

OH 83: A new early modern human fossil cranium from the Nduvu beds of Olduvai Gorge, Tanzania

Whitney B. Reiner¹  | Fidelis Masao^{2,3} | Sabrina B. Sholts⁴ | Agustino Venance Songita³ | Ian Stanistreet^{5,6} | Harald Stollhofen⁷ | R.E. Taylor⁸ | Leslea J. Hlusko¹

¹Department of Integrative Biology, University of California Berkeley, MC 3140, Berkeley, California 94720

²University of Dar es Salaam, Dar es Salaam, TZ 35091

³Conservation Olduvai Project, Dar es Salaam, TZ 35091

⁴Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560

⁵University of Liverpool, Liverpool, L69 3GP, UK

⁶The Stone Age Institute, Bloomington, Indiana 47407

⁷GeoZentrum Nordbayern, Universität Erlangen-Nürnberg, Erlangen, 91054, Germany

⁸University of California Riverside, Riverside, California 92521

Correspondence

Whitney B. Reiner, Department of Integrative Biology, University of California Berkeley, MC 3140, Berkeley, California 94720

Email: Whitney.Reiner@gmail.com

Funding information

National Science Foundation; Grant/Award Number: BCS 1025263 to LJH, Palaeontological and Scientific Trust (PAST), Johannesburg, South Africa to HS and IS

Abstract

Objective: Herein we introduce a newly recovered partial calvaria, OH 83, from the upper Nduvu Beds of Olduvai Gorge, Tanzania. We present the geological context of its discovery and a comparative analysis of its morphology, placing OH 83 within the context of our current understanding of the origins and evolution of *Homo sapiens*.

Materials and methods: We comparatively assessed the morphology of OH 83 using quantitative and qualitative data from penecontemporaneous fossils and the W.W. Howells modern human craniometric dataset.

Results: OH 83 is geologically dated to ca. 60–32 ka. Its morphology is indicative of an early modern human, falling at the low end of the range of variation for post-orbital cranial breadth, the high end of the range for bifrontal breadth, and near average in frontal length.

Discussion: There have been numerous attempts to use cranial anatomy to define the species *Homo sapiens* and identify it in the fossil record. These efforts have not met wide agreement by the scientific community due, in part, to the mosaic patterns of cranial variation represented by the fossils. The variable, mosaic pattern of trait expression in the crania of Middle and Late Pleistocene fossils implies that morphological modernity did not occur at once. However, OH 83 demonstrates that by ca. 60–32 ka modern humans in Africa included individuals that are at the fairly small and gracile range of modern human cranial variation.

KEYWORDS

evolution, paleoanthropology, paleontology, pleistocene, variation

1 | INTRODUCTION

Hominid crania from the Middle and Late Pleistocene are characterized by a mosaic of primitive traits shared with *Homo erectus* combined with derived morphologies of anatomically modern *Homo sapiens*, with a general shift from the earlier species to the later (Bruner, 2007; Reed & Tishkoff, 2006; Rightmire, 2008, 2009). The general pattern of changes

that mark the evolution of anatomically modern cranial morphologies from *H. erectus* include overall reductions in the size and robusticity of the cranial superstructures (crests and tori) (Rightmire, 2008), as well as increased parietal expansion and globularity of the brain case, frontal bone expansion in both the dimensions of breadth and along the sagittal plane, and retraction and size reduction of the facial skeleton (Lieberman, 1998; Rightmire, 2008). The specific combination of these derived and ancestral traits observed on different specimens is variable (Crevecoeur, Rougier, Grine, & Froment, 2009), revealing a mosaic pattern in the mode and tempo of human evolution. The morphological

Submitted for consideration as a research article in the American Journal of Physical Anthropology.

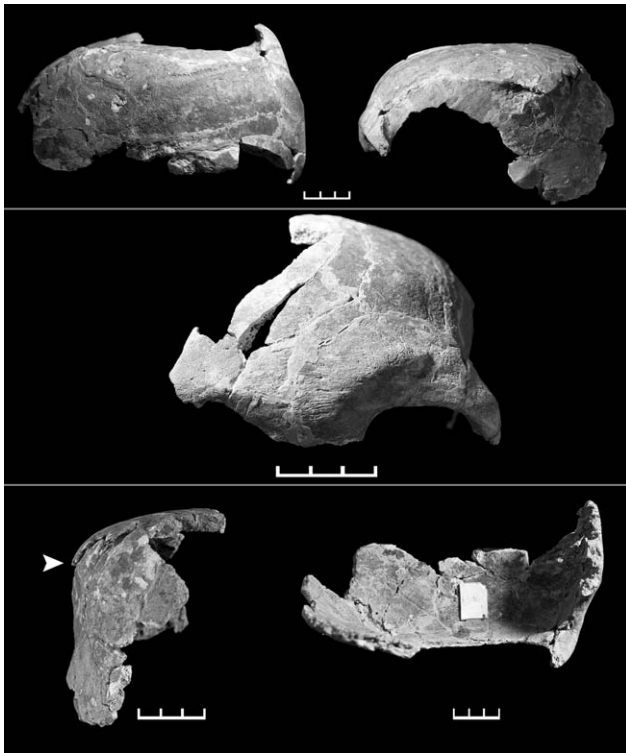


FIGURE 1 OH 83 rearticulated calvaria recovered from the surface. Center: OH 83 in *norma frontalis*. From top-right, and then clockwise: *Norma lateralis*, *norma basalis*, *norma occipitalis*, and *norma verticalis*. Arrow points to the left portion of the parietal that overhangs the vault, a clear indication of distortion. All scale bars are 3 cm length

heterogeneity among present-day modern humans further complicates our understanding of this matter (Haile-Selassie, Asfaw, & White, 2004).

