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Sexual dimorphism in the size and shape of the os coxae and the effects of micro-evolutionary processes.

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Abstract

Sexual dimorphism in the human pelvis has been studied widely for forensic purposes, but it is still unclear to what extent it varies among human populations. There is evidence that micro-evolutionary processes, both neutral (i.e. population history) and selective (e.g., thermoregulatory adaptation and size-related obstetrical constraints) contribute to explain pelvic variation among populations, but the extent to which these factors affect pelvic sexual dimorphism is unknown. In this study, I analyze sexual dimorphism of the os coxae in 20 globally-distributed human populations, using 3D morphometric data to separate the size and shape components of sexual differences. After evaluating population differences in the degree and pattern of sexual dimorphism, I test for the effect of population history, climate, and body size in shaping global diversity. The results show that size and shape dimorphism follow different patterns. Coxal size dimorphism is generally quite consistent through populations, with males bigger than females, but it appears to be reduced in small-bodied populations, possibly in relation to obstetrically-related selective pressures for a spacious birth canal. Beyond a general species-wide pattern of shape dimorphism, commonly used for forensic sex determination, other aspects of sexual differences in coxal shape vary among human populations, reflecting the effects of neutral demographic processes and climatic adaptation.

The pelvic region is the most sexually dimorphic region of the human skeleton, and, as such, is used widely for sex determination in forensic and archaeological contexts (Mays and Cox, 2000). Pelvic differences between the sexes have been related to on-going selection for a wider pelvic cavity in females than in males, necessary to provide a sufficiently spacious birth canal during parturition (Schultz, 1949; Leutenegger, 1974; Tague, 1989, 1991, 1995; Rosenberg and Trevathan, 1995; Correia et al., 2005; Weaver and Hublin, 2009). Given the universal nature of this type of selection in our species, it does not come as a surprise that a similar pattern of pelvic sexual dimorphism has been described for different human populations.

Comparisons of sexual dimorphism among populations have been limited, with most studies focusing on a small number of populations, mainly of European and African ancestry (e.g., Tague, 1992; Arsuaga and Carretero, 1994; Correia et al., 2005; Patriquin et al., 2005; Steyn and Patriquin, 2009). The few studies that compared a number of globally-distributed populations found support for a broadly similar pattern of pelvic sexual dimorphism across populations from different geographical regions (Weaver, 2002; Kurki, 2011). Overall, these studies confirm that females are relatively (and often absolutely) larger than males in the measurements of the birth canal, sub-pubic angle, pubic length, and width of the sciatic notch, and that this general pattern is valid independently of ancestry and geographical location (Murail et al., 2005; Steyn and Patriquin, 2009; Kurki, 2011).

Differences in the shape of the pelvis among human populations have, conversely, been widely documented (e.g., Derry, 1923; Işcan, 1983; Patriquin et al., 2002, 2003; Handa et al., 2008). One simple explanation for population differences in pelvic shape is that neutral evolutionary processes, such as population history, could have contributed to generating pelvic variation on a large geographical scale. This possibility is supported by two recent analyses of worldwide pelvic shape diversity, which have found that within-population pelvic shape variation decreases with distance from Africa (Betti et al., 2012, 2013), mirroring a similar decrease in heterozygosity in neutral genetic markers (Prugnolle et al., 2005; Ramachandran et al., 2005). The pattern has been explained as the effect of serial founder events during the human expansion out of Africa, and suggests a substantial signature of past population history in human pelvic shape variation.

There is also evidence of population differences in pelvic shape, especially pelvic breadth, in different climatic conditions, with modern human populations in high-latitude regions displaying relatively wider pelves than tropical populations (Ruff, 1993, 1994, 2002; Holliday, 1997; Weaver, 2002; Weaver and Hublin, 2009; Holliday and Hilton, 2010; Kurki, 2013). This pattern has been explained as the result of climatic adaptation, whereby wider trunks help reduce heat loss in cold environments by decreasing the surface-to-volume ratio of the body.

Homo sapiens evolved in Africa (Mellars, 2006a, b; Goebel, 2007; Henn et al., 2012), where most regions are characterized by a warm or hot climate. For endothermic species, such as humans, maintaining a stable body temperature in hot environments requires efficient heat dissipation; this is achieved through sweat evaporation at the body surface, which is facilitated by a high body surface-to-volume ratio. The relatively elongated body shape of most sub-Saharan African populations in respect to other human populations, and the associated increase in the surface-to-volume ratio, has been interpreted as a thermoregulatory adaptation to hot environments (e.g., Ruff, 1994, 2002; Holliday and Falsetti, 1995; Holliday, 1997; Holliday and Hilton, 2010). Following the same rationale, after the expansion out of Africa and the colonization of high-latitude regions, natural selection would have promoted new adaptations to colder environments. These new adaptations included a wider trunk and relatively shorter limbs, resulting in a lower surface-to-volume ratio which helped to maintain internal body temperature in cold regions. Differential climatic adaptation might, therefore, have contributed in generating extant population differences in body size and proportions, including pelvic shape and size (Trinkaus, 1981; Ruff, 1991, 1994; Holliday and Falsetti, 1995; Pearson, 2000; Stock, 2006; Weaver and Hublin, 2009).

Differences in average body size among populations have also been suggested to affect pelvic proportions. Kurki (2007) compared body size and pelvic dimensions in three populations that ranged from small (KhoeSan), through medium (Portuguese), to large body size (European-Americans). Kurki's results showed that some dimensions of the birth canal, especially of the midplane and outlet, are not significantly smaller in KhoeSan women relative to the other two populations, despite the former being significantly smaller in body size and in most of the other pelvic measurements (Kurki, 2007). Kurki interpreted the results as an indication that some obstetrical dimensions are evolutionarily protected and preserved independently of body size, due to strong stabilizing selection acting on the size of the female pelvic canal to maintain viable dimensions in small-size populations.

