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Sex differences in the pelvis did not evolve de novo in modern humans

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It is commonly assumed that the strong sexual dimorphism of the human pelvis evolved for delivering the relatively large human foetuses. Here we compare pelvic sex differences across modern humans and chimpanzees using a comprehensive geometric morphometric approach. Even though the magnitude of sex differences in pelvis shape was two times larger in humans than in chimpanzees, we found that the pattern is almost identical in the two species. We conclude that this pattern of pelvic sex differences did not evolve de novo in modern humans and must have been present in the common ancestor of humans and chimpanzees, and thus also in the extinct *Homo* species. We further suggest that this shared pattern was already present in early mammals and propose a hypothesis of facilitated variation as an explanation: the conserved mammalian endocrine system strongly constrains the evolution of the pattern of pelvic differences but enables rapid evolutionary change of the magnitude of sexual dimorphism, which in turn facilitated the rapid increase in hominin brain size.

No other bone in the human body differs, on average, as strongly between males and females as the pelvis. The pelvis is the only part of the human body for which females have larger average dimensions than males[1–5]. Compared with males, females have absolutely larger birth-relevant dimensions of the pelvic canal and a wider subpubic angle as well as a wider sciatic notch. This makes the human pelvis the most reliable anatomical structure for the sex determination of skeletal remains[6–9]. Following earlier work[10], we use 'female' and 'male' here to refer to humans of all genders with an anatomy that is commonly assigned to be female and male, respectively. The terms 'sex differences' and 'sexual dimorphism' are used synonymously.

Pelvic sex differences in humans and non-human primates have long been interpreted as evidence of selection acting on females for an obstetrically sufficient pelvis ('obstetric selection')[1,2,4,11–15]. However, the obstetric significance of sex differences in the pelvis is contentious among researchers[4,5,10,16–18]. Primates with high cephalopelvic ratios (large foetal heads relative to maternal pelvic dimensions) tend to exhibit strong pelvic sex differences[12,19,20]. Yet, the presence of mild differences in obstetrically less constrained species, such as great apes, calls into question the exclusive role of obstetric selection in producing these differences. Even in certain obstetrically unconstrained species, such as the Virginia opossum, a marsupial whose neonates comprise a mere 0.01% of maternal mass[21], pelvic sex differences are present independent of differences in body size. It has been suggested that pelvic sex differences can also, at least partially, arise from natural selection on other anatomical or physiological traits because steroid hormones do not only trigger dimorphic growth and remodelling in the pelvis but are also involved in numerous other developmental and physiological processes[4,10,18].

The evolution of bipedal locomotion coincided with massive changes in the human skeleton, including the pelvis, in both sexes[22–24]. But because of the scarcity of well-preserved pelvic fossil material, it remains unclear if the modern pelvic sex differences appeared with bipedalism in the Miocene to Pliocene or later with encephalization in the Pleistocene, or whether it preceded both of these processes. Inferences from the fossil record are also hampered by the unknown sex of the specimens. For example, at some point it was even argued that the fossil skeleton 'Lucy' (A.L. 288-1), which comprises one of the best-preserved female *Australopithecus* pelves, might be male[25–27].

Body proportions and stature correlate with pelvic form in humans[1,28–31], and some studies have suggested that the pelvic sex differences in the great apes are partly a consequence of body-size differences between the sexes[4,17,18]. However, for modern humans it has been shown that overall size differences contribute minimally to sex differences in pelvis shape[2].

In this Article, we address the evolutionary origin of human pelvic sex differences by a comprehensive geometric morphometric comparison of pelvic variation in modern humans and chimpanzees (*Pan troglodytes*), one of our closest living relatives (Fig. 1). Birth is an easier process in chimpanzees than in humans as the neonatal head comprises only approximately 70% of the smallest maternal pelvic dimension[12,14] and labour is typically shorter, although chimpanzee foetuses also appear to rotate during parturition, similarly but not identical to humans[32,33]. Nonetheless, chimpanzees are usually considered a species with little, if any, obstetrical constraint resulting from the bony pelvis. Most of the studies that investigated pelvic sex differences in chimpanzees have documented subtle differences in pelvic dimensions[4,18,20,34].

Results

We conducted a principal component analysis (PCA) of the Procrustes-aligned shape coordinates of 34 chimpanzee and 99 human individuals (Methods) to explore individual variation in pelvis shape. Humans and chimpanzees separated clearly along principal component (PC) 1 (79% of total shape variance), whereas the sex differences in both humans and chimpanzees were captured by PCs 2 and 3 (Fig. 2). Hence, the species differences in pelvis shape were clearly different (geometrically orthogonal) from the sex differences in the two species. In the plot of PC 2 versus PC 3, the four sex

