Contents lists available at ScienceDirect

Journal of Human Evolution

Virtual reconstruction of the *Australopithecus africanus* pelvis Sts 65 with implications for obstetrics and locomotion

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A B S T R A C T

Characterizing australopith pelvic morphology has been difficult in part because of limited fossilized pelvic material. Here, we reassess the morphology of an under-studied adult right ilium and pubis (Sts 65) from Member 4 of Sterkfontein, South Africa, and provide a hypothetical digital reconstruction of its overall pelvic morphology. The small size of the pelvis, presence of a preauricular sulcus, and shape of the sciatic notch allow us to agree with past interpretations that Sts 65 likely belonged to a female. The morphology of the iliac pillar, while not as substantial as in *Homo*, is more robust than in A.L. 288-1 and Sts 14. We created a reconstruction of the pelvis by digitally articulating the Sts 65 right ilium and a mirrored copy of the left ilium with the Sts 14 sacrum in Autodesk Maya. Points along the arcuate line were used to orient the ilia to the sacrum. This reconstruction of the Sts 65 pelvis looks much like a "classic" australopith pelvis, with laterally flared ilia and an inferiorly deflected pubis. An analysis of the obstetric dimensions from our reconstruction shows similarity to other australopiths, a likely transverse or oblique entrance of the neonatal cranium into the pelvic inlet, and a cephalopelvic ratio similar to that found in humans today.

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1. Introduction

The pelvis plays a key role in both locomotion and obstetrics, making it a particularly informative skeletal element for reconstructing the paleobiology of a hominin species. Pelvic morphology differs substantially between humans and apes (Weidenreich, 1913; Schultz, 1949; Robinson, 1972; Aiello and Dean, 2002), reflecting interspecific differences in body posture, locomotion, and obstetrics. Some of the morphologies related to bipedalism in the hominin pelvis are hypothesized to have made parturition more challenging—the "obstetrical dilemma" (Washburn, 1960, but see; Dunsworth et al., 2012; Warrener et al., 2015)—and many past studies have attempted to identify the relative importance of bipedality or childbirth on different pelvic morphologies (Rosenberg, 1992; Rosenberg and Trevathan, 1995; Kurki, 2011;

Wells et al., 2012), including in fossils (Tague and Lovejoy, 1986; Simpson et al., 2008; Kibii et al., 2011). However, the hominin fossil record has yielded relatively little pelvic material compared to other regions of the skeleton, impeding our ability to test models of locomotor and obstetric evolution in early hominins. The limited fossil pelvic material that has been preserved usually needs extensive reconstruction before analysis, as the thin cortical bone and highly curved surfaces of the pelvis make it susceptible to deformation, distortion, and crushing during taphonomic processes.

The subjectivity involved in said reconstructions of distorted fossils can result in a large degree of variability in the interpretation of hominin pelvic material. The two "classic" australopith pelves, A.L. 288-1 and Sts 14, have themselves been reconstructed multiple times. The contrasting reconstructions of A.L. 288-1 by Lovejoy (1979; Tague and Lovejoy, 1986), Schmid (1983), and Häusler and Schmid (1995) show differences in the orientation of the iliac blades and the inlet shape, with implications for both locomotion and obstetrics. Berge and Goularas (2010) see these differing

reconstructions as largely a function of the crushed and distorted sacroiliac joint in the A.L. 288-1 pelvis, illustrated clearly in Lovejoy (2005a:104, his Fig. 8). Sts 14 was originally reconstructed by Robinson (1972) only after dissolving away breccia using acetic acid and then using a substantial amount of plaster and glue, as well as a metal rod meant to reinforce the pubis (Day, 1973, 1978). Häusler and Schmid (1995) reconstructed Sts 14 by removing much of Robinson's plaster and instead physically mirror imaging the missing sections. They produced two reconstructions due to anatomical ambiguities at the sacroiliac joint and iliopubic angle, which Berge and Goularas (2010) attempted to correct for in their digital reconstruction.

These past attempts underscore that pelvic reconstructions, although enormously useful as a visual aid, represent morphological hypotheses. Teams working with the same set of fossils can produce different reconstructions and come to quite different conclusions (e.g., Ponce de León et al., 2008; Weaver and Hublin, 2009). One way to address the problem of reconstructive ambiguities in key fossils such as A.L. 288-1 and Sts 14 is to analyze and reconstruct additional fossil material with comparable anatomies, whereby a reconstruction of one fossil can be "checked" against another. Here, we study a partial but relatively unknown and mostly undistorted os coxae (i.e., an innominate or hipbone) from Sterkfontein Member 4, Sts 65, and provide a digital reconstruction that allows us to add to the ongoing dialogue about locomotion and obstetrics in *Australopithecus*.

Sts 65 is a right ilium and partial pubis of an adult hominin (Fig. 1). According to Tobias et al. (1977), it was recovered by John Robinson from Member 4 of Sterkfontein in the 1949 field season. Though the dates of the fossiliferous deposits at Sterkfontein have been contentious, recent work using U−Pb and U−Th techniques have allowed Pickering and Kramers (2010) to provide an age range for Member 4 of 2.0−2.6 Ma, using the flowstone bracketing the fossiliferous layers. Communication with the Ditsong Museum revealed little in the way of a specific day of discovery or stratigraphic provenance, as field notes from this season are unavailable or missing. Tobias et al. (1977) indicate that Sts 65 was recovered from the Sterkfontein main quarry (formerly called the 'Type Site'). Pickering and Kramers (2010) put the position of Broom's original excavations where Sts 5 was found at ~2.0 Ma, but the exact stratigraphic relationship between Sts 5 and Sts 65 is unknown. Although Sts 65 was not discovered with any associated craniodental remains, there is no reason to assume that it is not *Australopithecus africanus*. However, R. Clarke (1988, 2008, 2013) has proposed that there may be more than one species of australopith at Sterkfontein. This claim is difficult to assess until further material from this purported second species is described in more detail. Nevertheless, it is a consideration as we examine similarities and differences between Sts 65 and Sts 14.

Two other postcranial elements were originally associated with Sts 65, a proximal femur and a lumbar vertebral fragment. Wolpoff (1973) and McHenry (1974) note that the femur likely belongs to a baboon and we concur. Robinson (1972) mentions an associated lumbar vertebra, which consists only of the bases of the pedicles and the dorsal surface of the vertebral body. However, this lumbar vertebra is not currently curated with the pelvis at the Ditsong Museum and its whereabouts are currently unknown (as of 7/4/ 2013; Potze, pers. comm). Furthermore, Robinson (1972:113) writes that "This specimen is so fragmentary that there is no certainty that it actually belongs to *Homo africanus*, though I think it is likely that this is so." Given the uncertainty of both its taxonomic attribution and its current whereabouts, its utility in our study of the Sts 65 pelvis is limited.

Though the anatomy of Sts 65 has not been described in explicit detail, it is not without mention in the literature, mostly in contrast to the more complete Sts 14. Robinson (1972) devotes the most space to a discussion of Sts 65. Notably, in comparison with Sts 14, Robinson (1972) comes to the tentative conclusion that Sts 65 belongs to a male, citing a more flexed greater sciatic notch and the thickened iliac pillar (or acetabulocristal buttress). However, Wolpoff (1973), noting the presence of a preauricular sulcus, raises the possibility that Sts 65 is female, though he does also note that it is more "robustly developed" than Sts 14. Day (1978) also suggests that the pelvis is from a female, citing the "preauricular groove" as the primary piece of evidence. Lovejoy et al. (1973) mention Sts 65 in passing as part of a catalog of australopith pelvic material, though it is treated lightly in the body of the paper. McHenry (1975), as well as Häusler and Berger (2001), mention Sts 65 to note the presence of a pronounced iliac pillar, though they also observe that it is positioned differently in modern humans, as is the case in all australopiths. McHenry (1975) also reports some metrics on Sts 65, in the context of describing SK 3155. Both Arsuaga and Alonso (1983) and Arsuaga and Carretero (1994) describe the greater sciatic notch of Sts 65 as extremely open, a trait that they also ascribe to Sts 14, insinuating that both are likely female. Hager (1989) also identifies the sex of Sts 65 as female based on the posterior ilium, presumed pelvic inlet shape, and greater sciatic notch contour.
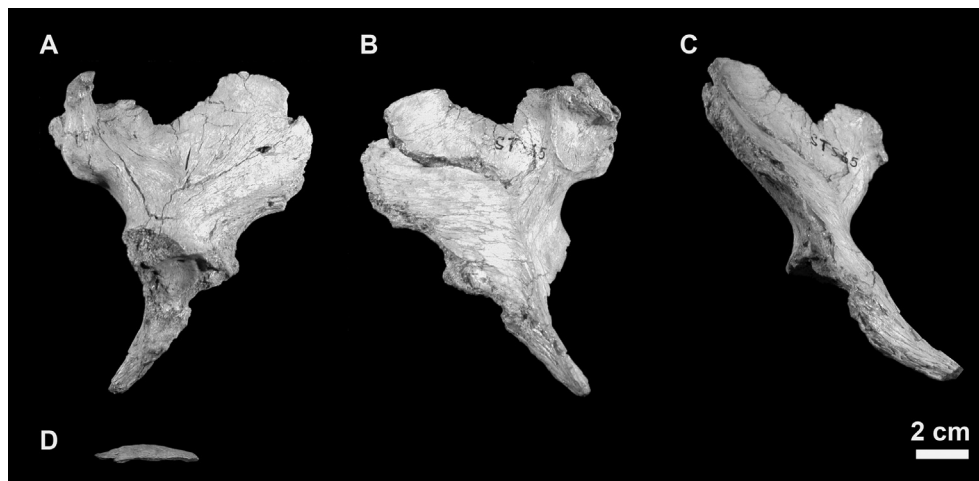

Figure 1. The Sts 65 pelvis. A) External view, B) Internal view, C) Anterior view, D) Piece of iliac crest.

