

**PROCEEDINGS OF
THE ROYAL SOCIETY B**
BIOLOGICAL SCIENCES

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

Journal:	<i>Proceedings B</i>
Manuscript ID	RSPB-2018-1807.R1
Article Type:	Research
Date Submitted by the Author:	01-Oct-2018
Complete List of Authors:	Betti, Lia; University of Roehampton, Department of Life Sciences Manica, Andrea; University of Cambridge, Zoology
Subject:	Evolution < BIOLOGY
Keywords:	human, pelvis, birth canal, obstetrical constraints, neutral variation, climate
Proceedings B category:	Evolution

SCHOLARONE™
Manuscripts

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

3 **Lia Betti^{*a}, Andrea Manica^b**

4 * Corresponding author Email: Lia.Betti@roehampton.ac.uk; tel.: +44 (0)1223 764722

5 ^aCentre for Research in Evolutionary, Social and Inter-Disciplinary Anthropology, Department of Life
6 Sciences, University of Roehampton, London, UK.

7 ^bDepartment of Zoology, University of Cambridge, Cambridge, UK.

8

9

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.

14

15 **Keywords:** human; pelvis; birth canal; obstetrical constraints; neutral variation; climate

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

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 pelvises [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 pelvises 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

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 pelvis were collected
19 following Kurki [28] (figure 1a and electronic supplementary material, table S1) from 348 female
20 individuals from 24 populations (figure 1b and electronic supplementary material, table S2 and table 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 S3).

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

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 $N_{\text{body size}}$), as a proxy for body size. Following Ruff [40], the femoral head diameter was estimated from
14 the acetabular diameter with the following formula:

$$\text{femoral diameter} = (0.945 \times \text{acetabular diameter}) - 6.1$$

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 S4](#)table 2). Geographic distance
24 from central sub-Saharan Africa (8°S 25°E), as hypothesized region of origin of our species, was

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

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 α -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.

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 Fst 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

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].

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 S⁴⁶). 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 2a),
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 2c). 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 3a 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 3b and electronic supplementary material, table S⁵⁷). 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 4a), mirroring the pattern shown by neutral

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 4b), 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 S~~68~~). 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 S~~79~~). 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 4c).

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 4d); 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 90th 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

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 ($R^2 = 0.19\text{--}0.28$; [29, 72]) and
3 consistent with previous results for the os coxae ($R^2 = 0.31\text{--}0.47$; [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 Mitteroecker [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 ($r=0.26\text{--}0.71$ 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 Khoisan 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 pelvis, however, is often

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 S~~810~~). 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 20th 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

- 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 **Acknowledgements**

10 A special thank to Ben Auerbach for making the Goldman dataset available to the scientific community,
11 and to Charles Roseman for useful advice in the early stages of this study. We are grateful to Ben
12 Auerbach, Brendon Billings, Michael Black, Jerome Cybulski, Gisselle Garcia-Pack, Lyman M. Jellema,
13 Natasha Johnson, Maureen Klemp, Osamu Kondo, Robert Kruszynski, Pasuk Mahakkanukrauh, Giorgio
14 Manzi, Philippe Mennecier, Marta Mirazon Lahr, Janet Monge, David Morris, Masaharu Motokawa,
15 Ogeto Mwebi, Tori Randall, Ana Luisa Santos, Maria Teschler-Nicola, Tim White, and Monica Zavattaro
16 for allowing access to the collections and for general assistance during data collection.

17 **Funding**

18 Wenner-Gren Foundation for Anthropological Research; the Ian and Christine Bolt Scholarship
19 (University of Kent); Sigma Xi Grant; European Union Synthesys Grants; American Museum of Natural
20 History Collection Study Grant; University of Kent Ph.D. Research Scholarship.

