JASs Journal of Anthropological Sciences Open Access
Research articles Vol. 99 (2021), pp. 117 - 134 e-pub ahead of print doi.10.4436/jass.99017

New insights on hip bone sexual dimorphism in adolescents and adults using deformation-based geometric morphometrics

Cinzia Fornai[1,2,3], Nicole M. Webb[1,4], Alessandro Urciuoli[5], Viktoria A. Krenn[1,2], Louise K. Corron[6] & Martin Haeusler[1]

1) *Institute of Evolutionary Medicine, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland*
e-mail: cinzia.fornai@univie.ac.at

2) *Department of Evolutionary Anthropology, University of Vienna, Djerassiplatz 1, 1030 Vienna, Austria*

3) *Vienna School of Interdisciplinary Dentistry, Wasserzeile 35, 34000 Klosterneuburg, Austria*

4) *Department of Palaeoanthropology, Institute for Archaeological Sciences, Senckenberg Centre for Human Evolution and Palaeoenvironment at Eberhard Karls University of Tübingen, Ruemelinstrasse 23, 72070, Tuebingen, Germany*
e-mail: nicole.webb@ifu.uni-tuebingen.de

5) *Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, Campus de la UAB. c/ de les columnes s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain*

6) *Department of Anthropology, University of Nevada, Reno, 1664 N. Virginia Street, Reno, NV 89557, USA*

Summary - *Morphological variation of the human pelvis, and particularly the hip bone, mainly results from both female-specific selective pressure related to the give birth of large-headed newborns, and constraints in both sexes for efficient bipedal locomotion, abdominal stability, and adaptation to climate. Hip bone morphology has thus been extensively investigated using several approaches, although the nuances of inter-individual and sex-related variation are still underappreciated, and the effect of sex on ontogenetic patterns is debated. Here, we employ a landmark-free, deformation-based morphometric approach to explore variation in modern human hip bone shape and size from middle adolescence to adulthood. Virtual surface models of the hip bone were obtained from 147 modern human individuals (70 females and 77 males) including adolescents, and young and mature adults. The 3D meshes were registered by rotation, translation, and uniform scaling prior to analysis in Deformetrica. The orientation and amplitude of deviations of individual specimens relative to a global mean were assessed using Principal Component Analysis, while colour maps and vectors were employed for visualisation purposes. Deformation-based morphometrics is a time-efficient and objective method free of observer-dependent biases that allows accurate shape characterisation of general and more subtle morphological variation. Here, we captured nuanced hip bone morphology revealing ontogenetic trends and sex-based variation in arcuate line curvature, greater sciatic notch shape, pubic body and rami length, acetabular expansion, and height-to-width proportions of the ilium. The observed ontogenetic trends showed a higher degree of bone modelling of the lesser pelvis of adolescent females, while male variation was mainly confined to the greater pelvis.*

Keywords - *Pelvic morphology, Sex-related variation, Ontogeny, Deformetrica, Diffeomorphism.*

Introduction

The human pelvis, and especially the hip bone, displays clear sexual dimorphism in both morphology and size (Waldeyer 1899; Krogman 1962; Ferembach et al. 1980; Brůžek 2002; İşcan and Steyn 2013; Klales 2020). Females have evolved a larger pelvic canal to allow for the passage of large-headed fetuses, while certain dimensions like bi-acetabular width and anteroposterior depth are constrained by the biomechanical requirements of upright bipedal locomotion (Abitbol 1987; Rosenberg 1992; Warrener et al. 2015; but see Washburn 1960) and possibly pelvic floor stability (Grunstra et al. 2019; Stansfield et al. 2021). These opposing selective pressures are commonly referred to as the "obstetrical dilemma" by Washburn (1960, see also Haeusler et al. 2021). This evolutionary trade-off is often used to explain the high degree of sexual dimorphism observed in the human pelvis, with females typically having larger overall pelvic canal dimensions and a markedly wider subpubic angle when compared to males. Furthermore, pelvic shape has been shown to vary in relation to body size (Fischer and Mitteroecker 2015, 2017), climate and stochastic evolutionary processes (see for example, Kurki 2007; Betti et al. 2013; Betti and Manica 2018; and further discussion in Mitteroecker et al. 2021).

These sex-related differences are also reflected in the shape and size of the isolated hip bone, with females showing a wider greater sciatic notch, a composite arch, an outward rotation of the ischium, and a medio-laterally elongated pubis (Genovés 1959). Pubic morphology is particularly dimorphic, with females usually possessing a ventral arc on the anterior aspect of the pubic body, a subpubic concavity, and a narrower medial aspect of the ischiopubic ramus accompanied by a discrete ridge (Phenice 1969; Klales et al. 2012;). Additionally, females are characterised by more triangular obturator foramina, relatively lower and more laterally divergent ilia, and smaller and more anterolaterally directed acetabula compared to males (Genovés 1959; İşcan and Steyn 2013. Additional sex characteristics of the hip bone include the relative size of the auricular surface and its elevation with respect to the rest of the iliac surface (Bass 1995) and the shape of the preauricular sulcus, although the mere presence of a groove in this region has been considered less reliable as an indicator of sex, particularly if the groove is faint (Brůžek 2002; Karsten 2018).

Pelvic sexual dimorphism is detectable as early as the fetal period and throughout childhood (Weaver 1980; Schutkowski 1993; Wilson et al. 2016), but becomes more pronounced at the onset of puberty, when male and female hip bones can be readily distinguished based on their general morphology (Brůžek 2002; Corron et al. 2021). Preliminary evidence suggests that female pelvic morphology diverges from that of males before adolescence (Huseynov et al. 2016), while further shape changes occur in both sexes before the adult shape is attained. In particular, Coleman (1969) noted that in females, both the ischial spine and the ilium undergo a medial to lateral reorientation and the superior pubic ramus elongates.

Despite these findings, pelvic ontogeny and the mechanisms guiding pelvic sexual dimorphism are still debated as the irregular morphology of the hip bone is also influenced by factors other than sex, including age, hormonal regulation, and body size, as well as ecological, nutritional, and climatic factors (e.g., Betti et al. 2013; Huseynov et al. 2016; Warrener et al. 2015; Wells 2017; Grunstra et al. 2019; Dunsworth 2020; Mitteroecker et al. 2021). Accordingly, the high degree of morphological variation of the hip bone is expected to manifest in increasing morphological overlap between the sexes. Moreover, it has been shown that morphological variation between the sexes is typical of many mammals. Thus, great apes display a similar pattern of sexual dimorphism in the pelvis, though at a different magnitude compared to humans (Huseynov et al. 2016; Fischer et al. 2021; Webb et al. 2021). Even species not subject to direct obstetric selective pressure, such as the marsupial Virginia opossum (*Didelphis virginiana*) show sexual dimorphism in certain pelvic features (Tague 2003).

The range of hip bone morphological variation has been extensively investigated using conventional approaches based on qualitative trait assessment and linear metrics (Buikstra and Ubelaker 1994; Rogers and Saunders 1994; Brůžek 2002), as well as landmark-based geometric morphometrics (Steyn et al. 2004;

Bytheway and Ross 2010; Charles 2010; Fischer and Mitteroecker 2017; Rmoutilová et al. 2017; Robertson et al. 2019; Cox 2021). Geometric morphometrics has become a preferred method in anthropology and other biological sciences for its ability to capture and retain the spatial relationship between landmark points, thereby providing more information about shape than previously unveiled by linear metrics (Bookstein 1991; Slice 2005; Weber and Bookstein 2011; Bookstein 2018). However, these methods rest on the assumption that the points used in the analyses are homologous, which means they are anatomically or ontogenetically correspondent. Accordingly, semilandmarks, which are geometrically homologous points, are often used for interlandmark shape analysis (Gunz et al. 2005; Gunz and Mitteroecker 2013). Although the concept of homology is at the very foundation of anthropometry, there are inherent limitations to its application, especially when comparing specimens from different genera (Zelditch et al. 1995). Rigorous landmark collection consequently requires highly experienced operators, and even adequate training or automated methods for landmark placement do not reduce the time-consuming nature of this process or its susceptibility to error (Fischer et al. 2019). Moreover, an extremely high number of points (including landmarks and semilandmarks) are necessary to represent an object in its entirety, particularly for a complex structure like the hip bone (e.g., Torres-Tamayo et al. 2018).

