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**BIOLOGICAL SCIENCES**

## Human variation in the shape of the birth canal is significant and geographically structured

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Manuscripts

1 **Human variation in the shape of the birth canal is significant and**

2 **geographically structured**

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1

1 **Abstract (200)**

2 The human birth canal shows a tight fit with the size of the neonate, which can lead to obstetric

3 complications. This is not the case in other apes, and has been explained as the outcome of conflicting

4 evolutionary pressures for bipedal locomotion and parturition of a highly-encephalised fetus. Despite

5 the suggested evolutionary constraints on the female pelvis, we show that women are, in fact,

6 extremely variable in the shape of the bony birth canal, with human populations having differently-

7 shaped pelvic canals. Neutral evolution through genetic drift and differential migration are largely

8 responsible for the observed pattern of morphological diversity, which correlates well with neutral

9 genetic diversity. Climatic adaptation might have played a role, albeit a minor one, with populations

10 from colder regions showing a more transversally oval shape of the canal inlet. The significant extent of

11 canal shape variation among women from different regions of the world has important implications for

12 modern obstetric practice in multi-ethnic societies, as modern medical understanding has been largely

13 developed on studies of European women.

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2

1    **Introduction**

2        The shape of the human pelvis is often interpreted as an evolutionary compromise between

3    conflicting selective pressures: a short and compact structure is favored for bipedal locomotion, but a

4    spacious pelvic canal is essential for parturition of a highly encephalized neonate [1-4] (but see [5-7] for

5    recent challenges to this hypothesis). These contradictory requirements are often referred to as the

6    "obstetrical dilemma" [8], whereby locomotory efficiency poses a limit to the size of the birth canal in

7    our species, sometimes leading to childbirth complications due to cephalo-pelvic disproportion (a

8    mismatch between the size of the fetus' skull and the mother's birth canal). Due to the tight fit between

9    neonatal size and canal size, the fetus needs to perform a series of rotations to successfully navigate the

10   mother's birth canal. During childbirth, the fetus' head and shoulders align with the wider, transversal

11   diameter of the canal entrance (inlet). Progressing through the pelvis, however, the fetus needs to turn

12   to adapt to the changing shape of the canal, which tends to be sagittally deeper at its midpoint

13   (midplane), and it is often transversally larger again at the outlet [9]. This set of rotations has been

14   explained as a further consequence of the obstetrical dilemma, and in particular of the need to maintain

15   an obstetrically sufficient pelvic canal despite the changes in pelvic shape that accompanied full bipedal

16   adaptation [4].

17       Because of the effects of the contrasting selective pressures for locomotion and childbirth, it can

18   be expected that human variation in pelvic canal size and shape would be limited by functional

19   constraints. The obstetrical dilemma has been often discussed in terms of constraints on pelvic breadth,

20   especially bi-acetabular breadth, for efficient locomotion[5, 10]; however, bipedal adaptations in the

21   pelvis involved wider changes in bone shape and relative position, which affected and potentially

22   constrained all measurements of the birth canal [11]. Tin contrast to these expectations, there is some

23   evidence , however, that women vary substantially in the shape of the birth canal. The presence of

24   individual variation became obvious with the introduction of X-ray pelvimetry as a standard prenatal

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1   examination, during the first half of the 20th century. Even though the measurements were mostly taken

2   from women of European descent, and therefore had limited geographic diversity, the variation in the

3   shape of the canal was revealed to be substantial. The data were used to define different pelvic types

4   based on the geometry of the pelvic inlet [12, 13]. Caldwell and Moloy's typology, in particular, became

5   widely used in the obstetrical literature: depending on the shape of the inlet, the female pelvis was

6   defined as platypelloid (transversally oval inlet), android (heart-shaped inlet), gynecoid (round inlet), or

7   anthropoid (sagittally oval inlet). The different types of pelvis, defined by the shape of the birth canal,

8   have been associated in some studies to different likelihood of childbirth complications, which tends to

9   be higher for the platypelloid and android pelves [12, 14-16].

10      Recent studies have confirmed individual variation in pelvic canal dimensions among women,

11   higher than reported for dimensions of the limbs [17, 18]. Moreover, canal shape and overall pelvic

12   shape show significant variation among different ethnic groups [17, 19-21]. One possible explanation for

13   population differences in pelvic canal shape is adaptation to local environments. Modern human

14   populations living in high-latitude regions have been shown to have relatively wider pelves than tropical

15   populations [22-25]. This difference has been interpreted as evidence of long-term thermoregulatory

16   adaptation, whereby a wider trunk might help reduce heat loss in cold environments by decreasing the

17   surface-to-volume ratio of the body [24]. If climatic adaptation affected the breadth of the pelvic girdle,

18   and indirectly the breadth of the canal, it could have contributed in generating differences in canal

19   shape between populations.

