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# Further assessment of a ~2-million-year-old hominin pelvis (DNH 43) from Drimolen Main Quarry, South Africa

The palaeocave site of Drimolen Main Quarry (DMQ) in Gauteng Province, South Africa, has produced fossil hominin material dating to 2.04–1.95 Ma, including craniodental remains attributed to *Paranthropus robustus* and the earliest specimen of *Homo erectus sensu lato* along with numerous postcrania of uncertain taxonomic affiliation. Among this collection is a partial pelvis (DNH 43), which includes the sacrum and elements of the right os coxae. Although previously described as showing similarities to the pelvis of *Australopithecus* and *Paranthropus*, comparisons across the broader hominin fossil record have been limited and DNH 43 has never been analysed quantitatively. Here we present a partial digital reconstruction of DNH 43 and compare it to an expanded data set of fossil specimens to determine its closest morphological affinities. Overall, the quantitative analysis is congruent with qualitative results reflecting the primitive features of DNH 43, suggesting an *Australopithecus/Paranthropus*-like anatomy, including small absolute size, relatively small sacroiliac articulation, moderately wide tuberoacetabular sulcus, gracile acetabulosacral buttress, and obstetric dimensions that are relatively broad. A study of this rare articulated pelvis shows that the orientation of the sacrum (pelvic incidence) is similar to that of recent *Homo sapiens*. Although DNH 43 shares some specific metric similarities with specimens MH2 (*Australopithecus sediba*) and OH 28 (cf. *Homo erectus*), the taxonomic relevance is unclear given the poor understanding of *Paranthropus* and early *Homo* postcranial variation. Affiliation with *Paranthropus robustus* (which dominates the DMQ craniodental assemblage) cannot be ruled out, and we consider assignment to that taxon to be a reasonable provisional attribution.

#### Significance:

- Associated pelvic elements (sacrum and ossa coxae) are rare in the hominin fossil record but provide information on overall body form, locomotion and obstetrics.
- Anatomical assessment and partial reconstruction of specimen DNH 43 from the Drimolen Main Quarry in the Cradle of Humankind, South Africa, thus provides additional insights into pelvic form in a ~2.0-million-year-old hominin.
- The fossil is best attributed to *Paranthropus robustus* and displays an overall primitive, gracile morphology, but presents with positioning of the sacrum similar to that of recent humans, which differs from prior interpretations of early hominin spinopelvic anatomy.

## Introduction

Palaeontological work at the palaeocave site of Drimolen Main Quarry (DMQ; 25°58'08" S, 27°45'21" E) in Gauteng Province, South Africa has produced significant fossil hominin material since excavations began in 1994.<sup>1</sup> The assemblage includes craniodental remains attributed to *Paranthropus robustus* and the earliest known specimen of *Homo erectus sensu lato* dating to between 2.04 Ma and 1.95 Ma, demonstrating that *Paranthropus* and *Homo* were effectively contemporaneous at the site and coeval with *Australopithecus* from nearby fossil localities in South Africa.<sup>2</sup> Numerous postcranial elements of uncertain taxonomic affiliation have also been recovered, but these have received little attention. Among these is a partial pelvis (DNH 43) with most of the sacrum (DNH 43A) and elements of the associated right os coxae (DNH 43B) preserved. Although some details about the recovery of the DNH 43 specimen are unclear, information on the relevant excavation history at the DMQ and what is known about the site context for the specimen is provided in the [Supplementary material](#), including a 3D plot of the fossil block's location within the quarry ([Supplementary figure 1A–C](#)).

The evolution of the pelvis bears on critical aspects of hominin biology, including locomotion, obstetrics, and variation in body size and shape related to climatic adaptation.<sup>3–8</sup> However, associated sacra and ossa coxae are especially rare in the early hominin fossil record<sup>9</sup>, making DNH 43 of particular interest. Gommery and colleagues<sup>9</sup> described the specimen qualitatively, noted its similarities to the pelvis of other early South African hominins, and attributed it to *Paranthropus robustus*. However, comparisons across the broader hominin fossil record are lacking and the specimen has never been analysed quantitatively. The objective of the present paper is to make 3D polygon models of DNH 43 available online (including a partial virtual reconstruction) and to compare the specimen metrically to an expanded data set of hominin pelvic material to (1) determine the closest overall morphological affinities of DNH 43 to test the hypothesis of taxonomic attribution to *P. robustus*<sup>9</sup>; (2) investigate aspects of the palaeobiology, including locomotor and obstetric implications; and (3) assess the possible sex of the specimen.

## Materials and methods

### Virtual reconstruction

A detailed description of DNH 43, including information on preservation, is provided by Gommery and colleagues<sup>9</sup>. For the current study, the DNH 43 pieces were surface scanned using an Artec Space Spider. The resulting surface

#### ARTICLE INCLUDES:

- ☒ Peer review
- ☒ [Supplementary material](#)

#### DATA AVAILABILITY:

- ☐ Open data set
- ☒ All data included
- ☐ On request from author(s)
- ☐ Not available
- ☐ Not applicable

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scans of the individual pieces of DNH 43, as well as the partial reconstruction, are provided in the University of the Witwatersrand's Drimolen Collection at <https://human-fossil-record.org>.

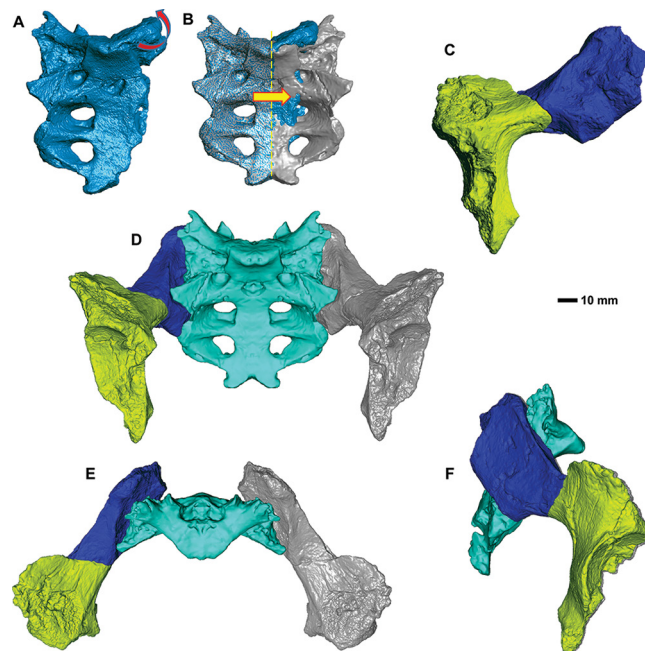
The sacrum (DNH 43A) includes a nearly complete plateau and most of the right side of the vertebrae, although the anterior aspect of the right-side ala is mostly missing. The left side of the sacral vertebral bodies and left-side ala are absent. The plateau exhibits plastic deformation such that the left half is shifted cranially; however, the right side is complete and undistorted (Figure 1A). On the right side, the cranial-most one-third of the sacral ala and auricular surface is absent, but the caudal two-thirds of the surface is reasonably well preserved and only minimally distorted. To partially reconstruct the sacrum, the virtual model of DNH 43A was sectioned at the midline and the more-complete right side was reflected to the left (Figure 1B) using Geomagic Control.

