



Testing the reliability of the rearticulation of osteological primate pelves in comparative morphological studies

Nicole Torres-Tamayo¹  | Todd C. Rae²  | Eishi Hirasaki³  | Lia Betti¹ 

¹Department of Anthropology, University College London, London, UK

²School of Life Sciences, University of Sussex, Brighton, UK

³Centre for Evolutionary Origins of Human Behavior, Kyoto University, Inuyama, Japan

Correspondence

Nicole Torres-Tamayo, Department of Anthropology, University College London, London, UK.

Email: nicoletorrestamayo@gmail.com

Funding information

Kyoto University Cooperative Research Programme; Leverhulme Trust, Grant/Award Number: RPG-2021-130; Great Britain Sasakawa Foundation, Grant/Award Number: B130

Abstract

The evolution of human pelvic form is primarily studied using disarticulated osteological material of living and fossil primates that need rearticulation to approximate anatomical position. To test whether this technique introduces errors that impact biological signals, virtual rearticulations of the pelvis in anatomical position from computed tomography scans were compared with rearticulated models from the same individuals for one female and one male of *Homo sapiens*, *Pan troglodytes*, *Macaca mulatta*, *Lepilemur mustelinus*, *Galago senegalensis*, and *Nycticebus pygmaeus*. “Cadaveric” pelvic bones were first analyzed in anatomical position, then the three bones were segmented individually, intentionally scattered, and “rearticulated” to test for rearticulation error. Three-dimensional landmarks and linear measurements were used to characterize the overall pelvis shape. Cadaveric and rearticulated pelves were not identical, but inter-specific and intra-specific shape differences were higher than the landmarking error in the cadaveric individuals and the landmarking/rearticulation error in the rearticulated pelves, demonstrating that the biological signal is stronger than the noise introduced by landmarking and rearticulation. The rearticulation process, however, underestimates the medio-lateral pelvic measurements in species with a substantial pubic gap (e.g., *G. senegalensis*, *N. pygmaeus*) possibly because the greater contribution of soft tissue to the pelvic girdle introduces higher uncertainty during rearticulation. Nevertheless, this discrepancy affects only the caudal-most part of the pelvis. This study demonstrates that the rearticulation of pelvic bones does not substantially affect the biological signal in comparative 3D morphological studies but suggests that anatomically connected pelves of species with wide pubic gaps should be preferentially included in these studies.

KEYWORDS

error, Haplorrhini, skeletal, Strepsirrhini, virtual

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *The Anatomical Record* published by Wiley Periodicals LLC on behalf of American Association for Anatomy.

1 | INTRODUCTION

An underlying issue in morphological studies of both neontological and palaeontological osteological material is the potential mismatch between the anatomical position of bones in the body and in postmortem (dry bone or fossil) reconstruction. This is inherent in situations requiring the rearticulation of multiple bones, such as the pelvis. A detailed understanding of the amount of variation introduced by the process of rearticulating osteological remains is unclear at present, but would be valuable, as such methodologically introduced variation could inadvertently affect locomotor and obstetric interpretations. To address this, the research described below uses geometric morphometrics of 3D virtual skeletal pelvises, based on full-body computed tomography (CT) scans of several species of primates, to determine the degree to which virtual rearticulations of the pelvis deviate from their shape in cadaveric specimens. This, in turn, will help to determine the level of confidence that can be attached to functional interpretations of the pelvis based on such methods.

1.1 | Anatomic considerations

The adult human pelvis is composed of two *ossa coxae*, the sacrum and the coccyx (Broek, 1911). The two *ossa coxae* articulate with the sacrum via the sacro-iliac joints in the posterior or dorsal part of the pelvis and may articulate or even fuse at the pubic symphysis in the ventral part of the pelvis (Todd, 1921). This skeletal anatomy creates a stable structure that has important functions in (1) locomotion, as body weight is transmitted to the lower limbs through the pelvic girdle, (2) childbirth, as the neonate must pass through the maternal birth canal, and (3) support of abdominal organs, both by the pelvis itself and the pelvic floor musculature that attaches to it, especially in orthograde taxa (Abitbol, 1988; Leutenegger, 1974; Lewton, 2022). To date, these considerations have been addressed primarily with respect to *H. sapiens* (e.g., Huseynov et al., 2016), but they are also relevant to the rest of the order Primates, in which a wider range of variation in pelvic form occurs.

The joints between the three pelvic bones provide the pelvis with some degree of flexibility that can be crucial for human childbirth (Gardner & Van Heuverswyn, 1940). The connective tissue between the *ossa coxae* at the pubic symphysis in humans is relaxed by hormones released in late stages of pregnancy and during childbirth to enlarge the birth canal to facilitate the passage of a relatively large fetus (Stolarczyk et al., 2021). This process has been hypothesized to be the reason why in humans the pubic

symphysis remains unfused throughout the entire life of the individual (Lovejoy, 2005). The sacro-iliac joints also allow some degree of mobility of the sacrum relative to the *ossa coxae*, increasing the size the pelvis outlet to facilitate birth (Vleeming et al., 2012). The sacro-iliac joints generally remain unfused throughout life in humans, although there are cases where one or the two *ossa coxae* fuse to the sacrum (Dar et al., 2008). Fusion of the sacro-iliac joint is more frequent in humans than a fused pubic symphysis, that is often manifested by degenerative bridging in pathological individuals or as a consequence of trauma (Schwarz & Schwarz, 1966).

In the wider context of non-human primates, however, the situation is considerably more variable. For example, the maroon leaf monkey *Presbytis rubicunda* and some gibbons such as *Hylobates lar* are reported to show frequent fusion of the two pubic corporae (Tague, 1993), while the pubic symphyses of other species such as the common marmoset *Callithrix jacchus* and the silvery lutung *Trachypithecus cristatus* are consistently unfused (Casteleyn et al., 2012; Tague, 1993). Thus, dry osteological pelvises of primates found in natural history collections exist in several states of disarticulation (Figure 1).

Researchers may find pelvic bones connected in anatomical position (Figure 1a) because of: (1) fused pelvic joints (e.g., the sacro-iliac joints, the pubic symphysis or both); (2) non-decomposed connective tissue holding the bones together; or (3) the presence of artificial material, for example, glue, putty, and wires. This last case is especially problematic when the three pelvic bones have been articulated incorrectly and are preserved in an anatomically inaccurate configuration. When the two *ossa coxae* are connected but the sacrum is separated (Figure 1b), it may be due to a partially or fully fused pubic symphysis or connective tissue/artificial material holding the two *ossa coxae* together. A common condition, and in some way the most challenging for the study of the complete pelvis, is when none of the pelvic joints have fused and there is no soft tissue or artificial material holding the bones together (Figure 1c). In this case, some form of rearticulation of the bones is necessary to restore the original conformation of the full pelvis to assess the shape and capacity of, for example, the birth canal.

1.2 | Challenges in the evaluation of the bony pelvis

Knowledge about pelvic allometric scaling, locomotor adaptations, phylogeny, neutral evolution, and human variation can be gleaned from analyses of isolated *ossa coxae* (Betti et al., 2013; Lewton, 2022; Mobb & Wood, 1997;

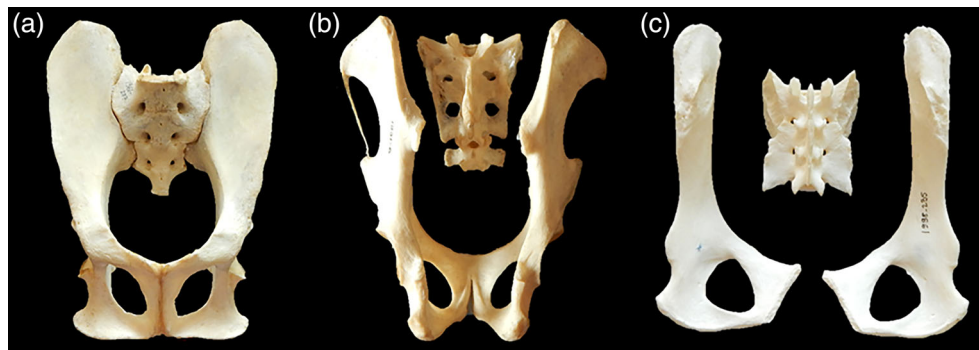


FIGURE 1 Pelvic anatomical conditions frequently encountered in osteological collections. (a) Anterior view of pelvic bones in anatomical connection of a male *Hylobates lar* MNHN-ZM-MO-1961-287; (b) Posterior view of two *ossa coxae* held together with a fused pubic symphysis and sacrum separated of a female *Propithecus verreauxi* MNHN-ZM-MO-1951-6; (c) Posterior view of three pelvic bones separated of a female *Alouatta seniculus* MNHN-ZM-MO-1998-235. The three specimens belong to the Collections de Vertébrés of the Musée Nationale d'Histoire Naturelle (Paris, France). Not to scale.

Wood & Chamberlain, 1986). Comprehensive studies of obstetric constraints by means of birth canal size and shape, however, ideally require anatomically connected pelvic girdles.

Long before contemporary imaging methods such as CT became a standard data collection technique, dry pelvic bones had been rearticulated to assess morpho-functional questions in primate comparative morphology. For example, sex differences in the primate bony pelvis were first evaluated via rearticulated dry pelvises using ligamentous preparations or held together by means of very thin layers of wax, cement and/or rubber (Schultz, 1949). Standard practice for many years has been to reconstruct the dry pelvis using rubber bands and/or putty or clay (e.g., Bonneau et al., 2012). Most studies that used rearticulated pelvises, often to evaluate intra-specific pelvic shape and size differences between females and males, include no compensation for musculoskeletal aspects of the pubic symphysis or sacro-iliac joints (Kurki, 2007, 2011; Moffett, 2017; Tague, 1989, 2000).

The possible variation introduced by rearticulation of dry osteological remains is rarely quantified in non-human primate comparative anatomy. Although some studies have addressed the issue of intra-observer error in such rearticulations (e.g., Hammond et al., 2016; Ward et al., 2018), rearticulated dry pelvises were not compared with *in vivo* pelvic shape. Such studies only quantify consistency across repeated rearticulations by a single observer, not their similarity to the form of the original anatomical structure in the body. Methodological variation, however, can be introduced when rearticulating osteological pelvises in this way, as demonstrated by comparison between cadaveric and dissected dry pelvises of the same human individuals. For example, Bonneau et al. (2012) showed that dissected pelvises rearticulated using rubber bands are not identical to the original cadaveric

pelvises in their 3D shape, nor in standard linear measurements, although the degree of variation introduced by rearticulation is small. With the increasing application of virtual techniques to the comparative analysis of skeletal form, manual rearticulations based on rubber bands and putty have increasingly been replaced by virtual rearticulation in studies of human and primate pelvic shape evolution (Fischer et al., 2021; Laudicina & Cartmill, 2023). The potential error induced by this type of re-articulation, however, has not been empirically evaluated, even though it is critically important when assessing variation in pelvic dimensions.