References

- [1] Schultz AH. 1949 Sex differences in the pelvis of primates. *Am. J. Phys. Anthropol.* **7**, 401-424. (doi:10.1002/ajpa.1330070307).
- [2] Leutenegger W. 1974 Functional aspects of pelvic morphology in simian Primates. *J. Hum. Evol.* **3**, 207-222.
- [3] Rosenberg K, Trevathan W. 1995 Bipedalism and human birth: the obstetrical dilemma revisited. *Evol. Anthropol.* **4**, 161-168.
- [4] Trevathan W, Rosenberg K. 2000 The shoulders follow the head: postcranial constraints on human childbirth. *J. Hum. Evol.* **39**, 583-586.
- [5] Dunsworth HM, Warrener AG, Deacon T, Ellison PT, Pontzer H. 2012 Metabolic hypothesis for human altriciality. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 15212-15216. (doi:10.1073/pnas.1205282109).
- [6] Wall-Scheffler CM. 2012 Energetics, locomotion, and female reproduction: implications for human evolution. *Annu. Rev. Anthropol.* **41**, 71-85. (doi:10.1146/annurev-anthro-092611-145739).
- [7] Warrener AG, Lewton KL, Pontzer H, Lieberman DE. 2015 A wider pelvis does not increase locomotor cost in humans, with implications for the evolution of childbirth. *PLOS ONE* **10**, e0118903. (doi:10.1371/journal.pone.0118903).
- [8] Washburn SL. 1960 Tools and human evolution. *Sci. Am.* **203**, 3-15.
- [9] Abitbol MM. 1991 Ontogeny and evolution of pelvic diameters in anthropoid primates and in *Australopithecus afarensis* (AL 288-1). *Am. J. Phys. Anthropol.* **85**, 135-148. (doi:10.1002/ajpa.1330850203).
- [10] Ruff C. 1995 Biomechanics of the hip and birth in early *Homo*. *Am. J. Phys. Anthropol.* **98**, 527-574.
- [11] Rosenberg KR. 1992 The evolution of modern human childbirth. *Am. J. Phys. Anthropol.* **35**, 89-124. (doi:10.1002/ajpa.1330350605).
- [12] Caldwell WE, Moloy HC. 1933 Anatomical variations in the female pelvis and their effect in labor with a suggested classification. *Am. J. Obstet. Gynecol.* **26**, 479-505. (doi:10.1016/S0002-9378(33)90194-5).
- [13] Greulich WW, Thoms H. 1938 The dimensions of the pelvic inlet of 789 white females. *Anat. Rec.* **72**, 45-51. (doi:10.1002/ar.1090720105).
- [14] Jagani N, Schulman H, Chandra P, Gonzalez R, Fleischer A. 1981 The predictability of labor outcome from a comparison of birth weight and x-ray pelvimetry. *Am. J. Obstet. Gynecol.* **139**, 507-511.
- [15] Stålberg K, Bodestedt Å, Lyrenås S, Axelsson O. 2006 A narrow pelvic outlet increases the risk for emergency cesarean section. *Acta Obstet. Gynecol. Scand.* **85**, 821-824. (doi:10.1080/00016340600593521).
- [16] Steer CM. 1975 *Moloy's evaluation of the pelvis in obstetrics*. Third edition ed. New York, Plenum Publishing Corporation.
- [17] Kurki HK. 2013 Skeletal variability in the pelvis and limb skeleton of humans: does stabilizing selection limit female pelvic variation? *Am. J. Hum. Biol.* **25**, 795-802. (doi:10.1002/ajhb.22455).
- [18] Wells JCK, DeSilva JM, Stock JT. 2012 The obstetric dilemma: an ancient game of Russian roulette, or a variable dilemma sensitive to ecology? *Am. J. Phys. Anthropol.* **149**, 40-71. (doi:10.1002/ajpa.22160).
- [19] Handa VL, Lockhart ME, Fielding JR, Bradley CS, Brubaker L, Cundiff GW, Ye W, Richter HE. 2008 Racial differences in pelvic anatomy by magnetic resonance imaging. *Obstet. Gynecol.* **111**, 914-920.
- [20] Kurki HK. 2013 Bony pelvic canal size and shape in relation to body proportionality in humans. *Am. J. Phys. Anthropol.* **151**, 88-101. (doi:10.1002/ajpa.22243).
- [21] Patriquin ML, Steyn M, Loth SR. 2002 Metric assessment of race from the pelvis in South Africans. *Forensic Sci. Int.* **127**, 104-113.

