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## The endocast morphology of LES1, *Homo naledi*

Shawn D. Hurst<sup>1</sup>, Ralph L. Holloway<sup>2</sup>, Antoine Balzeau<sup>3,4</sup>, Heather M. Garvin<sup>5,6</sup>, William B. Vanti<sup>7</sup>, Lee R. Berger<sup>6,8,9</sup>, and John Hawks<sup>6,10</sup>.

<sup>1</sup>Department of Biology, University of Indianapolis, Indianapolis, United States.

<sup>2</sup>Department of Anthropology, Columbia University, New York, United States.

<sup>3</sup>Département Homme et Environnement, Muséum National d'Histoire Naturelle, PaleoFED team, Paris, France.

<sup>4</sup>Department of African Zoology, Royal Museum for Central Africa, B-3080 Tervuren, Belgium

<sup>5</sup>Department of Anatomy, Des Moines University, Des Moines, United States

<sup>6</sup>Centre for the Exploration of the Deep Human Journey, University of Witwatersrand, Johannesburg South Africa.

<sup>7</sup>Science and Engineering Library, Columbia University, New York, United States.

<sup>8</sup>The National Geographic Society, Washington DC, United States

<sup>9</sup>The Carnegie Institution for Science, Washington D.C., United States

<sup>10</sup>Department of Anthropology, University of Wisconsin-Madison, Madison, United States.

\*Correspondence to: Shawn D. Hurst ([hursts@uindy.edu](mailto:hursts@uindy.edu))

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### Abstract

The evolutionary diversity across the genus *Homo* encompasses variation in brain size and overall brain shape. *Homo naledi*, from the Rising Star cave system of South Africa, is near the extreme of small brain size within *Homo* but is easily recognized as *Homo* in other aspects of endocast morphology. Previous work on the endocast of *H. naledi* has focused on cranial fossils from the Dinaledi Chamber. Here we add evidence of the endocast morphology of *Homo naledi* with the LES1 cranium from the Lesedi Chamber. This is the most complete representation of endocranial morphology yet known for *H. naledi* and confirms the anatomical form from more fragmentary material from the Dinaledi Chamber. Global endocast measurements show a posteriorly wide shape in *H. naledi* relative to endocranial volume. Qualitative description and metric comparisons show that LES1 and the DH3 endocast have derived morphology relative to chimpanzees and australopiths of the posterolateral frontal lobe and posterior occipital/parietal region. These traits are shared with *Homo sapiens* and endocasts of later *Homo erectus* and Neandertals. The orbital cap morphology may reflect a common ancestry of *H. naledi* with these groups, or parallelism between this smaller-brained lineage and species with larger brain sizes.

**Keywords:** Human evolution, brain, endocast, paleoneurology, *Homo naledi*

### 1. INTRODUCTION

Anthropologists long considered large brain size to be a defining feature of our genus (Leakey, Tobias, & Napier, 1964; Wood & Collard 1999; Garvin et al. 2017). Working with a less complete fossil record, researchers often interpreted the pattern of Pleistocene evolution of brain size as a gradual, geometric, or stepped increase over time, whether within a single evolving lineage (Lee & Wolpoff 2003) or across several taxa (Leigh 1992; Du et al. 2018). The discovery of Middle and Late Pleistocene species of *Homo* with absolutely and relatively small brain volumes, including *Homo naledi* and *Homo floresiensis*, has shown a greater diversity of brain size in extinct *Homo*. Analyses of endocasts have shown that despite their small brain sizes, *H. naledi* and *H. floresiensis* shared aspects of brain structure with *Homo sapiens* and some fossils of *Homo erectus* (Falk et al. 2005; Holloway et al., 2018). These findings suggested that brain structure, rather than brain size, may have been important to the initial evolution and diversification of *Homo* (Holloway et al., 2018).

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4 However, recent work has questioned this hypothesis by suggesting that the samples of early *H. erectus* from  
5 Dmanisi and the Turkana Basin have apelike frontal lobe organizations, while later samples of *H. erectus*  
6 include significant heterogeneity in this anatomical region (Ponce de León et al. 2021). They do this by  
7 implying that the position of the superior precentral sulcus relative to the coronal suture is predictive of the position  
8 of the inferior precentral sulcus relative to the orbital cap. This prediction does not hold. The entirety of the  
9 precentral sulcus is visible on DH3 and the inferior precentral sulcus is found posterior to the orbital cap as is seen  
10 in *Homo sapiens* rather than crossing the orbital cap as is seen in *Pan* (see Fig. 3 and especially Fig. S5 in  
11 Holloway et al. 2018). Here we provide further evidence that changes in brain structure were independent of  
12 changes in brain size during the initial evolution of *Homo* using diverse species including *Homo naledi*.

13  
14 We reconstructed and analyzed the endocast of the LES1 skeleton, from the Lesedi Chamber of the Rising  
15 Star cave system (Hawks et al. 2017). This skeleton is the most complete *H. naledi* individual yet described,  
16 with facial, mandibular, and vault morphology matching those of the Dinaledi Chamber sample (Hawks et al.  
17 2017, Berger et al. 2015). We examined the original fossil material and high-resolution three-dimensional (3D)  
18 surface models of the LES1 cranial remains to reconstruct the preserved portions of its endocast. This more  
19 complete specimen enabled us to test the anatomical conclusions previously obtained from the fragmentary  
20 endocasts of *H. naledi* from the Dinaledi Chamber (Holloway et al., 2018). With this additional data, we carried  
21 out metric analyses to compare *H. naledi* with a broad sample of recent humans (*H. sapiens*), chimpanzees  
22 (*P. troglodytes*), and fossil hominins. This work provides new quantitative data on the endocranial form of *H.*  
23 *naledi* in relation to fossil and extant hominins.

## 24 25 **2. MATERIALS AND METHODS**

26  
27 The *Homo naledi* sample comprises DH1, DH3 and DH4 as well as LES1. The fossil hominin comparative  
28 sample includes *A. africanus* (Sts 5, Sts 71, Sts 60), *Paranthropus robustus* (SK1585), *Paranthropus boisei*  
29 (KNM-WT 13750, 17000, OH 5, OMO 338), *H. habilis sensu lato* (KNM-ER 1805, 1813, OH 13 and 16), *H.*  
30 *floresiensis* (LB1), *H. erectus sensu lato* (KNM-WT 15000, KNM-ER 3733, 3883, OH 9, OH 12,  
31 Sambungmacan 3, Ngandong 7, 12, Ngawi, Sangiran 2, Zhoukoudian 3, 10, 12), *H. heidelbergensis* (Bodo,  
32 Broken Hill), *H. neanderthalensis* (La Chapelle-aux-Saints, Guattari, Saccopastore 1, Feldhofer, Reilingen,  
33 Krapina 3, Spy 2, Abri Pataud, and Cro-Magnon 1). Fossil specimens were included in this comparative  
34 sample that include the same anatomical area preserved in LES1. In addition, we included data from 45  
35 recent *H. sapiens*, 16 *P. paniscus*, and 15 *P. troglodytes* individuals (Balzeau & Gilissen 2010). All analyses  
36 were performed on endocast models obtained from surface scanning, CT, or microCT modalities as described  
37 in previous work (Holloway et al., 2018; Balzeau, Gilissen, Holloway, Prima, & Grimaud-Herve 2014; Balzeau  
38 & Gilissen 2010).

39  
40 Fragments comprising the LES1 cranial vault were scanned at the University of the Witwatersrand on a Nikon  
41 Metrology XTH 225/320 microtomography (microCT) scanner. Surface models of the ectocranial and  
42 endocranial surfaces were obtained from LES1 using a NextEngine 3D Scanner after physical reconstruction  
43 of the vault. Model processing was completed in Geomagic Wrap, with model lighting and curvature maps  
44 used to assist in evaluating endocast features. We created several physical models including 3D prints of the  
45 virtual endocast, a Smooth-On Equinox silicone cast made by S.H. from the interior surface of a 3D print of  
46 the skull reconstruction, and a Denstply Aquasil LV silicone cast made by R.H. from the interior of a 3D print  
47 made by W.V. from the virtual skull reconstruction by H.G. Endocast images presented in this manuscript are  
48 derived from the microCT models; both the microCT, surface scan, and physical models were reviewed for all  
49 qualitative descriptions. Sulci determination was made independently by three of us (SH, RLH and AB),  
50 followed by group discussions. Those features presented in this paper are limited to those in which there was a  
51 consensus on the features we could reasonably observe. Agreement on features between observers is  
52 particularly important given the qualitative nature of sulci identification and the reliance on subtle imprints in  
53 interpreting brain morphology.

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4 For metric analyses we selected anatomical landmarks that represent the preserved anatomical area of the *H.*  
5 *naledi* endocasts. Landmarks included the frontal pole (PF), the most lateral extension of the orbital cap (B;  
6 Balzeau et al. 2014), the temporal pole (TP), the point of maximal endocranial width (W), the temporo-  
7 cerebellar junction (TC), the point where the central sulci meet at their uppermost extension (C), the occipital  
8 pole (O), and endinion (E; Balzeau, Grimaud-Herve, & Gilissen 2011). Landmarks were positioned on each  
9 3D model with Avizo 7 software by a single observer (AB) and then recollected three months later to assess  
10 interobserver error. Intraobserver variation between those two trials was minimal (Figure S1), further  
11 confirmed by visual inspection.

12 We calculated all pairwise interlandmark distances, with mean,  $N$  and corrected coefficient of variation  $V^*$  for  
13 each taxon (Table S1, Supplementary File 1).  $V^*$  is a correction for small sample size bias in the estimate of  
14 CV, calculated as  $(1 + 1/4N) \times CV$ , where  $CV = SD/mean$ , both expressed in percentages (Sokal & Braumann  
15 1980; Wood & Lieberman 2001). Measurements were examined both in absolute scale and relative to the  
16 cube root endocranial volume of each individual specimen. Statistical procedures were conducted with PAST  
17 4.03 software (Hammer, Harper, & Ryan 2001).  
18

19 In addition to these landmarks, we used the protocol and data from a previous study on the third frontal  
20 convolution (Balzeau et al. 2014) to compare the size and shape of this anatomical area in DH3 and LES1 of  
21 *H. naledi* with our comparative dataset (Balzeau et al. 2014; Mounier, Noûs, & Balzeau 2020). In this protocol,  
22 three anatomical points delimit the third frontal convolution, characterizing its antero-posterior extension and  
23 its lateral extension relative to this length. These points are: the center of the relief corresponding to the orbital  
24 part of the third frontal convolution, located on the relief between the lateral orbital sulcus anteriorly and the  
25 horizontal ramus of the lateral fissure posteriorly; the second point occurs in the maximal curvature of the  
26 triangular part of the third frontal convolution that characterizes the lateral extension and bulging of the orbital  
27 cap; the third point was the upper aspect of the Sylvian valley between the opercular part of the third frontal  
28 convolution and the temporal lobe.  
29