To overcome the uncertainties associated with bony pelvis rearticulation, full bodies (i.e., including the soft tissue that holds the three pelvic bones together) are increasingly being used in studies of human and non-human primate morphology. In the advent of open science and data sharing, whole-body CT scans from living and cadaveric specimens are becoming increasingly available via online repositories. These CT scans contain anatomically connected pelvises that do not need to be rearticulated and have served as the main data source for many recent investigations (Brynskog et al., 2021; Buck et al., 2021; Huseynov et al., 2016, 2017; Kawada et al., 2020; Kubicka, 2023; Morimoto et al., 2023; Starrach et al., 2023; Torres-Tamayo et al., 2018; Torres-Tamayo, Martelli, et al., 2020; Torres-Tamayo, Schlager, et al., 2020; Uy & Laudicina, 2021; Waltenberger et al., 2022).

Historical osteological collections housed in institutions of natural history, however, contain valuable skeletal remains that have contributed to the progress of primate comparative anatomy since the beginning of the discipline (Tyson, 1699). Moreover, many of the non-human primate specimens present in these collections were collected in the organisms' natural habitat, unlike the bulk of available full-body CT scan sets, which consist

primarily of individuals raised in captivity, a situation that can affect skeletal health and, thus, skeletal form (Kohn & Lubach, 2019). For this reason, historical collections of disarticulated skeletons are still an important resource in comparative and functional morphology.

As the goal of morpho-functional investigations of rearticulated pelves is to better understand the relationship between anatomical form and its associated function(s), accurate pelvic rearticulation is crucial to avoid erroneous functional interpretations. This is especially true for the hominin fossil record, where pelvic remains are scarce and often the primary material from which inferences can be drawn about the locomotion, posture, and birthing process of extinct species (see, for example, pelvic reconstructions by Adegboyega et al., 2021; Berge & Goularas, 2010; Claxton et al., 2016; Häusler & Schmid, 1995; Laudicina et al., 2019; Lovejoy, 1979; Simpson et al., 2008; Weaver & Hublin, 2009). Fossil pelvic remains are overwhelmingly disarticulated, incomplete and/or distorted elements. Because of its fragility, the pubic region is normally missing in fossils and its absence adds more uncertainty to the articulation process of the pelvic girdle. To use these valuable natural history resources, both extant and fossil, to their fullest, it is necessary to determine if any error is introduced by rearticulation of separated skeletal

elements and, if so, how likely is it that this error will overshadow potential morpho-functional signals.

The current study tests whether the virtual rearticulation of osteological primate pelves introduces an error that may obscure inter-specific and intra-specific variation. Here, unedited virtual reconstructions of cadaveric pelves are compared with digitally separated and rearticulated pelves of the same individuals across several primate species.

2 | MATERIALS AND METHODS

2.1 | Sample: Inclusion and exclusion criteria

Primate species vary in their habitual posture, locomotor behavior and cephalo-pelvic proportions, all factors that have been linked to pelvic shape differences among species (Leutenegger, 1974; Lewton, 2010, 2015a, 2015b, 2022; Lovejoy, 2005; Moffett, 2017; Schultz, 1949; Ward et al., 2018). To ensure that the present results are applicable across the order, six extant species spanning different families are included (Figure 2): *H. sapiens* (Hominoidea-Hominidae), *Pan troglodytes* (Hominoidea-Hominidae), *Macaca mulatta* (Cercopithecoidea-Cercopithecidae), *Lepilemur*



FIGURE 2 Species included in this study. (a) *Homo sapiens*, (b) *Pan troglodytes*, (c) *Macaca mulatta*, (d) *Lepilemur mustelinus*, (e) *Galago senegalensis*, (f) *Nycticebus pygmaeus*. Images are not to scale. Photographs courtesy of All the World's Primates (<https://alltheworldsprimates.org/>), the Duke Lemur Center (<https://lemur.duke.edu/>) and Lemurs of Madagascar (<http://lemursofmadagascar.com/>).

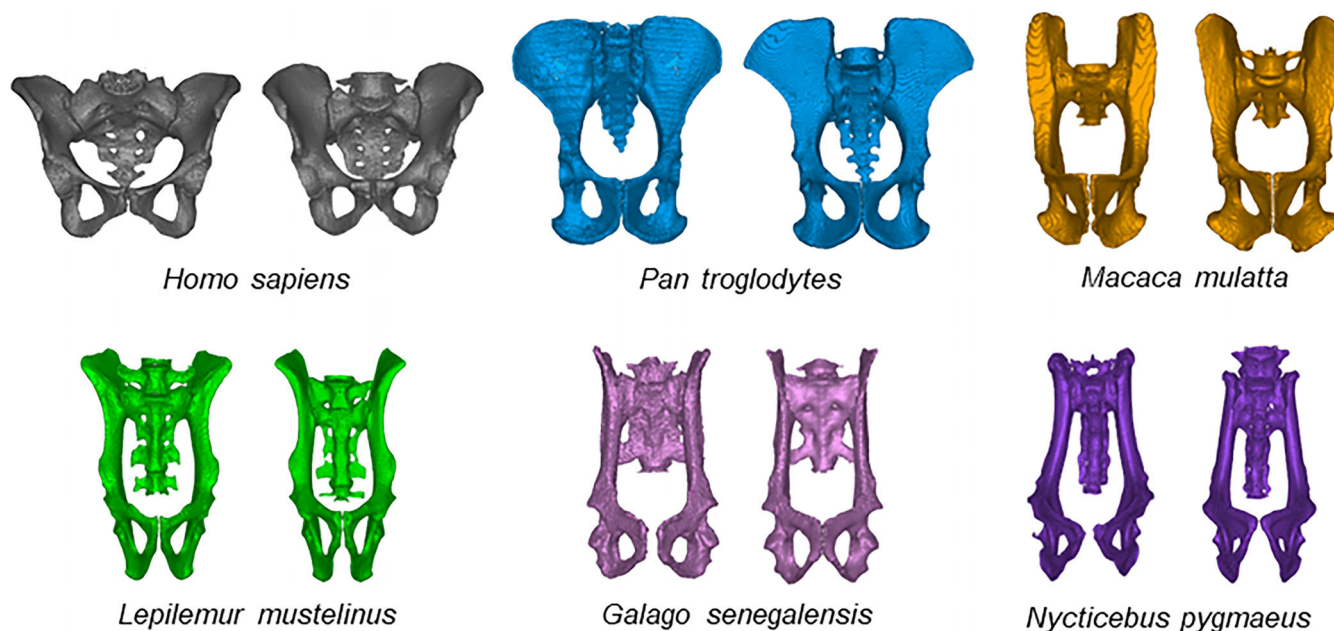


FIGURE 3 Virtual three-dimensional models of pelvis for the six primate species included in this study. Each species is represented by one female (left) and one male (right). The identities of the individuals can be found in Supplementary Table S1. Not to scale.

mustelinus (Lemuroidea-Lemuridae), *Galago senegalensis* (Lorisoidea-Galagidae) and *Nycticebus pygmaeus* (Lorisoidea-Lorisidae). Further details about the sample composition are given in Supplementary Table S1. For each species, whole-body CT scans were obtained for one female and one male adult individual so that intra-specific variation could include aspects of sexual dimorphism. All specimens were scanned either as well-preserved cadavers (frozen or in formalin) or as sedated living individuals. Specimens were chosen if they showed no-to-minimal bony asymmetry and pathology (see Supplementary Figure S1 for examples of excluded specimens), clearly displayed unfused pelvic joints (see Supplementary Figure S2 for examples of excluded specimens), and whose joints could be clearly visualized (see Supplementary Figure S3 for examples of excluded specimens).

2.2 | Data collection: Protocol design

The three pelvic bones of each pelvic girdle were manually segmented in the open-source software 3D Slicer (<https://www.slicer.org/>) (Kikinis et al., 2013), and 3D models of the 12 individuals were generated in STL file format (Figure 3). To evaluate the error introduced by digitally rearticulating separate pelvic bones, two studies were performed (Figure 4):

1. *Study 1*: The whole pelvis of cadaveric/living individuals was segmented from CT scans, creating a 3D model of the pelvic girdle in situ capturing the

original position of the three bones and the contribution of the soft tissues. The shape of the resulting anatomically connected pelvis was measured three times using 3D landmarks (see next section for details) on three different days by the same observer (N. T. T.), to estimate the intra-observer landmarking error.

2. *Study 2*: The three pelvic bones of cadaveric/living individuals were segmented individually and then randomly scattered in virtual space to simulate a situation in which isolated skeletal elements had been scanned (the most common occurrence when scanning museum specimens). The 3D models of the individual bones were then rearticulated three times on three different days by the same observer (N.T.T.) to estimate the intra-observer rearticulation error. The rearticulation of the pelvic bones was carried out in Artec Studio version 16 (<https://www.artec3d.com/>) by first digitally articulating the two *os coxae* and the sacrum at the sacroiliac joints. For this purpose, the auricular surface of the sacrum and of the left *os coxa* were preliminary aligned using three reference markers placed on the most superior, most ventral and most dorso-inferior points of the left iliac and sacral auricular surfaces (Supplementary Figure S4). The same procedure was applied to align the right *os coxa* and the sacrum. Then, the position of the bones was adjusted by taking the pubic symphysis joint into consideration and using the anatomical experience of the observer. Soft tissue contribution was assumed to be negligible at the level of the auricular surface (therefore simulating a manual rearticulation of