Developments within geometric morphometrics have led to a landmark-free, deformation-based geometric morphometric approach, recently introduced into the paleoanthropological literature (Beaudet et al. 2020; Urciuoli et al. 2020; 2021). This novel method offers the opportunity to conveniently study objects with irregular shape. The hip bone thus represents a suitable test case for landmark-free approaches (Kuchař et al. 2021) since its challenging anatomy commonly requires the use of less reliable Type II and Type III landmarks (Bookstein 1991, Weber and Bookstein 2011).

In this study, we aim to explore the morphological variation of the hip bone by applying deformation-based geometric morphometrics to 3D surface models from a sample of modern humans of known sex including both adolescents and adults. Using this novel approach, we expect to obtain detailed information regarding the role of sexual dimorphism in shaping hip bone morphology, and how it ultimately contributes to pelvic variation. Moreover, we explore ontogenetic shape changes occurring in the male and female hip bones between middle adolescence and adulthood with reference to previous qualitative observations (Coleman 1969; Corron et al. 2021) and geometric morphometric findings (Bilfeld et al. 2013; Huseynov et al. 2016).

Materials and Methods

Study sample and specimen preparation

The study sample was composed of 147 male (n = 76) and female (n = 71) modern human hip bones, 46 of which were of adolescents between the age of 15 and 18 years (25 males and 21 females) (Tab. 1). Chronological age was verified via associated medical records for 54 living individuals scanned at the Assistance Publique Hôpitaux de Marseille and 57 specimens belonging to the Weisbach osteological collection of the National History Museum Vienna. The rest of the sample (n = 36) was comprised of young and mature adults from skeletal collections (as specified in Table1) without degenerative changes, for whom exact age was unknown. All incomplete or pathological individuals were excluded from this study. The right hip bone was arbitrarily selected for all individuals. The pelvis shows fluctuating rather than directional asymmetry, ensuring its developmental stability (Brown et al. 2008; Tobolsky et al. 2016), and suggesting that laterality or asymmetry should not significantly affect the expression of sexual dimorphism or influence the outcomes of our analyses. Three-dimensional surface models of the hip bones were obtained using an optical 3D-surface scanner (QT Sculptor PT-M4c, https://www.polymetric.de;

***Tab. 1** - Demographic information for the study sample, including geographic origin, repository, age and sex. a: Anthropological Institute and Museum, University of Zurich, Zurich; b: Laboratory of Prehistoric Archaeology and Anthropology, University of Geneva, Geneva; c: Department of Evolutionary Anthropology, University of Vienna, Vienna; d: Department of Anthropology, Natural History Museum Vienna; e: Assistance Publique Hôpitaux de Marseille, Marseille; f: Musée de l'Homme, Paris*

ORIGIN	REPOSITORY	ADOLESCENTS		ADULTS	
		M	F	M	F
Africa	a	/	/	1	1
Europe	a; b; c; d; e	22	21	42	37
South-East Asia and Oceania	a; f	3	1	9	10
Total		**25**	**22**	**52**	**48**

Haeusler et al. 2004) for the osteological collection subsets, and segmenting the medical computed tomography scans using the Amira software (www.fei.com) for the clinical subjects. As several authors have demonstrated, the inclusion of 3D surface models obtained from different imaging techniques does not affect study outcomes (Waltenberger et al. 2021). Instances of minor taphonomic damage of the skeletal hip bones were virtually repaired using the Geomagic Design X software (https://it.3dsystems.com).

As a preprocessing step for deformation-based geometric morphometric analysis, each surface model was smoothed and cleaned, which eliminated minor imperfections such as holes or inverted triangles to restore surface continuity. The meshes were also decimated to 50,000 (± 100) triangles to reduce computational processing time without compromising surface accuracy and enable comparability in terms of number of faces. Possible detrimental effects of the decimation process to the models (Veneziano et al. 2018) were limited by the high quality and smoothness of the original meshes and, therefore, did not compromise the accuracy of the virtual models. The meshes were subsequently aligned to a randomly chosen reference specimen (see Bookstein 1991) by means of rigid and uniform transformations with scaling, using the 'align surfaces' module of Amira and its 'rigid + uniform' option, which equates to a classical Procrustes superimposition. The pre-alignment was performed to ensure that all the specimens were translated and oriented to the same global reference (Durrleman et al. 2012b; Beaudet et al. 2016; 2021; Zanolli et al. 2018). The scaling factors were recorded for use in subsequent size analyses. The aligned surfaces were then converted into legacy VTK files using the open-source software Paraview v. 5.6.0 (www.paraview.org).

Deformation-based geometric morphometrics analysis

The legacy VTK files were imported into Deformetrica v. 4.2 (www.deformetrica.org; Bône et al. 2018) for the deformation-based shape analysis. This landmark-free method computes deformations of each specimen from the sample's mean shape, a theoretical specimen calculated from all the specimens in the sample, based on the geometric correspondence between continuous surfaces (Glaunès and Joshi 2006; Durrleman et al. 2012b; Bône et al. 2018). The deformations are then described by means of diffeomorphisms, which are invertible and continuous mathematical functions used to map differentiable manifolds, a manifold being a topological space that locally approximates a linear space (Krantz et al. 2013). Unlike landmark-based geometric morphometrics, deformation-based morphometrics allows for direct assessment of shape differences between surfaces. Moreover, shape variation is quantified based on momentum vectors exemplifying the magnitude and direction of surface deformations attached to previously identified control points rather than based on the distances between paired homologous landmark points (Durrleman et al. 2012a, b).

Previous work has shown that deformation-based morphometrics produces comparable outcomes to landmark-based 3D geometric morphometrics (Urciuoli et al. 2018, 2020). As a first step, Deformetrica computes a template surface representing the sample's mean shape and identifies a set of control points placed at the most variable regions of that template. The template is then warped to match the other included specimens (or targets), and deformations are quantified by attaching momentum vectors to the control points describing the magnitude and direction of each deformation. The number of control points is automatically identified and optimised by the software based on the Kernel width specified by the user (Bône et al. 2018). The Kernel width is a sensitivity parameter that must be optimised to ensure that the deformation from the global mean to the target specimens is accurate, namely that the deformed global mean surface perfectly matches the model of each of the target specimens. Test runs on sample subsets are necessary for the user to identify the correct Kernel width. The shape analysis was performed at the Barcelona Supercomputing Center to reduce computation time using the MinoTauro GPU cluster computer (www.bsc.es/marenostrum/minotauro).

Patterns of shape variation were inspected using principal component analysis (PCA) on the deformation fields (i.e., the raw shape data obtained by combining the momenta and control points stemming from the deformation analysis; Supplementary Data 1 and 2) using the *ade4* (v.1.7-16) package (Dray and Dufour 2007) for the R statistical environment (R Development Core Team 2021). To assess allometric trends, we performed major axis regressions of each of the first three principal component (PC) scores against the natural logarithm of the inverted scaling factor (computed during the alignment of the surfaces) using the function 'lmodel2' of the *lmodel2* R package (v.1.7-3) (Legendre 2018). The significant PCs were identified using the 'getMeaningfulPCs' function of the *Morpho* R package (v.2.9) (Schlager 2013). The differences between the four groups (i.e., adult males, adult females, adolescent males, and adolescent females) were statistically assessed using a MANOVA test with Bonferroni correction in PAST (https://palaeo-electronica.org). In addition, we performed a Wilcoxon-Mann-Whitney test with Bonferroni correction on each of the first three PCs, using the 'pairwise.wilcox.test' function of the *stats* R package. The scaling factors used for standardising the models were normalised (i.e., inverted) prior to visualisation in boxplots and analysed using the Mann-Whitney U test. To evaluate ontogenetically derived variation, and the appearance and expression of sexual dimorphism, cumulative displacement variations of male and female adult hip bones from the adolescent global mean were rendered with colour maps. Additionally, momentum vectors representing deformation from the global mean were used to represent maximum local displacements at the most variable regions of the hip bone. Accuracies of classification into male and female sexes were assessed using linear Discriminant Function Analysis (DFA) of the PC scores, an approach widely adopted in biological anthropology (e.g., Franklin et al. 2005; Krishan et al. 2016; Oikonomopoulou et al. 2017). Principal components were incrementally added to the model until classification accuracy was maximised. Thus, the addition of further PCs after that would have consistently provided lower classification accuracies. DFA models for male and female adults only, and male and female adolescents only were calculated after running separate PCAs for the adult and the adolescent subsamples. We then contrasted our results with those obtained by Robertson et al. (2019), who also used DFA to evaluate classification accuracy of male and female adult hip bones, based on traditional landmark-based geometric morphometrics. This offered the possibility to directly compare the outcomes of their classic geometric morphometric approach using 32 and 17 pelvic landmarks with our deformation-based geometric morphometrics approach.