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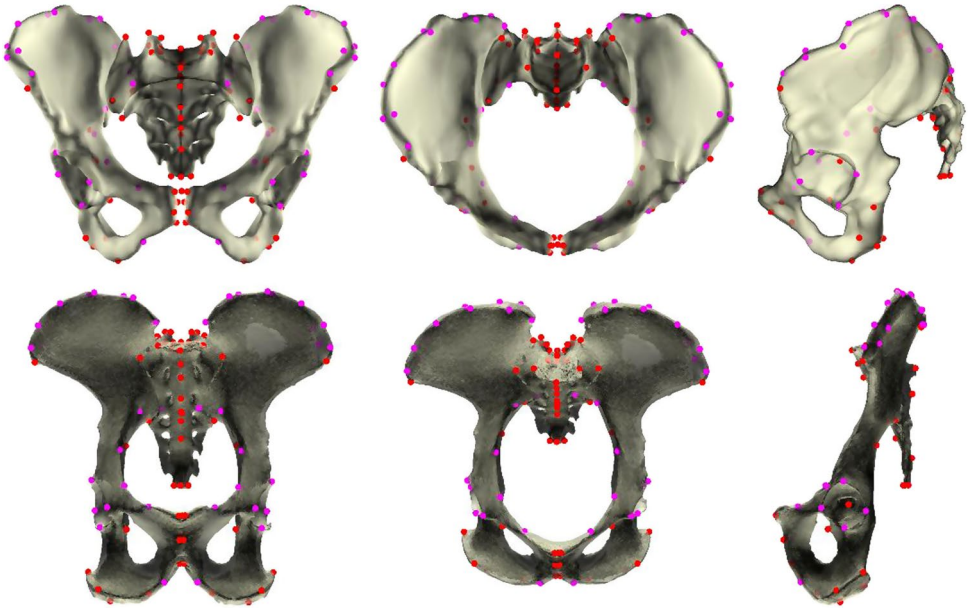

Fig. 1 | Landmarks and semilandmarks. The 109 3D landmarks (red) and semilandmarks (magenta) used in this study, shown on the mean female human pelvis shape (top row) and the mean female chimpanzee pelvis shape (bottom row) of this sample in anterior (leftmost), superior (centre) and lateral (rightmost) views. The surface models are semi-transparent so that all landmarks are visible.

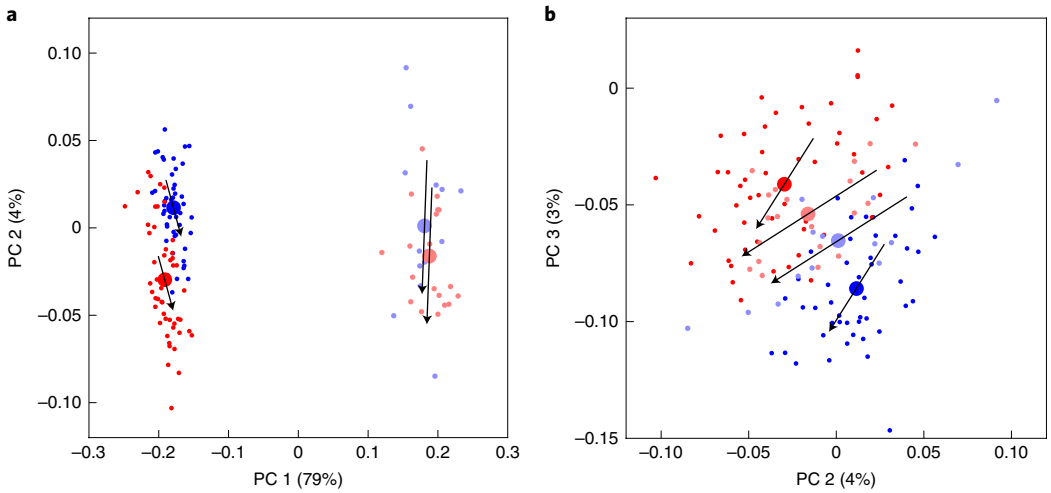

Fig. 2 | Joint PCA of pelvis shape for humans and chimpanzees. a, PC 1 versus PC 2. **b**, PC 2 versus PC 3. Each small point corresponds to an individual (humans: males in blue, females in red; chimpanzees: males in light blue, females in light red). The larger points in the same colours correspond to the sex means of each species. The arrows are the species-specific allometry vectors (coefficient vectors from the pooled within-sex regression of pelvis shape on centroid size, projected into the PC spaces), indicating that the average shape pattern is associated with an increase in pelvis size. Note that they are not sex-specific but are superimposed twice on the sex means of each species (Methods and Extended Data Fig. 1).

means were almost collinear, indicating that the pattern of sex differences is very similar in humans and chimpanzees (almost parallel mean difference vectors; Fig. 2b). However, the overall magnitude of sex differences in chimpanzees, as measured by the Procrustes distance between male and female mean shapes, was only 52% of that in humans.

Because humans have a much larger body size than chimpanzees and males are larger than females in both species, we investigated allometry, the association of size and shape, in each species (pooled within sex). We found that the pattern of pelvic allometry was similar in both species but clearly distinct from the directions of sexual dimorphism and the species differences (Fig. 2). Similar results were obtained when using non-pelvic body size proxies instead of pelvic centroid size to estimate allometry (Extended Data Figs. 1 and 2).

The similar pattern of sex differences in humans and chimpanzees is also obvious from the three-dimensional (3D) visualizations of male and female pelvis shapes (Fig. 3). In both species, the relative transverse diameter of the pelvic inlet and the subpubic angle were larger in females compared with males. Females had a sacrum that was, on average, relatively broader but shorter than in males. Males had relatively larger and more flared iliac blades than females.