Given the body of evidence pointing to significant population differences in pelvic shape due to population history (i.e. neutral evolutionary processes) and differential selective pressures, it is relevant to consider whether or not these micro-evolutionary processes affected pelvic sexual dimorphism in human populations. Beyond the general species pattern of pelvic dimorphism, which ensures that females have viable birth canal dimensions, it is possible that population-specific or region-specific characteristics in sexual differences contribute to the variation visible today (González et al., 2007). Geographically-closer populations might be expected to display more similar patterns of dimorphism in respect to distant populations, as a reflection of shared population history. If climatic adaptation indeed promoted changes in pelvic shape in human populations, these changes could have had repercussions on the degree and pattern of sexual dimorphism in different climates. While the selection of a large, obstetrically capacious pelvis might conflict with the thermoregulatory needs of a narrow pelvis in hot climates, such a dilemma might not present itself in cold climates, where a large pelvis would be climatically favored (Weaver and Hublin, 2009). Obstetrical constraints, if stronger in small-bodied populations as suggested by Kurki (2007), could increase pelvic dimorphism in these populations in respect to others characterized by larger body size. In a larger study, Kurki (2011) found only two pelvic measurements that appeared to be more sexually dimorphic in small-bodied populations than in larger-bodied ones: the anterior-posterior dimensions of the midplane and outlet, both obstetrically-relevant dimensions. The results are suggestive, although Kurki concluded that they were not strong enough to support a direct relationship between obstetrical selection and level of pelvic dimorphism.

Pelvic differences between the sexes are easily identified by the unaided eye and are particularly accentuated in the pubic region and in the shape of the sciatic notch (e.g., Phenice, 1969; Ferembach et al., 1980; Işcan and Derrick, 1984; Sutherland and Suchey, 1991). Visual sex determination takes advantage of these broad morphological differences, which are evaluated by eye independently of size variation. When it comes to *measuring* the level of sexual dimorphism in different human populations, however, the focus shifts from the shape of these pelvic regions to individual measurements. In recent decades, pelvic sexual dimorphism in human populations has been measured and compared by means of indices of size dimorphism, which compare the size of specific pelvic measurements between the sexes. Several studies show how some pelvic traits (e.g., diameter of the false pelvis, hip bone length and ischial length) vary in accordance with sexual differences in body size, being larger in males than in females. Other traits, on the other hand, including measurements of the birth canal, pubic length, and bi-acetabular breadth, show the opposite pattern, with females larger than males despite the reverse relation in body size (Tague, 1992; Correia et al., 2005; Kurki, 2007, 2011). The presence of a reverse pattern in size dimorphism for obstetrically-relevant pelvic measurements can be seen as evidence of a significant effect of stronger female obstetrical constraints.

By comparing single measurements, these studies cannot give an estimation of the level of general shape dimorphism (i.e. somewhat analogous to the visual evaluation used for sex determination), although differences in shape can be inferred by the fact that various pelvic measurements are associated with different levels and patterns of size dimorphism. When no correction for the size of the individuals is applied to the data, the indices of sexual dimorphism carry information relative to both the shape and size of the pelvis in the two sexes, and do not allow the separation of the two components of dimorphism (Arsuaga and Carretero, 1994). For example, traits that appear to be virtually identical in size in males and females can instead appear notably dimorphic when general pelvic size is taken into account and different pelvic proportions are revealed. The separation of the size and shape component is extremely important, as it is possible that sexual dimorphism in size and in shape follow different patterns, as emerged in the case of growth trajectories during the development of pelvic sexual dimorphism in rats (*Rattus norvegicus;*Berdnikovs et al., 2007).

In this study, sexual dimorphism of the os coxae was evaluated in 20 globally-distributed human populations in its separate components of size and shape variation. The population samples were chosen in order to represent different geographical regions and climatic conditions, as well as human variation in body size. The aims of the study can be summarized as follow:

1) To evaluate population differences in sexual size and shape dimorphism for the os coxae.

2) To investigate the effects of population history in shaping population differences in sexual dimorphism. Due to more recently shared ancestry and on-going gene flow, geographically proximate populations can be expected to share a similar level of sexual dimorphism in respect to populations further away from one another. This pattern is often referred to as Isolation-By-Distance (Wright, 1943; Malécot, 1969; Crow and Kimura, 1970; Morton, 1973).

3) To test for possible effects of climate on sexual dimorphism.

4) To test if differences in sexual dimorphism are related to male and female body size, thereby testing the hypothesis that small-bodied populations have an increased level of pelvic sexual dimorphism.

MATERIALS AND METHODS

Morphometric data of the os coxae were collected in the form of 27 3D landmarks (Supplementary material, Table S1) for 1,144 individuals (634 males and 510 females) representing 20 globally-distributed human populations (Table 1, Fig. 1). The minimum sample size for the populations is 8 individuals, with an average sample size of 31.7 and 25.5 individuals for males and females, respectively.

Only individuals whose iliac crest was completely fused were measured for this study. Determination of sex, when not recorded at the death of the individual, was performed using standard non-metric methods (Phenice, 1969; Işcan and Derrick, 1984; Sutherland and Suchey, 1991); the accuracy of such visual determination has been tested on a more extensive dataset by Betti et al. (2013), and deemed extremely high.

Unilateral data were collected on the best preserved (i.e. most complete) os coxae. Intra-observer error was tested on three ossa coxarum from two females and a male, by performing five repeat measurements of all landmarks. Following von Cramon-Taubadel et al. (2007), only landmarks with a standard deviation below 1 mm were selected.

Differences in position, rotation, and size among individual configurations were corrected by generalized Procrustes superimposition (Gower, 1975; Rohlf and Slice, 1990) in Morphologika 2.5 (O'Higgins and Jones, 1998). Female and male individual landmark configurations were pooled together and subjected to the same Procrustes superimposition in Morphologika. Individual centroid size was set aside to compare size differences between the two sexes. In addition, landmark coordinates in Procrustes and tangent space were used to analyze sexual differences in shape. New morphometric variables were also extracted by performing a Principal Component Analysis (PCA) in Morphologika on the covariance matrix of the Procrustes coordinates (as projected on the tangent space). The resultant PC scores, representing 100% of the total shape variance, were used as morphometric data in some of the shape analyses.

Pair-wise geographical distances among populations were calculated as the shortest route on landmasses, avoiding areas with a mean altitude higher than 2,000 m above sea level (Manica et al., 2005; Prugnolle et al., 2005). In order to ensure connections between continents, a land bridge was assumed across the Bering Strait and additional land bridges were used to connect the Malay Peninsula and Australia, through the major Indonesian islands.

