101-1416	Right distal tibia	42.2
U.W. 101-1518	Left distal tibia	29.8
Fibula		
U.W. 101-181	Distal fibular shaft	26.9
U.W. 101-416	Left proximal fibular shaft	28.7
U.W. 101-449	Proximal fibular shaft	25.9
U.W. 101-508	Right fibular midshaft	47.9

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