

A One-Million-Year-Old Hominid Distal Ulna From Olduvai Gorge, Tanzania

Leslea J. Hlusko,^{1*} Whitney B. Reiner,¹ and Jackson K. Njau^{2,3}

¹Human Evolution Research Center and Department of Integrative Biology, University of California Berkeley, Berkeley, CA 94720

²Department of Geological Sciences, Indiana University, Bloomington, IN 47405

³The Stone Age Institute, Bloomington, IN 47407

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ABSTRACT *Objective:* Our aim was to recover new evidence of the evolution of the hominid lineage.

Methods: We undertook paleontological fieldwork at Olduvai Gorge, Tanzania, in one of the richest paleoanthropological sites in the world, documenting the evolution of our lineage and its environmental contexts over the last 2 million years.

Results: During field work in 2012, the Olduvai Vertebrate Paleontology Project discovered the distal end of a

hominid ulna (OH 82) on the north side of Olduvai Gorge a few meters west of the Third Fault, eroding from Bed III sediments that are ~1 million years in age. *Discussion:* The size and morphology of this distal ulna falls within the normal range of variation seen in humans, although at the larger end of the distribution. *Am J Phys Anthropol* 000:000–000, 2015. © 2015 Wiley Periodicals, Inc.

In 2012, as part of the Olduvai Vertebrate Paleontology Project, WBR recovered the distal end of a hominid¹ ulna at Olduvai Gorge, Tanzania. Here we provide a brief report on the geological context for the discovery and a short comparative description. This fossil was originally given specimen number OVPP-11. In the tradition of numbering hominids from Olduvai Gorge sequentially, it is renamed OH 82² (following OH 80, Domínguez-Rodrigo et al., 2013, and OH 81, Domínguez-Rodrigo et al., 2012).

Of the ~75 hominids recovered from Olduvai Gorge to date, we can confidently discern five that likely derived from Bed III or possibly undifferentiated Bed III/IV sediments: OH 12, OH 22, OH 28, OH 29, OH 34, OH 51, OH 59 (Leakey, 1971; Rightmire, 1980; Leakey and Roe, 1994). Of these, OH 28 (left femoral shaft and os coxae) and OH 34 (femur and tibia) are the only postcrania, making this new specimen the only hominid upper limb bone known from the Bed III/IV sediments at Olduvai Gorge.

GEOLOGICAL CONTEXT OF DISCOVERY

The geological sequence at Olduvai Gorge is divided into Beds I through IV with the Masek, Ndutu, and the Naisiusiu Beds on top of Bed IV (Hay 1976, 1990). The base of Bed I is ~2.03 Ma, and the youngest archaeological strata date to about 1,300 BP (Hay, 1976; Tamrat et al., 1995; Blumenschine et al., 2003; McHenry et al., 2008, Deino, 2012).

OH 82 was discovered near the Third Fault. The base of the sequence here is marked by the Bed I lavas overlain by Beds I through IV, with more recent sediments

above that (see Fig. 1B, modified from Hay, 1976). The contact between Beds II and III is disconformable and obvious in this area of the Gorge, as the Bed III sediments are distinctive in their red color (primarily claystones consisting of a large amount of volcanic detritus) in contrast to the gray of Bed II. Bed IV sediments are brown, as can also be seen in Figure 1, with an erosional surface at the contact with Bed III (Hay, 1976).

OH 82 was found on a scree slope eroding from the red claystones of Bed III (Fig. 1D). All of the fossils recovered in this area were stained black, have similar preservation, and could be traced to a fossiliferous horizon <2 m above the Bed II/III contact. As no other fossiliferous horizons were found in the area, and no other types of preservation occurred in this fossil assemblage, we conclude that this fossil derived from Bed III.