20      Obstetrically-related selection might have also played a role. Childbirth complications are

21   expected to have a considerable direct effect on the fitness of a woman, which would be decreased *in*

22   *primis* by her death or injury, but also by the death or parturition-induced disabilities of the newborn. A

23   recent study suggested that shorter women, who on average have a higher incidence of cephalo-pelvic

24   disproportion [26], tend to have a rounder, obstetrically more effective birth canal [27]. The birth canal

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1    of small bodied populations, such as the KhoeSan, has also been shown to be larger than expected in

2    some dimensions [28].

3        Neutral processes such as genetic drift and migration can also be expected to generate

4    geographic variation, and have been shown to be important factors in explaining human variation in

5    both cranial and pelvic shape [29-34]. Indeed, these neutral processes likely played a bigger role than

6    climatic selection in shaping population differences in pelvic shape [35].

7        Understanding the extent to which women vary in the shape and size of the birth canal, and the

8    processes involved in shaping such variation, is important in many respects. Despite some indication of

9    substantial geographic diversity, modern obstetric textbooks are still relying on a typological description

10   of shape variation largely based on women of European descent. An update seems necessary, especially

11   in an increasingly multiethnic society. A better understanding of the range of modern birth canal

12   variation is also crucial to interpret the changes in pelvic shape that accompanied hominin evolution and

13   their relationship with obstetrical adaptations.

14       In this study, we evaluate global variation in the size and shape of the female birth canal, and we

15   test the relative importance of selective and neutral processes in shaping their geographic diversity.

16

17   **Materials and methods**

18       Measurements of the main diameters of the birth canal of rearticulated pelves were collected

19   following Kurki [28] (figure 1*a* and electronic supplementary material, table S1) from 348 female

20   individuals from 24 populations (figure 1*b* and electronic supplementary material, table S2table 1)

21   covering multiple continents. The samples come from different periods, ranging from the second

22   millennium BCE to the modern era (electronic supplementary material, table S31).

23       Sex was determined using standard non-metric methods [36, 37], which have been shown to

24   have high accuracy (88–96%) [36, 38, 39]. The pelvis was rearticulated by fitting as closely as possible

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1    the sacrum and the two ossa coxarum at the auricular surface. The gap at the level of the pubic

2    symphysis was filled with plasticine without altering the relative position of the bones, and the

3    rearticulated structure was kept firmly together using elastic bands. An internal caliper was used to

4    measure the anteroposterior and mediolateral diameters of the three planes of the canal. From the raw

5    data, inlet, midplane and outlet indices were estimated by dividing the respective anteroposterior

6    diameter by the mediolateral diameter, and the indices were used as canal shape data in all the

7    analyses.  Canal size was estimated as the sum of the geometric mean of the diameters in each plane.

8    The geometric mean was preferred to the arithmetic mean because it uses a product of the canal

9    diameters, therefore better resembling the area of the canal. The supero-inferior diameter of the

10   acetabulum (from the point on the acetabulum margin where ilium and ilio-pubic ramus meet and the

11   point furthest away) was measured in most of the individuals, excluding the individuals whose pelvis had

12   been mounted and could not be disassembled (see ~~electronic supplementary material, table S2~~table 1,

13   $N_{body\ size}$), as a proxy for body size. Following Ruff [40], the femoral head diameter was estimated from

14   the acetabular diameter with the following formula:

15                    *femoral diameter = (0.945 x acetabular diameter) - 6.1*

16          The estimated femoral head diameter was then used to calculate likely body mass using the

17   mean result of three different equations, as suggested by Auerbach and Ruff [41]: McHenry's [42]

18   formula for small-bodied samples, Grine et al. [43] formula for large-bodied samples, and Ruff et al. [44]

19   for females of European and African ancestry from a modern US samples. The combination of the three

20   equations reduces the likelihood of a bias in body mass estimation when using human populations of

21   different body sizes and proportions.

22          The location of each population was recorded as the coordinates of the centroid of the region

23   that the population likely inhabited (electronic supplementary material, table S~~4~~2). Geographic distance

24   from central sub-Saharan Africa (8°S 25°E), as hypothesized region of origin of our species, was

6

1    estimated as the shortest distance on land avoiding long sea crossing and mountain ranges over 2,000

2    m. of altitude [45]. The average minimum temperature of the coldest month and the average maximum

3    temperature of the warmest month for the population centroids (electronic supplementary material,

4    table S24) were obtained from WorldClim [www.worldclim.org; 46] as interpolated GIS layers at 30 arc-

5    second definition (*ca.* 1 km).