The partial right os coxae (DNH 43B) is preserved in two pieces that refit cleanly at a postmortem break approximately midway along the acetabulosacral buttress, which is the bony strut connecting the sacroiliac joint and the hip (Figure 1C). The anterior portion includes most of the lunate surface of the acetabulum (missing the superomedial and inferomedial horns), allowing for measurement of the superoinferior diameter. A small anterior portion of the iliac blade (which is mostly missing otherwise) projects superolaterally from the anterior inferior iliac spine, which is present but weathered. The superior portion of the ischium is preserved, including a somewhat polished ischial spine and approximately 1 cm of bone inferior to it. The ischial tuberosity is almost entirely absent, but a lip of bone representing the superior edge of what would be the roughened tuberosity is discernible, allowing assessment of the tuberoacetabular sulcus width. The posterior portion of DNH 43B includes a complete auricular surface and much of the iliac tuberosity. The iliac tuberosity is damaged posterolaterally such that the posterior-superior and posterior-inferior iliac spines are absent.

The two pieces of the os coxae were fitted together virtually and reflected to generate a left side for articulation with the reconstructed sacrum (Figure 1D–F). Each piece of DNH 43A and B was 3D printed using a Lulzbot Taz 6 printer (an 'extrusion' printer using fused-deposition modelling with a polylactic acid printing filament) at a layer height of 0.1 mm. The 3D prints were manipulated physically to evaluate the fit and to ground-truth the virtual articulation.

#### Comparative sample

To evaluate the closest morphological affinity of DNH 43, it was compared to a sample of recent *Homo sapiens* (12 male and 13 female individuals) and several fossil hominin specimens. The recent human sample for analysis of the isolated pieces came from the Maxwell Museum of Anthropology at the University of New Mexico and access followed the relevant research and ethics reviews of that institution. Fossils included specimens typically attributed to *Australopithecus afarensis* (AL 288-1), *A. africanus* (Sts 14 and Stw 431), *A. sediba* (MH1 and MH2), *Paranthropus robustus* (SK 50, SK 3155b, TM 1605), *Homo* sp. (likely representing various taxa including *Homo erectus* and its probable immediate descendants<sup>10,11</sup>: Arago XLIV, Kabwe E. 719, KNM-ER 1808, KNM-ER 3228, KNM-ER 5881, KNM-WT 15000 and OH 28), *H. floresiensis* (LB1), Neanderthals (Amud 1, Kebara 2, Krapina 207, Neanderthal 1, and Tabun C1), and early *H. sapiens* (Omo-Kibish 1 and Skhul IV). Comparative metric assessment of the articulated pelvis included additional data from the literature allowing the consideration of material attributed to either *Homo* sp. or Neanderthals (Sima de los Huesos Pelvis 1 and Pelvis 2)<sup>12</sup>, *H. erectus* (BSN49/P26)<sup>13</sup>,



**Figure 1:** Three-dimensional polygon models derived from surface scanning of DNH 43: (A) sacrum (DNH 43A) with arrow indicating cranially directed deformation of the left side of the sacral plateau; (B) bisection and reflection of the relatively undistorted right side to reconstruct the left side; (C) medial view of the two refit pieces of the os coxae (DNH 43B); (D) anterior view of the articulated pelvis with the reconstructed sacrum and the right os coxae reflected to reproduce the left side; (E) superior view of the articulated pelvis; and (F) lateral view of the articulated pelvis.

although some have argued this could represent *P. bosei*<sup>14</sup>, a late Pleistocene *Homo sapiens* specimen (Ohalo II)<sup>15</sup>, along with larger data sets of obstetric breadths and pelvic incidence from recent *H. sapiens* populations<sup>15,16</sup> and modern *Pan troglodytes*<sup>15,17</sup>.

### Measurements and analysis

Measurements were taken on 3D scans of the individual DNH 43A and DNH 43B specimens and compared with data from the fossil and recent *H. sapiens* samples. Measurements were taken by author E.B. (based on landmarks placed on the 3D scans using Stratovan Checkpoint, except for the sciatic notch proportions and measurements on the articulated reconstruction, which were taken by author C.M.O. using Geomagic Control or taken from the literature where indicated. Analysis of three repeated trials by the relevant observer returned mean technical errors of measurement<sup>18</sup> of  $\pm 0.4$ – $0.8$  mm (0.4–3.1% relative error) for the linear metrics of the os coxa and sacrum,  $\pm 0.6^\circ$  (0.8% relative error) for sciatic notch angle, and  $\pm 0.02$  (1.1% relative error) for the sciatic notch proportion ratio indicating good precision. Differential preservation limited measurement of some fossils, so analyses included subsamples accordingly. More detailed definitions of measurements and landmarks are provided in Supplementary table 1 and Supplementary figure 2.

Sacrum measurements captured total craniocaudal length and maximum mediolateral and anteroposterior dimensions of the plateau. Sacral proportions and shape have been suggested to differ among early hominin fossil taxa with possible taxonomic implications.<sup>19</sup>

Analysis of the os coxae focused on measurements available on as many fossils as possible, following metrics from Churchill et al.<sup>20</sup> The width of the tuberoacetabular sulcus (TAS: the ‘gap’ between the superior-most aspect of the ischial tuberosity and the inferior margin of the acetabulum) and breadth of the auricular surface (AUR) were evaluated relative to the superoinferior acetabular diameter (AD). Recent humans and fossils attributed to *Homo* tend to have a narrow tuberoacetabular sulci compared to earlier hominins, including *Australopithecus* and *Paranthropus*.<sup>20–22</sup> The index of the acetabulosacral buttress thickness (ASBT: mediolateral breadth superior to the greater sciatic notch) to the acetabulosacral buttress load arm (ASLA: anteroposterior length from acetabulum to the auricular surface) captures the relative robusticity of the lower ilium. Members of the genus *Homo* typically exhibit thicker acetabulosacral buttresses.<sup>10,20</sup> In addition to bivariate plots to examine the scaling of specific metrics, a cluster analysis of the indices TAS:AD  $\times$  100, AUR:AD  $\times$  100 and ASBT:ASLA  $\times$  100 was conducted using the unweighted pair group method with arithmetic mean (UPGMA) to assess the closest overall metric affinities.