30 We examined interlandmark distances with both univariate and multivariate methods. For each distance we  
31 compared groups using adjusted z-scores (Azs) (Scolan, Santos, Tillier, Maureille, & Quintard 2012), in which  
32 95% of the variation of the reference population is included between  $-1$  and  $+1$ . An Azs lower than  $-1$  or  
33 higher than  $+1$  is, therefore, outside 95% of the variation of the reference population. Our multivariate  
34 analyses included both principal component analyses (PCA) and linear discriminant analyses (LDA). Each of  
35 these was applied to absolute interlandmark distances and distances relative to the cube root endocranial  
36 volume of each specimen. In our LDA analyses we assigned most of our comparative sample to species  
37 groups, except for pooling *Australopithecus* and *Paranthropus*. Five fossil individuals were treated as  
38 unknowns with no *a priori* group assignments: the two *H. naledi* specimens (DH3 and LES1), the two *H.*  
39 *habilis* endocasts (KNM-ER 1813 and KNM-ER 1805) and LB1, holotype of *H. floresiensis*.  
40

### 41 3. RESULTS

42 **3.1 Preservation.** The largest contiguous endocast surface of LES1 represents most of the left frontal,  
43 parietal, and temporal lobes, the superolateral aspect of the right frontal lobe, a portion of the left occipital  
44 lobe, a portion of the right parietal lobe, and the leftmost part of the cerebellum (Figure 1). Both left and right  
45 frontal poles are present on this preserved surface. Posteriorly, the preserved portion of the occipital bone  
46 does not extend to the midline. The endocranial surface is additionally represented on non-contiguous  
47 fragments of the right parietal, right temporal, and occipital. The cranial base of LES1 is not preserved, aside  
48 from a portion of the left lateral orbitofrontal, the basioccipital portion of the occipital bone, and fragments of  
49 left and right petrosals. On the contiguous endocast surface, there are four notable missing portions of 10-20  
50 mm dimensions on the left endocast surface of the posterior frontal lobe, the temporal lobe, and the parietal  
51 lobe. Small cracks are visible across the reconstructed endocast surface representing junctions between  
52 cranial fragments. These cracks are mostly obvious interruptions of an otherwise smooth endocast surface.  
53 The bone fragments that constitute the vault exhibit no crushing, matrix expansion, or plastic distortion (Hawks  
54 et al. 2017, de Ruiter et al. 2019), and the preserved endocast surface appears to be free of any large-scale  
55 deformation. The external markings associated with the posterior portion of *M. temporalis* exhibit asymmetry  
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4 between the left and right temporal bones, possibly associated with pathology of the right suprameatal region  
5 (Hawks et al. 2017; de Ruiter et al. 2019) but we do not note any obvious signs of pathology on the endocast  
6 surface.

7  
8 **3.2 Qualitative description.** More of the left orbital surface is present on LES1 than on any of the Dinaledi  
9 endocrania. The lateral part of the left middle orbital gyrus and the anterior part of the left posterior orbital  
10 gyrus as well as the entire left anterior and lateral orbital gyri are present. There is no evidence of a fronto-  
11 orbital sulcus incising the orbital margin. The frontal pole of the right hemisphere is slightly rostral in position to  
12 that of the left hemisphere, reflective of a right frontal petalia (Figures 1, S2-S3). The left lateral fissure with  
13 lateral (Sylvian) notch is present and ascending and horizontal rami of the lateral fissure are visible (Figure 1).  
14 The major frontal sulci incise the orbital margin at positions similar to modern human endocasts but grow  
15 fainter posteriorly (Figure 1). In contrast to the orbital surface, the dorsolateral surface of the anterior endocast  
16 has little detail. Portions of the precentral and central sulci are present (Figure 1).

17  
18 The posterior endocast has little detail (Figures 1, S2). The sigmoid sinus is about 17.5 mm posterior to the  
19 foramen spinosum and middle meningeal artery. The sinus ends about 20 mm inferiorly. The upper part of the  
20 sigmoid sinus leads into a slightly elevated transverse sinus approximately 3 mm thick, and which terminates  
21 approximately 10 mm anterior to the mid-sagittal plane. The anatomy does not make clear whether the flow  
22 from the longitudinal sulcus was to the left or right side. The lateral part of the cerebellar lobe is rounded and  
23 full, and the greater horizontal cerebellar sulcus is visible extending from mid-sigmoid sinus to the inferior  
24 portion of the lateral sinus. Roughly 35 mm from the sigmoid sinus is the inferior portion of the remnant of the  
25 lambdoid suture, which is slightly visible for about 28 mm before ending in the broken portion of the parietal  
26 lobe. While very dim, it does appear in the expected area under the remnant, partially absorbed lambdoid  
27 suture seen on the ectocranium. Roughly 20 mm posterior to the lower limb of the suture is a faint groove,  
28 concave medially, which we believe is an outline of the left occipital pole, which is roughly 15 mm anterior to  
29 the mid-sagittal plane.

30  
31 There is a deformity of the sigmoid sinus where it appears that the most inferior portion of the sigmoid sinus  
32 has been displaced medially. At the posterior extension of this inferior part of the sinus there is a hole on the  
33 endocranial surface that corresponds to the course of a diploic vein. A meningeal vein also continues  
34 posteriorly in this area in the continuation of the sinus. The sinus was possibly doubled, with the inferior one  
35 covering the sinus in the expected position, while the posterior extension has not been marked on the  
36 endocranial surface, possibly because it continued inside the brain. We regard the small crescentic groove as  
37 part of the occipital lobe just lateral to where the true occipital pole would be. There is no evidence for an  
38 inferior parietal sulcus on either side of the parietal lobe.

39  
40 **3.3 Metric analyses.** Our metric analyses add new information about the *H. naledi* endocasts in comparison  
41 with the broader sample of fossil and recent material. The most interesting findings concern the quantitative  
42 assessment of the third frontal convolution. This anatomical area is well defined on both DH3 and LES1.  
43 Across all samples, variation ( $V^*$ ) is similar in extent for the measurements of this region (Table 1). However,  
44 the absolute and relative dimensions for this anatomical area are different among hominid groups. Despite  
45 their small endocranial volumes, the two *H. naledi* specimens, DH3 and LES1, each have absolute third  
46 frontal convolution measures that enter the upper half of the variation for *H. sapiens*, *H. erectus*, and *H.*  
47 *neanderthalensis*. When examined relative to the cube root of endocranial volume, *H. naledi* ranks among the  
48 highest values in these samples of *Homo*. Both absolute and relative values for the *H. naledi* specimens are  
49 far above *Pan*, *Australopithecus*, and *Paranthropus* (Balzeau et al. 2014).

50  
51 Global interlandmark distances reflect the small size of LES1 and other *H. naledi* endocasts. Absolute  
52 measures of *H. naledi* overlap the range of variation of *Au. africanus*, *Paranthropus*, and *H. habilis* (Table S1).  
53 These absolute measures tend to be significantly smaller than *H. sapiens* and larger than *Pan* (Table S3).  
54 When interlandmark distances are considered relative to cube root endocranial volume (Table S2), *H. naledi*  
55 endocasts are relatively larger than both *H. sapiens* and *Pan* for distances from frontal pole to the endocast's  
56 maximum width and the frontal pole to the temporo-cerebellar junction (Table S4). Both these measures  
57 suggest a wide endocast relative to volume, particularly posteriorly (Table S1, S2, Supplementary File 1).  
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4 The first two components of the principal component analysis (PCA) computed on the absolute interlandmark  
5 distances represent respectively 86.4% and 5.9% of the total variance (Figures S4-S5). Loadings of all the  
6 variables are positive in PC1 which is strongly related to endocranial volume; PC2 encompasses mostly  
7 within-species variation seen across the broad sample. To explore the extent of shape differentiation of  
8 groups, we conducted linear discriminant analysis (LDA) on the same absolute data (Figures 2, S6). LDA  
9 provided good separation of groups with similar brain sizes and did separate the *H. naledi* endocasts from *H.*  
10 *habilis* and *Australopithecus*, but size was the largest contributor to group separation. To examine variation in  
11 shape relative to endocranial size, we computed a relative LDA with interlandmark distances scaled to cube  
12 root endocranial volume (Figure S7). This analysis also produced good separation of *H. sapiens*, *Pan*,  
13 *Australopithecus-Paranthropus* and *H. erectus*, while Neandertals overlap with *H. sapiens* and *H. erectus*.  
14 This analysis separated the two *H. habilis* endocasts from both *Australopithecus-Paranthropus* and *Pan*. As in  
15 the absolute LDA, LB1 of *H. floresiensis* clusters with *Pan*. LES1 plots in an area of extensive overlap  
16 between species, near Abri Pataud (*H. sapiens*), Bodo (Middle Pleistocene human), Ngandong 7 (*H. erectus*)  
17 and one *P. paniscus* individual, although this relative LDA does distinguish it clearly from *Australopithecus*  
18 and *Paranthropus*.  
19

20 In sum, *H. naledi* generally resembles other hominins with small brain size in absolute measurements. Where  
21 it is more distinctive is in its low but posteriorly located maximal width and long distance to the junction of the  
22 frontal and parietal lobes, particularly when scaled by cube root endocranial volume. The *H. naledi* endocasts  
23 contrast metrically from other hominins with small brain size in the orbital cap, which is comparable in absolute  
24 and relative size to species of *Homo* with much larger brain sizes. This portion of the LES1 endocast is similar  
25 to that in the smaller DH3, and the variation between these two is comparable to variation observed in other  
26 species of hominins.  
27

#### 28 4. DISCUSSION

29

30 The anatomy of LES1 confirms the size and form of the orbital cap in *H. naledi*. Some have suggested that the  
31 morphology of the orbital cap is not reliably assessed in an endocast (Ponce de León et al. 2021). The  
32 discovery of LES1 enabled us to test this assertion for *H. naledi* with a new endocast not included in our  
33 previous examinations from the Dinaledi Chamber. Both qualitative and quantitative analyses show  
34 consistency between LES1 and other *H. naledi* endocasts, show that *H. naledi* had a level of variation in this  
35 region comparable to that seen in extant species, and confirm the shared morphology of *H. naledi* with *H.*  
36 *sapiens*, Neandertals, and some specimens of *H. erectus*. This shared morphology across lineages that  
37 otherwise differ in size and global endocast shape suggests that this frontal lobe morphology retained  
38 adaptive value across lineages with varied ecologies, body sizes, and life histories. It has been suggested that  
39 the functions of this brain area in communication (Balzeau et al. 2014; Schoenemann & Holloway 2016),  
40 social and emotional cognition (Kringelbach & Rolls 2004), and possibly tool manufacture (Stout, Toth,  
41 Schick, & Chaminade 2008; Putt, Wijeakumar, Franciscus, & Spencer 2017) may have been important to the  
42 origin and evolution of *Homo*.

43 A broad array of work shows that different lineages within *Homo* exhibited diverse evolutionary patterns in  
44 endocast shape and size. The early evolution of *H. sapiens* involved shape changes to the endocast, but little  
45 increase in brain size (Hublin et al. 2017). The evolution of *H. neanderthalensis* from earlier to later samples  
46 involved endocast shape changes together with an increase in endocranial volume (Poza-Rey, Gomez-  
47 Robles, & Arsuaga 2019). *Homo erectus* increased in brain size across its long existence, and comparisons of  
48 endocast shape between early African and later Asian samples of *H. erectus s.l.* (sometimes distinguished as  
49 two species, *H. ergaster* and *H. erectus*) show contrasts between these regional samples (Pearson, Polly, &  
50 Bruner 2021).  
51

52 With this growing evidence of evolutionary diversity in brain shape across *Homo*, lineages with smaller brain  
53 sizes, like *H. naledi*, *H. habilis*, and *H. floresiensis*, are of great interest. At present, only a handful of  
54 endocasts representing these lineages are complete enough to consider global aspects of endocast shape. It  
55 is not clear whether *H. floresiensis*, *H. naledi*, or both may have evolved from ancestors with larger brain size.  
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4 The endocast shape of LB1 (*H. floresiensis*), while sharing some aspects of endocast shape with *H. erectus*,  
5 occupies a very distinctive place in shape space compared to either *H. erectus* or other hominins (Falk et al.  
6 2005); although some have suggested that pathology may play a role in the morphology of this individual  
7 (Holloway 2010). Neubauer and colleagues (Neubauer, Hublin, & Gunz 2018) included KNM-ER 1813 (*H.*  
8 *habilis*) and KNM-ER 1470 (*H. rudolfensis*) in a morphometric analysis of endocranial shape in *H. erectus*,  
9 finding that these two endocasts each are distinct from *H. erectus* and *H. sapiens* in different shape  
10 dimensions. In our present study, we find that the lateral and posterior cranial shape of *H. naledi* sets it apart  
11 from *H. habilis* although the two species overlap in size.

