

Global Geometric Morphometric Analyses of the Human Pelvis Reveal Substantial Neutral Population History Effects, Even across Sexes

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Abstract

Recent applications of population genetic models to human craniodental traits have revealed a strong neutral component to patterns of global variation. However, little work has been undertaken to determine whether neutral processes might also be influencing the postcranium, perhaps due to substantial evidence for selection and plastic environmental responses in these regions. Recent work has provided evidence for neutral effects in the pelvis, but has been limited in regard to shape data (small numbers of linear measurements) and restricted only to males. Here, we use geometric morphometric methods to examine population variation in the human os coxae (pelvic bone) in both males and females. Neutrality is examined via apportionment of variance patterns and fit to an Out-of-Africa serial founder effect model, which is known to structure neutral genetic patterns. Moreover, we compare males and females directly, and the true versus false pelvis, in order to examine potential obstetrical effects. Our results indicate evidence for substantial neutral population history effects on pelvic shape variation. They also reveal evidence for the effect of obstetrical constraints, but these affect males and females to equivalent extents. Our results do not deny an important role for selection in regard to specific aspects of human pelvic variation, especially in terms of features associated with body size and proportions. However, our analyses demonstrate that at a global level, the shape of the os coxae reveals substantial evidence for neutral variation. Our analyses thus indicate that population variation in the human pelvis might be used to address important questions concerning population history, just as the human cranium has done.

Citation: Betti L, von Cramon-Taubadel N, Manica A, Lycett SJ (2013) Global Geometric Morphometric Analyses of the Human Pelvis Reveal Substantial Neutral Population History Effects, Even across Sexes. PLoS ONE 8(2): e55909. doi:10.1371/journal.pone.0055909

Editor: John H. Relethford, State University of New York College at Oneonta, United States of America

Received: November 5, 2012; **Accepted:** January 3, 2013; **Published:** February 7, 2013

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Funding: This study was funded by the Wenner-Gren Foundation for Anthropological Research (<http://www.wennergren.org/>, fieldwork dissertation grant #8289), a Ian and Christine Bolt scholarship from the University of Kent (http://www.kent.ac.uk/scholarships/postgraduate/christine_bolt.html), Sigma Xi (<http://www.sigmaxi.org/>, grant G20100315153260), two grants from the SYNTHESYS Project (<http://www.synthesys.info/>) which is financed by European Community Research Infrastructure Action under the FP7 "Capacities" Program, the American Museum of Natural History (<http://www.amnh.org/>, collection study grant), and a University of Kent Ph.D. research scholarship. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

In recent years, the study of human morphological variation has seen a shift of attention from mainly selective processes to the neutral component of shape variation (i.e., due to genetic drift and migration) [1]. Most of this work has been carried out on craniodental traits, showing how variation in cranial and dental morphology largely mirrors neutral genotypic variation in modern human populations (e.g., [2–14]). Neutrality of cranial variation at a global level has been inferred on the basis of three main approaches [15]: examination of the apportionment of phenotypic variance at different geographic levels, directly comparing phenotypic distance to neutral genetic distance, and testing for the preservation of serial founder events which occurred during the expansion of our species out of Africa.

Lewontin [16] was the first to describe the apportionment of genetic variance within human populations and between major geographic regions. Specifically, he showed how the large majority of human genetic diversity is present at the local population level (~85%), while only about 6% of variation separates what had

conventionally been conceived of as the major “racial” groups [16]. The same method has since been applied to a range of neutral genetic markers (e.g., [17,18]) and to craniometric variation, confirming the same general apportionment pattern [2,3,7]. Conversely, it has been shown that traits under selection, for example human skin color variation, tend to have relatively small within-population diversity (~9%), while most of the variation lies between populations and between geographic regions [3]. Therefore, despite the fact that the microevolutionary significance of Lewontin’s findings may have been overstated (e.g., [19–21]), variance apportionment patterns do distinguish effectively between largely neutrally evolving phenotypes, such as human cranial shape, and strongly selected phenotypes, such as human skin color.

Direct comparison of genetic and phenotypic distances between populations also confirmed a substantial neutral signal in cranial variation [6,8,9,13,14,22,23]. Moreover, cranial differences between human populations were shown to follow the same Isolation By Distance (IBD) pattern previously described for genetic

distance [24,25], whereby a decrease of genetic and phenotypic similarity between pairs of populations accompanies increasing geographic separation, due to reduced gene flow over larger distances [4,26].

Finally, within-population cranial diversity, like genetic diversity, reveals a clear signature of the expansion of the human species out of the African continent. Genetic diversity (heterozygosity) was shown to decrease with increasing distance from sub-Saharan Africa, a pattern that has been explained as the signature of serial founder events that accompanied the colonization of other continents [27–29]. Subsamples of established populations would move to new areas, founding new communities that would in time be the origin of further expansion by a new sub-population. With each founding event, some genetic diversity is lost at random, creating the described worldwide pattern. The presence of the same, if somewhat weaker, signature in craniodental variation is additional evidence of the overall neutrality of cranial variation [10–12,30].

Only very recently has the same interest in neutral processes shaping human variation been extended to the postcranium [31], where variation in different populations has otherwise been addressed mainly in terms of selection and plastic reactions to the environment (e.g., [32–38]). Betti et al. [31] showed how various regions of the postcranium, specifically the pelvis and long bones, reflect differently the signature of the Out-of-Africa (OoA) expansion. In particular, the pelvis, like the cranium, reveals a clear signature of the past population expansion, while the pattern is absent in long bones, which in turn seem to be affected by climate. The preservation of the signature of ancient demographic events in the pelvis, as for the cranium, suggests a substantial fit to a neutral model of phenotypic variation in this anatomical region.