The Sts 65 pelvis is overdue for a more complete analysis. Modern techniques, such as 3D surface modeling and digital reconstruction, provide us access to data that were previously unavailable. The presence of another semi-complete australopith reconstruction allows us to compare it directly with modern human, ape, and hominin pelves and their reconstructions to assess variation and to test locomotor and obstetric hypotheses in *Australopithecus*.

2. Materials and methods

2.1. Anatomical description

Sts 65 is a right partial hipbone preserving parts of the ilium and pubis (Fig. 1). The ischium is not preserved. The fossil is badly weathered in places and has several large cracks. Due to Robinson's choice of an acid preparation technique, the bone was dipped in a varnish-like hardener that gives the appearance of the bone being held together with glue in places. However, distortion is minimal, with the exception of some lateral translation of the iliac tuberosity. The superior iliac breadth is a minimum of 97.3 mm. Almost the entirety of the superior pubic ramus is preserved, which is unusual in a fossil hominin. Unfortunately, the pubic symphysis itself is not preserved. Following Tague and Lovejoy (1986), the measurement of the iliopectineal line from the apex of the auricular surface to the end of the preserved pubis is 9.7 cm, which is only slightly shorter than Sts 14 at 10.0 cm, and substantially shorter than A.L. 288-1 at 12 cm. The pubis angles inferiorly as in other known australopiths, with the exception *Australopithecus sediba* (Kibii et al., 2011). The pubis is heavily weathered with cracks running along the main axis of the superior ramus. A fragment of cortical bone has flaked from the superior ramus just medial to the acetabulum. There is a strong pectineal line that remains raised throughout much of the length of the pubis. At the junction with the ilium, the pectineal line becomes less pronounced and grades into an arcuate line, which can be traced as an elevated surface to the border with the auricular surface. The dorsal surface of the superior pubic ramus presents heavily weathered cracks running primarily along its long axis. There is a single vertical crack 19.7 mm from the medial end of the preserved pubis.

A jagged break separates the ilium from an unrecovered ischium, and thus the ischial spine is not present. The bone around the greater sciatic notch is very well preserved, lacking the weather cracks seen in other areas of the fossil. The notch as preserved is 26.5 mm wide from the edge of the auricular surface to the break in the ilium, and 10.8 mm deep relative to a straight line connecting these points. It is U-shaped and quite symmetrical. Just lateral to the greater sciatic notch is a thickening of bone, the acetabulosacral buttress, which measures 16.4 mm at its thickest point. The auricular surface is well preserved, showing a moderately fine-grained surface texture with very little evidence of billowing. It is 21.7 mm in maximum length (mostly SI) and 17.3 mm in width, and has a subtle lunate shape. Posterior and inferior to the auricular surface is a non-articular part of the bone in which a large (2.6 mm diameter) circular puncture hole can be found. Inferior to the auricular surface is a preauricular sulcus measuring 2.9 mm wide and 13.3 mm in preserved length (Fig. 2).

The iliac fossa has many weathering cracks. There is a large crack, 53.5 mm long and in places as wide as 5.2 mm, mediolaterally oriented through the middle of the iliac fossa. However, this crack does not penetrate to the dorsal side of the ilium save for a circular puncture, and the surrounding bone does not appear to have any distortion. The iliac fossa is generally flat, but becomes slightly concave in the center of the ilium. There is damage to the anterior inferior iliac spine (AIIS), though the remnants of it can be

Figure 2. The preauricular surface of Sts 65. The preauricular sulcus in Sts 65 is ambiguous in character. While there does not appear to be any distinct pitting, it is also closed on its lateral border. Note the lack of piriform tubercle. The sulcus most clearly resembles the "i-f-f" morph as defined in Bruzek (2002).

seen just superior to the acetabulum. The cortex overlying the AIIS has been stripped away, exposing the underlying trabecular bone. The anterior inter-spinal notch is preserved and is 24.6 mm wide and 7.5 mm deep, separating the damaged AIIS from the inferior border of the anterior superior iliac spine (ASIS), which has also been stripped away from the iliac crest, exposing underlying trabecular bone. A large portion of the anterior iliac crest (34.1 mm) is sheared away anteriorly, leaving exposed trabecular bone. This is not an unfused apophyseal surface given the exposure of formed spongy bone and the lack of the irregular cartilaginous surface of an epiphysis. This damaged anterior iliac crest terminates in a missing part of the ilium—the start of the large crack in the center of the ilium. Beyond the crack, the iliac crest (with exposed trabecular bone) continues another 26.9 mm before reaching a large missing portion of the ilium and iliac crest. However, the most posterior 18.3 mm of the ilium is preserved. The posterior superior iliac spine (PSIS) is well preserved, though there is a small piece of this anatomy that has flaked off and is held in place by glue. There are cracks circling the base of the iliac tuberosity indicating that it has been distorted, resulting in a dorsal and slightly inferior shift to this entire region of the bone. This shifting has resulted in what McHenry (1975) called a "peculiar" posterior projection, though we regard this as distortion and not normal anatomy. There is a clear separation between the medial edge of the auricular surface and the distorted fragment of the posterior ilium, which is at most 4.7 mm wide. Bringing these two pieces together again would result in the posterior inferior iliac spine being slightly more anterior and superior than is currently found. Perhaps most notable about the PSIS is the presence of a fused apophysis. There is a faint epiphyseal line still detectable, indicating a relatively recent fusion, but this anatomy leaves little doubt that Sts 65 is from at least a young adult.

The dorsal (gluteal) fossa is heavily weathered with cracks, many of which emanate from a region just superior to the acetabulum and proceed throughout the ilium (as illustrated by Robinson [1972:Fig. 32]). The gluteal fossa is concave posteriorly, but becomes flatter anteriorly. Along the anterior portion of the ilium is a strong iliac pillar, ~13.0 mm in maximum thickness. The position of the Sts 65 iliac pillar has been described as anteriorly-positioned, similar to other australopiths and unlike the more posterior position found in *Homo* (Ward et al., 2015). The iliac crest

is damaged preventing one from tracing the iliac pillar superiorly to the iliac tubercle. There is a 6.3 × 2.6 mm hole at the terminus of a crack just posterior to the iliac pillar, which penetrates obliquely through the ilium and emerges through the large crack anteriorly. Superior to this hole, just posterior to the iliac pillar, is a faint but palpable linear rugosity—the anterior gluteal line. Posteriorly, there is a faint vertical rugosity—the posterior gluteal line.

The entire rim of the acetabulum is weathered away, and the entire ischium together with the inferior portion of the ilium is broken off, producing a 22.4 mm mediolateral (ML) × 20.6 mm anteroposterior (AP) triangular shaped region with exposed trabecular bone. The most lateral part of this region is the rim of the acetabulum. The articular surface of the acetabulum is a maximum of 27.2 mm ML and 22.3 mm AP. There is a circular hole in the superior part of the acetabulum, perhaps a carnivore tooth mark.

Associated with Sts 65 is a small piece of the iliac crest. It is 52.2 mm in total length and about 8.5 mm at its thickest point. This is not an unfused epiphysis since the break reveals internal spongy bone. In superior view, this part of the crest is sigmoid in shape. It is not thick enough to be part of the most anterior section of the broken iliac crest (anterior to the large crack). It appears to fit best, both in thickness and in curvature, articulating with the anterior section of the iliac crest just posterior to the large crack. However, there is no direct contact between this piece and the rest of the ilium, and no attempt was made to virtually attach them.

2.2. Reconstruction

The original fossil was examined by two of us (AGC and JMD) and scanned with a NextEngine 3D surface laser scanner at the Ditsong Museum in Pretoria, South Africa. The digital scan was imported as a polygonal surface in the stereolithography (.stl) file format and mirrored in Maya (Autodesk Inc., 2012). As there is no sacrum associated with Sts 65, the Sts 14 sacrum was used as the best available match in terms of size (see below). We scanned a cast of the sacrum and mirrored it in Maya using the methods outlined below. Following Berge and Goularas (2010), we digitally removed the reconstructed right half and mirrored the preserved left half of the Sts 14 sacrum by choosing three landmarks: one on the anterior sacrum and two posteriorly. The anterior landmark corresponds to the point just superior to the broken transverse line (the superior-most border between the fused sacral vertebrae). The posterior landmarks correspond to apices on the sacral crest. A plane of symmetry was constructed using these three points, and the anterior point was selected to serve as the pivot during the transformations. The Mirror Cut tool in Maya was used to then mirror the right half along the plane of symmetry and pivot point. This mirroring of the sacrum was necessary due to the substantial plaster reconstruction of the right half by Robinson. A series of comparative linear measurements were taken on originals of both Sts 14 and Sts 65 (see Table 1) to determine if any scaling of the Sts 14 sacrum was necessary. Though they have differences in preservation, we

found that Sts 65 and Sts 14 have eight measurements that are comparable. These metrics are partially based on those found in Wolpoff (1973), though all measurements in this paper were taken by AGC. Those on Sts 65 and Sts 14 were taken on the original fossils, the others were taken from high-quality casts from the collection of Boston University. The right half of Sts 14 was measured, as it is the more complete hipbone. The logged geometric mean (LGM) of a series of linear measurements can be used as a reliable estimate of overall size (Mosimann and James, 1979; Madar et al., 2002). Given that the LGMs of Sts 14 and Sts 65 are virtually identical, scaling the Sts 14 sacrum for our reconstruction does not appear to have any support.