While it is agreed that Bed III sediments were deposited ~1 Ma, the exact boundaries on the age are somewhat uncertain (Hay, 1976; Cerling and Hay 1986; Tamrat et al., 1995; McHenry et al., 2007). McHenry et al. (2007: 210) provide a detailed discussion and conclude that the Bed II/III contact is likely older than the 1.15 Ma originally reported by Hay (1976) and may be as old as 1.28 Ma given magnetostratigraphic results

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*Correspondence to: Leslea Hlusko, Human Evolution Research Center and Department of Integrative Biology, University of California Berkeley, Berkeley, CA 94720. E-mail: hlusko@berkeley.edu

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¹Hominidae is used here as the sister group to the African apes, and includes all taxa on the human lineage since the split with chimpanzees, following White (2002).

²OH stands for Olduvai Hominid.

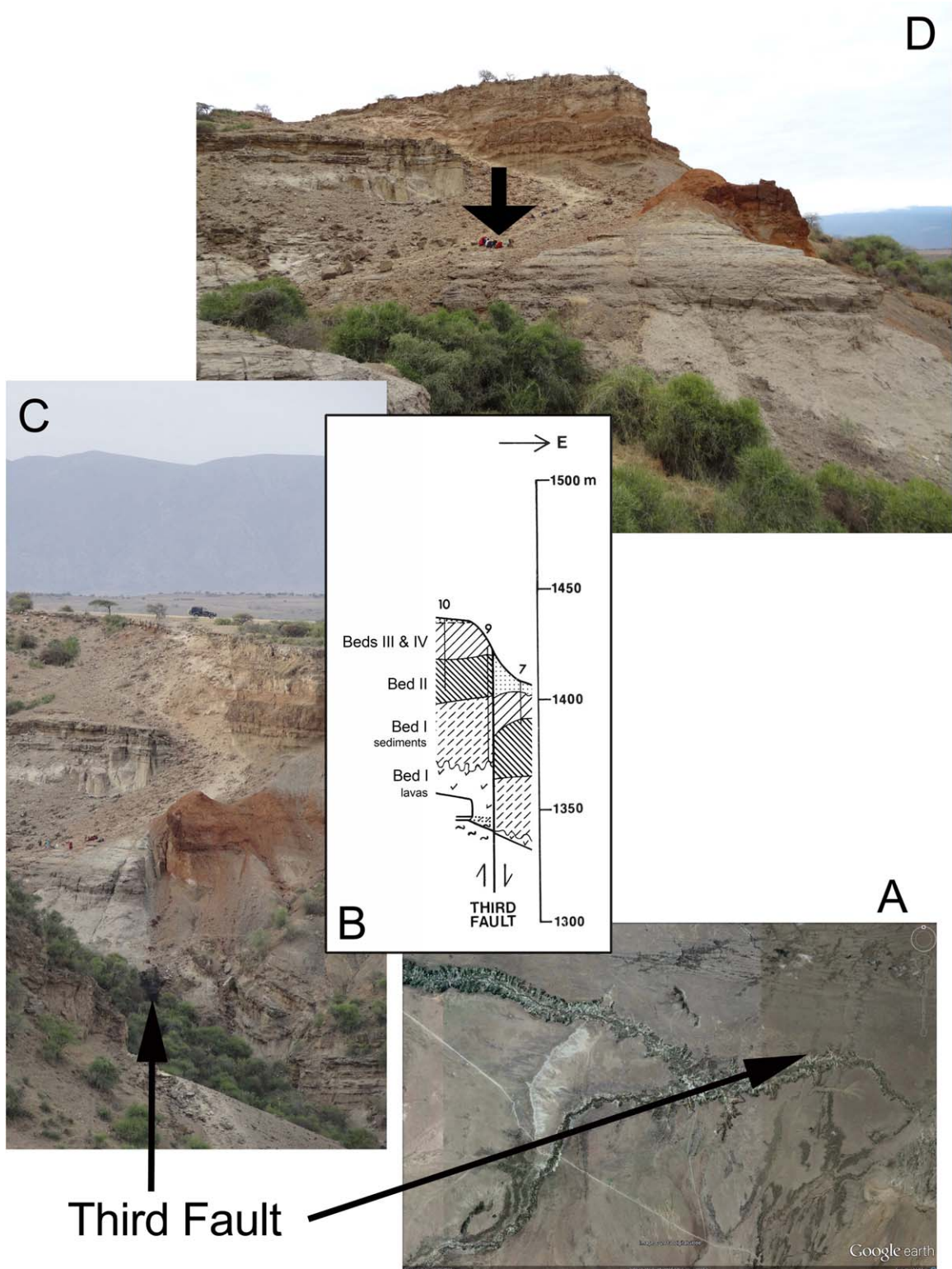


Fig. 1. Geological context for the recovery of OH 82. **A:** Satellite imagery from Google Earth© with an arrow indicating the location of the Third Fault. **B:** Excerpt of stratigraphic column from Hay (1976) indicating the four main sedimentological horizons exposed at the Third Fault. **C:** A view from the south side of the gorge, looking towards the north side where OH 82 was found. People, some dressed in red, are visible on the west side of the fault as they crawl along the surface looking for additional fragments of the specimen. For orientation, the people are more readily visible in 1D. **D:** Photographer was standing just west of where OH 82 was found at the northern side of the gorge at the Third Fault. The large black arrow in 1D shows where the fossil was found. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE 1. Measurements of the OH 82 distal ulna and comparative specimens