Fossil, archaeological, and genetic evidence indicate an African origin for anatomically modern *H. sapiens* (AMHS) around 200 ka, followed by a range expansion beyond Africa between 190–70 ka (Cann, 2001; Cann, Stoneking, & Wilson, 1987; Clark et al., 2003; Day & Stringer, 1982; Haile-Selassie et al., 2004; Henshilwood & Marean, 2003; Kocher & Wilson, 1991; Llorente et al., 2015; McBrearty & Brooks, 2000; McDermott et al. 1996; Relethford & Jorde, 1999; Relethford, 2001; Stoneking, Sherry, Redd, & Vigilant, 1993; Stringer, 2002; Tishkoff et al., 1996; Trinkaus, 2005; White et al., 2003). Skeletal remains from the Middle Pleistocene (ca. 780–120 ka, Cohen, Finney, Gibbard, & Fan, 2013) have been differentiated at the subspecies level (*Homo sapiens idaltu*) on the basis of robust craniofacial morphology and a number of cranial vault dimensions exceeding the modern human range of variation in length (White et al., 2003). Newly discovered fossil crania from the Late Pleistocene (ca. 120–11 ka (Cohen et al., 2013)) of Africa increase the morphological information for the time period following *H. s. idaltu*, thereby improving our understanding of intra- and interspecific variation for *Homo* and the origins and early diversification of our species (Crevecoeur et al., 2009; Haile-Selassie et al., 2004; Stojanowski, 2014; Tryon et al., 2015; White et al., 2003).

With this in mind, we announce the discovery of a fossil calvaria recovered from Olduvai Gorge, Tanzania (Figure 1). Here, we present the initial description and metric data for OH 83, along with a morphological description of the fossil and preliminary analyses.

In 2009, as part of the Conservation Olduvai Project (COP) directed by F.M., A.V.S. found a few small fragments of a hominid fossil eroding from Nduvu Beds on the northern side of Olduvai Gorge. The University of Dar es Salaam's archaeology field school and COP ran a controlled excavation under the direction of F.M. during which additional, larger fragments (see Figure 2) were recovered *in situ* 110–280 cm below the surface. The larger pieces of the partial crania, and the majority of the smaller fragments were recovered through excavation. We associated the few surficial fragments with those recovered through excavation because there are no duplicated identifiable elements (MNI = 1) and size and preservation are in accord with the rearticulated calvaria. Hereafter designated “OH 83”, the specimen and associated fragments are housed in the Natural History Museum (NHM) in Arusha, Tanzania.

1.1 | Geological and geochronological context of OH 83

The sediments naturally exposed at Olduvai Gorge are approximately 100 m thick and divided into seven beds, numbered sequentially from oldest to youngest, with the base of Bed I dated to ~2 mya and the uppermost part of Bed IV dated to ca. 600,000 ka (Hay, 1976) (Figure 3). The stratigraphic units younger than Bed IV (the Masek, Nduvu and Naisiusiu Beds) have been the subject of considerably less geological research than the lower stratigraphic units (Beds I–IV) (Skinner, Hay, Masao, & Blackwell, 2003). OH 83 was discovered eroding from sediments of the Nduvu Beds, near archeological locality PLK (Hay, 1976) and geological locality 23 (Hay, 1976), situated on the downthrown side of FLK Fault between the Fourth and Fifth Faults on the north side of the main gorge (Figure 3). Based on our field observations, the sediments at locality 23 compare best to the massive “eolian tuff” facies (Hay, 1976) of the upper unit of the Nduvu Beds.

Although multiple attempts to date the Nduvu Beds have been made with varying success (Hay, 1976) (see references in Millard, 2008, and also Leakey, Hay, Thurber, Protsch, & Berger, 1972; Bada, 1981; Bada and Protsch, 1973; Macintyre, Mitchell, & Dawson, 1974), altogether the results suggest that the upper unit represents the period from ca. 60–32 ka and the lower unit spans from about 400–60 ka (Hay, 1976). While these age estimations for the Nduvu Beds are still debated to some extent, in part because distinguishing between sediments of the upper and lower units of Nduvu Beds exposures can be especially difficult along the rim of the gorge, Hay's age estimates for the upper and lower units of the Nduvu Beds are provisionally accepted (Eren, Durant, Prendergast, & Mabulla, 2014; Hay, 1976; Manega, 1993; Skinner et al., 2003). Recent archaeological survey of the upper unit of the Nduvu Beds has confirmed the presence of lithic technology from the Middle Stone Age (MSA) (Eren et al., 2014), which indicates



FIGURE 2 OH 83 cranial and dental fragments recovered *in situ*. Length of scale bar for cranial fragments is 6 cm length. Length of scale bar for teeth is 3 cm

an absolute lower age boundary of ca. 200 ka that is far below the older date for the upper Ndutu.

Radiocarbon (^{14}C) dating was attempted on an equid molar discovered in the excavation of OH 83. Attempts to isolate >30 kDa molecular weight organics were made on tooth material taken from three different points on the molar. Unfortunately, all organic constituents of the molar were degraded beyond use for this method. It is unclear whether the degradation is a factor of age, depositional setting, or a combination of both, due to the complex manner by which environmentally related biogeochemical processes are compounded. It is possible that the lack of organic matter is exclusively a result of the molar's age having surpassed the limits of the ^{14}C dating method, as accurate

^{14}C age determinations are difficult to obtain on materials older than 30 ka (Wood, 2015) and the maximum effective measurement limit is around 40 ka (Taylor & Bar-Yosef, 2014). However, this does not rule out that these sediments represent the upper unit of the Ndutu Beds, since this unit extends to 60 ka (Hay, 1976).

While the age of OH 83 remains to be more definitively determined, we place OH 83 within the age range of the upper unit of the Ndutu Beds, between 60 and 32 ka based on the available evidence. OH 83 is now the fourth hominid cranial fossil discovered in the uppermost beds of Olduvai Gorge, following three previously described specimens (OH 11 (Rightmire, 1980); OH 23 (Leakey, 1971); OH 1968 (Von Zieten, 2009).

