

# Allometry and Sexual Dimorphism in the Human Pelvis

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## ABSTRACT

Sexual dimorphism in the human pelvis has evolved in response to several jointly acting selection regimes that result from the pelvis' multiple roles in locomotion and childbirth, among others. Because human males are, on average, taller than females, some aspects of sexual dimorphism in pelvis shape might result from allometry, the association between stature and pelvis shape across individuals. In this study, they aimed to disentangle and quantify the two components contributing to pelvic sex differences: the allometric component, which emerges as a consequence of dimorphism in stature, and the remaining non-allometric sexual dimorphism component. A geometric morphometric analysis of a dense set of 3D landmarks, measured on 99 female and male adult individuals was conducted. While pelvis size was similar in both sexes, the average differences in pelvis shape reflected the well-documented pattern of sexual dimorphism. There was almost no overlap between females and males in shape space. Their analysis showed that pelvis size and shape were similarly associated with stature in both sexes. It was found that dimorphism in the height-to-width ratio of the pelvis and in the orientation of the iliac blades was largely allometric, whereas dimorphism in the subpubic angle and the relative size and distance of the acetabula was largely non-allometric. It was concluded that, in contrast to the overall pelvic proportions, sexual dimorphism in the birth-relevant pelvic dimensions was mainly of non-allometric origin and was presumably mediated via steroid hormone secretion during puberty. *Anat Rec*, 300:698–705, 2017. © 2017 Wiley Periodicals, Inc.

**Key words:** obstetric dilemma; human evolution; morphometrics

## INTRODUCTION

The complex geometry of the human pelvis reflects its multiple functional roles: support of the upper vertebral column, locomotion, and childbirth. The well-known pelvic sexual dimorphism is linked to obstetric requirements. The pelvic canal is wider and differently shaped in females than in males (Schultz, 1949; Rosenberg, 1992; Tague, 1992; Rosenberg and Trevathan, 1995; Fischer and Mitteroecker, 2015; Huseynov et al., 2016). Sex differences in the pelvis have been described qualitatively by visual inspection as well as quantitatively by numerous measurements. Pelvic dimorphism has been

used reliably for sex determination in various archeological, anthropological, and forensic contexts (Hanna et al., 1953; Stewart, 1954; Davivongs, 1963; Kelley, 1979;

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Seidler, 1980; Bruzek, 2002; Patriquin et al., 2003; İřcan, 2005; Steyn and İřcan, 2008). A classic variable for sex determination, the ischium-pubic index (Schultz, 1930; Washburn, 1948; Schultz, 1949; Leutenegger, 1970), relates the dimensions of the sexually dimorphic pubis to the ischium, a measure correlating with body size (Leutenegger, 1970).

Sex differences in the pelvis are thought to be sex-specific solutions to different selection pressures that have acted on the two sexes throughout the evolution of modern humans: only female pelvises must be able to accommodate the fetus during childbirth. Efficiency for bipedal locomotion and sufficiency for obstetric requirements are likely to be among the most important selection regimes acting on pelvic morphology (Grabowski, 2012; Grabowski and Roseman, 2015). The relevance of obstetric selection for the origin of pelvic sexual dimorphism is supported by comparative studies in primates, which show that species with large neonates also have large sexual dimorphism (Leutenegger, 1974; Rosenberg, 1992; Ridley, 1995; Wells et al., 2012; Dunsworth and Eccleston, 2015).

Human females and males also differ in body height: on average, males are taller than females. The major part of dimorphism both in stature and pelvic morphology emerges during puberty (Coleman, 1969; Mobb and Wood, 1977; LaVelle, 1995) by the sex-specific interaction of steroid hormones and the GH/IGF-1 axis (Rogol et al., 2002; Styne, 2003). For that reason, there is a certain consensus in the literature that while part of the sex differences are likely a consequence of obstetric selection in females, the remaining part can be linked to sex differences in body size (Mobb and Wood, 1977; Steudel, 1981; Wood and Chamberlain, 1986; Tague, 1992; Arsuaga and Carretero, 1994; Kurki, 2011, 2013). All of these studies found some correlations between stature and certain selected pelvic dimensions and concluded that sexual dimorphism in the pelvis is—in part—a consequence of the sexually dimorphic body height. However, these studies disagree about the extent to which stature accounts for pelvic dimorphism between the sexes. One reason is that the estimates tend to depend on the specific distance measurements that were taken. Results on single distance measurements are difficult to interpret if they are considered separately, without reference to other dimensions. For example, as some pelvic dimensions are absolutely larger in females and others are larger in males, measures of overall pelvic size based on only a small number of pelvic measurements depend highly on the specific choice of measurements and may thus be misleading. A few linear dimensions cannot adequately represent the complex geometry of the pelvis; its analysis requires an inherently multivariate approach. This is the approach we choose to take in this study.