Climatic data were obtained from WorldClim (http://www.worldclim.org) as interpolated values from globally-distributed climatic stations (Hijmans et al., 2005), with a definition of 30 arc-second (ca. 1 km). The climatic data included average minimum temperature of the coldest month, average maximum temperature of the warmest month, and annual precipitation.

Indices of sexual dimorphism in size and shape

Sexual dimorphism in size has been studied widely in animal species. There is, however, no unequivocal way of defining size dimorphism, and several indices have been developed over the years. A review of the most common indices of size dimorphism concluded that most indices behave similarly when size differences between the sexes are not too marked, as in the case of modern humans (Smith, 1999). Lovich and Gibbons' (1992) ratio was chosen from among the range of indices used in other studies as it is broadly equivalent to the shape dimorphism index (Schutz's shape index 2) described below.

$$\textit{Lovich and Gibbons' ratio (LGR):} \qquad \left(\frac{\bar{S}_m}{\bar{S}_f}\right) - 1$$

where $\bar{S}_m$ and $\bar{S}_f$ are the mean male and mean female centroid size. The larger sex is always at the numerator, and the index is given an arbitrary positive value when males are larger, and a negative value when females are larger.

An additional index of size dimorphism, recently introduced by Schutz and colleagues (2009), was also computed and used in the following analyses. Most of the common indices of size dimorphism are ratios, and have been criticized for their tendency to follow a skewed and non-normal distribution (Atchley et al., 1976). Schutz and colleagues devised an index of size dimorphism that, not being a ratio, overcomes such criticism.

$$\textit{Schutz's size index (SSI):} \qquad \frac{(\bar{S}_m - \bar{S}_f)^2}{Var_m + Var_f}$$

where $\bar{S}_m$ and $\bar{S}_f$ are the mean male and mean female centroid size, and Var_m and Var_f are the respective sample variances. An important advantage of using Schutz's index is that it takes into account the dispersion around the mean for each sex. Sexual dimorphism can in fact be defined not only by the distance between the means of the two sexes, but also by the level of superimposition of the two distributions, which is partly related to within-sex variance (Marini et al., 1999). If male and female distributions overlap, at equal distance between the sexes' means, a smaller variance would lead to a more limited superimposition between individuals of the two sexes. Hence, although the distance between the means of the two sexes remains identical, smaller within-sex variances would achieve a greater separation between males and females, and the population could be considered more dimorphic than in cases of larger variances (Marini et al., 1999).

Sexual dimorphism in shape is more difficult to evaluate, since shape is a multivariate property of an object, and very little work has been done on it. Only recently has the application of geometric morphometric methods to landmark data allowed a clearer separation between the geometric properties of ‘shape’ and isometric scaling. Schutz and colleagues recently devised two new shape indices, especially created for geometric morphometric data (Schutz et al., 2009).

Schutz’s shape index 1 (SShI.1): $\frac{D^2_{\bar{m}\bar{f}}}{Var_m+Var_f}$

where $D^2_{\bar{m}\bar{f}}$ is the squared Procrustes distance between the mean male and female landmark configurations for each population, and Var_m and Var_f are the sample shape variance in males and females. This index is analogous to SSI, but adapted to use for a complex multivariate property like shape.

Schutz’s shape index 2 (SShI.2): $\left(\frac{\sum D^2_{mf}}{\sum D^2_{ij}} - 1\right)$

where $\sum D^2_{mf}$ is the mean pair-wise squared Procrustes distance between males and females (i.e. the distance of each male to any female of that population, repeated for all males and then averaged) and $\sum D^2_{ij}$ is the mean pair-wise Procrustes distance between individuals i and j, both of the same sex, of whichever sex is more disparate and has the greatest mean distance. The index is effectively analogous to Lovich and Gibbons’ index of size dimorphism, readapted to be used for shape variables. The authors of the index originally assigned a positive value when males were more disparate and a negative value when females had the largest shape variation. In the present dataset, however, the average pair-wise Procrustes distance between sexes is always higher than among individuals of each sex, and assigning a positive or negative sign depending on which sex is the most disparate returns a discontinuous distribution of the index. To avoid this problem, SShI.2 will always have a positive sign in this study, independently of which sex has the highest shape variation (Supplementary material, Fig. S1).

All of the described shape and size indices return a single value: a measure of the magnitude of sexual dimorphism (Table 2) which is independent of sample size and is comparable across species/populations and across anatomical regions within species. For all indices, Shapiro-Wilk tests revealed no significant deviation from normality. All index calculations were performed in R (R Core Team, 2013).

Given the rarity of osteological remains for certain populations, some of the sample sizes in the present study are less than optimal, leading to some error in the estimation of the population parameters used to compute the indices of sexual dimorphism. Cardini and Elton (2007) showed that, at least for their sample of 400 vervet monkey crania, it is possible to estimate average population size very accurately from subsamples as small as 10 individuals, whilst more than 30 individuals are needed for a reasonably precise estimation of size variance. The opposite is true for shape parameters, where an accurate estimation of population shape variance can be achieved from very small samples, but the computation of average shape is accompanied by a large error when fewer than 30 individuals are available. Extending Cardini and Elton's (2007) results to the present study, we can expect the highest uncertainty for Schutz's shape index 1, while Lovich and Gibbons' ratio is likely to be acceptably accurate even for small population samples. Any error due to insufficient sampling would have a confounding effect in the subsequent analyses, making it more difficult to detect significant patterns and associations of variables.

Statistical analyses

Analysis of variance was used to test if individual size (ANOVA) or shape (MANOVA) vary significantly in relation to sex or populations, or the interaction between the two variables. As MANOVA requires that the data be in Euclidean space, the points in Procrustes space were projected on a tangent Euclidean space in Morphologika, and subjected to Principal Component

Analysis (PCA). The individual PC scores were then used as new shape variables for the MANOVA test (Gündüz et al., 2007).