	DV breadth	ML breadth	Styloid length	Total ulnar length	Radio-ulnar articular height
<i>Homo sapiens</i> ^a					
N	57	50	57	49	43
Average	19.5	16.6	4.9	257.4	7.7
StDv	1.8	1.6	1.2	16.7	1.1
<i>Pan</i> ^a					
N	6	6	6	6	6
Average	19.9	17.8	6.5	275.6	5.8
StDv	1.4	1.2	0.5	11.7	1.0
<i>Gorilla</i> ^a					
N	5	5	5	5	
Average	26.0	25.7	7.8	338.9	8.6
StDv	3.4	3.9	1.3	37.1	1.0
<i>Pongo</i> ^a					
N	2	2	2	2	2
Average	21.7	22.7	5.1	356.3	6.7
A.L. 137-48B ^b	—	—	4.6	—	—
A.L. 333-12 ^b	18.5	18.3	6.1	—	—
AL 288-1 ^{a,c}	13.5	12.1	4.5	—	4.7
A.L. 438-1 ^d	20.1	17.5	6.5	278	—
MH2 ^e	16.5	15.8	6.0	246	5.2
Stw 326 ^f	14.5	14	—	—	—
Stw 398b ^f	16.5	14.2	—	—	—
OH 82	21.5	16.9	6.7	—	8.4

^aData are from the University of California Berkeley's collections.

^bData are from Lovejoy et al., 1982.

^cData are from Johanson et al., 1982.

^dData are from Drapeau et al., 2005.

^eMeasurements were taken from a cast provided by L. Berger.

^fData are from Menter, 2002.

Measurements are in mm. DV = maximum dorsoventral dimension of the distal ulna in standard anatomical position (dorsopalmar); ML = maximum mediolateral dimension of the distal ulna; "styloid length" = maximal proximodistal length of the styloid process from the depth of the articular disk attachment; "radioulnar articular height" = the maximal proximodistal height of the radioulnar articular surface, measured in parallel to the proximodistal axis of the bone; "total ulnar length" = the maximum proximodistal length of the ulna including the styloid process.

from Tamrat et al. (1995). Cerling and Hay (1986) adjust Hay's (1976) original date for the Bed III/IV contact from 0.7 to 0.83 Ma, with the Bed III/IV contact at the Matuyama-Brunhes transition, now recognized at 0.78 Ma (Tamrat et al., 1995). We conclude that Bed III sediments date between 1.2 and 0.83 Ma, providing a median age of 1 Ma for OH 82.