It is a long-standing tradition in biometrics to study the association of body proportions or body shape with overall body size, typically referred to as “allometry” (Gould, 1966; Huxley, 1932). Based on estimates of such associations across individuals *within* one sex or species, the differences *between* sexes or species can be partitioned into two components, one that is attributable to allometry and one non-allometric component (Bookstein, 1991; Klingenberg, 1998, 2016; Mitteroecker et al., 2004a, 2013).

In this study, we aim to disentangle and quantify the two components contributing to pelvic sex differences: (i) the pattern and magnitude of sexual dimorphism that emerges as a consequence of body size dimorphism (the “allometric component”), and (ii) the remaining “non-allometric sexual dimorphism.” We apply geometric morphometric methods to fine-resolution landmark data that capture the complex three-dimensional geometry of the pelvis.

## MATERIAL AND METHODS

This study is based on a data set established by Herbert Reynolds and colleagues in 1982 using a large number of pelvises from skeletons from the Hamann-Todd collection at the Cleveland Museum of Natural History. Reynolds et al. articulated the pelvises and measured 3D landmark coordinates using a Hewlett Packard digitizer. Stature was measured earlier, before skeletonization of the human bodies. A more detailed description of the data acquisition, preparation, and measurement accuracy can be found in Reynolds et al. (1982) (available for download from <http://www.dtic.mil/dtic/tr/fulltext/u2/a118238.pdf>) as well as in Fischer and Mitteroecker (2015).

From the data set established by Reynolds et al. we used a subsample consisting of 99 American Whites (46 males, 53 females). As some landmarks were frequently missing from the data set, we selected a subset of 71 3D landmarks per pelvis based on their availability in the sample and the quality of their definition. This subsample was earlier used in another study by the authors (Fischer and Mitteroecker, 2015) and it is available online (<http://datadryad.org/resource/doi:10.5061/dryad.2d728>). We reconstructed the missing landmarks (3.7% of all landmarks) by thin-plate spline interpolation using the mean pelvis shape of our sample as a reference (Bookstein, 1989; Mitteroecker and Gunz, 2009). Reynolds et al. (1982) measured most landmarks on the left hemipelvis only. To restore the data for the right hemipelvis, we estimated the midplane as a least-squares fitted plane to the unpaired landmarks (Gunz et al., 2009) and mirrored the unpaired landmarks across this midplane. This routine produced bilaterally symmetric configurations of 126 3D landmarks per pelvis (Fig. 1).

The 99 configurations of 126 landmarks were then superimposed by a generalized Procrustes analysis, which standardizes the landmark configurations for variation in position, scale, and orientation. The resulting Procrustes shape coordinates represent the shape of the pelvis only, whereas information about the overall pelvis size is represented by the centroid size of the landmark configurations (square root of the summed squared distances of the landmarks from their centroid, which is the average landmark position). To assess the static allometry of pelvis size, which describes the rate at which overall pelvis size increases with body height in our sample, we regressed log centroid size on log body height, separately for females and males (Huxley, 1932).

We performed a principal component analysis (PCA) of the Procrustes shape coordinates, jointly for males and females. Sexual dimorphism was computed as the difference between average male and female pelvis shape. Allometry, the dependence of pelvis shape on