Evaluating the effects of micro-evolutionary processes on the magnitude of size and shape sexual dimorphism. The presence of a neutral pattern of Isolation-By-Distance (IBD) in the differences in sexual size and shape dimorphism was tested with a Mantel test. A matrix of between-population Euclidean distance of dimorphism was created for each of the indices, and then correlated with the matrix of between-population geographical distance.

In order to test for a correlation between body size and the level of sexual dimorphism, an estimate of individual body mass was derived from acetabular height (Ruff, 2010). First, acetabular height (distance between landmark 14 and 15, see Table S1) was used to estimate femoral head diameter, using the equation developed by Ruff (2010). Femoral head diameter has been used by several authors as a proxy for body mass in modern humans and extinct hominins, due to its weight-bearing role in locomotion. McHenry's (1992) formula to derive body mass from the estimated femoral head diameter was selected because it was originally developed from osteometric measurements taken from human populations from a variety of body sizes.

The indices of size and shape sexual dimorphism were regressed on the populations' average female and male body size, to test for a correlation between body size and the level of sexual dimorphism. The different indices were also regressed on the three climatic variables, to test for a correlation between climate and level of sexual dimorphism.

For all factors, the regression was tested with a Generalized Least Square analysis in R (GLS; function *gls*, library *nlme*). The GLS function can control for spatial autocorrelation (SAC), when present, thereby taking into account any effect of neutral population history when testing for the effect of other variables. Taking into consideration neutral patterns of variation is fundamental in these analyses, as they can have a confounding effect. For example, phylogeographic relationships among human populations have been shown to have a significant effect on sexual dimorphism in stature (Gustafsson and Lindenfors, 2004, 2009) and to act as a confounding factor when testing for the relationship between human stature dimorphism and latitude (Gustafsson and Lindenfors, 2009).

The GLS algorithm calculates pair-wise geographical distances between populations from spatial coordinate data, computing Euclidean distances between coordinate points, and uses this information to model SAC. However, geographical distances between human populations are here estimated as shortest routes of migration instead of linear distances and are effectively non-Euclidean distances. To overcome the problem, Multi-Dimensional Scaling (MDS) was applied to the original matrix of overland geographical distance, returning new orthogonal axes that could be used as spatial coordinates by the GLS function; a Mantel test confirmed that original and new distances, calculated from five MDS variables, were highly correlated ($r = 0.999$ and p-value < 0.001). Different autocorrelation structures were fitted to the data in the GLS models, and an ANOVA test was carried out to test the significance of the contribution of each spatial autocorrelation structure to the model. When the contribution was significant, the structure associated with the largest decrease in AIC (Akaike Information Criterion; Akaike, 1973) was chosen for the analyses; a gaussian or an exponential correlation structure appeared to be the most suitable in all cases.

Evaluating the effects of micro-evolutionary processes on the pattern of shape sexual dimorphism. In order to test if populations differ in the pattern, and not only the degree, of shape dimorphism, differences in shape between males and females were analyzed using individual PC axes. Each PC represents a separate component of shape variation, and the magnitude and direction of sexual differences along these axes can be used to investigate population patterns of shape sexual dimorphism. Only PCs that explain a minimum of 1% of variance were included in these analyses (PC 1–22). A Student's t-test was performed to isolate PCs that significantly separate the sexes in at least one population. An alpha level of 0.01 was chosen for this analysis, instead of the 0.05 probability threshold used in the other analyses. A stricter threshold would have further reduced the risk of false positives in multiple tests, but false positives are less problematic, in this particular instance, than a too strict, preemptive exclusion of PCs from the following analyses. For each of these PCs, the difference between the average male score and the average female score was computed for all populations, giving an indication of the direction (males > females, or vice versa) of dimorphism for a particular component of shape.

The presence of a neutral IBD signature in these PCs was tested by computing a matrix of between-population Euclidean distances in sexual differences over all PCs, and correlating it to geographical distance using a Mantel test. A significant result would suggest that geographically closer (i.e. genetically closer) populations share a more similar pattern of sexual dimorphism, implying a significant effect of neutral demographic processes on coxal shape dimorphism. The effect of climate and of body size on the pattern of dimorphism in individual PCs was evaluated using a GLS analysis, as detailed above.

Except where differently specified, significance was set at $p < 0.05$.

RESULTS

Sexual dimorphism in size

In all examined populations, males appear to have bigger coxal bones than females (Table 3). A two-way ANOVA test reveals that there are significant differences in size between the sexes and among population samples. However, the interaction between population and sex was not a significant factor, implying that there is no significant difference among populations in the amount of sexual size dimorphism (Table 4).

A Mantel test was used to compare population differences in the magnitude of sexual size dimorphism and geographical distance; the results were not significant for either of the two indices (LGR and SSI). The lack of a significant correlation suggests that the population levels of sexual size dimorphism do not follow an Isolation-By-Distance pattern.

No correlation with climate was highlighted by the GLS models for any of the indices of sexual size dimorphism. On the other hand, the models revealed a significant correlation with male (but not female) body size in both indices (r^2 = 0.258 and p-value = 0.022 for LGR; r^2 = 0.257 and p-value = 0.023 for SSI), with smaller average male size associated with lower sexual size dimorphism. No significant spatial autocorrelation was detected or corrected for.

Sexual dimorphism in shape

A MANOVA test for the effects of population and sex on the shape variables returned significant results for both sex and population, as well as for the interaction between the two variables (Table 5). As for coxal size, coxal shape is significantly different between the two sexes and among at least some of the populations. The fact that the interaction term is also significant means that, in contrast to sexual size dimorphism, sexual shape dimorphism varies significantly among populations.

A simple plot (Fig. 2) of the first two principal components of shape shows that males and females are almost completely separated along PC 1 (PC 1 explaining 16.10% of variance and PC 2 8.87% of variance). As PC 1 separates the two sexes very well, differences in landmark configurations between the two extremes of this PC axis are informative regarding shape differences between males at one end, and females at the other. Indeed, the extreme landmark configurations associated with hyper-feminine and hyper-masculine configurations show clear differences in the shape of the os coxae, which are in line with commonly described traits of sexual dimorphism (e.g., Brothwell, 1981; White et al., 2012). The pubis is relatively elongated in females and the acetabulum appears to be relatively larger in males. The area of the sciatic notch (as defined by landmarks 2, 3 and 4) is much more open in females, which also show a shorter and more posteriorly elongated ilium. Finally, females have a more laterally placed ischial tuberosity and ischial spine, and a more posterior position of the auricular surface, that altogether contribute in creating a more spacious cavity for the female birth canal (Fig. 3).