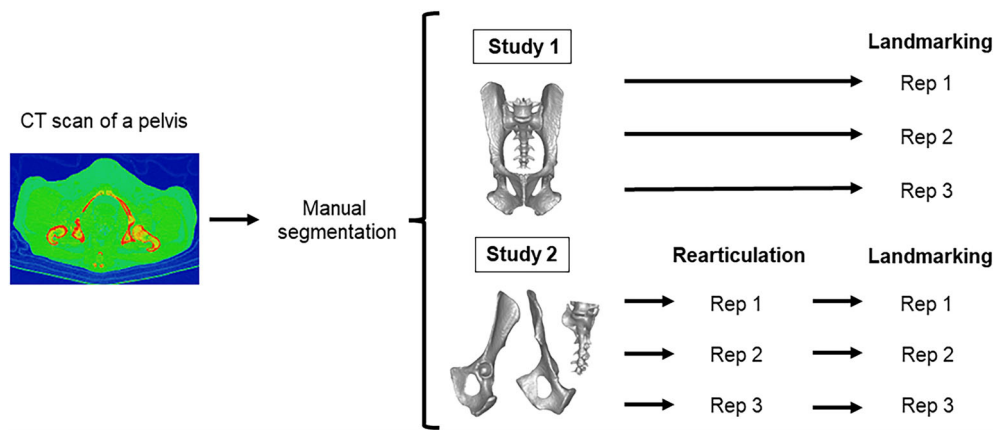


FIGURE 4 Data acquisition protocol. In study 1, the resulting 3D pelvic bones are an anatomically connected pelvic girdle that is landmarked three times (rep = repetition). In study 2, the 3D pelvic bones were randomly scattered, then rearticulated three times and each resulting rearticulated pelvis was landmarked once. “Rep” means repetition and refers to the repeated landmarking and rearticulation. The pelvis illustrated in the protocol belongs to the adult male *Macaca mulatta* individual ucd:39650 from the California National Primate Centre, UC Davis (California, USA) and is available from Morphosource.

the sacrum with the ilia on dry bone specimens), while no assumptions of a particular joint thickness were made for the pubic symphysis, the pubic gap being dictated by the posterior articulation of the girdle and only adjusting for the alignment of the symphysis at the center. This approach was chosen because the sacro-iliac joints are good anchor points at the posterior part of the pelvis due to the close match of the joint surfaces on the two articulating bones, while there is large variation in the size of the gap at the pubic symphysis. Each resulting rearticulated pelvis was measured once by the same observer (N. T. T.), using the same set of landmarks as for Study 1. This second study allows the assessment of the combined effects of the intra-observer re-articulation error and landmarking error.

2.3 | Analyses

A total of 53 landmarks, plus 215 semilandmarks distributed along 11 curves, were placed by the same researcher (N. T. T.) on the virtual pelvic models to capture the 3D shape of the pelvis (Figure 5, Supplementary Table S2). The resulting x , y , z raw landmark coordinates of the 72 specimens (six species, two individuals per species, 6 landmarking repetitions per pelvis) were subjected to generalized Procrustes analysis (GPA; Gower, 1975) that translates, rotates, and scales the configurations to remove any variation not related to the actual shape of the pelvis. This process transforms the raw coordinates into Procrustes shape coordinates that were further analyzed by means of standard geometric morphometric analyses.

For a preliminary exploration and intuitive visualization of the inter-specific and intra-specific variation within the sample and of the (dis)similarities between the cadaveric and the rearticulated pelvises, a shape space principal component analysis (PCA) was performed. A more comprehensive quantification of the similarities and differences between the specimens of our sample was carried out by calculating the Euclidean distance between sets of Procrustes shape coordinates (i.e., Procrustes distances, the squared root of summed squared inter-landmark distances between corresponding landmarks; Mitteroecker & Gunz, 2009) between all possible pairs of pelvises and carrying out a pairwise comparison between groups. The calculated Procrustes distances within groups were visualized by means of box-and-whiskers plots. Additionally, two Nested Procrustes MANOVA (model: shape \sim species/individual) were performed in the cadaveric (Study 1) and in the rearticulated (Study 2) samples separately to disentangle the amount of inter-specific (species as factor), intra-specific (individual/sex as factor) and residual variation (here interpreted as intra-observer landmarking-only error in Study 1 and intra-observer landmarking plus re-articulation error in Study 2).

Finally, to quantify the impact of rearticulation error on the birth canal diameters traditionally measured in biological anthropology (adapted from Tague, 2000 to suit a variety of primate species), six inter-landmark distances (in millimetres, mm) between relevant landmarks were extracted (Table 1). For dorso-ventral diameters measured from the left and right pubes, the mean between both values was calculated and used in subsequent analyses. The mean values were calculated for the

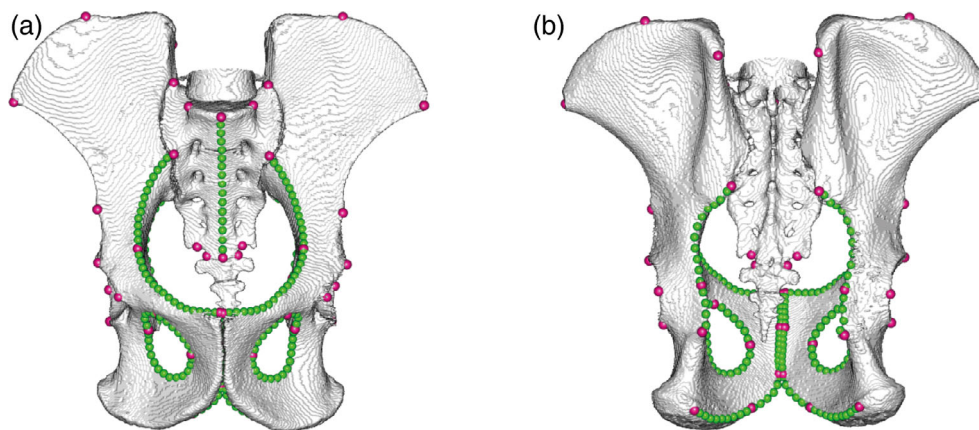


FIGURE 5 A total of 53 fixed landmarks (pink) and 215 semilandmarks along 11 curves (green) in a male chimpanzee pelvis. (a) Anterior or ventral view. (b) Posterior or dorsal view. The pelvis mesh used to illustrate the landmarks and semilandmarks belong to the adult male *Pan troglodytes* individual Ypm Mam 015939 from the Vertebrate Zoology Division–Mammalogy, Yale Peabody Museum and available in Morphosource.

TABLE 1 Traditional birth canal diameters and first-last landmarks enclosing them. For diameters measured in the left (L) and right (R) side, the mean between both values was calculated.

Diameter	Definition	Landmarks
DV inlet diameter (L and R)	From the <i>promontorium</i> to dorsomedial aspect of superior border of pubis	28–13 (L) 29–13 (R)
ML inlet diameter	Maximum transverse distance between <i>lineae terminales</i>	52–53
DV midplane diameter (L and R)	From semilandmark 123 ^a to dorsomedial aspect of inferior border of pubis	32–123 ^a (L) 33–123 ^a (R)
ML midplane diameter	Distance between <i>spinae ischiadicae</i>	24–25
DV outlet diameter (L and R)	From most caudal midpoint of <i>apex sacralis</i> to dorsomedial aspect of inferior border of pubis	30–15 (L) 31–15 (R)
ML outlet diameter	Distance between <i>tubera ischiadica</i> ^b	42–43 ^b

Abbreviations: DV, dorso-ventral; ML, medio-lateral.

^aDue to the highly variable number of sacral vertebrae in the species included, it was not possible to measure the AP midplane diameter from the point “between fourth and fifth sacral vertebrae” as traditionally described for humans (Tague, 2000). Instead, the tenth semilandmark (sml 123) of the sacral curve composed of 15 semilandmarks and thus representing 2/3 of the sacrum was taken as starting point of the DV midplane diameter. Note that this point might not be best suited to measure this obstetrical diameter, but the aim of this study is not evaluating the birth canal diameters but assessing the measurement error between repetitions.

^bThe points of measurement on the ischial tuberosities are located along the medial margin at the widest transverse diameter. Their location may be uncertain in those species where the ischial tuberosities are not very pronounced or in those individuals where the scan resolution is lower.

cadaveric and rearticulated pelvis; the difference between the cadaveric and rearticulated diameters for each specimen was calculated using the mean for the two conditions and expressed as percentage over their mean.

All the analyses were carried out in the open-source R software (R Core Team, 2023), specifically in the packages *Morpho* (Schlager, 2017), *geomorph* version 4.0.5 (Adams et al., 2022) and *RRPP* version 1.3.1 (Collyer & Adams, 2018), and in PAST version 4.13 (Hammer et al., 2001).

3 | RESULTS

3.1 | Morphological affinities and differences in the sample

Inter-specific differences are clear in the first two principal components of the shape space PCA (Figure 6).

Principal component 1 (PC1) explains more than 50% of the total variation of the sample and appears to reflect some residual size variation (due to allometry) and phylogenetic differences between species, as well as adaptations to bipedal locomotion in *H. sapiens*; humans plot in the lowest PC1 values, and their distinctive pelvic shape is clearly separated from that of the non-human primates, that plot towards higher PC1 values. *H. sapiens* pelvis are cranio-caudally short and medio-laterally wide in relative terms and show a relatively short distance between the sacro-iliac joint and the acetabulum. The sacrum is relatively short and curved. The pelvic inlet is round, and the iliac blades curve to lie in the sagittal plane, with a very marked anterior projection of the anterior-superior and

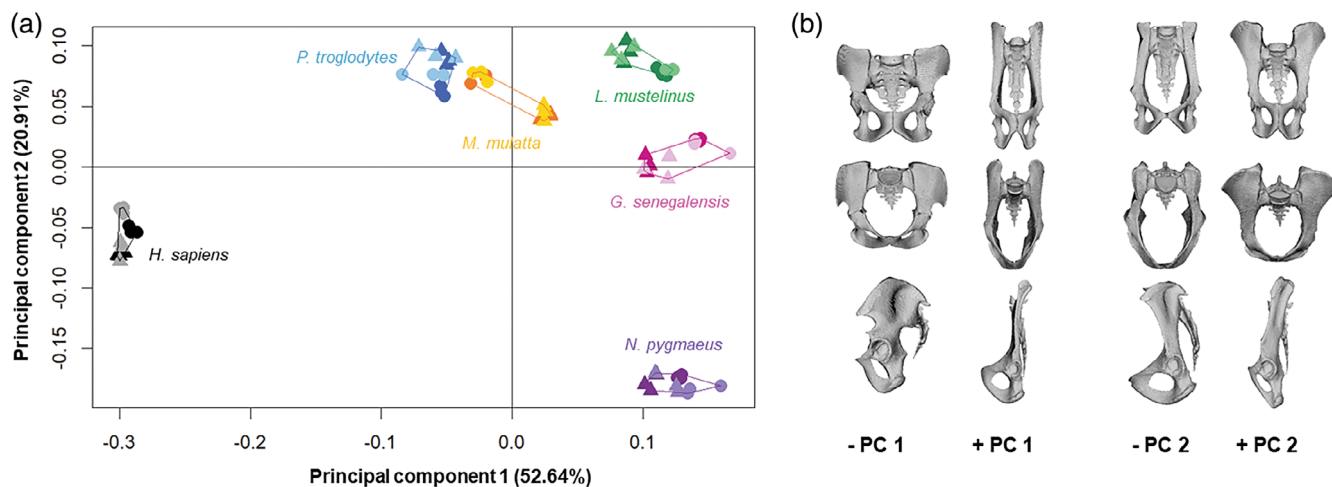


FIGURE 6 Shape space principal component analysis showing the main shape variation of the sample. (a) PCA plot of PC1 and PC2 (>70%). Triangles: females; circles: males; dark colors: cadaveric individuals; light colors: rearticulated individuals. (b) Pelvis shapes at the maximum and minimum PC scores values of PC1 and PC2 in frontal view (first row), superior view (second row) and left lateral view (third row). The pelvis mesh used as reference in the thin plate spline warping belongs to the adult male *Macaca mulatta* individual ucd:39650 from the California National Primate Centre, UC Davis (California, USA) and is available from Morphosource.