Because of the undistorted state of preservation of the Sts 65 fossil at the sacroiliac joint, our reconstruction was relatively simple (Fig. 3). First, we rotated the ilium with respect to the sacrum. Three points along the apex of the iliac arcuate line were defined, along with three corresponding points on the sacral arcuate line. A curve-fitting algorithm implemented in Maya effectively created an arc using both point triads that followed their respective arcuate lines. Planes were constructed through both arcs and then aligned until the arcs through the linea terminalis formed an uninterrupted curve. This is largely similar to the method of iliosacral alignment used to reconstruct the A. sediba pelvis (Kibii et al., 2011: Fig. S3). Corresponding points on either side of the auricular surfaces were chosen as well, in order to minimize the distance between the two elements. As Berge and Gommery (1999) point out, the epiphyseal lamina on the anterior part of the left sacral auricular surface of Sts 14 is missing, likely due to its juvenile age. Thus, we did not minimize the distance between the anterior-most points on the auricular surface, instead leaving ~5 mm of space between them. Once these alignments were made, the ilium was mirrored and matched on the left side using the same methods. Researcher intervention was kept to a minimum once the points were selected along the arcuate line, but some slight manual manipulation was necessary in order to overcome digital overlap of the elements. Measurements of the digital reconstruction were taken in Maya, as well as the NIH software ImageJ. Pelvic measurements (see Table 2) were primarily derived from those defined in Tague and Lovejoy (1986), Häusler and Schmid (1995), and Berge and Goularas (2010).

The pubic symphysis is unfortunately not preserved. This means that much care must be placed in orienting the reconstruction at the sacroiliac joint, as we have no way of independently confirming that we have angled the hipbones correctly without the anterior constraints provided by the pubic symphysis. However, the iliopectineal line in Sts 65 (9.7 cm) is close in length to the same measurement in Sts 14 (10.0 cm). Furthermore, direct digital overlay of the two specimens (Supplementary Online Material [SOM] Fig. 1) strongly suggests that the pubis in Sts 65 is nearly complete. Nevertheless, the absence of the pubic symphysis forces us to estimate the anteroposterior dimension of the pelvic inlet by connecting the preserved medial part of the Sts 65 pubis via inferred lines. To provide room for error, we did this in three

Table 1
Comparative measurements on fossil hominin pelves.

| Metric	Sts 65	Sts 14	A.L. 288-1	ER 3228	OH28	SK 3155
Auricular surface height	22	26	29	43	44	35
Auricular surface width	17	16	15	20	19	17
Iliac pillar thickness	13	12	11	24	18	15
PIIS to anterior notch	78	79	72	100	101	78
Greater sciatic notch to anterior notch	48	47	50	71	68	53
Auricular surface to pubis	83	81	NA	NA	NA	NA
Posterior arcuate line	28	23	30	20	28	25
Arcuate line to anterior notch	32	35	30	58	56	47
LGM	1.516	1.513	1.456	1.604	1.601	1.520
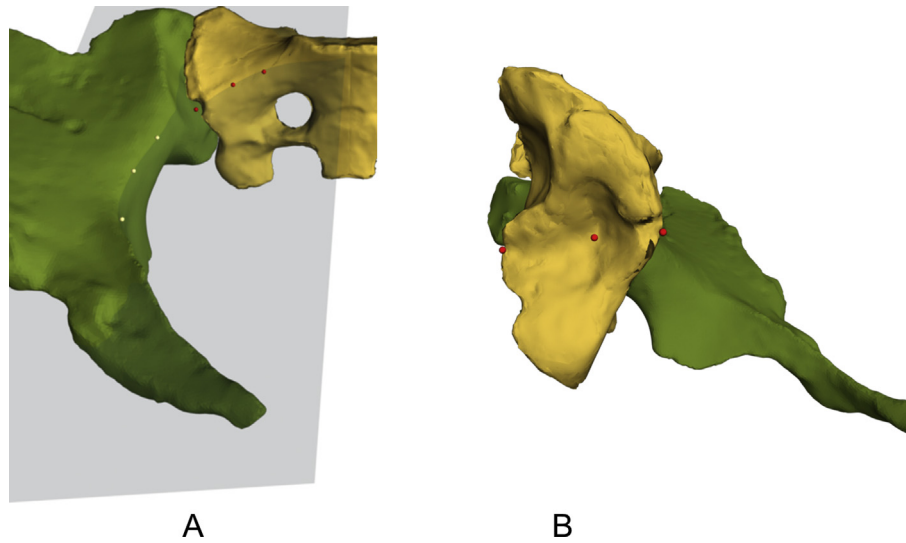
Figure 3. Method of reconstruction. A) Shown are the points chosen at the apex of the arcuate line on both the sacrum and the ilium, as well as the plane used to align them. Note the space corresponding to the missing epiphyseal lamina at the anterior aspect of the sacroiliac joint. B) The points on the auricular surface used to align the sacroiliac joint.

different ways. First, we connected the ends of the pubic rami via a "shortest" horizontal line. This is likely the minimum possible limit of an AP inlet diameter, reflecting the unlikely possibility of the pubic rami deflecting posteriorly. Second, using a series of points on the arcuate line and superior pubic ramus, we used a curve-fitting equation to connect the rami with a curved line. Qualitative observations of reconstructed hominin (A.L. 288-1, Sts 14, MH 2, BSN49/P27) and modern human pelves indicate that this is the most anatomically likely reconstruction of the pubic symphysis. Lastly, we used two points on each of the superior pubic rami to connect theoretical lines at an angle, showing the possibility that the pubic rami could have continued anteriorly. This is the ventral-most, if anatomically unlikely, position of the pubic symphysis and thus represents the extreme maximum possible AP inlet diameter.

To provide a range of possible values in the mediolateral dimension, we reconstructed the Sts 65 pelvis using the same methods described above with the sacrum of the *Australopithecus afarensis* female A.L. 288-1 (Lucy), which is notably wider than that of Sts 14. Given that this sacrum is wider than Sts 14 and from a different species of australopith, it likely represents an extreme possible ML width for the reconstructed Sts 65 pelvis. A.L. 288 has a fully fused epiphyseal lamina, thus, there was no need to compensate for its absence as in Sts 14. Unless noted otherwise, however, discussion of the reconstructed Sts 65 pelvis refers to the reconstruction using the Sts 14 sacrum.

2.3. Digital articulation error study

An error study was performed in order to assess how well the digital articulation methods used to reconstruct Sts 65 align ossa coxae to sacra. Modern human hipbones and matching sacra from three adults (male = 2, female = 1) were CT scanned at Stony Brook University. Osteological specimens were selected from the Stony Brook University teaching collections and are therefore of uncertain ancestry. Individuals were sexed following Bruzek (2002). Scans were processed, converted to polygonal models in .stl format, and digitally articulated by one of us (AGC) following the procedure used for Sts 65. For each individual, the sacrum was mirrored and the left hipbone was articulated producing a "hemipelvis." The left hipbone was then mirrored to produce a full pelvis. The full pelvis was exported from Maya and imported into Landmark Editor software (Wiley et al., 2005). A single observer (ASH) then placed the following three-dimensional landmarks on the pelves: the left ASIS, the center of the left acetabular fossa, the most superior and anterior point on the pubic symphysis, the left ischial spine, and the most dorsal midline point on the lumbosacral surface. The raw coordinates (x, y, z) of these landmarks were exported from Landmark Editor.

Each of the three bony pelves were then manually articulated following methods described in Hammond (2013) and consistent with re-assembly methods used by others (e.g., Li, 2002:; Bonneau

Table 2
Dimensions and indices of pelvic reconstructions.[a]

	Sts 65	Sts 65 (Lucy sacrum)	Sts 14[b]	Sts 14[c]	A.L. 288[d]	A.L. 288[e]	MH-2[f]	BSN49/P27[g]	*Homo sapiens*[h]	*Pan* (F)[h]	*Gorilla* (F)[h]	*Pongo* (F)[h]
Pelvic Breadth	≥224.9	251.1	256.3	230	258	268	250	288	259	254	331	241
AP Inlet	82.8	82.7	83	89	76	77.5	81.7	98	109	143	167	147
ML Inlet	101.5	109	116	101	132	124	117.6	124	131	105	123	110
Inlet shape (AP/ML)	0.82	0.76	0.72	0.88	0.58	0.63	0.69	0.79	0.83	1.36	1.36	1.34

[a] Given the damaged iliac crest, pelvic breadth in Sts 65 is a low estimate. A lower inlet shape ratio is more platypelloid.
[b] From Berge and Goularas (2010).
[c] From Häusler and Schmid (1995).
[d] From Schmid (1983).
[e] From Tague and Lovejoy (1986).
[f] From Kibii et al. (2011).
[g] From Simpson et al. (2008).
[h] From Tague (1991).

et al., 2012; Brown, 2015). Sculpting putty was placed between the pubic symphyses (approximately 3 mm thick) and the auricular surfaces (approximately 3 mm thick), and the pelvic girdles were held together with large rubber bands. Past work has shown that re-assembling pelves with putty results in reconstructions that more closely approximate the original pelvis shape (i.e., with cartilages present) than is achieved from articulating dry bones (Li, 2002). Sacroiliac cartilage thickness was selected based on studies which have found human adult sacroiliac cartilage to be approximately 3 mm thick (Schunke, 1938; Lawson et al., 1982; McLauchlan and Gardner, 2002), but perhaps up to 6 mm thick in younger individuals (MacDonald and Hunt, 1952; Bowen and Cassidy, 1981). We selected the thinner cartilage values (3 mm) for the sacroiliac joint in this error study because our digital methods do not actively simulate cartilage, though some space was left between the auricular surface and the sacrum. It is reported that the human interpubic fibrocartilage disc is approximately 7 mm wide (Bonneau et al., 2012 and references therein), but the thickness of this fibrocartilage probably differs across species and individuals of differing size (Li, 2002), and so there is some uncertainty about what the best thickness for this structure would be in Sts 65. It is worth noting that the thickness of the sculpting putty at the sacroiliac joint should be more influential than the putty placed at the pubic symphysis, because the digital articulation methods only align the pelvis elements (i.e., sacrum and hipbone) at the sacroiliac joint.

After re-assembling the pelvis, the same observer (ASH) then digitized the same five landmarks (i.e. left ASIS, the center of the left acetabular fossa, the most superior and anterior point on the pubic symphysis, the left ischial spine, the dorsal midline point on the lumbosacral surface) on the bony pelvis using a microscribe. Manual articulation and landmarking were performed three consecutive times for each of the three pelves. The intraobserver precision between repeated articulation and landmarking trials was low, with the maximum difference between interlandmark distances being 2.5 mm in this study. This level of intraobserver precision is only slightly larger than error levels reported for other Microscribe studies working from stationary (i.e., not repeatedly articulated) objects (e.g., Singleton, 2002; von Cramon-Taubadel et al., 2007).