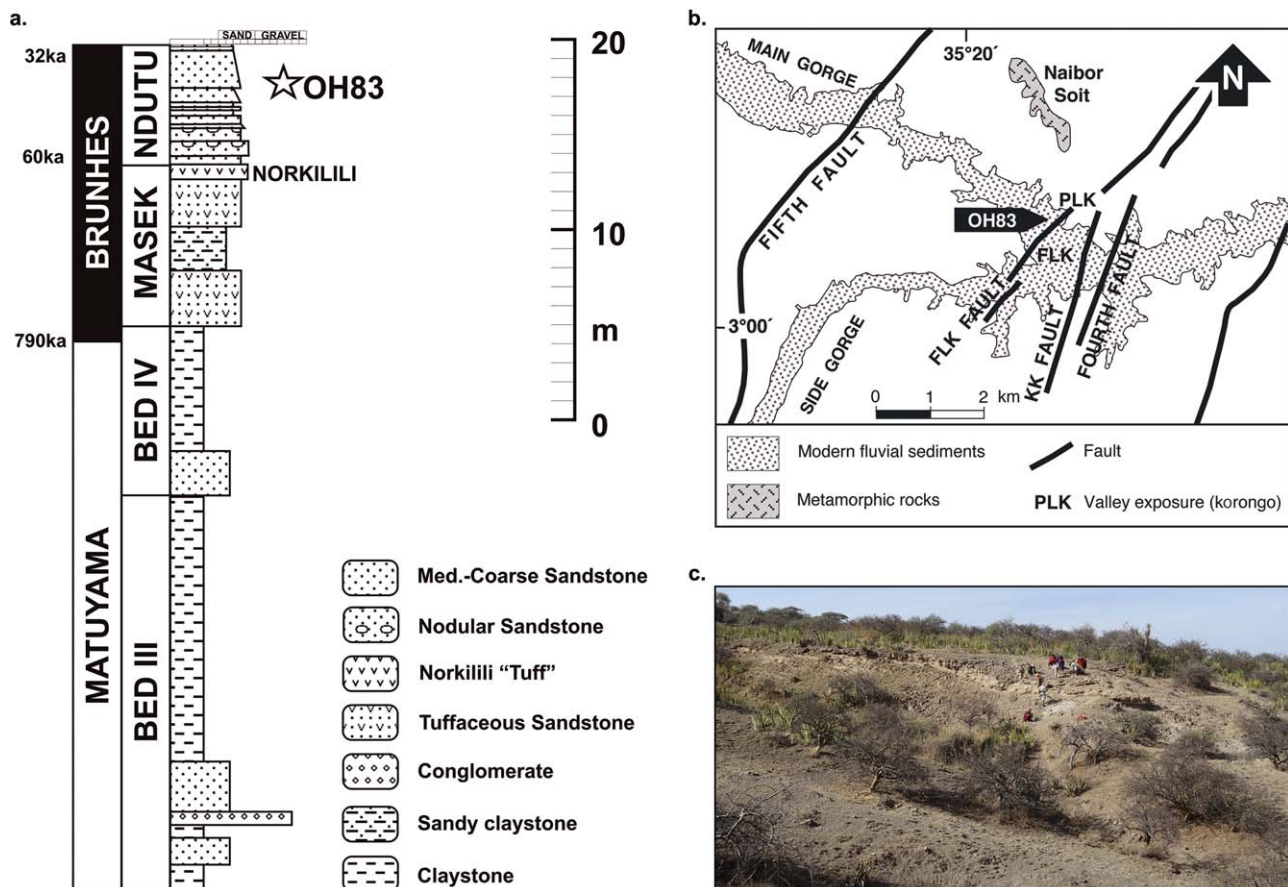


FIGURE 3 Geological context of OH 83. (a) Generalized stratigraphic column of the area on the downthrown side of the FLK Fault where OH 83 was found. Incorporates data from measured section of Loc. 23 of Hay (1976), (b) Depiction of geology at PLK (Loc. 23 of Hay, 1976), (c) photograph showing topography of OH 83's site of discovery; team members of the Olduvai Vertebrate Paleontology Project in this photograph provide a sense of scale.

1.2 | Anatomical description

OH 83 is composed mainly of the frontal and left parietal bones; neither the facial skeleton nor the basicranium is preserved (Figure 1). The right half of the neurocranium is almost entirely absent. As the occiput is not preserved, maximum cranial length cannot be measured, but the maximum length of the preserved cranial vault is 179.8 mm. Similarly, OH 83's preservation precludes the measurement of maximum cranial breadth, but the maximum width of preserved left half of the cranial vault is 57.4 mm.

The OH 83 frontal preserves the glabellar region, the superior half of the orbital region, and the majority of the squamous portion. The orbital region is broken superior to the level of nasion so that only about one-third of the superior-most portion of the orbit is preserved. The width of the preserved frontal between the medial-most extent of the orbital rims is 26.5 mm. The right side of the frontal squama is preserved near bregma at its superior-most extent, and it extends inferolaterally toward the level of supraglabella to the partially preserved right orbit. The left half of the frontal squama is present and complete. The supraorbital region's supraciliary arches are moderately pronounced and medially divided by a bilaterally arched glabella that is somewhat prominent, but only projects minimally beyond the superomedial corners of the orbits. The medial and lateral segments of the brow ridges are clearly differentiated from one another. In addition to its vertically oriented frontal squama at the region of the forehead, the supraorbital morphology of OH 83 is characteristic of the derived condition within recent *Homo* that is seen in AMHS (Rightmire, 1996).

For the right parietal, OH 83 preserves only a small fragment that articulates with the left parietal along the sagittal plane near the vertex. Although nearly complete, the left parietal around the midline is not preserved in the posterior region, but the inferolateral portion that would have articulated with the left posterior half of the occipital bone is present. The lateral side of the left parietal is broken inferior to the temporal line. The border of the break follows the squamous suture that would have been present during life, and a small portion of the left temporal bone preserving the supramastoid crest is preserved.

Most of OH 83's surface anatomy is not well preserved, most likely due to post-depositional processes leading to compaction, or erosion by windblown sands (Stojanowski, 2013). Two meningeal grooves are visible on the endocranial vault surface of the left parietal. On the ectocranial surface, parietal striae are visible on the inferolateral extension of the left parietal and the superior temporal line is clearly demarcated. Enough of the coronal suture is preserved to allow for the estimation of bregma at the midline, but unlike the frontal, the left parietal is only preserved lateral to the midsagittal plane. As a result, the sagittal suture is not preserved. However, OH 83 appears to preserve a metopic suture remnant, a feature only seen in 1–10% of adult modern humans worldwide (Byers, 2005).