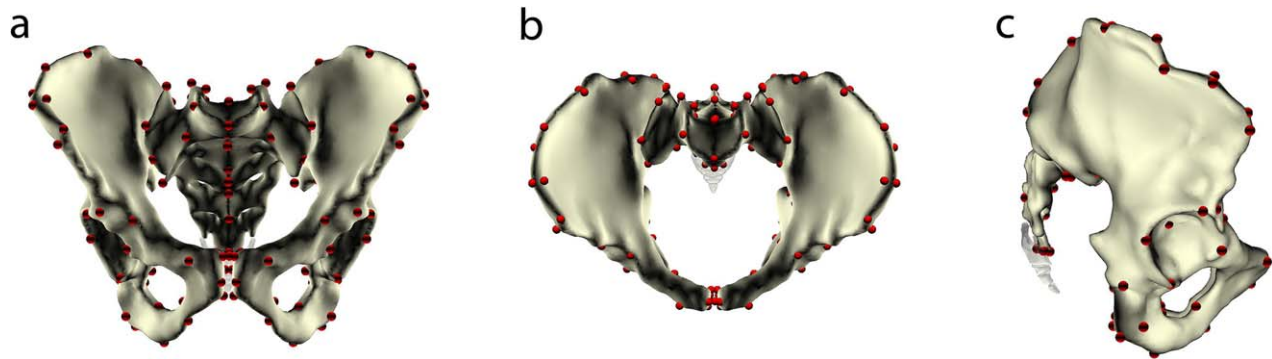


Fig. 1. Positions of landmarks. The data we used in this study consists of a dense set of 3D landmarks, 126 3D points per pelvis, here shown as red spheres on the mean pelvis shape, in anterior (a), superior (b), and lateral (c) view.

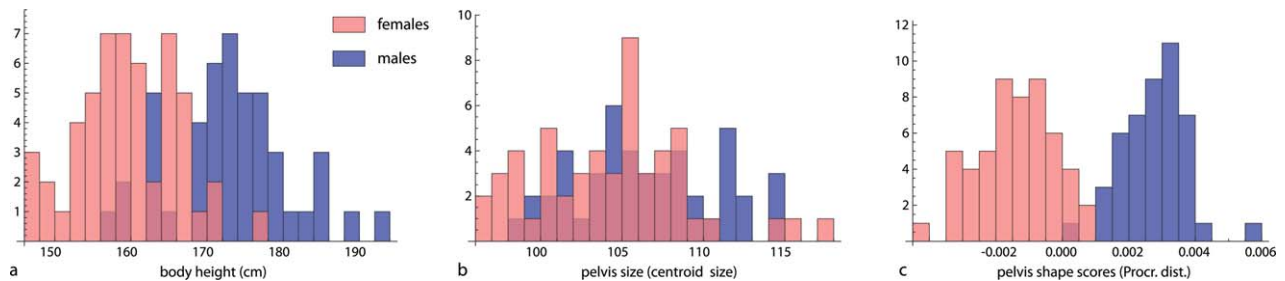


Fig. 2. Histograms for (a) body height, (b) pelvic centroid size, and (c) pelvic shape scores, separately for females (pink) and males (blue). Bars that overlap between females and males are indicated in purple. Body size is more dimorphic than pelvic centroid size; pelvic shape

scores even show almost no overlap. The shape scores shown in (c) were computed by projecting the Procrustes coordinates onto the sexual dimorphism vector; they represent the individual expression of the maximally dimorphic shape features.

body size, was estimated by regression of the Procrustes coordinates on body height, separately for males and females (multivariate linear ordinary least squares regressions). Statistical significance of mean differences and regressions were estimated by permutation tests (5,000 random permutations).

Sexual dimorphism and allometry were represented as vectors in shape space, which had  $123 \times 3 = 369$  dimensions for our data (with 362 degrees of freedom due to the standardization for position, scale, and orientation). The sexual dimorphism vector contains the differences between male and female means for all 369 shape variables. The allometry vector comprises the 369 slopes from the regression of the shape coordinates on body height, describing how pelvis shape would change in response to one unit change in body height (mm). We scaled this vector with the dimorphism in body height. If these two vectors are of similar direction and length in shape space, sexual dimorphism can largely be attributed to allometric effects.

Total sexual dimorphism can be decomposed in an allometric and a non-allometric component in different ways. One classic approach is to compute the non-allometric component as the difference vector between male and female mean shapes in the subspace orthogonal to the allometry vector (Burnaby, 1966; Mitteroecker

et al., 2004b). The allometric and non-allometric vectors computed this way are orthogonal and thus allow for a sum-of-squares decomposition. Because the interpretation of orthogonality as geometric independence rests on a number of assumptions (Huttenberger and Mitteroecker, 2011; Mitteroecker and Huttenberger, 2015), we performed an alternative computation of the non-allometric component by subtracting from the sexual dimorphism vector the allometry vector scaled by the dimorphism in body height (135.5 mm). This is equivalent to the vector of partial regression coefficients resulting from the regression of shape on both body height and sex. These vectors are not orthogonal but are independent of the spatial distribution and redundancy of landmarks (because the computation is performed for each shape coordinate separately) and thus biologically easier to interpret.