6        In the absence of available genetic and morphological data from the same individuals, we

7    assembled a set of populations with genetic information that matched our samples based on geographic

8    location and ancestry. We selected populations from the Human Origin dataset [47], which have been

9    typed for 594,924 Single Nucleotide Polymorphisms (SNPs). As it was impossible to find a suitable match

10   for all skeletal populations, the analyses which involved genetic data were run on a subset of the data

11   (electronic supplementary material, table S35).

12   *Variation in shape and size*

13       To evaluate the geographic pattern of variation in the shape of the birth canal, we compared the

14   variation in pelvic indices among continents using ANOVA and a post-hoc Tukey test. North African (here

15   represented by Egypt) and European populations were analyzed together, as movement of people

16   across and around the Mediterranean appears to have been higher than across the Sahara desert [48,

17   49].

18       The overall worldwide magnitude of shape variation in the birth canal was evaluated by

19   comparing the coefficient of variation (CV) of the three canal indices with other indices of body

20   proportions known to vary between human populations. Brachial (the maximum length of the radius

21   divided by the maximum length of the humerus) and crural (the maximum length of the tibia divided by

22   the maximum length of the femur) indices, and an index of general body shape (bi-iliac breadth divided

23   by maximum femoral length), were calculated for all female individuals in the Goldman dataset

24   [http://web.utk.edu/~auerbach/GOLD.htm; 50]. The dataset is freely available and includes 48

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1    populations from five continents; it is expected to include a wider range of body shape and size variation

2    than the dataset compiled for this study. Worldwide (species) variation in canal size was evaluated by

3    comparing the CV of the six canal measurements from this study with the CV of limb bones' length

4    (radius, humerus, tibia and femur) and pelvic width (bi-iliac breadth) for all female individuals in the

5    Goldman dataset. We calculated an empirical 95% confidence interval by employing a jackknife

6    approach, excluding a population at a time; the confidence interval was estimated by multiplying the

7    standard error by the $\alpha$-level critical value of a Student's t distribution with number of populations - 1

8    degrees of freedom.

9    *Tests of neutral evolution*

10    Neutral processes such as drift and migration are expected to shape genetic and phenotypic

11    variation within a species both in the presence and in the absence of selection, and reflect the vagaries

12    of past population history. Indeed, the geographic pattern of modern human genetic variation has been

13    shown to be largely the outcome of neutral evolution, and has been used to reconstruct the

14    demographic history of our species from its origin in Africa throughout its expansion into other

15    continents [51-53]. Directional selection can also play a role in shaping genetic and phenotypic variation,

16    and many phenotypes have a further layer of variability added by developmental plasticity in response

17    to the environment. Despite these caveats, in the absence of strong selection or high plasticity (i.e., in

18    traits with relatively high heritability) phenotypic variation will reflect past population history [29, 54].

19    For the reasons mentioned above, when evaluating the geographic pattern of human birth canal

20    variation, we start from the null hypothesis that geographic patterns reflects past population history;

21    significant deviations above and beyond this simple expectation can be taken as potentially representing

22    the effects of natural selection. If the shape of the birth canal evolved mainly neutrally in our species, in

23    the absence of strong selection or high environmental plasticity, we would expect a pattern of variation

24    similar, albeit noisier, to the one shown by neutral genetic variation.

8

1    The presence of a signature of past population history was evaluated in two different ways:

2    1)    phenotypic diversity should decline with increasing distance from sub-Saharan Africa,

3    due to the iterative founder effect that accompanied the colonization of the other continents [52];

4    2)    there should be a significant correlation between genetic and phenotypic distance

5    between populations.

6    To test for the signature of the Out-of-Africa expansion, individual within-population variances

7    were calculated as the average of the trace of the variance-covariance phenotypic matrix of canal

8    indices, and regressed on population distances from central sub-Saharan Africa [31].

9    Relethford and Blangero's [55] method was used to calculate a matrix of between-population

10   phenotypic distances (Q), while correcting for small populations sample sizes [56]. This approach treats

11   the canal indices as quantitative traits, whereby different genetic loci have an equal and additive effect

12   [55]. In the absence of an estimate of the additive genetic covariance matrix, the phenotypic covariance

13   matrix was used as an approximation under the assumption of proportionality [57]. Given the lack of

14   heritability estimates for the canal measurements, total heritability was assumed in all analyses. Since

15   phenotypic distances as estimated in the Q matrix are effectively ratios, the distance matrix was

16   normalized using an arcsine square root transformation [33]. For the genetic data, after thinning SNP in

17   linkage disequilibrium using PLINK (v1.07) [58] with parameters --indep-pairwise 50 10 0.1, we

18   computed pairwise between-population $F_{st}$ using Arlequin [59]. The correlation between pairwise

19   between-population phenotypic and genetic distances was tested using a Mantel test with 10,000

20   randomizations.