The OH 83 partial calvarium bears clear indications of post-mortem distortion. On the left lateral side of the calvarium a posterior portion of parietal overhangs the vault (see arrow in Figure 1), which is an obvious artifact of preservational distortion that does not reflect the biology of the individual during life. White (2003) provides a cautionary

tale that demonstrates post-mortem distortion in hominid fossils should be carefully considered. We interpret distortion in OH 83 as primarily affecting the cranial breadth dimension, but cannot rule out possible effects on other dimensions, such as the relatively long anteroposterior dimension of the preserved cranial vault in comparison to breadth.

OH 83 represents a mature adult, on the basis of overall cranial size and closure of the preserved coronal suture. The preservational state of OH 83 prohibits a confident estimation of sex for this individual. However, its small overall vault size and gracility of the preserved superstructures may indicate that it is female.

Although limited in number due to poor preservation, OH 83's traits are morphologically characteristic of AMHS. The frontal bone of OH 83 is characterized by a weakly developed torus with clear differentiation of its medial and lateral aspects, the frontal squama is high and vertically oriented, and bossed, and its weak glabellar prominence and broad upper face are all modern and expressed within the range of variation seen in living people. The cranial vault of OH 83 is modern in its long, generally globular form and overall morphology, aligning it with anatomically modern humans.

2 | MATERIALS AND METHODS

2.1 | Comparative samples

The fossil sample used for comparative analyses are crania from the Middle Pleistocene to the Early Holocene in Africa and the Levant, a spatio-temporal context that subsumes OH 83 (Table 1). Measurements for the fossils were taken from published literature, and when available, compared to physical measurements we collected from research quality casts at the Human Evolution Research Center at the University of California, Berkeley (Table 2).

The modern human samples used for comparative analyses are the archaeological and historic populations represented in the Howells craniometric dataset (1973; 1989; 1995; <http://web.utk.edu/~auerbach/HOWL.htm>). This dataset compiles cranial measurements of over 2500 adult individuals from 28 Late Holocene populations worldwide. For our comparative analyses, we parsed the total dataset into groups according to geographic region: Americas, Asia, Australasia, Europe, North Africa, Polynesia, and Sub-Saharan Africa (Table 3).

Sexual dimorphism almost certainly contributes to the range of variation in the comparative fossil sample. While sex may be estimated for some of the more complete fossils, it would be untenable to estimate sex for others and risk increasing potential error in the comparative analyses. Consequently, although the Howells dataset includes sex estimations for all individuals, the males and females were combined as a pooled sex sample of modern humans to mirror the fossil sample.

2.2 | Cranial measurements

Twenty-seven cranial fragments and three teeth were found in association with the main calvarial pieces of OH 83. While the main calvarial pieces and associated cranial fragments are similar in preservational

TABLE 1 List of comparative fossil material with estimated geological ages

Country	Specimen	Age	References
Ethiopia	Omo I, II ^a	195 kya	Day and Stringer, 1991; McDougall et al., 2005; Feibel, 2008
	Herto (BOU-VP/16-1)	160–154 kya	Clark et al., 2003; White et al., 2003
Kenya	Eliye Springs (ES-11693)	> 200 kya ^b	Bräuer and Leakey, 1986; Bräuer, 2008; Cieri et al., 2014
	LH 1	> 46 kya	Tryon et al., 2015
Egypt	Nazlet Khater 2	40–35 kya	Thoma, 1984; Pinhasi and Semal, 2000; Crevecoeur and Vilotte, 2006; Crevecoeur, 2008; Crevecoeur et al., 2009; Vermeersch, 2010
Nigeria	Iwo Eleru	ca. 11.7–16.3 kya	Harvati et al., 2011
Morocco	Dar es Soltane II	150–8 kya	Millard, 2008
	Jebel Iroud 1	190–90 kya	Grün and Stringer, 1991; Hublin, 1991; Smith et al., 2007
S. Africa	Border Cave 2	115–90 kya	Grün and Beaumont, 2001
	Fish Hoek	35 kya	Protsch, 1974
	Hofmeyr	36.2 ± 3.3 kya	Grine et al., 2007
	Florisbad	290–230 kya	Grün et al., 1996
	Saldanha	1 mya < 600 kya	Klein, Avery, Cruz-Urbe, and Steele, 2007
Sudan	Singa	145.5 ± 7.5 – 89 ± 9.3 kya	McDermott et al., 1996
Tanzania	LH 18	3–200 kya	Magori and Day, 1983; Manega, 1995
	Ndutu	400 kya	Manega, 1995
Zambia	Kabwe 1	4–300 kya ^b	Klein, 1999
Israel	Manot 1	54.7 ± 5.5 kya	Hershkovitz et al., 2015
	Skhul IV, V	135–100 kya	Grün et al., 2005
	Qafzeh 1,2,6,9	115–92 kya	Vandermeersch, 1981; Schwarcz et al., 1988; Valladas et al., 1988
	Zuttiyeh	5–200 kya	Huxtable, 1990; Mercier et al., 1995; Mercier and Valladas, 2003; Freidline et al., 2012

^aOmo I was recovered *in situ* during excavation. Omo II was found on the surface, its age is estimated on the basis of stratigraphic correlation with Omo I (Leakey, 1969; McDougall et al., 2005; Fleagle et al., 2008).

^bIndicates age is estimated due to absence of context for stratigraphic location of the fossil when discovered (Bräuer and Leakey, 1986; Woodward, 1921).

state, they do not conjoin (Figures 1 & 2). We focus our analysis here on the larger elements of the OH 83 calvaria.

2.2.1 | 3D laser scanning

Given OH 83's fragile state of preservation, we used a three-dimensional (3D) laser scanner to facilitate measurement (Kuzminsky & Gardiner, 2012). We created a digital 3D model of OH 83 using a NextEngine Desktop 3D laser scanner (NextEngine Inc., Santa Monica, CA) at the National Museum of Natural History, Arusha, Tanzania. The NextEngine scanner uses lasers and a camera to capture surface geometry and full-color photo data from the scanned object, which is then rendered and measurable as a digital 3D model. The scanner was set to the standard capture settings for larger objects, e.g., a human cranium (Sholts, Wärmländer, Flores, Miller, & Walker, 2010), with a geometric point resolution of 75 dots per inch (DPI) and 150 DPI color. The fossil was scanned multiple times at different angles. Following scanning, we

manually aligned the images via common points and removed overlapping meshes using ScanStudio PRO 1.6.3 software (NextEngine Inc. 2006–2008), and following data processing, the completed 3D model (Figure 4) was imported into RapidWorks 2.3.2 software (Rapidform, Sunnyvale, CA, 2006). Using digital tools to create geometric points and measure distances on 3D models, we placed points at craniometric landmarks and recorded the linear distances between them. To facilitate accurate point placement, high-resolution photographs of the specimen were used to identify sutures and topographic anatomy when they were not easily discernible, which is especially common in 3D laser scanned models of crania exhibiting deterioration or discoloration (Sholts, Flores, Walker, & Wärmländer, 2011).