Because such a decomposition requires similar allometric relationships in males and females, we compared the directions of the sex-specific allometry vectors and the sexual dimorphism vector in the subspace of the first three principal components (PCs 1–3). To assess if these vectors are sufficiently represented in the low-dimensional space, we expressed the squared norm of the regressions vectors within the space of the first three PCs to the squared norm of the vectors in full shape

space. The pooled within-sex allometry for females and males was estimated by a multivariate regression of shape on body size with sex as a covariate.

For morphological interpretation, the components of sexual dimorphism and allometry were visualized by thin-plate spline deformations (Bookstein, 1989, 1991) of a 3D surface model of an articulated pelvis (turbosquid.com, product ID 710664, Oormi Creations), on which we also measured the 126 3D landmarks using the software Amira (version 5.4.5, FEI Visualization Sciences Group, Bordeaux, France). All statistical analyses and

visualizations were performed with Mathematica 8 (Wolfram Research, Inc., Champaign, IL).

## RESULTS

Despite the clearly dimorphic body height (Fig. 2a), pelvis size—as measured by centroid size—was not clearly dimorphic between females and males (Fig. 2b). On average, males were 135.5 mm or 1.9 standard deviations (s.d.) taller than females, whereas average male centroid size was only 0.5 s.d. larger than female centroid size. Within the sexes, however, pelvic size and body height were positively correlated ( $r = 0.77$  in males and  $0.73$  in females). Pelvic size was negatively allometric in both sexes; the allometric coefficients from the log–log regression are  $0.70$  (standard error:  $0.09$ ) in males and  $0.80$  (standard error:  $0.10$ ) in females (Fig. 3).

In contrast to pelvis size, the shape of the pelvis differed substantially between females and males ( $P < 0.001$ ). The first three principal components accounted for 44% of shape variation and the sexes showed little overlap in these three dimensions (Fig. 4). The shape scores along the axis determined by the sexual dimorphism vector were almost perfectly separated between the sexes, showing a mean difference of 4.0 s.d. (Fig. 2c). We also performed a quadratic maximum-likelihood classification with leave-one-out cross-validation. This led to a classification success of 98% (only 2 out of the 99 individuals were misclassified based on the first 5 PCs). Compared with males, the female pelvis was broader and flatter. Females had shorter but more laterally extending iliac blades, a relatively larger and rounder pelvic inlet, a shorter and more outward projecting sacrum, and a wider subpubic angle (Fig. 5).

Sexual dimorphism was well represented within the first three PCs (96% of the squared length of the dimorphism vector was captured by PCs 1–3). The dimorphism

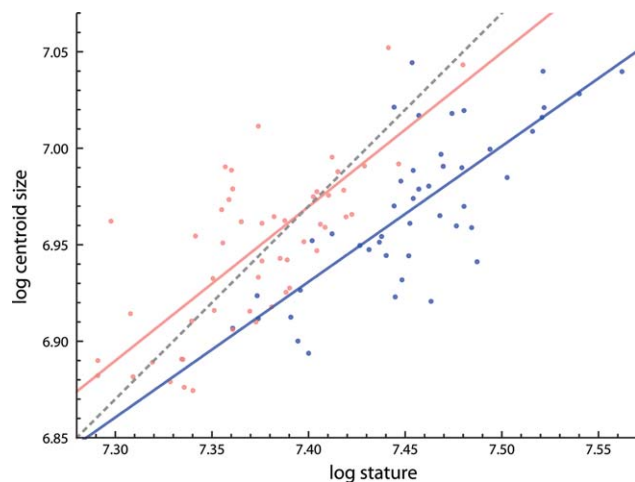


Fig. 3. Linear regression of log centroid size on log body height, separately for females (pink) and males (blue). Each point corresponds to an individual. The allometric coefficients, that is, the slopes of the regression lines, are similar for both sexes and clearly smaller than 1, indicating a negative static allometry of pelvis size. For comparison, the isometric line (gray dashed) with a slope of 1 is also shown.