MATERIALS AND METHODS

In addition to a review of the published literature, the morphological and metric characteristics of OH 82 were compared with 72 specimens of extant hominoids held within the various collections at the University of California Berkeley (see Table 1). The extant collections included 57 modern humans (primarily Native Californian), six *Pan* (five *P. troglodytes* and one *P. paniscus*), five *Gorilla*, and two *Pongo*. Sample compositions were roughly half male and half female. Casts of four fossil hominoids were also available for study (A.L. 137-48B, A.L. 288-1, A.L. 333-12, and MH2).

Given the general hominoid morphology of this specimen and that the only hominoid found to-date at Olduvai Gorge are members of the Hominidae, our null hypothesis is that this specimen represents a 1 million year old member of this Linnean Family. Below we present data that cannot reject this hypothesis.

RESULTS

OH 82 is the distal end of a right ulna, broken 39.2 mm proximal to the distal articular surface (Fig. 2).

This specimen has a reduced styloid process compared to Old World Monkeys, similar to humans and other extant apes. It lacks an articular facet with the triquetral and pisiform, a condition typical of humans and extinct hominids. The ulnar head, radial articulation, and extensor carpi ulnaris groove of OH 82 are encompassed within modern human variation. There is no groove, or fovea, separating the head from the styloid process, a configuration not uncommon in humans, and the styloid process projects straight from the shaft. OH 82 falls within, but towards the larger end of the range of the metric and morphological variation seen in modern humans (Fig. 3, Table 1, and also Van Der Heijden et al., 2005; Sharma et al., 2011).

Comparative fossil material is sparse as complete distal ulnae are rarely preserved. There are two other ulnae from Olduvai Gorge. OH 36 is an almost complete ulna from Upper Bed II, originally assigned to *H. erectus* (Day, 1986; Tobias, 1991) and later to *Australopithecus cf. boisei* (Walker and Leakey, 1993; Wood et al., 1998; Aiello et al., 1999; McHenry et al., 2007). Aiello et al. (1999: 102) conclude that the robusticity of OH 36 exceeds that seen in modern humans, as well as what is characteristic of other fossil hominids. The second Olduvai ulna is from the partial skeleton OH 62 from Bed I (Johanson et al., 1987). While neither of these two specimens preserves the distal end, and so direct comparison with OH 82 is not possible, the distal-most anterior-posterior dimensions are as follows: OH 36 = 13.9 mm, OH 62 = 9.2 mm. OH 82's proximal-most anterior-posterior dimension is 13 mm. These dimensions demonstrate