Results

Hip bone shape variation

The results of the PCA on the momentum vectors, representing deformations from the global mean, are presented in Figure 1 and Supplementary Videos 1-4. PC1 (15% of total variance explained) showed a general grouping of males vs. females based on several morphological features. For instance, variation in the robusticity (thickness) of the hip bone was noticeable, with males being more robust than females except for the posterior region of the ilium and the iliac crest, which were relatively more robust in females. In females, a wider greater sciatic notch, a more everted ischium, longer and more slender pubic rami, and a wider pubic body collectively resulted in a broader pelvic inlet and outlet. The auricular surface varied from being depressed in males to elevated in females (see PC1 warpings in Figure 1), contributing to increased medio-lateral width of the pelvic inlet in females by accentuating the curvature of the *linea terminalis*. The widening of the greater sciatic notch corresponded to a cranio-caudally shorter posterior region of the ilium, as if resorption had occurred at its inferior border between the posterior inferior iliac spine and the deepest point of the greater sciatic notch. Thus, with respect to males, females presented with a relatively broader iliac blade. The broader pubic body and elongated pubic rami in females produced a typically wide subpubic angle and contributed to the concave appearance of the lower border of the inferior pubic ramus as well as the more triangular shape of the foramen obturatum. The pubic symphysis was of similar cranio-caudal length for both sexes. The characteristic pre-auricular sulcus could be discerned in females on the inferior side of the sacroiliac joint, and a retro-auricular depression was visible between the protruding auriculum and the most posterior region of the iliac tuberosity (see PC1 warpings in Figure 1). Furthermore, variation was detected in the relative expansion of the acetabulum, which was wider for males than for females. Along PC1, differences between all group means were significant except for those between adolescent and adult males (Tab. 2). Moreover, a statistically significant, albeit weak, negative allometric trend was found along PC1 (adjusted R^2: 0.1063; F-statistic: 18.36; p-value < 0.0001).

Principal Component 2 (12% of total variance) reflected ontogenetic trends with adolescents showing a straighter arcuate line and a shorter pubis than adults, resulting in a relatively medio-laterally narrower pelvic inlet. Ontogenetic shape changes also involved a rearrangement of the ilium, which was more vertical in adults, while the superior pubic ramus was more posteriorly oriented near the symphysis (see PC2 warpings in Figure 1). Adolescent and adult males were more similar in shape compared to adolescent and adult females. Shape differences between adolescent and adult means were significant for both males and females, while none of the differences between male and female adolescents, adults or both were statistically significant (Tab. 2). A significant but weak allometric trend was observed along PC2 (adjusted R^2: 0.0345; F-statistic: 6.22; p-value = 0.0138).

Males and females were best separated in the PC1-PC3 plot. Shape changes along PC3 (8% of total variance) reflected the expansion of the iliac blade in both breadth and height, and the concomitant medio-lateral shortening of the pubis. For the same PC1 scores, males tended to have higher PC3 scores than females, which, in terms of morphology, reflected a greater expansion of the ilium in males for similar pubic length to females (see PC3 warpings in Figure 1). Along PC3, males and females (considering adolescents only, adults only, or all individuals together) differed significantly. The differences between adolescent and adult females were also significant, but adolescent males did not differ significantly from adult males or adult females (Tab. 2). Allometry was significant along PC3 (adjusted R^2: 0.1861; F-statistic: 34.38; p-value < 0.0001), where the observed shape changes were positively correlated with the size of the specimens.

Group mean differences

The surface deviations of the male and female adult means and the male and female adolescent means from the global adolescent mean are illustrated in Figures 2 and 3 (see also Supplementary Videos 5-16). The MANOVA was performed using the first 26 PCs corresponding to 90% of total variance explained.

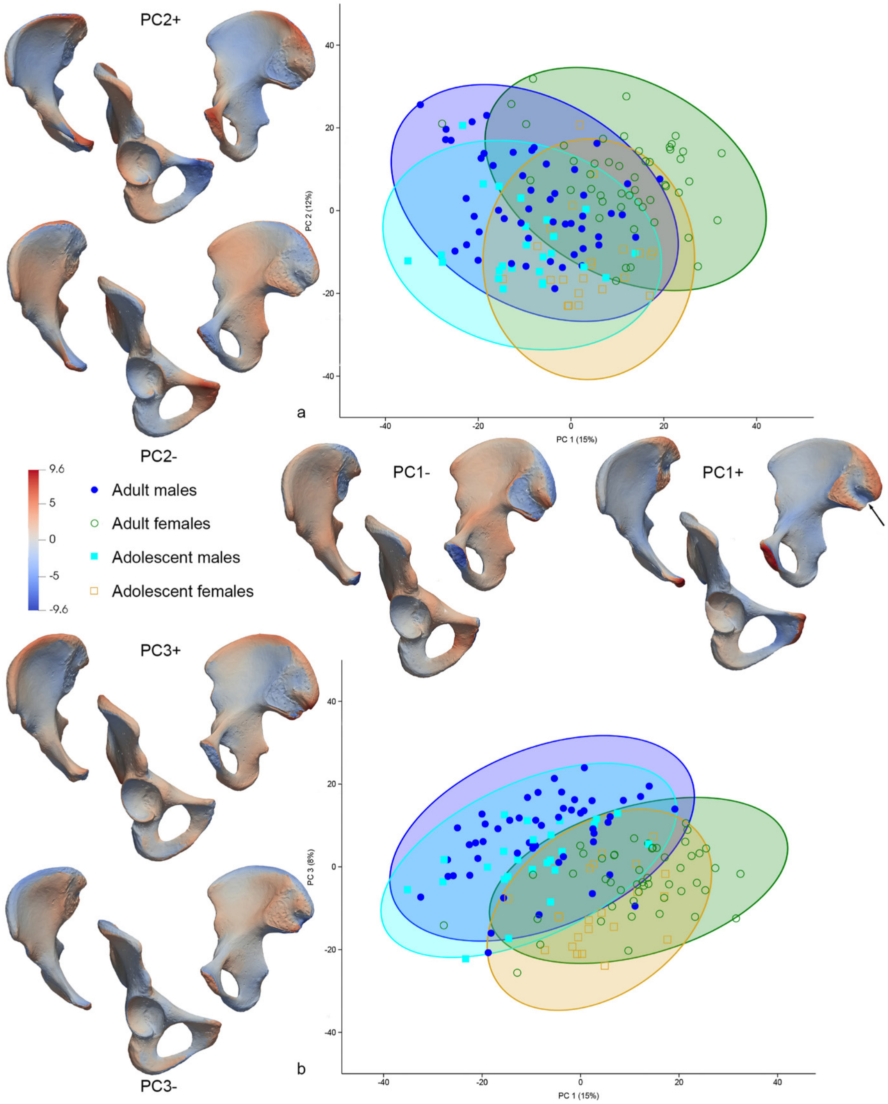

Fig. 1 – ***Score plots derived from PCA performed on the deformation fields from the global mean. The associated warped models are shown at the extremes of the range of distribution along the first three principal components (PCs). Positive deformations are mapped in warm (red) gradient colours, while negative deformations are in cold (blue) gradient colours. Given a certain region, a positive deformation signifies a volume increase to the surface reference. Accordingly, a negative deformation signifies a decrease in volume. The male (closed symbols) and female (open symbols) adolescents (squares) and adults (circles) are enclosed within 95% prediction ellipses in the plots. a. PC1-PC2 plot showing sex-related variation along PC1 and an ontogenetic trend along PC2. Along PC1, hip bones vary mostly in terms of relative width of the greater sciatic notch, length of the pubis and outward rotation of the ischium. The retro-auricular surface, pronounced in females, is indicated by a black arrow. Variation along PC2 is driven by a medio-lateral expansion of the pelvic inlet. b. The PC1-PC3 plot distinguishes best between males and females by combining the most commonly described sex-related shape changes observed along PC1 with the relative expansion of the ilium along PC3. Colour bar values in mm.***

