The evolution of the human pelvis: changing adaptations to bipedalism, obstetrics and thermoregulation

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The fossil record of the human pelvis reveals the selective priorities acting on hominin anatomy at different points in our evolutionary history, during which mechanical requirements for locomotion, childbirth and thermoregulation often conflicted. In our earliest upright ancestors, fundamental alterations of the pelvis compared with non-human primates facilitated bipedal walking. Further changes early in hominin evolution produced a platypelloid birth canal in a pelvis that was wide overall, with flaring ilia. This pelvic form was maintained over 3–4 Myr with only moderate changes in response to greater habitat diversity, changes in locomotor behaviour and increases in brain size. It was not until Homo sapiens evolved in Africa and the Middle East 200 000 years ago that the narrow anatomically modern pelvis with a more circular birth canal emerged. This major change appears to reflect selective pressures for further increases in neonatal brain size and for a narrow body shape associated with heat dissipation in warm environments. The advent of the modern birth canal, the shape and alignment of which require fetal rotation during birth, allowed the earliest members of our species to deal obstetrically with increases in encephalization while maintaining a narrow body to meet thermoregulatory demands and enhance locomotor performance.

1. Introduction

The human pelvis is a remarkable structure that plays a central role in many critical biological processes, most notably bipedal locomotion, thermoregulation and parturition (childbirth). Each of these processes is essential enough to survival and reproductive success as to be under strong pressure from natural selection [1–4]. As a result, the fossil record of the evolution of the human pelvis over the past 4.5 Myr reveals a profound story concerning selective priorities during different phases of human evolution, and elucidates the essential constraints that formed our modern anatomical condition.

Pelvic anatomy impacts human performance. To walk upright in an energetically efficient manner with a minimal risk of injury, the pelvis must be robust and have a shape that maximizes muscle lever arms and minimizes load [5–11]. The ability to regulate body temperature is affected by the width and depth of the pelvis, which plays a crucial role in determining overall body proportions and the body’s surface area-to-mass ratio, thereby influencing heat loss through the body’s surface [12,13]. Finally, and most critically from a selective standpoint, pelvic shape must allow the delivery of a healthy infant without harm to the mother [14]. These goals are not all achieved by the same pelvic morphology, yet all three demands must be met. Therefore, selection has favoured compromises between these often contradictory pressures [15–17].

The results of these compromises can be seen in our hominin ancestors’ pelvic morphology at every stage of evolution of the lineage, with different aspects of hominin ecology playing a more or less dominant role in driving pelvic form at different times. The changes in pelvic anatomy over time in our lineage appear to reflect changes in locomotion, habitat, climate, brain
size and subsistence behaviour (behaviours related to the acquisition of food), and therefore tell the story of human evolution with remarkable depth.

To consider the role of the pelvis in locomotion, obstetrics and thermoregulation and the way in which these different pressures affected pelvic anatomy, we follow the approach of Lovejoy et al. [20] and divide the pelvis into upper and lower halves (dashed white line in figure 1). In the upper half, changes in the height and position of the iliac blades (alae or wings of the ilia) influence the leverage of muscles that abduct or extend the hip joint, the range of motion in the lumbar vertebral column, and the height of the centre of mass, all of which affect the ability to balance the body over the legs during a striding bipedal gait. In addition, the position of the iliac blades affects trunk width and impacts thermoregulation. But the upper half of the pelvis has a limited influence on parturition; the proportions of the birth canal are determined by structures in the lower pelvis.

2. Pelvic morphology in humans and non-human primates
The overall form of the pelvis in hominins is dramatically different from other primates in many key ways that reveal human adaptations to bipedalism, thermoregulation and parturition (see [22,23] and summaries in the literature; [7,9,24] for more details). The mechanical goals of modern bipedalism appear to be to walk with long strides, with high mechanical efficiency, while not falling over [5]. Thus, the ability to balance our upper body on long extended limbs is seen as a central pressure for pelvic anatomy in humans. The curvature in the lower back (lumbar lordosis) helps balance the upper body over the pelvis. In the upper half of the pelvis, the size, shape and orientation of the iliac blades differ between apes and humans in a way that reflects our commitment to striding bipedal locomotion (figure 1). Our iliac blades are shorter than those of apes, lowering our centre of mass and avoiding entrapment of the lumbar vertebrae by the iliac blades, thus allowing lumbar lordosis [11,20,21].

Our iliac blades are also reoriented compared with non-human apes (figure 1). The iliac blades in non-human primates are tall, flat plates and oriented in the coronal plane, allowing the gluteal muscles, which arise from the external surface of the iliac blade and insert on the proximal femur, to run posteriorly over the hip and extend (retract) the thigh [6,7,25–27]. In modern humans, in contrast, the iliac blades curve around the side of the body (facing laterally) and flare outward, producing the characteristic bowl shape of the modern human pelvis and allowing the lesser gluteals—especially gluteus