TABLE 2 Procrustes distances reflecting the inter-specific and intra-specific variation in the cadaveric (Cad) and in the rearticulated (Rea) pelvis. In both the rearticulated and the cadaveric pelvis, this variation was assessed by calculating the Procrustes distances between the three landmarking repetitions of the female individual and the three landmarking repetitions of the male individual across all possible pairs.

		<i>Homo sapiens</i>		<i>Pan troglodytes</i>		<i>Macaca mulatta</i>		<i>Lepilemur mustelinus</i>		<i>Galago senegalensis</i>		<i>Nycticebus pygmaeus</i>	
		Cad	Rea	Cad	Rea	Cad	Rea	Cad	Rea	Cad	Rea	Cad	Rea
Inter-specific variation	<i>Pan troglodytes</i>	Max	0.338	0.339									
		Mean	0.327	0.320									
		Min	0.314	0.291									
	<i>Macaca mulatta</i>	Max	0.394	0.390	0.212	0.230							
		Mean	0.369	0.370	0.196	0.202							
		Min	0.335	0.343	0.176	0.179							
	<i>Lepilemur mustelinus</i>	Max	0.464	0.470	0.232	0.256	0.238	0.234					
		Mean	0.439	0.441	0.214	0.220	0.214	0.214					
		Min	0.415	0.412	0.189	0.176	0.199	0.184					
	<i>Galago senegalensis</i>	Max	0.468	0.486	0.273	0.311	0.268	0.277	0.187	0.184			
		Mean	0.445	0.451	0.251	0.265	0.244	0.246	0.166	0.170			
		Min	0.419	0.418	0.235	0.231	0.223	0.211	0.138	0.150			
<i>Nycticebus pygmaeus</i>	Max	0.464	0.498	0.343	0.383	0.318	0.340	0.305	0.308	0.264	0.273		
	Mean	0.447	0.469	0.319	0.345	0.293	0.304	0.284	0.292	0.244	0.247		
	Min	0.432	0.440	0.307	0.313	0.267	0.271	0.269	0.275	0.228	0.226		
Intra-specific variation		<i>Homo sapiens</i>		<i>Pan troglodytes</i>		<i>Macaca mulatta</i>		<i>Lepilemur mustelinus</i>		<i>Galago senegalensis</i>		<i>Nycticebus pygmaeus</i>	
		Cad	Rea	Cad	Rea	Cad	Rea	Cad	Rea	Cad	Rea	Cad	Rea
	Max	0.174	0.173	0.151	0.148	0.115	0.117	0.118	0.127	0.130	0.135	0.131	0.136
	Mean	0.162	0.149	0.139	0.133	0.108	0.102	0.105	0.113	0.109	0.114	0.126	0.119
Min	0.155	0.132	0.131	0.116	0.103	0.094	0.096	0.099	0.096	0.088	0.118	0.107	

Note: In this study, intra-specific variation = inter-individual variation which includes inter-sex variation.

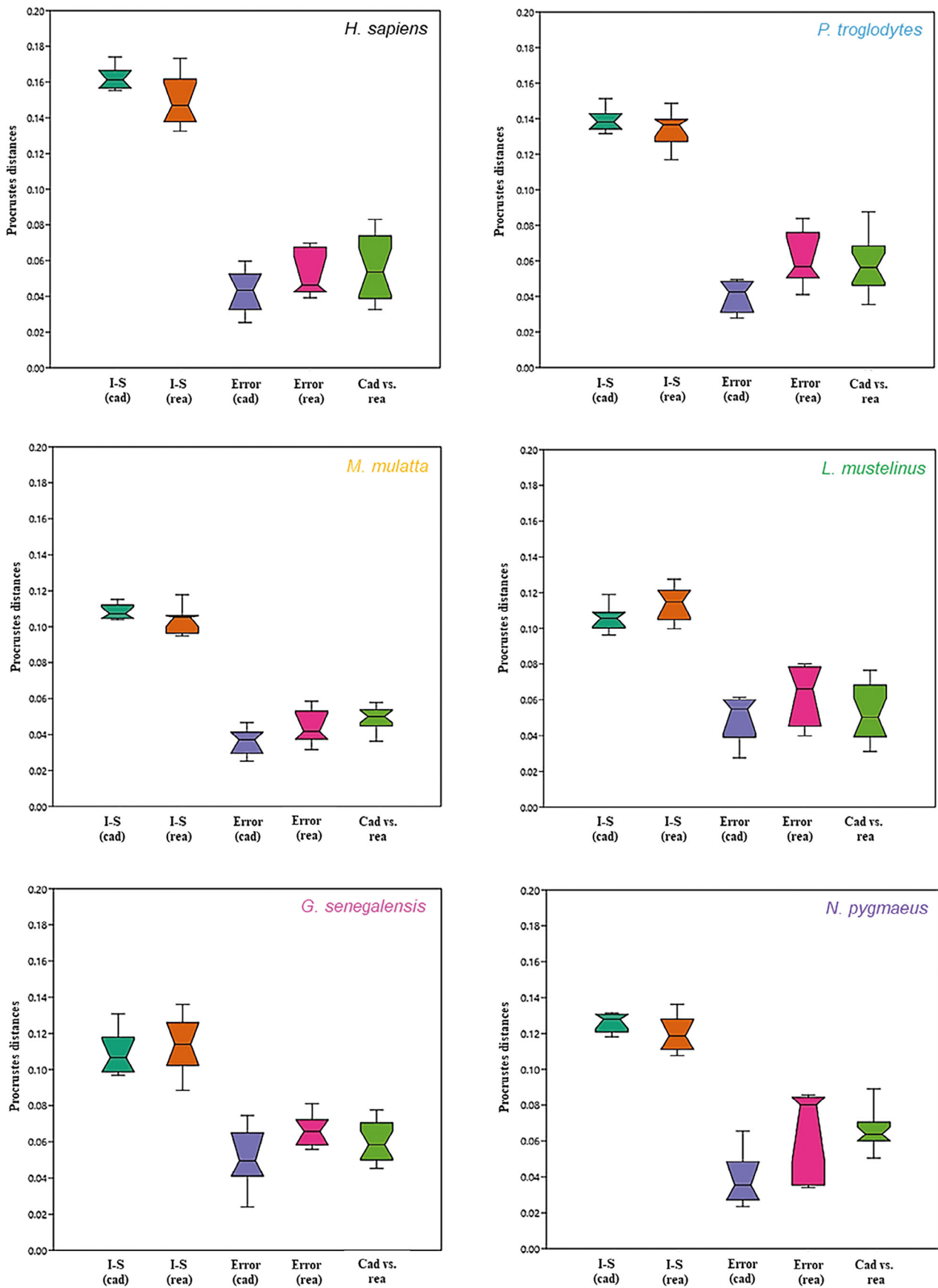


FIGURE 7 Legend on next page.

anterior-inferior iliac spines. The strepsirrhines *L. mustelinus*, *G. senegalensis*, and *N. pygmaeus* show the most distinct pelvis shape when compared to *H. sapiens*, falling towards the highest PC1 values. These primates show a medio-laterally narrower pelvis and a relatively longer and flatter sacrum, and their iliac blades protrude well above the sacrum. The pelvic inlet is extremely oval in the sagittal plane, and the iliac blades are more coronally oriented, with less marked iliac spines. *P. troglodytes* and *M. mulatta* plot in intermediate PC1 values as expected based on phylogenetic relationships and show a pelvic shape that is intermediate between the two morphological trends described above.

Principal component 2 (PC2) explains ~21% of the total variation of the sample. In the lowest PC2 scores, pelvises show remarkably narrow iliac blades in relation to the sacrum, although these morphological differences appear to be largely driven by the peculiarities of pelvic shape of *N. pygmaeus*, which sits at the extreme negative values of the axis. The pelvic inlet is oval in the sagittal plane. The pubis and the anterior-superior iliac spines are anteriorly projected, and the ischio-pubic rami and the inferior ischial rami are relatively long, with a very short pubic symphysis. In the pelvic outlet, the ischial spines protrude well into the midline of the pelvic cavity and the sub-pubic angle is remarkably open. Towards higher PC2 scores, the sacrum is narrow in relation to the width of the iliac blade, which protrudes well above the sacrum. The pelvic inlet is oval shaped with the relatively longer diameter in the sagittal plane, but not as markedly as in negative PC2 scores, as the ischio-pubic rami do not project as far ventrally.

Both PC1 and PC2 reflect morphological trends associated with differences between species, which are represented here by one female and one male individual. The inter-specific differences are so pronounced that consistent trends linked to pelvis shape sexual dimorphism are not captured in the PC1-PC2 projection.

The PCA plot also shows that, for the same individual, the cadaveric and the rearticulated pelvises are not identical, due to the effect of landmarking and rearticulation error. These measurement differences, however, are relatively small compared with inter-individual differences, as a separation between the female and the male individual is observable in both the cadaveric and the rearticulated pelvises within each species. The single female and single male

composition of the study sample, however, is insufficient to interpret these differences between individuals as a measure of pelvis shape sexual dimorphism. These differences, that include the effect of individual variation and sexual dimorphism, will be hereafter referred to as inter-individual differences within each species.