***Tab. 2** – P-values from the cross-validated ANOVA of the first three PCs with Bonferroni correction. Significant values (p < 0.05) are in bold.*

PC1	ADULT FEMALES	ADOLESCENT FEMALES	ADULT MALES	ALL FEMALES
ADOLESCENT FEMALES	**0.0281**	-	-	-
ADULT MALES	**<0.0001**	**0.0014**	-	-
ADOLESCENT MALES	**<0.0001**	**0.0001**	1.0000	-
ALL MALES	-	-	-	**<0.0001**

PC2	ADULT FEMALES	ADOLESCENT FEMALES	ADULT MALES	ALL FEMALES
ADOLESCENT FEMALES	**<0.0001**	-	-	-
ADULT MALES	0.0544	**<0.0001**	-	-
ADOLESCENT MALES	**<0.0001**	0.6470	**0.0005**	-
ALL MALES	-	-	-	0.1200

PC3	ADULT FEMALES	ADOLESCENT FEMALES	ADULT MALES	ALL FEMALES
ADOLESCENT FEMALES	**0.0132**	-	-	-
ADULT MALES	**<0.0001**	**<0.0001**	-	-
ADOLESCENT MALES	0.0720	**0.0005**	0.0768	-
ALL MALES	-	-	-	**<0.0001**

After a Bonferroni correction, all groups were found to differ significantly. Male and female adult means differed ($p < 0.0001$) mainly for the shape changes described by PC1 and PC3, which involved sexually dimorphic features of the greater and lesser pelvis. The male mean could be distinguished from the female mean by its robustness, a more vertical and expanded ilium, a narrower and deeper greater sciatic notch, a straighter arcuate line, shorter pubic rami, a narrower pubic body, and a more inward-oriented ischial tuberosity. The colour maps also showed a more pronounced anterior inferior iliac spine in the male mean, as well as a flattened groove in the preauricular region, a non-elevated auricular surface, and a thinner post-auricular region. The acetabulum was also relatively larger in males than in females.

Typical male and female configurations were already visible in adolescents, thus their means differed significantly ($p = 0.0031$). The shape changes between adolescent and adult means were significant for both females (p-value < 0.0001) and males (p-value = 0.0007). Adolescents showed less robust iliac crests and more vertical ilia than adults. The arcuate line was less curved in adolescents, resulting in a medio-laterally narrower pelvic inlet. Additionally, the superior rim

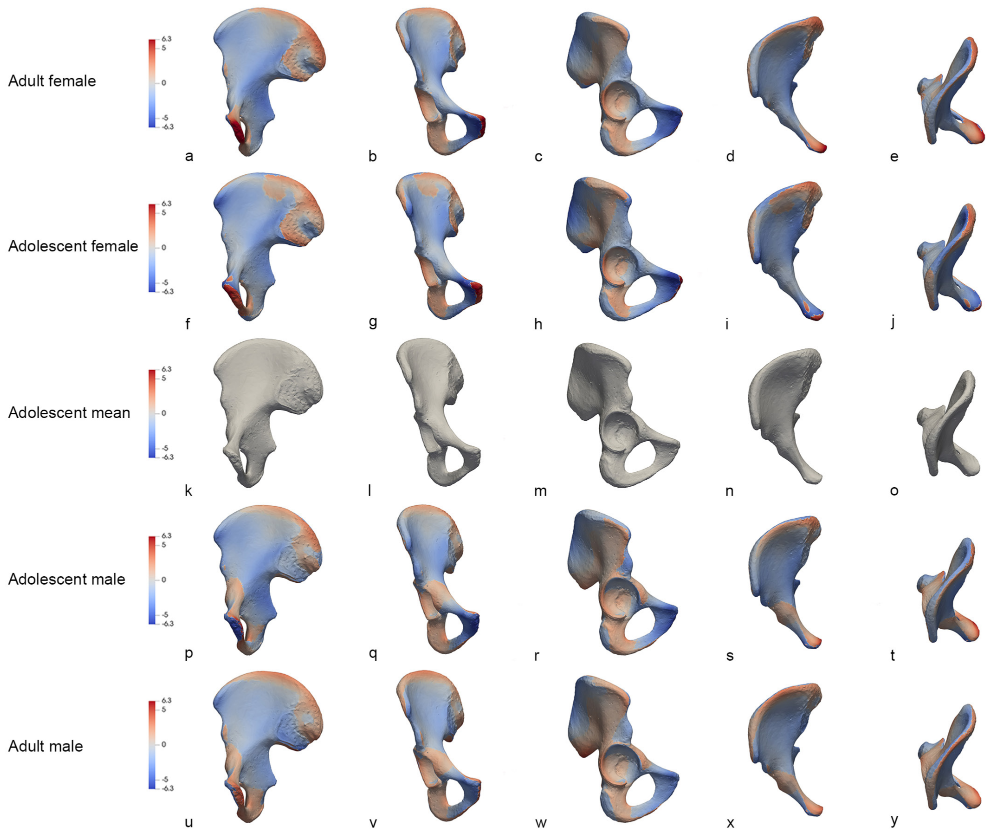

***Fig. 2** – Surface models of the group means of adult females (a-e), adolescent females (f-j), adolescent males (p-t) and adult males (u-y) showing areas of main deformation (positive deviations in red, negative in blue) from the adolescents mean (k-o, in grey) in internal (a,f,k,p,u), frontal (b,g,l,q,v), lateral (c,h,m,r,w), superior (d,i,n,s,x), and vertical (e,j,o,t,y) views. Positive deformations are mapped in warm (red) gradient colours, while negative deformations are in cold (blue) gradient colours. Given a certain region, a positive deformation signifies a volume increase to the surface reference. Accordingly, a negative deformation signifies a decrease in volume. The group means of adult and adolescent females deviate from those of adolescent and adult males for their wider greater sciatic notch, elongated pubic body, depressed preauricular sulcus and elevated auricular surface. Adolescent and adult males possess cranio-caudally higher ilia than females. The adult female mean can be distinguished from the adolescent female mean by features leading to a mediolaterally wider pelvic inlet, a more everted ischial tuberosity, protruding post-auricular area and a posteriorly deflected superior pubic body near the pubic symphysis. Adult males differ from adolescent males by a higher robusticity of the middle and anterior sections of the iliac crest and the anterior inferior iliac spine. Adolescent males and females differ from adults by their more medially oriented iliac blades. Colour bar values in mm.*

of the symphysis was anteriorly deflected. The female adults differed from the female adolescents by their longer superior pubic ramus, while the most visible shape change for males was represented by the expansion of the ilium, which became taller in adults.