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**Figure 1.** The pelvis in (L to R) modern human (*Homo sapiens*), early hominins and chimpanzee (*Pan troglodytes*). In the anterior view (upper), note shortening of the height of the body (1) and blade (3) of the ilium in *Homo* compared with *Pan*, which lowers the centre of mass in the former. The iliac blade is also more laterally placed and the sacrum is wider in humans (2), which eliminates the entrapment of the lower lumbar vertebrae seen in the chimpanzee (2). In the lateral view (lower), note especially the coronal orientation of the iliac blade in the chimpanzee compared with the more laterally rotated blade in the hominins, which allows gluteal muscles that arise from the external surface of the ilium and attach to the greater trochanter of the femur to act as abductors of the thigh and, when the lower limb is in stance phase, to counteract tipping of the pelvis. In addition note the length of the ischium in *Homo* compared with *Pan*. Like chimpanzees, the ischium in *Ar. ramidus* is relatively long, indicating a potential mosaic evolution of the pelvis in early hominin evolution. The ischium is the site of attachment for hamstring and sacrotuberous ligament; the small triangles indicate the orientation of the ischial tuberosity, which is directed inferiorly in *Ar. ramidus* and the chimpanzee but more posteriorly in *A. afarensis* and modern humans. (Adapted from references [20,21].)
tuberosity, resists sacral rotation and is loaded under tension, which runs from the sacrum and coccyx to the ischial (lower end), along with the coccyx. The sacrotuberous ligament, which faces posteriorly, depressing the sacral promontory and elevating its apex, improves the leverage for the hamstrings, but also reflects the rotational pattern in the human in which the infant’s head enters the birth canal facing laterally, but then rotates at the midplane and exits the outlet facing posteriorly. Also note that in the two hominins, the infant’s head exits the pelvis more anteriorly, under the ischiopubic rami. (b) Midsagittal (above) and coronal (below) sections through a modern human female pelvis, illustrating the three major planes of the birth canal. (a adapted from [24,33]; b from [1]).

Changes in the lower half of the pelvis—sacrum, ischium and pubis—affect the anteroposterior (A–P) and transverse diameters of the birth canal as well as the attachment sites for ligaments that connect the ischium and sacrum, and for the hamstrings and adductor muscles. Most notably, the ischium in apes is long, and the ischial tuberosity where the hamstrings and the sacrotuberous ligament attach faces downward (figure 1), whereas in humans, the ischium is shortened [22,23]. Because the human thigh is relatively long, this means that the insertion site for the hamstrings is pulled further away from the origin [7,11,22]. In addition, the ischial tuberosity is more robust than in apes, and angled with part of it facing upwards [7,11,22]. The position and form of the ischial tuberosity in humans not only improves the leverage for the hamstrings, but also reflects increased tension from the sacrotuberous ligament. The lumbosacral joint is located anterior to the sacroiliac joint in humans, and so body weight tends to rotate the sacrum anteriorly, depressing the sacral promontory and elevating its apex (lower end), along with the coccyx. The sacrotuberous liga-

Figure 2. (a) ‘Midwife’s’ (inferior or lithotomy position) view of the birth canal in a chimpanzee (P. troglodytes), A. afarensis (A.L. 288 – 1, ‘Lucy’) and a modern human female. The position of the infant’s head at the three major planes of the birth canal is shown. Note the non-rotational birth in apes in which the infant’s head faces anteriorly throughout, the contrasting non-rotational pattern in the australopithecine in which the infant’s head faces laterally throughout, and the rotational pattern in the human in which the infant’s head enters the birth canal facing laterally, but then rotates at the midplane and exits the outlet facing posteriorly. (b) Midsagittal (above) and coronal (below) sections through a modern human female pelvis, illustrating the three major planes of the birth canal. (a adapted from [24,33]; b from [1]).

by body weight during bipedal standing and walking [7,11,22,31].

The situation is quite different in humans. Humans have a relatively narrow birth canal in the A–P plane, possibly, in part, because of the needs for efficient balancing in bipedal locomotion. The human sacrum is unique in forming a bony posterior/superior wall of the birth canal [23,33]. The result is a pelvic inlet that is wider mediolaterally than anteroposteriorly (i.e. transverse diameter is long relative to the anatomical conjugate, between the pubic symphysis and sacral promon- tory; [1,33,35,36]). In compensation, the modern human birth canal at its more inferior levels is enlarged in humans, especially in women. This expansion is accomplished through the anterior rotation and sagittal curvature of the sacrum,
along with overall A–P expansion of the pelvis provided mostly by lengthening of the pubic rami [33,36]. These changes are accompanied by shortening and flaring of the ischia, which result in a wider subpubic angle and a greater distance between the ischial spines (figure 2). When looked at as a canal with a superior inlet and inferior outlet, the changing shape of the human birth canal is clear: although there is variation [37], in general, the human female pelvis is wide mediolaterally at its inlet, whereas the midplane and outlet are wider anteroposteriorly (figure 2; [1,35]).

The contrasts between the human pelvis and that of apes, in combination with the relatively large body size and cranial size of human neonates, have a profound effect on human infant delivery: we experience a birth process that is unusual, if not unique [1,24,34]. A human infant must perform a series of twists and turns during parturition to enable the widest dimensions of its body to pass through the changing dimensions of the maternal birth canal, a process called rotational birth. A human infant’s head enters the inlet facing laterally, and then rotates, usually to face backwards, as it exits through the more anteroposteriorly oriented outlet (figure 2). Although the precise orientation of the infant may vary depending on variations in the shape of the maternal birth canal, this rotation during birth is consistent among humans [4]. In contrast with an ape baby, who passes through the outlet posteriorly between the ischial tuberosities, a human baby emerges more anteriorly, under the ischiopubic rami, owing to the inferior position of the sacrum [33,35].