12 The LES1 endocast adds to the evidence that *H. naledi* had a relatively and absolutely large orbital cap with  
13 morphology similar to *Homo* species that have larger brain sizes (Holloway et al., 2018). The current study of  
14 *H. naledi* material does not address whether this morphology is shared with early fossils of *H. erectus*  
15 including the Dmanisi sample, which have been suggested to differ from later *H. erectus* and *H. sapiens*  
16 based on the position of the superior precentral sulcus relative to the coronal suture (Ponce de León et al.  
17 2021); however this condition does not appear to be predictive of orbital cap morphology (Holloway et al.  
18 2018). Previous work suggested that some early African and Indonesian representatives of *H. erectus* had  
19 smaller orbital cap areas than later *H. erectus* (Balzeau et al. 2014), and the current study places *H. naledi*  
20 among the larger *H. erectus* and *Homo sapiens* samples—in contrast to *H. floresiensis* and *H. habilis*  
21 endocasts. It is possible that this morphology links *H. naledi* with later *H. erectus* and *H. sapiens*, consistent  
22 with the hypothesis that these may share a common ancestor in the later Early Pleistocene (Dembo et al.  
23 2016). Alternatively, orbital cap morphology may exhibit significant parallelism between these lineages.  
24 Testing these alternatives would benefit from closer morphological assessment of this region in hominins that  
25 have been underrepresented in studies of complete endocasts.

#### 26 **AUTHOR CONTRIBUTIONS:**

27  
28 SH performed research, analyzed data, presented the research at conference, helped write the paper, and  
29 did manuscript editing. RH did fossil reconstruction, performed research, analyzed data, and did manuscript  
30 editing; AB designed research, performed research, analyzed data, helped write the paper, and did  
31 manuscript editing; HM created 3D scans, did fossil reconstruction, analyzed data, and did manuscript  
32 editing; WV generated 3D prints of endocasts; LB designed research, led excavation and research, created  
33 3D scans, analyzed data, and did manuscript editing; JH designed research, led excavation and research,  
34 analyzed data, helped write the paper, and did manuscript editing.  
35

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37  
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42

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## Figure and Table Legends

### Figure 1.

LES1 (*Homo naledi*) virtual endocast illustrated in (A) left lateral; (B) superior; and (C) rostral views. Ideograms of the cranial vault illustrate each angle. (D) Left lateral view with sulci and fissures drawn for illustration: 1. Superior frontal sulcus; 2. middle frontal sulcus; 3. inferior frontal sulcus; 4. ascending ramus of the lateral fissure; 5. horizontal branch; 6. precentral sulcus; 7. central sulcus; 8. lateral fissure; 9. transverse fissure; 10. inferior portion of sigmoid sinus. (E) Oblique detail view of the LES1 left orbital cap, unlabeled (left) and labeled (right) 1. Horizontal branch; 2. ascending ramus of the lateral fissure.

### Figure 2.

Results of linear discriminant analyses (LDA). (A) LDA based on absolute interlandmark distances. In this analysis, axis 1 is strongly correlated with endocranial volume, while axis 2 correlates with endocast height relative to length, attaining separation of modern and Neandertal crania (left) and *H. naledi* from *H. habilis* and *Australopithecus-Paranthropus* (right). (B) LDA based on interlandmark distances relative to cube root endocranial volume. In these results, *H. naledi* is not clearly separated from *H. erectus* or *P. paniscus*, and LES1 falls in an area of extensive overlap of *H. sapiens*, *H. erectus*, and *P. paniscus*. Individuals near LES1 in this comparison are Abri Pataud (*H. sapiens*), Ngandong 7 (*H. erectus*), Bodo (Middle Pleistocene human) and two *P. paniscus* individuals.

### Figure 3.

Bivariate plot of the size of the third frontal convolution (square root, noted 3Fc, in mm) and of the endocranial volume (cube root, noted Endo V, in mm) in *Pan paniscus* (triangles), *Pan troglodytes* (inverted triangles), *H. sapiens* (circles), fossil *H. sapiens* (black circles), fossil hominins (black diamonds: T: Taung, 17k: KNM-WT 17000, 1470: KNM-ER 1470, 1813: KNM-ER 1813, 3733: KNMER 3733, 3883: KNM-ER 3883, 15k: KNM-WT 15000, OH 9, D: Dmanisi 9002, T2: Trinil 2, S2: Sangiran 2, S17: Sangiran 17, M: Mojokerto, Ng7: Ngandong 7, Ng12: Ngandong 12, Sm3: Sambungmacan 3, S3: Zhoukoudian Ckn. E 1.PA.16, S12: Zhoukoudian Ckn. L 2.PA.100, LB 1: Liang Bua 1, SV: Skhūl V, Ar: Arago, B: Bodo, K: Kabwe 1, JB1: Jebel Irhoud 1, P: Petralona, S: Salé) and Neandertals (red circle, F: Feldhofer, LC: La Chapelle-aux-Saints 1, LF1: La Ferrassie 1, Gu: Guattari, Gi: Gibraltar, K3: Krapina 3, Q5: La Quina H5, Sa: Saccopastore, TC1: Tabun C1, TT: Teshik Tash, SII: Spy 10 modified from Mounier and al., 2020). The green circle refers to the two analysed *Homo naledi* specimens.

### Table 1.

Measurements of the third frontal convolution (mean values for HF3: height of the 3rd frontal convolution, LF3: length of the 3rd frontal convolution both are in mm, SF3: surface of the 3rd frontal convolution in mm<sup>2</sup>, HF3r and LF3r are dimensions for HF3 and LF3 relative to cube root endocranial volume; *N*: number of individuals *V*\*: coefficient of variation corrected for small samples) in the different analyzed samples. See also Supplemental File 1.

### Supplementary Figure S1.

Landmarks used in metric analyses. PF= Frontal pole; B= most lateral extension of the orbital (Broca's) cap; TP= Temporal pole, W=Point of maximal endocranial width; TC= Temporo-cerebellar junction, C= Point where the central sulci meet at their uppermost extension; O= Occipital pole; E= Endinion.

### Supplementary Figure S2.

Preservation of LES1 endocast compared to individuals from the Dinaledi Chamber. LES1 (top left) preserves nearly all the left side of the endocast except for the extremely posterior portion of the occipital lobe and cerebellum. It also preserves some portions of the right parietal lobe and most of the right frontal lobe contiguous with the left side. DH3 (top right) preserves left frontal, left temporal, and left parietal portions with a portion of the left cerebellum but none of the right

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4 side. DH1 (middle right) preserves the posterior endocranial surface and portions of both parietal  
5 lobes on two different preserved portions of the cranium. DH2 (middle left, shown here reversed)  
6 preserves portions of both parietal lobes, right temporal, and right occipital portions. DH4 (bottom  
7 left, shown here reversed) preserves portions of right cerebellar, occipital, temporal, and parietal  
8 lobes. DH3 has the best gyral and sulcal detail, with LES1 approaching this level of detail in  
9 selected portions.

#### 10 **Supplementary Figure S3.**

11 LES1 silicone endocast physical model in left lateral (top) and basal (bottom) views. This model  
12 uses comparative data to build the basicranial anatomy. The measured volume of this  
13 reconstruction is 590cc, smaller than the digital reconstruction which had a volume of 610cc  
14 (Holloway et al., 2018). 1, Meningeal vessel; 2, lambdoid suture; 3, small sulcus of occipital lobe and  
15 pole; 4, sigmoid sinus; 5, interior portion of sigmoid sinus, displaced; 6, greater cerebellar horizontal  
16 sulcus.

#### 17 **Supplementary Figure S4.**

18 Results of principal components analysis (PCA) based on interlandmark distances. PC1 accounts  
19 for 86.4% of the variance and has positive weights on all underlying interlandmark distances.  
20 The rank order of fossil hominins on this axis is basically in order of endocranial volume. PC2  
21 accounts for 5.9% of the variance and appears to show a degree of within-group variation in each  
22 sample.  
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#### 24 **Supplementary Figure S5.**

25 Results of principal components analysis (PCA) based on interlandmark distances relative to  
26 cube root endocranial volume. In this analysis, PC1 still appears correlated with endocranial size,  
27 although with length relative to height reflected in this dimension.  
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#### 29 **Supplementary Figure S6.**

30 Results of linear discriminant analysis (LDA) based on absolute interlandmark distances. These  
31 results are also reported in main text Figure 2, here provided with all fossil hominin individuals  
32 labeled. Axis 1 is strongly correlated with endocranial volume, while axis 2 separates samples  
33 based on dimensions associated with endocast length relative to height. *H. naledi* in this analysis  
34 is well discriminated from other samples of similar endocranial volume, including *H. habilis*,  
35 *Australopithecus-Paranthropus*, and *H. erectus*.

#### 36 **Supplementary Figure S7.**

37 Results of linear discriminant analysis (LDA) based on interlandmark distances relative to cube  
38 root endocranial volume. These results are also reported in main text Figure 2, here provided with  
39 all fossil hominin individuals labeled.  
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#### 41 **Table S1.**

42 Data for endocranial measurements between pairs of points (mean value in mm, N: number of  
43 individuals, V\*: coefficient of variation corrected for small samples) in the different analyzed  
44 samples. PF= frontal pole; B= most lateral extension of the orbital (Broca's) cap; TP= Temporal  
45 pole, W=Point of maximal endocranial width; TC= Temporo-cerebellar junction, C= Point where  
46 the central sulci meet at their uppermost extension; O= Occipital pole; E= Endinion. See also  
47 Supplemental Excel file.  
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#### 49 **Table S2.**

50 Data for *relative* endocranial measurements between pairs of points (N:  
51 number of individuals, V\*: coefficient of variation corrected for small samples) in the different  
52 analyzed samples. PF= frontal pole; B= most lateral extension of the orbital (Broca's) cap; TP=  
53 Temporal pole, W=Point of maximal endocranial width; TC= Temporo-cerebellar junction, C=  
54 Point where the central sulci meet at their uppermost extension; O= Occipital pole; E= Endinion.  
55 See also Supplemental Excel file. "r" indicates these are relative measurements. See also  
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4 Supplemental Excel file.  
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6 **Table S3.**

7 Data for endocranial measurements between pairs of points (mean value in mm) individual values for  
8 the different *H. naledi* fossils and Azs scores relative to the comparative samples. PF= frontal pole;  
9 B= most lateral extension of the orbital (Broca's) cap; TP= Temporal pole, W=Point of maximal  
10 endocranial width; TC= Temporo-cerebellar junction, C= Point where the central sulci meet at their  
11 uppermost extension; O= Occipital pole; E= Endinion. See also Supplemental Excel file.  
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13 **Table S4.**