Classification accuracy

The number of PCs that could be used until the classification accuracy started to consistently decrease was 26 (Supplementary Fig. S1). We achieved classification accuracies ranging from 70.0% to 100.0% (Tab. 3). In particular, the

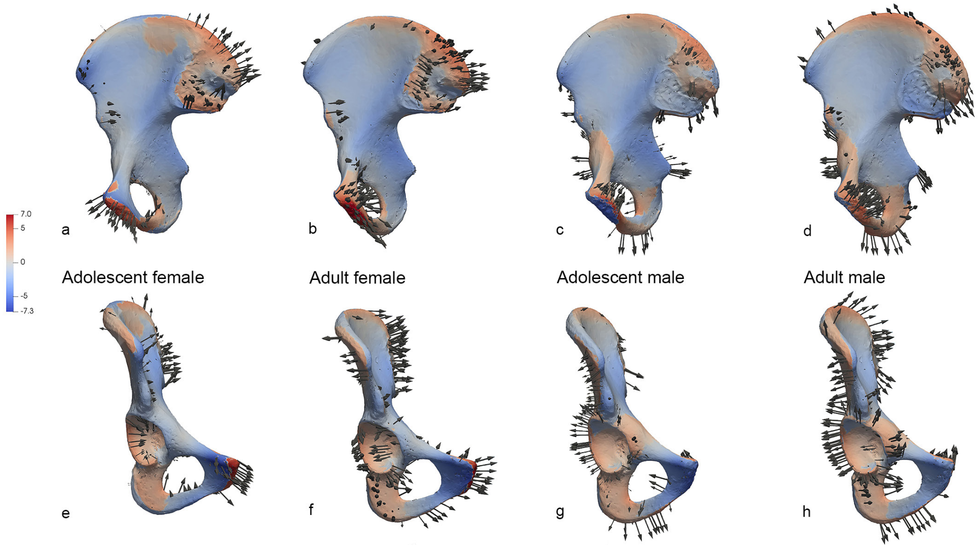

***Fig. 3** – Surface models of the hip bone in internal (a-d) and lateral (e-h) views with scaled vectors attached to the control points showing the direction and magnitude of deformation (magnified 20 times to allow appreciation of the deformations) from the adolescent mean to the group means of the adolescent (a,e) and adult (b,f) females, and adolescent (c,g) and adult (d,h) males. Positive deformations are also mapped in warm (red) gradient colours, while negative deformations are in cold (blue) gradient colours. Given a certain region, a positive deformation signifies a volume increase to the surface reference. Accordingly, a negative deformation signifies a decrease in volume. Colour bar values in mm.*

highest accuracies were obtained for the classification of the sexes within the entire sample (females = 97.1%; males = 94.7%) or into female or male adults only (females = 94.0%; males = 94.0%). The results for the adults were slightly lower than those achieved by Robertson et al. (2019) in their geometric morphometric analysis of a different sample of adult hip bone using a configuration of 17 landmarks (females = 99.2%; males = 97.8%) or 32 landmarks (females = 97.6%; males = 97.5%). Classification accuracies in the present male and female adolescent groups were higher for females (100.0%) than for males (84.0%). Accuracy decreased for the classification based on four groups (female adults = 82.0%; female adolescents = 85.0%; male adults = 78.0%; male adolescents = 84.0%), while accuracies were lowest when classifying males or females into adolescents and adults (male adolescents = 84.0%; male adults = 78.0%) (female adolescents = 70.0%; female adults = 78.0%).

Discussion

The modern human pelvis has been intensively investigated for its biological relevance in relation to sex estimation, locomotion, and birth (see references in Haeusler et al. 2021). Thus, appreciating the nuances of its morphological variation is crucial for disentangling the adaptive and functional significance of its characteristics. The hip bone is the most sexually dimorphic bone of the human skeleton because of differential local growth that contributes to shaping a more spacious birth canal in females (e.g., Huseynov et al. 2016; Robertson et al. 2019). Our deformation-based geometric morphometric investigation of the human hip bone, a large and complex anatomical object, successfully captured important large-scale, but also subtle morphological patterns of variation that previously required the application of a combination of methods. It allowed us to intuitively visualise

***Tab. 3** - Cross-validated classification results based on the first 26 PCs, derived from the Discriminant Function Analysis. The percentages of correctly classified individuals are given for each subgroup.*

	ADULT FEMALES	ADOLESCENT FEMALES	ADULT MALES	ADOLESCENT MALES
ADULT FEMALES	82.0	14.0	0.0	4.0
ADOLESCENT FEMALES	10.0	85.0	0.0	5.0
ADULT MALES	4.0	0.0	78.0	18.0
ADOLESCENT MALES	0.0	4.0	12.0	84.0
Overall classification accuracy: 81.38%; Kappa statistic: 0.74				

	ADULT FEMALES	ADULT MALES	ADULT FEMALES*	ADULT MALES*
ADULT FEMALES	94.0	6.0	99.2	0.8
ADULT MALES	6.0	94.0	2.2	97.8
Overall classification accuracy: 94.00%; Kappa statistic: 0.88				

	ADOLESCENT FEMALES	ADOLESCENT MALES
ADOLESCENT FEMALES	100.0	0.0
ADOLESCENT MALES	16.0	84.0
Overall classification accuracy: 91.11%; Kappa statistic: 0.82		

	ALL FEMALES	ALL MALES
ALL FEMALES	97.1	2.9
ALL MALES	5.3	94.7
Overall classification accuracy: 95.86%; Kappa statistic: 0.92		

	ADULT FEMALES	ADOLESCENT FEMALES
ADULT FEMALES	78.0	22.0
ADOLESCENT FEMALES	30.0	70.0
Overall classification accuracy: 75.71%; Kappa statistic: 0.45		

	ADULT MALES	ADOLESCENT MALES
ADULT MALES	78.0	22.0
ADOLESCENT MALES	16.0	84.0
Overall classification accuracy: 80.00%; Kappa statistic: 0.58		

* In Robertson et al. 2019

Tab. 4 – Significance values (p-values) from the MANOVA performed using the first 26 PCs with Bonferroni correction.

	ADULT FEMALES	ADULT MALES	ADOLESCENT FEMALES
ADULT MALES	<0.0001	-	-
ADOLESCENT FEMALES	<0.0001	<0.0001	-
ADOLESCENT MALES	<0.0001	0.0007	0.0031

gross morphological variation while permitting quantitative assessment of the magnitude and direction of local shape changes (Fig. 3). The convenient visual depictions produced with the Deformetrica approach provided insights into subtle shape changes that significantly informed our understanding of hip bone variation. As such, this method offered all the advantages of geometric morphometrics using dense landmark configurations while avoiding the associated drawbacks related to time-consuming landmark collection and susceptibility to placement error.

We detected similar morphological signals to those previously obtained using other approaches, from qualitative observations (Coleman 1969; Corron et al. 2021), to linear measurements (Mestekova et al. 2015), and more sophisticated landmark-based geometric morphometric approaches (Bilfeld et al. 2013, Huseynov et al. 2016; Robertson et al. 2019). As already noticed by Coleman (1969), we confirmed that the morphological heterogeneity of the hip bone is accentuated in the anatomical regions formed by more than one bony element (e.g., the acetabulum, obturator foramen, ilio-pubic eminence, greater sciatic notch, etc.). Morphological differences between males and females also extended to the ilium, which is craniocaudally shorter, and thus relatively broader, in females. In fact, the reduced height of the posterior region of the ilium might be associated to the widening of the greater sciatic notch. Further, the elevation of the auricular area contributes to the medio-lateral width of the pelvic canal in females (see Figure 1). This is compatible with the fact that the sacrum is not as highly dimorphic as one would expect by considering the total degree of pelvic sexual dimorphism (Flander 1978; Zech et al. 2012; Zhan et al. 2018; Krenn et al. 2021; but see Rusk and Ousley 2016).

While most sexually dimorphic traits, such as the width of the greater sciatic notch, the curvature of the pelvic inlet, and the orientation of the ischiatic tuberosity are already present during adolescence, they become more pronounced in female adults (Figs. 2, 3). The ontogenetic trends we registered in the male and female hip bones and their related shape changes add to previous observations by Huseynov et al. (2016), who found that the female pelvis deviates from males starting from puberty in terms of maturation and development of sexually dimorphic traits. Based on a landmark-based geometric morphometric study of the ilium, Bilfeld et al. (2013) concluded that divergent ontogenetic trajectories between males and females establish already beginning from the age of 9 years. This notion was corroborated by Corron et al. (2021) who observed the timing of maturation of the pelvic epiphyseal sites in relation to the appearance of sexually dimorphic traits. The differential growth of the hip bone in males and females is reflected by substantial bone modelling occurring in the regions of the ischium, the ischio-pubic ramus, the pubis and the auriculum, resulting in larger morphological differences of the lesser pelvis between adolescent and adult females than between adolescent and adult males (Figs. 2, 3). Huseynov et al. (2016) found that, during adolescence to early adulthood, the female pelvis models towards a pelvic canal shape increasingly suitable for parturition. Our data confirm that female adolescents and adults differ significantly, showing that continued, obstetrically relevant pelvic directional growth occurs during adolescence in females. Particularly, the adult female hip bone is characterized by a more curved arcuate line than in female adolescents and an elongated superior pubic ramus, leading to a larger pelvic inlet. We also observed that the adolescent male hip bone goes through significant shape changes, too, before reaching the adult configuration. However, these changes mostly concern the iliac blade, while the lesser pelvis grows in a similar fashion to females but to a lesser degree.