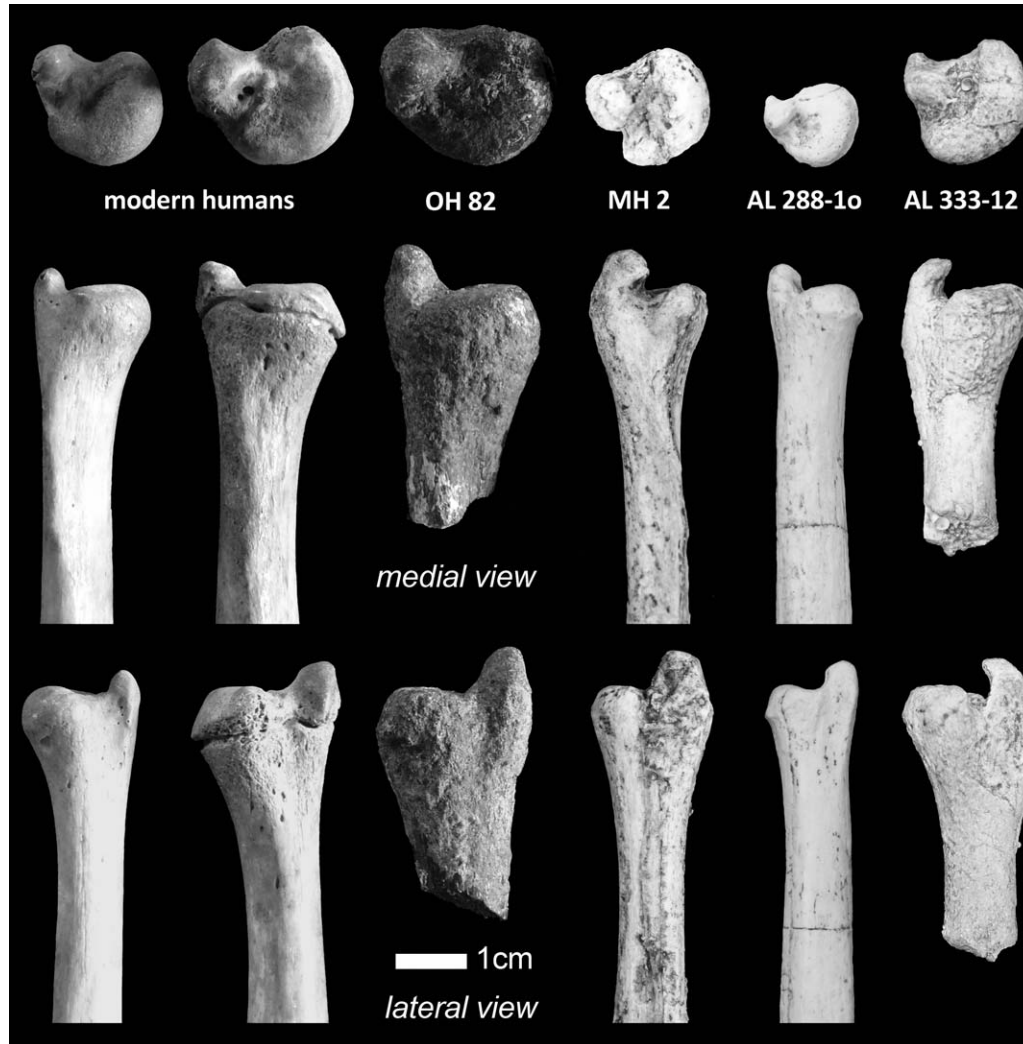


Fig. 2. OH 82 shown with two modern human specimens to the left and casts of three fossil hominid distal ulnae to the right. All specimens are from the right side. The distal end is shown at the top. In the distal view, MH2's morphology medial to the styloid process is notably distinct. We are uncertain as to whether this is a real anatomical difference or an artifact of cast quality. Note that the 1cm scale is approximate and these photos are not suitable for taking measurements. Refer to Table 1 for specific measurements.

that OH 62's shaft circumference at the distal end is considerably more slender than is OH 82. That said, OH 62 is also more slender than is A.L. 288-1, making it one of the thinnest known in the hominid fossil record (Johanson et al., 1987; see Fig. 3).

Turning to the geologically older comparative specimens brings us to the fossil record of the Omo and Afar regions. Omo L 40-19 from the Omo Shungura Formation is dated to 2.3 Ma (Feibel et al., 1989) and has been assigned to *A. boisei* (Howell and Wood, 1974; McHenry et al., 1976; Howell et al., 1987; Aiello and Dean 1990). It derives from a hominid of substantial body or forearm size (Richmond et al., 2002), but again, the distal end is broken and it lacks the styloid process (Howell and Wood, 1974).