2.2.2 | Data collection

We collected seven linear distance measurements from six craniometric landmarks preserved on OH 83 (Table 4). For each distance, one of

TABLE 2 Cranial measurements of the fossils used in comparative analyses

Specimens	STB	XFB	FRC	FMB
Border Cave 2	—	—	116.3 ^a	105.0 ^a
Dar es Soltane II	—	132.0 ^a	—	—
Eliye Springs ^b ES - 11693	105.0 ^c	118.0 ^c	116.5 ^c	—
Fish Hoek	121.6 ^a	105.0 ^d	122.9 ^a	103.0 ^a
Florisbad	—	137.0 ^e	117.0 ^e	130.0 ^f
Herto BOU-VP-16/1	96.0 ± 3.0 ^g	120.0 ± 5 ^g	124.8 ^a	130.0 ± 2 ^g
Hofmeyr	—	117.0 ^h	112.0 ^h	—
Iwo Eleru	112.0 ⁱ	115.0 ⁱ	114.0 ⁱ	111.0 ⁱ
Jebel Irhoud 1	113.0 ^j	120.0 ^k	109.5 ^a	116.0 ^a
Kabwe 1	111.0 ^a	118.0 ^a	120.5 ^a	127.0 ^f
LH 1	—	111.0 ^l	120.0 ^l	107.4 ^l
LH 18	92.2 ^f	112.7 ^a	115.7 ^a	105.0 ^f
Ndutu Lake	115.4 ^m	112.0 ⁿ	—	—
Nzalet Khater 2	—	122.0 ^h	116.0 ^h	—
Omo I	124.0 ⁱ	110.5 ^m	130.0 ⁱ	122.0 ⁱ
Omo II	117.1 ¹	120.0 ^a	124.3 ^f	—
Qafzeh 1	114.0 ^a	114.7 ^a	—	114.5 ^a
Qafzeh 2	110.5 ^a	98.7 ^a	113.7 ^a	—
Qafzeh 6	109.0 ^a	125.0 ^o	114.0 ^o	—
Qafzeh 9	112.7 ^f	117.0 ^o	115.0 ^o	—
Saldanha	—	112.0 ⁿ	116.0 ⁿ	117.0 ^p
Singa	—	105.0 ^q	—	—
Skhul IV	—	121.0 ^o	118.0 ^o	—
Skhul V	—	114.0 ^o	106.0 ^o	—
Zuttiyeh	106.9 ^a	109.0 ^a	110.0 ^a	—

All measurements in mm. “—” indicates that measurement could not be collected either because the specimen is incomplete or deformed in that region.

^aMeasurement collected by one of the authors (WBR) using research quality cast at HERC, University of California Berkeley.

^bSpecimen has a pathology that may affect its measurements (Bräuer et al., 2003).

^cBräuer & Leakey, 1986.

^dKeith, 1931.

^eDreyer, 1935.

^fMagori, 1980.

^gWhite et al., 2003.

^hCrevecoeur et al., 2009.

ⁱMeasurement in parentheses (Stringer, 1974).

^jStringer, 1974.

^kHublin, 1992.

^lTryon et al., 2015.

^mMeasurement collected by one of the authors (WBR) using research quality cast/reconstruction at HERC, University of California Berkeley.

ⁿRightmire, 2008.

^oVandermeersch, 1981.

^pSinger, 1954. Measurement includes a query.

^qWells, 1951.

us (W.B.R.) collected at least three repeated measurements based on iterations of point placement. Intraobserver error ranged between 0.5–4.9%. Due to the lack of preservation of the right side of the cranial vault, we relied on the bilateral symmetry of the skull for all breadth measurements requiring paired osteometric points. These measurements (BFM, FMB, STB, XFB, WFB) were calculated by measuring the distance from the preserved (left) paired cranio-metric point to the mid-sagittal plane, and doubling the result. The mid-sagittal plane was

TABLE 3 Regional divisions used for the Howells comparative modern human dataset (Howells, 1973; 1989; 1995)

Geographic Region	Population
Asia N = 665	Ainu
	Andaman
	Anyang
	Atayal
	Buriat
	Hainan
Americas N = 389	N. Japan
	Philippines
	S. Japan
Australasia N = 298	Arikara
	Eskimo
	Peru
Europe N = 317	Santa Cruz
	Australia
	Tasmania
North Africa N = 111	Tolai
	Berg
	Norse
Sub-Saharan Africa N = 373	Zalavar
	Egypt
	Bushman
Polynesia/ Micronesia N = 371	Dogon
	Teita
	Zulu
Total N = 2,524	Easter Island
	Guam
	S. Maori
	N. Maori
	Moriiori
	Mokapu



FIGURE 4 Image of three-dimensional scan depicting OH 83 in *norma frontalis*.

identified in the 3D model as corresponding with the midline of the metopic suture remnant. The frontal (nasion-bregma) chord was measured, although the location of nasion was estimated at the most inferior midline point on the frontal bone; however small, there is potential for error introduced by this estimation. Opisthocranium could not be estimated without significant potential error. In consequence, glabella-occipital length (GOL) was not included in the comparative analyses, but the anteroposterior length of the preserved remains was included in the morphological description. Eurion could not be located on the lateral portion of the parietal or the squama of the temporal bone, due to the poor preservation of OH 83, preventing a confident estimation of maximum cranial breadth (XCB). For this reason, XCB is also omitted from the comparative analyses. Instead, the maximum width of the left half of the cranial vault, measured from the lateral-most preserved part of the left side of the vault to the midline was included in the morphological description.