14 Data for relative endocranial measurements between pairs of points individual values for the different  
15 *H. naledi* fossils and Azs scores relative to the comparative samples. PF= frontal pole; B= most  
16 lateral extension of the orbital (Broca's) cap; TP= Temporal pole, W=Point of maximal endocranial  
17 width; TC= Temporo-cerebellar junction, C= Point where the central sulci meet at their uppermost  
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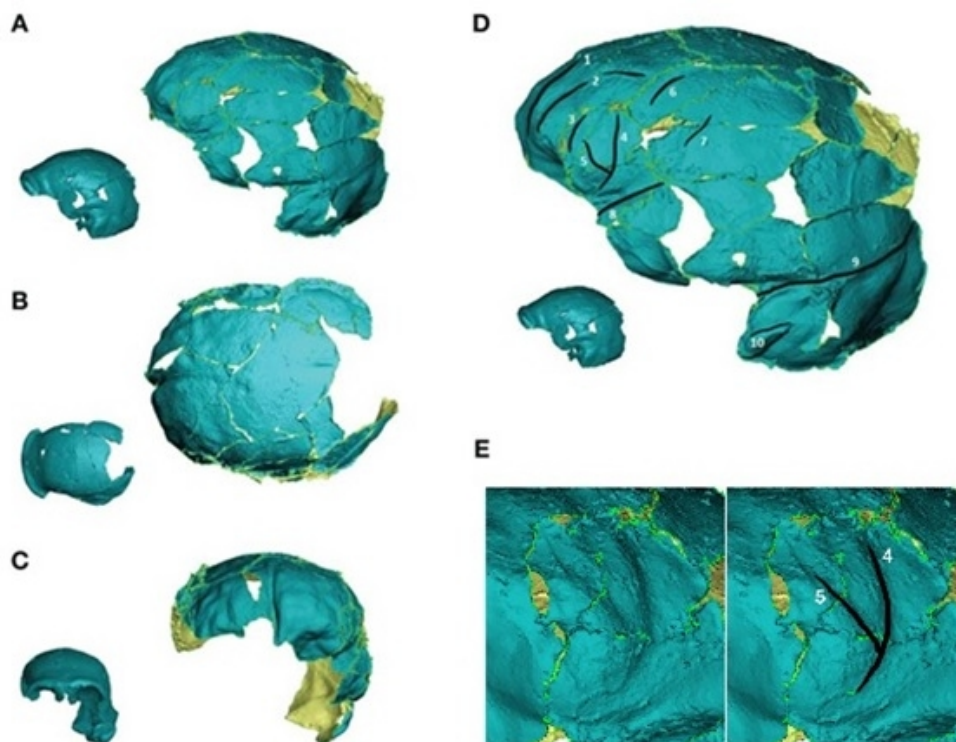


Figure 1.

LES1 (*Homo naledi*) virtual endocast illustrated in (A) left lateral; (B) superior; and (C) rostral views. Ideograms of the cranial vault illustrate each angle. (D) Left lateral view with sulci and fissures drawn for illustration: 1. Superior frontal sulcus; 2. middle frontal sulcus; 3. inferior frontal sulcus; 4. ascending ramus of the lateral fissure; 5. horizontal branch; 6. precentral sulcus; 7. central sulcus; 8. lateral fissure; 9. transverse fissure; 10. inferior portion of sigmoid sinus. (E) Oblique detail view of the LES1 left orbital cap, unlabeled (left) and labeled (right) 1. Horizontal branch; 2. ascending ramus of the lateral fissure.

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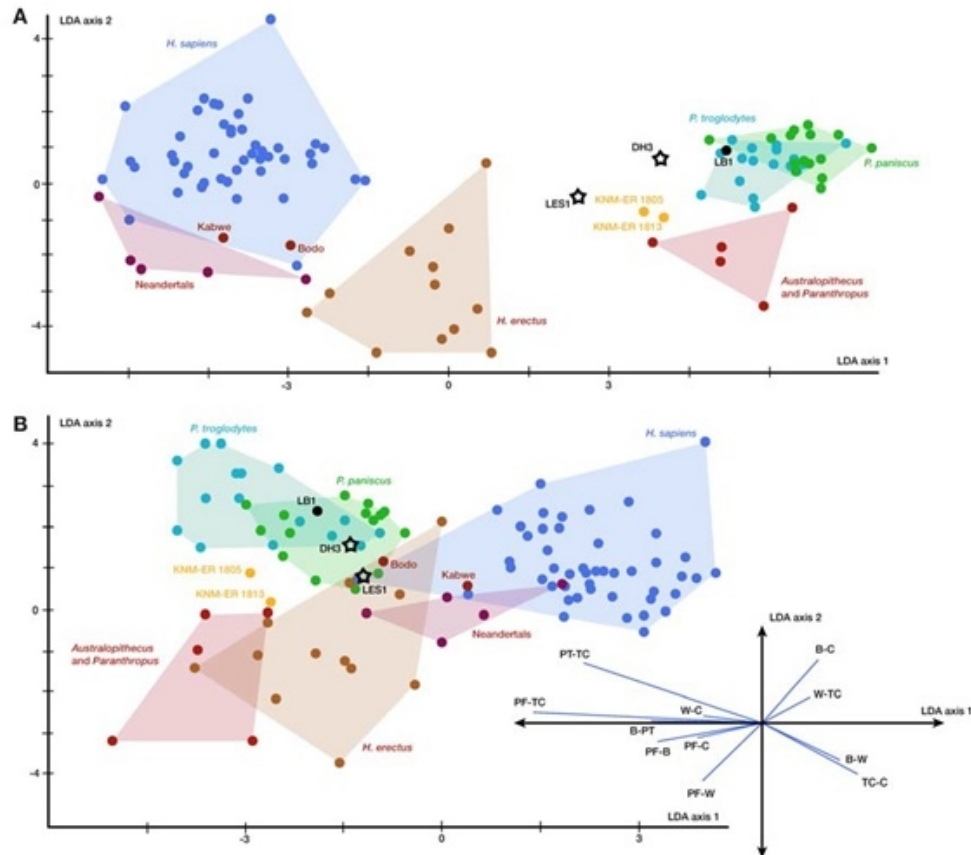


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Results of linear discriminant analyses (LDA). (A) LDA based on absolute interlandmark distances. In this analysis, axis 1 is strongly correlated with endocranial volume, while axis 2 correlates with endocranial height relative to length, attaining separation of modern and Neandertal crania (left) and *H. naledi* from *H. habilis* and *Australopithecus-Paranthropus* (right). (B) LDA based on interlandmark distances relative to cube root endocranial volume. In these results, *H. naledi* is not clearly separated from *H. erectus* or *P. paniscus*, and LES1 falls in an area of extensive overlap of *H. sapiens*, *H. erectus*, and *P. paniscus*. Individuals near LES1 in this comparison are Abri Pataud (*H. sapiens*), Ngandong 7 (*H. erectus*), Bodo (Middle Pleistocene human) and two *P. paniscus* individuals.

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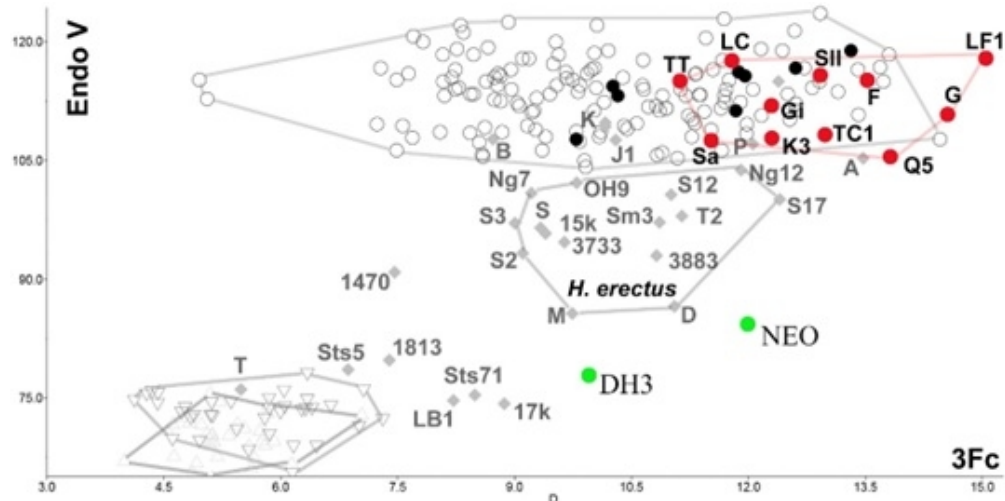
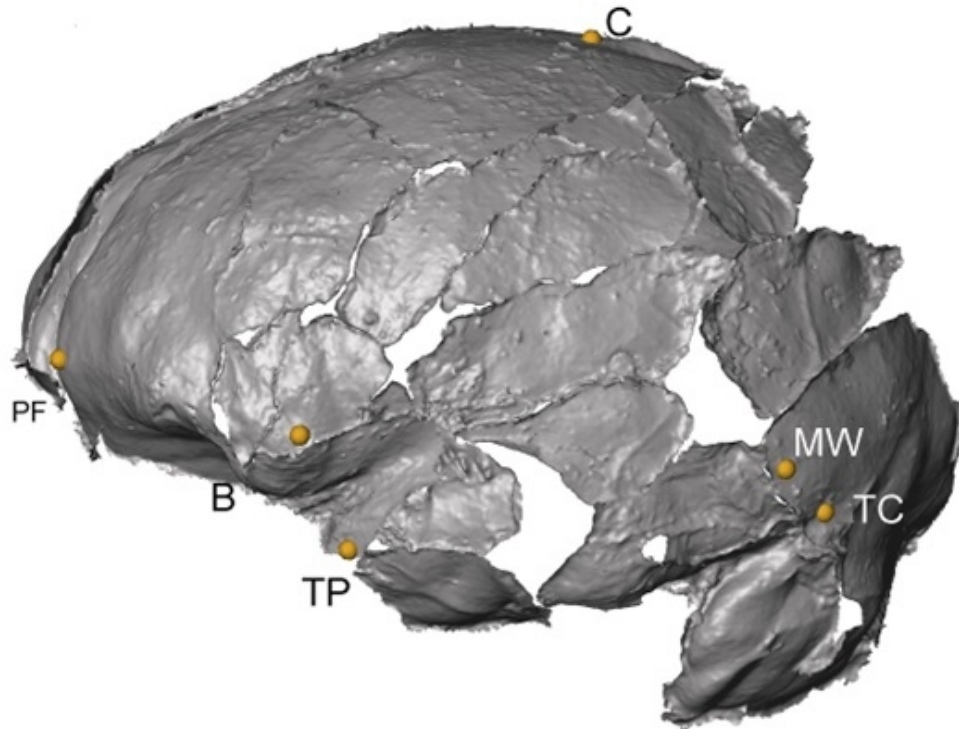