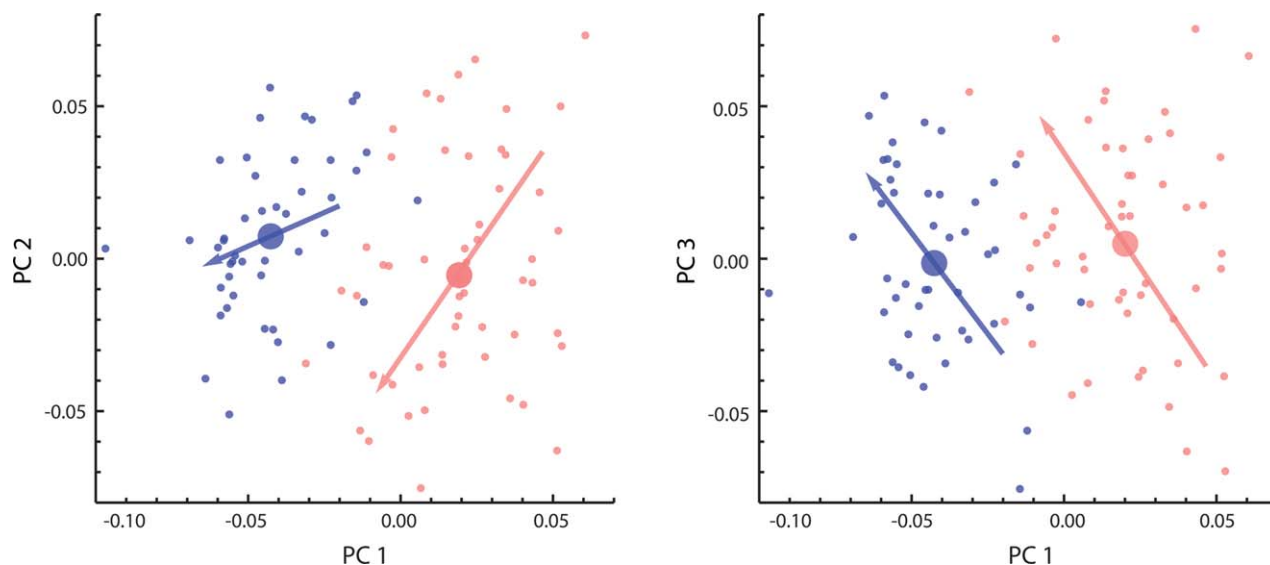


Fig. 4. Principal components (PCs) of pelvis shape. Each point corresponds to an individual (females are pink, males blue). The female and male mean shapes are indicated as large points. The sex-specific allometry vectors were projected onto the planes defined by PC1 and PC2 in (a) and PC2 and PC3 in (b), and multiplied by 300. They describe the pelvic shape change that corresponds to a change in body height of 300 mm, pointing from the shapes of small individuals to that of tall individuals.