21   *The effects of climate*

22   Climatic-related directional selection was evaluated by testing for a correlation between

23   pairwise between-population phenotypic distances and temperature differences. In order to take into

24   account the underlying pattern of genetic similarity due to past demographic events, the correlation

9

1    between phenotypic and temperature differences was also calculated while correcting for genetic

2    distance (in the reduced dataset) using a partial Mantel test. The analyses were repeated for each pelvic

3    index.

4    *Obstetrically-related selection*

5        In the absence of a measure of stature, small body mass was used as an indication of women at

6    higher risk of cephalo-pelvic disproportion. It has been suggested that obstetric selective pressures led

7    to a relatively more spacious birth canal in small women [28]. We tested this hypothesis of a non-linear

8    relationship between canal size and body mass by means of linear, quadratic and cubic regression

9    analyses. Variation in canal shape with body size was explored by plotting the three indices against body

10   mass, to test whether small women tend to have a rounder and obstetrically more efficient birth canal

11   [27]. All analyses were performed using the software R version 3.4 [60].

10

1    **Results**

2         Human variation in the shape of the birth canal appears to be geographically structured. Figure

3    2 shows the variation in canal indices in different continents, highlighting the geographic pattern of

4    variation. An analysis of variance (ANOVA) and post hoc Tukey tests showed that most of these

5    differences are highly significant (electronic supplementary material, table S4~~6~~). Sub-Saharan African

6    populations are overall characterized by a deeper birth canal in the anterior-posterior direction,

7    throughout the three planes (inlet, midplane, and outlet), while Native American populations fall at the

8    other extreme of variation with a more transversally-wide canal. Asian and European/North African

9    populations show an intermediate morphology (figure 2). The differences are particularly obvious for

10   the inlet, which tends to be more markedly oval in Americans and Europeans/North Africans (figure 2*a*),

11   and for the outlet, which tends to be sagittally-oval in sub-Saharan Africans and Asians, while it is

12   generally transversally-oval in Americans and Europeans/North Africans (figure 2*c*). It is worth noting,

13   however, that canal variation is continuous and without abrupt differences between regions, when

14   analyzed at the single populations' level (figure 3*a* and electronic supplementary material, figure S1).

15        The magnitude of shape variation, measured as coefficient of variation (CV), is similar ~~between~~

16   among the three planes, and consistently higher than the other body proportion indices and

17   measurements (figure 3*b* and electronic supplementary material, table S5~~7~~). The comparative indices

18   are known to vary significantly between human populations, and have been suggested to have been

19   under climatically-driven divergent selection [22, 23]. The fact that the birth canal indices show a higher

20   CV is, therefore, remarkable and unexpected.

21        *Tests of neutral evolution*

22        Strong evidence of neutral evolution of the shape of the canal comes from the fact that within-

23   population phenotypic diversity tends to decrease with increasing geographic distance from sub-

24   Saharan Africa ($R^2$= 0.435, $F_{1,22}$=16.95, p<0.001, figure 4*a*), mirroring the pattern shown by neutral

11

1     genetic markers [52] and related to the serial founder events that accompanied the Out-of-Africa

2     expansion. Phenotypic distance between populations is significantly correlated with genetic distance ($R^2$

3     = 0.242, Mantel p < 0.001; figure 4*b*), providing additional evidence that neutral evolutionary processes

4     played an important role in shaping canal variation on a global scale.

5     *The effects of climate*

6         The analyses revealed no significant correlation between overall canal shape differences and

7     temperature differences between populations, before or after correcting for genetic distance (electronic

8     supplementary material, table S6~~8~~). When the three planes were analyzed separately, however, a ~~small~~

9     ~~but~~ significant correlation was found between inlet shape differences and temperature differences

10     (electronic supplementary material, table S7~~9~~). The correlation was still significant after correcting for

11     pairwise genetic distances. The inlet tends to be more transversally oval in colder climates ($R^2$=0.394,

12     $F_{1,22}$=14.29, p=0.001; figure 4*c*).