A linear regression model was used to test if differences in PC 1 scores (i.e. separating males and females) were driven by allometric changes related to bigger male size, using coxal centroid size as independent variable. Although the model returned a significant correlation (p-value < 0.001), the fraction of variance explained was extremely small ($r^2 = 0.044$), therefore supporting the conclusion that PC 1 captures sexual shape dimorphism largely independently of coxal size.

Population differences in the magnitude of sexual shape dimorphism, as measured by the two indices (SShI.1 and SShI.2), are not significantly correlated with geographical distance, suggesting that the level of shape dimorphism in different populations does not reflect the underlying neutral IBD pattern.

No correlation with climate or body size was detected by the GLS models for the two indices of sexual shape dimorphism. No significant spatial autocorrelation was detected or corrected for.

When the *pattern* of sexual shape dimorphism, instead of the *magnitude* of dimorphism, was examined, a different set of results were obtained. Out of the 22 individual PCs selected for this analysis, 13 were significantly different in the two sexes in at least one population, suggesting that sexual dimorphism goes beyond the (stronger) species-wide pattern identified by PC 1. Differences between males and females in these 13 PCs varied among populations (Supplementary material, Table S2), in accordance with the results of the MANOVA analysis which revealed significant differences in shape dimorphism among populations.

The population values of male-female difference for these PCs were used to build a pair-wise distance matrix of shape dimorphism between populations, which appeared to be significantly correlated with geographical distances ($r^2 = 0.150$, p-value < 0.001). Differences in the pattern of shape dimorphism increase with geographical distance, as expected under an IBD model, suggesting a significant effect of neutral demographic processes.

When values for single PCs were regressed on average male and female size, the analyses returned no significant results, indicating that variation in body size does not explain population differences in sexual shape dimorphism.

Temperature was significantly correlated with sexual differences in two of the PCs. Sexual differences on PC 4 returned a significant correlation with maximum temperature ($r^2 = 0.291$, p-value = 0.014), even after accounting for SAC (p-value = 0.001). Different extremes of temperature appear to be associated with an inverse pattern of sexual dimorphism (Fig. 4a). Morphological differences along PC 4 mainly focus on the ilium, with at one extreme a long iliac blade that curves anteriorly towards the pubis, and at the other extreme a flatter and shorter iliac blade whose anterior spines remain more laterally and posteriorly positioned. In cold environments, males appear to have a more elongated and curved ilium than females, while the opposite pattern is apparent in hot climates. Sexual differences on PC 12 also showed a significant correlation with maximum temperature ($r^2 = 0.273$, p-value = 0.018), and no spatial autocorrelation. Lower temperature corresponds to larger differences between the sexes (Fig. 4b), which mainly regard the shape on the acetabulum. In cold environments, the anterior end of the lunate surface tends to be shorter in females, terminating before the edge of the acetabulum, while males tend to have a more extended lunate surface. Although sexual differences on PC 4 and PC 12 show a significant relationship with climate, it is worth noting that not all populations appear to be sexually dimorphic in respect of these aspects of shape, and that the sexual differences themselves are not as marked as for PC 1 (Table S2).

DISCUSSION

Human pelvic variation has been shown to be affected by both neutral processes (Betti et al., 2012, 2013) and selective processes related to thermoregulatory adaptation (e.g., Ruff, 1994; Holliday and Hilton, 2010) and obstetrical constraints (e.g., Kurki, 2007). However, the influence of these micro-evolutionary processes on pelvic sexual dimorphism is still largely unexplored. By looking at global variation in the shape and size of the os coxae, this study is the first that directly addresses these questions by comparing a large number of human populations. In addition, this study separates and independently analyzes sexual size and shape dimorphism in the os coxae, allowing for the possibility that the size and shape components of dimorphism follow different developmental trajectories in humans, as suggested for other species (Berdnikovs et al., 2007).

Sexual differences in the size of the os coxae follow a similar pattern in all human populations, with males consistently exhibiting larger coxal bones than females. This pattern is in agreement with human sexual size dimorphism in other skeletal parts and general body size, with males on average larger than females (e.g., Stini, 1974; Ross and Ward, 1982; Ruff, 1987, 2002). The results might at first seem at odds with previous reports of bigger pelvic size in females (e.g., Berge et al., 1984; Tague, 1992; Kurki, 2011), but the discrepancy is easily explained by the fact that previous studies included measurements of the pelvic cavity in the analyses. The size of the cavity is not necessarily related to the size of the bones that form it (i.e. the sacrum and the two coxal bones), as its size will also depend on the shape of the bones themselves. Indeed, the present results, where the female os coxae appears consistently smaller than the male one, suggest that differences in the shape of the bones must be responsible for the relatively (and often absolutely) larger female pelvic cavity. Variation in the shape of the sacrum can also contribute to the size of the birth canal, although males have on average larger sacra (Tague, 2007)

Sexual dimorphism in shape, once size has been taken into account, is significant, and reflects known sex differences in pelvic characteristics that have been widely used in visual sex determination (e.g., Phenice, 1969; Ferembach et al., 1980; Işcan and Derrick, 1984; Sutherland and Suchey, 1991). These differences in shape, including the relative position of the ischial tuberosity, sciatic spine and auricular surface, clearly contribute to creating a larger pelvic cavity and birth canal in females. Interestingly, the indices of size and shape dimorphism are not strongly correlated (LGR vs. SShI2: $r^2 = 0.09$, p-value = 0.19; SSI vs. SShI1: $r^2 = 0.22$, p-value = 0.04), suggesting that different developmental processes account for the two aspects of coxal dimorphism.

Beyond a general, species-wide pattern of shape dimorphism, captured by the first Principal Component axis and largely in agreement with the classic morphological differences used for visual sex determination, substantial population differences emerge. The results of the MANOVA and of the single PCs analyses suggest that population differences in sexual shape dimorphism exist, although they appear to be limited to relatively minor aspects of shape variation and do not contradict the evidence for a more general pattern shared by all human populations (Murail et al., 2005; Steyn and Patriquin, 2009; Kurki, 2011).