Morphology of the sciatic notch in DNH 43B was quantified to investigate the possibility of assigning sex to this specimen and other early hominins based on recent human criteria. The greater sciatic notch shows sexual dimorphism in recent *H. sapiens*, with female individuals typically exhibiting a wider notch that is relatively symmetric with the apex shifted anteriorly such that the anterior and posterior arcs are closer in length than in male individuals.<sup>13,23</sup> Thus, the sciatic notch angle (SNA) was used to quantify the ‘openness’ of the notch while the relative position of the notch’s apex quantified the sciatic notch proportions (SNP) following the method from reference.<sup>13</sup>

Mediolateral (transverse) dimensions with locomotor and obstetric implications were measured on the virtually articulated pelvis. These included the mediolateral diameter of the pelvic inlet (between the most lateral points on the right and left arcuate lines), the bispinous breadth (between right and left ischial spines quantifying the mediolateral dimension of the obstetric midplane) and biacetabular breadth (between the centres of the right and left acetabulae). Without a pubis, reconstruction of the anterior enclosure of the inlet is impossible and anteroposterior dimensions are unmeasurable. Sacral orientation, which is related to the degree of lumbar lordosis, varies among non-hominins, *Australopithecus*, and later members of the genus *Homo*.<sup>15</sup> Relative to extant apes, *H. sapiens* exhibit a high degree of anterior sacral tilt, which corresponds to an increased lumbar lordosis to position the superincumbent body weight over the hips.<sup>15</sup> Sacral orientation

(Supplementary figure 3) was assessed in DNH 43 by quantifying pelvic incidence using a method following Peleg et al.<sup>24</sup> and comparing it with data from Been and colleagues<sup>15</sup>.

### Results

The DNH 43A sacrum has a minimum craniocaudal length of  $\sim 72$  mm. This is probably an underestimate as only a portion of the fifth sacral vertebra is intact, but it closely matches the length of specimen AL 288-1 (73.5 mm) attributed to *A. afarensis*. The reconstructed sacral plateau measures 16.6 mm anteroposteriorly by 29.3 mm mediolaterally. An index of sacral plateau proportions is compared among hominins in Figure 2A. DNH 43A shows its closest affinities with sacra attributed to *A. afarensis* and *A. africanus*, although one male human matches DNH 43A in having a similarly anteroposteriorly compressed plateau.

Measurements of the DNH 43B os coxae are shown in Table 1, along with a comparative sample of fossils and recent *H. sapiens*. Fossils are grouped in Table 1 for brevity and the most useful overall comparisons, but individual specimen data are provided in Supplementary table 2. Bivariate plots of tuberoacetabular sulcus width versus acetabular diameter, auricular breadth (AUR) versus acetabular diameter, and acetabulosacral buttress thickness versus acetabulosacral load arm are shown in Figure 2B–D.

The UPGMA cluster analysis results are shown in Figure 3. The dendrogram exhibits two primary clusters: the recent *H. sapiens* sample plus the LB1 *H. floresiensis* specimen and a fully fossil hominin cluster. Within the fossil cluster, there are two further main divisions: (1) a cluster that includes DNH 43B along with ossa coxae assigned to *Australopithecus* or *Paranthropus* plus the OH 28 specimen (cf. *Homo erectus*); and (2) a cluster including ossa coxae referring to various Pleistocene members of the genus *Homo* (including early taxa such as *H. erectus* and later groups such as Neanderthals and ‘early *H. sapiens*’). Within the first cluster, DNH 43B shows its closest linkages to OH 28 and MH2 (*Australopithecus sediba*) (Figure 3).

Greater sciatic notch measurements (SNA and SNP) are shown in Table 1 and Figure 4. Mean SNA for female *H. sapiens* ( $81.9^\circ$ ; standard deviation = 5.7; range: 75.0–93.9°) is significantly different from that for the male *H. sapiens* ( $67.7^\circ$ ; standard deviation = 4.0; range: 59.4–72.6°) ( $t = 7.14$ ,  $p < 0.001$ ). The SNPs also differ significantly ( $t = 3.8$ ,  $p < 0.001$ ) between recent human female individuals (mean = 0.38; standard deviation = 0.08; range: 0.31–0.52) and male individuals (mean = 0.24; standard deviation = 0.10; range: 0.12–0.45). For both variables, DNH 43B falls at the high end of the range for female *H. sapiens*.

Measurements from the articulated DNH 43 pelvis are provided in Table 2. DNH 43 has a pelvic inlet and bispinous breadth that are somewhat narrow mediolaterally but a biacetabular breadth similar to other individuals, including recent *H. sapiens* (which are absolutely broad when compared to *P. troglodytes*). The pelvic incidence angle of  $56^\circ$  (Supplementary figure 3) falls close to the *H. sapiens* mean ( $54 \pm 10^\circ$  standard deviation) and is higher than those for all other fossil hominins and 4.5 standard deviations above the *P. troglodytes* mean ( $29 \pm 6^\circ$  standard deviation).

### Discussion

In absolute measurements, DNH 43 is small and similar to specimens attributed to *Paranthropus* and *Australopithecus* (Tables 1 and 2; Figure 2). The close correlations among acetabulum size, femoral head size and body mass<sup>14</sup> suggest that the individual represented by DNH 43 would have been of a similar overall body size to these early hominin taxa.