For a better comparison of the pattern of sex differences between humans and chimpanzees, independent of the strong species differences in pelvis shape, we added the chimpanzee vector of sex

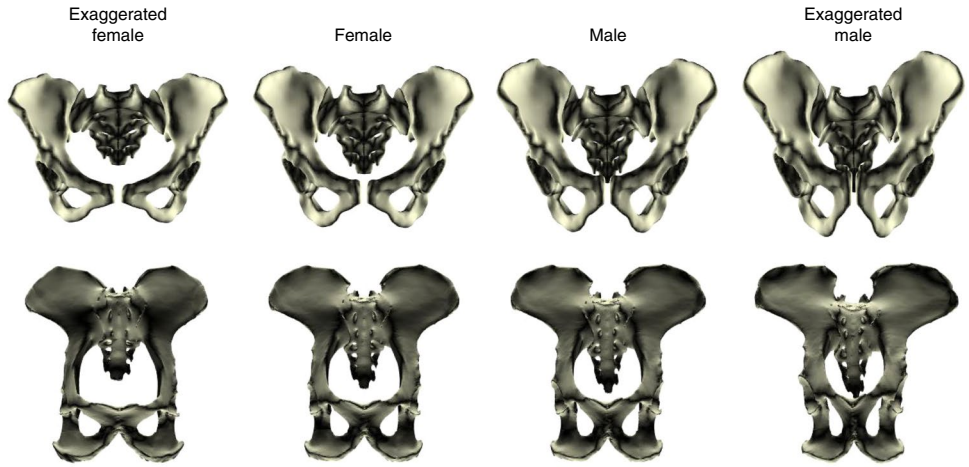

Fig. 3 | Sex differences in pelvis shape for humans (top row) and chimpanzees (bottom row). Visualizations were created by warping, separately for each species, one specimen's surface mesh to the female and male mean shapes using thin-plate spline interpolation. Average female and male shapes are shown together with two-fold extrapolations of the sex differences ('exaggerated female' and 'exaggerated male'; Methods).

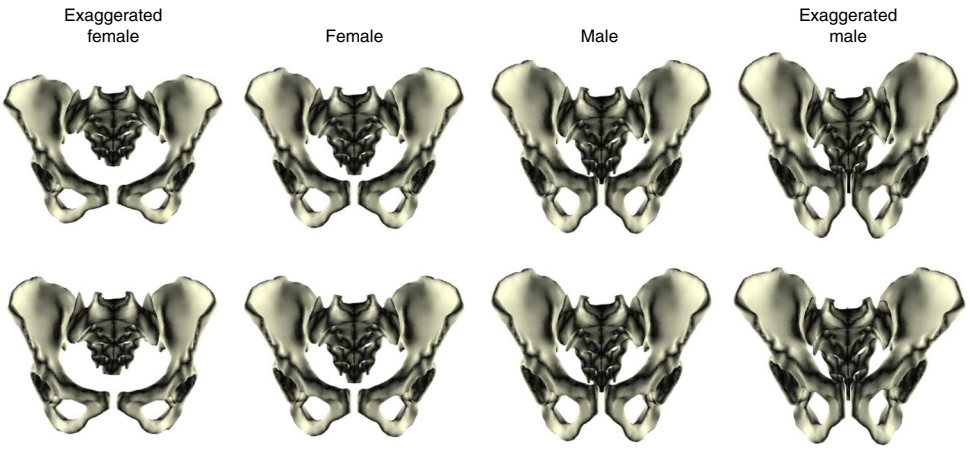

Fig. 4 | A comparison of pelvic sex differences in humans and chimpanzees independent of the species differences. The top row depicts the original sex differences in humans (as in Fig. 3). The bottom row shows the pattern of sex differences (mean difference vector) in chimpanzees added to the human sex means after scaling it to the same magnitude (that is, to the same length) as the human vector. These visualizations are virtually identical between humans and chimpanzees, reflecting the very similar pattern of sexual differences in the two species, regardless of the differences in magnitude.

differences to the human sex means, after scaling the chimpanzee vector to the same length as the human sex difference vector (in units of Procrustes distance). In other words, we added the chimpanzee dimorphism, scaled to the same magnitude as the human dimorphism, to the human female mean shape and we subtracted this scaled chimpanzee dimorphism from the human male mean shape. This resulted in almost perfect reconstructions of the human sex differences in pelvis shape (Fig. 4), showing that the pattern of sex differences is indeed almost the same in the two species.

To assess sex differences in the birth canal more specifically, we conducted a separate analysis of pelvic inlet shape. The most relevant dimensions of the birth canal are determined by the pelvic inlet, which is the superior or coronal part of the pelvic canal, as well as the pelvic midplane and outlet. For the inlet, which is most readily comparable between humans and chimpanzees, the pattern of sex differences was once again very similar in the two species. On average, the transverse diameter of the inlet was relatively wider in females for both humans and chimpanzees, yielding an overall rounder birth canal in females compared with males (Fig. 5). Inlet size, calculated as the area of the polygon defined by the inlet landmarks, was larger in females than in males in both species (on average, 11% larger in human females compared with males and 10% larger in chimpanzees; Extended Data Fig. 3).

Discussion

The human pelvis must accommodate a large foetus during birth and allow for upright locomotion, two traits that are considered central to hominin evolution. From this human-centred perspective, our finding that chimpanzees basically have the same pattern of pelvic sex differences as humans appears surprising.