The differential growth of the ilium during adolescence was already described by Coleman (1969), who noted that in males, the anterior part of the iliac crest corresponding to the anterior superior iliac spine is more laterally flaring than females, while the posterior portion of the ilium is more laterally deflected. In accordance with the greater muscularity, the anterior superior, and especially the anterior inferior iliac spines were more robust in males. The anterior inferior iliac spine represents the origin of the *rectus femoris* muscle that might be more developed in males compared to females. Dimorphic differences in hip bone robusticity might be driven by the same growth patterns observed in other bones. In fact, a general increase in the robusticity of long bones has been observed after the adolescent growth spurt (Rantalainen et al. 2016). This phenomenon is more pronounced in males than in females, and the timing at which dimorphic differences in robusticity become evident varies between different skeletal elements (Iuliano-Burns et al. 2009).

Another geometric morphometric analysis of the adult pelvis by Fischer and Mitteroecker (2017) revealed that differences in orientation of the iliac blades between males and females were mostly a consequence of differences in overall stature. Thus, taller persons, typically males, present with a relatively taller and narrower pelvis and inwardly rotated iliac blades while shorter individuals, typically females, show a relatively wider pelvis with shorter and laterally-extending iliac blades. The direction of the deformation fields observed for males and females in the present study (Fig. 3) could be interpreted in light of these previous findings, although body height was not known for the individuals considered here.

In addition to sex-based variation, subtle allometric patterns emerged. As expected, female shape changes were associated with smaller sizes. Smaller individuals tended to possess a longer superior pubic ramus and an antero-posteriorly narrower and supero-inferiorly shorter ilium, regardless of their sex. This finding is compatible with the existence of obstetrical constraints in females (see detailed discussion in Fischer and Mitteroecker 2015; Fischer et al. 2021; Haeusler et al. 2021) and can possibly reflect genetic stability preserving the structural integrity of pelvic morphology in both sexes.

By adding to these previous findings, we are thereby confirming the utility of deformation-based morphometrics to analyse sex- and age-related shape changes of the hip bone. Using configurations of 32 or fewer landmarks, Robertson et al. (2019) concluded that a 17-landmark configuration was the most appropriate to capture male and female hip bone morphological differences, allowing them to reach the highest classification accuracies within their adult sample (see our Table 2). Using a much higher number of variables (~50,000, equivalent to the number of surface polygons representing each specimen), we achieved a marginally lower sex classification accuracy for the adult specimens, which means that a deformation-based geometric morphometric analysis of the entire hip bone decreases accuracy by only a small percentage. Since the current work and the study by Robertson et al. (2019) use different samples, the respective outcomes are not directly comparable. Nevertheless, our evaluation still shows that expected sex-based differences and resulting classification accuracies into male and female categories can be achieved using both geometric morphometric approaches.

According to the findings in Huseynov et al. (2016), we are aware that the possible inclusion of hip bones from mature individuals might have confounded the interpretation of sex-related morphological variation within the adult sample. Further studies focussing entirely on samples of known age and similar origin might allow for a higher resolution of shape changes occurring during the different phases of adulthood. Although most of our sample (122/147) was from Central Europe, we could speculate that the overlap between the different age and sex groups might also partially derive from geographical heterogeneity. Based on results obtained for the sacrum (Krenn et al. 2021), we would expect that using a more geographically homogeneous sample could have led to better separation between the groups and, therefore, higher classification accuracies.

Acknowledgements

We thank the following persons and institutions for granting access to or otherwise facilitating data acquisition: Karin Wilschke-Schrotta and Sabine Eggers, Department of Anthropology, Natural History Museum Vienna; Kathia Chaumoitre, UMR7268 Anthropologie bioculturelle, Droit, Ethique et Sante and Assistance Publique des Hôpitaux de Marseille, Marseille; Martin Friess and Véronique Laborde, Musée de l'Homme, Paris; Marcia Ponce de León, Marc Scherrer, Jody Weissmann, Anthropological Institute and Museum, University of Zurich, Zurich; Jocelyne Desideri, Laboratory of Prehistoric Archaeology and Anthropology, University of Geneva, Geneva; Harald Wilfing, Katrin Schäfer, Katarina Matiasek, Department of Evolutionary Anthropology, University of Vienna, Vienna. We thank Stephanie Cole, University of Nevada, Reno, and Yaroslav Brůžek, Université de Bordeaux, UMR 5199 PACEA, and Charles University, Prague, for the in-depth conversations on subadult sex estimation, sexual dimorphism, and maturation of the pelvis.

The Barcelona Supercomputing Center granted computational time to AU (project No BCV-2020-1-0008). C.F., N.M.W., V.A.K. and M.H. were financially supported by the Swiss National Science Foundation (SNF grant No 31003A_176319/1). AU was funded by the Agencia Estatal de Investigación (PID2020-117289GB-I00 and PID2020-116908GB-I00, AEI/FEDER, EU) and the Generalitat de Catalunya (CERCA Programme).

Author contributions

CF, NMW, and MH initiated the project; NMW and VK prepared and aligned the surface data; AU performed the deformation-based morphometric analysis; CF and AU produced tables and visualisations; all authors discussed the results and their interpretation; CF wrote the manuscript with the contribution of all authors.

References

Abitbol MM (1987) Obstetrics and posture in pelvic anatomy. J Hum Evol 16:243–255. https://doi.org/10.1016/0047-2484(87)90001-7

Bass WM (1995) Human Osteology: a Laboratory and Field Manual, Missouri Archaeological Society, Columbia, Mo.

Beaudet A, Clarke RJ, Heaton JL, et al (2020) The atlas of StW 573 and the late emergence of human-like head mobility and brain metabolism. Sci Rep 10:4285. https://doi.org/10.1038/s41598-020-60837-2

Beaudet A, Dumoncel J, Thackeray JF, et al (2016) Upper third molar internal structural organization and semicircular canal morphology in Plio-Pleistocene South African cercopithecoids. J Hum Evol 95:104-20. https://doi.org/10.1016/j.jhevol.2016.04.004

Beaudet A, Holloway R, Benazzi S (2021) A comparative study of the endocasts of OH 5 and SK 1585: Implications for the paleoneurology of eastern and southern African *Paranthropus*. J Hum Evol 156:103010. https://doi.org/10.1016/j.jhevol.2021.103010

Betti L, Manica A (2018) Human variation in the shape of the birth canal is significant and geographically structured. Proc Royal Soc B 285:20181807. https://doi.org/10.1098/rspb.2018.1807

Betti L, Von Cramon-Taubadel N, Manica A, et al (2013) Global geometric morphometric analyses of the human pelvis reveal substantial neutral population history effects, even across sexes. PLoS One 8:e55909. https://doi.org/10.1371/journal.pone.0055909

Bilfeld MF, Dedouit F, Sans N, et al (2013) Ontogeny of size and shape sexual dimorphism in the ilium: a multislice computed tomography study by geometric morphometry. J Forensic Sci 58:303–310. https://doi.org/10.1111/1556-4029.12037