The shape of the pelvis has long been the focus of attention of paleoanthropologists (e.g. [39–49]), as well as physical anthropologists interested in modern human biology and variation (e.g., [33,50–56]). Being involved in two fundamental activities, locomotion and childbirth, the pelvis is under complex and conflicting constraints, often referred to as the obstetrical dilemma [57–59]. While bipedal locomotion privileges narrow pelvises, parturition of a large-brained neonate requires that the birth canal be wide enough to allow the passage of the skull. These conflicting factors led to a close fit between the size of the modern human birth canal and the neonate skull which is absent in other apes, accompanied by increased danger of complications during childbirth. This problem may also additionally be confounded by climatic adaptation in humans [48]. Indeed, there is evidence that climate independently affected the form of the pelvis following the colonization of high latitude regions by modern humans. Various studies have found that human populations living in colder climates have relatively wider pelvises that help reduce heat loss by decreasing the surface-to-volume ratio of the body [32,33,35,48,60]. Acetabular diameter is also related to body mass [61,62] and, therefore, could also be subject to climatic adaptation via Bergmann's [63] rule.

Despite the large body of literature suggesting that selection and evolutionary constraints have affected the morphology of the human pelvis, the results of Betti et al. [31] clearly point to the persistence of a neutral signal, related to population history, in pelvic shape variation that has not been completely erased by selection. However, such results were obtained with a less than ideal dataset, with strong limitations in respect to shape representation (only three pelvic measurements) and in the absence of female individuals for a comparison between the sexes. Hence, further and more detailed testing of the neutral model is warranted.

In this study, in the absence of matched genetic samples for our phenotypic data, the fit to a neutral model for global shape variation in the human pelvis will be assessed via two of the aforementioned methods. The presence of the Out-of-Africa (OoA) demographic signature on the pelvis will be examined in greater detail and in both sexes, on a dataset compiled to maximize shape definition (using 3D morphometric data of the os coxae) and to better represent global variation (larger and a more homogeneous distribution of population samples). These data also facilitate a methodological comparison of 3D geometric (landmark) data versus inter-landmark distance data in addressing questions of this type. Additionally, an overview of the apportionment of variance will also be carried out, in order to evaluate whether global patterns of within- and between-population pelvic shape variation apportion in a similar way to neutrally evolving genotypes/phenotypes or to non-neutral phenotypes such as human skin color variation.

In addition, we also consider the possible confounding effect of obstetrical constraints on neutral variation. Obstetrical constraints may have a direct effect on internal population variance due to strong stabilizing selection [64], whose effect is to reduce genetic and phenotypic variance. For instance, Kurki [65] has shown that in populations characterized by small body size, females retain similar dimensions of the birth canal as in larger-bodied populations. This suggests that some obstetrical dimensions are evolutionary protected and preserved, thus helping maintain viable canal dimensions in small-size populations. Indeed, complications during parturition are expected to have a considerable direct effect on the fitness of a woman, which would be decreased *in primis* by her death, but also by the death or parturition-induced disabilities of the newborn [64,65]. Given the potential strength of the selective pressure acting on the pelvis, we can expect that obstetrical constraints might affect the shape of the os coxae, reducing within-population variability, at least in females. Obstetrical constraints may be expected to act mainly on the area of the birth canal, and in general on what is often referred to as the “true pelvis” (e.g., [66]). The cavity of the pelvis is in fact often divided into two areas: the “true pelvis” (or “lesser pelvis”), which includes the space internal to the pelvic girdle situated below the pelvic brim, and the “false pelvis” (or “greater pelvis”), which includes the internal pelvic space above the pelvic brim (Figure 1). The part of the os coxae that contributes to the true pelvis might, therefore, be under stronger constraints than the part not directly involved in parturition (false pelvis). The presence of such constraints could, therefore, decrease the strength of the neutral pattern in the female phenotype, particularly in the true pelvis. We test these predictions here by comparing male and female pelvic shape in terms of relative goodness of fit to the serial founder effect (OoA) model, both in terms of overall pelvic shape, and in terms of two alternative landmark configurations that deliberately differ in respect to coverage of the true pelvis versus the false pelvis.

Materials and Methods

Morphometric data for the os coxae were collected by one of us (LB) in 1,443 adult individuals, 891 males and 552 females, curated at several osteological collections (Table 1). Only individuals whose iliac crest was completely fused were measured in this study. The dataset comprises 27 male and 20 female globally distributed population samples, with a minimum sample size of 16 individuals per population, and an average sample size of 33 and 27.6 individuals for males and females, respectively.

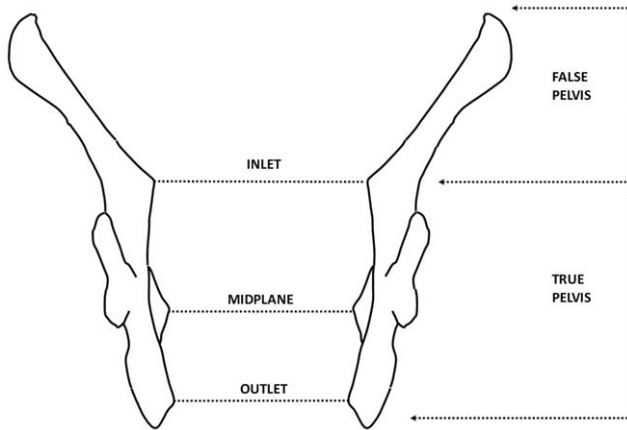


Figure 1. Diagram of the true and false pelvis. Inlet, midplane and outlet refer to the different planes of the birth canal (figure redrawn after [51,65,66]).