13     *Obstetrically-related selection*

14         There is a linear increase in birth canal size with body mass, as estimated from the acetabular

15     diameter ($R^2$=0.215, $F_{1,325}$=88.74, p<0.001). The residuals of the linear regression do not show any

16     remaining effect of body mass on canal size (figure 4*d*); moreover, adding a quadratic ($F_{1,325}$= 0.004;

17     p=949) and cubic term ($F_{1,324}$=0.045; p=0.835) to the regression model does not improve the fit. The

18     results, therefore, fail to support the hypothesis that smaller women have a larger-than-expected birth

19     canal. Furthermore, we could not identify any obvious difference in canal shape between women of

20     different body masses (electronic supplementary material, figure S2).

21

1    **Discussion**

2    Women are remarkably variable in the shape of the birth canal. The three planes that define the

3    geometry of the passage vary widely between individuals, in contrast with the expectations of a highly

4    constrained structure under strong selective pressures. The classic narrative of the "obstetrical

5    dilemma" sees the birth canal as a tight compromise between a narrow, locomotory efficient pelvis and

6    a wide, obstetrically sufficient pelvic canal, implying that functional constraints should limit female

7    variation in the shape of the canal. This is clearly incorrect.

8    Several authors have recently criticized the notion of an "obstetrical dilemma", first of all by

9    showing that the larger female pelvis is not less efficient than the narrower male pelvis during walking

10    or running [5-7] (but see [61]). Grabowski and colleagues [62, 63] showed that the human pelvis is a less

11    constrained structure than in other apes, with lower covariance between pelvic traits, allowing it to

12    evolve in more independent directions. The findings presented here provide additional evidence that

13    the classic hypothesis of human pelvic evolution as a strict functional compromise might need to be

14    rethought in a less simplistic way.

15    On the other hand, injuries or death of the mother and the newborn during parturition are not

16    rare, especially in areas of the world where modern medical assistance is not readily available [64].

17    Wells and colleagues [18] suggest that obstetrical difficulties could have been exacerbated in recent

18    human evolution by the adoption of agriculture. The shift in diet associated with food production could

19    have increased neonatal growth and level of adiposity, resulting in a tighter fit with the birth canal.

20    Changes in diet and lifestyle in the last century, leading to the modern obesity epidemic, might have

21    further increased relative neonatal size, as evidenced by the positive correlation between maternal

22    obesity and fetal macrosomia (i.e. fetal weight exceeding the $90^{th}$ percentile of birth weight in a given

23    population) [65]. In this sense, the occurrence of cephalo-pelvic disproportion and related childbirth

1    complications would not be (solely) the consequence of an evolutionary compromise, but evidence of

2    recent shifts in subsistence.

3         When analyzed at a global scale, variation in the shape of the birth canal is geographically

4    structured and women in different regions of the world tend to have, on average, a differently shaped

5    canal.

6         Climate could be expected to have played a role in increasing canal variation, as differences in

7    minimum temperature, in particular, have been shown to explain some human variation in body

8    proportions, cranial morphology, and crucially pelvic breadth and the shape of the os coxae [24, 25, 30,

9    35, 66-69]. Unexpectedly, however, differences in overall canal shape between populations are not

10   correlated to temperature differences, and a significant , but small, correlation was found only for the

11   shape of the inlet. Instead, large part of the variation in canal shape is explained by neutral genetic

12   differences between populations, suggesting that most of the observed canal differences might have

13   stemmed from the stochastic effects of genetic drift that accompanied the geographic expansion of our

14   species.

15        *Homo sapiens* originated in Africa and dispersed rapidly into new continents in the last 60-100

16   thousand years, a relatively recent time (see [70] for a recent review of the evidence). The combination

17   of a small founding population size [71] and a quick dispersal meant that a series of genetic bottlenecks

18   accompanied the colonization of new areas of the world. Each founding event, in fact, was achieved by a

19   subpopulation carrying only a portion of the ancestral population's genetic diversity. The signature of

20   these serial founding events is evident in modern populations' genetic variation, whereby genetic

21   diversity decreases with increasing distance from Africa (and number of founding events in the

22   population's history) [52]. Within-population variance in birth canal shape also declines with distance for

23   sub-Saharan Africa, reflecting the effects of the same demographic processes. Not only is this clear

24   evidence that canal variation has been shaped by past population history, but the signal appears to be

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1     particularly strong. Distance from Africa explains a remarkable 43.5% of canal diversity within human

2     populations, a proportion higher than that reported for the cranium ($R^2$ = 0.19–0.28; [29, 72]) and

3     consistent with previous results for the os coxae ($R^2$ = 0.31–0.47; [31]).

4           Differences in the shape of the canal between populations are significantly correlated with

5     neutral genetic distances, confirming the important role of neutral evolutionary processes and past

6     demographic events in generating the observed geographic pattern in canal morphology. Shape

7     differences between main geographic regions have likely arisen from a stochastic drift towards different

8     average shapes along the various routes of expansion out of Africa and into new continents.