Four interlandmark distances were calculated between sacral and hipbone landmarks (i.e., the ASIS, acetabular fossa center, ischial spine, and pubic symphysis to the dorsal point on S1) from both the manually and digitally articulated pelves. Raw differences (mm) and percent differences are reported (Table 3). Interlandmark distances between the digitally and manually articulated pelves did not typically differ by more than 5%, which was <5 mm for most distances. It was expected that the position of the pubic symphysis of the digitally articulated pelvis, which is formed by a single hipbone aligned to the sacrum, would have a higher rate of error than the other landmarks given that any subtle misalignments that occur at the sacroiliac joint would be amplified distally. Indeed, the largest difference observed between the manual and digital articulations was in the distance between the superior pubic symphysis and the dorsal S1 landmark in Specimen 2 (7.44—8.45% difference). The error study suggests that the method of digital alignment works reasonably well (i.e., converges on the same pelvic dimensions as manual articulation), but, as a matter of caution, interpretations derived from reconstructions using these methods should acknowledge that there is a certain level of uncertainty inherent in this articulation technique, as has been found by others (Bonneau et al., 2012).

2.4. Obstetric methods

Determining the obstetric challenges faced by the Sts 65 female first requires an estimation of the neonatal cranial volume in *Australopithecus africanus*, and then a comparison of that volume with the maximum neonatal cranial volume and/or linear dimensions that would be allowed through a corresponding pelvic inlet. We are aware that cranial dimensions do not pose the only obstetric challenge and that the neonatal shoulder width is likely to be a critical component as well (Trevathan and Rosenberg, 2000). However, given that this pelvis preserves only an inlet and neonatal shoulder width is not known for *A. africanus*, we have characterized obstetrics in Sts 65 based primarily on cephalopelvic proportions.

The maximum neonatal brain volume capable of being birthed by Sts 65 was calculated based on the minimum AP dimension of the pelvic inlet. The AP dimension of the inlet has been used to estimate the maximum permitted brain size of a potential neonate in the *Homo erectus* pelvis from Gona, Ethiopia (Simpson et al., 2008:SOM, pp. 26—27), and we follow the same methodology, though other approaches exist (Frémondière and Marchal, 2013). It is noteworthy that the AP inlet is not the minimum dimension of the birth canal in most modern humans (transverse midplane), Sts 14 (AP midplane), or A.L. 288-1 (AP outlet), making this approach rather conservative (Tague and Lovejoy, 1986; Tague, 1989; Berge and Goularas, 2010). However, it is the minimum dimension known from the Sts 65 pelvis and, thus, the most informative dimension for calculating the maximum sized brain capable of being birthed by this female. Because the heads of human neonates enter the pelvic inlet transversely or obliquely, the biparietal width of the skull roughly corresponds to the AP inlet. In humans, the biparietal dimensions are 5—8 mm smaller than the AP depth of the inlet due to soft tissue (Levi and Erbsman, 1975; Kurki, 2007; Simpson et al., 2008). Given the roughly 10—11 cm width of the modern human female pelvic inlet (Kurki, 2007), we estimate after accounting for soft-tissue that the maximum biparietal width capable of passing through the Sts 65 (and other primates') pelvic inlet is, generously, 95% of the AP depth of the pelvic inlet, assuming that the cephalopelvic dimensions are essentially those found in modern women. Following Simpson et al. (2008), the occipitofrontal length of the cranium was calculated as 1.22 times

Table 3
Comparison of interlandmark distances (absolute [mm] and percent difference [%]) for each digitally articulated pelvis with the manually re-assembled pelvis.

		ASIS: dorsal S1	Acetabular fossa: dorsal S1	Ischial spine: dorsal S1	Pubic symphysis: dorsal S1
Specimen 1	Manual articulation 1	2.23 (1.68%)	4.86 (4.41%)	7.21 (6.71%)	3.57 (2.66%)
	Manual articulation 2	2.95 (2.21%)	4.95 (4.49%)	6.92 (6.43%)	2.72 (2.02%)
	Manual articulation 3	0.48 (0.37%)	5.40 (4.90%)	6.66 (6.18%)	2.96 (2.20%)
Specimen 2	Manual articulation 1	0.10 (0.07%)	5.02 (4.25%)	2.14 (1.74%)	11.65 (8.11%)
	Manual articulation 2	0.94 (0.67%)	4.10 (3.48%)	2.06 (1.68%)	12.12 (8.45%)
	Manual articulation 3	1.37 (0.99%)	3.06 (2.61%)	1.93 (1.58%)	10.72 (7.44%)
Specimen 3	Manual articulation 1	0.04 (0.03%)	3.79 (3.38%)	0.28 (0.37%)	4.04 (3.01%)
	Manual articulation 2	1.96 (1.40%)	5.18 (4.64%)	0.81 (0.67%)	6.50 (4.89%)
	Manual articulation 3	1.21 (0.86%)	3.90 (3.48%)	0.78 (0.22%)	5.51 (4.13%)

the biparietal breadth (which is an average of the human ratio at 1.26 and the chimpanzee at 1.18 found in Tague and Lovejoy, 1986), and the cranial height as between 60 and 70% the biparietal breadth (also following Simpson et al., 2008, who in turn follow Tague and Lovejoy, 1986). With these three dimensions, we calculated a rough estimate of allowed cranial capacity by treating the skull as an ellipsoid with diameters a, b, and c, cranial height, occipitofrontal length, and biparietal breadth:

$$\text{maximum allowed neonate cranial capacity} = \pi/6 \text{ abc}$$

Comparative data for ape neonatal cranial capacity (DeSilva and Lesnik, 2006, 2008) and pelvic dimensions (Tague and Lovejoy, 1986; Tague, 1991; Kurki, 2011) were obtained from published sources.

The maximum neonatal cranial volume capable of passing through the Sts 65 pelvic inlet was then compared to regression-based estimates of brain size at birth in fossil hominins (DeSilva and Lesnik, 2008) using the OLS equation:

$$\begin{aligned}\log (\text{neonatal cranial capacity}) &= 0.7246 \\ &\times \log (\text{adult cranial capacity}) \\ &+ 0.3146\end{aligned}$$

This equation predicts the neonate cranial capacities of both humans and great apes, and it is thus reasonable that australopiths had a largely similar relationship between neonate and adult brain size. Given this assumption, adult brain size in *A. africanus* averages 466.8 cm^3 ($n = 8$), predicting a neonatal cranial capacity averaging 177.1 cm^3 (95% C.I. 155.8–201.3 cm^3; DeSilva and Lesnik, 2008). This volume was compared to estimates of allowed neonatal cranial volume using the Simpson et al. (2008) method described above by dividing the latter by the former. In this index, a value of one indicates that the allowed cranial volume and the predicted cranial volume match perfectly. A value of less than one indicates a tighter fit, while greater than one predicts a more spacious birth canal and presumably an easier birth. In addition, we used a second method for calculating the neonatal brain volume capable of being birthed by Sts 65, using the same human neonatal growth-based approach used to estimate *H. erectus* neonatal size from the KNM-WT 15000 pelvis (Walker and Ruff, 1993). The biparietal breadth of the neonate was calculated as described above and then matched to the most size-appropriate modern human developmental time in weeks (Levi and Erbsman, 1975). This temporal value was then converted to a cranial volume using the human brain growth equation reported by Dobbing and Sands (1978).

Finally, the cranial capacity calculated using DeSilva and Lesnik (2008) was converted back into linear dimensions of a neonatal skull by employing the same ratios used by Simpson et al. (2008; e.g., occipitofrontal length is 1.22× biparietal breadth) and treating the skull as an ellipsoid with the dimensions in the above ratios. It is then possible, by comparing these expected neonate cranial diameters to the observed inlet dimensions, to test whether or not these early hominin neonates could have entered the birth canal sagittally like modern apes, or had to have entered the birth canal obliquely or transversely as occurs in humans today (Fig. 4).

3. Results

The Sts 65 pelvic reconstruction created here looks much like the "classic" australopith pelves A.L. 288-1 and Sts 14 (Fig. 5). The ilia are laterally flared and the pubis is inferiorly deflected. The iliac crest, though incomplete, has a clear sigmoid curvature. However, the developed iliac pillar is unusual for an australopith, indicating that Sts 65 is perhaps trending towards later Pleistocene hipbones

with regard to robusticity. Table 2 shows the measurements taken on the completed reconstructions, as well as comparative fossil and extant samples. The inlet is relatively more anteroposteriorly elongated than in other known australopiths, with the exception of Häusler and Schmid's reconstruction of Sts 14. The missing ischium in the original fossil means that the entire "true pelvis" is unavailable for analysis, so we are unable to evaluate the pelvic midplane or outlet. Unfortunately, the preservation in Sts 65 precludes us from confidently taking cross-pelvic measurements, such as pelvic and biacetabular breadths, from the completed reconstruction.