doi:10.1371/journal.pone.0055909.g001

Sex of the individuals, whenever unknown, was assessed visually by LB following standard non-metric methods [67–69]. The morphometric data consist of a set of 27 landmarks on the os coxae (Figure 2, Table 2), obtained using an Immersion 3D Microscribe digitizer. The data were collected unilaterally, for the best preserved side (i.e. complete), allowing inclusion of individuals with an incomplete preservation of the entire pelvic girdle. The set of landmarks was specifically designed to represent the complex shape of the os coxae and minimize inter-observer error. Five repeat measurements of all landmarks were performed on three os coxae from different individuals, and landmarks associated with a standard deviation over 1 mm were excluded [70]. Differences in position, rotation and size between individual configurations were corrected by generalized Procrustes superimposition [71–74] in Morphologika 2.5 [75], in males and females separately. The centroid size for each os coxae configuration was retrieved after the superimposition. New morphometric variables in the form of Principal Component (PC) scores were extracted from the whole 3D configuration of the os coxae by performing a Principal Component Analysis (PCA) in tangent shape space on the covariance matrix of the Procrustes coordinates. The obtained PC scores, representing 100% of the total shape variance, were used as morphometric data in the following analyses.

Accuracy of Visual Sex Determination

Visual methods of sex assessment were developed originally mainly for individuals of European ancestry, and their efficacy in individuals from different continents is largely unknown. In order to test for the accuracy of visual determination of sex in the global dataset under study, a specific test was developed using the available 3D data. Male and female individuals were pooled together and subjected to full Procrustes superimposition. Discriminant analysis was run in R version 2.14 [76] on the PC scores of a subset of the individuals (169 males and 165 females) of known sex obtained from forensic or cemetery collections (Table 3, DB1). The selected individuals were chosen from populations of different continents, in order to represent ethnic and geographic variation. The resulting discriminant function was applied separately to the remaining individuals of known sex available in the dataset (Table 3, DB2), and to all individuals whose sex had been visually estimated (Table 3, DB3). The results of the discriminant function were compared to the actual sex of one

Table 1. Population samples and institutions where material is hosted.

| Region | Males | Females | Institution |
|-------------------------------|-------|---------|-------------------------|
| <i>Africa</i> | | | |
| Botswana, Tswana | 33 | 30 | UW |
| Egypt dynastic | 34 | 17 | AMNH, NM |
| Kenya, Kykuyu | 40 | 30 | NMK |
| Lesotho, Sotho | | 34 | UW |
| Malawi | 33 | | UW |
| Nubia | 33 | 25 | NM |
| South Africa, Khoi-San | 26 | 21 | AMNH, MGM, NHM, UW |
| South Africa, Venda | 29 | | UW |
| Swaziland | 39 | 20 | UW |
| <i>Europe</i> | | | |
| Austria | 70 | 16 | CMNH, NM |
| France | 28 | 23 | MdH |
| Ireland | 28 | | CMNH |
| Italy | 33 | | CMNH, MNdAE |
| Portugal | 42 | 42 | CU |
| Western Russia | 26 | | CMNH |
| <i>Asia</i> | | | |
| Ainu, Japan | 23 | 20 | KU, TU |
| India | 28 | | AMNH, MdH, MoM, NHM, UW |
| Iran | 32 | 22 | UP |
| Japan | 45 | 37 | AMNH, KU, MdH, NH |
| Thailand | 37 | 36 | CMU, MdH |
| <i>America</i> | | | |
| Alaska, Point Hope | 38 | 35 | AMNH |
| Argentina, Patagonia | 33 | 23 | MdH, MNdAE |
| Canada, Sadiermiut | 24 | 24 | MCC |
| Chile, Fuegians | 17 | | MNdAE, NHM, UR |
| Native Californians | 36 | 31 | UCB |
| Peru | 31 | 33 | MdH, UCB |
| South Dakota, Arikara | 35 | 33 | UTK |
| Tennessee, Late Mississippian | 18 | | UTK |

AMNH = American Museum of Natural History, New York; CMNH = Cleveland Museum of Natural History, Ohio; CMU = Chiang Mai University, Thailand; CU = Coimbra University, Portugal; KU = Kyoto University, Japan; MCC = Musée Canadien des Civilisations, Gatineau, Canada; MdH = Musée de l'Homme, Paris, France; MGM = McGregor Museum, Kimberley, South Africa; MNdAE = Museo Nazionale di Antropologia e Etnologia, Firenze, Italy; MoM = San Diego Museum of Man, California; NHM = Natural History Museum, London, UK; NM = Naturhistorisches Museum, Wien, Austria; NMK = National Museum of Kenya, Nairobi, Kenya; TU = Tokyo University, Japan; UTK = University of Tennessee at Knoxville; UCB = University of California at Berkeley; UP = University of Pennsylvania at Philadelphia; UR = University of Rome "La Sapienza", Italy; UW = University of Witwatersrand, Johannesburg, South Africa. doi:10.1371/journal.pone.0055909.t001

dataset and the estimated sex of the other, and the rate of individuals with matching sex was calculated. If visual sex determination has a high accuracy, we can expect the discriminant function to give a similar rate of matching sex individual in both datasets. The proportion of individuals with the correct matching sex was very similar in the known and unknown sex database