Finally, even if the delivery of its large head is successful, a human infant’s bony, rigid shoulders pose another significant obstacle to birth [1,35]. We share wide shoulders in common with the great apes, but ape mothers are generally able to deliver their infants’ shoulders without difficulty because of their relatively large and comparatively straight birth canals. In humans, however, shoulder dystocia is a serious potential complication in childbirth, and further con- tortions are required from the infant to squeeze its shoulders through the birth canal. After its head emerges, the baby must rotate twice more, so that its shoulders can align first with the pelvic inlet and then with the outlet [24]. Trevathan and Rosenberg have argued [24,35,38] that passage of the infant’s shoulders may have influenced the size and shape of the human pelvis as much as head size.

Skeletal anatomy, whether of the mother’s pelvis or the infant’s head and shoulders, is not the only factor influencing the pattern and degree of difficulty of birth in humans. The soft tissues of the pelvic cavity and vagina are compressed or stretched during delivery, facilitating passage of the infant. The effects of the hormone relaxin are another important factor promoting successful parturition. Relaxin production by the ovaries and uterus increases towards the end of pregnancy, increasing the elasticity of the pelvic ligaments [39,40]. This allows some mobility in the maternal pelvis in response to pressure from the fetal head and shoulders: the bones of the pelvis can spread apart somewhat at the pubic symphysis and sacroiliac joints, and the sacrum can rotate anteriorly to facilitate exit of the fetal head through the pelvic outlet [39,40]. In addition, the bones of the fetal skull are pliable and are moulded during passage through the birth canal [41]. However, endocrine effects on parturition in extinct animals are difficult if not impossible to ascertain, and neonatal remains are vanishingly rare in the fossil record owing to their great fragility [1]. The morphology of the maternal pelvis, therefore, provides the best information about the process of birth in extinct hominins, and this review focuses on inferences made from fossil pelvic anatomy.

3. Pelvic evolution in early (non-Homo) hominins

An examination of pelvic anatomy in the fossil record reveals the varying pressures on the pelvis during human evolution. The evolution of the pelvis in the earliest hominins—Ardipithecus ramidus, Australopithecus afarensis, Au. africanus and the more recent Au. sediba—shows derived features relative to apes, patterns that make enormous logical biomechanical sense in terms of the appearance and evolution of bipedalism in our lineages. It is well known that there is considerable and often rancorous debate about the nature of locomotion in early hominins: was it like modern humans, like that of chimpanzees, or something in between? It is not the goal of this paper to revisit this debate; the details can be found in the original works [7,26,27,42], in more recent summaries [10,11,21,43–47] and a myriad of articles in between. With the recent description of Ar. ramidus [20,48], there is no longer debate about whether there was a phase of non-human-like bipedalism in our lineage. The debate now is simply about how long that form of locomotion lasted, and how it is reflected in the anatomy of the pelvis. Some argue that full human-like locomotion arose with Au. afarensis (see reference [11] for a summary), whereas others argue that it appeared only in Homo erectus (see [46] for a summary).

Our earliest detailed knowledge of the hominin pelvis comes from fossils of Ardipithecus ramidus, from Ethiopia 4.4 million years ago (Ma) [20,52]. Although the Ar. ramidus pelvis required extensive reconstruction, most agree that it displays a ‘mosaic’ pattern: the upper half of the pelvis is substantially changed relative to apes, whereas the lower half retains more primitive features [20]. The iliac blades are repositioned and flare laterally compared with apes, improving gluteal lever- age and allowing control of side-to-side balance during walking (figure 1). In addition, the change in iliac blade shape and position appears to reduce lumbar entrapment and to facilitate the development of lumbar lordosis. Reflecting on the selective factors that drove changes in iliac height, Lovejoy & McCollum ([21], p. 3297) recently argued that ‘the favourable position of the anterior gluteal muscles in homini- ids allows them to control pelvic tilt during single support can now be seen to have been largely a refinement that followed the initial primary adoption of a lordotic spine with an emancipated caudal-most lumbar vertebra’. In contrast to changes in the ilium, the long ischium of Ar. ramidus is reported to be more like that of living apes, with a hamstrings tuberosity that points downward (figure 1). Lovejoy et al. [20], p. 71) argue that this suggests that Ar. ramidus was ‘... an effective upright walker’ and that ‘it could also run, but probably with less speed and efficiency than humans’.

The shape of the pelvis in the early African australopithecines Australopithecus afarensis and Au. africanus, which post-date Ar. ramidus by 1–2 Myr, has been described in detail previously (see [6,7,9,11,26,27,53–56]), and the two species are for the purpose of this paper considered similar (though see reference [56] for a sense of the variation) and will be discussed together. As in Ar. ramidus, the iliac blades of Au. afarensis and
*Au. africanus* are vertically shortened and have moved laterally compared with living apes ([27]; but see reference [7] for a contrary view), and also exhibit great lateral flare, meaning they extend laterally out over the hip joint and femoral neck (figure 3). The pelvis overall is extremely wide, wider than in any modern human of their small size [55], with a wide interacetabular distance, making it broader mediolaterally than anteroposteriorly (i.e. platypelloid in shape).