3.1. Obstetric results

We agree with earlier assessments made by Wolpoff (1973), Day (1978), and Hager (1989) that Sts 65 is female. There are three major pieces of evidence for this. First, given that most interpretations of australopith body size sexual dimorphism claim that males were significantly larger than females (Richmond and Jungers, 1995; Plavcan, 2001; Plavcan et al., 2005) and that Sts 65 is at least a young adult and unlikely to grow much more, the small size of this fossil alone allows us to infer that it probably belonged to a female. The presence of a preauricular sulcus on the ilium (Fig. 2), as also noticed by Wolpoff (1973) and Day (1978), gives more weight to this assertion. Many authors have interpreted the preauricular sulcus as direct evidence of past parity (Cox and Scott, 1992, but see; Spring et al., 1989). Some studies tend to treat the preauricular sulcus as a trait of singular expression, but Houghton (1974) divides it into two distinct morphs—only one of which is well correlated to parturition. Bruzek (2002) also recognizes a number of different morphs, some of which occur more often in one sex than the other. The Sts 65 preauricular sulcus does not appear to bear resemblance to any of the three male morphs as described in Bruzek (2002), but rather to one of the "other female forms." We contend that the sulcus present in Sts 65 bears resemblance to Bruzek's "i-f-f" morph, described as a "little depression with closed border, with intermediate aspects of positive relief" (Bruzek, 2002). Regardless, a preauricular sulcus of any morph occurs with greater prevalence in modern females than in males (Dunlap, 1981; Bruzek, 2002; Royer, 2009; Novak et al., 2012). If australopiths followed this pattern, it seems likely that Sts 65 belonged to a female. Finally, the width of the greater sciatic notch is often used to sex modern human pelves and can be done to a reasonable degree of reliability (Buikstra and Ubelaker, 1994; Walker, 2005). Most of these methods are comparative scoring standards, however, and are of less use to paleoanthropologists. Simpson et al. (2008), in their analysis of the Gona pelvis, quantify the shape of the sciatic notch by drawing an inferred line between the ischial spine and the sacroiliac ligament tubercle, and a perpendicular line to the deepest part of the notch (the inflection point). The position of the point where the two lines meet quantifies the shape of the greater sciatic notch. Males and females overlap in their ranges only in a limited sense (males = 2.8–5.2, females = 0.9–3.5; Simpson et al., 2008). Though the ischial spine on Sts 65 is incomplete, we could estimate the inflection point at approximately 0.5, solidly grouping it with modern females. We understand that the sample of australopith fossil pelves is not large enough for us to determine whether or not the greater sciatic notch is truly a sexually dimorphic trait, but the fact that the Sts 65 pelvis groups with modern human females to the exclusion of modern males is consistent with the overall morphological pattern seen in this fossil. We would also add that the two fragmentary australopith pelves that are generally attributed to males (StW 431 and KSD-VP-1/1) are both large and are said to have relatively narrower greater sciatic notches (Kibii and Clarke, 2003; Haile-Selassie et al.,
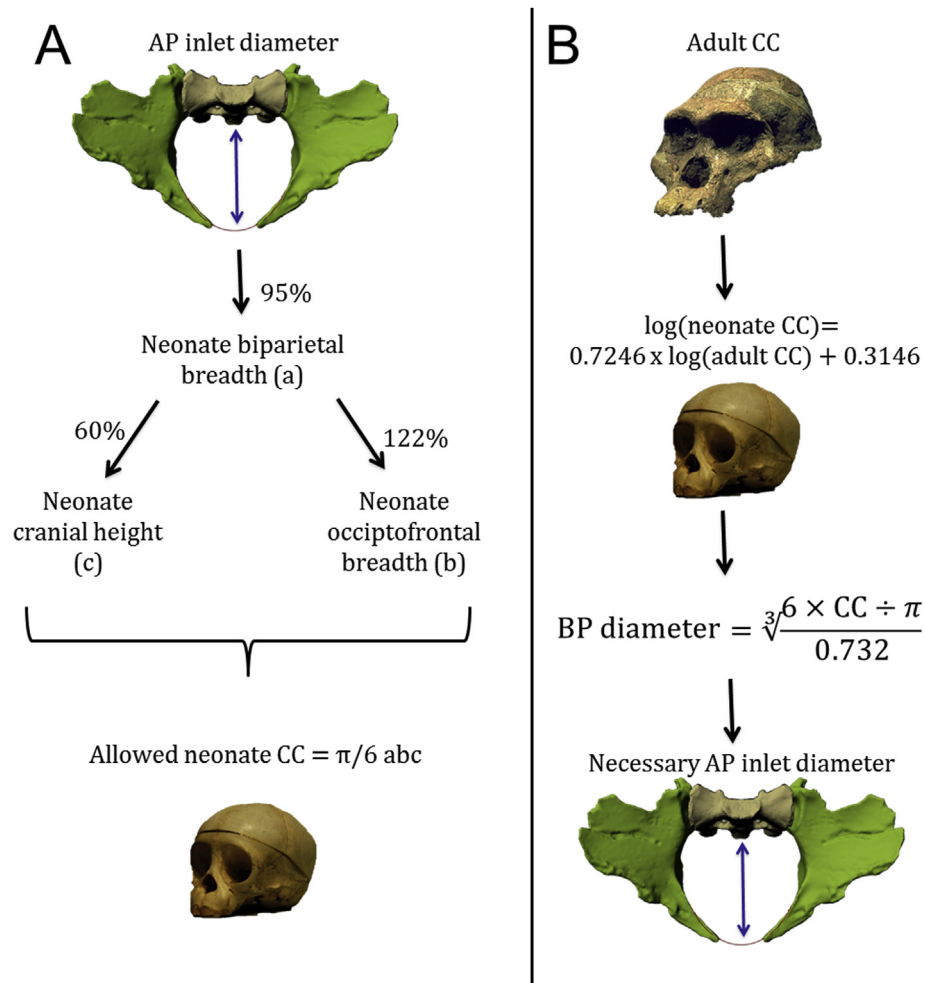
Figure 4. Visualization of obstetric calculations. A) The anteroposterior (AP) inlet diameter can be used to calculate the maximum neonatal cranial capacity (CC) capable of being birthed by Sts 65. This approach follows Simpson et al. (2008). B) Given the strong correlation between adult and neonatal cranial capacity across catarrhines (DeSilva and Lesnik, 2008), we employed a regression-based approach to estimating neonatal cranial capacity in *Australopithecus africanus*. Treating the neonatal cranium as an ellipsoid, the biparietal (BP) diameter of an infant with a cranial capacity of 177 cc can be calculated.
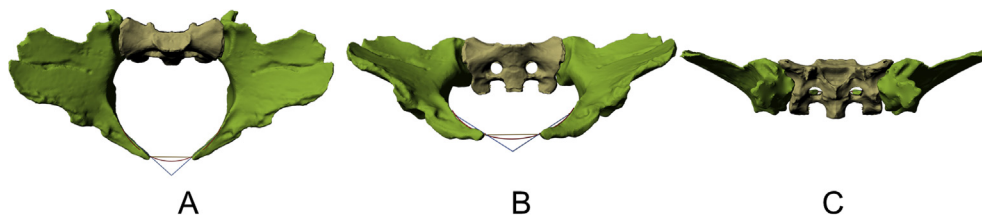

Figure 5. The Sts 65 pelvis as reconstructed with the mirrored Sts 14 sacrum and possible anterior limits to the pelvic inlet. A) Superior view, B) Anterior view, C) Posterior view. Note the gynecoidal pelvic inlet and flaring ilia typical of australopiths. The curve is likely the most anatomically accurate of the three possible contacts connecting the incomplete pubic symphysis.

2010), at least in comparison to the small size and wide sciatic notches of Sts 65, Sts 14, and A.L. 288-1.

If Sts 65 belonged to an adult female, an obstetric analysis is warranted. The AP dimension of the inlet has been used to estimate the maximum permitted brain size of a potential neonate, as described above (Simpson et al., 2008). Because of the incompleteness of the pubic ramus, we were forced to connect the apices of the mirrored rami with three imaginary lines (Fig. 5) that represent the range of possible connections. As discussed earlier, we think that the curve-fitting method most closely approximates anatomical reality given qualitative comparisons with Sts 14, A.L.

288-1, BSN49/P27, and modern human pelves. This approach yields an AP inlet of approximately 82.8 mm, nearly identical to the AP inlet of the Sts 14 pelvis (Berge and Goularas, 2010). The AP inlet dimension of Sts 65 remains nearly identical (82.7 mm) even if the Lucy sacrum is used, demonstrating that variation in the ML dimension of the sacrum used in our reconstruction does not impact the limiting obstetric dimension (AP).

Based on this AP inlet dimension, the Sts 65 pelvis would have been able to birth an infant with a cranial capacity of 186 cm^3, only 5% larger than the regressed mean for *A. africanus* (177 cm^3), and well within the 95% C.I. (155–201 cm^3) of neonatal brain size

predicted using regression based estimates from adult cranial capacity (DeSilva and Lesnik, 2008, Table 4, Fig. 6). However, the estimated minimum and maximum AP diameters yield allowed neonate cranial capacities of 162 and 273 cm³ for Sts 65. We view this as the largest possible neonate that could be birthed through the Sts 65 pelvic inlet. This is both anatomically unlikely (given the morphology of the pubic rami as stated above) and much smaller than the regressed estimate of a modern human neonate (355 cm³). The predicted biparietal diameter of a neonate that could be birthed through the Sts 65 pelvis is equivalent to a human at a gestational age of 29 weeks (Levi and Erbsman, 1975), which corresponds to a cranial volume of 188.2 cm³ (Dobbing and Sands, 1978), only 6.3% larger than the regression-based predictions of neonatal brain size in an A. africanus (DeSilva and Lesnik, 2008) and nearly identical to the 186 cm³ calculated using the Simpson et al. (2008) method.

Converting the possible Sts 65 neonate back into linear dimensions allows us to directly compare inlet dimensions with neonate cranial measurements. Working backwards from the regression-based volume equation, an A. africanus neonate with a 177 cm³ brain would have a biparietal breadth of 7.7 cm, an occipito-frontal length of 9.2 cm, and a cranial height of 4.5 cm. These dimensions are similar to, though slightly larger than, a chimpanzee neonate (Tague and Lovejoy, 1986). As seen in Table 4, the ratio of predicted biparietal breadth to AP inlet diameter

(necessary vs. actual AP diameter) in later hominins and humans is unchanged, centered at just above 100%. Ape comparisons can be made by using the transverse, rather than the AP, dimension of the inlet, in order to align the biparietal breadth with its theoretically limiting dimension. Applying this approach, apes possess birth canals that are far in excess of the 100% ratio between pelvic inlet and neonatal dimensions found in modern humans: chimpanzees (252%), orangutans (271%), and gorillas (323%). Both reconstructions of Sts 14 (using the AP inlet) are above 100%, while reconstructions of A.L. 288-1 are between 83 and 88%. Our most anatomically likely (curved line connecting the pubis) reconstruction of Sts 65 yields a percentage of 105%.