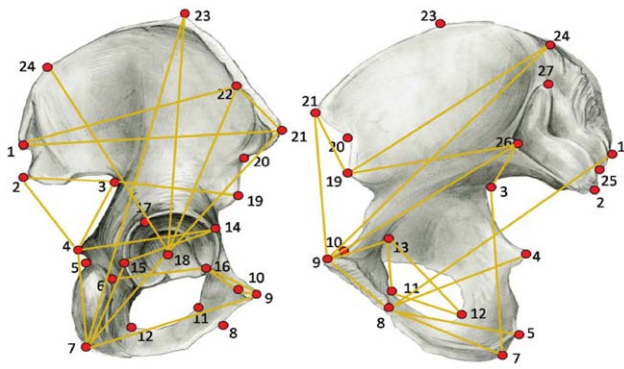


Figure 2. Landmarks and inter-landmark distances. Landmarks and linear distances used in the study are shown on right os coxae (lateral view shown on left, medial view shown on right).
doi:10.1371/journal.pone.0055909.g002

(99.04% and 98.87% respectively), supporting the validity of the visual sex determination.

Apportionment of Variance

Population samples (Table 1) were assigned to different continents (Africa, Europe, Asia, and America) and the relative apportionment of variance at the population and continent level was calculated as in [3,77].

The method is based on a quantitative genetics model, where each locus has an equal and additive effect. It requires the computation of an R matrix of scaled variances and covariances around the regional mean allele frequencies [78,79]. In the absence of an estimate of the additive genotypic covariance matrix, the phenotypic covariance matrix is used, assuming total heritability. Given the small sample size of some of the populations, a correction for sampling error was included in the calculation of the R matrix, as suggested by [77]. Unbiased F_{ST} values were extracted from the R matrix as the weighted average diagonal of the R matrix:

$$F_{ST} = \sum_{i=1}^g w_i r_{ii}$$

Table 2. Definition of landmarks used in this study.

| Landmark | Definition |
|----------|--|
| 1 | Apex of the posterior superior iliac spine* |
| 2 | Apex of the posterior inferior iliac spine* |
| 3 | Point of maximum curvature in the greater sciatic notch* |
| 4 | Tip of the ischial spine. The lower point of the tip is taken when the spine is not triangular in shape* |
| 5 | Point where the transverse ridge meets the medial edge of the ischial tuberosity* |
| 6 | Apex of the ischium tubercle |
| 7 | Farthest point of ischial curve from the centre of the obturator foramen |
| 8 | Most inferior point on the inferior edge of the medial aspect of the pubic symphysis* |
| 9 | Most superior point on the superior edge of the medial aspect of the pubic symphysis* |
| 10 | Apex of the pubic spine |
| 11 | Most anterior point of the obturator foramen |
| 12 | Most posterior point of the obturator foramen |
| 13 | Most superior point of the obturator foramen |
| 14 | Point on the acetabulum margin corresponding to where ilium and ilio-pubic ramus meet |
| 15 | Point on the acetabulum margin furthest away from landmark 14 |
| 16 | Most inferior point of the anterior end of the lunate surface of the acetabulum |
| 17 | Point on the acetabulum margin furthest away from landmark 16 |
| 18 | Center of the acetabular fossa |
| 19 | Apex of the anterior inferior iliac spine* |
| 20 | Deepest point of the interspinal notch |
| 21 | Apex of the anterior superior iliac spine* |
| 22 | Midpoint of the supero-lateral edge of the cristal tubercle* |
| 23 | Most superior point of the iliac crest, in measuring position |
| 24 | Point where the lateral margin of the iliac crest meets the superior end of the posterior gluteal line* |
| 25 | Point where the posterior margin of the auricular surface meets the margin of the ilium. |
| 26 | Point where the arcuate line meets the auricular surface of the ilium* |
| 27 | Most postero-superior point on the auricular surface of the ilium* |

The os coxae is orientated in lateral view and the posterior iliac spines together with the edge of the ischial tuberosity lie on an imaginary y-axis with respect to the observer. When possible, Weaver's [60] landmark definitions have been used (highlighted by an asterisk, [60]).
doi:10.1371/journal.pone.0055909.t002

Table 3. Subsets of the original dataset used to test the accuracy of visual sex determination.

| Population samples | Males (N) | Females (N) | Total (N) |
|--------------------|-----------|-------------|-----------|
| DB1 | 169 | 165 | 334 |
| Africa | 62 | 64 | |
| Europe | 70 | 65 | |
| Asia | 37 | 36 | |
| DB2 | 253 | 59 | 312 |
| Africa | 79 | 21 | |
| Europe | 157 | 10 | |
| Asia | 17 | 28 | |
| DB3 | 469 | 328 | 797 |
| Africa | 126 | 92 | |
| Europe | | 6 | |
| Asia | 111 | 51 | |
| Americas | 232 | 179 | |

The numbers refer to the number of individuals (N). DB1: known-sex individuals used to derive the discriminant function; DB2: different subset of known-sex individuals; DB3: estimated-sex individuals.
doi:10.1371/journal.pone.0055909.t003

Where g is the number of populations, and w is the relative population size of population i . In the absence of any specific information, identical *population* size was assumed for all populations and w was set as a vector of 1. The apportionment of variance was explored at a hierarchical level, following [16] and subsequent analogous works:

AR = variance among geographic regions (in this case continents);

AL = variance among local populations within regions;

WL = variance within local populations.