The extreme width of the australopithecine pelvis has presented enormous challenges for interpretation. Lovejoy and co-workers [6,11,20,25,59] see it as part of a larger complex of lateral iliac flare and long femoral necks that produce human-like hip kinetics. Ruff [10,60] has also argued that this morphological complex is related to hip mechanics, suggesting that the iliac flare provides better leverage for the gluteal muscles to balance the pelvis (but see [61,62]), and moderates forces applied to the lower limb joints. However, in contrast to Lovejoy and co-workers, Ruff contends that this arrangement would also increase mediolateral (M–L) loading of the femur (but see [61,62]), and moderate forces applied to the lower limb joints. Our work supports Rak’s idea with an experimental study [67] that tested for relationships between lower limb length and locomotor variables (stride length, speed and pelvic rotation) in modern humans. Our work supports Rak’s hypothesis: when people with short legs (as in australopithecines) walk faster, they show pronounced increases in pelvic rotation, which increases their stride length. Whitcome et al. [68] similarly found that women take longer strides relative to leg length when walking than men do, probably thanks to their broader pelvises. However, it is unclear how much the energetic cost of locomotion may actually have been elevated by the broad pelvis in australopithecines [32,62], and whether any increase in cost would have been offset by the energetic advantages of a longer stride. Stern [46] raised concerns that we share about the costs of vertical oscillations and stride length, suggesting that specific stride lengths and levels of centre of mass oscillation may provide energetic efficiency. Work by Wall-Scheffler and co-workers [69,70] suggests that a broad pelvis may provide the additional important benefit of increasing speed flexibility relative to locomotor cost, especially in short-legged individuals. Furthermore, Wall-Scheffler and co-workers have found that a wider pelvis reduces the cost of carrying an infant, which would have been an important energy drain for early female bipeds [69,71,72].

![Figure 3. Anterior and superior views of the pelvis in (a) female *A. afarensis* (‘Lucy’), (b) female *H. erectus* (Gona), (c) male *H. heidelbergensis* (Atapuerca Pelvis 1) and (d) female modern *H. sapiens*. The bones are shown to approximately the same scale. (e) Comparison of pelvic shape and body proportions in *H. erectus*, *A. afarensis* and modern *H. sapiens*. Note the relatively broad pelvis in *A. afarensis*, and the great degree of iliac flare in both fossil hominins. As iliac flare and pelvic width decrease the body shape becomes relatively narrow, promoting effective heat loss. (a,b and d from [57]; c from [37]; e by J. Gurche from [58]).](http://rstb.royalsocietypublishing.org/)
The functional significance of anatomical changes in the lower half of the pelvis is even more ambiguous. *Australopithecus afarensis* and *Au. africana* have anatomy that is intermediate between *Ar. ramidus* and modern humans. The sacrum is placed relatively posteriorly compared with apes, and like the pelvic inlet, the lower planes of the birth canal in early hominins are platypelloid in shape (figures 2 and 3; [11]). The position and shape of the ischial tuberosity and attachment sites for the hamstrings (figure 1) have been a subject of significant debate [6,7,11,20,26,27,53,73]. Some researchers [6] argued that australopithes in had poor leverage for their hamstrings, whereas others [7] argued that the leverage was strong; these differing results could be explained, in part, by differing methodologies and indices against which leverage is measured. In addition, the relative flatness of the sacrum and the orientation of the ischial tuberosity in *Australopithecus* compared with modern humans suggest that the sacrotuberosous ligament was less robust, and vertical loading during locomotion was reduced [7].

The presence of a platypelloid birth canal from the inlet through to the outlet in *Au. afarensis* and *Au. africana* suggests to most authors that *Australopithecus* had a unique type of non-rotational birth (figure 2). The neonate's head would have entered the inlet facing laterally, and remained in that position until it exited the outlet [24,33,74]. Importantly, Trevathan & Rosenberg [38] have pointed out that the birth could not have been truly non-rotational, because as in modern humans, the infant would have to rotate after emergence of the head to allow passage of its wide, rigid shoulders. In notable contrast, Borge & Goularais [56] reconstructed Sts 14 as less platypelloid than previously thought, and said that *Au. africana* had a ‘human-like movement of rotation and flexion of the fetal skull’ during birth ([56], p. 262; see also [36,75]). Neonatal head size relative to the size of the birth canal in australopithes was probably closer to apes than humans ([33,75–77]; but see [1,36]), and the M–L wide and A–P narrow pelvis is seen by most authors as a barrier to birth of infants with relatively large brains (see [16] for a review of encephalization and birth in fossil hominins).

The relative importance of obstetric versus locomotor or thermoregulatory demands (or even neutral evolutionary processes) in determining pelvic morphology in extinct homin species could be illuminated by an assessment of sexual dimorphism, because obstetric constraints affect females, whereas other selective pressures would presumably affect both sexes equally. In modern humans, for example, pelvic breadth is related to climate in the same manner in males and females [13], but a number of features of the female bony pelvis increase the size of the birth canal relative to males [78]. Unfortunately, the fossil record of the hominin pelvis is so sparse that it is usually impossible to make comparisons between male and female anatomy for any particular species [17,36,79]. In fact, because evolution has produced in fossil hominin pelvises ‘a combination of traits in an extinct animal that is duplicated by no living creature’ [80, p. 110], it is often very difficult even to assign a sex to any given fossil [2,33,36,81–83].