2.2.3 | Data validation

As the comparative datasets for the fossil and modern human samples are composed of direct measurements on the physical specimens with calipers rather than indirect measurements on digital 3D models, we performed a validation study to assess potential measurement error in the comparative analyses. Eleven modern human crania from the Phoebe A. Hearst Museum of Anthropology (PAHMA) were selected on the basis of preservation and measured by W.B.R. with calipers following Howells (1973) protocols and with digital 3D methods as outlined for OH 83 above (Supporting Information Table S1). Evaluations of measurement error comparing direct anthropometry and indirect

measurement of digital models produced by laser scanning and other 3D surface capture systems have indicated that 3D systems-based measurements are accurate and reliable for research and clinical use (Fourie, Damstra, Gerrits, & Ren, 2011). Following Fourie et al. (2011), we calculated average error (AE) and average percentage error (APE) for caliper and 3D-model based measurements (Supporting Information Table S2). Mean AE for all cranial measurements was 0.76 mm, and ranged from 0.18–1.44 mm. Mean APE was 0.69% and ranged from 0.1–1.7%. Mean error values were comparable to those reported by Fourie et al.'s (2011) measurements on laser scanner models for AE (0.89 mm) and APE (1.48%), indicating they are sufficiently reliable for use in our comparative analyses of OH 83.

2.2.4 | Quantitative comparisons

Descriptive statistics were calculated in RStudio (2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL <http://www.rstudio.com/>) and GGPlot2 (H. Wickham. ggplot2: Elegant Graphics for Data Springer-Verlag New York, 2009). We compared the four linear distances measurable on OH 83 that are also included in the Howells dataset (1973, 1989, 1995): Bifrontal breadth (FMB), bistephanic breadth (STB), frontal chord (FRC), and maximum frontal breadth (XFB). The Howells data and OH 83 are also compared to a sample of other fossil data from roughly penecontemporaneous sites across the Old World.

3 | RESULTS

3.1 | Morphological trait comparison

The Ndutu cranium (distinct from OH 83 from the Ndutu Bed at Olduvai Gorge) was found near Lake Ndutu less than 50 km from Olduvai Gorge. This cranium has an estimated age of ca. 600–300 ka (Clarke, 1976; Millard, 2008), securely placing it in the Middle Pleistocene. Both OH 83

TABLE 4 Measurements collected from three-dimensional scan of OH 83

Cranial measurement	Abbrev.	
Bistephanic breadth [†]	STB	90.71 ^a
Maximum frontal breadth [†]	XFB	95.58 ^a
Frontal chord [†]	FRC	114.94
Bifrontal breadth [†]	FMB	120.57 ^a
Upper facial breadth ^b	BFM	128.24 ^a
Minimum frontal breadth ^c	WFB	89.97 ^a
Glabella-bregma chord ^d	GBC	112.66

All measurements are in mm and each is used as defined by Howells (1973), except BFM, WFB, and GBC.

[†]Measurements used in our statistical analyses comparing OH 83 to fossil hominids and Holocene modern humans from the Howells dataset (1973, 1989).

^aMeasurement calculated from the preserved (left) paired craniometric point to the midline and multiplying that by two.

^bFollowing White et al., 2011.

^cFollowing Buikstra and Ubelaker, 1994.

^dMeasurement taken as the direct distance from glabella to bregma.

and the Ndutu crania are relatively small; estimated cranial capacity for the Ndutu cranium is 1,110 cm³ (Clarke, 1976). Due to the preservation of OH 83, further comparison on the cranial size of these two fossils is limited. Similar to other Middle Pleistocene hominid crania including Kabwe 1 (Woodward, 1921) and Herto (BOU-VP-16/1) (White et al., 2003), the Ndutu cranium (1990; Clarke, 1976) is more robust in the supraorbital and glabellar regions than OH 83, which is similarly gracile to the Omo I reconstruction (Day, 1969) and Eliye Springs. In comparison to the dimensions of the frontal squama of the Ndutu cranium (Clarke, 1976), Dar es Soltane II, and the preserved squama on Iwo Eleru (Harvati et al., 2011), the frontal squama of OH 83 is more vertical and thus more modern in its appearance. The frontal squama of Omo I (Day, 1969) and Zuttiyeh (Freidline, Gunz, Janković, Harvati, & Hublin, 2012) are also morphologically modern in this way, although less so than OH 83. The Skhul and Qafzeh hominid crania, for the most part, appear to have slightly higher, more modern frontal squama, but larger brow ridges than OH 83. The Saldanha specimen from South Africa exhibits a supraorbital region that is quite robust with an almost inflated appearance over the orbits, morphology which is not present on the relatively gracile supraorbital region of OH 83. The moderate angle of the parietals toward the sagittal suture and vertically-oriented lateral walls of the cranial vault expressed in the Manot 1 specimen from Israel (Hershkovitz et al., 2015), as well as the Skhul and Qafzeh hominids, are morphologies that are also expressed in OH 83.

Compared with Holocene populations of *H. sapiens*, OH 83 shows an overall pattern of modern human cranial morphology. OH 83 is gracile in almost all respects, and the slight glabellar prominence and slight rugosity of the supraorbital region are well within the expected range of variation for modern humans. While the cranial vault appears to be low and long relative to its breadth, this is an artifact of preservation and distortion due to post-depositional processes and is not representative of what the cranium looked like during its life.

3.2 | Craniometric comparison

Box plots showing the distribution of measurements, mean, and 95% confidence interval of the median for the modern human comparative sample, with OH 83 and the comparative fossil sample superimposed are shown in Figure 5. Mean and standard deviation values for the modern human sample by geographic region are reported in Appendix 1. For STB (90.71 mm) and XFB (95.58 mm), OH 83 falls at the lower end of the range compared to the fossil and modern data, and outside the 95% confidence interval. Two of the East African specimens, Herto and LH 18, also fall at the low end of the range for STB, but for XFB, OH 83 falls nearest Qafzeh 2 from Israel. For FMB (120.57 mm), OH 83 falls at the upper end of the range for modern humans. For FRC (114.94 mm), OH 83 fits well within the range for modern human variation, and is nested within the comparative fossil specimens.