Population levels of size and shape dimorphism, estimated by the various indices, do not reflect an isolation-by-distance pattern, as would be expected under a model of neutral evolution. A possible explanation for the lack of a neutral signature is that natural selection had a significant impact, therefore disrupting the underlying neutral pattern. Climatic adaptation, for example, has been associated with population differences in pelvic breadth (Ruff, 1994; Holliday and Falsetti, 1995; Holliday, 1997; Holliday and Ruff, 2001; Ruff, 2002), and it could have affected the magnitude of sexual dimorphism. However, the indices of size and shape sexual dimorphism are not correlated to the three climatic variables tested in this study, therefore rejecting the hypothesis that the level of sexual dimorphism varies in accordance to climatic extremes.

The indices can only inform of the magnitude of sexual dimorphism, which can be a very poor indicator of population differences in shape dimorphism, where the same level of dimorphism can be achieved by a wide variety of morphological differences. Between-population differences in the pattern of shape dimorphism (i.e. how single components of shape vary between the sexes) tend to follow neutral expectations, albeit weakly. It appears that, although the *degree* of sexual size and shape dimorphism does not reflect the neutral genetic pattern related to population history, the *manner* in which the two sexes differ in some aspects of shape is significantly different in the various populations, broadly in accordance with an isolation-by-distance model. The analyses also reveal a significant correlation between temperature and certain aspects of shape dimorphism, suggesting that climatic adaptation affected the pattern of coxal sexual dimorphism in human populations.

Variation in body size has also been related to pelvic shape and size, at least in females. Evolutionary protection of obstetrical dimensions has been suggested to have led to an allometric relationship between birth canal dimensions and stature/body size, so that smaller females do not have proportionally small pelvic canals (Tague, 2000; Kurki, 2007). To test this hypothesis, Kurki (2007) compared pelvic sexual dimorphism in three populations of different body size, and found evidence of relatively larger female pelvic dimensions in the KhoeSan small-bodied population in respect to larger-bodied populations of European ancestry. She explained the pattern as the effect of obstetrically-related evolutionary constraints, which promoted the preservation of relatively large antero-posterior pelvic canal dimensions despite the population's smaller body size.

It is difficult to translate the pattern highlighted by Kurki (2007) on canal dimensions into expectations for the size and shape of the os coxae. I have shown that sexual differences in coxal size mirror body size dimorphism, with males bigger than females. Therefore, larger pelvic cavities in females seem to be mainly achieved by differences in shape of the coxal bones instead of size differences alone. A preservation of pelvic canal dimensions in small-bodied populations could be attained by either increasing shape sexual dimorphism in the os coxae and/or decreasing size dimorphism. In other words, female ossa coxarum could be larger than expected, in respect to males, in small-bodied populations, therefore returning a relatively larger pelvis, or they could be hyper-feminine in their shape and generate a larger cavity by more extreme changes in their morphology. The results of this study suggest that size dimorphism indeed decreases in smaller-bodied populations, while no correlation was found between body size and shape dimorphism. Obstetrical constraints might have played a role by reducing sexual size dimorphism in small-bodied populations, without affecting shape dimorphism. However, lower coxal size dimorphism in small-bodied populations could also be explained by a general decrease in body size dimorphism with no direct effect of obstetrical constraints.

In conclusion, this study shows that the male and female ossa coxarum differ significantly in both size and shape. Despite the fact that the female pelvis has been shown to be absolutely larger than the male one in most obstetrically-related measurements, the present results demonstrate that the general size of the os coxae follows the pattern of the rest of the skeleton, with males larger than females. The discrepancy is likely related to the focus of previous studies on the size of the pelvic cavity instead of the actual pelvic bones. A larger birth canal is achieved in females by changes in the shape of the ossa coxarum instead of by an increase in the size of the coxal bones *per se*.

Sexual size dimorphism is higher in populations with larger body size. Lower sexual size dimorphism in smaller populations might be related to selective pressure to maintain an obstetrically-sufficient pelvic size despite a smaller body size. Neither population history nor climate seems to have affected population *levels* of size or shape sexual dimorphism. On the other hand, neutral processes, and to a lesser extent temperature, partially explain population differences in some aspects of shape dimorphism, suggesting that micro-evolutionary processes played a role in generating global variation in sexual dimorphism of the os coxae.

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Tables

TABLE 1. Population samples and institutions where the material is curated.

Region	**Males**	**Females**	**Institution**[a]
Africa			
Botswana, Tswana	33	30	UW
Egypt dynastic	34	17	AMNH, NM
Kenya, Kykuyu	40	30	NMK
Nubia	33	25	NM
South Africa, KhoeSan	26	21	AMNH, MGM, NHM, UW
Swaziland	39	20	UW
Europe			
France	28	23	MdH
Portugal	42	42	CU
Asia			
Ainu, Japan	23	20	KU, TU
Iran	32	22	UP
Japan	45	37	AMNH, KU, MdH, NH
Philippines, ‘negritos’	8	8	MdH
Thailand	37	36	CMU, MdH
America			
Alaska, Point Hope	38	35	AMNH
Argentina, Patagonia	33	13	MdH, MNdAE
Canada, Sadiermiut	24	24	MCC

Chile, Fuegians	17	10	MNdAE, NHM, UR
Native Californians	36	31	UCB
Peru	31	33	MdH, UCB
South Dakota, Arikara	35	33	UTK

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[a] *(AMNH = American Museum of Natural History, New York, USA; 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; NHM = Natural History Museum, London, UK; NM = Naturhistorisches Museum, Wien, Austria; NMK = National Museum of Kenya, Nairobi, Kenya; TU = Tokyo University, Japan; UCB = University of California at Berkeley, USA; UP = University of Pennsylvania at Philadelphia, USA; UR = University of Rome "La Sapienza", Italy; UTK = University of Tennessee at Knoxville, USA; UW = University of Witwatersrand, Johannesburg, South Africa).*

TABLE 2. Indices of sexual size and shape dimorphism.