If F_{RT} is F_{ST} calculated among regions, and F_{LT} is F_{ST} calculated among local populations, then:

$$AR = F_{RT}$$

$$AL = F_{LT} - F_{RT}$$

$$WL = 1 - F_{LT}$$

Assessing Fit to the Out-of-Africa Model

Within-population phenotypic diversity was calculated as the trace of the variance-covariance matrix of the PC scores [80,81], which is effectively a sum of each PC's within-population variance. Following [10], all potential origins of human expansions were represented as a grid of equally spaced points (5° latitude/longitude) distributed over Africa, Eurasia, Australia and the Americas. Geographic distance from each potential origin was calculated as the shortest route over land avoiding areas with an altitude greater than 2,000 m (computed using the graph theory approach described by [82]).

To test for the signature of the serial founder effect, a linear regression analysis was implemented in R, where phenotypic multivariate variance was dependent on geographic distance from the origin of expansion. The analyses were repeated for all possible origins, in order to identify the origin associated with the lowest AIC (Akaike Information Criterion, [83]) for both males and females.

Analogous published works on the cranium used linear measurement data to quantify shape variation [10,12,30]. To allow a more direct comparison with previous studies, 39 linear

Euclidean distances between landmarks were extracted from the 3D data (Figure 2). The measurements were size adjusted by dividing each inter-landmark distance by centroid size (i.e. the square root of the sum of the squared Euclidean distances from each landmark to the centroid). Following the Relethford-Blangero [79] method, the inter-landmark distances were subject to a z-score transformation which standardizes all measurements by subtracting the population's mean and dividing the result by the population's standard deviation, erasing the effect of scale differences and allowing a direct comparison between measurements. Within-population variance was computed for the linear measurements and regressed on the distance from the centroid of the area within 4 points of delta AIC of the single most supported origin.

Obstetrical Constraints

To test for the possible effect of obstetrical constraints on the os coxae, two new configurations of 17 landmarks were created from the full set of landmarks, broadly related to the shape of the true and false pelvis (Figure 3). The region of the acetabulum was included in both configurations, therefore maintaining useful shape information regarding the position of the landmarks in respect to the axis of the body. The OoA model was then tested separately on both configurations, using the methods described above.

Results

Apportionment of Variance

The relative apportionment of within- and between-population phenotypic variance at a regional (continental) and local level is very similar for the os coxae as to the pattern described for neutral genetic markers and craniometric data, with the large majority of shape variance found within local populations (i.e., >90%; Table 4). This contrasts sharply with the apportionment pattern for skin color, where within-population variation only accounts for less than 10% of the total diversity. Therefore, these results are consistent with the suggestion that global patterns of variation in the shape of the os coxae can largely be attributed to neutral evolutionary processes.

Out-of-Africa Model

The test of the iterative founder effect model on all possible origins gave very similar results in males and females (Figure 4). In both sexes, the "best" origin (i.e., the origin associated with the lowest AIC) was found in South Africa (25°S 20°E for males and 30°S 20°E for females). Expanding the confidence interval to all origins within 4 points of AIC from the best model returned an area that matches very closely the whole African continent, with a centroid in central sub-Saharan Africa (5°N 25°E).

Within-population variance shows a significant decline with increasing distance from the centroid of the most supported area of origin (i.e. 5°N 25°E) in both males and females (Table 5, Figure 5), confirming the results of [31] in showing a clear neutral signature of the OoA expansion in pelvic shape variation. The pattern appears stronger in males than in females ($r^2 = 0.466$ and $r^2 = 0.305$, respectively). Repeating the analyses on inter-landmark distances gave very similar results ($r^2 = 0.376$ in males and $r^2 = 0.315$ in females; Table 5).

The possible presence of a bias towards lower variances in smaller samples could in principle affect the OoA pattern. A simple regression analysis, however, showed no significant relationship between phenotypic variance and sample size ($r^2 = 0.097$, p-value = 0.11 in males; $r^2 = 0.066$, p-value = 0.281

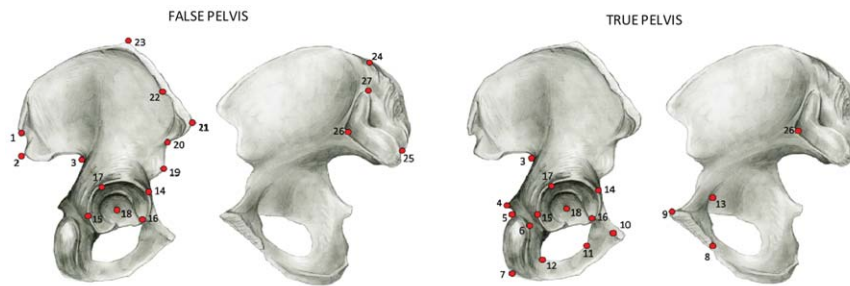


Figure 3. Landmark configurations for regions of the os coxae associated with the false and true pelvis. The acetabular region is included in both configurations.

doi:10.1371/journal.pone.0055909.g003

in females) nor between sample size and distance from Africa ($r^2 = 0.070$, p -value = 0.182 in males; $r^2 = 0.042$, p -value = 0.385 in females).

The results indicate that the neutral demographic pattern is stronger in males than in females. To test if the difference could be due to the more numerous population samples available for males ($N = 27$) compared to females ($N = 20$), the analyses were repeated on a subset of 19 populations that included individuals from both sexes. No difference between the sexes was highlighted in landmark data ($r^2 = 0.292$ and $r^2 = 0.284$ in males and females respectively) nor the linear distances ($r^2 = 0.318$ and $r^2 = 0.341$ in males and females respectively).