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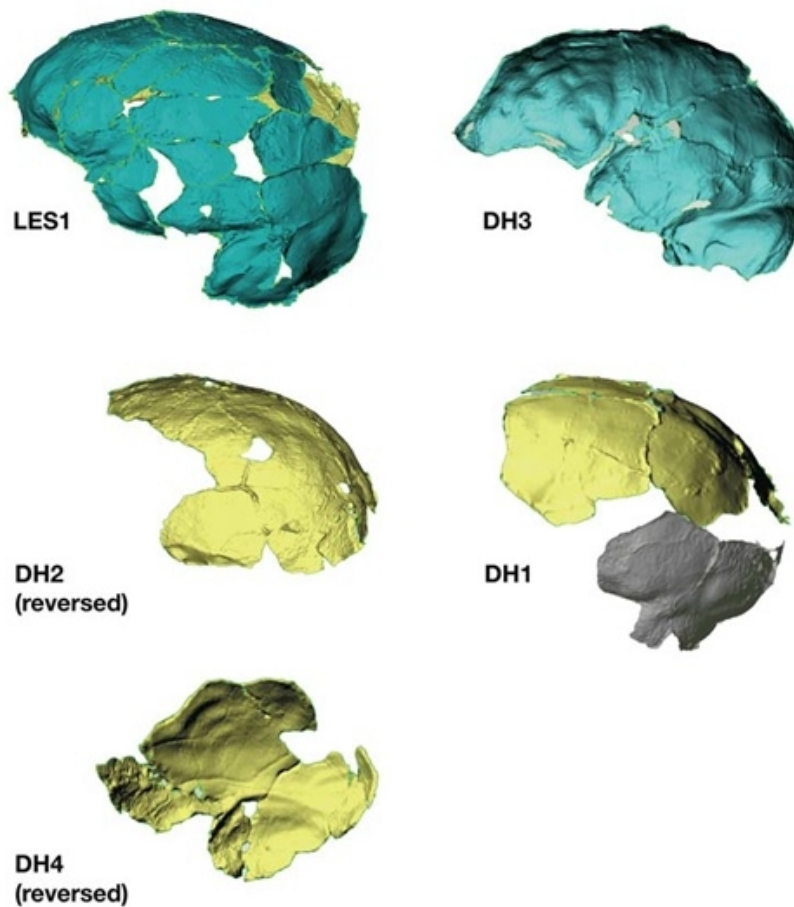
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Landmarks used in metric analyses. PF= Frontal pole; B= most lateral extension of the orbital (Broca's) cap; TP= Temporal pole, W=Point of maximal endocranial width; TC= Temporo-cerebellar junction, C= Point where the central sulci meet at their uppermost extension; O= Occipital pole; E= Endinion.

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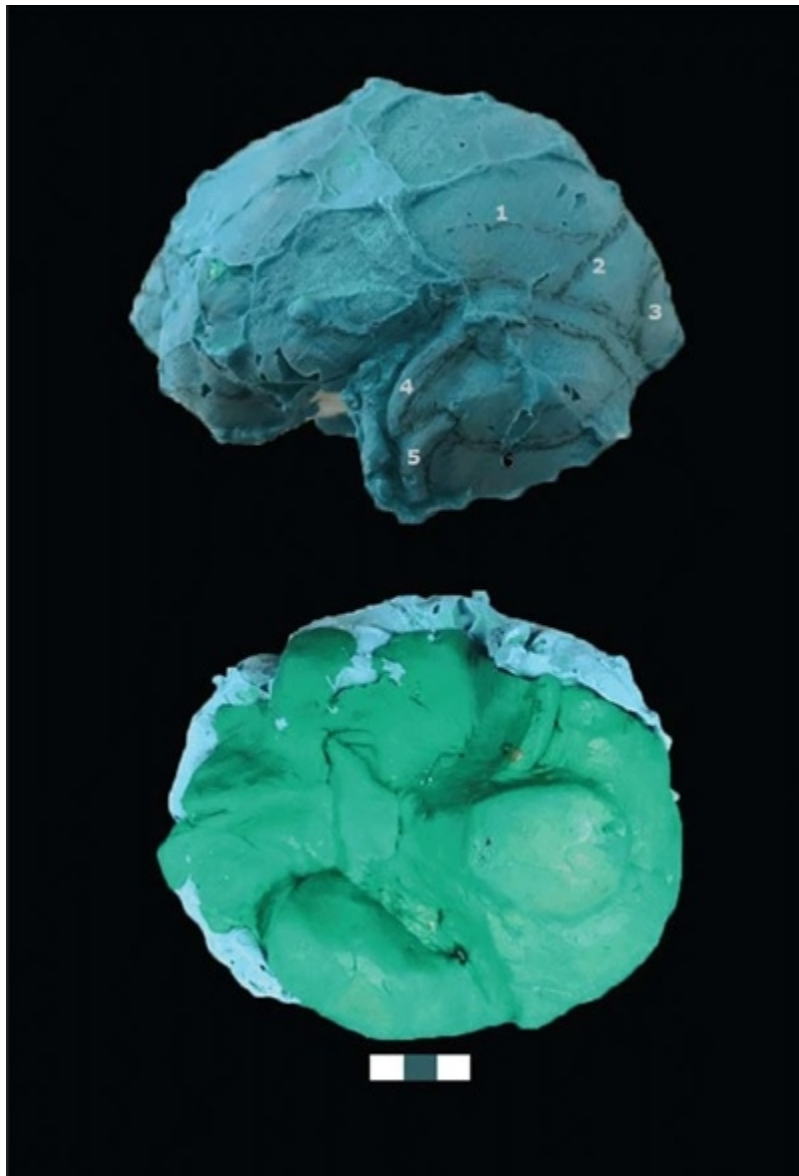




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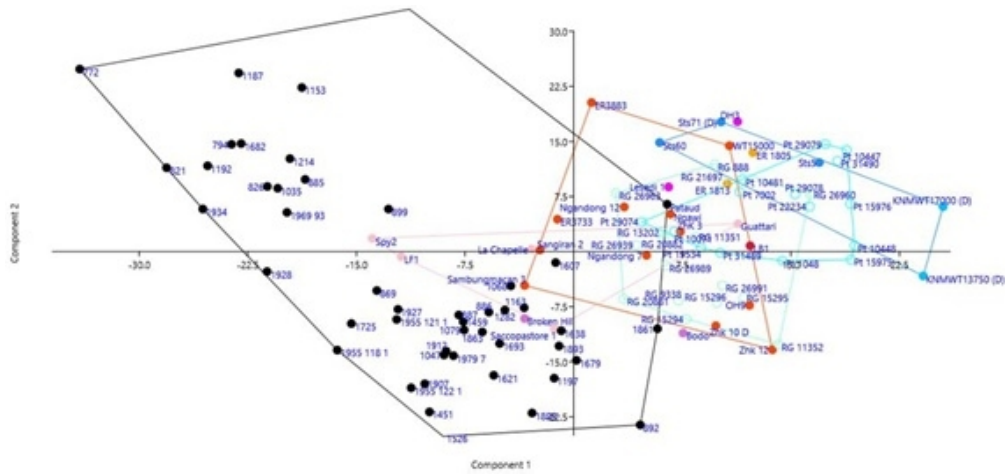


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LES1 silicone endocast physical model in left lateral (top) and basal (bottom) views. This model uses comparative data to build the basicranial anatomy. The measured volume of this reconstruction is 590cc, smaller than the digital reconstruction which had a volume of 610cc (Holloway et al., 2018). 1, Meningeal vessel; 2, lambdoid suture; 3, small sulcus of occipital lobe and pole; 4, sigmoid sinus; 5, interior portion of sigmoid sinus, displaced; 6, greater cerebellar horizontal sulcus.

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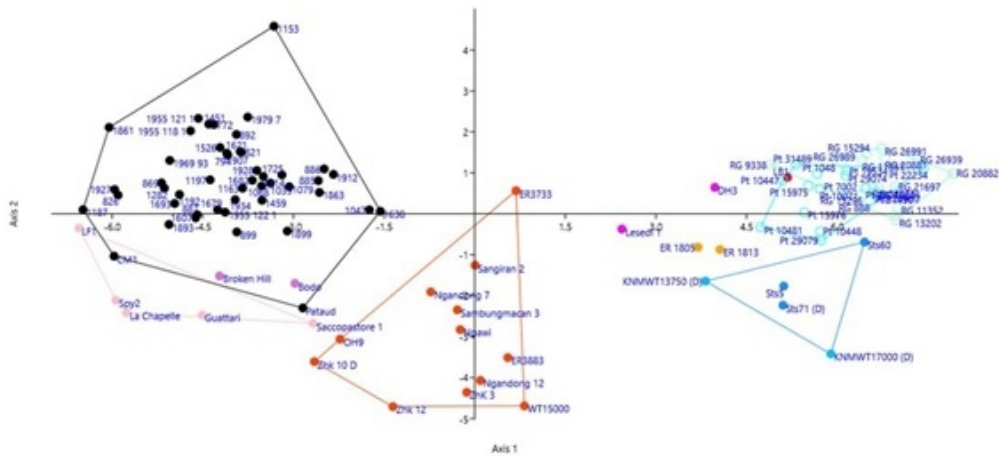




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Results of principal components analysis (PCA) based on interlandmark distances relative to cube root endocranial volume. In this analysis, PC1 still appears correlated with endocranial size, although with length relative to height reflected in this dimension.

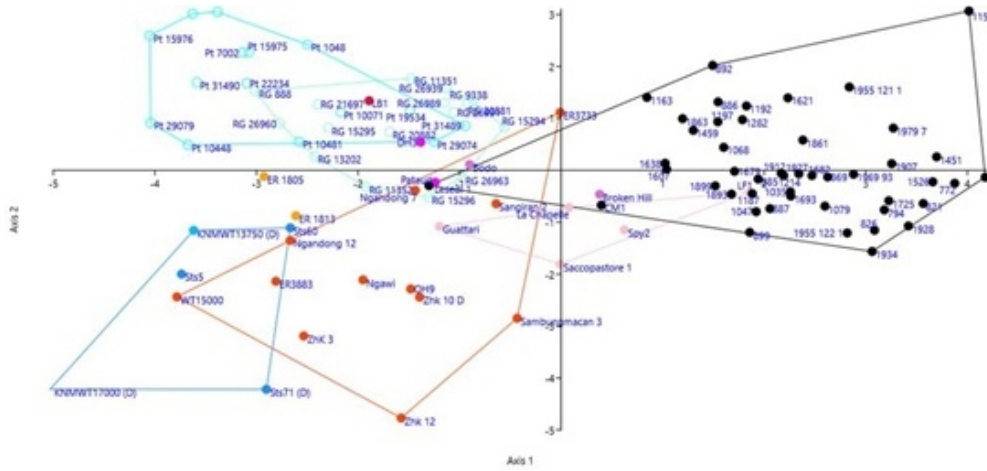
150x70mm (96 x 96 DPI)



Supplementary Figure S6.

Results of linear discriminant analysis (LDA) based on absolute interlandmark distances. These results are also reported in main text Figure 2, here provided with all fossil hominin individuals labeled. Axis 1 is strongly correlated with endocranial volume, while axis 2 separates samples based on dimensions associated with endocranial length relative to height. *H. naledi* in this analysis is well discriminated from other samples of similar endocranial volume, including *H. habilis*, *Australopithecus-Paranthropus*, and *H. erectus*.

148x67mm (96 x 96 DPI)



Supplementary Figure S7.  
Results of linear discriminant analysis (LDA) based on interlandmark distances relative to cube root endocranial volume. These results are also reported in main text Figure 2, here provided with all fossil hominin individuals labeled.