The assemblage of *A. afarensis* specimens from Hadar include several distal ulnae ranging across the distribution of body sizes. On the small end of the scale, the A.L. 288-1 partial skeleton preserves right and left distal ulnae, A.L. 288-1o and A.L. 288-1u, respectively

(Johanson et al., 1982). The right specimen is better preserved, enabling measurement of features on the distal end, (Table 1 and Fig. 3). Other Hadar specimens include A.L. 137-48B and A.L. 333-12 (the latter shown in Fig. 2; Lovejoy et al., 1982). While A.L. 333-12 has a groove separating the semilunar surface and the styloid process, A.L. 137-48B does not. A.L. 137-48B's styloid process also projects in a straight line from the axis of the ulnar shaft as does OH 82's, unlike what is preserved in A.L. 333-12 (where the styloid process curves radially). The more recently discovered A.L. 438-1a (Drapeau et al., 2005) dates to 2.94 Ma. This is one of the largest specimens of *A. afarensis* known and the first complete ulna of this species. It is also the closest in size to OH 82 (see Table 1 and Fig. 3) and has a straight styloid process, more like OH 82, A.L. 137-48B, and A.L. 288-1 compared to A.L. 333-12. Unfortunately, the older 3.58 Ma ulna from Woranso-Mille, Ethiopia, (KSD VP 1/1) lacks the distal end (Haile-Selassie et al., 2010).

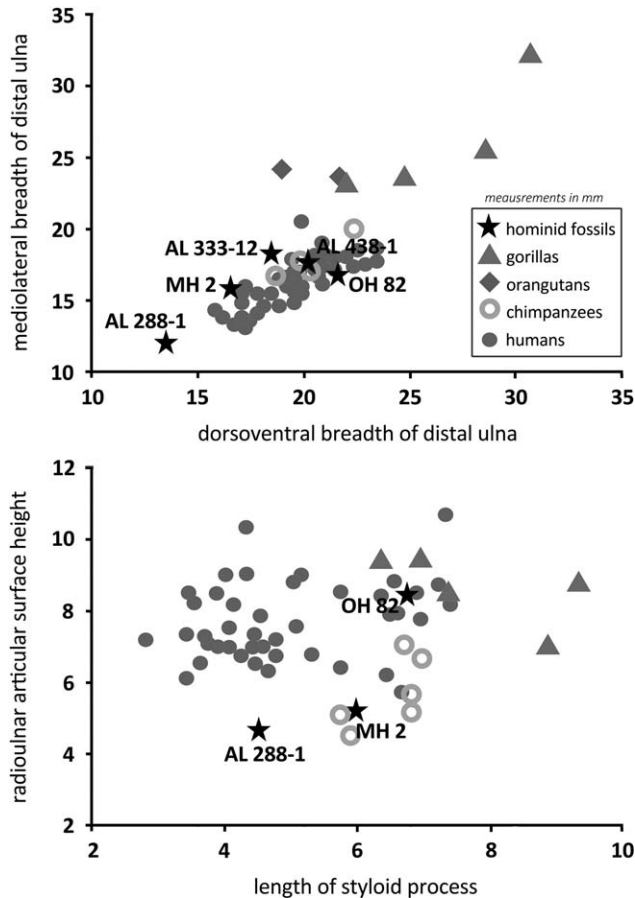


Fig. 3. Bivariate plots of four measurements (in mm) characterizing the distal ulna: dorsoventral breadth plotted against mediolateral breadth and length of the styloid process relative to radioulnar articular surface height. See Table 1. OH 82 falls comfortably within the larger end of the range of variation for humans.

Of the fossil hominid ulnae from the Plio-Pleistocene sites of Kenya, none preserve the distal end (e.g., KNM-BK 66, Solan and Day, 1992; KNM-ER 1808 and KNM-ER 3956, Leakey and Walker, 1985; and KNM-WT 15000, Walker and Leakey, 1993).

While there are numerous partial ulnae from South African sites (e.g., DNH 109, Gallgher and Menter, 2011; SKX 8761, Susman, 1989; Stw 108 and 113, Senut and Tobias, 1989; Stw 431, Toussaint et al., 2003; and TM 1517, Broom, 1942), only three preserve the distal end: Stw 326 and Stw 398B (Menter, 2002), and MH 2 (Berger et al., 2010). Two of these have a complete styloid process: Stw 326 and MH 2 (described as *A. sediba*; Berger et al., 2010). All three of these specimens are notably smaller than OH 82 (Table 1, Fig. 3).