The analyses showed a lower OoA signal in the true pelvis with respect to the false pelvis (Table 5). Moreover, average within-population variance is lower in the true pelvis (0.0026 in both males and females using 19 populations) than in the false pelvis (0.0041 and 0.0040 in males and females, respectively using 19 populations). The results are in line with what would be expected if obstetrical constraints were indeed affecting the true pelvis. However, results were virtually identical between males and females, both in the strength of the OoA signal and in within-population pelvic variation (0.0058 and 0.0057 in males and females, respectively, using 19 populations) suggesting that the constraints, if present, do not affect female pelvic shape to a greater extent than male shape.

Discussion

It is clear from the results that at a global level, the shape of the os coxae reflects the effects of ancient demographic events on genetic diversity, as expected under a model of neutral phenotypic evolution. The pattern of variance apportionment at a regional and local level is consistent with previous analyses of neutral genetic markers and (largely neutral) craniometric traits [3,17,18,84,85], and opposite to the pattern shown by skin color, which has been attributed to strong natural selection (Table 4) [3,86]. The analysis assessing all possible origin points found that the best supported origin lay in sub-Saharan Africa, consistent with previous assessments of neutral genetic markers [10] and also equivalent analyses of craniometric data [10,12]. Phenotypic diversity, moreover, declines with increasing distance from sub-Saharan Africa ($r^2 = 0.31$ – 0.47), following the same pattern described in neutral genetic markers [27–29] and craniodental traits [10–12,30]. The results are particularly striking as the pattern appears stronger than found previously on a more limited set of pelvic measurements ($r^2 = 0.15$) [31], or even in larger studies of cranial variation ($r^2 = 0.19$ – 0.28) [12,30]. These results would obviously benefit from further investigation via directly matched global samples of cranial and postcranial remains. However, it is worth emphasizing that given the small sample size of some groups, we can expect the presence of some “noise” in the analyses, which would primarily affect the regression

Table 4. Apportionment of genetic and phenotypic variance.

| Data | Reference | Number of regions | Variance components (%) | | |
|----------------------------------|---------------|-------------------|-------------------------|---|-------------------------------|
| | | | Among regions (AR) | Among local populations within regions (AL) | Within local populations (WL) |
| Blood polymorphisms | [16] | 7 | 6.3 | 8.3 | 85.4 |
| Blood polymorphisms | [84] | 6 | 10.4 | 5.6 | 84.0 |
| Microsatellite DNA | [17] | 5 | 10.0 | 5.5 | 84.5 |
| RFLPs, 16 loci | [17] | 5 | 8.0 | 8.4 | 83.6 |
| RFLPs, 79 loci | [17] | 4 | 11.7 | 3.9 | 84.5 |
| Craniometrics* $h^2 = 0.55$ | [3] | 6 | 14.6 | 6.7 | 78.8 |
| Skin color $h^2 = 0.66$ | [3] | 5 | 87.9 | 3.2 | 8.9 |
| Pelvic shape (males) $h^2 = 1$ | Present study | 4 | 2.6 | 4.8 | 92.6 |
| Pelvic shape (females) $h^2 = 1$ | Present study | 4 | 3.3 | 6.4 | 90.3 |

Results as reported in some of the cited works and in the present study. Only studies comparing at least 4 main geographic regions were included. The present study assumes complete heritability thus generating minimum F_{ST} values. Craniometric average heritability based on [103] and skin color heritability based on [104].

doi:10.1371/journal.pone.0055909.t004

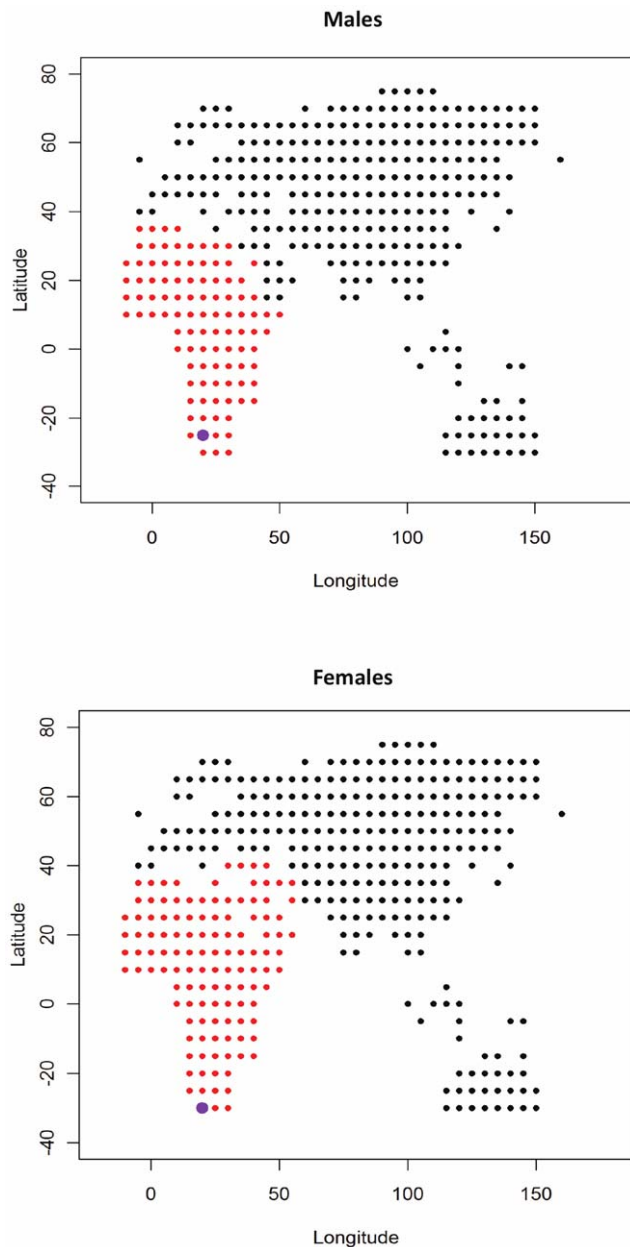


Figure 4. Points of origin of human expansion tested in males (above) and females (below). The origin that returned the highest correlation between phenotypic variance and geographic distance is highlighted with a larger dot. The origins that gave a regression model within 4 points of delta AIC from the best origin are highlighted by red dots. Americas not shown but included in analysis. doi:10.1371/journal.pone.0055909.g004