Human pelvic morphology is thought to be the result of an evolutionary trade-off: obstetric sufficiency imposes selection for a spacious birth canal, whereas the biomechanics of bipedal locomotion and pelvic floor stability during erect posture impose selection for a narrow pelvis[1,13,23,35–38]. Additionally, it has been suggested that an expanded female pelvic canal may also be developmentally induced by the spatial requirements of the uterus, vagina and gonads[10]. Clearly, obstetric selection for a more spacious birth canal is considerably weaker in chimpanzees than in humans, but also the antagonistic selection for a less expansive birth canal is likely to be much

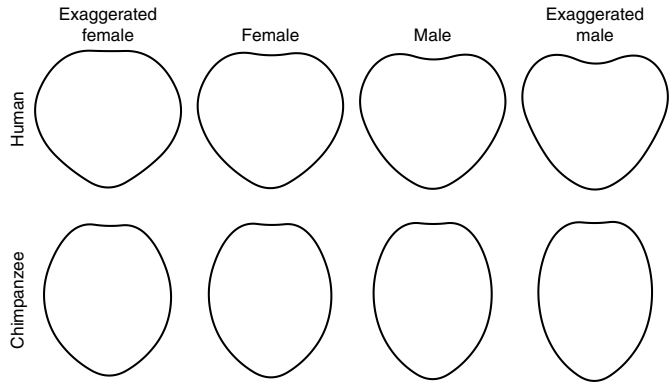

Fig. 5 | Sex differences in the pelvic inlet in humans and chimpanzees. The pelvic inlet is the superior part of the birth canal (Fig. 1). Sex differences in the inlet (humans: top row, chimpanzees: bottom row) are shown together with three-fold extrapolations of the sex differences ('exaggerated female' and 'exaggerated male'). The symphysis pubis lies at the bottom of each curve and the sacrum at the top. In humans, and especially in males, the sacral promontory protrudes into the pelvic canal, which is not the case in chimpanzees.

weaker in chimpanzees as they are not bipedal. The optimal 'compromise morphology' of the chimpanzee pelvis may therefore still comprise a certain degree of sexual dimorphism, despite chimpanzee neonates being relatively small. This may explain the magnitude of pelvic dimorphism in chimpanzees[4,18,34] and other great apes[4,8], as documented by earlier studies.

It is less obvious why the pattern of pelvic sex differences in chimpanzees so closely resembles that in humans, despite the difference in the magnitude of dimorphism and all the differences in parturition and biomechanics. The striking similarity in pelvic sex differences suggests that they did not evolve de novo in modern humans but were already present in the common ancestor of humans and chimpanzees, and thus also in the extinct *Homo* and *Australopithecus* species and putative hominins (for example, *Sahelanthropus*), albeit at different magnitudes.

It is likely, however, that the pattern of sex differences in the pelvis is much older and of early mammalian or even amniote origin. Difficult labour owing to large foetuses is not unique to humans but can be found in several other primates (for example, gibbons, macaques and squirrel monkeys). Bats, seals, several rodents and even most ungulates all have relatively larger neonates than humans[11]. Species with large neonates also tend to exhibit more pronounced sex differences[11,18,20,39]. Reptiles and birds lay eggs, but may nonetheless face similar 'obstetric' challenges when egg size is large relative to maternal body size, as in the kiwi bird[40] and small-bodied turtles[41,42]. Indeed, sex differences in the pelvis have been documented for all major placental clades (Afrotheria[43], Euarchontoglires[44,45], Eulipotyphla[11], Chiroptera[11,46,47], Cetartiodactyla[48–50], Carnivora[51,52] and Xenarthra[45]), and the pattern of pelvic sex differences appears to be similar between these groups (and similar to the human pattern) with differences concentrated predominantly in the pubic region. Similar subtle pelvic sex differences exist in some reptiles[53,54] and birds[55]. This leads us to hypothesize that a sexually dimorphic pelvis existed already in early mammals or potentially even in amniotes and that it constitutes the ancestral condition for mammals. We propose that this common ancestor had already evolved sexual dimorphism in the pelvis to facilitate giving birth to large offspring or, alternatively, for laying large eggs relative to adult body size.

Even some mammals with tiny neonates exhibit subtle sex differences in the pelvis. Marsupial bony pelves provide ample space for their small foetuses and obstetric selection clearly cannot explain the presence of pelvic sex differences. Yet, some of their sexually dimorphic features are similar to the human pattern[21]. We propose that pelvic sex differences in mammal species where birth is completely unconstrained by the bony pelvis are a 'vestigial pattern:' developmental remnants that were obstetrically adaptive in early mammalian or amniote ancestors. Because of the underlying hormonal induction, it might be difficult to evolutionarily remove pelvic sex differences completely, even when they are no longer necessary for parturition, as in marsupials. Subtle sex differences might not carry a fitness disadvantage and therefore simply persist as vestigial traits.