A rare glimpse of pelvic sexual dimorphism in an early hominin is provided by the recently described 1.9 Myr old South African species *Australopithecus sediba*. These fossils have garnered attention because of their age (close to some of the oldest specimens of *Homo erectus*) and because of arguments that they may be ancestral to *Homo* [84]. Pelvic fossils from a male and a female have been recovered, and although conclusions must be tempered by the male’s juvenile status, Kibii et al. [84], p. 1408) report that *Au. sediba* ‘may not have expressed the marked sexual dimorphism characteristic of modern humans’; neither the male nor the female exhibits the suite of traits that characterizes the respective sex in *H. sapiens*. Furthermore, despite the fact that *Au. sediba*’s pelvic inlet (in the male and the female specimen) is somewhat rounder compared with earlier australopithes, it also had a small adult brain size, and therefore Kibii et al. argue that any *Homo*-like aspects of the pelvis are not related to increased neonatal cranial size and are not explicable by obstetric requirements. They conclude that ‘birthing of larger-brained babies was not driving the evolution of the pelvis at this time’ ([84], p. 1407), and that if these changes in *Au. sediba* are functionally relevant rather than part of a phylogenetic signal, they represent locomotor rather than obstetric demands.

The overall pattern of pelvic morphology in *Au. sediba* is complex and differs from both earlier australopithes and early *Homo*. Kibii et al. [84] report that these specimens not only retain the wide interacetabular distance, long pubic rami and sacral shape of prior australopithes, but also have *Homo*-like features including shorter, more vertical ilia and a shortened ischium with an everted ischial tuberosity. Their explanation for these features is complex, noting at some points that it is possible that the shortened ischium is due to pleiotropy associated with other pelvic changes, and at others arguing for a phylogenetic affinity with *Homo*, rather than novel locomotor or obstetric requirements. Kibii et al. also point out that *Au. sediba*’s relatively M–L broad birth canal (and long femoral neck), but smaller degree of iliac flare, may present a challenge for Ruff’s model of australopithecine hip biomechanics [10,84]. A conclusive interpretation of the complex and potentially mosaic features of the pelvis of *Au. sediba* will require more material from adult members of this species and a more extensive biomechanical analysis like those applied to earlier fossil hominins.

What is there to make of the overall picture of the australopithecine pelvis? Changes in the iliac blade in our early ancestors compared with other primates is a response to fundamental needs for pelvic balance in bipedal walking, whereas changes in ischial and pubic shape are more complex. Some researchers are convinced that the nature of locomotion in early hominins was close to that of modern humans, and differences between australopithes and *Homo* reflect obstetric changes [11,20,21]. Other researchers take a different view and argue that there were major locomotor differences between australopithes and *Homo* (see [7,46,84]), and counter that pelvic differences reflect both locomotor and obstetric needs. In this formulation, there were multiple phases of locomotor evolution in australopithes, and obstetric concerns played a relatively minor role until the evolution of *Homo* species and possibly not until *H. sapiens* specifically.

In our estimation, early stages of hominin pelvic evolution reflect clear pressures for locomotion without an obvious nod towards either obstetric or thermoregulatory pressures. Although such pressures were certainly present prior to 2 Ma, they were neither dominant nor even equal to pressures of bipedal locomotion on pelvic form. Whatever the adaptive or functional significance of australopithecine pelvic morphology may be, it is intriguing that virtually the
same suite of anatomical features is seen in the pelvis of another hominin from the opposite side of the globe and millions of years later. The small-bodied, short-legged, small-brained hominin Homo floresiensis (the ‘Hobbit’)—from Java as recently as 17 000 years ago [85,86]—has a pelvis that is strikingly similar to that of Au. afarensis [87,88], suggesting similar adaptive pressures despite great geographical and chronological distance.

4. Pelvic evolution in fossil Homo

The genus Homo emerged in the early Pleistocene, just after 2 Ma, and the first representatives of H. sapiens appear in the fossil record around 200 thousand years ago (kya). The scarcity of relevant fossils in the intervening period makes interpretation difficult, but some evolutionary patterns over time are evident. The pelvises of early Homo, although similar in overall form to earlier hominins, do have derived traits that distinguish them from australopithecines. Many of these are probably related to changes in locomotor behaviour. Once established in the Early Pleistocene, pelvic morphology in archaic Homo seems to be largely characterized by morphological stasis over time. However, some trends towards modern human anatomy can be seen later in the Pleistocene, most likely adaptations to birthing larger-brained babies. A new additional source of variation in genus Homo is thermoregulatory adaptation to increasingly diverse environments.