Population	**Lovich and Gibbons' ratio**	**Schutz's size index**	**Schutz's shape index 1**	**Schutz's shape index 2**
Ainu	0.033	0.378	5.801	0.213
Alaska	0.054	1.127	5.715	0.190
Arikara	0.028	0.417	7.901	0.267
Botswana	0.047	0.613	6.261	0.229
California	0.035	0.550	10.425	0.383
Egypt	0.039	0.322	11.007	0.426
France	0.064	1.253	5.835	0.170
Tierra del Fuego	0.014	0.069	9.999	0.238
Iran	0.058	0.611	5.943	0.147
Japan	0.024	0.151	7.530	0.312
Kenya	0.044	0.479	5.631	0.159
KhoeSan	0.024	0.119	7.833	0.243
Nubia	0.048	0.742	8.492	0.239
Patagonia	0.050	0.571	9.382	0.284
Peru	0.045	0.665	9.952	0.424
Philippines	0.029	0.177	10.43	0.204
Portugal	0.043	0.461	7.674	0.321
Sadiermiut	0.034	0.310	10.217	0.429
Swaziland	0.038	0.463	8.013	0.324
Thailand	0.025	0.205	8.598	0.355

TABLE 3. Average male and female centroid size for all populations.

Population	**Average male size**	**Average female size**
Ainu	370.007	358.343
Alaska	383.086	363.496
Arikara	384.113	373.591
Botswana	359.239	343.064
California	386.144	373.174
Egypt	368.500	354.835
France	392.617	369.061
Fuegian	366.179	361.264
Iran	389.470	368.058
Japan	360.382	351.884
Kenya	355.025	339.992
KhoeSan	332.910	325.229
Nubia	373.424	356.462
Patagonia	388.772	370.252
Peru	365.923	350.219
Philippines	330.827	321.420
Portugal	374.978	359.427
Sadiermiut	387.485	374.651
Swaziland	357.999	344.903
Thailand	364.529	355.525

TABLE 4**.** Results of the ANOVA test for differences in size between sexes, between populations, and for the interaction between sex and population.

Factors	**Degrees of freedom**	**F-value**	**P-value**
Population	19	52.854	<0.001
Sex	1	249.584	<0.001
Population:Sex	19	1.275	0.191

TABLE 5. Results of the MANOVA test for differences in shape between sexes, between populations, and for the interaction between sex and population.

Factors	**Degrees of freedom**	**Pillai's trace**	**Approximate F-value**	**P-value**
Population	19	6.432	7.255	<0.001
Sex	1	0.893	117.141	<0.001
Population:Sex	19	2.139	1.799	<0.001

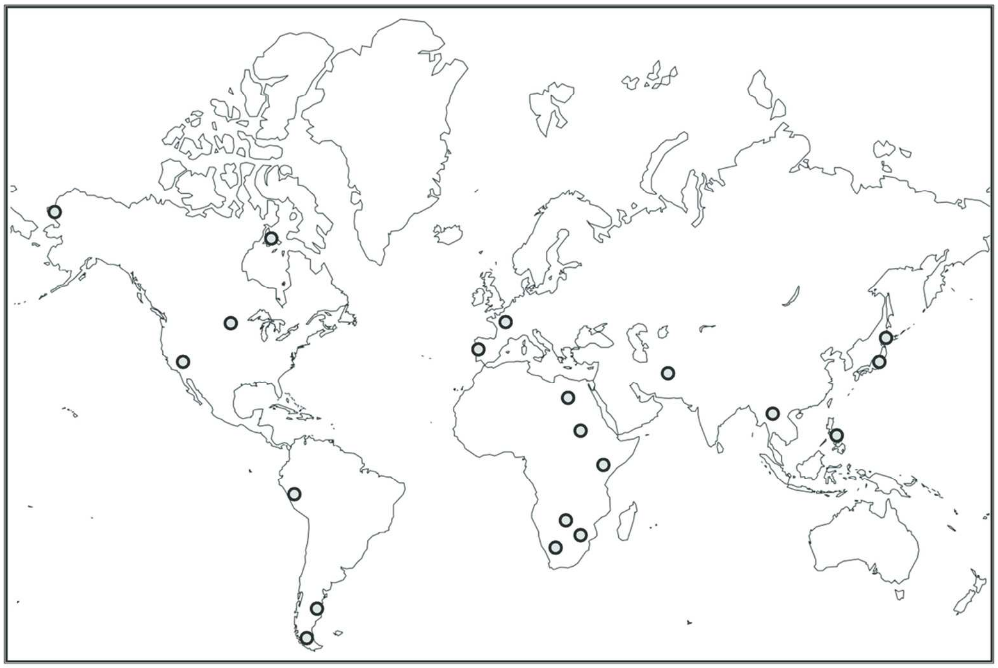
Figures

Fig. 1. Geographical location of the population samples.

Fig. 2. Plot of the first two principal components, highlighting the differences between males (points) and females (crosses).

Fig. 3. Differences in landmark configurations along PC 1. The right os coxae is orientated in order to highlight the major changes along the PC axis, approximately in posterior, medial and superior view from top to bottom. Extreme female configurations are on the left (lowest values of PC 1), and extreme male configuration are on the right (highest values of PC 1). To help the interpretation of the configurations, the area of the auricular surface in colored in red, the acetabulum in yellow, and the posterior part of the ischial tuberosity (defined by landmarks 5, 6 and 7) in light blue. (**a**) Approximate posterior view; (**b**) approximate medial view; (**c**) approximate superior view (pubis pointing downwards). The arrows point to the ischial spine.

Fig. 4. Plot of the regression (OLS) of maximum temperature on sexual differences for PC 4 (**a**; $r^2 = 0.291$) and PC 12 (**b**; $r^2 = 0.273$).