The DNH 43A sacral plateau is relatively narrow in the anteroposterior dimension compared with the mediolateral dimension, linking it with early hominins including *A. afarensis* and *A. africanus* versus the recent *H. sapiens* sample (Figure 2A). The Kebara 2 sacrum is also anteroposteriorly compressed, although it overlaps the low end of the human sample (as does the Sts 14 specimen attributed to *A. africanus*). However, although the sacral plateau is not well preserved in the Sts 431 sacrum (attributed to *A. africanus*) or for that of MH2 (*A. sediba*), the sacral body in these specimens is somewhat thicker anteroposteriorly than those of DNH 43A, AL 288-1, and Sts 14<sup>28</sup>, suggesting some

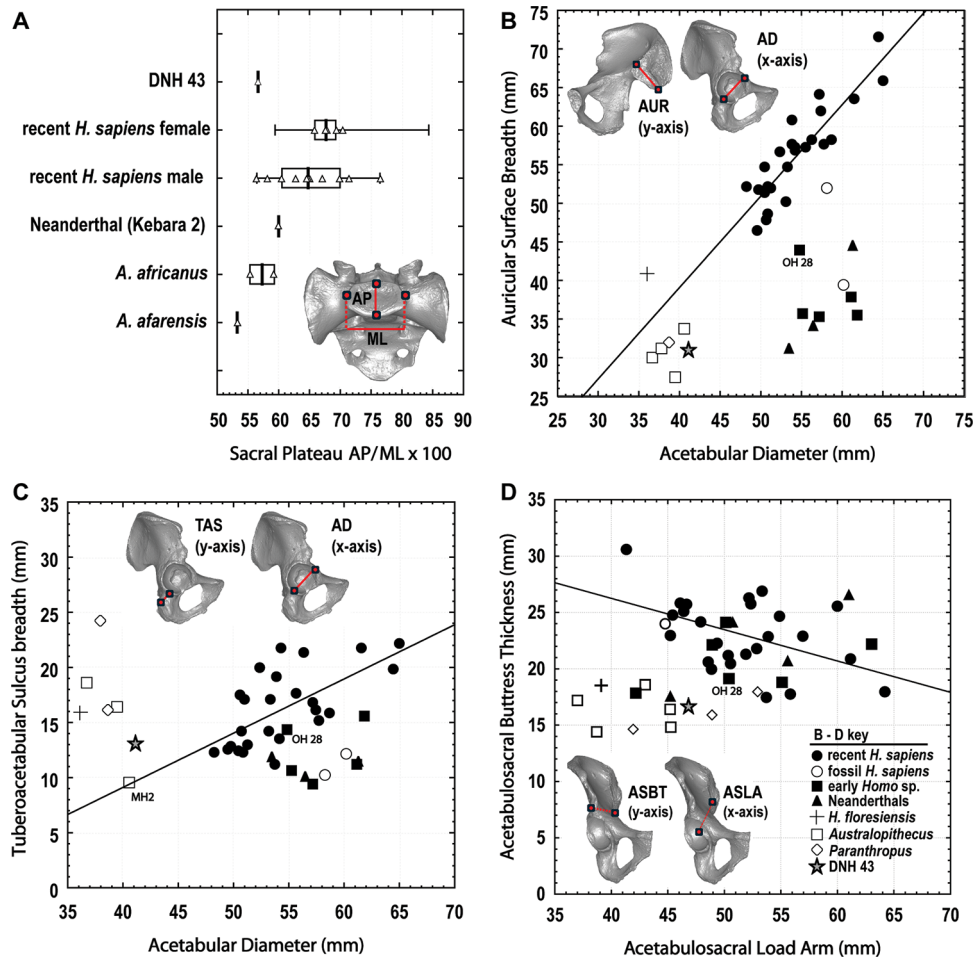


**Table 1:** Summary data for the os coxae measurements

	AD	TAS	ASBT	ASLA	SNA	SNP	AUR	TAS/AD × 100	ASBT/ASLA × 100	AUR/AD × 100
<b>DNH 43</b>	41.1	13.2	16.6	46.8	87.3	0.48	31.2	32.1	35.5	75.9
<b><i>Australopithecus</i></b>										
N	3	3	5	5	2	2	4	3	5	4
Mean	38.2	17.5	16.3	41.8	90.8	0.27	28.6	45.9	35.0	75.2
Standard deviation	1.8	4.7	1.7	3.8	–	–	2.6	13.8	5.6	6.5
Minimum	36.8	9.5	14.4	37.0	85.9	0.25	27.3	23.3	32.8	69.1
Maximum	40.7	18.6	18.6	45.3	95.6	0.28	33.7	50.5	46.5	82.8
<b><i>H. floresiensis</i></b>	36.0	15.9	18.5	39.1	81.0	0.44	41.0	44.2	47.4	113.8
<b><i>H. sapiens fossil</i></b>										
N	2	2	1	2	2	2	2	2	2	2
Mean	59.3	11.1	24.0	54.7	81.1	0.41	45.7	18.7	53.6	77.3
Minimum	58.3	10.1	24.0	44.8	80.4	0.34	39.4	17.4	53.6	65.4
Maximum	60.3	12.1	24.0	64.6	81.8	0.48	52.0	20.0	53.6	89.1
<b><i>H. sapiens recent</i></b>										
N	25	25	25	25	25	25	25	25	25	25
Mean	54.5	16.3	23.0	51.6	75.1	0.31	56.3	29.7	45.4	103.1
Standard deviation	4.5	3.5	3.2	5.4	8.7	0.11	6.0	5.2	9.6	5.4
Minimum	48.3	11.2	17.5	41.3	59.4	0.12	46.4	20.8	28.0	93.7
Maximum	65.0	22.1	30.6	64.2	93.9	0.52	71.4	40.0	74.0	112.7
<b><i>Homo sp.</i></b>										
N	5	5	6	7	5	4	5	5	6	5
Mean	58.1	12.2	20.7	50.2	79.3	0.30	37.6	20.9	40.5	65.0
Standard deviation	3.3	2.6	2.5	7.4	6.8	0.07	3.7	4.3	5.6	8.8
Minimum	54.9	9.3	17.8	41.7	73.4	0.22	35.2	16.2	34.2	57.2
Maximum	62.0	15.5	24.1	63.0	86.3	0.36	43.9	26.0	48.1	80.1
<b>Neanderthals</b>										
N	4	4	4	4	3	3	3	3	4	3
Mean	57.8	9.7	22.3	53.1	64.7	0.16	36.5	19.5	41.9	63.6
Standard deviation	3.4	3.0	3.9	6.7	7.7	0.07	7.0	2.2	4.7	7.7
Minimum	53.6	5.3	17.6	45.2	59.8	0.08	31.1	17.8	37.3	58.1
Maximum	61.3	11.8	26.6	61.0	73.6	0.22	44.4	22.0	47.6	72.4
<b><i>P. robustus</i></b>										
N	2	2	3	3	2	2	2	2	3	2
Mean	38.4	20.2	16.2	47.9	82.6	0.50	39.0	52.7	33.2	101.7
Standard deviation	–	–	1.7	5.6	–	–	–	–	2.2	–
Minimum	38.0	16.1	14.6	41.9	80.7	0.49	31.8	41.5	30.8	82.0
Maximum	38.8	24.2	18.0	52.9	84.5	0.51	46.1	63.8	34.9	121.3

\*AD, acetabular diameter (superoinferior); TAS, tuberoacetabular sulcus breadth; ASBT, acetabulosacral buttress thickness; ASLA, acetabulosacral load arm; SNA, sciatic notch angle; SNP, sciatic notch proportions; AUR, auricular surface breadth. All measurements included were taken for the current study with the exception of ASBT and ALSA for MH2 taken from Churchill et al.<sup>20</sup> Data for individual specimens are provided in the supplementary material.