9           Recent studies have suggested that selection might have acted in several ways to reduce the risk

10    of cephalo-pelvic disproportion during childbirth. For example, women with a smaller head tend to give

11    birth to small-headed babies [73], while women with a larger head, who are more likely to give birth to

12    babies with a larger head, tend to have a rounder and obstetrically more capable birth canal [27].

13    Fischer and Mitteroeker [27] also reported a rounder birth canal in shorter women, which are at higher

14    risk of childbirth complications [26], but such a pattern was not observed in this study using body size as

15    a proxy for stature. The use of estimated body mass instead of stature might account for the difference

16    in results, despite stature and femoral head diameter being moderately correlated (r=0.26-0.71 in

17    European- and African-Americans [74]). We also did not observe a relatively more spacious canal in

18    smaller women, as suggested by Kurki's [28] study comparing small-bodied KhoeSan women and larger-

19    bodied European women.

20          The remarkable diversity of the human birth canal highlighted by this study, both within and

21    between human populations, has important implications for the interpretation of pelvic morphology in

22    extinct hominins. Paleoanthropologists have studied the size and shape of the birth canal in several

23    extinct hominin species, to identify at what point in human evolution obstetrical constraints became an

24    important factor. The comparison between hominin and modern human pelves, however, is often

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1  performed without explicitly accounting for the range of variation in modern humans [75-77]. This is

2  particularly problematic because of the bias in the human populations used for comparative studies,

3  with populations of European ancestry being over-represented or sometimes used as the sole

4  representative group [78, 79].

5        The canal indices of extinct hominins often fall within the range of modern human variation,

6  especially for the most recent species (electronic supplementary material, table S8~~10~~). Human variation

7  between geographically diverse modern populations is substantial, and can help put the differences

8  between some of the fossils into perspective. A similar degree of variation in canal morphology between

9  fossil individuals is very likely to be due to the effect of genetic drift; it would not necessarily imply

10 adaptation by natural selection and a significant change in obstetrical constraints and birth mechanism

11 in hominin species, as has been suggested before [10, 25, 80].

12      The magnitude of canal shape variation in human populations revealed by this study sits in stark

13 contrast with the simplified description of the typical human canal morphology in many anatomy books.

14 The description is often based on the most common shape in European individuals, and does not take

15 into account the wide range of variation showed by our species. The rotation movements required by

16 the fetus to negotiate the twisting passage are also generally reported based on an average European

17 experience. Substantial differences in the shape of the canal in modern populations, especially in the

18 outlet, might translate into differences in the fetal movements and presentation. Indeed, X-ray studies

19 of labouring women, from the first half of the 20$^{th}$ century, provide some evidence of differences in

20 foetal presentation during labour depending on the shape of the mother's pelvic inlet [16]. The head of

21 the foetus tends to align to the wider diameter of the inlet at engagement. A different rotation of the

22 fetus from the norm might, therefore, occur in women with a differently shaped canal, and should not

23 necessarily be interpreted as a problem. Given the geographic differences in canal shape among modern

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1    populations showed by this study, a wider range of variation in childbirth might be especially expected

2    in modern multi-ethnic societies, and should be taken into account in obstetric practice.

1    **Data**

2    The dataset supporting this article has been uploaded on Dryad (doi:10.5061/dryad.1gk3014).

3    **Competing interests**

4    We have no competing interests.

5    **Authors' contributions**

6    LB contributed to the design the study, collected the pelvic measurements, analyzed the data, and

7    wrote the manuscript. AM contributed to the design of the study, analyzed the genetic data, and

8    contributed to the writing and editing of the manuscript.

9    **Aknowledgements**

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**Table and figure captions**

**Table 1.** Skeletal samples included in the study. N $_{body\ size}$ is the number of individuals for whom it was possible to estimate body size based on the size of the acetabulum.

**Figure 1.** Pelvic canal measurements (*a*) and population samples (*b*) used in this study. A = anteroposterior (AP) diameter of the inlet, from the sacral promontory to the dorsomedial superior pubis; B = AP diameter of the midplane, from the junction of the fourth and fifth sacral vertebrae to the dorsomedial inferior pubis; C = AP diameter of the outlet, from the apex of the fifth sacral vertebrae to the dorsomedial inferior pubis; D = mediolateral (ML) diameter of the inlet, as maximum distance between the linea terminalis; E = ML diameter of the midplane, as distance between the ischial spines (often approximated due to damage to the spines); F= ML diameter of the outlet between the inner margins of the transverse ridge of the ischial tuberosities.