Developmentally, the pattern of pelvic sex differences is largely determined by the spatial distribution of oestrogen, androgen and relaxin hormone receptors and by hormonally induced bone remodelling[56,57]. In humans, for instance, these hormones have been shown to orchestrate pelvic bone remodelling during puberty, but sex differences in the pelvic receptors for these hormones have already developed in the foetus[58,59]. The magnitude of pelvic dimorphism may also be influenced by the wide pleiotropic effects of oestrogen hormones on other tissues, including pelvic soft tissue. Indeed, it has been reported that different trunk elements show a similar pattern of morphological integration in humans and chimpanzees, albeit at different magnitudes[30,60].

As most aspects of the endocrine system are highly conserved among vertebrates, we propose that the genetic–developmental machinery underlying pelvic sex differences has also stayed relatively stable during primate and maybe even amniote evolution. However, we suggest that the developmental 'knob' that regulates this machinery, namely the amount and duration of hormone secretion as well as the overall reactivity of the corresponding receptors in the pelvis, is much more evolvable and can adapt rapidly. This discrepancy in evolvability may account for the conserved pattern of pelvic sex differences among primates and mammals and the highly variable magnitude. Hence, when the size of the neonatal brain increased substantially in the human lineage during the Pleistocene[61,62], the genetic and developmental mechanisms to evolve a more spacious female pelvis were already in place, they did not need to evolve anew. This evolutionary co-option has led to the modern human pelvic dimorphism, which is outstanding in magnitude among most primates but probably similar in pattern to most other mammals.

This idea closely resembles the concept of 'facilitated variation'[63], which is a central concept in evolutionary developmental biology and the extended evolutionary synthesis[64,65]. It proposes that 'weak regulatory linkage' of conserved genetic and developmental 'core components' has greatly enhanced the evolvability of complex organisms. A classic example is sex determination and sex-specific development. Once sex is determined, the genetics and physiology of sex-specific development are strongly conserved in vertebrates (conserved core components). But the way in which sex is determined (that is, the switch that turns on male or female development) varies considerably across lineages[66–69]. We propose that the genetic and developmental mechanisms responsible for pelvic sex differences are themselves conserved core components with a highly evolvable regulatory control.

Support for the facilitated variation hypothesis of pelvic sex differences comes from the comparison of human populations. A reanalysis of the data from DelPrete[70] showed that all populations have a very similar pattern of pelvic sex differences despite ample variation in the magnitude of dimorphism, as predicted by our hypothesis (Extended Data Fig. 4). So far, no broad quantitative comparison of pelvic sex differences across primates, mammals and amniotes has been conducted. Our hypothesis provides the testable prediction that the pattern, but not the magnitude, of pelvic sex differences is largely conserved across mammals and other amniotes, despite very different obstetric and biomechanical requirements.

Methods

Our study sample comprised 34 adult chimpanzee pelves (20 female, 14 male) and 99 adult human pelves (53 female, 46 male). On each pelvis, 44 anatomical 3D landmarks and 65 curve semilandmarks were collected. For the chimpanzees, we measured these points manually on 3D surface models of pelves in the software Amira-Avizo (Thermo Fisher Scientific). The chimpanzee sample included 10 specimens segmented from whole-body computerized-tomography (CT) scans from the Primate Research Institute of the University of Kyoto, 20 CT-scanned disarticulated pelves available as individual bones from the Center for Academic Research and Training in Anthropogeny (which we recomposed digitally using the software Geomagic), and four surface-scanned pelves available as individual bones from the Natural History Museum in Vienna, which we also recomposed digitally using Geomagic (Supplementary Table 1). One chimpanzee specimen had missing landmarks, which were imputed by thin-plate spline deformation of the sample average[71].

For the human sample, a set of pelvic landmarks homologous to those in the chimpanzees was selected from a larger, existing dataset collected from skeletons of white North Americans housed at the Hamann-Todd collection[1,2,72,73]. These data were collected by physically articulating the sacrum and left coxal bone before measuring the 3D landmarks with a Hewlett-Packard digitizer[72]. As landmarks were only measured on the left hemipelvis they were mirrored across the midplane, which was estimated as a least-squares fitted plane to the unpaired landmarks. In the original human sample, 3.6% of all landmarks were missing, which were also imputed by thin-plate spline deformation of the sample average[71].

The landmark data of all 133 pelves were subjected to generalized Procrustes analysis, standardizing for variation in overall position, scale and orientation[74–76]. The positions of the semilandmarks along their curves were estimated by the sliding-landmark algorithm, which minimizes the bending energy, a measure of local shape differences, between the individuals and the sample mean shape[77,78].

Sexual dimorphism in pelvis shape was visualized by warping a 3D surface model to the female and male mean shapes, separately for humans and chimpanzees, using thin-plate spline interpolation. For the chimpanzees, a surface model of one specimen in our sample was used. For visualizing the human landmark data, we used another surface model of a human pelvis that was not part of our sample (www.turbosquid.com human anatomy series, product ID 710664, Oormi Creations), on which we measured the same 3D landmarks using the software Amira-Avizo.

To extrapolate the pattern of sexual dimorphism for effective visualization, we produced exaggerated female and exaggerated male pelvis shapes by adding or subtracting one additional sexual-dimorphism vector to the sex means, separately for each species, leading to a two-fold extrapolation of the actual magnitude of dimorphism. To compare individual variation and sexual dimorphism in pelvis shape between humans and chimpanzees, we performed a joint PCA of the pelvic shape coordinates of the two species.