coefficient of the OoA model. Therefore, the results reported in Table 5 should be considered as minimal values.

One possible reason for the difference highlighted between this study and analogous tests of the OoA pattern on the pelvis and the cranium could be the nature of the data themselves. All previous studies made use of linear measurement data collected using caliper-based traditional morphometric methods. Repeating the analyses on inter-landmark distances, however, returned very similar results ($r^2 = 0.32-0.37$), again supporting a very strong OoA pattern in the pelvis. It appears, therefore, that independently of the specific category of data, global shape variation of the

os coxae reflects the neutral signature of population history in *Homo sapiens*. A comparison with the weaker OoA signal found by [31] using only three pelvic measurements suggests that the number and the choice of traits, more than the type of data employed, affects the overall results. This would imply that although a strong signal can be detected even with a small number of traits, well-chosen variables that give a higher definition of shape will enhance the capability of the analyses to capture weaker signals. Hence, the number of variables and an accurate representation of the general shape are important factors to take into consideration in this type of study.

Other sources of variation are of course possible, such as differences in activity levels and diet, which could in principle affect pelvic shape [37,87–89]. Being impossible to test for these potentially confounding variables with the present dataset, we can only assume that part of the variation in pelvic shape in our samples could be accounted for by plastic reactions to unknown factors. However, even if present, their effect is not strong enough to obliterate the signature of ancient population history.

Our analyses testing for obstetrical constraints in shape variation indicated no difference in the neutral OoA pattern between males and females, a difference that would be expected if constraints were stronger in females than in males. This result is consistent with Tague's [51] finding that males are not necessarily more variable in pelvic morphology than females. It is also consistent with recent suggestions that the obstetric dilemma may be influenced more by maternal energetics than pelvic morphology per se [90,91]. However, it is important to note that our analyses did not include the sacrum, which is also a component of variation in obstetric dimensions (although see [31]). Indeed, the demographic signature does appear to be weaker in certain functional (i.e. the obstetrically related) regions of the os coxae than in others. The fact that the false pelvis shows a stronger neutral pattern of variation, and a higher overall average variation in shape than the (obstetrically-related) true pelvis, suggests that obstetrical constraints might indeed have an influence on some pelvic traits. At the very least, our analyses indicate that different regions of the pelvis preserve a neutral signal to different extents in a similar vein to the human cranium [7–9,13,14,22,92,93].

In summary, the shape of the os coxae reveals a surprisingly strong signature of ancient population history and an overall neutral pattern of variance apportionment, despite the fact that some aspects of pelvic form have been demonstrated to be subject to selective pressures (e.g., [32,33,35,60]). Moreover, although our results reveal some potential for obstetrical effects to be exerting an effect on population variance, these are not preeminent in terms of obliterating the underlying neutral pattern. However, it is important to underline that the present results, based on *within*-population shape diversity, cannot be interpreted as an indication of no effect of selective factors on pelvic shape differences *between* populations. Indeed, our results are in line with suggestions that the effects of climatic selection in the human pelvis may have been more prevalent on aspects of size (via Bergmann's [63] rule) than they have on global patterns of *shape* variation [31]. Future work should investigate the extent to which climatic selection has contributed to deviations from total fit to the neutral model; assessing its contribution in *relative* rather than absolute terms.

Our overall main finding of a substantial component of neutral shape variation in the human pelvis is important in the light of studies of the human cranium (e.g., [2,6–9,94]). Such studies have highlighted that human cranial variation can largely be thought of as a proxy for neutral genetic variation in terms of understanding