Table 2 summarizes inter-specific and intra-specific (inter-individual & inter-sex) variation by means of Procrustes distances. Inter-specific variation of the sample is similar when assessed in the cadaveric and in the rearticulated pelvises. In the cadaveric sample, mean inter-specific distance ranges from 0.447 (separating *H. sapiens* from *N. pygmaeus* as the most different species) to 0.166 (separating *L. mustelinus* from *G. senegalensis* as the most similar species). In the rearticulated pelvises, this variation is very similar and ranges from 0.469 (from *H. sapiens* to *N. pygmaeus*) to 0.170 (from *L. mustelinus* to *G. senegalensis*). Within each species, the intra-specific variation in the cadaveric and rearticulated pelvises are of similar magnitude, and smaller than inter-specific distances (Table 2, Figure 7). Both the inter- and the intra-specific variation in either the cadaveric or the rearticulated pelvises are notably higher than the error introduced by landmarking or by rearticulation of the same individual (Figure 7, Supplementary Table S4), meaning that the intra-observer landmarking-only error (for cadaveric pelvises) and the combined rearticulation and landmarking error (for rearticulated pelvises) are negligible compared to the intra-specific variation or the inter-specific variation of the sample. As expected, the intra-observer landmarking-only error is lower than the intra-observer rearticulation and landmarking error for the two sexes within the six species (Figure 7, Supplementary Table S4), indicating that additional error, albeit quite small, is introduced by the rearticulation process. However, cadaveric and rearticulated pelvises of the same individual are substantially more similar to each other than the pelvises of two different individuals of the same species are to each other (Table 2, Supplementary Table S4), indicating that such error does not substantially confound inter-individual variation.

The results of the nested Procrustes MANOVAs (Supplementary Table S5) show that inter-specific individual differences in pelvic shape as indicated by the mean square ($MS_{\text{cad}} = 0.2622$; $MS_{\text{rea}} = 0.2757$) are an order of magnitude higher than intra-specific differences ($MS_{\text{cad}} = 0.0222$; $MS_{\text{rea}} = 0.0192$), which are themselves about 10× higher

FIGURE 7 Box-and-whisker plots of the Procrustes distances calculated in this study. I-S (cad) and I-S (rea) indicate the intra-specific (I-S) variation in the cadaveric (cad) and in the rearticulated (rea) pelvises respectively. Error (cad) indicates the Procrustes distances between the different landmarking repetitions (intra-observer landmarking-only error) assessed in cadaveric pelvises. Error (rea) indicates the Procrustes distances between the different rearticulations (intra-observer rearticulation & landmarking error). Cad vs. Rea indicates shape differences between cadaveric and rearticulated pelvises. Data of male and female individuals are combined.

TABLE 3 Linear measurements comparisons (in mm) between the cadaveric (cad) and the rearticulated (rea) pelvis. For each measurement, the mean difference is expressed as percentage (% Δ) of the absolute difference between the value in the cadaveric pelvis and in the value in the rearticulated pelvis divided by the mean value between the cadaveric and the rearticulated pelvis, following Bonneau et al. (2012).

		Mean inlet DV	Mean inlet ML	Mean midplane DV	Mean midplane ML	Mean outlet DV	Mean outlet ML
<i>Homo sapiens</i> F	Cad	120.37	126.74	131.80	107.72	122.60	117.74
	Rea	119.69	125.57	130.03	106.80	120.60	117.58
	% Δ	0.57	0.93	1.35	0.86	1.65	0.14
<i>H. sapiens</i> M	Cad	113.59	122.84	124.01	101.94	95.09	114.84
	Rea	110.42	122.55	123.27	98.19	93.90	113.94
	% Δ	2.83	0.23	0.60	3.74	1.26	0.76
<i>Pan troglodytes</i> F	Cad	144.80	104.78	133.30	102.93	138.39	110.97
	Rea	142.05	104.70	131.73	100.14	137.69	108.50
	% Δ	1.91	0.08	1.18	2.74	0.51	2.24
<i>P. troglodytes</i> M	Cad	143.92	114.23	115.88	96.23	111.68	109.68
	Rea	140.44	113.50	115.45	95.44	111.15	108.91
	% Δ	2.45	0.64	0.34	0.82	0.48	0.70
<i>Macaca mulatta</i> F	Cad	66.48	53.24	63.79	39.33	74.42	34.36
	Rea	66.29	53.23	63.57	38.39	73.69	32.69
	% Δ	0.28	0.01	0.35	2.42	0.98	4.96
<i>M. mulatta</i> M	Cad	65.13	55.72	63.19	54.19	73.91	41.89
	Rea	64.11	52.90	63.06	50.83	73.67	39.50
	% Δ	1.59	5.20	0.21	6.40	0.33	5.89
<i>Lepilemur mustelinus</i> F	Cad	28.06	18.48	23.38	13.83	20.81	10.08
	Rea	27.91	18.29	23.30	13.50	20.73	9.98
	% Δ	0.52	1.03	0.35	2.41	0.38	1.04
<i>L. mustelinus</i> M	Cad	26.23	15.21	21.62	13.53	18.67	8.30
	Rea	25.37	14.95	20.88	13.33	18.53	8.15
	% Δ	3.36	1.67	3.48	1.45	0.73	1.77
<i>Galago senegalensis</i> F	Cad	22.38	12.28	17.93	13.96	16.94	11.39
	Rea	22.26	11.83	17.86	13.33	16.91	10.06
	% Δ	0.50	3.79	0.37	4.60	0.18	12.41
<i>G. senegalensis</i> M	Cad	21.39	11.38	16.54	11.32	15.11	8.26
	Rea	21.36	11.30	16.44	11.06	15.08	7.96
	% Δ	0.15	0.70	0.62	2.27	0.17	3.69
<i>Nycticebus pygmaeus</i> F	Cad	28.93	15.86	24.92	9.02	21.65	13.84
	Rea	28.60	15.50	24.85	8.01	21.58	12.39
	% Δ	1.16	2.26	0.28	11.82	0.33	11.00
<i>N. pygmaeus</i> M	Cad	29.18	15.96	23.44	8.38	23.07	10.69
	Rea	28.89	15.54	23.17	7.36	22.54	9.50
	% Δ	1.01	2.66	1.15	13.04	2.34	11.71

Note: Values in bold indicate those percentual differences between cadaveric and rearticulated pelvis that are >10%.

Abbreviations: DV, dorso-ventral; ML, medio-lateral.

than the landmarking error in the cadaveric individuals ($MS_{cad} = 0.0010$) or the rearticulation and landmarking error in the rearticulated pelvis ($MS_{rea} = 0.0018$). The error due to the rearticulation process, based on these results, can be estimated to be about the same magnitude as the landmarking error, doubling the mean square value in respect to the simple process of landmarking, and substantially lower than intra-specific or inter-specific variation.

3.2 | Analyses of linear canal measurements

Linear measurements (mm) taken repeatedly on cadaveric and on rearticulated pelvis are shown in Supplementary Table S6, and a summary of the comparison of these

measurements is shown in Table 3. For a better visualization, the percentual mean differences between cadaveric and rearticulated pelvis have been illustrated in Figure 8. These results show that the pelvic diameters measured in the rearticulated specimens tend to be smaller than in the corresponding cadaveric specimens for all the individuals and all the repetitions included in this study.

For all the dorso-ventral measurements, none of the species shows a percentual difference between the cadaveric and the rearticulated pelvis that exceeds 5% (Table 3, Figure 8). In fact, the male *L. mustelinus* differences are the only ones to exceed 3%. For the medio-lateral inlet diameter, none of the species exceeds 5% difference, except for the male *M. mulatta* that is slightly above that value (5.2%). This male *M. mulatta* maintains this trend in the medio-lateral midplane and outlet diameters that also exceed 5%.

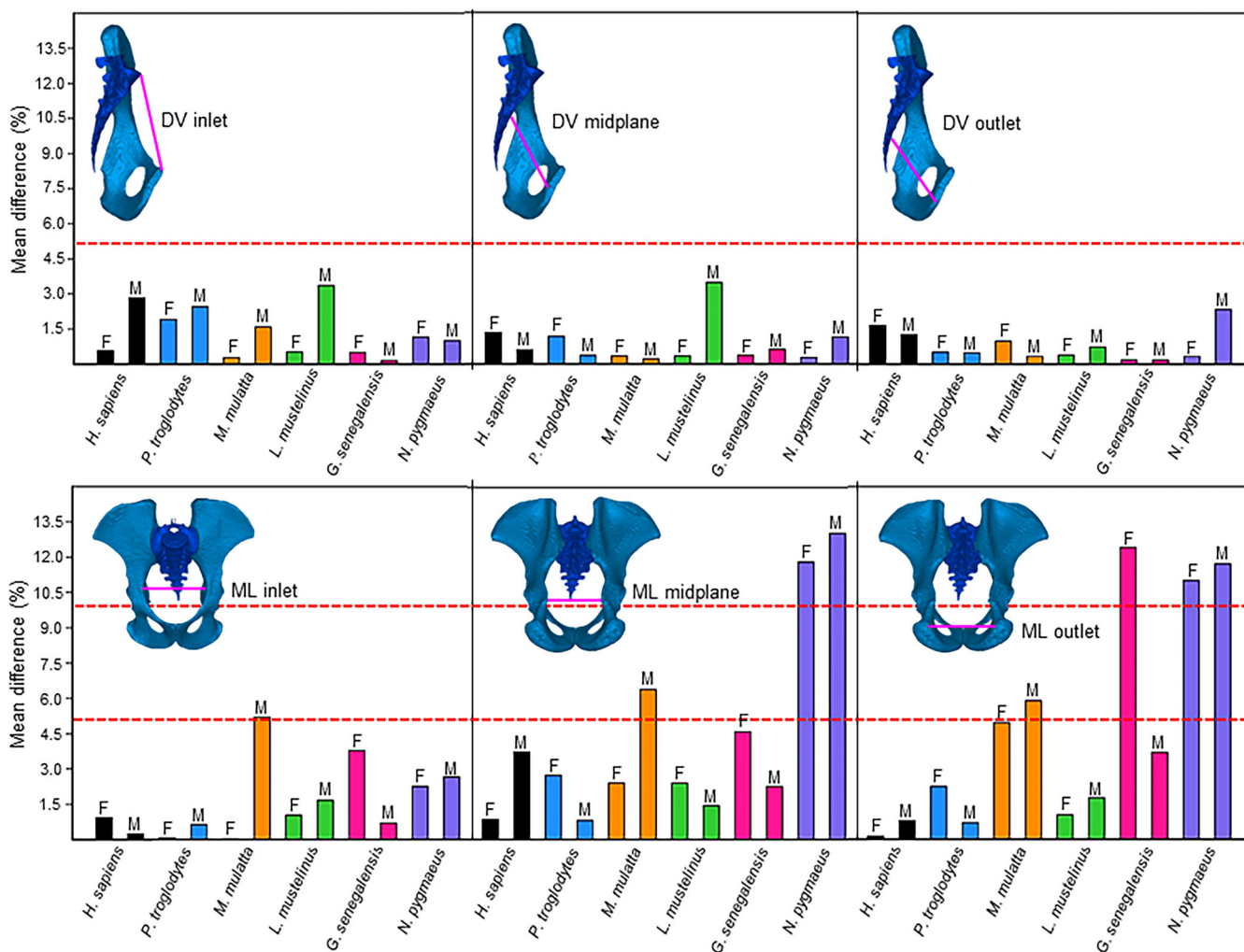


FIGURE 8 Bar charts showing percentual differences of the linear measurements between cadaveric and rearticulated pelvis. Dashed lines indicate mean differences of 5% for the dorso-ventral diameters and of 5% and 10% for the medio-lateral diameters. DV: dorso-ventral; ML: medio-lateral; F: female; M: male. The pelvis mesh used to illustrate the pelvic diameters belongs to the adult male *Pan troglodytes* individual Ypm Mam 015939 from the Vertebrate Zoology Division–Mammalogy, Yale Peabody Museum, available from Morphosource.