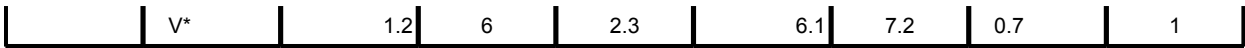
144x67mm (96 x 96 DPI)

|                            |      | HF3  | LF3  | SF3   | HF3r | LF3r |
|----------------------------|------|------|------|-------|------|------|
| <i>H. naledi</i>           | mean | 6.5  | 36.8 | 120.6 | 8    | 45.5 |
|                            | N    | 2    | 2    | 2     | 2    | 2    |
|                            | V*   | 17.5 | 13.6 | 30.8  | 10.8 | 6.9  |
| <i>H. sapiens</i>          | mean | 5.6  | 36.7 | 105.7 | 5    | 32.4 |
|                            | N    | 139  | 139  | 139   | 139  | 139  |
|                            | V*   | 26.1 | 12   | 34.2  | 26.2 | 12.8 |
| <i>P. paniscus</i>         | mean | 2.4  | 23.6 | 29.1  | 3.5  | 33.6 |
|                            | N    | 35   | 35   | 35    | 35   | 35   |
|                            | V*   | 20.7 | 9.2  | 24.3  | 20.7 | 8.5  |
| <i>P. troglodytes</i>      | mean | 2.9  | 22   | 32.2  | 4    | 30.2 |
|                            | N    | 36   | 36   | 36    | 36   | 36   |
|                            | V*   | 25   | 9.3  | 30.3  | 26   | 9.2  |
| <i>H. erectus</i>          | mean | 6.4  | 34.7 | 111.3 | 6.6  | 35.7 |
|                            | N    | 12   | 12   | 12    | 12   | 12   |
|                            | V*   | 26.7 | 20.1 | 41    | 26.1 | 13.7 |
| <i>H. neanderthalensis</i> | mean | 7.5  | 35.2 | 167.7 | 6.7  | 31.2 |
|                            | N    | 11   | 11   | 11    | 11   | 11   |
|                            | V*   | 27.9 | 34   | 19.9  | 26   | 32.1 |

|                            |    | PF<br>-B | PF<br>-C | PF<br>-W | PF- TC | B- TP | B- W | B- C |
|----------------------------|----|----------|----------|----------|--------|-------|------|------|
|                            | me | 38       | 79       | 94       | 104    | 19    | 62   | 76   |
| <b>H. naledi</b>           | an | 6        | 2        | 5        | 0.7    | 5     | 0.9  | 8    |
|                            | N  | 2        | 2        | 2        | 2      | 2     | 2    | 2    |
|                            | V* | 14       | 10       |          |        |       | 4    |      |
|                            |    | 4        | 1        | 7.2      | 4.9    | 8.8   | 3    | 9.9  |
|                            | me | 50       | 11       | 11       | 123    | 24    | 71   | 10   |
| <b>H. sapiens</b>          | an | 5        | 0.1      | 3.3      | 0      | 6     | 0.8  | 7    |
|                            | N  | 45       | 45       | 45       | 45     | 45    | 45   | 45   |
|                            | V* |          |          |          |        | 25    | 15   |      |
|                            |    | 7        | 6.4      | 6.9      | 5      | 2     | 0.5  | 5.9  |
|                            | me | 34       | 68       | 72       | 86     | 20    | 41   | 63   |
| <b>P. paniscus</b>         | an | 9        | 2        | 6        | 7      | 5     | 0.7  | 8    |
|                            | N  | 16       | 16       | 16       | 16     | 16    | 16   | 16   |
|                            | V* |          |          |          |        | 13    | 12   |      |
|                            |    | 8.7      | 6.7      | 5.6      | 4.8    | 4     | 0.8  | 6    |
|                            | me | 38       | 76       | 77       | 93     | 21    | 43   | 70   |
| <b>P. troglodytes</b>      | an | 6        | 0        | 4        | 0      | 8     | 0.3  | 5    |
|                            | N  | 15       | 15       | 15       | 15     | 15    | 15   | 15   |
|                            | V* |          |          |          |        | 12    | 12   |      |
|                            |    | 7.3      | 6.2      | 7.4      | 5      | 7     | 0.1  | 5.3  |
|                            | me | 50       | 10       | 10       | 119    | 28    | 62   | 91   |
| <b>H. erectus</b>          | an | 9        | 3.8      | 7.5      | 0.9    | 2     | 0.4  | 3    |
|                            | N  | 12       | 12       | 12       | 12     | 12    | 12   | 12   |
|                            | V* | 11       |          |          |        | 14    | 11   |      |
|                            |    | 6        | 7.1      | 4.5      | 4.4    | 7     | 0.3  | 6.4  |
|                            | me | 54       | 11       | 12       | 131    | 31    | 75   | 10   |
| <b>H. neanderthalensis</b> | an | 8        | 2        | 3.3      | 0.5    | 1     | 0.5  | 4.1  |
|                            | N  | 7        | 6        | 7        | 6      | 6     | 7    | 6    |
|                            | V* |          |          |          |        | 15    | 10   |      |
|                            |    | 6.5      | 6.6      | 6.1      | 5.9    | 4     | 0.2  | 7.7  |
|                            | me | 43       | 80       | 92       | 108    | 19    | 56   | 72   |
| <b>H. habilis</b>          | an | 1        | 7        | 9        | 0.8    | 1     | 0    | 1    |
|                            | N  | 3        | 2        | 3        | 2      | 2     | 3    | 2    |
|                            | V* |          |          |          |        | 18    | 18   |      |
|                            |    | 3.3      | 0        | 5.9      | 5.1    | 7     | 0    | 0.3  |
|                            | me | 40       | 76       | 82       | 99     | 23    | 47   | 64   |
| <b>Au. africanus</b>       | an | 8        | 1        | 9        | 5      | 8     | 0.1  | 3    |
|                            | N  | 3        | 3        | 3        | 3      | 3     | 3    | 3    |
|                            | V* | 13       |          |          |        | 14    | 10   |      |
|                            |    | 7        | 7.7      | 1.5      | 5.9    | 0     | 0.2  | 4.7  |
|                            | me | 45       | 72       | 82       | 104    | 20    | 46   | 66   |
| <b>Paranthropus</b>        | an | 6        | 1        | 6        | 0.4    | 8     | 0.2  | 2    |
|                            | N  | 2        | 2        | 3        | 3      | 3     | 3    | 3    |
|                            | V* |          | 10       |          |        |       | 24   | 11   |



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| TP- TC | TC<br>-C | W- TC | W<br>-C | W<br>-E | C- O | TC<br>-O | E- O | W<br>-O |
|--------|----------|-------|---------|---------|------|----------|------|---------|
| 67     | 81       | 19    | 74      | 65      | 87   | 46       | 18   | 62      |
| 3      | 8        | 4     | 0.8     | 0       | 7    | 8        | 0    | 0.8     |
| 2      | 3        | 4     | 3       | 2       | 1    | 2        | 2    | 2       |
|        |          | 15    | 4       | 0       |      |          | 14   | 6       |
| 4.4    | 3.6      | 9     | 9       | 0       |      | 2.3      | 0.3  | 0       |
| 73     | 11       | 37    | 92      | 91      | 10   | 75       | 26   | 90      |
| 9      | 1.3      | 4     | 0.3     | 0.9     | 7.3  | 2        | 0.1  | 0.5     |
| 45     | 45       | 45    | 45      | 45      | 45   | 45       | 45   | 45      |
|        |          | 31    | 10      | 6       |      |          | 15   | 6       |
| 7.9    | 5.2      | 6     | 0.9     | 4       | 6.2  | 8.4      | 0    | 4       |
| 54     | 66       | 20    | 60      | 59      | 63   | 39       | 14   | 55      |
| 4      | 1        | 6     | 0.9     | 0.4     | 0    | 9        | 0.8  | 0.7     |
| 16     | 16       | 16    | 16      | 16      | 16   | 16       | 16   | 16      |
|        |          | 21    | 5       | 6       |      |          | 14   | 8       |
| 7.2    | 4.9      | 9     | 6       | 5       | 6.6  | 7.4      | 0.6  | 7       |
| 59     | 66       | 23    | 63      | 62      | 57   | 41       | 13   | 58      |
| 3      | 5        | 0     | 0.7     | 0.2     | 7    | 6        | 0.8  | 0.5     |
| 15     | 15       | 15    | 15      | 14      | 14   | 14       | 14   | 14      |
|        |          | 17    | 5       | 5       |      | 10       | 14   | 8       |
| 7.4    | 5.7      | 4     | 7       | 0       | 9.6  | 3        | 0    | 4       |
| 70     | 93       | 24    | 84      | 79      | 92   | 61       | 26   | 77      |
| 5      | 4        | 8     | 0.9     | 0.7     | 9    | 5        | 0.6  | 0.8     |
| 12     | 12       | 13    | 12      | 13      | 12   | 13       | 13   | 13      |
|        |          | 14    | 9       | 9       |      | 13       | 17   | 14      |
| 7.5    | 7        | 4     | 3       | 0       | 6.8  | 5        | 0.6  | 0.1     |
| 74     | 11       | 30    | 98      | 86      | 10   | 76       | 32   | 88      |
| 9      | 2.9      | 5     | 0.8     | 0.6     | 7.7  | 0        | 0.2  | 0.3     |
| 6      | 6        | 7     | 7       | 6       | 7    | 6        | 6    | 7       |
| 13     |          | 18    | 3       | 3       |      |          | 11   | 5       |
| 2      | 5.6      | 2     | 7       | 7       | 3.7  | 4.8      | 0.9  | 9       |
| 65     | 81       | 28    | 69      | 67      | 79   | 38       | 20   | 57      |
| 5      | 9        | 3     | 0.8     | 0.9     | 8    | 1        | 0.3  | 0.6     |
| 2      | 3        | 3     | 3       | 3       | 3    | 3        | 3    | 4       |
|        |          | 11    | 10      | 8       |      |          | 18   | 8       |
| 8.6    | 5.2      | 0     | 0       | 4       | 5.3  | 1.4      | 0.5  | 1       |
| 62     | 75       | 28    | 58      | 61      | 72   | 35       | 17   | 54      |
| 1      | 0        | 4     | 0.7     | 0.6     | 5    | 9        | 0.5  | 0.2     |
| 3      | 3        | 3     | 3       | 3       | 3    | 3        | 3    | 3       |
|        |          | 14    | 5       | 12      |      | 12       | 23   | 16      |
| 7      | 7.6      | 7     | 5       | 0.3     | 5.7  | 1        | 0.1  | 0.1     |
| 63     | 74       | 25    | 70      | 67      | 74   | 44       | 18   | 64      |
| 8      | 2        | 4     | 0.1     | 0.5     | 2    | 3        | 0.6  | 0.2     |
| 3      | 4        | 5     | 4       | 5       | 4    | 5        | 5    | 5       |
|        |          | 31    | 11      | 16      |      | 11       | 20   | 16      |