- [22] Cowgill LW, Eleazer CD, Auerbach BM, Temple DH, Okazaki K. 2012 Developmental variation in ecogeographic body proportions. *Am. J. Phys. Anthropol.* **148**, 557-570. (doi:10.1002/ajpa.22072).
- [23] Holliday TW, Hilton CE. 2010 Body proportions of circumpolar peoples as evidenced from skeletal data: Ipiutak and Tigara (Point Hope) versus Kodiak Island Inuit. *Am. J. Phys. Anthropol.* **142**, 287-302. (doi:10.1002/ajpa.21226).
- [24] Ruff C. 1994 Morphological adaptation to climate in modern and fossil hominids. *Am. J. Phys. Anthropol.* **37**, 65-107.
- [25] Weaver TD, Hublin JJ. 2009 Neandertal birth canal shape and the evolution of human childbirth. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 8151-8156. (doi:10.1073/pnas.0812554106).
- [26] Prasad M, Al-Taher H. 2002 Maternal height and labour outcome. *J. Obstet. Gynaecol.* **22**, 513-515.
- [27] Fischer B, Mitteroecker P. 2015 Covariation between human pelvis shape, stature, and head size alleviates the obstetric dilemma. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 5655-5660. (doi:10.1073/pnas.1420325112).
- [28] Kurki HK. 2007 Protection of obstetric dimensions in a small-bodied human sample. *Am. J. Phys. Anthropol.* **133**, 1152-1165. (doi:10.1002/ajpa.20636).
- [29] Betti L, Balloux F, Hanihara T, Manica A. 2009 Ancient demography, not climate, explains within-population phenotypic diversity in humans. *Proc. R. Soc. Lond. B Biol. Sci.* **276**, 809-814.
- [30] Betti L, Balloux F, Hanihara T, Manica A. 2010 The relative role of drift and selection in shaping the human skull. *Am. J. Phys. Anthropol.* **141**, 76-82.
- [31] 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**, e55909.
- [32] Harvati K, Weaver TD. 2006 Human cranial anatomy and the differential preservation of population history and climate signatures. *Anat. Rec. Part A* **288A**, 1225-1233.
- [33] Roseman CC. 2004 Detecting interregionally diversifying natural selection on modern human cranial form by using matched molecular and morphometric data. *Proc. Natl. Acad. Sci. U. S. A.* **101**, 12824-12829.
- [34] Betti L. 2017 Human variation in pelvic shape and the effects of climate and past population history. *The Anatomical Record* **300**, 687-697. (doi:10.1002/ar.23542).
- [35] Betti L, von Cramon-Taubadel N, Manica A, Lycett SJ. 2014 The interaction of neutral evolutionary processes with climatically-driven adaptive changes in the 3D shape of the human os coxae. *J. Hum. Evol.* **73**, 64-74. (doi:https://doi.org/10.1016/j.jhevol.2014.02.021).
- [36] Phenice TW. 1969 A newly developed visual method of sexing the os pubis. *Am. J. Phys. Anthropol.* **30**, 297-301.
- [37] Sutherland LD, Suchey JM. 1991 Use of the ventral arc in pubic sex determination. *J. Forensic Sci.* **36**, 501-511.
- [38] McFadden C, Oxenham MF. 2016 Revisiting the Phenice technique sex classification results reported by MacLaughlin and Bruce (1990). *Am. J. Phys. Anthropol.* **159**, 182-183. (doi:doi:10.1002/ajpa.22839).
- [39] Ubelaker D, Volk C. 2002 A test of the Phenice method for the estimation of sex. *J. Forensic Sci.* **47**, 19-24.
- [40] Ruff C. 2010 Body size and body shape in early hominins - implications of the Gona pelvis. *J. Hum. Evol.* **58**, 166-178.
- [41] Auerbach BM, Ruff CB. 2004 Human body mass estimation: a comparison of "morphometric" and "mechanical" methods. *Am. J. Phys. Anthropol.* **125**, 331-342. (doi:10.1002/ajpa.20032).
- [42] McHenry HM. 1992 Body size and proportions in early hominids. *Am. J. Phys. Anthropol.* **87**, 407-431. (doi:10.1002/ajpa.1330870404).