## Sexual dimorphism

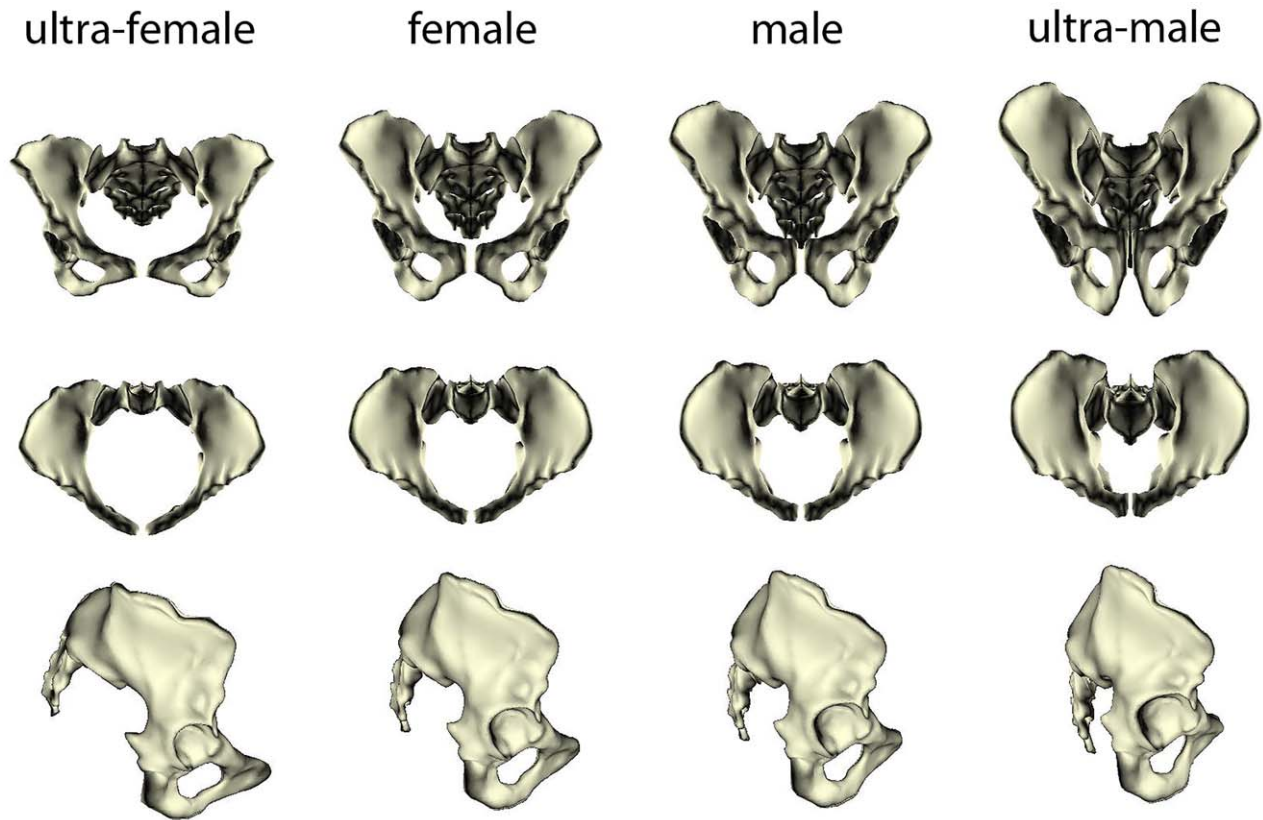


Fig. 5. Sexual dimorphism in pelvis shape. Shown are the average female and male pelvis shapes in the sample, together with fivefold extrapolations of the sexual dimorphism vector ("ultra-female" and "ultra-male"), each in anterior, superior, and lateral view (top, middle, and bottom rows, respectively).

vector closely aligned with PC1 (Fig. 4), the direction of maximum variance in pelvic shape space.

The regressions of shape on body height were significant in both sexes ( $P < 0.001$  for both tests). For males and females, 65% and 49% of the squared length of the allometry vectors were represented by the first three PCs, respectively. While these sex-specific allometry vectors shared a similar direction, they clearly differed in direction from sexual dimorphism, indicating divergent shape patterns underlying allometry and sexual dimorphism. This was also confirmed by the orthogonal decomposition of sexual dimorphism into an allometric and a non-allometric component. Allometry accounts for only 7% of the squared length of the dimorphism vector.

Compared with shorter persons, tall persons had, on average, a relatively taller and narrower pelvis with iliac blades that were more inward rotated (Fig. 6; note that because this analysis is of the shape of the pelvis, increase or decrease of certain dimensions are relative to the overall size of the pelvis, as measured by centroid size). The relative height of the sacrum and the symphysis increased with stature. Taller persons also had a more oval pelvic cavity with an outward-projecting pubic symphysis, whereas short persons had a rounder pelvic cavity.

Both ways of computation yielded very similar visualizations of the non-allometric component. Figure 6 shows the non-allometric component computed as the difference between the sexual dimorphism vector and the scaled allometry vector. This component captures the features of sexual dimorphism that are independent of allometry: Compared with males, females had a relatively flatter and wider pelvis and shorter iliac blades. The distance between the acetabula was relatively larger in females than in males. The female inlet was wider, the subpubic angle was larger, and the sacrum was shorter and more outward projecting than in males.

## DISCUSSION

In this article, we present a geometric morphometric study of pelvis form, based on a dense set of 3D landmarks that comprehensively represent the gross morphology of the pelvis. While we found that overall pelvic size, computed as centroid size, was similar in both sexes, the shape of the pelvis differed considerably. In fact, the distributions of male and female pelvis shape showed only very little overlap, allowing for a reliable sex identification (98% correctly classified individuals).