4. Discussion

This study finds that Sts 65, though similar to Sts 14, is different in important ways and is evidence for intraspecific variation in pelvic morphology in female Au. africanus. Sts 65 has a thicker iliac pillar and may represent a generally more robust individual. Additionally, the shape of the pelvic inlet is also distinct from other australopiths, being relatively more anteroposteriorly elongated (that is, gynecoid) than any known australopith (see Table 2, Inlet Shape). There is a large amount of intraspecies variation in this trait (Walrath, 2003; Kurki, 2011), however, so it is not necessary to treat our finding as any sort of species-level distinction.

Table 4
Dimensions and obstetric calculations of fossil and modern pelves for both transverse (a) and sagittal (b) entry into the pelvic inlet.

Transverse entry (BP-sagittal)

		AP diameter	Allowed neonate BP (95%)	Allowed neonate OF	Allowed neonate height	Allowed neonate CC	Regressed neonate CC	Cranial index (allowed/regressed CC)	Predicted neonate BP	Necessary AP diameter	Necessary vs actual AP
Sts 65	Curve	82.8	78.7	96.0	47.2	186.4	177.1	1.05	77.4	81.27	102%
	Min	79	75.1	91.6	45.0	161.9	177.1	0.91	77.4	81.27	97%
	Max	94	89.3	108.9	53.6	272.8	177.1	1.54	77.4	81.27	116%
Sts 65 w/A.L.	Curve	82.7	78.6	95.8	47.1	185.8	177.1	1.05	77.4	81.27	102%
288 sacrum	Min	78.5	74.6	91.0	44.7	158.9	177.1	0.90	77.4	81.27	97%
	Max	94.7	90.0	109.8	54.0	278.9	177.1	1.58	77.4	81.27	117%
Sts 14[a]		83	78.9	96.2	47.3	187.8	177.1	1.06	77.4	81.27	102%
Sts 14[b]		89	84.6	103.2	50.7	231.5	177.1	1.31	77.4	81.27	110%
A.L. 288[c]		76	72.2	88.1	43.3	144.2	173.8	0.83	76.8	80.64	94%
A.L. 288[d]		77.5	73.6	89.8	44.2	152.9	173.8	0.88	76.8	80.64	96%
MH-2[e]		81.7	77.6	94.7	46.6	179.1	164.2	1.09	75.3	79.07	103%
BSN49/P27[f]		98	93.1	113.6	55.9	309.1	287.4	1.08	90.8	95.34	103%
Homo sapiens[g]		109	103.6	126.3	62.1	425.3	354.9	1.20	97.4	102.27	107%
Pan (F)[g]		143	135.9	165.7	81.5	960.4	153.2	6.27	71	73.6	194%

Sagittal entry (OF-sagittal)

		AP diameter	Allowed neonate OF (95%)	Allowed neonate BP	Allowed neonate height	Allowed neonate CC	Regressed neonate CC	Cranial index (allowed/regressed CC)	Predicted neonate OF	Necessary AP diameter	Necessary vs actual AP
Sts 65	Curve	82.8	78.7	64.5	38.7	102.7	177.1	0.58	94	98.7	84%
	Min	79	75.1	61.5	36.9	89.2	177.1	0.50	94	98.7	80%
	Max	94	89.3	73.2	43.9	150.2	177.1	0.85	94	98.7	95%
Sts 65 w/A.L.	Curve	82.7	78.6	64.4	38.6	102.3	177.1	0.58	94	98.7	84%
288 sacrum	Min	78.5	74.6	61.1	36.7	87.5	177.1	0.49	94	98.7	80%
	Max	94.7	90.0	73.7	44.2	153.6	177.1	0.87	94	98.7	96%
Sts 14[a]		83	78.9	64.6	38.8	103.4	177.1	0.58	94	98.7	84%
Sts 14[b]		89	84.6	69.3	41.6	127.5	177.1	0.72	94	98.7	90%
A.L. 288[c]		76	72.2	59.2	35.5	79.4	173.8	0.46	94	98.7	77%
A.L. 288[d]		77.5	73.6	60.3	36.2	84.2	173.8	0.48	94	98.7	79%
MH-2[e]		81.7	77.6	63.6	38.2	98.6	164.2	0.60	92	96.6	85%
BSN49/P27[f]		98	93.1	76.3	45.8	170.2	287.4	0.59	111	116.55	84%
Homo sapiens[g]		109	103.6	84.9	50.9	234.2	354.9	0.66	124	130.2	84%
Pan (F)[g]		143	135.9	111.4	66.8	528.9	153.2	3.45	83	87.15	164%

[a] From Berge and Goularas (2010).
[b] From Häusler and Schmid (1995).
[c] From Schmid (1983).
[d] From Tague and Lovejoy (1986).
[e] From Kibii et al. (2011).
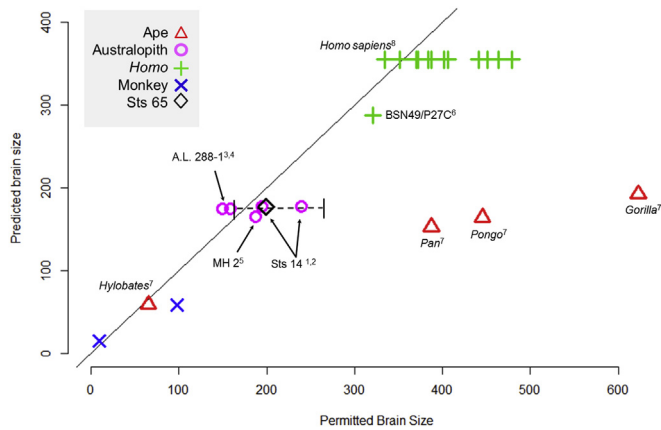[f] From Simpson et al. (2008).
[g] From Tague (1991).

Figure 6. Permitted vs. predicted neonate brain size. Scatter plot illustration of cephalopelvic disproportion index as described in the text. Both axes are in cm³. Permitted brain size calculated from the AP inlet dimension as in Simpson et al. (2008), with the exception of the hominoids where we used the ML inlet dimension. The diagonal line represents a 1-to-1 ratio between the estimated permitted brain size and the predicted brain size based on the regressions of DeSilva and Lesnik (2008). Data points to the right of the line indicates a value greater than 1, where the permitted brain size is larger than the predicted one and may be indicative of a relatively easy birthing process. The dashed horizontal line indicates the range of possible Sts 65 values based on different reconstructions of the pubic symphysis. Comparative data were obtained from [1]Berge and Goularas (2010), [2]Häusler and Schmid (1995), [3]Schmid (1983), [4]Tague and Lovejoy (1986), [5]Kibii et al. (2011), [6]Simpson et al. (2008), [7]Tague (1991), [8]Kurki (2011).

4.1. Error and limitations

There are uncertainties in our reconstruction and analysis that must be acknowledged. Our reconstruction is a heuristic model, and as such there is inherent error (Table 3). Sources of error may derive from aspects of the modeling itself, including issues with aligning the pelvis and sacrum incorrectly and/or from not modeling soft tissues at the site of articulation (i.e., articulating bony sacrum on bony hipbone). However, the measurement most pertinent to an obstetric analysis (pubic symphysis to dorsal S1) had an average percent difference between manual and digital reconstruction of about 4.8%, and this percent difference will likely not affect the obstetric results in any significant manner, as this is already within the range of variation produced by our three possible AP diameter estimates.

We may also have introduced error in using the Sts 14 sacrum as a substitute for the Sts 65 sacrum (not preserved). Our reconstruction assumes that Sts 65 had sacral dimensions and proportions that closely approximate the Sts 14 sacrum. To account for inter-individual differences in sacroiliac proportions, we also reconstructed Sts 65 with the A.L. 288-1 sacrum, which resulted in a slightly wider and more platypelloid (relatively mediolaterally broad) inlet (by 5 mm). Importantly, using the A.L. 288-1 sacrum did not result in a substantial difference in the AP dimension, which is the smaller and, therefore, limiting dimension in the australopith inlet. In other words, using different australopith sacra did not alter the AP dimension, the important variable in estimating obstetric challenges faced by early hominins.

Another source of potential error relates to the fact that the Sts 65 pubic symphysis is not preserved. We acknowledge that the AP inlet measurement is inherently an estimate as a result. The extreme ranges of possible AP inlet diameters in our reconstruction of Sts 65 are between 79 and 94 mm. Because only slight linear changes to the pelvis can dramatically alter the volume of the cranium that can fit into the birth canal (Epstein, 1973), these ranges yield extreme minimum and maximum values of neonatal

cranial capacity between 162 and 273 cm³. However, these extremes of possible AP diameters for Sts 65 are anatomically unlikely, and we stress that our curve-fitting approach not only yields an AP inlet value almost identical to that of the Sts 14 pelvis, but almost certainly approaches anatomical reality more closely than either of the alternatives.

Finally, it is possible that we have misidentified the sex of this individual. If this is the case, it goes against three major pieces of evidence in favor of a female assignment. The presence of a pre-auricular sulcus is considered by many to be a reliable indicator of sexing a human pelvis. Though we don't yet understand the pattern of pelvic sexual dimorphism within the australopiths, size has been used as a proxy for sex. This may well prove not to be the case, but for now we cannot help but point out that Sts 65 is small—roughly the same size as Sts 14, considered by most scholars to be from a female (Wolpoff, 1973; Day, 1978; Arsuaga and Carretero, 1994). Were Sts 65 male, we would have to drastically reevaluate how we approach sexual dimorphism in australopiths. Third, the shape of the greater sciatic notch points to a female designation, though the sciatic notch is wide in general in australopiths (Arsuaga and Carretero, 1994).