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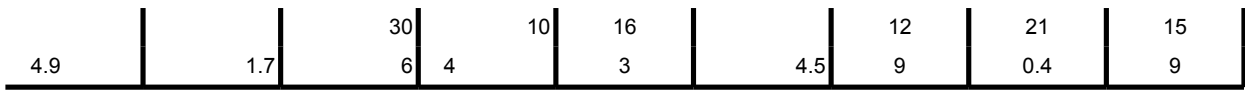
|                            |          | PF-<br>Br | PF-<br>Cr  | PF-<br>Wr  | PF-<br>TCr | B-<br>TPr | B-<br>Wr | B-<br>Cr  |
|----------------------------|----------|-----------|------------|------------|------------|-----------|----------|-----------|
| <b>H. naledi</b>           | me<br>an | 47<br>5   | 97<br>5    | 116<br>0.5 | 129<br>0.1 | 24<br>2   | 77<br>6  | 94<br>0.6 |
|                            | N        | 2         | 2          | 2          | 2          | 2         | 2        | 2         |
|                            | V*       | 7.2       | 2.9        | 0          | 2.3        | 15<br>9   | 2.9      | 2<br>7    |
| <b>H. sapiens</b>          | me<br>an | 45<br>4   | 98<br>9    | 101<br>0.8 | 110<br>0.6 | 22<br>1   | 64<br>5  | 96<br>0.1 |
|                            | N        | 45        | 45         | 45         | 45         | 45        | 45       | 45        |
|                            | V*       | 6.4       | 5.3        | 5.8        | 3.7        | 24<br>3   | 14<br>7  | 4<br>3    |
| <b>P. paniscus</b>         | me<br>an | 49<br>4   | 96<br>6    | 102<br>0.8 | 122<br>0.7 | 29<br>1   | 59<br>0  | 90<br>0.3 |
|                            | N        | 16        | 16         | 16         | 16         | 16        | 16       | 16        |
|                            | V*       | 9.3       | 6.8        | 5.1        | 3          | 12<br>2   | 12<br>3  | 5<br>8    |
| <b>P. troglodytes</b>      | me<br>an | 53<br>1   | 104<br>0.5 | 106<br>0.2 | 127<br>0.9 | 29<br>9   | 59<br>5  | 96<br>0.9 |
|                            | N        | 15        | 15         | 15         | 15         | 15        | 15       | 15        |
|                            | V*       | 4.6       | 6.7        | 4.6        | 2.8        | 12<br>6   | 10<br>4  | 5<br>3    |
| <b>H. erectus</b>          | me<br>an | 51<br>6   | 105<br>0.3 | 109<br>0.3 | 121<br>0.7 | 28<br>7   | 63<br>6  | 92<br>0.7 |
|                            | N        | 12        | 12         | 12         | 12         | 12        | 12       | 12        |
|                            | V*       | 7.7       | 4          | 5.5        | 2.9        | 14<br>9   | 14<br>5  | 5<br>2    |
| <b>H. neanderthalensis</b> | me<br>an | 48<br>4   | 98<br>0    | 108<br>0.9 | 116<br>0.5 | 27<br>6   | 66<br>5  | 91<br>0.1 |
|                            | N        | 7         | 6          | 7          | 6          | 6         | 7        | 6         |
|                            | V*       | 7.2       | 3.2        | 2.8        | 5.3        | 16<br>1   | 6.5      | 4<br>7    |
| <b>H. habilis</b>          | me<br>an | 51<br>9   | 98<br>9    | 111<br>0.7 | 133<br>0.2 | 23<br>3   | 67<br>1  | 88<br>0.3 |
|                            | N        | 3         | 2          | 3          | 2          | 2         | 3        | 2         |
|                            | V*       | 7.1       | 3.6        | 2.8        | 1.5        | 15<br>2   | 14<br>4  | 3<br>3    |
| <b>Au. africanus</b>       | me<br>an | 53<br>6   | 100<br>0.3 | 109<br>0.3 | 131<br>0   | 31<br>4   | 62<br>2  | 84<br>0.7 |
|                            | N        | 3         | 3          | 3          | 3          | 3         | 3        | 3         |
|                            | V*       | 10<br>3   | 5          | 2.8        | 2.4        | 13<br>0   | 13<br>2  | 1<br>2    |
| <b>Paranthropus</b>        | me<br>an | 59<br>9   | 94<br>6    | 106<br>0.5 | 134<br>0.6 | 26<br>8   | 59<br>2  | 85<br>0   |
|                            | N        | 2         | 2          | 3          | 3          | 3         | 3        | 3         |

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|--|----|-----|-----|-----|-----|----|----|---|
|  |    |     |     |     |     | 11 | 21 | 7 |
|  | V* | 2.7 | 6.7 | 2.7 | 3.5 | 0  | 0  | 4 |

| TP-TCr    | TC-Cr      | W-TCr     | W-Cr      | W-Er      | C-Or       | TC-Or     | E-Or       | W-Or      |
|-----------|------------|-----------|-----------|-----------|------------|-----------|------------|-----------|
| <b>83</b> | <b>100</b> | <b>24</b> | <b>91</b> | <b>81</b> | <b>106</b> | <b>58</b> | <b>22</b>  | <b>78</b> |
| <b>2</b>  | <b>0.3</b> | <b>2</b>  | <b>8</b>  | <b>3</b>  | <b>0.4</b> | <b>7</b>  | <b>0.5</b> | <b>8</b>  |
| 2         | 3          | 4         | 3         | 2         | 1          | 2         | 2          | 2         |
| 11.6      | 3          | 20        | 1.9       | 5         |            | 7.3       | 9          | 10        |
|           |            | 2         |           |           |            |           | 4          | 9         |
| <b>66</b> | <b>100</b> | <b>33</b> | <b>83</b> | <b>82</b> | <b>96</b>  | <b>67</b> | <b>23</b>  | <b>81</b> |
| <b>5</b>  | <b>0</b>   | <b>5</b>  | <b>0</b>  | <b>6</b>  | <b>4</b>   | <b>6</b>  | <b>0.4</b> | <b>3</b>  |
| 45        | 45         | 45        | 45        | 45        | 45         | 45        | 45         | 45        |
| 7.5       | 3.9        | 31        | 10        |           |            |           | 14         |           |
|           |            | 0         | 8         | 5.3       | 5.5        | 7.9       | 0.6        | 6         |
| <b>77</b> | <b>93</b>  | <b>29</b> | <b>86</b> | <b>84</b> | <b>89</b>  | <b>56</b> | <b>20</b>  | <b>78</b> |
| <b>0</b>  | <b>5</b>   | <b>0</b>  | <b>2</b>  | <b>1</b>  | <b>1</b>   | <b>5</b>  | <b>0.9</b> | <b>9</b>  |
| 16        | 16         | 16        | 16        | 16        | 16         | 16        | 16         | 16        |
| 5.8       | 3.4        | 20        |           |           |            |           | 12         |           |
|           |            | 6         | 4.7       | 5.1       | 5.3        | 8.5       | 0.4        | 8.3       |
| <b>81</b> | <b>91</b>  | <b>31</b> | <b>87</b> | <b>84</b> | <b>78</b>  | <b>56</b> | <b>18</b>  | <b>79</b> |
| <b>5</b>  | <b>4</b>   | <b>7</b>  | <b>5</b>  | <b>8</b>  | <b>8</b>   | <b>7</b>  | <b>0.8</b> | <b>8</b>  |
| 15        | 15         | 15        | 15        | 14        | 14         | 14        | 14         | 14        |
| 5.8       | 4.4        | 19        |           |           |            |           | 15         |           |
|           |            | 0         | 4.3       | 4.5       | 9          | 9.5       | 0          | 7.6       |
| <b>71</b> | <b>94</b>  | <b>25</b> | <b>86</b> | <b>81</b> | <b>94</b>  | <b>62</b> | <b>27</b>  | <b>79</b> |
| <b>6</b>  | <b>9</b>   | <b>4</b>  | <b>2</b>  | <b>4</b>  | <b>3</b>   | <b>7</b>  | <b>0.2</b> | <b>3</b>  |
| 12        | 12         | 13        | 12        | 13        | 12         | 13        | 13         | 13        |
| 5.7       | 5.3        | 14        |           |           |            |           | 16         | 10        |
|           |            | 0         | 7.3       | 5.3       | 3.9        | 9.9       | 0.5        | 0         |
| <b>66</b> | <b>99</b>  | <b>27</b> | <b>86</b> | <b>76</b> | <b>94</b>  | <b>66</b> | <b>28</b>  | <b>77</b> |
| <b>3</b>  | <b>3</b>   | <b>0</b>  | <b>8</b>  | <b>2</b>  | <b>5</b>   | <b>8</b>  | <b>0.4</b> | <b>6</b>  |
| 6         | 6          | 7         | 7         | 6         | 7          | 6         | 6          | 7         |
| 12.8      | 3.7        | 15        |           |           |            |           | 13         |           |
|           |            | 5         | 4.6       | 3.9       | 2.9        | 4         | 0.1        | 7.5       |
| <b>80</b> | <b>98</b>  | <b>33</b> | <b>83</b> | <b>81</b> | <b>95</b>  | <b>45</b> | <b>24</b>  | <b>68</b> |
| <b>1</b>  | <b>3</b>   | <b>9</b>  | <b>7</b>  | <b>5</b>  | <b>8</b>   | <b>8</b>  | <b>0.4</b> | <b>6</b>  |
| 2         | 3          | 3         | 3         | 3         | 3          | 3         | 3          | 4         |
| 5.1       | 0.8        | 9.2       | 6.5       | 8.8       | 3.5        | 3         | 0.1        | 8.3       |
| <b>81</b> | <b>98</b>  | <b>37</b> | <b>77</b> | <b>81</b> | <b>95</b>  | <b>47</b> | <b>23</b>  | <b>71</b> |
| <b>7</b>  | <b>8</b>   | <b>4</b>  | <b>4</b>  | <b>1</b>  | <b>6</b>   | <b>3</b>  | <b>0.1</b> | <b>3</b>  |
| 3         | 3          | 3         | 3         | 3         | 3          | 3         | 3          | 3         |
| 3.6       | 5.6        | 11        |           | 10        |            | 12        | 22         | 14        |
|           |            | 1         | 3.2       | 1         | 3.3        | 0         | 0.3        | 1         |
| <b>82</b> | <b>96</b>  | <b>32</b> | <b>90</b> | <b>86</b> | <b>96</b>  | <b>57</b> | <b>24</b>  | <b>82</b> |
| <b>2</b>  | <b>1</b>   | <b>6</b>  | <b>9</b>  | <b>8</b>  | <b>2</b>   | <b>1</b>  | <b>0</b>   | <b>6</b>  |
| 3         | 4          | 5         | 4         | 5         | 4          | 5         | 5          | 5         |