The average pattern of sexual dimorphism that we found matches the well-known pattern of sexual

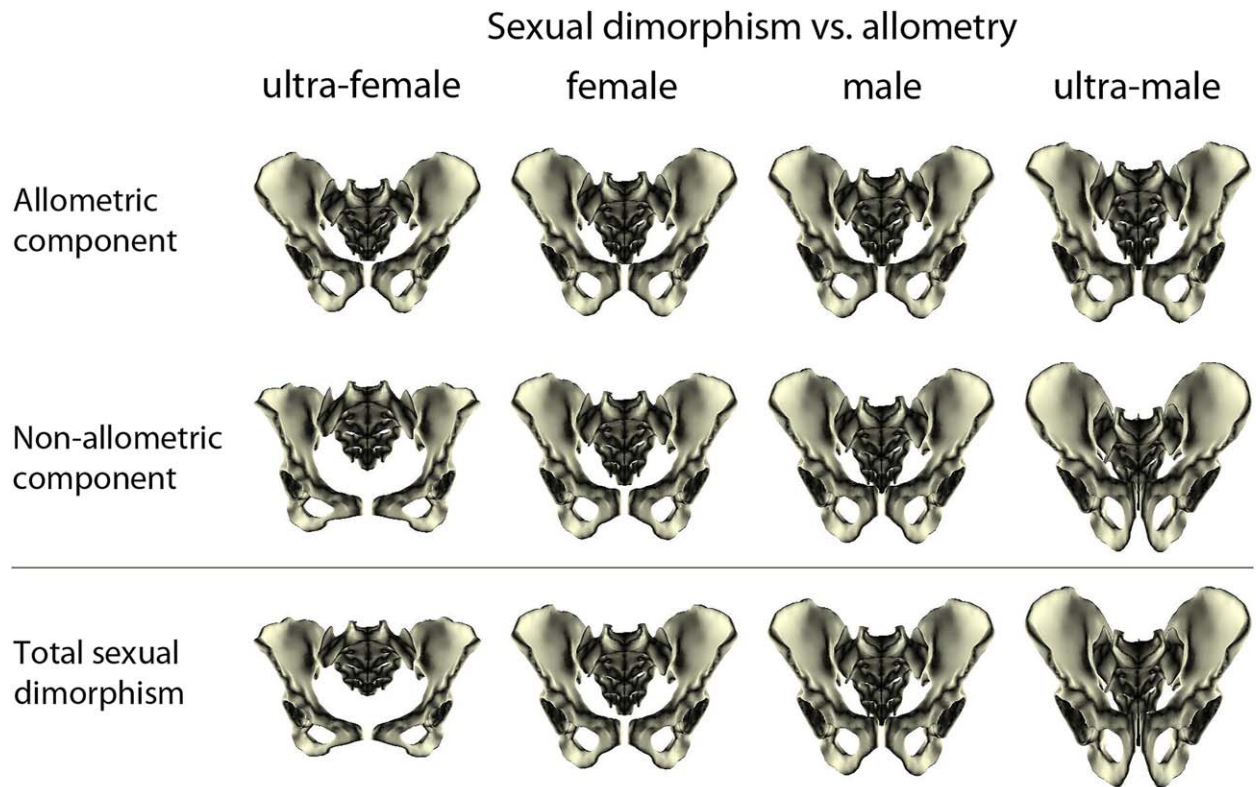


Fig. 6. Decomposition of sexual dimorphism. The total sexual dimorphism in pelvis shape (bottom row) is disentangled into its two components: the allometric component (top row) and the non-allometric component (middle row). Each row contains the corresponding female and male shapes, together with fivefold extrapolations of their

difference (“ultra-female” and “ultra-male”). The allometric component is the pooled within-sex regression vector, scaled to the actual and the extrapolated body height dimorphism between males and females, respectively. The non-allometric component is the difference between the sexual dimorphism vector and the scaled allometry vector.

dimorphism documented in the literature (Wood and Chamberlain, 1986; Tague, 1992; Arsuaga and Carretero, 1994; LaVelle, 1995). Most of these sex differences appear to be adaptations to the obstetric demands in females as they enlarge the birth canal: females have a relatively larger and rounder pelvic cavity, a shorter and more posteriorly projecting sacrum, a wider subpubic angle, and smaller acetabula with a larger distance between them.

Pelvic allometry—the association of pelvis shape and stature—was similar in females and males (for a sex-specific visualization see also Fischer and Mitteroecker, 2015). Together with the overall body proportions, the pelvis becomes taller and narrower with increasing stature. The geometry of the pelvic inlet, by contrast, is differently linked to body height: on average, short persons have a rounder pelvic cavity and a more outward-projecting sacrum than tall persons.