4 | DISCUSSION AND CONCLUSIONS

The Middle and early-Late Pleistocene represents the transition between *H. erectus* and the earliest appearances of *H. sapiens* ca. 200

ka (Fu et al., 2013; Henshilwood & Marean, 2003; Magori, 1980; McBrearty & Brooks, 2000; McDougall, Brown, & Fleagle, 2005; Poznik et al., 2013; Rightmire, 2008; Scozzari et al., 2014; Trinkaus, 2005; White et al., 2003). Specimens from <200 ka tend to exhibit traits more similar to recent modern humans (Rightmire, 2009), such as the Herto crania (*H. s. idaltu*, dated to 160–154 ka). This specimen, while being robust, is more similar to the anatomically modern end of the *H. erectus*–*H. sapiens* spectrum with respect to its occipital flexion, anteriorly projecting supraorbital region, and parietal curvature (White et al., 2003).

There have been numerous attempts to biologically define *H. sapiens* (Day & Stringer, 1982; Lieberman, McBratney, & Krovitz, 2002; Stringer, Hublin, & Vandermeersch, 1984; Tattersall & Schwartz, 2008). Attempts to characterize morphological traits that define humans in the fossil record rely heavily on cranial anatomy (Day & Stringer, 1982; Stringer et al. 1984; Tattersall & Schwartz, 2008). These efforts have not met wide agreement by the scientific community due, in part, to the mosaic patterns of cranial variation represented by the fossils (Bräuer & Leakey, 1986; Lieberman et al., 2002) and the morphological heterogeneity present in living modern humans (Haile-Selassie et al., 2004; Howells, 1973, 1989; Lahr, 1996). The irregular, mosaic pattern of trait expression in the crania of Middle and Late Pleistocene fossils implies that morphological modernity did not occur at once (McBrearty & Brooks, 2000; Reed & Tishkoff, 2006; Trinkaus, 2005).

OH 83 adds to the current understanding of early modern humans by adding to the fossil record, and by expanding the dataset for Late Pleistocene hominid crania. The initial description we present here demonstrates that *Homo sapiens* in Africa exhibited morphologically modern cranial characters by 60–32 ka. But, that said, the metric data for OH 83 do not specifically cluster with the Africans sampled by Howells, 1973, 1989). The early fossils of *H. sapiens* demonstrate that the patterns of ancestry that characterize present-day human cranial variation were not present as of 160 ka (White et al., 2003). Perhaps these geographic clusters of cranial variation still had not coalesced by the time of OH 83, as this specimen does not cluster with the Africans sampled by Howells. However, the data available to adequately explore this possibility are quite limited due to the fragmentary nature of OH 83, and much further research on additional fossil material is needed to say anything more conclusive on this matter.

While we know that many aspects of the cranial vault bones are influenced by genetic effects (Sherwood & Duren, 2013; Sherwood et al., 2008, 2011; Susanne, 1977; Šešelj, Duren, & Sherwood, 2015), we still know very little about the genetic architecture that underlies the development of, or variation in, cranial features such as glabellar prominence or overall cranial vault shape (Boas, 1912, 1928; Kohn, 1991; Sherwood & Duren, 2013; Šešelj et al., 2015). Until we have a better grasp of the biological etiology of these morphologies, a cautious interpretation of the skeletal evidence is that the morphological variation of Middle and Late Pleistocene African hominid crania signifies population-level, rather than species-level differences.

Given the genetic evidence for small population sizes for the lineage ancestral to humans over the past million years, which is estimated