**Figure 2.** Variation in the inlet (*a*), midplane (*b*) and outlet (*c*) indices within four major geographic regions. The boxes represent the interquartile distance, the whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range, and outliers are highlighted as open circles. The ovals on the left represent the extremes of shape observed in this study for each of the canal planes. The endpoints of the color bars link pairs of regions with significantly different canal shapes (see results of post-hoc Tukey tests in electronic supplementary material, table S4).
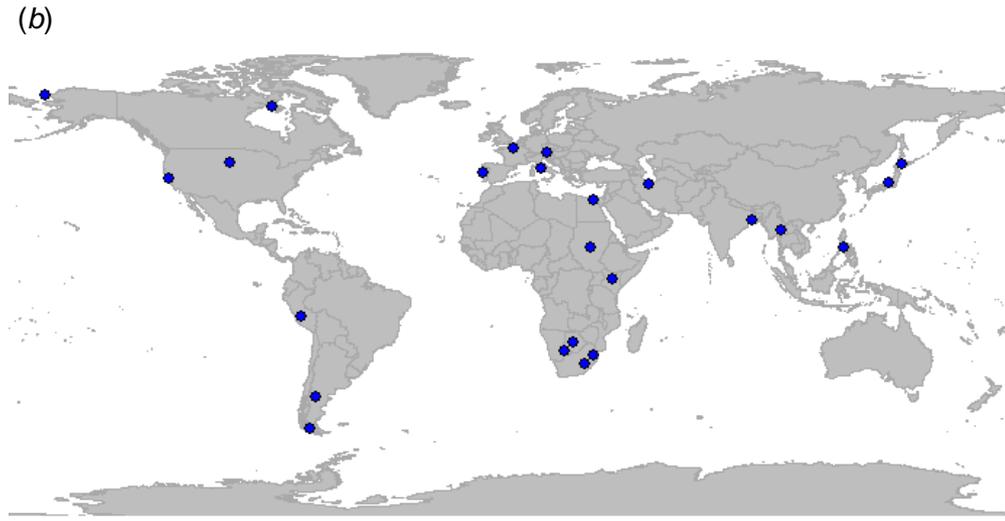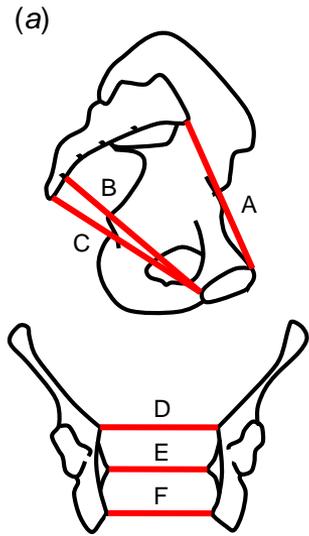
**Figure 3.** 3D plot of population averages for the inlet, midplane and outlet indices (*a*) and coefficient of variation for various postcranial indices and measurements (*b*). Populations from four geographic regions are highlighted in different colours in panel (*a*) (Africa = green, Asia = yellow, Europe and North Africa = red, Americas = blue). Panel (*b*) reports the coefficient of variation (CV) for the birth canal (in blue; this study) and other postcranial indices and measurements (in white; Goldman dataset). Indices are highlighted by an asterisk; pelvis/femur refers to pelvic breadth divided by femoral length. The 95% confidence interval obtained after a jackknife procedure is shown in red.
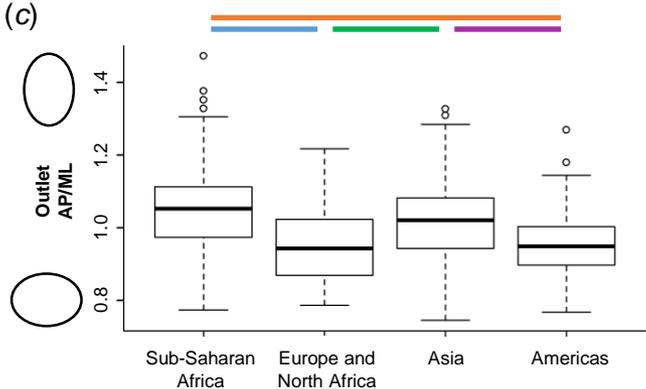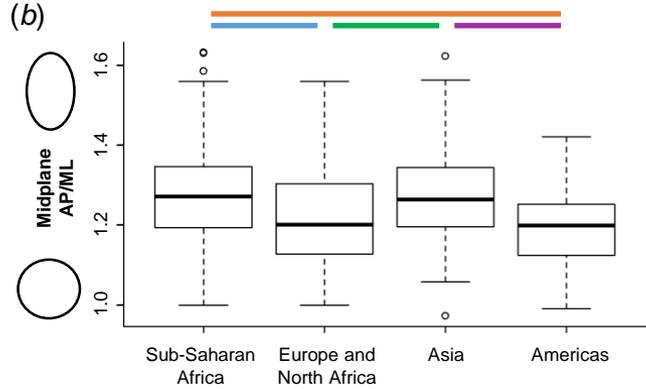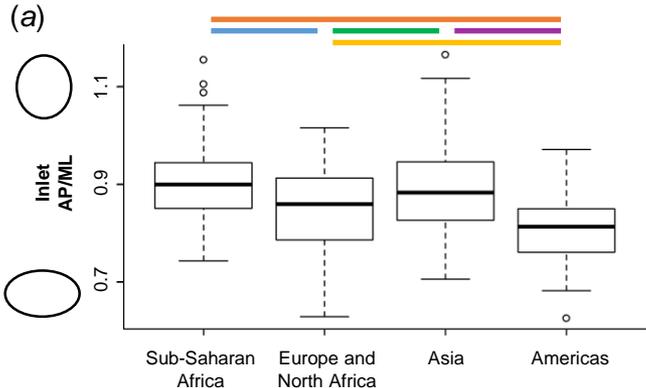
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**Figure 4: Graphical representation of the key results**. (*a*) plot of within-population phenotypic distance and geographic distance from central sub-Saharan Africa; (*b*) plot of between-population phenotypic distance and genetic distance; (*c*) plot of the population average inlet index against minimum temperature; (*d*) plot of the residuals of the regression of canal size on body mass, against body mass.
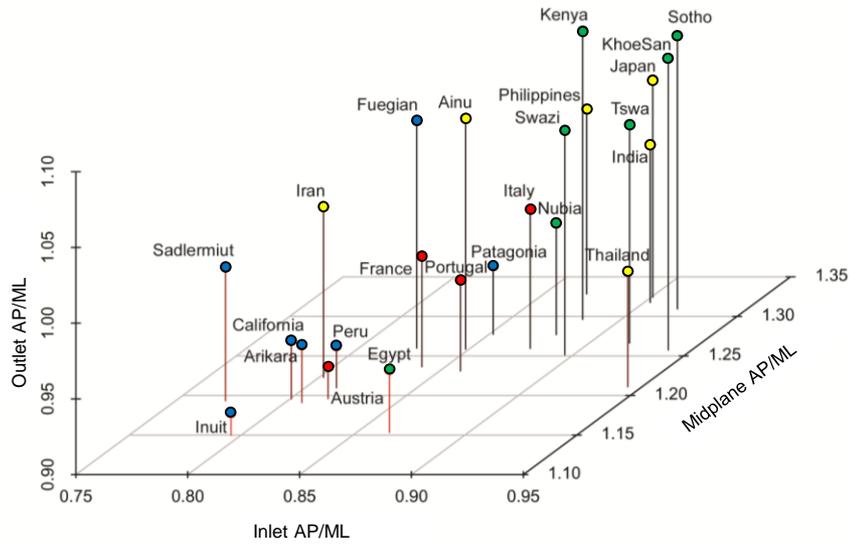
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**Tables**