4.2. Locomotion

Classic *Australopithecus* pelves (A.L. 288-1, Sts 14) are typically described as having short, flaring ilia, a wide bi-acetabular breadth, mediolaterally long pubic rami, large iliopubic and subpubic angles, small acetabulae with a small anterior lunate horn, a broad platypelloid inlet, and a low level of overall robusticity. Indeed, Sts 65 appears to have had short and flaring ilia, but there is a moderate level of robusticity in the Sts 65 pelvis compared to other australopiths (A.L. 288-1, Sts 14). The robusticity in Sts 65 (Fig. 7) is found specifically in the iliac pillar, and not necessarily the acetabulosacral buttress (poorly developed) or the acetabulospinal buttress (not fully preserved).

A pronounced iliac pillar has been proposed to relate to the frequent contraction of gluteus medius and minimus during walking (Day, 1971; Robinson, 1972), which theoretically requires a thicker, stronger ilium in the region of muscular origin. The particularly well-developed iliac pillar seen in Middle Pleistocene *Homo*, such as OH 28 and KNM-ER 3228, has been inferred to suggest powerful hip abductor function and probably a high activity level (Ruff, 1995).

It is usually assumed that a strong iliac pillar is accompanied by a large iliac tubercle, which is located at the superior aspect of the iliac pillar. Robinson (1972) proposed that the presence of a strong iliac tubercle in some hominin pelves indicates a well-developed iliotibial band. The iliotibial band contributes to lateral knee stability, particularly during extension, and probably reduces stress on the femur during stance phase (Rohlmann et al., 1980). Discussions of hominin iliac morphology typically focus on the gluteal muscles and iliotibial tract, but the abdominal obliques and transversus abdominus muscles also insert along the iliac crest and tubercle (see Häusler, 2002) and are probably also relevant to anterior iliac crest morphology. Despite the role of abdominal musculature in torso stability, the influence of trunk musculature as it relates to different patterns of pelvic flaring and iliac crest robusticity is unstudied. Unfortunately, the iliac crest where the iliac tubercle would have been located was not preserved with the Sts 65 pelvis, and so it cannot provide additional information about hip or trunk soft tissue attachments.

The poorly developed acetabulosacral buttress in *Australopithecus*, including Sts 65, suggests only low levels of weight transfer in the pelvis. A pronounced acetabulosacral buttress is associated with weight-bearing because this thickened region of
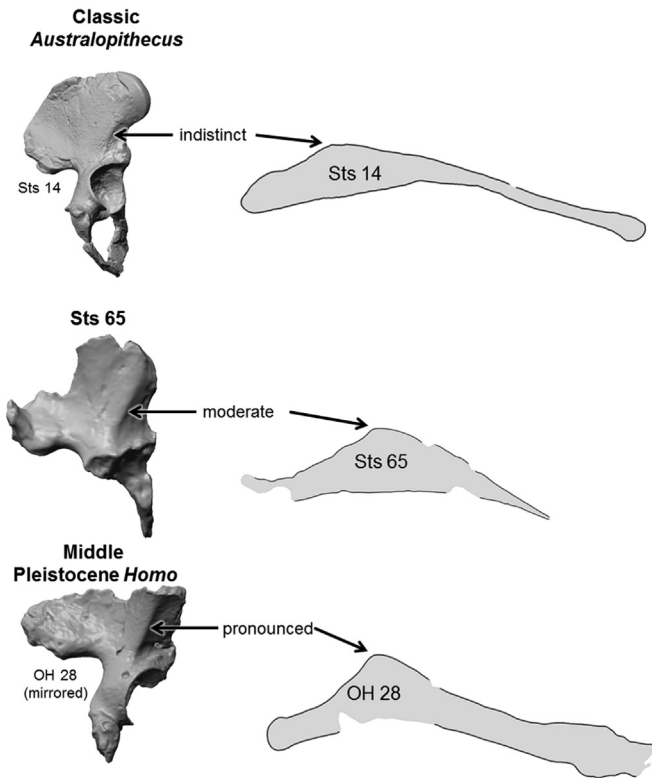
Figure 7. Iliac pillar morphology in classic *Australopithecus*, Sts 65, and early fossil *Homo*. Externally, the iliac pillar is indistinct in Sts 14, moderate in Sts 65, but thick in OH 28. Cross-sections taken from polygonal models at the level of the anterior inferior iliac spine and perpendicular (normal) to the long-axis of the iliac pillar show a similar pattern. In cross-section, the anterior portion of the ilium is equally thick in Sts 14, with moderate buttressing in Sts 65, and a thick and triangular buttress seen in OH 28. Original cortex is outlined in black on cross-sections to illustrate cracks or broken areas of the fossils. Cross-sections are oriented with the lateral portion of the ilium at the top, anterior ilium to the left, medial ilium at the bottom, and posterior ilium to the right. Sts 65 was laser scanned from the original, the other comparative fossils were scanned from casts. OH 28 is a left innominate that has been mirrored. Images of fossils, and cross-sectional renderings, are not to the same scale.

bone, from the superior portion of the acetabulum vertically to the auricular surface, corresponds to the route of weight transfer between the hip and sacroiliac joints. The australopith acetabulosacral buttress (e.g., A.L. 288-1, Sts 14, SK 3155b, SK 50) is both relatively thinner and less robust compared to Pleistocene *Homo* (e.g., OH 28, KNM-ER 3228, KNM-ER 1808, UA-173/405, Broken Hill E.719; Day, 1971; Robinson, 1972; Rose, 1984; Stringer, 1986; Macchiarelli et al., 2004). The difference in robusticity of the acetabulosacral buttress is most noticeable closer to the hip joint and can be easily appreciated by viewing the greater sciatic notch inferiorly. That the australopith acetabulosacral buttress is thinner near the hip joint is interesting given that it builds on additional lines of evidence suggesting australopiths had decreased force transmitted across the hip. To begin with, *Homo* is characterized by a larger hip joint size than australopiths (Ruff, 1995, 1998, 2010), probably due to selection for a bipedal hip joint that can regulate and/or reduce stress in articular cartilage and the underlying bone (Ruff et al., 1993; Ruff, 1995; Hammond et al., 2010). This marked shift in postcranial morphology is probably associated with the increased joint loading accompanying long-distance travel (Jungers, 1988). Additionally, australopiths would have presumably had lower joint reaction forces during abduction of the pelvis on the femur during stance phase due to their flaring ilia and relatively long femoral neck lengths, which would have increased the

moment arm of the lesser gluteal muscles (Lovejoy et al., 1973; Lovejoy, 1975, 2005b).

The presence of a moderate iliac pillar but an underdeveloped acetabulosacral buttress in Sts 65 suggests there may be more morphological diversity than previously inferred from "classic" gracile *Australopithecus* specimens such as A.L. 288-1 and Sts 14. Interestingly, the pelvic morphology of *A. sediba* has been described as sharing *Homo*-like features (e.g., a moderate sigmoid curvature to the iliac crest, a deep gluteus medius fossa, vertically oriented iliac blades, and medially positioned anterior superior iliac spine), but has an iliac pillar that is not robust (Kibii et al., 2011; Simpson et al., 2014), potentially signaling multiple pelvic morphologies in South African hominins. This would not be a surprise given the number of findings in recent years that suggest there were probably multiple locomotor adaptations in *Australopithecus*. The most compelling evidence for multiple locomotor adaptations comes from foot bones from Hadar (*A. afarensis*, 3.2 Ma) and Woranso-Mille (3.4 Ma; Haile-Selassie et al., 2012) suggesting two different Pliocene hominin foot morphologies, the former showing evidence of a stiff longitudinal arch (Ward et al., 2011) in a non-grasping foot (Latimer and Lovejoy, 1990), and the latter maintaining an *Ardipithecus*-like opposable big toe (Haile-Selassie et al., 2012). Additionally, the calcaneal morphology of chronologically later *A. sediba* (1.977 Ma) is suggestive of possibly a third locomotor adaptation in *Australopithecus* (DeSilva et al., 2013). The predominant view of this genus has been one of stasis, whereby the general australopith bauplan was maintained throughout the lineage in both eastern and southern Africa (e.g., McHenry, 1986). The emerging picture of the australopiths is that it is a grade of hominin that was continually evolving, displaying a range of locomotor morphologies in different lineages and at different times.