Interestingly, the medio-lateral midplane and outlet diameters show a remarkably high difference in the female individual of *G. senegalensis* and in the female and male individuals of *N. pygmaeus* compared to the other species (Table 3). The difference in the medio-lateral outlet diameter of female *G. senegalensis* is >10% and of female and male *N. pygmaeus* exhibit a difference of >10% for the medio-lateral diameters of the midplane and of the outlet. The fact that differences between cadaveric and rearticulated pelvises that are >10% are found only in the medio-lateral diameters of the caudal-most part of the pelvis (midplane and outlet) suggests that these diameters are more affected by the rearticulation error than the medio-lateral diameters of the cranial-most part of the pelvis and the dorso-ventral diameters. It is also worth noting that these larger differences are found in the smallest of the species in the sample, and that the ratio of skeletal element size to scan resolution may be a contributing factor.

4 | DISCUSSION

The current study represents the first assessment of the potential shape variation (both in 3D and in linear dimensions) introduced by the rearticulation of dry bones in primate comparative anatomy. Overall, the adopted protocol for virtual rearticulation of the two *ossa coxae* and the sacrum of primates leads to pelvic girdle reconstructions with a level of accuracy acceptable for most comparative studies. The error introduced by the rearticulation is relatively small and unlikely to substantially affect 3D shape analyses of intra-specific (sexual) or inter-specific variation.

The same is generally true for pelvic linear dimensions, although the process of rearticulation appears to have a disproportionately larger effect on medio-lateral pelvic measurements in those species with a relatively large pubic gap (Figure 2) and/or relatively small pubic body and small sacro-iliac articular surface (e.g., *G. senegalensis*, *N. pygmaeus*). It is possible that the wider flexibility of the girdle derived from the pubic gap and the short pubic body, along with the relatively small articular surfaces used to anchor the rearticulation of the three elements, are responsible for the higher error value and lead specifically to an underestimation of medio-lateral pelvic canal measurements. This error is nonetheless expected to be smaller than that resulting from alternative rearticulation strategies that do not leave any gap between the pubic bones (Kurki, 2007, 2011; Tague, 1989, 2000). It is worth noting that small sacro-iliac articular surfaces do not seem to affect the accuracy of the dorso-ventral measurements as much, suggesting that the reconstruction protocol outlined above reproduces the angle of the sacrum concerning the ilia well in all species.

4.1 | Implications of the potential rearticulation error in pelvis studies

The present results demonstrate that for the three anthropoid primate species (*H. sapiens*, *P. troglodytes*, and *M. mulatta*), the shape variation introduced by virtual rearticulation does not substantially affect 3D pelvic shape nor pelvic linear dimensions. These results are consistent with those reported previously for *H. sapiens* (Bonneau et al., 2012) and confirm that the pelvis can be reliably reconstructed in *P. troglodytes* and *M. mulatta*, species that are frequently used in studies of primate comparative anatomy (Buck et al., 2021; Fischer et al., 2021; Morimoto et al., 2023). The results also support the assumption of earlier comparative analyses that variation introduced by rearticulation of the separate dry osteological pelvic bones does not substantially affect the inter- or intra-specific signal in comparative 3D morphological studies. This in turn justifies the use of dry osteological material as rearticulated pelvises in future studies of functional morphology in extant anthropoid primates.

The situation might be different, however, for studies addressing morpho-functional questions in the bony pelvic girdle of strepsirrhines, especially when the aim is evaluating pelvic size and shape employing pelvic linear dimensions. The two small-bodied size strepsirrhines included in this study (*G. senegalensis* and *N. pygmaeus*) show substantial differences in the medio-lateral dimensions of the midplane and outlet when compared to their cadaveric counterparts. These are species in which there is a substantial pubic gap, particularly in females, and a relatively small pubic body and sacro-iliac articular surface; it is likely that the inaccuracies in reassembling the girdle derived from the difficulty in estimating the size of the pubic gap, together with the relatively small joint surfaces used to anchor the rearticulation of the three elements. This highlights the need for particular attention to pelvic rearticulation of species with these characteristics, where an underestimation of female pelvic size could ultimately lead to erroneous interpretations of pelvic sexual dimorphism (or lack thereof). Scans of cadaveric and/or living small-bodied strepsirrhines, where they are available, could help avoid this issue.

The reconstruction of extinct hominin pelvises might also be affected by this potential source of error, as all known fossil pelvises show a pubic gap. This may not be a serious issue, however, as the results above demonstrate that the relatively small degree of rearticulation error in humans does not seem to substantially obscure the biological intra-specific signal (Bonneau et al., 2012, and the present study). Given that the results above suggest that the relative size of the joint surfaces might affect how successful the rearticulation is, however, hominin species

with small sacro-iliac joint surfaces relative to the acetabular diameter, such as australopithecines (Berge & Kazmierczak, 1986; Kibii et al., 2011), might be more sensitive to this rearticulation process than humans and other hominins with relatively large pelvic joints. The frequent incompleteness, fragmentation, and distortion of the fossils are likely to add further uncertainty to the pelvic reconstruction that is probably more substantial than the error introduced by the rearticulation of the three pelvic bones.

These sorts of potential difficulties are highlighted by previous attempts to rearticulate the pelvis of the widely studied *Australopithecus afarensis* specimen A.L. 288-1, dated to 3.2 Ma from the Hadar region of Ethiopia (Johanson et al., 1982). Fossil preservation and differing reconstruction protocols and articulation criteria have resulted in alternative functional interpretations. The initial manual reconstruction of the A.L. 288-1 pelvis was performed without compensation for the soft-tissue of the sacro-iliac joint and the pubic symphysis (Lovejoy, 1979). A later (but still manual) effort resulted in a differently shaped birth canal, changing the functional interpretations of this pelvic shape in terms of birth rotation (Häusler & Schmid, 1995). A subsequent virtual reconstruction of the A.L. 288-1 pelvis, which included consideration of the associated soft tissues, resulted in a lower estimated body mass (Brassey et al., 2018), but has also been criticized for inadequately characterizing the sacroiliac articulation while maintaining adequate spacing for articular cartilage (Wiseman, 2023). These differing reconstructions of the pelvis of the same hominin specimen, used to make interpretations about obstetrics, body mass and locomotion, have almost certainly been affected by the potential error introduced by pelvis reconstruction and, indeed, were instigated on the basis of such assumed errors having affected previous reconstructions. The uncertainties affecting these reconstructions are not only rearticulation-based, as the distortion of the fossils may also have an impact on the resulting pelvis. While the incomplete and/or distorted fossils can be virtually restored using statistical reference-based techniques (Amano et al., 2022; Gunz et al., 2009; Weber & Bookstein, 2011; Zollikofer et al., 2005), rearticulation error still needs to be addressed to avoid adding further uncertainty to the already challenging fossil reconstruction process.

4.2 | Other considerations and conclusions

The repeated rearticulations carried out in this experiment did not model the soft tissue thickness of the sacroiliac and pubic symphysis joints, as there are no available

data of pelvic joint thickness for primate species, with the exception of *H. sapiens* (Li, 2002; Vleeming et al., 2012). The rearticulation was performed without simulating the presence of soft tissue at the sacro-iliac joint to maintain the protocol consistent across species and similar to the strategy used for isolated osteological remains. The study, however, allowed for an unspecified gap at the pubic symphysis, whose size was determined by the shape of the individual pelvis after articulation at the dorsal/posterior joints. This flexibility is essential, given the large variability in pubic gap size across and within species. While the results show an underestimation of medio-lateral pelvic diameters in rearticulated pelvis with a larger pubic gap, the directional bias towards smaller canal measurements would have been further exacerbated by the commonly employed strategy of always having the *osssa coxae* touch at the symphysis. This consideration is particularly important in studies of sexual dimorphism in the pelvic canal, in which sexual differences in canal diameters are interpreted as evidence of obstetric constraints in primates.

While the effect of the rearticulation error did not appear to overshadow individual/sexual differences within species, this rearticulation experiment was not intended to assess pelvic sexual dimorphism. One female and one male per species do not allow to estimate sexual shape dimorphism within the species, as differences between them are indistinguishable from inter-individual differences and might not be representative. To assess the extent to which the sexual dimorphic signal may be altered by the rearticulation process, it is necessary to re-evaluate these findings on larger sample sizes.

It should be noted that this study uses cadaveric specimens, which might not be fully accurate models of the specimens during life due to postmortem alteration of the soft tissues. Different types of body preservation (e.g., frozen bodies, bodies preserved in formalin) likely alter the soft tissue, although the extent of such changes is unclear, especially in the pelvis. It is also important to note that this study assesses the rearticulation error introduced by the same observer (intra-observer error) but does not evaluate potential errors introduced by different observers (inter-observer error). In the case of multiple observers, it can be expected that inter-observer error will affect both the articulation and the landmarking process (Chollet et al., 2014; Robinson & Terhune, 2017). So, this protocol of error assessment should be complemented with an error study between observers, that is, another researcher(s) with pelvic anatomy experience should attempt to rearticulate the pelvic bones to see if/how this affects the results. Finally, while this study has relevance for manual rearticulations of osteological specimens, especially in supporting the role of the sacro-iliac joint as

the anchor of the pelvic reconstruction and the importance of leaving the pubic gap flexible instead of forcingly close it, it should be stressed that the results reported are for digital articulations and cannot be directly translated for physical rearticulations.