**Table 1.** Skeletal samples included in the study. N $_{body\ size}$ is the number of individuals for whom it was possible to estimate body size based on the size of the acetabulum.

| Region | N $_{tot}$ | N $_{body\ size}$ |
| --- | --- | --- |
| *Africa* | | |
| Botswana, Tswana | 18 | 18 |
| Kenya, Kykuyu | 21 | 21 |
| Lesotho, Sotho | 21 | 21 |
| Nubia | 17 | 16 |
| South Africa, Khoe-San | 12 | 12 |
| Swaziland | 16 | 16 |
| *Europe/North Africa* | | |
| Austria | 13 | 13 |
| Egypt dynastic | 9 | 9 |
| France | 15 | 15 |
| Italy | 6 | 6 |
| Portugal | 25 | 25 |
| *Asia* | | |
| Ainu, Japan | 13 | 3 |
| India | 11 | 6 |
| Iran (Iron Age) | 11 | 11 |
| Japan | 21 | 21 |
| Philippines, 'negritos' | 8 | 8 |
| Thailand | 21 | 20 |
| *America* | | |
| Alaska, Ipiutak and Tigara | 21 | 21 |
| Argentina, Patagonia | 7 | 7 |
| Canada, Sadlermiut | 9 | 9 |
| Chile, Fuegians | 9 | 9 |
| Native Californians | 15 | 15 |
| Peru | 13 | 13 |
| South Dakota, Arikara | 16 | 15 |

(a)

(b)