4.3. Obstetrics

The living apes and monkeys have neonates that enter the pelvic inlet with the head oriented in the sagittal plane, and it is likely that the chimpanzee/human last common ancestor did so as well. Modern human neonates, however, usually enter the pelvic inlet obliquely or in the transverse dimension—with the occipitofrontal diameter of the head lined up with the transverse dimension of the inlet. The mechanics of parturition in australopiths have been primarily inferred based on reconstructions of two fossils: A.L. 288-1 and Sts 14 (Berge et al., 1984; Tague and Lovejoy, 1986; Rosenberg, 1992; Häusler and Schmid, 1995; Abitbol, 1996; Berge and Goularas, 2010; Frémondière and Marchal, 2013). Here, even in the absence of an associated sacrum, we attempted to reconstruct the obstetric challenges encountered by a third female *Australopithecus*, Sts 65. We find that in Sts 65, as in other australopiths and modern humans, the neonate probably entered the pelvic inlet in a transverse or oblique orientation given the narrow AP dimensions of the female pelvis. In fact, the AP dimensions are so narrow on some fossil pelves (A.L. 288-1) that it is likely that the infant entered the birth canal with the head flexed, presenting the narrower suboccipito-bregmatic dimension of the skull into the inlet (Tague and Lovejoy, 1986; Abitbol, 1996; Berge and Goularas, 2010). We present the pelvic inlet as a perfect oval (Fig. 8A and B), though we acknowledge that this is not entirely accurate given the anteriorly projecting sacral promontory. It is thus entirely likely that following Joulin's law (1864), the entry into the pelvic inlet was oblique, rather than perfectly transverse. Importantly, an oblique entry into the pelvic inlet would permit proper space for both the maximum (occipitofrontal) dimension of the head, but also the wide and perpendicularly oriented shoulders (Abitbol, 1996; Trevathan and Rosenberg, 2000).
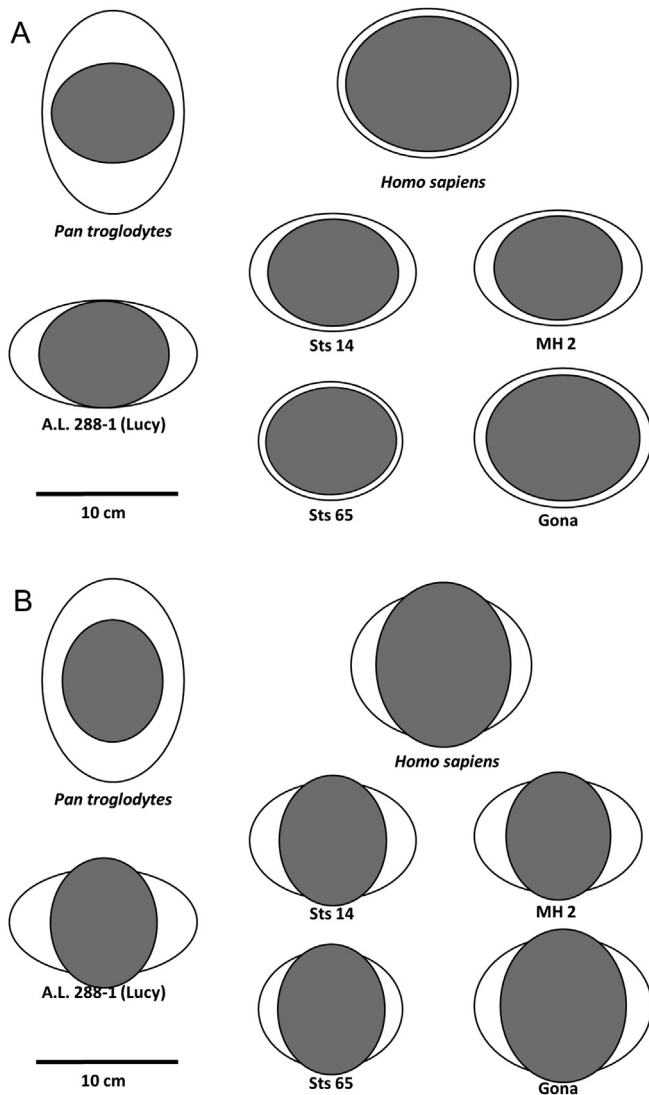
Figure 8. A and B. Geometry of engagement of the fetal head with the female inlet. Diagrams after Schultz (1949) and Rosenberg (1992). The dark ovals represent the neonate cranium, while the clear ovals represent the size and shape of the pelvic inlet. The size and shapes of the extinct hominin neonate crania were based on taking the regressed CC from DeSilva and Lesnik (2008) and reverse-calculating the dimensions of an ellipsoid with known volume and proportions. These illustrations do not include soft tissue and are only inlet dimensions and, therefore, do not necessarily reflect the minimum obstetric diameters. The dimensions of A.L. 288-1 and Sts 14 are taken from the reconstructions of Tague and Lovejoy (1986) and Berge and Goularas (2010), respectively. A) Scenario in which all neonates enter the inlet transversely. B) Scenario in which all neonates enter the pelvic inlet sagitally. This entry into the birth canal occurs in chimpanzees, but is restricted in humans and all fossil hominins. Transverse or oblique entry into the birth canal has occurred in the hominin lineage for at least the last 3.2 Ma.

Thus, evidence from other australopith pelves as well as Sts 65 suggests that a transverse or oblique entry evolved at least by 3.2 Ma, because the ape-like sagittal entry is simply not possible. If the occipitofrontal diameter of the neonatal cranium lined up with the sagittal plane of the inlet during delivery in Sts 65 (as happens in apes), using the same approach described in the methods section, the largest theoretical neonate cranium that could fit through the 8.3 cm inlet is 103 cm^3—a neonate with a brain only slightly larger than a neonatal olive baboon's and well below the average chimpanzee neonatal brain size (DeSilva and Lesnik, 2006). Even if we have underestimated the AP inlet of Sts 65, the AP inlet dimensions of other female australopiths—Sts 14 (8.3 cm), MH2

(8.2 cm), and A.L. 288-1 (7.6 cm)—result in the same conclusion that only a neonate with a brain the size of a baby baboon's could be birthed sagitally in australopiths. Head flexion would undoubtedly ease the difficulty of a sagittal birth, but we find it much more likely that, following Joulin's Law (1864), early hominins entered the birth canal transversely or obliquely. In fact, this is true of all four female australopith pelves (Fig. 8). Even a relatively anteroposteriorly elongated pelvis such as Sts 65 requires the neonate to enter the birth canal transversely. It is possible that this method of parturition is the default in hominins, regardless of variation in pelvic dimensions.

The transverse entry of an infant into the birth canal, especially when combined with the trend towards larger-brained infants later in human evolution, would have made birth substantially more difficult and likely contributed to the necessity for rotational birth at some point in human evolution, whether in the Pliocene (Berge et al., 1984; Häusler and Schmid, 1995; Berge and Goularas, 2010) or later in the Pleistocene (Weaver and Hublin, 2009). Though Sts 65 appears to have birthed infants with a comparable amount of difficulty to both Sts 14 and modern humans (Table 4, Fig. 6), we unfortunately cannot use Sts 65 to test the proposed presence of rotational birth in *A. africanus* (Häusler and Schmid, 1995; Berge and Goularas, 2010) given the nature of its preservation and the lack of a midplane or outlet.

Even with a transverse or oblique entry into the birth canal, we find that Sts 65 was likely birthing an infant with a head size that is approximately equal to the maximum allowable dimensions as estimated from the pelvic inlet. The estimated neonatal cranial capacity of *A. africanus* is ~177 cm^3, while the Sts 65 pelvis is spacious enough to birth an infant ~186–188 cm^3. Given that the midplane and outlet dimensions are unknown in Sts 65, and these are the limiting dimensions in modern humans, A.L. 288-1, and Sts 14, birth most likely was even more difficult for Sts 65 than calculated here. In terms of cephalopelvic proportions, our findings are consistent with that previously calculated for Sts 14 (Berge and Goularas, 2010) and with modern humans. It is therefore possible that these australopiths had a labor comparable to that of modern humans (contra Leutenegger, 1972, 1982), perhaps even necessitating the conspecific assistance that characterizes human parturition (Trevathan, 1987; Rosenberg, 1992; Rosenberg and Trevathan, 2002). Consistent with the cephalopelvic indices calculated here, is recent evidence suggesting that *A. africanus* had delayed fusion of the metopic suture, meaning that the anterior cranial bones would have been more flexible, allowing for cranial deformation during birth (Falk et al., 2012; but see; Holloway et al., 2014).

We note that the obstetric ratios between "allowed" and "possible" neonate cranial dimensions do not appear to shift between the South African australopiths, *H. erectus*, and modern humans, despite a substantial increase in encephalization occurring throughout this time (Table 4). As brains increased in size, so too did pelvic dimensions, resulting in similar cephalopelvic ratios through the Plio-Pleistocene (Fig. 8, Table 4), though fluctuations in the degree of cephalopelvic disproportion due to other factors acting on pelvic morphology and neonatal size (e.g., nutrition, thermoregulation) likely occurred (Wells et al., 2012). The link between pelvic morphology and neonatal brain size has been established in humans today (Fischer and Mitteroecker, 2015), and there appears to have been parallel evolution of pelvic morphology and encephalization through the Plio-Pleistocene.

Cephalopelvic disproportion is unlikely to have influenced the length of human gestation or the timing of birth (Dunsworth et al., 2012). Additionally, obstetric modifications to the female pelvis appear to have not compromised locomotor energetics (Dunsworth et al., 2012; Warrener et al., 2015). These findings challenge the obstetrical dilemma as it was originally framed (Washburn, 1960).

However, if the cephalopelvic index is a proxy for laborious parturition, then, compared at least to the apes, hominins have been uniquely challenged with a difficult and potentially dangerous birth process since at least 3.2 Ma. Given the small pelvic changes required to ease this tight fit (Epstein, 1973) and the apparent absence of locomotor consequences for these changes (Warrener et al., 2015), it remains unclear why this pelvic shape would have been selectively beneficial in female australopiths. The conserved cephalopelvic ratio between australopiths and modern humans is consistent with antagonistic selective pressure between neonate brain size and maternal pelvic size. It is unlikely that the female pelvis could get substantially larger and wider without a corresponding increase in body size. Perhaps the substantial increase in body size in the Early Middle Pleistocene is partially an allometric consequence of the pressure for a larger pelvis in order to birth larger brained neonates.

5. Conclusion

The description, reconstruction, and analysis of an additional australopith pelvis is significant because it has allowed us to assess variation and test hypotheses about locomotion and obstetrics. It further cements the use of digital 3D imaging as a valuable tool in reconstructive methods by allowing researchers to develop multiple hypothetical reconstructions of fossil pelves. We tested our methods of aligning a sacrum and hipbones for cases when the pubic symphysis is not preserved, and found that the sacroiliac joint is acceptable to use as a primary alignment site for reconstructing pelves. Our hypothetical reconstruction of Sts 65 is largely consistent with other australopiths, but shows a heretofore unseen degree of intraspecific variation in both features related to locomotion and those related to obstetrics. The large iliac pillar belies the overall small size of the specimen and suggests that there was also a degree of intraspecific locomotor diversity. Despite the intrageneric variation found in the pelvic inlet, birth in australopiths appears to have been consistently difficult, with modern human-like cephalopelvic proportions for the last 3 million years. An oblique or transverse entry into the birth canal also appears to have characterized all known australopiths, meaning that the shift from sagittal-to-transverse entry occurred long before the significant increase in encephalization in *Homo*. The morphology of the Sts 65 pelvis differs from Sts 14 primarily in the shape of the pelvic inlet and in the more robust iliac pillar, extending the known range of variation in female *Australopithecus africanus* pelves.

Supplementary Online Material

Supplementary online material related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2016.06.001.

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