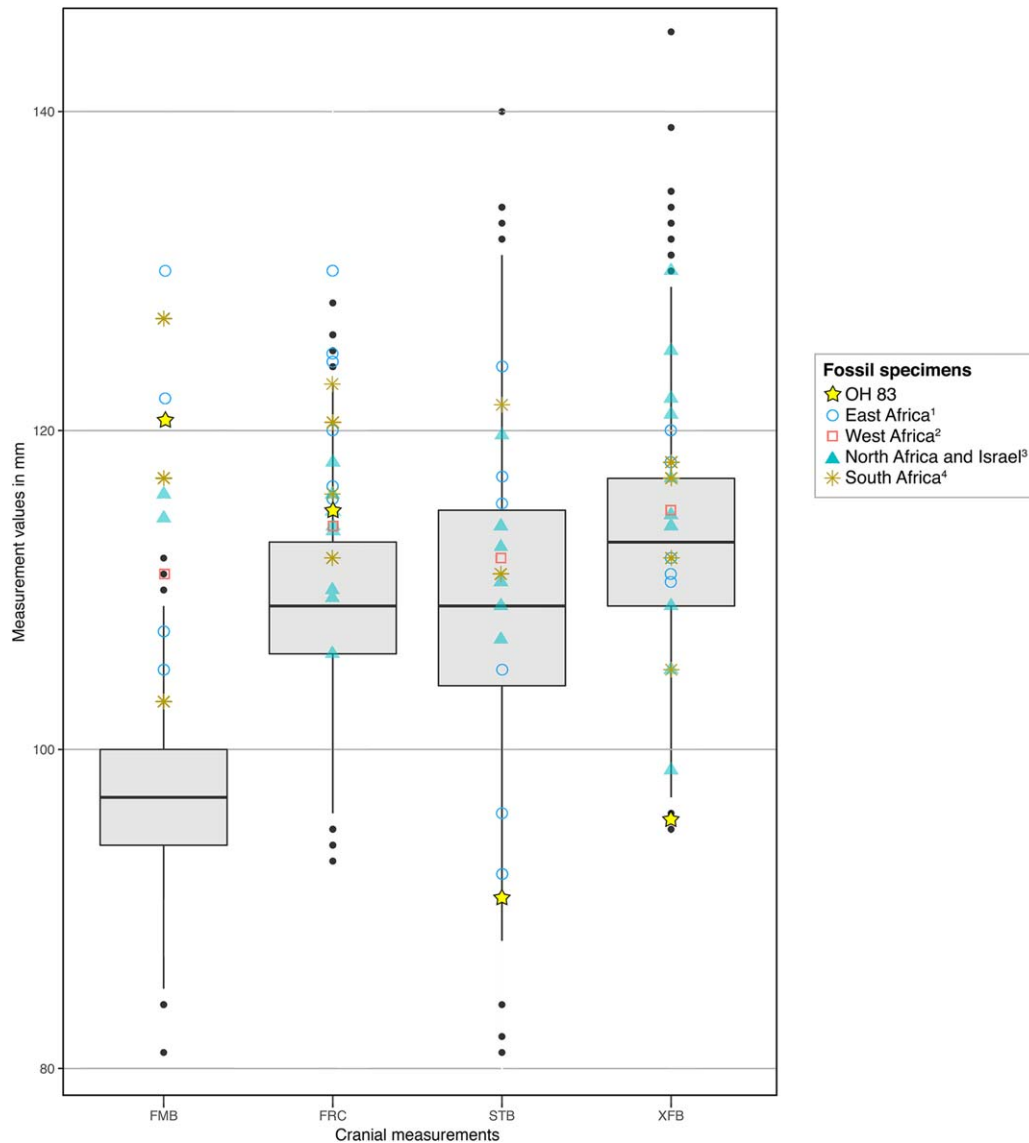


FIGURE 5 Box plots representing the range of modern human variation for four cranial measurements (see Appendix 1 for summary data). Box and whisker plots indicate 95% confidence limits of the distribution of Howells' data (1973, 1989, 1995) for four cranial measurements. Superimposed on these box plots are OH 83 and a sample of penecontemporaneous fossils (see Tables 1–3). All data are reported in mm. Shapes refer to the fossil specimens, the yellow stars refer to OH 83. Individual measurements are plotted for the comparative fossils, but specimens are depicted by shapes that refer to the fossil's geographic region: ¹Eastern Africa: Omo I and II, Herto, Eliye Springs, LH 1, LH 18, Ndutu Lake; ²Western Africa: Iwo Eleru; ³Northern Africa and Israel: Dar es Soltane II, Jebel Irhoud 1, Singa, Nazlet Khater 2, Skhul IV and V, Qafzeh 1, 2, 6, and 9, Zuttiyeh; ⁴Southern Africa: Kabwe 1, Border Cave 2, Fish Hoek, Hofmeyr, Florisbad, Saldanha. Individual specimen measurements are listed in Table 2

to have fluctuated between 40,000 to 100,000 individuals (Lahr & Foley, 1998; Rogers & Jorde, 1995; Sherry, Harpending, Batzer, & Stoneking, 1997; Takahata, Satta, & Klein, 1995), it is likely that the demography of African *Homo* fluctuated considerably. Some of the morphological variation at this time would be the result of adaptation to local environments, leading to morphological divergence between populations. However, Lahr and Foley (1998) note that this population structure also leads to variation that is not the result of genetic effects, or which is genetic in origin but not necessarily adaptive to the environment (i.e., genetic drift and gene flow). Because of its morphological

overlap with non-African humans (Figure 5), OH 83 provides support for this observation.

Our study demonstrates that morphologically and metrically, OH 83 falls within the range of variation observed in *Homo sapiens*. The metric data alone are less convincing than are the morphological data, but we reiterate that the crania shows clear evidence of taphonomic distortion and as such, standard linear metrics should not be considered in isolation. Our interpretation of the cranial morphology of OH 83 is that it should be placed taxonomically within anatomically modern humans. As is always the case in an historical science such as

paleoanthropology, only fieldwork and the discovery of more hominid remains will elucidate the transition from *H. erectus* to *H. sapiens*, and how population variation was patterned as our species evolved. For now, the discovery of OH 83 demonstrates that a fully anatomically modern human, indistinguishable from living people, died in northern Tanzania ca. 60–32 ka.

ACKNOWLEDGMENTS

This project would not have been possible without the support and assistance of: Dr. H. Mshinda, Director General, Commission for Science and Technology; Mr. J. Paresso and Mr. J. Temba, Tanzanian Department of Antiquities; Ms. V. Ufunguo, Ngorongoro Conservation Area Authority; Mrs. F. Mangalu, Director of the National Natural History Museum, Arusha; J. Njau; T. White, and the Human Evolution Research Center. We also acknowledge the collaboration of J. R. Southon, Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory, University of California, Irvine, and support from the Gabrielle R. Vierra Memorial Fund. Thanks to J. Hofmeister, M. Brasil, L. Chang, and T. Monson for assistance RStudio. Special thanks to colleagues in the Department of Integrative biology for their feedback: J. Carlson, M. Huffman, M. Yang, H. Kurkjian, and C. Jennings; and to J. Reed, A. Johnson, and W.P. Reiner for providing invaluable feedback and support. This article was greatly improved by comments from the associate editor and two anonymous reviewers. This research is based upon work supported by the National Science Foundation under Grant No. BCS 1025263 to L.J.H. and based upon work supported by the Palaeontological and Scientific Trust to H.S. and I.S. This material will be submitted as partial fulfillment of Reiner W.B.'s doctoral dissertation at the University of California Berkeley.

ORCID

Whitney B. Reiner  <http://orcid.org/0000-0003-3346-4808>

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Reiner WB, Masao F, Sholts SB, et al. OH 83: A new early modern human fossil cranium from the Nduu beds of Olduvai Gorge, Tanzania. *Am J Phys Anthropol*. 2017;164:533-545. <https://doi.org/10.1002/ajpa.23292>

APPENDIX : MEAN AND STANDARD DEVIATION OF CRANIAL MEASUREMENTS FOR MODERN SAMPLE

		Americas	Asia	Australasia	Europe	North Africa	Polynesia/Micronesia	Sub-Saharan Africa
Measurement	n =	389	665	298	317	111	371	373
STB	mean	106.28	111.75	101.97	116.47	111.41	108.69	108.14
	std dev	6.63	7.30	6.32	6.73	5.49	6.37	6.99
XFB	mean	112.39	115.36	108.76	118.74	113.51	112.43	111.16
	std dev	4.94	6.83	4.60	5.81	5.03	4.98	5.78
FRC	mean	108.51	109.47	107.59	109.84	110.11	113.25	108.18
	std dev	5.07	5.38	5.10	4.89	5.22	5.39	5.15
FMB	mean	96.08	96.02	99.46	96.92	93.97	98.08	97.45
	std dev	4.08	4.78	4.30	3.75	3.61	3.96	4.41

Craniometric data from Howells (1973, 1989, 1995).
 Mean in mm, rounded to the nearest hundredth.