Allometry, the association of size and shape, was estimated by an ordinary least-squares regression of the shape coordinates on the landmarks' centroid size, separately for each species but pooled within males and females[76,79]. Additionally, we regressed the pelvic shape coordinates on body size (stature in humans and femur head diameter in chimpanzees). The vectors of regression coefficients were orthogonally projected onto the PC planes (PC 1–2 and PC 2–3) and superimposed on the two sex means.

To assess sex differences in the size and shape of the birth canal more specifically, we used a sub-sample of 12 landmarks delineating the pelvic inlet, from the sacral promontory along the linea terminalis to the pubic symphysis. These 3D landmarks were projected onto a least-squares fitted plane and the size of the inlet was calculated as the area of the polygon defined by the projected inlet landmarks. The sliding-landmarks algorithm[77,78] was applied once again to the resulting two-dimensional landmarks, which were then subjected to Procrustes analysis and PCA. All analyses and all figures were produced using the software Wolfram Mathematica 12.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are openly available in an OSF repository[80], https://osf.io/bd4gw/.

Code availability

The code written to analyse the data is openly available in an OSF repository[80], https://osf.io/bd4gw/.

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Author contributions

B.F. designed the comparative study. N.D.S.G., E.Z. and B.F. developed the chimpanzee landmark scheme and E.Z. and N.D.S.G. acquired the chimpanzee data. N.D.S.G. and B.F. derived the homologous landmark scheme. B.F. acquired the human data. B.F. and P.M. cleaned and analysed the data. B.F., N.D.S.G. and P.M. wrote the paper. All authors commented on the paper.

Competing interests

The authors declare no competing interests.

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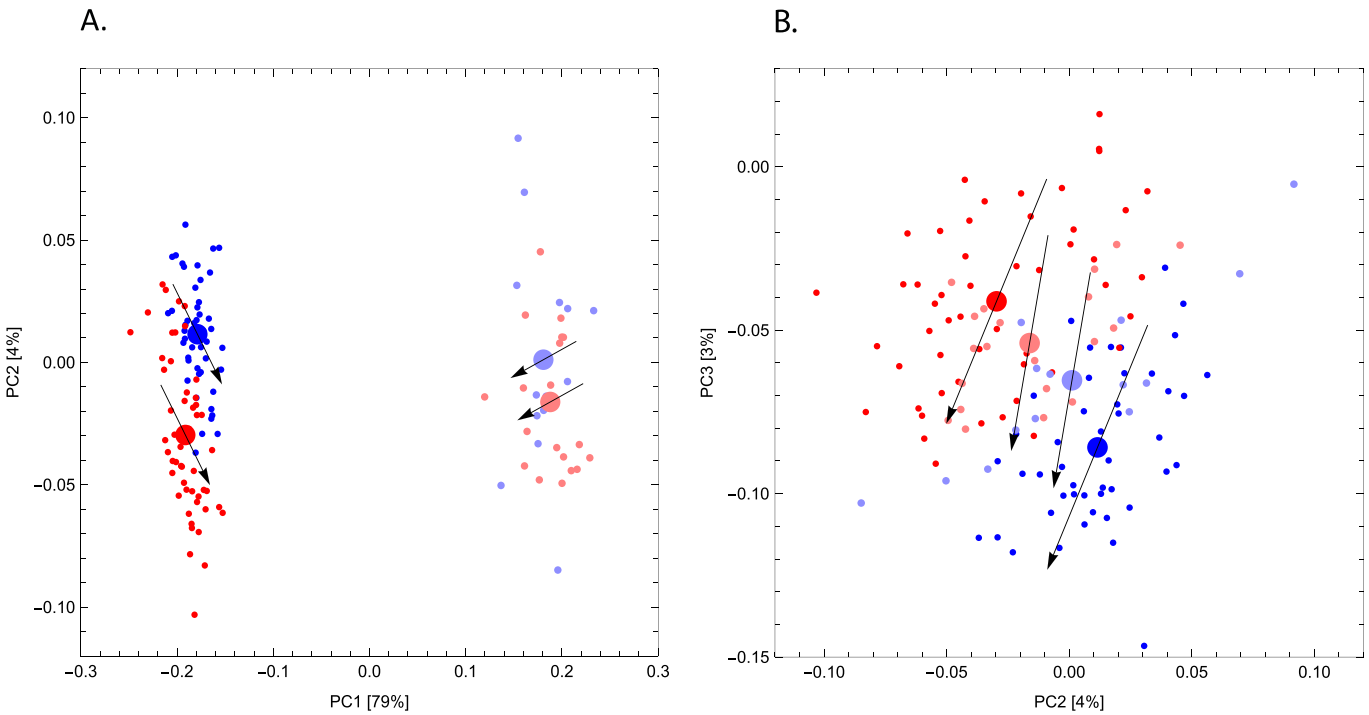
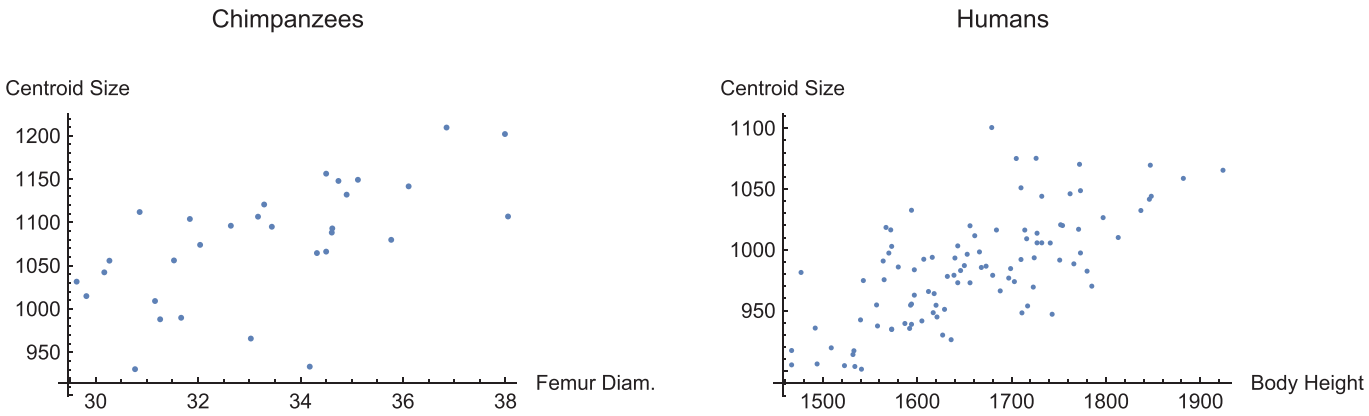
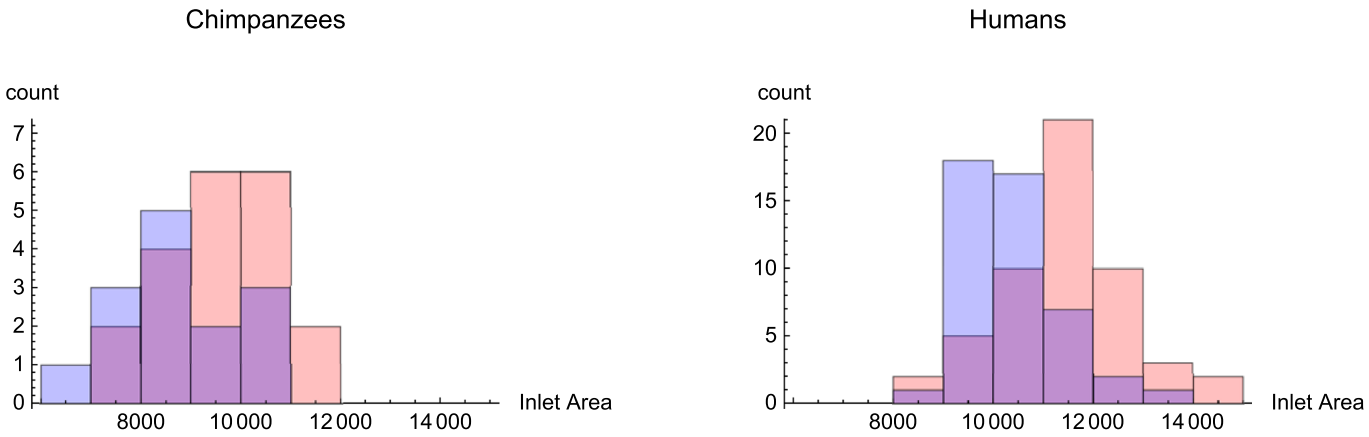