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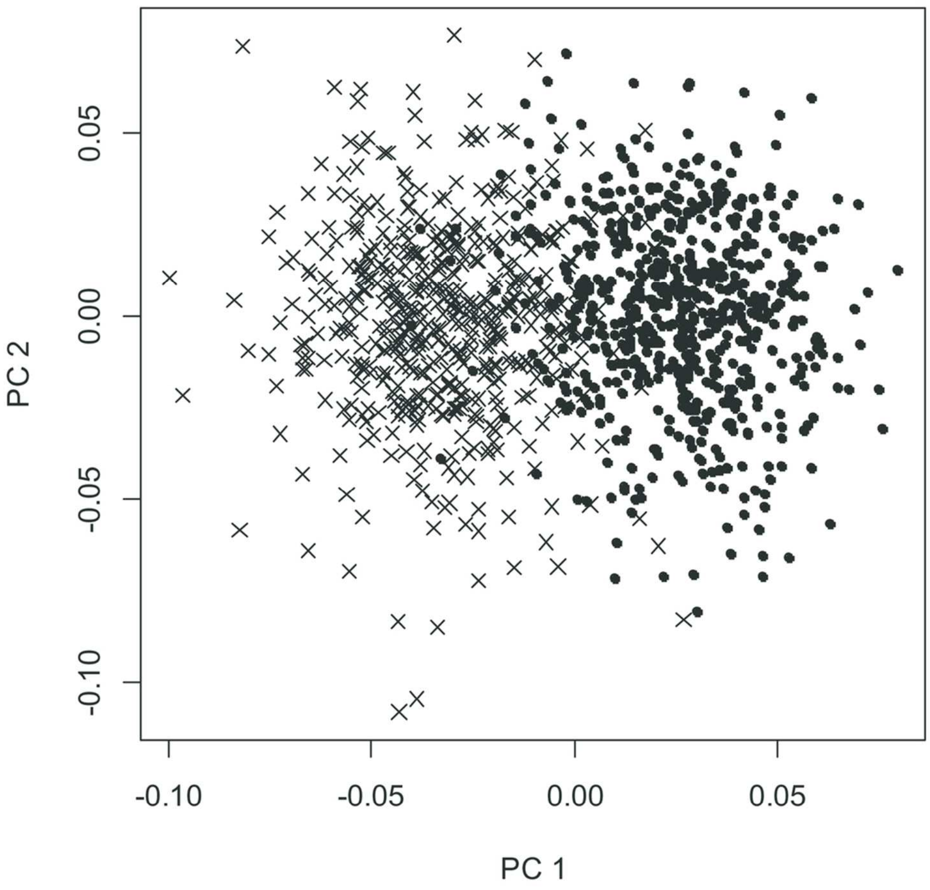

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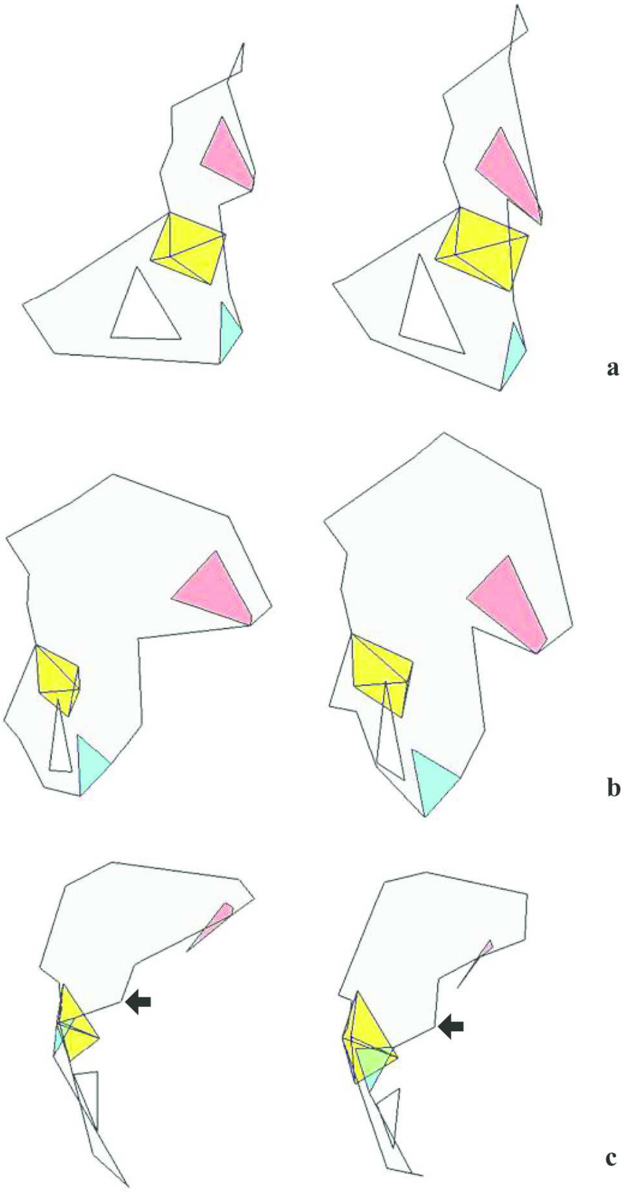

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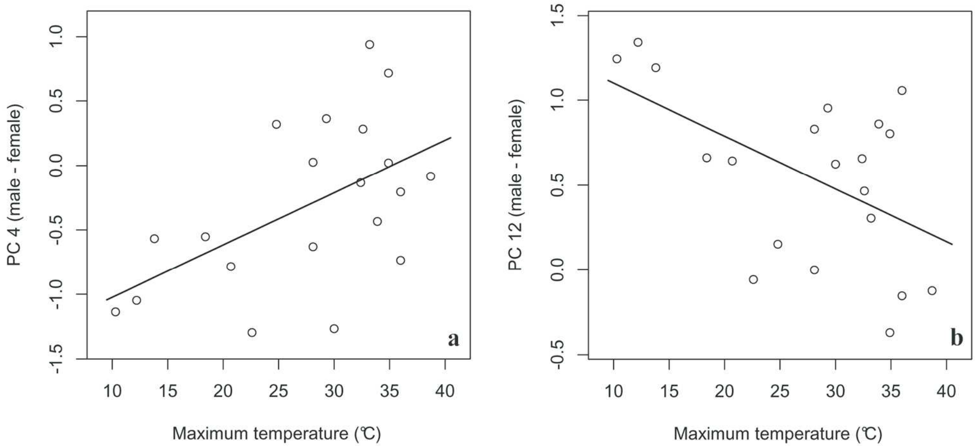

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