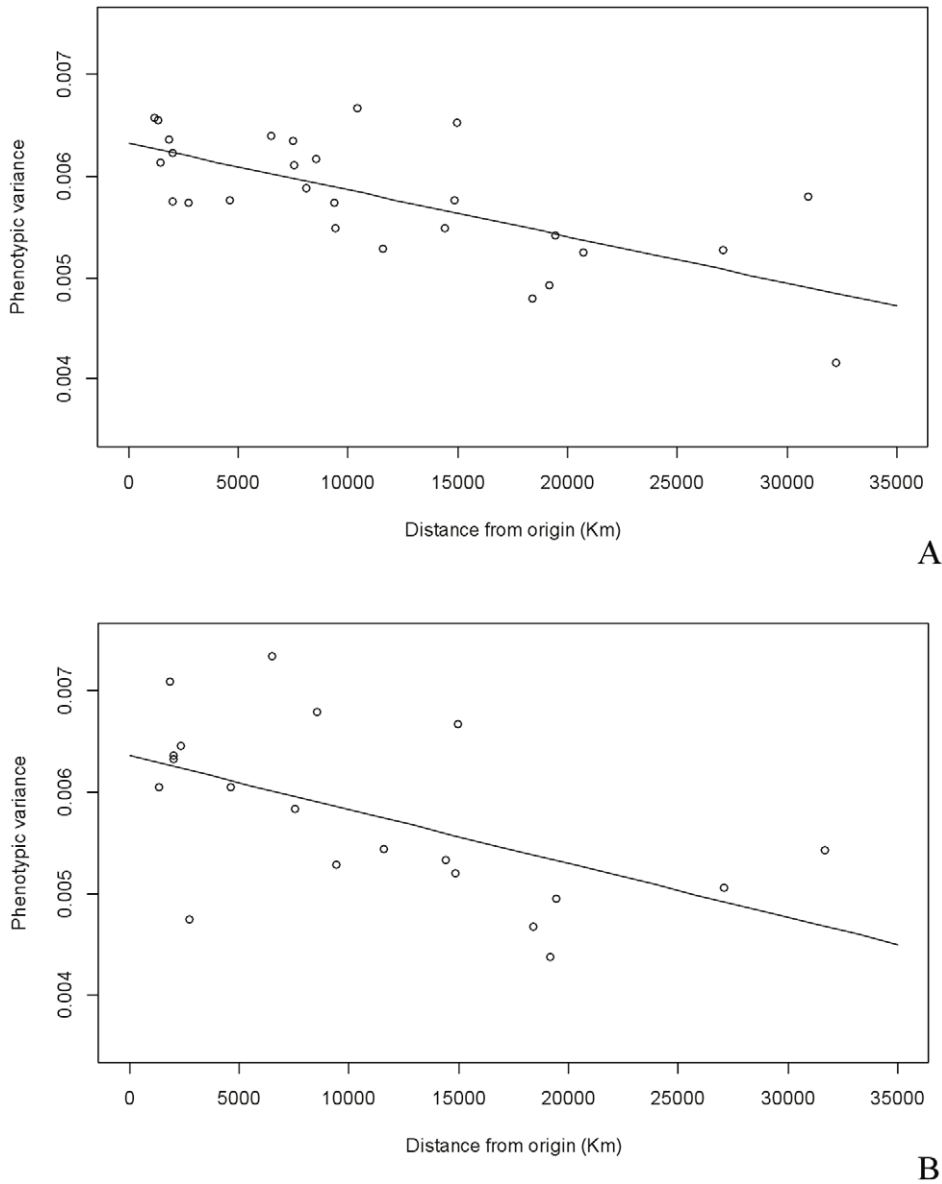


Figure 5. Out-of-Africa pattern. Plot of within-population phenotypic variance on distance from the sub-Saharan African centre of origin for males (A) ($r^2=0.466$; p -value <0.001) and females (B) ($r^2=0.305$; p -value = 0.012) (Table 5). The difference between males and females disappears when equal numbers of populations (i.e. 19) are used for males ($r^2=0.292$; p -value = 0.017) and females ($r^2=0.284$; p -value = 0.019) (Table 5). doi:10.1371/journal.pone.0055909.g005

Table 5. Results of linear regression models.

| MALES | R ² | P-value | FEMALES | R ² | P-value |
|------------------------------|----------------|---------|------------------------------|----------------|---------|
| PhVar~Dist | 0.466 | <0.001 | PhVar~Dist | 0.305 | 0.012 |
| PhVar~Dist (linear) | 0.376 | <0.001 | PhVar~Dist (linear) | 0.315 | 0.010 |
| PhVar~Dist (19 pop.) | 0.292 | 0.017 | PhVar~Dist (19 pop.) | 0.284 | 0.019 |
| PhVar~Dist (linear, 19 pop.) | 0.318 | 0.012 | PhVar~Dist (linear, 19 pop.) | 0.341 | 0.009 |
| PhVar~Dist (true pelvis) | 0.382 | <0.001 | PhVar~Dist (true pelvis) | 0.210 | 0.042 |
| PhVar~Dist (false pelvis) | 0.419 | <0.001 | PhVar~Dist (false pelvis) | 0.313 | 0.010 |

PhVar: phenotypic variance; Dist: distance from the African origin; linear: analysis performed on inter-landmark distances; 19 pop.: analysis performed on a subsample of 19 populations for which both male and female individuals were available. doi:10.1371/journal.pone.0055909.t005

past population history [1,15], leading to insights into factors such as the divergence of Neanderthals and modern humans [95,96], the dispersal of modern humans [10,30,97], the demographic signature of the Neolithic expansion [98,99], and the settlement of the Americas (e.g., [100–102]). Our study indicates that shape data for the human pelvis might provide an important adjunct to, or substitute for, cranial data in anthropological questions of this type.

Acknowledgments

We are grateful to Benjamin Auerbach, Brendon Billings, Michael Black, Jerome Cybulski, Gisselle Garcia-Pack, Lyman M. Jellema, Natasha

Johnson, Maureen Klemp, Osamu Kondo, Robert Kruszynski, Pasuk Mahakkanukrauh, Giorgio Manzi, Philippe Mennecier, Janet Monge, David Morris, Masaharu Motokawa, Ogeto Mwebi, Tori Randall, Ana Luisa Santos, Maria Teschler-Nicola, Tim White, and Monica Zavattaro for allowing access to the collections and for general assistance. We wish to thank Brian Campbell for the original drawings of the os coxae. John Relethford and two anonymous reviewers provided helpful comments on a previous version of this paper.

Author Contributions

Conceived and designed the experiments: LB NvCT SJL. Performed the experiments: LB. Analyzed the data: LB AM. Contributed reagents/materials/analysis tools: AM. Wrote the paper: LB NvCT SJL.

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