**Figure 2:** Anteroposterior versus mediolateral proportions of the sacrum (A) and bivariate plots of three features of the os coxae demonstrating scaling relationships between the auricular surface breadth and the superoinferior acetabular diameter (B), tuberoacetabular sulcus breadth and superoinferior acetabular diameter (C), and the acetabulosacral buttress thickness versus the acetabulosacral load arm (D). In all cases, the plotted least-squares regression lines are fit solely to the recent *Homo sapiens* sample. Inset images illustrate the variables in each plot as demonstrated on a human individual.

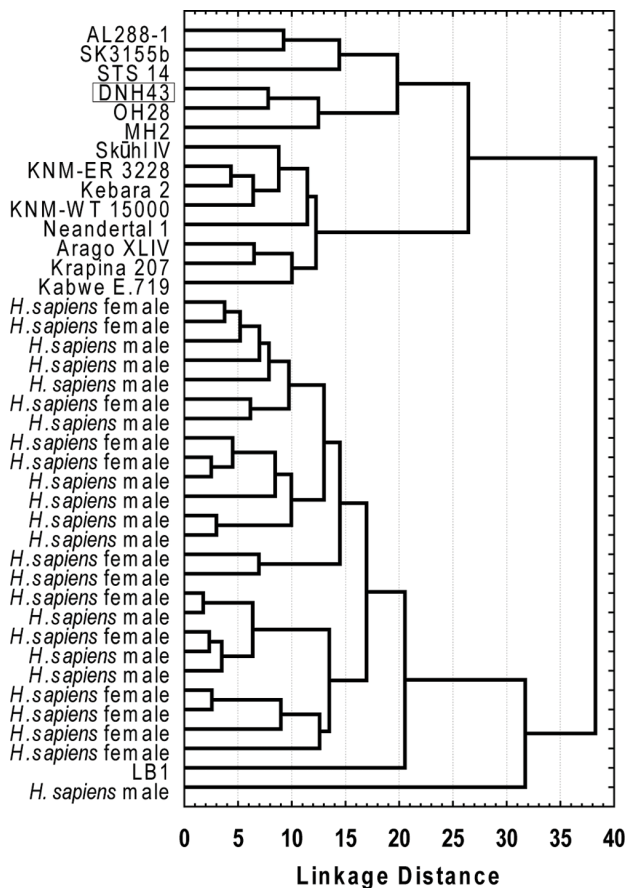
variation in sacral robusticity within *Australopithecus* that might have taxonomic implications, including heterogeneity in the Sterkfontein sample<sup>19</sup>. Unfortunately, there are no sacral specimens attributed to *Paranthropus* against which DNH 43A can be compared.

The DNH 43B os coxae exhibits an auricular surface that is small relative to the size of the acetabulum (Figure 2B) and a transverse acetabular sulcus that is only moderately wide relative to the size of the acetabulum (Figure 2C). As with most of the *Australopithecus* and *Paranthropus* specimens sampled, DNH 43B has a gracile communication between the sacroiliac joint and hip joint with an acetabulosacral buttress that is slender relative to its length (Figure 2D), as reflected in its low ASBT/ASLA  $\times 100$  index (Table 1).

Considering indices TAS:AD  $\times 100$ , AUR:AD  $\times 100$  and ASBT:ASLA  $\times 100$  together in the UPGMA cluster analysis (Figure 3), DNH 43B has its closest linkage with specimen OH 28 (*Homo cf. erectus*) while its next closest linkage is to specimen MH2 (*Australopithecus sediba*). DNH 43B, OH 28, and MH2 all form a direct 'sister' group with the branch that includes the *Australopithecus* and *Paranthropus* specimens to the exclusion of most of the individual fossils typically attributed to the various *Homo* taxa. Although this reflects a general 'early hominin-grade' morphology for DNH 43, the pattern of clustering within DNH 43's group suggests that the quantified characters have limited utility in resolving taxonomy at a finer scale. The linkage distances that separate individual specimens within the *Australopithecus*/*Paranthropus* cluster are relatively small despite ostensibly representing at least four and possibly five different early hominin taxa; in fact, they do not exceed

the largest distances separating specimens of the recent *H. sapiens* sample. Linkage of DNH 43 with OH 28 might reflect some 'early *Homo*' characteristics in DNH 43B and the MH2 os coxae. Indeed, the MH2 pelvis has been argued to display some *Homo*-like features<sup>20,28</sup>, and craniodental characters tentatively suggest a close common ancestor<sup>33</sup>. Alternatively, these results may simply reflect variability in the expression of shared primitive features among *Australopithecus*/*Paranthropus* and early *Homo* species. While MH2 is closer in absolute size to DNH 43 and represents *A. sediba* from the nearby Malapa site in South Africa, which is contemporaneous with the DMQ assemblage<sup>2</sup>, the UPGMA link with OH 28 should be considered with greater caution based solely on the three included indices. OH 28 is much larger in absolute dimensions (Figure 2B–D) and exhibits an exceptionally robust acetabulocristal buttress (Supplementary figure 4) – characters expressed strongly in other ossa coxae attributed to early *Homo* sp.<sup>34</sup> but not evident in either DNH 43B or MH2. Indeed, Rose<sup>34</sup> noted close overall similarities among specimens such as OH 28, KNM-ER 3228, and recent *H. sapiens* vis-à-vis *Australopithecus* and *Paranthropus* in terms of iliac features.