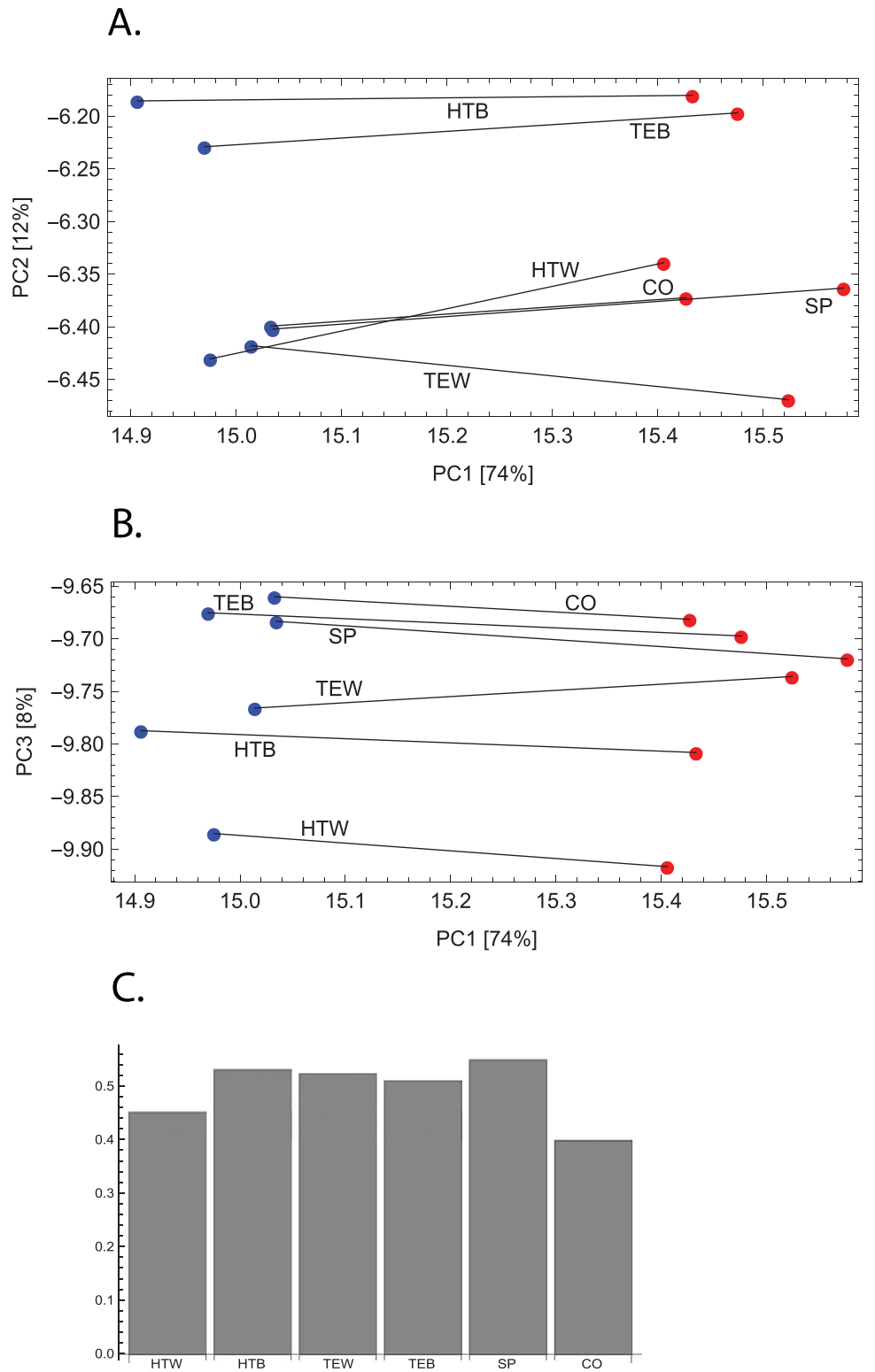
Extended Data Fig. 1 | Principal component analysis (PCA) of pelvis shape, jointly for humans and chimpanzees. The black arrows represent the allometry vectors, which were estimated here using a non-pelvic size measure for each species (femoral head diameter in chimpanzees and body height in humans, compare Extended Data Fig. 2) in contrast to Fig. 2, where they were estimated based on pelvic centroid size. For these non-pelvic size variables, z-scores were computed independently for each species. The allometry vectors were then estimated by regressing the shape coordinates on the z-scores for each species and projected into the PC spaces. As in Fig. 2, the allometry vectors are species-specific but not sex-specific. The vectors are shown twice, superimposed on the sex means for each species. The direction of allometry is distinct from the direction of sex differences in both species. The individual data shown are the same as in Fig. 2. Each small point corresponds to an individual (humans: males=blue, females=red; chimpanzees: males=light blue, females=light red). The larger points in the same colors correspond to the sex means for each species.