In summary, this study establishes an accessible protocol to test the reliability of the intra-observer rearticulation of osteological primate pelves in comparative morphological studies, that can be extended to other species. The results show that, although the 3D shape of the pelvis does not seem markedly affected by the rearticulation, the medio-lateral pelvic linear dimensions of small-bodied species with relatively small articular surfaces and a wide pubic gap can be underestimated. To avoid the uncertainties of pelvic rearticulation in such species, (a) anatomically connected pelves can (and perhaps should) be included, but care should be taken for specimens with dried soft tissue that is likely to have shrunk and to have reduced any existing pubic gap, or (b) specimens should be CT scanned as the highest resolution possible to maximize accuracy in the rearticulation process. Finally, the described protocol can be adapted to other anatomical structures that require manual rearticulation to be analyzed in anatomical connection, such as the vertebral column or the articulation of the cranium and the mandible.

AUTHOR CONTRIBUTIONS

Nicole Torres-Tamayo: Conceptualization; investigation; methodology; writing – original draft; writing – review and editing; formal analysis; data curation; visualization. **Todd C. Rae:** Conceptualization; investigation; funding acquisition; validation; writing – review and editing; supervision; project administration; visualization; data curation; resources. **Eishi Hirasaki:** Writing – review and editing; data curation; resources; validation; visualization. **Lia Betti:** Conceptualization; investigation; funding acquisition; writing – review and editing; project administration; supervision; visualization; data curation; resources.

ACKNOWLEDGMENTS

This study was funded by a Great Britain Sasakawa Foundation (B130), a Leverhulme Trust Project grant (RPG-2021-130), and the Kyoto University Cooperative Research Programme Award. We are grateful to Steven Heritage and Amanda Mazza (Duke Lemur Center, USA), Laura T. Buck (University of Liverpool, UK), Yuki Kinoshita (Kyoto University, Japan), the Duke Lemur Center (Durham, NC, USA), the Rhesus Macaque Admixture Project of the California National Primate Research Center (University of California, Davis, USA), the Izu Shaboten Zoo (Shizuoka, Japan), the Great Ape Information Network (GAIN), and the Digital Morphology Museum of the now-defunct Kyoto University

Primate Research Institute, Morphosource (<https://www.morphosource.org/>) and the New Mexico Decedent Image Database (<https://nmdid.unm.edu/>) for providing access to the information and material included in this study. We also thank Noel Rowe, Marc Myers, All The World's Primates (<https://www.alltheworldsprimates.org/>), Sara Sorraia, David Haring, the Duke Lemur Center and Lemurs of Madagascar (<http://lemursofmadagascar.com/>) for generously sharing photographs of primates to compose Figure 1. Many thanks to C. Owen Lovejoy (Kent State University, USA) and Martin Haeusler (University of Zürich, Switzerland) for providing technical details of their reconstructions of A.L. 288-1 and Sts 14 pelves, and Kristi L. Lewton (University of Southern California, USA) for constructive feedback about the anatomy of the primate pelvis. We are grateful to Ashley Hammond (American Museum of Natural History, USA) and an anonymous reviewer for the time they invested to help improve this manuscript. Finally, we want to say thanks to Carla San Román (Universidad Autónoma de Madrid) for assisting in the figures formatting.

DATA AVAILABILITY STATEMENT

All the procedures can be performed in open-source software and all the necessary data and scripts are available in this publication, making the protocol reproducible and replicable by everybody interested in testing the effect of this potential source of error in their studies. The segmented 3D models used in this study (with the exception of that of the female chimpanzee Koko, see below), as well as the landmark coordinates collected on these 3D models and the R-scripts used to perform the analyses are available in Open Science Framework (<https://osf.io/69nvq/>). The CT data have not been made openly available in OSF as these data are easily accessible through the corresponding institution and/or online repository. For anyone interested in getting access to the CT scans, the sample composition and relevant institutions/repositories of provenance are detailed in Supplementary Table S1. Regarding the *Pan troglodytes* female Koko, unrestricted distribution of the CT scan and the 3D model to third parties is not allowed by the Center for the Evolutionary Origins of Human Behavior (EHUB), Kyoto University. To get access to these data, please, contact the corresponding author and/or the co-author Dr. Eishi Hirasaki (hirasaki.eishi.6x@kyoto-u.ac.jp).

ORCID

Nicole Torres-Tamayo  <https://orcid.org/0000-0003-2504-3886>

Todd C. Rae  <https://orcid.org/0000-0002-4010-5945>

Eishi Hirasaki  <https://orcid.org/0000-0001-7849-1936>

Lia Betti  <https://orcid.org/0000-0003-2895-9718>

REFERENCES

- Abitbol, M. M. (1988). Evolution of the ischial spine and of the pelvic floor in the Hominoidea. *American Journal of Physical Anthropology*, 75(1), 53–67.
- Adams, D. C., Collyer, M. L., Kaliontzopoulou, A., & Baken, E. K. (2022). Geomorph: Software for geometric morphometric analyses. R Package Version 4.0.4. <https://cran.r-project.org/package=geomorph>
- Adegboyega, M. T., Stamos, P. A., Hublin, J. J., & Weaver, T. D. (2021). Virtual reconstruction of the Kebara 2 Neanderthal pelvis. *Journal of Human Evolution*, 151, 102922.
- Amano, H., Rae, T., Tsoukala, E., Nakatsukasa, M., & Ogiyama, N. (2022). Computerized restoration of a fossil cranium based on selective elimination of estimated taphonomic deformation. *American Journal of Biological Anthropology*, 178, 448–460.
- Berge, C., & Goullaras, D. (2010). A new reconstruction of Sts 14 pelvis (*Australopithecus africanus*) from computed tomography and three-dimensional modeling techniques. *Journal of Human Evolution*, 58(3), 262–272.
- Berge, C., & Kazmierczak, J. (1986). Effects of size and locomotor adaptations on the hominid pelvis: Evaluation of australopithecine bipedality with a new multivariate method. *Folia Primatologica*, 46(4), 185–204.
- Betti, L., von Cramon-Taubadel, N., Manica, A., & Lycett, S. J. (2013). Global geometric morphometric analyses of the human pelvis reveal substantial neutral population history effects, even across sexes. *PLoS One*, 8(2), e55909.
- Bonneau, N., Bouhallier, J., Simonis, C., Baylac, M., Gagey, O., & Tardieu, C. (2012). Shape variability induced by reassembly of human pelvic bones. *American Journal of Physical Anthropology*, 148(1), 139–147.
- Brassey, C. A., O'Mahoney, T. G., Chamberlain, A. T., & Sellers, W. I. (2018). A volumetric technique for fossil body mass estimation applied to *Australopithecus afarensis*. *Journal of Human Evolution*, 115, 47–64.
- Broek, A. J. (1911). Ueber Geschlechtsunterschiede im Becken bei Primaten Archiv für Anatomie und Physiologie. *Biodiversity Heritage Library*, 21, 163–184.
- Brynskog, E., Iraeus, J., Reed, M. P., & Davidsson, J. (2021). Predicting pelvis geometry using a morphometric model with overall anthropometric variables. *Journal of Biomechanics*, 126, 110633.
- Buck, L. T., Katz, D. C., Ackermann, R. R., Hlusko, L. J., Kanthaswamy, S., & Weaver, T. D. (2021). Effects of hybridization on pelvic morphology: A macaque model. *Journal of Human Evolution*, 159, 103049.
- Casteleyn, C., Bakker, J., Breugelmans, S., Kondova, I., Saunders, J., Langermans, J. A. M., Cornillie, P., Van den Broeck, W., Van Loo, D., Van Hoorebeke, L., Bosseler, L., Chiers, K., & Decostere, A. (2012). Anatomical description and morphometry of the skeleton of the common marmoset (*Callithrix jacchus*). *Laboratory Animals*, 48, 152–163.
- Chollet, M. B., Aldridge, K., Pangborn, N., Weinberg, S. M., & DeLeon, V. B. (2014). Landmarking the brain for geometric morphometric analysis: An error study. *PLoS One*, 9(1), e86005.
- Claxton, A. G., Hammond, A. S., Romano, J., Oleinik, E., & DeSilva, J. M. (2016). Virtual reconstruction of the *Australopithecus africanus* pelvis Sts 65 with implications for obstetrics and locomotion. *Journal of Human Evolution*, 99, 10–24.
- Collyer, M. L., & Adams, D. C. (2018). RRPP: An R package for fitting linear models to high-dimensional data using residual randomization. *Methods in Ecology and Evolution*, 9(2), 1772–1779.
- Dar, G., Khamis, S., Peleg, S., Masharawi, Y., Steinberg, N., Peled, N., & Hershkovitz, I. (2008). Sacroiliac joint fusion and the implications for manual therapy diagnosis and treatment. *Manual Therapy*, 13(2), 155–158.
- Fischer, B., Grunstra, N. D., Zaffarini, E., & Mitteroecker, P. (2021). Sex differences in the pelvis did not evolve de novo in modern humans. *Nature Ecology & Evolution*, 5(5), 625–630.
- Gardner, W. U., & van Heuverswyn, J. (1940). Inhibition of pelvic changes occurring during pregnancy in mice by testosterone propionate. *Endocrinology*, 26, 833–836.
- Gower, J. C. (1975). Generalized Procrustes analysis. *Psychometrika*, 40, 33–51.
- Gunz, P., Mitteroecker, P., Neubauer, S., Weber, G. W., & Bookstein, F. L. (2009). Principles for the virtual reconstruction of hominin crania. *Journal of Human Evolution*, 57(1), 48–62.
- Hammer, O., Harper, D. A. T., & Ryan, P. D. (2001). Past: Paleontological statistics software package for education and data analysis. *Paleontologia Electronica*, 4(1), 1–9.
- Hammond, A. S., Plavcan, J. M., & Ward, C. V. (2016). A validated method for modelling anthropoid hip abduction in silico. *American Journal of Physical Anthropology*, 160(3), 529–548.
- Häusler, M., & Schmid, P. (1995). Comparison of the pelvis of Sts 14 and AL288-1: Implications for birth and sexual dimorphism in australopithecines. *Journal of Human Evolution*, 29(4), 363–383.
- Huseynov, A., Ponce de León, M. S., & Zollikofer, C. P. (2017). Development of modular organization in the chimpanzee pelvis. *The Anatomical Record*, 300(4), 675–686.
- Huseynov, A., Zollikofer, C. P., Coudyzer, W., Gascho, D., Kellenberger, C., Hinzpeter, R., & Ponce de León, M. S. (2016). Developmental evidence for obstetric adaptation of the human female pelvis. *Proceedings of the National Academy of Sciences of the United States of America*, 113(19), 5227–5232.
- Johanson, D. C., Lovejoy, C. O., Kimbel, W. H., White, T. D., Ward, S. C., Bush, M. E., Latimer, B. M., & Coppens, Y. (1982). Morphology of the Pliocene partial hominid skeleton (AL 288-1) from the Hadar formation, Ethiopia. *American Journal of Physical Anthropology*, 57(4), 403–451.
- Kawada, M., Nakatsukasa, M., Nishimura, T., Kaneko, A., & Morimoto, N. (2020). Covariation of fetal skull and maternal pelvis during the perinatal period in rhesus macaques and evolution of childbirth in primates. *Proceedings of the National Academy of Sciences of the United States of America*, 117(35), 21251–21257.
- Kibii, J. M., Churchill, S. E., Schmid, P., Carlson, K. J., Reed, N. D., De Ruiter, D. J., & Berger, L. R. (2011). A partial pelvis of *Australopithecus sediba*. *Science*, 333(6048), 1407–1411.
- Kikinis, R., Pieper, S. D., & Vosburgh, K. G. (2013). 3D slicer: A platform for subject-specific image analysis, visualization, and clinical support. In *Intraoperative imaging and image-guided therapy* (pp. 277–289). Springer.
- Kohn, L. A. P., & Lubach, G. R. (2019). Postcranial skeletal differences in free-range and captive-born primates. *The Anatomical Record*, 302(5), 761–774.
- Kubicka, A. M. (2023). Changes in plasticity of the pelvic girdle from infancy to late adulthood in *Homo sapiens*. *Scientific Reports*, 13(1), 1–8.
- Kurki, H. K. (2007). Protection of obstetric dimensions in a small-bodied human sample. *American Journal of Physical Anthropology*, 133(4), 1152–1165.