Bône A, Louis M, Martin B, et al (2018) Deformetrica 4: an open-source software for statistical shape analysis. In: Reuter M, Wachinger C, Lombaert H, Paniagua B, Lüthi M & Egger B (eds.) Shape in Medical Imaging, Springer, Cham.
Bookstein FL (1991) Morphometric Tools for Landmark Data: Geometry and Biology, Cambridge University Press, Cambridge.
Bookstein FL (2018) A Course in Morphometrics for Biologists: Geometry and Statistics for Studies of Organismal Form, Cambridge University Press, Cambridge.
Brown WM, Price ME, Kang J, et al (2008) Fluctuating asymmetry and preferences for sex-typical bodily characteristics. Proc Natl Acad Sci USA 105:12938-12943. https://doi.org/10.1073/pnas.0710420105
Brůžek J (2002) A method for visual determination of sex, using the human hip bone. Am J Phys Anthropol 117:157–168. https://doi.org/10.1002/ajpa.10012
Buikstra JE, Ubelaker DH (1994) Standards for data collection from human skeletal remains: Proceedings of a seminar at the Field Museum of Natural History, organized by Jonathan Haas (3rd ed.), Arkansas Archeological Survey, Fayetteville.
Bytheway JA, Ross AH (2010) A geometric morphometric approach to sex determination of the human adult os coxa. J Forensic Sci 55:859–864. https://doi.org/10.1111/j.1556-4029.2010.01374.x
Charles BE (2010) A Geometric Morphometric Analysis of the Human Ossa Coxae for Sex Determination, Master of Science, Boston University, Boston.
Coleman WH (1969) Sex differences in the growth of the human bony pelvis. Am J Phys Anthropol 31:125–151. https://doi.org/10.1002/ajpa.1330310202
Corron LK, Santos F, Adalian P, et al (2021) How low can we go? A skeletal maturity threshold for probabilistic visual sex estimation from immature human os coxae. Forensic Sci Int 325:110854. https://doi.org/10.1016/j.forsciint.2021.110854
Cox SL (2021) A geometric morphometric assessment of shape variation in adult pelvic morphology. Am J Phys Anthropol 176:652–671. https://doi.org/10.1002/ajpa.24399
Dray S, Dufour A (2007) The ade4 package: Implementing the duality diagram for ecologists. J Stat Softw 22:1–20. https://doi.org/0.18637/jss.v022.i04
Dunsworth HM (2020) Expanding the evolutionary explanations for sex differences in the human skeleton. Evol Anthropol 29:108–116. https://doi.org/10.1002/evan.21834
Durrleman S, Pennec X, Trouvé A, et al (2012a) Comparison of the endocranial ontogenies between chimpanzees and bonobos via temporal regression and spatiotemporal registration. J Hum Evol 62:74–88. https://doi.org/10.1016/j.jhevol.2011.10.004
Durrleman S, Prastawa M, Korenberg JR, et al (2012b) Topology preserving atlas construction from shape data without correspondence using sparse parameters. Med Image Comput Comput Assist Interv 15:223–230. https://doi.org/10.1007/978-3-642-33454-2_28
Ferembach D, Schwidetzky I, Stoukal M (1980) Recomendations for age and sex diagnosis of skeletons. J Hum Evol 9:517–549. https://doi.org/10.1016/j.jchb.2005.07.002
Fischer B, Grunstra NDS, Zaffarini E, et al (2021) Sex differences in the pelvis did not evolve de novo in modern humans. Nat Ecol Evol 5:625–630. https://doi.org/10.1038/s41559-021-01425-z
Fischer B, Mitteroecker P (2015) Covariation between human pelvis shape, stature, and head size alleviates the obstetric dilemma. Proc Natl Acad Sci USA 112:5655–5660. https://doi.org/10.1073/pnas.1420325112
Fischer B, Mitteroecker P (2017) Allometry and sexual dimorphism in the human pelvis. Anat 300:698–705. https://doi.org/10.1002/ar.23549
Fischer MCM, Krooß F, Habor J, et al (2019) A robust method for automatic identification of landmarks on surface models of the pelvis. Sci Rep 9:13322. https://doi.org/10.1038/s41598-019-49573-4
Flander LB (1978) Univariate and multivariate methods for sexing the sacrum. Am J

Phys Anthropol 49:103–110. https://doi.org/10.1002/ajpa.1330490116
Franklin D, Freedman L, Milne N (2005) Sexual dimorphism and discriminant function sexing in indigenous South African crania. HOMO 55:213–228. https://doi.org/10.1016/j.jchb.2004.08.001
Genovés S (1959) L'estimation des différences sexuelles dans l'os coxal: différences métriques et différences morphologiques. Bull Mem Soc Anthropol Paris X:3–95. https://doi.org/10.3406/bmsap.1959.2750
Glaunès J, Joshi S. (2006) Template estimation form unlabeled point set data and surfaces for Computational Anatomy. 1st MICCAI Workshop on Mathematical Foundations of Computational Anatomy: Geometrical, Statistical and Registration Methods for Modeling Biological Shape Variability, Oct 2006, Copenhagen, Denmark. https://hal.archives-ouvertes.fr/hal-00263576.
Grunstra NDS, Zachos FE, Herdina AN, et al (2019) Humans as inverted bats: A comparative approach to the obstetric conundrum. Am J Hum Biol 31:e23227. https://doi.org/10.1002/ajhb.23227
Gunz P, Mitteroecker P (2013) Semilandmarks: a method for quantifying curves and surfaces. Hystrix 24:103–109. https://doi.org/10.4404/hystrix-24.1-6292
Gunz P, Mitteroecker P, Bookstein F (2005) Semilandmarks in Three Dimensions. In: Slice DE (ed.) Modern Morphometrics in Physical Anthropology, Springer, Boston, MA.
Haeusler M, Grunstra NDS, Martin RD, et al (2021) The obstetrical dilemma hypothesis: there's life in the old dog yet. Biol Rev 96:2031–2057. https://doi.org/10.1111/brv.12744
Haeusler MF, Schweitzer W, Braun M, et al (2004) Evaluation von 3D-Scanner für den Einsatz in der Rechtsmedizin. Rechtsmedizin 14:356–357.
Huseynov A, Zollikofer CPE, Coudyzer W, et al (2016) Developmental evidence for obstetric adaptation of the human female pelvis. Proc Natl Acad Sci USA 113:5227–5232. https://doi.org/10.1073/pnas.1517085113
İşcan MY, Steyn M (2013) The Human Skeleton in Forensic Medicine, Springfield, Thomas.
Iuliano-Burns S, Hopper J, Seeman E (2009) The age of puberty determines sexual dimorphism in bone structure: A male/female co-twin control study. J Clin Endocrinol Metab 94:1638–1643. https://doi.org/10.1210/jc.2008-1522
Karsten JK (2018) A test of the preauricular sulcus as an indicator of sex. Am J Phys Anthropol 165:604–608. https://doi.org/10.1002/ajpa.23372
Klales AR (2020) Sex estimation using pelvis morphology. In: Klales AR (ed.) Sex Estimation of the Human Skeleton: History, Methods, and Emerging Techniques, Academic Press.
Klales AR, Ousley SD, Vollner JM (2012) A revised method of sexing the human innominate using Phenice's nonmetric traits and statistical methods. Am J Phys Anthropol 149:104–114. https://doi.org/10.1002/ajpa.22102
Krantz SG, Parks HR, 6.2.4. PT (2013) The implicit function theorem: history, theory, and applications, Birkhäuser, Basel.
Krenn VA, Fornai C, Webb NM, et al (2021) Sex determination accuracy in a Central European sample using the human sacrum. Anthropol Anz https://doi.org/10.1127/anthranz/2021/1415
Krishan K, Chatterjee PM, Kanchan T, et al (2016) A review of sex estimation techniques during examination of skeletal remains in forensic anthropology casework. Forensic Sci Int 261:165.e1-8. https://doi.org/10.1016/j.forsciint.2016.02.007
Krogman WM (1962) The Human Skeleton in Forensic Medicine, Thomas, Springfield.
Kuchař M, Henyš P, Rejtar P, et al (2021) Shape morphing technique can accurately predict pelvic bone landmarks. Int J Legal Med 135:1617–1626. https://doi.org/10.1007/s00414-021-02501-6
Kurki HK (2007) Protection of obstetric dimensions in a small-bodied human sample. Am J Phys Anthropol 133:1152–1165. https://doi.org/10.1002/ajpa.20636
Legendre P (2018) Lmodel2: Model II Regression. https://cran.r-project.org/web/packages/lmodel2/index.html.
Mestekova S, Brůžek J, Veleminska J, et al (2015) A test of the DSP sexing method on