Extended Data Fig. 2 | Pelvic centroid size vs. femoral head diameter in chimpanzees and body height in humans, respectively. Correlations for these pairs of size measures were 0.62 in chimpanzees and 0.70 in humans. Femoral head diameter was available for 31 out of 34 chimpanzees and stature was available for all 99 human individuals.



Extended Data Fig. 3 | Inlet area in mm² in humans and chimpanzees for females (red) and males (blue). Inlet area was calculated as the area of the polygon defined by the 2D inlet landmarks. Humans: female mean=11540 (sd=1248), male mean=10376 (sd=1047); Chimpanzees: female mean=9517 (sd=1107), male mean=8661 (sd=1263).



Extended Data Fig. 4 | Reanalysis of data from DelPrete (2019). These data comprise means for females and males of 26 pelvic variables (linear distances, curved distances, and circumferences) from 6 populations (skeletal collections): White individuals from Hamann-Todd collection (HTW, 60 males, 59 females); Black individuals from Hamann-Todd (HTB, 60 m., 60 f.); Whites from Terry collection (TEW, 52 m., 52 f.), Blacks from Terry collection (TEB, 52 m., 52 f.); Coimbra collection (CO, 84 m., 71 f.); Spitalfields collection (SP, 31 m., 35 f.). We conducted a principal component analysis of these data. Shown are the sex means of males (blue) and females (red) for each population within the first three principal components (accounting for 94% of the total variance). The sex difference vectors (lines connecting the sex means) of the six populations are close to parallel in the first three principal components (panels A and B), illustrating the similar pattern of sex differences in the pelvis between human populations, despite some variation in magnitude (panel C). The magnitude was calculated as the Euclidean length of the sex differences vector.

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Data exclusions	No individuals were excluded.
Replication	The dataset was carefully cleaned before the analysis. All steps of our analysis are fully reproducible and the data and code will be shared upon publication.
Randomization	Before measurement, individual chimpanzee pelvises were randomized. All 3D measurements were subsequently taken by a single person, one of the authors. For the human sample, the data used here were part of a larger, existing dataset.
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Field-collected samples	No involvement of field-collected samples.
Ethics oversight	No ethics oversight required as only museum material and surface models from online repositories were measured.

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