- Kurki, H. K. (2011). Pelvic dimorphism in relation to body size and body size dimorphism in humans. *Journal of Human Evolution*, 61(6), 631–643.
- Laudicina, N. M., & Cartmill, M. (2023). Bony birth-canal dimensions and obstetric constraints in hominoids. *American Journal of Biological Anthropology*, 180(3), 442–452.
- Laudicina, N. M., Rodriguez, F., & DeSilva, J. M. (2019). Reconstructing birth in *Australopithecus sediba*. *PLoS One*, 14(9), e0221871.
- Leutenegger, W. (1974). Functional aspects of pelvic morphology in simian primates. *Journal of Human Evolution*, 3, 207–222.
- Lewton, K. L. (2010). *Locomotor function and the evolution of the primate pelvis (PhD Dissertation)*. Arizona State University.
- Lewton, K. L. (2015a). Allometric scaling and locomotor function in the primate pelvis. *American Journal of Physical Anthropology*, 156(4), 511–530.
- Lewton, K. L. (2015b). Pelvic form and locomotor adaptation in strepsirrhine primates. *The Anatomical Record*, 298(1), 230–248.
- Lewton, K. L. (2022). An integrative approach to examining the influences of size, phylogeny, and locomotion on os coxae shape variation in primates. *American Journal of Biological Anthropology*. <https://doi.org/10.1002/ajpa.24665>
- Li, Y. (2002). *Postnatal development of pelvic sexual dimorphism in four anthropoid primates (PhD Dissertation)*. The Johns Hopkins University.
- Lovejoy, C. O. (1979). A reconstruction of the pelvis of A.L. 288-1 (Hadar Formation, Ethiopia). *American Journal of Physical Anthropology*, 50, 460.
- Lovejoy, C. O. (2005). The natural history of human gait and posture: Part 1. Spine and pelvis. *Gait and Posture*, 21(1), 95–112.
- Mitteroecker, P., & Gunz, P. (2009). Advances in geometric morphometrics. *Evolutionary Biology*, 36, 235–247.
- Mobb, G. E., & Wood, B. A. (1997). Allometry and sexual dimorphism in the primate innominate bone. *American Journal of Anatomy*, 150(4), 531–537.
- Moffett, E. A. (2017). Dimorphism in the size and shape of the birth canal across anthropoid primates. *The Anatomical Record*, 300(5), 870–889.
- Morimoto, N., Kawada, M., Tomizawa, Y., Kaneko, A., & Nishimura, T. (2023). Pelvic shape change in adult Japanese macaques and implications for childbirth at old age. *Proceedings of the National Academy of Sciences of the United States of America*, 120(30), e2300714120.
- R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing <https://www.R-project.org/>
- Robinson, C., & Terhune, C. E. (2017). Error in geometric morphometric data collection: Combining data from multiple sources. *American Journal of Physical Anthropology*, 164(1), 62–75.
- Schlager, S. (2017). Morpho and Rvcg-shape analysis in R. In G. Zheng, S. Li, & G. Székely (Eds.), *Statistical shape and deformation analysis* (pp. 217–256). Academic Press.
- Schultz, A. H. (1949). Sex differences in the pelvis of primates. *American Journal of Physical Anthropology*, 7(3), 401–424.
- Schwarz, G., & Schwarz, G. S. (1966). Noninfectious symphyseal bridging and pseudo-marsupial bones. *American Journal of Roentgenology*, 97(3), 687–692.
- Simpson, S. W., Quade, J., Levin, N. E., Butler, R., Dupont-Nivet, G., Everett, M., & Semaw, S. (2008). A female *Homo erectus* pelvis from Gona, Ethiopia. *Science*, 322(5904), 1089–1092.
- Starrach, T., Schmidhuber, L., Elger, L., Franz, M., Buechel, J., Hübener, C., Kolben T., Koliogiannis V., Mahner S., Hasbargen U., & Fischer, B. (2023). Pelvic inlet area is associated with birth mode. *Acta Obstetrica et Gynecologica Scandinavica*, 102(1), 59–66.
- Stolarczyk, A., Stępiński, P., Sasinowski, Ł., Czarnocki, T., Dębiński, M., & Maciag, B. (2021). Peripartum pubic symphysis diastasis-practical guidelines. *Journal of Clinical Medicine*, 10(11), 2443.
- Tague, R. G. (1989). Variation in pelvic size between males and females. *American Journal of Physical Anthropology*, 80(1), 59–71.
- Tague, R. G. (1993). Pubic symphyseal synostosis and sexual dimorphism of the pelvis in *Presbytis cristata* and *Presbytis rubicunda*. *International Journal of Primatology*, 14, 637–654.
- Tague, R. G. (2000). Do big females have big pelvises? *American Journal of Physical Anthropology*, 112(3), 377–393.
- Todd, T. W. (1921). Age changes in the pubic bone. V. Mammalian pubic metamorphosis. *American Journal of Physical Anthropology*, 4, 333–406.
- Torres-Tamayo, N., García-Martínez, D., Nalla, S., Barash, A., Williams, S. A., Blanco-Pérez, E., Mata-Escolano, F., Sanchis-Gimeno, J. A., & Bastir, M. (2018). The torso integration hypothesis revisited in *Homo sapiens*: Contributions to the understanding of hominin body shape evolution. *American Journal of Physical Anthropology*, 167(4), 777–790.
- Torres-Tamayo, N., Martelli, S., Schlager, S., García-Martínez, D., Sanchis-Gimeno, J. A., Mata Escolano, F., Nalla, S., Ogihara, N., Oishi, M., & Bastir, M. (2020). Assessing thoraco-pelvic covariation in *Homo sapiens* and *Pan troglodytes*: A 3D geometric morphometric approach. *American Journal of Physical Anthropology*, 173, 514–534.
- Torres-Tamayo, N., Schlager, S., García-Martínez, D., Sanchis-Gimeno, J. A., Nalla, S., Ogihara, N., Oishi, M., Martelli, S., & Bastir, M. (2020). 3D geometric morphometrics of thorax-pelvis covariation and its potential for predicting the thorax morphology: A case study on Kebara 2 neandertal. *Journal of Human Evolution*, 147, 102893.
- Tyson, E. (1699). Orang-outang sive *Homo sylvestris*: or The Anatomy of a Pygmie compared with that of a Monkey, an Ape, and a Man. <https://archive.org/details/orangoutangsiveh00tyso/page/n19>
- Uy, J., & Laudicina, N. M. (2021). Assessing the role of the pelvic canal in supporting the gut in humans. *PLoS One*, 16(10), e0258341.
- Vleeming, A., Schuenke, M. D., Masi, A. T., Carreiro, J. E., Danneels, L., & Willard, F. H. (2012). The sacroiliac joint: An overview of its anatomy, function and potential clinical implications. *Journal of Anatomy*, 221(6), 537–567.
- Waltenberger, L., Rebay-Salisbury, K., & Mitteroecker, P. (2022). Are parturition scars truly signs of birth? The estimation of parity in a well-documented modern sample. *International Journal of Osteoarchaeology*, 32(3), 619–629.
- Ward, C. V., Maddux, S. D., & Middleton, E. R. (2018). Three-dimensional anatomy of the anthropoid bony pelvis. *American Journal of Physical Anthropology*, 166(1), 3–25.

- Weaver, T. D., & Hublin, J. J. (2009). Neandertal birth canal shape and the evolution of human childbirth. *Proceedings of the National Academy of Sciences*, *106*(20), 8151–8156.
- Weber, G. W., & Bookstein, F. L. (2011). *Virtual anthropology: A guide to a new interdisciplinary field*. Springer.
- Wiseman, A. L. (2023). Three-dimensional volumetric muscle reconstruction of the *Australopithecus afarensis* pelvis and limb, with estimations of limb leverage. *Royal Society Open Science*, *10*(6), 230356.
- Wood, B. A., & Chamberlain, A. T. (1986). The primate pelvis: Allometry or sexual dimorphism? *Journal of Human Evolution*, *15*(4), 257–263.
- Zollikofer, C. P. E., de León, M. S. P., Lieberman, D. E., Guy, F., Pilbeam, D., Likius, A., Mackaye, H. T., Vignaud, P., & Brunet, M. (2005). Virtual cranial reconstruction of *Sahelanthropus tchadensis*. *Nature*, *434*(7034), 755–759.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Torres-Tamayo, N., Rae, T. C., Hirasaki, E., & Betti, L. (2023). Testing the reliability of the rearticulation of osteological primate pelves in comparative morphological studies. *The Anatomical Record*, 1–18. <https://doi.org/10.1002/ar.25366>