Unfortunately, specimens SK 50 and TM 1605, usually considered to represent *P. robustus* from the sites of Swartkrans and Kromdraai, respectively<sup>5</sup>, could not be included in the cluster analysis because damage precludes accurate measurement of the auricle breadth in both specimens and acetabular diameter in TM 1605. However, in preserved anatomy, these specimens exhibit apparently plesiomorphic characteristics of the lower os coxae. SK 50 has the widest tuberoacetabular sulcus relative to the acetabular diameter of any specimen in the sample and the acetabulosacral buttress is gracile



**Figure 3:** Dendrogram from the UPGMA cluster analysis.

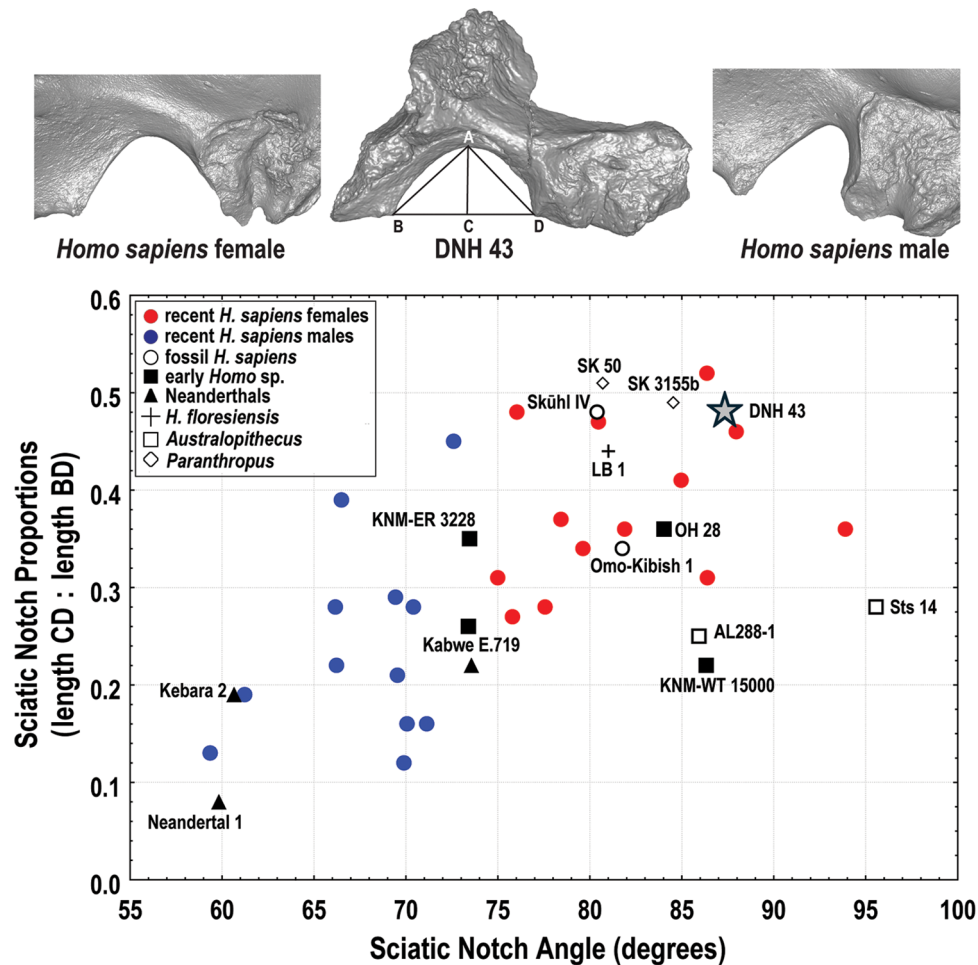
relative to the acetabulosacral load arm in both SK 50 and TM 1605. It should be cautioned that even for these specimens from Swartkrans (whose craniodental sample is overwhelmingly attributed to *P. robustus*), the association with *Paranthropus* is circumstantial, lacking direct association with taxonomically identifiable jaws and teeth, and early *Homo* also occurs at the site.

*P. robustus* is the most frequently sampled hominin at DMQ<sup>1,35,36</sup>, which has produced remarkably complete cranial remains of the species<sup>37,38</sup>. The morphology preserved in DNH 43 cannot rule out an affiliation with that taxon corresponding with the initial description.<sup>9</sup> However, early *Homo* (including *Homo erectus sensu lato*) has been documented at DMQ<sup>2</sup>, so caution is warranted. Associated craniodental and pelvic remains of definitive early *Homo* are scarce generally<sup>10,11</sup> and unknown from the South African record, although *H. naledi* may represent a relatively plesiomorphic member of the genus<sup>10</sup>. Much of the postcranial skeleton is variable among fossil samples thought to represent taxa of truly early *Homo*.<sup>11</sup> *Homo naledi* pelvic remains from the Rising Star Cave system preserve fragmented ossa coxae that evince an *Australopithecus/Paranthropus*-like lateral iliac flare with an anteriorly placed and lightly expressed acetabulocrystal buttress and an absolutely narrow acetabulosacral buttress but short 'Homo-like' load arm<sup>21</sup> and a narrow tuberoacetabular sulcus. Notably, the LB1 *H. floresiensis* pelvis also exhibits a laterally flared ilium similar to *Australopithecus* and *Paranthropus*.<sup>39</sup> Although LB1 clusters with a single recent male *H. sapiens* individual in the UPGMA analysis (Figure 3) due primarily to its relatively large auricular surface (Figure 2B), it shows a relatively wide tuberoacetabular sulcus (Figure 2C) and gracile acetabulosacral buttress relative to load arm (Figure 2D), which is considered to be plesiomorphic.<sup>39</sup> The small body size of both *H. floresiensis* and *H. naledi* and their somewhat different morphologies of the lower os coxae suggest variation in these traits may not be the result of allometric effects (i.e. 'Homo-like' features do not necessarily covary with differences in

overall body size). Uncertainty concerning the magnitude of variation in these features among early diverging members of the genus *Homo* makes it difficult to evaluate their taxonomic utility vis-à-vis DNH 43.