CT images from a modern French sample. J Forensic Sci 60:1295–1299. https://doi.org/10.1111/1556-4029.12817
Mitteroecker P, Grunstra NDS, Stansfield E, et al (2021) Did population differences in human pelvic form evolve by drift or selection? Bull Mém Soc Anthropol Paris 33:10–25. https://doi.org/10.4000/bmsap.7460
Oikonomopoulou EK, Valakos E, Nikita E (2017) Population-specificity of sexual dimorphism in cranial and pelvic traits: evaluation of existing and proposal of new functions for sex assessment in a Greek assemblage. Int J Legal Med 131:1731–1738. https://doi.org/10.1007/s00414-017-1655-x
Phenice TW (1969) A newly developed visual method of sexing the os pubis. Am J Phys Anthropol 30:297–302. https://doi.org/10.1002/ajpa.1330300214
R Development Core Team (2021) R: A language and environment for statistical computing R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available: http://www.R-project.org.
Rantalainen T, Weeks BK, Nogueira RC, et al (2016) Long bone robustness during growth: A cross-sectional pQCT examination of children and young adults aged 5–29 years. Bone 93:71–78. https://doi.org/10.1016/j.bone.2016.09.015
Rmoutilová R, Dupej J, Veleminska J, et al (2017) Geometric morphometric and traditional methods for sex assessment using the posterior ilium. Leg Med (Tokyo) 26:52–61. https://doi.org/10.1016/j.legalmed.2017.03.004
Robertson HI, Pokotylo DL, Weston DA (2019) Testing landmark redundancy for sex-based shape analysis of the adult human os coxa. Am J Phys Anthropol 169:689–703. https://doi.org/10.1002/ajpa.23860
Rogers T, Saunders S (1994) Accuracy of sex determination using morphological traits of the human pelvis. J Forensic Sci 39:1047–1056. https://doi.org/10.1520/JFS13683J
Rosenberg KR (1992) The evolution of modern human childbirth. Yearb Phys Anthropol 35:89–124. https://doi.org/10.1002/AJPA.1330350605
Rusk KM, Ousley SD (2016) An evaluation of sex- and ancestry-specific variation in sacral size and shape using geometric morphometrics. Am J Phys Anthropol 159:646–654. https://doi.org/10.1002/ajpa.22926
Schlager S (2013) Soft-tissue reconstruction of the human nose: population differences and sexual dimorphism. PhD dissertation, University of Freiburg.
Schutkowski H (1993) Sex determination of infant and juvenile skeletons: I. Morphognostic features. Am J Phys Anthropol 90:199–205. https://doi.org/10.1002/ajpa.1330900206
Slice DE (ed.) (2005) Modern morphometrics in physical anthropology, Kluwer Academic/Plenum Publishers, New York.
Stansfield E, Kumar K, Mitteroecker P, et al (2021) Biomechanical trade-offs in the pelvic floor constrain the evolution of the human birth canal. Proc Natl Acad Sci USA 118:e2022159118. https://doi.org/10.1073/pnas.2022159118
Steyn M, Pretorius E, Hutten L (2004) Geometric morphometric analysis of the greater sciatic notch in South Africans. HOMO 54:197–206. https://doi.org/10.1078/0018-442X-00076
Tague RG (2003) Pelvic sexual dimorphism in a metatherian, *Didelphis virginiana*: implications for eutherians. J Mammal 84:1464–1473. https://doi.org/10.1644/BME-009
Tobolsky VA, Kurki HK, Stock JT (2016) Patterns of directional asymmetry in the pelvis and pelvic canal. Am J Hum Biol 28:804-810. https://doi.org/10.1002/ajhb.22870
Torres-Tamayo N, García-Martínez D, Nalla S, et al (2018) The torso integration hypothesis revisited in *Homo sapiens*: Contributions to the understanding of hominin body shape evolution. Am J Phys Anthropol 167:777–790. https://doi.org/10.1002/ajpa.23705
Urciuoli A, Zanolli C, Almécija S, et al (2021) Reassessment of the phylogenetic relationships of the late Miocene apes *Hispanopithecus* and *Rudapithecus* based on vestibular morphology. Proc Natl Acad Sci USA 118:e2015215118. https://doi.org/10.1073/pnas.2015215118
Urciuoli A, Zanolli C, Almécija S, et al. (2018) Analysis of the primate vestibular apparatus: a comparison of 3D geometric morphometric and

diffeomorphism approaches. Proceedings of the European Society for Human Evolution, Faro, Portugal.
Urciuoli A, Zanolli C, Beaudet A, et al (2020) The evolution of the vestibular apparatus in apes and humans. eLife 9:e51261. https://doi.org/10.7554/eLife.51261
Veneziano A, Landi F, Profico A (2018) Surface smoothing, decimation, and their effects on 3D biological specimens. Am J Phys Anthropol 166:473–480. https://doi.org/10.1002/ajpa.23431
Waldeyer HWG (1899) Das Becken. Topographisch-anatomisch mit besonderer Berücksichtigung der Chirurgie und Gynäkologie, Cohen, Bonn.
Waltenberger L, Rebay-Salisbury K, Mitteroecker P (2021) Three-dimensional surface scanning methods in osteology: A topographical and geometric morphometric comparison. Am J Phys Anthropol 174:846–858. https://doi.org/10.1002/ajpa.24204
Warrener AG, Lewton KL, Pontzer H, et al (2015) A wider pelvis does not increase locomotor cost in humans, with implications for the evolution of childbirth. PLoS One 10:e0118903. https://doi.org/10.1371/journal.pone.0118903
Washburn SL (1960) Tools and human evolution. Sci Am 203:63–75. https://doi.org/10.1038/scientificamerican0960-62schul
Weaver DS (1980) Sex differences in the ilia of a known sex and age sample of fetal and infant skeletons. Am J Phys Anthropol 52:191–195. https://doi.org/10.1002/ajpa.1330520205
Webb NM, Fornai C, Krenn VA, et al (2021) Do chimpanzees really have a spacious birth canal? A reanalysis of cephalopelvic proportions and implications for the obstetrical dilemma in humans. Am J Phys Anthropol Supplement 71:111–112.
Weber GW, Bookstein FL (2011) Virtual Anthropology: A Guide to a New Interdisciplinary Field, Vienna, Austria, Springer.
Wells JC (2017) The New "Obstetrical Dilemma": Stunting, Obesity and the Risk of Obstructed Labour. Anat 300:716–731. https://doi.org/10.1002/ar.23540
Wilson LaB, Ives R, Humphrey LT (2016) Quantification of 3D curvature in the iliac crest: Ontogeny and implications for sex determination in juveniles. Am J Phys Anthropol 162:255–266. https://doi.org/10.1002/ajpa.23114
Zanolli C, Pan L, Dumoncel J, et al (2018) Inner tooth morphology of *Homo erectus* from Zhoukoudian. New evidence from an old collection housed at Uppsala University, Sweden. J Hum Evol 116:1-13. 10.1016/j.jhevol.2017.11.002
Zech WD, Hatch G, Siegenthaler L, et al (2012) Sex determination from os sacrum by postmortem CT. Forensic Sci Int 221:39–43. https://doi.org/10.1016/j.forsciint.2012.03.022
Zelditch ML, Fink WL, Swiderski DL (1995) Morphometrics, homology, and phylogenetics: Quantified characters as synapomorphies. Syst Biol 44:179–189. https://doi.org/10.2307/2413705
Zhan MJ, Fan F, Qiu LR, et al (2018) Estimation of stature and sex from sacrum and coccyx measurements by multidetector computed tomography in Chinese. Leg Med 34:21–26. https://doi.org/10.1016/j.legalmed.2018.07.003

Editor, Giovanni Destro Bisol