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|                                | PF-B        | PF-C        | PF-W        | PF-TC      | B-PT        | B-W         | B-C         | PT-TC       |
|--------------------------------|-------------|-------------|-------------|------------|-------------|-------------|-------------|-------------|
| <b>Lesedi 1</b>                | <b>42.1</b> | <b>84.2</b> | <b>98.8</b> | <b>108</b> | <b>18.5</b> | <b>64.6</b> | <b>81.6</b> | <b>65.4</b> |
| <i>Azs H. sapiens</i>          | -1.2        | -1.8        | -0.9        | -1.2       | -0.5        | -0.3        | -2          | -0.7        |
| <i>Azs Pan panis</i>           | 1.1         | 1.6         | 3           | 2.3        | -0.4        | 2           | 2.2         | 1.3         |
| <i>Azs Pan trogl</i>           | 0.3         | 0.5         | 1.6         | 1.3        | -0.2        | 2           | 1           | 1.1         |
| <i>Azs H. erectus</i>          | -0.7        | -1.2        | -0.8        | -1         | -1.1        | 0.1         | -0.7        | -0.4        |
| <i>Azs H. neand</i>            | -1.6        | -1.6        | -1.3        | -1.2       | -0.8        | -0.5        | -1.2        | -0.2        |
|                                |             |             |             |            |             |             |             |             |
| <b>DH3</b>                     | <b>35.1</b> | <b>74.1</b> | <b>90.2</b> | <b>102</b> | <b>20.6</b> | <b>61.3</b> | <b>72</b>   | <b>69.2</b> |
| <i>Azs H. sapiens</i>          | -2.1        | -2.5        | -1.5        | -1.7       | -0.3        | -0.5        | -2.7        | -0.4        |
| <i>Azs Pan panis</i>           | 0           | 0.6         | 2           | 1.6        | 0           | 1.7         | 1           | 1.8         |
| <i>Azs Pan trogl</i>           | 0.3         | 0.5         | 1.6         | 1.3        | -0.2        | 2           | 1           | 1.1         |
| <i>Azs H. erectus</i>          | -1.2        | -1.8        | -1.6        | -1.5       | -0.8        | -0.1        | -1.5        | -0.1        |
| <i>Azs H. neand</i>            | -1.6        | -1.6        | -1.3        | -1.2       | -0.8        | -0.5        | -1.2        | -0.2        |
|                                |             |             |             |            |             |             |             |             |
| <b>DH1</b>                     |             |             |             |            |             |             |             |             |
| <i>Azs H. sapiens</i>          |             |             |             |            |             |             |             |             |
| <i>Azs Pan paniscus</i>        |             |             |             |            |             |             |             |             |
| <i>Azs Pan troglodytes</i>     |             |             |             |            |             |             |             |             |
| <i>Azs H. erectus</i>          |             |             |             |            |             |             |             |             |
| <i>Azs H. neanderthalensis</i> |             |             |             |            |             |             |             |             |
|                                |             |             |             |            |             |             |             |             |
| <b>DH4</b>                     |             |             |             |            |             |             |             |             |
| <i>Azs H. sapiens</i>          |             |             |             |            |             |             |             |             |
| <i>Azs Pan paniscus</i>        |             |             |             |            |             |             |             |             |
| <i>Azs Pan troglodytes</i>     |             |             |             |            |             |             |             |             |
| <i>Azs H. erectus</i>          |             |             |             |            |             |             |             |             |
| <i>Azs H. neanderthalensis</i> |             |             |             |            |             |             |             |             |



|    | TC-C        | W-TC        | W-C         | W-E         | C-O         | TC-O        | E-O         | W-O         |
|----|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| 1  |             |             |             |             |             |             |             |             |
| 2  |             |             |             |             |             |             |             |             |
| 3  | <b>82.4</b> | <b>16.2</b> | <b>76.6</b> |             |             |             |             |             |
| 4  | -2.5        | -0.9        | -0.8        |             |             |             |             |             |
| 5  |             |             |             |             |             |             |             |             |
| 6  | 2.3         | -0.5        | 2.1         |             |             |             |             |             |
| 7  | 1.6         | -0.5        | 1.3         |             |             |             |             |             |
| 8  | -0.8        | -1.1        | -0.5        |             |             |             |             |             |
| 9  |             |             |             |             |             |             |             |             |
| 10 | -2          | -0.9        | -2.7        |             |             |             |             |             |
| 11 |             |             |             |             |             |             |             |             |
| 12 | <b>78.8</b> | <b>20.1</b> | <b>71</b>   |             |             |             |             |             |
| 13 |             |             |             |             |             |             |             |             |
| 14 | -2.8        | -0.7        | -1.1        |             |             |             |             |             |
| 15 | 1.8         | 0           | 1.4         |             |             |             |             |             |
| 16 | 1.6         | -0.5        | 1.3         |             |             |             |             |             |
| 17 |             |             |             |             |             |             |             |             |
| 18 | -1          | -0.6        | -0.8        |             |             |             |             |             |
| 19 | -2          | -0.9        | -2.7        |             |             |             |             |             |
| 20 |             |             |             |             |             |             |             |             |
| 21 |             |             |             |             |             |             |             |             |
| 22 | <b>84.1</b> | <b>18.3</b> | <b>77</b>   | <b>64.9</b> | <b>87.7</b> | <b>46.1</b> | <b>19.6</b> | <b>60.5</b> |
| 23 | -2.3        | -0.8        | -0.8        | -2.3        | -1.5        | -2.3        | -0.8        | -2.5        |
| 24 | 2.6         | -0.2        | 2.2         | 0.7         | 2.7         | 1           | 1           | 0.5         |
| 25 |             |             |             |             |             |             |             |             |
| 26 | 1.6         | -0.5        | 1.3         | 0.4         | 2.5         | 0.5         | 1.4         | 0.2         |
| 27 | -0.6        | -0.8        | -0.4        | -0.9        | -0.4        | -0.8        | -0.7        | -0.7        |
| 28 | -2          | -0.9        | -2.7        | -2.6        | -2          | -3          | -1.2        | -2.1        |
| 29 |             |             |             |             |             |             |             |             |
| 30 |             |             |             |             |             |             |             |             |
| 31 |             | <b>23</b>   |             | <b>65</b>   |             | <b>47.5</b> | <b>16.4</b> | <b>65.2</b> |
| 32 |             | -0.6        |             | -2.3        |             | -2.2        | -1.2        | -2.1        |
| 33 |             |             |             |             |             |             |             |             |
| 34 |             | 0.3         |             | 0.7         |             | 1.2         | 0.3         | 0.9         |
| 35 |             | -0.5        |             | 0.4         |             | 0.6         | 0.6         | 0.6         |
| 36 |             | -0.2        |             | -0.9        |             | -0.8        | -1          | -0.5        |
| 37 |             | -0.9        |             | -2.6        |             | -2.9        | -1.5        | -1.8        |
| 38 |             |             |             |             |             |             |             |             |
| 39 |             |             |             |             |             |             |             |             |
| 40 |             |             |             |             |             |             |             |             |
| 41 |             |             |             |             |             |             |             |             |
| 42 |             |             |             |             |             |             |             |             |
| 43 |             |             |             |             |             |             |             |             |
| 44 |             |             |             |             |             |             |             |             |
| 45 |             |             |             |             |             |             |             |             |
| 46 |             |             |             |             |             |             |             |             |
| 47 |             |             |             |             |             |             |             |             |
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| 51 |             |             |             |             |             |             |             |             |
| 52 |             |             |             |             |             |             |             |             |
| 53 |             |             |             |             |             |             |             |             |
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|                                | PF-Br     | PF-Cr     | PF-Wr      | PF-TCr     | B-PTr     | B-Wr      | B-Cr      | PT-TCr    |
|--------------------------------|-----------|-----------|------------|------------|-----------|-----------|-----------|-----------|
| <b>Lesedi 1</b>                | <b>50</b> | <b>99</b> | <b>117</b> | <b>127</b> | <b>22</b> | <b>76</b> | <b>96</b> | <b>77</b> |
| <i>Azs H. sapiens</i>          | 0.7       | 0         | 1.2        | 2          | 0         | 0.6       | 0         | 1.1       |
| <i>Azs Pan paniscus</i>        | 0         | 0.2       | 1.2        | 0.6        | -1        | 1.1       | 0.5       | 0         |
| <i>Azs Pan troglodytes</i>     | -1        | 0         | 1          | 0          | -1        | 1.2       | 0         | 0         |
| <i>Azs H. erectus</i>          | 0         | -1        | 0.5        | 0.7        | -1        | 0.6       | 0.3       | 0.6       |
| <i>Azs H. neanderthalensis</i> | 0.1       | 0.1       | 1          | 0.6        | -1        | 0.9       | 0.5       | 0.5       |
|                                |           |           |            |            |           |           |           |           |
| <b>DH3</b>                     | <b>45</b> | <b>96</b> | <b>117</b> | <b>131</b> | <b>27</b> | <b>79</b> | <b>93</b> | <b>89</b> |
| <i>Azs H. sapiens</i>          | 0         | 0         | 1.2        | 2.4        | 0.4       | 0.8       | 0         | 2.3       |
| <i>Azs Pan paniscus</i>        | 0         | 0         | 1.2        | 1          | 0         | 1.3       | 0.2       | 1.3       |
| <i>Azs Pan troglodytes</i>     | -2        | -1        | 1          | 0.4        | 0         | 1.5       | 0         | 0.8       |
| <i>Azs H. erectus</i>          | -1        | -1        | 0.5        | 1.2        | 0         | 0.7       | 0         | 1.9       |
| <i>Azs H. neanderthalensis</i> | 0         | 0         | 1          | 0.9        | 0         | 1.1       | 0.2       | 1         |
|                                |           |           |            |            |           |           |           |           |
| <b>DH1</b>                     |           |           |            |            |           |           |           |           |
| <i>Azs H. sapiens</i>          |           |           |            |            |           |           |           |           |
| <i>Azs Pan paniscus</i>        |           |           |            |            |           |           |           |           |
| <i>Azs Pan troglodytes</i>     |           |           |            |            |           |           |           |           |
| <i>Azs H. erectus</i>          |           |           |            |            |           |           |           |           |
| <i>Azs H. neanderthalensis</i> |           |           |            |            |           |           |           |           |
|                                |           |           |            |            |           |           |           |           |
| <b>DH4</b>                     |           |           |            |            |           |           |           |           |
| <i>Azs H. sapiens</i>          |           |           |            |            |           |           |           |           |
| <i>Azs Pan paniscus</i>        |           |           |            |            |           |           |           |           |
| <i>Azs Pan troglodytes</i>     |           |           |            |            |           |           |           |           |
| <i>Azs H. erectus</i>          |           |           |            |            |           |           |           |           |
| <i>Azs H. neanderthalensis</i> |           |           |            |            |           |           |           |           |

| TC-Cr      | W-TCr     | W-Cr      | W-Er      | C-Or       |
|------------|-----------|-----------|-----------|------------|
| <b>97</b>  | <b>19</b> | <b>90</b> |           |            |
| 0          | -1        | 0.4       |           |            |
| 0.5        | -1        | 0.5       |           |            |
| 0.6        | -1        | 0.3       |           |            |
| 0.2        | -1        | 0.3       |           |            |
| 0          | -1        | 0.3       |           |            |
|            |           |           |           |            |
| <b>102</b> | <b>26</b> | <b>92</b> |           |            |
| 0.2        | 0         | 0.5       |           |            |
| 1.2        | 0         | 0.6       |           |            |
| 1.2        | 0         | 0.5       |           |            |
| 0.6        | 0.1       | 0.4       |           |            |
| 0.2        | 0         | 0.5       |           |            |
|            |           |           |           |            |
| <b>102</b> | <b>22</b> | <b>93</b> | <b>79</b> | <b>106</b> |
| 0.3        | -1        | 0.6       | 0         | 0.9        |
| 1.3        | -1        | 0.8       | -1        | 1.7        |
| 1.2        | -1        | 0.7       | -1        | 1.8        |
| 0.6        | 0         | 0.5       | 0         | 1.5        |
| 0.3        | -1        | 0.7       | 0.3       | 1.7        |
|            |           |           |           |            |
|            | <b>30</b> |           | <b>84</b> |            |
|            | 0         |           | 0.1       |            |
|            | 0.1       |           | 0         |            |
|            | 0         |           | 0         |            |
|            | 0.5       |           | 0.3       |            |
|            | 0.3       |           | 1         |            |