(a) Early Homo

Patterns of pelvic evolution in earliest Homo are obscured by continuing uncertainty about taxonomy [19,60,83,89–92] and the almost total absence of pelvic fossils that are associated with diagnostic craniodental remains (the one notable exception being the Nariokotome H. erectus skeleton from Kenya [93]). Furthermore, although hominins spread out of Africa during the Early Pleistocene and into Europe and Asia [94,95], pelvic fossils of early Homo have been recovered exclusively from Africa [2]. The available evidence, however, suggests that the morphology of the pelvis in these early members of our genus (specimens typically referred to H. erectus, but sometimes to H. ergaster, H. habilis or H. rudolfensis [60]) remained largely consistent for at least a million years (see [60,96–99]). The pelvis retains the primitive overall form established in early hominins—mediolaterally broad and anteroposteriorly narrow, with a platypelloid birth canal and laterally flaring iliac blades (figure 3; [2,60,66,74,100])—but there are changes compared with earlier australopithecines that appear to reflect ecological and behavioural changes occurring in our genus.

Ruff [10,60] has proposed that many features of pelvic morphology in early Homo are part of a single biomechanical complex that increases the leverage of the gluteal abductors, as in the australopithecines. However, changes in locomotor behaviour also appear to be reflected in some aspects of pelvic morphology [60,96–99]. Open, grassy savannahs first became a major component of the African landscape in the Early Pleistocene [101–104], and many authors have suggested that greater mobility in early Homo, along with increased exposure to heat from the sun, required improvements in locomotor efficiency [10,105–109]. The pelvis of H. erectus, while broad compared with modern humans, was narrower relative to body height than in the australopithecines (figure 3; [2,60]). This change in proportions, combined with longer lower limbs and higher cranial indices [110], would have allowed H. erectus to walk farther at a lower energetic cost (although some studies suggest that a broad pelvis may improve some aspects of walking economy [70,111]).

Endurance running may have been a component of the hominin locomotor repertoire for the first time in H. erectus [108,112]. Novel adaptations to running may include the overall narrower pelvis, large and deep acetabulae, more sagittally curved iliac blades, increased ligamentous stabilization of the pelvic joints and more powerful muscles [82,108,111]. With these morphological changes, movements of the trunk and hip were decoupled, allowing more movement between the two, the trunk was better stabilized, and joint stress was reduced, making running a viable subsistence behaviour for H. erectus.

Other features of the pelvis in early Homo are probably related to parturition. The primitive platypelloid birth canal suggests that these hominins would have also retained the presumed primitive non-rotational birth mechanism of the australopithecines [2,60,74]. However, some expansion in relative A–P dimensions of the birth canal did occur, primarily through upward rotation of the pubic rami (figure 3; [60,82]). This enlargement is probably related to an increase in neonatal brain size. There was an initial jump in encephalization (relative brain size) over australopithecines with the origins of the genus [60,113,114], and non-rotational birthing of a relatively larger-brained and larger-shouldered infant would explain the continued need for the M–L broad true pelvis [2,38]. Subsequently, levels of encephalization in H. erectus remained largely unchanged, because further brain size expansion accompanied proportional increases in body size [60,113,114]. This stasis in relative brain size may account for the long-term consistency in pelvic morphology in the species.

Finally, thermoregulation, while probably not a major selective force acting on the australopithecines, became increasingly important for Homo owing to climatic change and geographical radiations into more varied habitats[2,13]. As discussed in §3, a wider body conserves heat, whereas a narrower body increases heat loss [8,9]. In a series of exhaustive studies, Ruff has demonstrated that pelvic bi-iliac breadth (intercristal diameter) varies with latitude among modern humans [2,12,13,115], and fossil hominins show the same pattern, with those from warmer climates, including African earliest Homo, having smaller pelvic breadths than those from colder climates [2,12,13,116] (although see [18]).

An exception to the prevailing pattern of pelvic morphology in early Homo is the Ethiopian Gona pelvis, dating to 1.4–0.9 Ma and identified by its discoverers as an adult female H. erectus (figure 3; [82]). Although Gona is similar in some ways to other H. erectus specimens, it differs in key features. Most notably, the Gona pelvis is even broader overall, but has a more gynecoid (rounder) birth canal with a particularly large pelvic outlet. Simpson et al. [82,83] argue based on this specimen that adaptations to birthing larger-brained infants, including perhaps rotational birth, arose earlier than previously suspected. Another surprise, especially considering the great breadth of the Gona pelvis, is the very diminutive body size implied by its small acetabulae, which are more similar in size to those of australopithecines than to other H. erectus [2,82]. In contrast to the majority of the fossil evidence, which suggests that body sizes in H. erectus were in the modern human range (summarized in reference [2], although see [90,117,118]), Gona indicates either very high levels of sexual dimorphism or
great intraspecific variation in body size [82,83]. Ruff [2] has questioned these unexpected conclusions about H. erectus, countering that Gona may in fact represent Australopithecus (see [83] for Simpson et al.’s response).

In sum, early Homo provides another illustration of powerful, conflicting selective pressures acting on the pelvis: while a greater overall width was beneficial for non-rotational parturition, a narrower pelvis was more advantageous in terms of both locomotor efficiency and thermoregulation in hot climates. However, it is important to keep in mind the lessons of the Gona fossil, which, like Au. sediba, shows that there was significant postcranial diversity among Pleistocene hominins, and details of mosaic evolution in specific populations may contrast with overall long-term trends [92].