Sex attribution of the DNH 43 pelvis remains uncertain. The specimen has an 'open' greater sciatic notch and the apex of the notch is situated anteriorly, giving it a semicircular appearance similar to what is observed commonly in the pelvises of recent *H. sapiens* female individuals. However, whether sexually dimorphic aspects of the modern human pelvis also characterise fossil taxa is not established.<sup>13</sup> Furthermore, the acetabular diameter of DNH 43 is somewhat larger than all *Australopithecus* and *Paranthropus* specimens sampled (Table 1); thus, an appeal to overall size does not further clarify whether DNH 43 is male or female. The rest of the fossils span the distribution of male and female individuals for both greater sciatic notch variables (Table 1 and Figure 4), although there is some clustering by group. If the sexually dimorphic features of recent *H. sapiens* characterise the fossil populations, then these clusters probably represent sampling error (i.e. mostly male or female individuals sampled in a fossil group). Neanderthal specimens included in the sample all exhibit a more 'male-like' sciatic notch (however, Tabun C1, which is thought to be female<sup>32</sup> could not be measured due to taphonomic damage), while the 'early *Homo* sp.' group all fall within the female distribution or close to the male-female borderline. Interestingly, all specimens typically assigned to *Paranthropus* fall at the high end of the female distribution of the two variables along with DNH 43. SK 50 exhibits some taphonomic damage to the posterior that might have a small effect on sciatic notch measurements. However, our observations on the fossil indicate that the crushing would have had at most the effect of narrowing the observed notch. As such, our metrics should be considered a minimum and 'reconstruction' of the damaged area would further exaggerate the already 'female-like' qualities of the morphology. In contrast, pelvises attributed to *A. afarensis* (AL 288-1), *A. africanus* (Sts 14), and the subadult *H. erectus* (KNM-WT 15000) show an unusual combination of a wide sciatic notch angle ('female-like') coupled with a more posterior notch apex ('male-like') (Figure 4). However, the KNM-WT 15000 measurement is based on fairly heavy reconstruction of the pelvis<sup>29</sup>, which warrants some caution (although in our assessment it provides a reasonable estimate). Based on a broader evaluation of pelvic morphology, AL 288-1 and Sts 14 are generally considered to represent the female sex of their respective taxa due to small size<sup>40</sup> (but see Hausler and Schmid<sup>41</sup>) and KNM-WT 15000 is considered to represent a young male individual.<sup>29</sup> Among Neanderthals, Krapina 207 is an older subadult individual with an unfused iliac crest, which also falls closest to the recent human female distribution and there could be an ontogenetic influence on sciatic notch form, although this is uncertain (Figure 4). Determining whether specimens such as KNM-WT 15000, AL 288-1 and Sts 14 are outliers, or if the unusual combination of these greater sciatic notch features has phylogenetic valence, will require an expanded fossil sample.

Compared with available comparative material (Table 2), the DNH 43 pelvis is wide mediolaterally when considering a reasonable proxy of overall body size (superioinferior acetabular diameter). A mediolaterally broad pelvis is often considered a plesiomorphic trait associated with *Australopithecus*, although it is retained in the few available pelvises of early *Homo*.<sup>4,13</sup> The mediolateral breadth of DNH 43 is especially pronounced when considering the width between the hip joints (biacetabular breadth) and the narrowest point in a hominin birth canal (bispinous breadth). Indexed against the acetabular diameter, the biacetabular breadth of DNH 43 is 301% and bispinous breadth is 257% that of the acetabulum size. These relative dimensions are exceeded only in *A. afarensis* specimen AL288-1 (335% and 274%) and the BSN49/P27 pelvis (possibly a female *H. erectus*) at 320% and 280% of the superoinferior acetabular diameter.<sup>12</sup> The *A. sediba* specimen MH2 is similar to DNH43 in biacetabular breadth relative to the acetabular diameter (300%). Among other absolutely wide fossil pelvises, the biacetabular diameter of Kebara 2 is 228% that of the acetabular diameter (no bispinous diameter is available), although Kebara 2 is probably a male individual. The Sima de los Huesos Pelvis 1 biacetabular and bispinous breadths are respectively 235% and 198% of the reported<sup>12</sup> superoinferior diameter of the acetabulum (58.8 mm).



**Figure 4:** Examples of greater sciatic notch morphology (top: oriented in medial view with sacroiliac joint to the right) in DNH 43 versus a recent *Homo sapiens* female and male and a bivariate plot (bottom) of the sciatic notch proportions versus the sciatic notch angle in DNH 43 and the comparative sample.

In contrast to the early hominin fossil sample, in female *H. sapiens*, the mean biacetabular and bispinous breadths (Table 2) are 230% and 225% that of the mean acetabular diameter, while the same male dimensions are 196% and 172%, respectively. The exceptionally wide bispinous and biacetabular breadths of DNH 43 suggest a capacious pelvic outlet that might indicate a non-rotational birth mechanism as sometimes inferred for *Australopithecus*.<sup>25,42</sup> A pelvis that is mediolaterally broad from hip joint to hip joint may also influence lower limb kinematics by maintaining stride length in individuals with relatively shorter hindlimbs via the recruitment of greater pelvic rotation.<sup>43–45</sup> However, such an arrangement does not appear to increase locomotor cost.<sup>46</sup> A better sample of articulated fossil pelvises will shed further light on our understanding of the evolution of hominin encephalisation and its evolutionary interplay with locomotor biomechanics, although much of the theoretical and empirical basis of this relationship remains controversial.<sup>3,7,47–51</sup>

The pelvic incidence of DNH 43 (Table 2; Supplementary figure 3) indicates an anterior tilt to the sacrum and concomitant lumbosacral alignment that would facilitate a human-like lumbar lordosis.<sup>15</sup> Although the 56° pelvic incidence of DNH 43 is higher than the human mean and values for single specimens of *A. afarensis* (42°) and *A. africanus* (45°), all three of these fossils fall comfortably within the variation documented for recent *H. sapiens*.<sup>15</sup> Sts 14 is within one lower standard deviation of the human mean of 54° and AL 288-1 is well within the range (32–84°) (Table 2). In contrast, DNH 43 and the *Australopithecus* specimens highlight the peculiarly low pelvic incidence demonstrated for members of the Neanderthal lineage.<sup>15</sup> Kebara 2 and both Sima de los Huesos pelvises fall over two standard deviations below the human mean (Table 2), although pathology in Pelvis 1 from Sima de los Huesos might influence pelvic incidence.<sup>15</sup> Further

work investigating variation in late Pleistocene spinopelvic anatomy is warranted. Nevertheless, these data suggest spinopelvic mechanics in *Australopithecus* (and likely *Paranthropus* if DNH 43 indeed represents the genus) were similar to recent *H. sapiens* in how they positioned the torso and head over the hip joint during bipedal posture and locomotion.