DISCUSSION

The primate wrist is derived relative to many other mammals in its lack of ulnar articulation with the triquetral and pisiform, interpreted as evidence of increased mobility of the hand in a climbing rather than cursorial animal (reviewed in Lewis, 1965 and Almquist, 1992). Within the primates, the wrist joints of hominoids are distinct from the anatomy of the Old World Monkeys in having a meniscus separating the ulna from the

carpal bones (e.g., Lewis, 1972; O'Connor, 1975). While there is consensus among scientists that the lack of articulation between the distal ulna and the wrist bones is reflective of a shift away from weight-bearing during locomotion among the hominoids (but see Elmer, 2011), the details of what that activity may have actually been are still debated (e.g., Lewis, 1972; Corruccini, 1978; Sarmiento, 1988; Marzke et al., 1992; Wolfe et al., 2006; Kivell and Schmitt, 2009; Rohde et al., 2010).

While there are distinct types of variation within the carpals of extant hominoid taxa (e.g., Sarmiento, 1988), the skeletal morphology of the distal end of the ulna is remarkably variable within great apes such that variation between them does not provide for solid generic differentiation. For example, large humans can have a cartilage configuration around the styloid process that is also seen in gorillas (Sarmiento, 1988), and occasionally, human ulnar styloid processes have triquetral articulation (Biyani et al., 1990), although this extreme length often correlates with ulnar styloid impaction syndrome (Tomaino et al., 2001; Van Der Heijden et al., 2005). When it comes to the hominid lineage, the shape of the proximal ulna and the curvature of the shaft is typically taxonomically diagnostic, but the anatomy of the ulnar distal end is dominated by the morphology associated with the intra-articular meniscus, and is therefore relatively consistent in shape even in geologically older specimens (e.g., Hadar, Ethiopia, Lovejoy et al., 1982; Drapeau et al., 2005; Lovejoy et al., 2009). As such, this isolated fragment of distal ulna represents the remains of a large hominoid. Given that the only large hominoid discovered at Olduvai Gorge to date are those within the Hominidae, and that we cannot demonstrate morphology on OH 82 that cannot be encompassed within the variation seen in extant humans, we identify this specimen as a member of the human lineage separate from that of the other apes.

Historically, fossils from Olduvai Gorge have figured prominently in our understanding of the evolution of human manipulative abilities (e.g., Napier 1962; and see Marzke and Marzke, 2000). Leakey, Tobias, and Napier write in their revised diagnosis of the genus *Homo* that "...the hand is capable not only of a power grip but of, at the least, a simple and usually well developed [sic] precision grip" (1964:7). Within their diagnosis for the new species *H. habilis*, they note that, "the hand bones differ from those of *H. sapiens* in robustness" (1964:8), but without mention of the ulna's role in the wrist, as there had not yet been an ulna recovered from Olduvai at that time.

OH 82's size and robusticity suggests that whichever hominid it may represent, this individual was also robust. For the distal ulna at least, that robusticity and morphology was not beyond the range of variation typical of modern humans (although robusticity has been debated as a possibly archaic *H. sapiens* characteristic in reference to the 110,000–60,000 year old ulna from Klasies River Mouth, see Churchill et al., 1996 and Groves, 1998). OH 82 further evinces the long temporal stability in the morphological variation of the distal ulna—a configuration shared with chimpanzees, gorillas, and orangutans reflecting the intra-articular meniscus and a lack of os daubentonii. With luck and continued field work, carpal bones of this antiquity may also be found, elucidating the timing and ecological contexts of the more derived elements of the wrist of *Homo* hypothesized to have evolved as early as 1.4 Ma (Ward et al.,

2014), or as recently as 800,000 years ago (e.g., Tocheri et al., 2007, 2008).

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