(b) Middle Pleistocene Homo

Africa, Europe, the Middle East and East Asia have all produced fossil human pelvises from the Middle Pleistocene (about 800–100 kya). As in earlier Homo, the available evidence again suggests that the overall primitive pelvic form was retained in archaic (pre-modern) humans without major changes throughout most of this time period [37]. The biomechanics of bipedalism had reached an essentially modern state in H. erectus in the Early Pleistocene [108], so any changes in pelvic morphology during the Middle Pleistocene are unlikely to reflect major locomotor adaptations. Ecogeographic patterns in pelvic breadth indicate that thermoregulatory constraints continued to play an important role [2] throughout the Pleistocene. However, the demands of parturition became ever more critical: trends towards modern human morphology during this time become more clear and are probably related to increases in encephalization and concomitant requirements for birthing larger-brained babies. Populations from the later Middle Pleistocene exhibit mosaic evolution and diversity in anatomical details, and the modern human pelvic form (with narrower overall breadth and a birth canal requiring rotational birth) seems to appear between 200 and 100 kya, with the origin of H. sapiens.

Pelvic anatomy in H. heidelbergensis (sometimes referred to as ‘Archaic H. sapiens’[8]) is known primarily from high-latitude individuals from Europe and Asia (figure 3; [37,97,116,119,120]). These pelvises are very large overall and remarkably wide: the specimens from Atapuerca (Spain) and Jinniushan (China), for example, have the largest bi-iliac diameter of the birth canal and a high degree of iliac flare in H. heidelbergensis—although generally less than in earlier Homo [2,37,100,116,119,120]. Again, these two aspects of pelvic breadth are probably linked biomechanically [2,60]. The birth canal is broad both at the inlet, partly because of long superior pubic rami, and at the outlet; the shape of the midplane is not clear owing to poor preservation of the iliac spines in the relevant fossils [2,37,60,74,116,119].

The pelvis in Neanderthals is typically very similar to H. heidelbergensis in its morphology and large size [1,74,100,120–126] (but see [127]). Except for a few uniquely derived characteristics, particularly in the cross-sectional shape of the superior pubic ramus (see [100,120] for reviews), recent work has shown that most of the features of the Neanderthal pelvis that were once thought to be distinctive are in fact retained primitive traits [37,100,119–121,123,128].

The shape of the birth canal in most Middle Pleistocene Homo specimens was primitive relative to modern humans (although some may have indices within the modern human range [16,37,116]). This implies a primitive (non-rotational) birth mechanism in both H. heidelbergensis and Neanderthals, although this is debated partly because of the paucity and incompleteness of pelvic fossils [1,2,16,37,96,124,129]. However, birth canal size in Middle Pleistocene Homo is clearly larger than in earlier hominins, generally within the modern human range [16,74,79,119,121,124,127]. Presumably this enlargement is related to increases in infant size. Adult body size in H. heidelbergensis and the Neanderthals, which was within or above the modern human range, changed little during the Middle Pleistocene, but adult brain size did increase [24,60,74,113,114,116]. Fossil evidence suggests that Neanderthal infants were born with a body and head size similar to modern newborns, implying a similar level of obstetric difficulty in Neanderthals and modern humans [1,16,74,77,124] and probably ‘obligate midwifery’ (cf. [35,130]). Finally, it is also of interest that these are the first humans in which sexual dimorphism in the pelvis can be clearly observed, and the pattern differs from modern humans. While the birth canal is larger in females than males, this is primarily owing to rotation of the pubis, rather than lengthening as in modern humans. In archaic Middle Pleistocene Homo, the pubic rami are actually longer in males than in females [74,79,116,120,121,124].

5. The evolution of the modern human pelvis

European Neanderthals maintained this archaic complex of pelvic anatomy (and possibly birth mechanism) well into the Late Pleistocene ([125,131]; but see [127]). However, some human populations during the late Middle Pleistocene, particularly in Africa and the Middle East, where H. sapiens evolved, were characterized by a mix of primitive traits and ones that are derived in the direction of modern humans. The Late Middle Pleistocene fossil pelvis from Broken Hill (Kabwe), Zambia, for example, is largely modern in appearance but is associated with a clearly archaic skull [132] and does have some primitive traits (see [2,133,134]). Arensburg & Belfer-Cohen [123] identify a similar mosaic in populations of late Middle Pleistocene hominins from Israel. They point to modern traits in pelvic fossils generally classified as Neanderthals (such as Kebara 2 and Tabun C) and retained primitive features in early ‘anatomically modern H. sapiens’ such as Skhul IV and IX [123] (but see [122]). This mix of traits is what might be expected in closely related groups with a rapidly evolving new morphology. An alternative explanation could be interbreeding between groups that display different morphologies, but this hypothesis would be difficult to test based on the small samples available.

When exactly modern human pelvic anatomy first appeared is unclear at this time, but it must be near the end of the Middle Pleistocene, and certainly by 100 kya. The earliest likely examples are found in individuals from East Africa and the Middle East, although the late Middle Pleistocene pelvic fossil record from Africa is particularly sparse [2]. The Omo I partial skeleton from Ethiopia, described as ‘the oldest well-dated anatomically modern human fossil’
(135), has been dated to approximately 195 kya—interestingly, twice the age of the intermediate or mosaic populations from Israel. However, there are traits throughout the skeleton that differentiate it from modern humans, some of which appear to be primitive (135). Pearson et al. (135) described the Omo I partial hip bone, but primarily with respect to sex and age inferences; no archaic features are mentioned, and no assessments of functional anatomy or phylogenetic implications have been made thus far (and may not be feasible given the fragmentary nature of the specimen).