## Conclusion

Overall, the quantitative analysis presented here is congruent with prior qualitative results reflecting the primitive features of DNH 43. *Paranthropus robustus* is a reasonable taxonomic assignment given the overall plesiomorphic morphology and that *P. robustus* remains dominate the DMQ hominin assemblage. However, caution is warranted as *H. erectus sensu lato* is documented at DMQ<sup>2</sup> and well-associated cranial and postcranial remains are scarce for both *Paranthropus* and early *Homo*. Because phylogenetic analyses based primarily on craniodental character sets indicate that *Paranthropus* and *Homo* may represent sister groups<sup>33</sup>, these taxa would be expected to share some postcranial features based on that common ancestry. Consequently, basal members of *Homo* might be difficult to identify based solely on the pelvic traits visible in DNH 43. Thus, taxonomic assignment of postcranial remains such as DNH 43 may be subject to revision with a better understanding of the postcranial anatomy of *Paranthropus* and early *Homo*, which overlapped chronologically in both southern<sup>2</sup> and eastern Africa<sup>52</sup>.

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**Table 2:** Measurements of the articulated pelvis

Taxon/group and specimen(s)	Mediolateral breadth of pelvic inlet (mm)	Biacetabular breadth (mm)	Bispinous breadth (mm)	Pelvic Incidence (degrees)
<b>DNH 43<sup>a</sup></b>	108.9	123.6	106.3	56
<b><i>Australopithecus afarensis</i></b>				
AL 288-1 <sup>b</sup>	132	118	101	42 <sup>c</sup>
<b><i>Australopithecus africanus</i></b>				
Sts 14 <sup>d</sup>	116.8	107.5	89.0–93.1	45 <sup>c</sup>
Sts 65 <sup>e</sup>	101.5 (109)	–	–	–
<b><i>Australopithecus sediba</i></b>				
MH 2 <sup>f</sup>	117.6	122.3	–	–
<b><i>Homo erectus</i></b>				
KNM-WT 15000 <sup>g</sup> (subadult)	100	102	–	–
<b><i>Homo cf. erectus</i></b>				
BSN 49/P27 <sup>h</sup>	124.5	131.0	114.5	–
<b><i>Homo heidelbergensis</i></b>				
Sima de los Huesos:				
Pelvis 1 <sup>i</sup>	139.3	138	116.4	28 <sup>c</sup>
Pelvis 2	–	–	–	33 <sup>c</sup>
<b>Neanderthal</b>				
Kebara 2 <sup>j</sup>	138	129	–	34 <sup>c</sup>
Tabun C1 <sup>k</sup>	131	133.8	–	–
<b><i>Homo sapiens</i> (fossil)</b>				
Ohalo II	–	–	–	52 <sup>c</sup>
<b><i>Homo sapiens</i> (recent)<sup>l</sup></b>	132.5 ± 7.5	121.1 ± 8.1	117.2 ± 1.0	54 ± 10 <sup>c</sup>
	(female <i>n</i> = 218)	(female <i>n</i> = 163)	(female <i>n</i> = 143)	range:
	1274 ± 7.4	111.2 ± 6.7	97.3 ± 9.2	32 – 84
	(male <i>n</i> = 237)	(male <i>n</i> = 200)	(male <i>n</i> = 162)	( <i>n</i> = 53)
<b><i>Pan troglodytes</i><sup>m</sup></b>	100 ± 12.6	105.8 ± 35.6	–	29 ± 6 <sup>c</sup>
	<i>n</i> = 29	<i>n</i> = 29		<i>n</i> = 8

<sup>a</sup> DNH 43: all measurements from current study

<sup>b</sup> AL 288-1 breadth of pelvic inlet and bispinous breadth from Tague and Lovejoy<sup>25</sup>; biacetabular breadth from Berge and Goularas<sup>17</sup> based on Schmid<sup>26</sup>

<sup>c</sup> All pelvic incidence data (except for DNH 43) are from Been et al.<sup>15</sup>

<sup>d</sup> Sts 14: breadth measurements are from Berge and Goularas<sup>17</sup>

<sup>e</sup> Sts 65: breadth of the pelvic inlet (with higher-end estimate based on reconstruction with AL 288-1 sacrum) from Claxton et al.<sup>27</sup>

<sup>f</sup> MH2: breadth measurements from Kibii et al.<sup>28</sup>

<sup>g</sup> KNM-WT 15000: breadth measurements from Walker and Ruff<sup>29</sup>

<sup>h</sup> BSN49/P27: breadth measurements from Simpson et al.<sup>13</sup>

<sup>i</sup> Sima de los Huesos Pelvis 1: breadth measurements are from Bonmati et al.<sup>12</sup>

<sup>j</sup> Kebara 2 biacetabular breadth is the mean of two reconstructions from Adegboyega et al.<sup>30</sup> and bispinous breadth is from Rak<sup>31</sup>

<sup>k</sup> Tabun C1: pelvic inlet breadth from Weaver and Hublin<sup>32</sup> and biacetabular breadth measured on the 3D reconstruction from Weaver and Hublin<sup>32</sup>

<sup>l</sup> Recent *Homo sapiens* breadth of pelvic inlet, biacetabular breadth, and bispinous breadth data represent the weighted mean of six populations ± standard deviations from Tague<sup>16</sup>

<sup>m</sup> *Pan troglodytes* mediolateral breadth of pelvic inlet and biacetabular breadth data from Berge and Goularas<sup>17</sup>



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## Data availability

All the data supporting the results of this study are included in the article itself and in the [supplementary material](#). For the current study, the DNH 43 pieces were surface scanned using an Artec Space Spider. The resulting surface scans of the individual pieces of DNH 43 as well as the partial reconstruction are provided in the University of the Witwatersrand's Drimolen Collection at <https://human-fossil-record.org>.

## Declarations

We have no competing interests to declare. We have no AI or LLM use to declare. This work appears in whole or in part in a thesis/dissertation.

## Authors' contributions

E.B.: Conceptualisation, methodology, sample analysis, data collection, validation; writing – the initial draft; writing – revisions. A.S.H.: Methodology, data collection, validation, writing – revisions. A.G.W.: Methodology, validation, writing – revisions. M.S.M.: Methodology, data collection. M.W.T.: Methodology, data collection. S.E.B.: Conceptualisation, methodology, data collection, project leadership, project management. A.I.R.H.: Conceptualisation, methodology, data collection, project leadership, project management, funding acquisition. D.S.S.: Conceptualisation, methodology, project leadership, project management, funding acquisition, writing – revisions. C.M.O.: Conceptualisation, methodology, sample analysis, validation, data collection, student supervision, project leadership, project management, funding acquisition, data curation, writing – the initial draft, writing – revisions. All authors read and approved the final manuscript.

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