In Fischer and Mitteroecker (2015), we suggested that the rounder inlet shape in shorter persons might be due to the higher obstetric selection pressure in shorter women. It is well-known that shorter women, on average, have harder births than taller women (Baird, 1952; Molloy, 1969; Camilleri, 1981; Dougherty and Jones, 1988; Parsons et al., 1989). In particular, the risk of birth complications increases if the father is much taller than the mother (Dougherty and Jones, 1988). For that reason, the optimal pelvis shape, as a compromise

between obstetric and biomechanical demands, is expected to differ between short and tall women. We suggest that the evolved pattern of pelvic allometry contributes to ameliorate the obstetric dilemma (Washburn, 1960) and that it may be an adaptive response to the complex selection regime acting on the human pelvis.

Recently, Washburn’s obstetrical dilemma hypothesis (Washburn, 1960) has been challenged by researchers who evaluated if wider pelvic dimensions negatively affect walking and running efficiency (Dunsworth et al., 2012; Warrener et al., 2015). These two studies found no evidence that a narrow pelvic morphology contributes to more energy-efficient bipedal locomotion. Elsewhere (Huseynov et al., 2016), this work is already cited as “falsifying the obstetrical dilemma.” However, in our view, discarding this classic hypothesis on these grounds is premature. We suggest that further empirical work based on larger sample sizes is needed to assess the validity of Washburn’s hypothesis and to account for the large morphological variation within the sexes. It must also be taken into account that evolution does not optimize individual morphologies or functionality, but instead population fitness (e.g., Arnold et al., 2001; see also Mitteroecker and Fischer, 2016).

Because males are, on average, taller than females, some of the average pelvic sex differences can be explained as an allometric consequence of this dimorphism in body size. Figure 5 contrasts the allometric

and the non-allometric components of sexual dimorphism. Dimorphism in the overall height-to-width ratio of the pelvis, including the orientation of the iliac blades, is largely allometric, whereas the subpubic angle and the relative size of the acetabula does not scale with body height; sexual dimorphism in these features cannot be explained by allometry. The shape of the pelvic inlet is also related to stature: taller individuals have a more oval-shaped pelvic inlet than shorter individuals. Similarly, the average male inlet is more oval than that of females. However, the allometric effect on pelvic inlet shape does not suffice to explain the entire dimorphism. The dimorphism in inlet shape is larger than predicted for the dimorphism in stature. Likewise, the allometry of the length and orientation of the sacrum matches the pattern of sexual dimorphism, but it does not suffice to explain the magnitude of sexual dimorphism.

It is difficult to quantify the degree to which allometry accounts for pelvic sexual dimorphism. In any such composite quantity, the different anatomical regions are weighted by the number of landmarks per region, which involves some arbitrariness (Huttegger and Mitteroecker, 2011). One such quantification, the angle in shape space between the common allometry vector and the sexual dimorphism vector, was 75° for our sample (and 71° in the space of the first three PCs; see Fig. 4), indicating the dominance of non-allometric effects over allometry. Similarly, when sexual dimorphism is decomposed orthogonally into an allometric and a non-allometric component, the squared length of the allometry vector accounts for only 7% of the squared length of the dimorphism vector. Such summary quantities, however, should be interpreted with care.

In ontogenetic development, the larger part of the dimorphism in pelvis shape as well as in stature emerges during puberty (Coleman, 1969; Mobb and Wood, 1977; LaVelle, 1995; Huseynov et al., 2016), even though pelvic remodeling has been shown to extend into late adulthood (Huseynov et al., 2016; Mitteroecker and Fischer, 2016). During prepubertal growth, which is largely under the control of thyroid hormones and the GH/insulin-like growth factor axis, body height and pelvis are only slightly dimorphic (Rogol et al., 2002; Styne, 2003; Frelat and Mitteroecker, 2011). The pubertal growth spurt coincides with a massive increase in GH secretion and is initiated by gonadal steroid hormones (predominantly testosterone in males and estradiol in females) and the adrenal androgens (primarily DHEAS). Also the sex-specific pubertal growth of the pelvis is due mainly to steroid hormones, even though GH receptors are present in the pelvis as well. The postmenopausal shape change in the female pelvis also coincides with a drop in female steroid hormone secretion. It thus seems possible that the allometric association of stature and pelvis shape is primarily mediated via GH, while the non-allometric sex differences result from the sex-specific action of steroid hormones.

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