Whether the modern human pelvis was present at 200 kya will have to wait for more complete fossils or at least a more detailed analysis of the Omo I specimen. The 100–95 000 year old Qafzeh 9 H. sapiens skeleton from Israel provides the next example of likely anatomically modern pelvic anatomy. Although it is badly crushed, its morphology appears to match that of H. sapiens [122,123]. Qafzeh 9 is contemporaneous with the Skhul individuals [137], providing further evidence that modern morphology evolved in a mosaic fashion in the Middle East.

Early anatomically modern fossil pelvises, like those of later H. sapiens, were narrower overall compared with archaic humans, with a low degree of iliac flare. The birth canal was equivalent or larger in size and had changed in shape, becoming less platypelloid throughout, with a shortening of the pubic rami, especially in males [100,120]. The birth canal now varied in proportions along its length: the inlet retained its M–L orientation (although less pronounced), especially in females, whereas the midplane and outlet became larger in the A–P dimension. The fossil evidence suggests, therefore, that the modern human pattern of rotational birth evolved only with the origin of H. sapiens [2,74] (although there is some disagreement [124,129]).

What adaptive scenario can explain this dramatic change in morphology? The answer may involve conflicts between thermoregulation and obstetrics. In cold-adapted hominins such as Jinniushan or the Neanderthals, there was no thermoregulatory constraint on widening the pelvis to increase birth canal size (and therefore infant brain size [2,74]). However, among tropical humans, obstetric and thermoregulatory pressures on the pelvis are in direct conflict. Weaver & Hublin [74] and Ruff [2] have proposed that during the Middle Pleistocene, further increases in pelvic breadth among low-latitude hominins were impossible because of heat dissipation requirements. Instead, pressure for narrow-bodied women to birth larger-brained babies eventually resulted in yet another morphological compromise in the pelvis: the capacity of the birth canal was enlarged by increasing its A–P diameter, particularly at the midplane and outlet, whereas its M–L dimensions simultaneously narrowed. The resulting twist in orientation allowed the true pelvis to accommodate a larger-brained infant without also widening the body [138].

The relationship between body size and shape, overall pelvic size and shape, and birth canal size and shape in modern humans is complex [3,15,17,18,79,138–141]. With the evolution of the modern pelvis, the size of the birth canal was essentially decoupled from the size of the body: birth canal proportions in modern humans do not necessarily correlate with body proportions [138,141,142]. A recent study by Kurki [142] determined that among modern humans, birth canal transverse breadth may be constrained by climate, with lower-latitude populations having relatively narrower dimensions, but the anteroposterior breadth of the birth canal appears more free to vary in order to maintain obstetric capacity.

While it has been shown that thermoregulation is an important factor influencing variation in pelvic dimensions between anatomically modern human populations [3,12,13], the way in which obstetrics influences variation among populations, or even between males and females, is unclear. Evolutionary theory would suggest that because ‘selection intensity and phenotypic variability are inversely related’ ([143], p. 59), there should be sexual dimorphism in the variability of pelvic morphology, with variation in the size and shape of the female birth canal limited by obstetric demands. However, the nature and extent of sexual dimorphism in the modern pelvis are particularly complex, and a large number of studies have produced no clear indication that obstetric constraints produced between-sex differences in variability [3,18,138,139,141–143]. To further complicate matters, work by Betti and co-workers [3,18,141] has suggested that among modern humans, neutral evolutionary processes reflecting demographic history have also been important in determining variation in pelvic form (see also [17]).

In any case, whatever the patterns of intraspecific variation, recent and fossil H. sapiens populations from both warm and cold climates show reduced pelvic breadth compared with archaic humans from similar latitudes [2,13,138,144]. As anatomically modern humans spread out from their origins in Africa into higher latitudes [3], they adapted, as earlier hominins had, by evolving wider bodies to improve heat retention [2,12,13,138,145], but no modern H. sapiens populations evolved the primitive platypelloid birth canal and great iliac flare of archaic humans. In addition to its thermoregulatory and obstetric benefits, the narrower modern pelvis and accompanying decrease in body mass may have conferred biomechanical and energetic advantages in walking [146] (but see [15,32,62]), or perhaps improved the adaptive advantages of high mobility, or of running as a subsistence behaviour [111,147] (see also [148]). Through the evolution of the uniquely shaped birth canal, modern humans have been able to birth larger-brained infants, while maintaining the flexibility to adapt body breadth to varying habitats and at the same time improving locomotor performance.

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Endnotes

1Betti and co-workers [3,18] have shown that in addition to selection based on thermoregulatory and locomotor constraints, neutral evolutionary processes have also had a significant effect on pelvic shape variation among modern humans (see §3). However, the fossil record is insufficient to allow investigation of the extent of neutral evolution of the pelvis in extinct humans.
References


In the following discussion, we refer to the humans that succeed H. erectus and predate the Neanderthals, sometimes referred to as ‘Archaic Homo sapiens’, as Homo heidelbergensis, regardless of their geographical origin. We acknowledge that there is a great deal of disagreement regarding Middle Pleistocene human phylogenetics, and we use this nomenclature not to take a taxonomic position but to clarify discussion.