- [43] Grine FE, Jungers WL, Tobias PV, Pearson OM. 1995 Fossil *Homo* femur from Berg Aukas, northern Namibia. *Am. J. Phys. Anthropol.* **97**, 151-185. (doi:10.1002/ajpa.1330970207).
- [44] Ruff CB, Scott WW, Liu AYC. 1991 Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *Am. J. Phys. Anthropol.* **86**, 397-413. (doi:10.1002/ajpa.1330860306).
- [45] Manica A, Prugnolle F, Balloux F. 2005 Geography is a better determinant of human genetic differentiation than ethnicity. *Hum. Genet.* **118**, 366-371.
- [46] Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005 Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965-1978.
- [47] Lazaridis I *et al.* 2014 Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature* **513**, 409-413. (doi:10.1038/nature13673).
- [48] Font-Porterias N, Solé-Morata N, Serra-Vidal G, Bekada A, Fadhlaoui-Zid K, Zalloua P, Calafell F, Comas D. 2018 The genetic landscape of Mediterranean North African populations through complete mtDNA sequences. *Ann. Hum. Biol.* **45**, 98-104. (doi:10.1080/03014460.2017.1413133).
- [49] Henn BM *et al.* 2012 Genomic ancestry of North Africans supports back-to-Africa migrations. *PLOS Genetics* **8**, e1002397. (doi:10.1371/journal.pgen.1002397).
- [50] Auerbach BM, Ruff CB. 2006 Limb bone bilateral asymmetry: variability and commonality among modern humans. *J. Hum. Evol.* **50**, 203-218.
- [51] Pagani L *et al.* 2016 Genomic analyses inform on migration events during the peopling of Eurasia. *Nature* **538**, 238-242. (doi:10.1038/nature19792).
- [52] Prugnolle F, Manica A, Balloux F. 2005 Geography predicts neutral genetic diversity of human populations. *Curr. Biol.* **15**, R159-R160.
- [53] Li H, Durbin R. 2011 Inference of human population history from individual whole-genome sequences. *Nature* **475**, 493-496. (doi:10.1038/nature10231).
- [54] Manica A, Amos W, Balloux F, Hanihara T. 2007 The effect of ancient population bottlenecks on human phenotypic variation. *Nature* **448**, 346-348.
- [55] Relethford JH, Blangero J. 1990 Detection of differential gene flow from patterns of quantitative variation. *Hum. Biol.* **62**, 5-25.
- [56] Relethford JH, Crawford MH, Blangero J. 1997 Genetic drift and gene flow in post-famine Ireland. *Hum. Biol.* **69**, 443-465.
- [57] Cheverud JM. 1988 A comparison of genetic and phenotypic correlations. *Evolution* **42**, 958-968.
- [58] Purcell S *et al.* 2007 PLINK: a tool set for whole-genome association and population-based linkage analyses. *Am. J. Hum. Genet.* **81**, 559-575. (doi:10.1086/519795).
- [59] Excoffier L, Lischer HEL. 2010 Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* **10**, 564-567. (doi:10.1111/j.1755-0998.2010.02847.x).
- [60] R Core Team. 2017 R: a language and environment for statistical computing. (Vienna, R Foundation for Statistical Computing).
- [61] Ruff C. 2017 Mechanical constraints on the hominin pelvis and the “obstetrical dilemma”. *Anat. Rec.* **300**, 946-955. (doi:10.1002/ar.23539).
- [62] Grabowski MW. 2013 Hominin obstetrics and the evolution of constraints. *Evol. Biol.* **40**, 57-75. (doi:10.1007/s11692-012-9174-7).
- [63] Grabowski MW, Polk JD, Roseman CC. 2011 Divergent patterns of integration and reduced constraint in the human hip and the origins of bipedalism. *Evolution* **65**, 1336-1356. (doi:10.1111/j.1558-5646.2011.01226.x).

- [64] Abou Zahr C, Wardlaw T. 2004 *Maternal mortality in 2000: estimates developed by WHO, UNICEF and UNFPA*. Geneva, World Health Organization.
- [65] Wells JCK. 2017 The new “obstetrical dilemma”: stunting, obesity and the risk of obstructed labour. *Anat. Rec.* **300**, 716-731. (doi:10.1002/ar.23540).
- [66] Noback ML, Harvati K, Spoor F. 2011 Climate-related variation of the human nasal cavity. *Am. J. Phys. Anthropol.* **145**, 599-614. (doi:10.1002/ajpa.21523).
- [67] Tilken MJ, Wall-Scheffler C, Weaver TD, Steudel-Numbers K. 2007 The effects of body proportions on thermoregulation: an experimental assessment of Allen's rule. *J. Hum. Evol.* **53**, 286-291. (doi:10.1016/j.jhevol.2007.04.005).
- [68] Holliday TW. 1997 Body proportions in Late Pleistocene Europe and modern human origins. *J. Hum. Evol.* **32**, 423-447.
- [69] Katzmarzyk PT, Leonard WR. 1998 Climatic influences on human body size and proportions: ecological adaptations and secular trends. *Am. J. Phys. Anthropol.* **106**, 483-503. (doi:10.1002/(sici)1096-8644(199808)106:4<483::aid-ajpa4>3.0.co;2-k).
- [70] Nielsen R, Akey JM, Jakobsson M, Pritchard JK, Tishkoff S, Willerslev E. 2017 Tracing the peopling of the world through genomics. *Nature* **541**, 302-310. (doi:10.1038/nature21347).
- [71] Schiffels S, Durbin R. 2014 Inferring human population size and separation history from multiple genome sequences. *Nat. Genet.* **46**, 919-925. (doi:10.1038/ng.3015).
- [72] von Cramon-Taubadel N, Lycett SJ. 2008 Brief communication: human cranial variation fits iterative founder effect model with African origin. *Am. J. Phys. Anthropol.* **136**, 108-113.
- [73] Leary S et al. 2006 Geographical variation in relationships between parental body size and offspring phenotype at birth. *Acta Obstet. Gynecol. Scand.* **85**, 1066-1079. (doi:10.1080/00016340600697306).
- [74] Giroux CL, Wescott DJ. 2008 Stature estimation based on dimensions of the bony pelvis and proximal femur. *J. Forensic Sci.* **53**, 65-68. (doi:doi:10.1111/j.1556-4029.2007.00598.x).
- [75] Berge C, Gouleras D. 2010 A new reconstruction of Sts 14 pelvis (*Australopithecus africanus*) from computed tomography and three-dimensional modeling techniques. *J. Hum. Evol.* **58**, 262-272.
- [76] Kibii JM, Churchill SE, Schmid P, Carlson KJ, Reed ND, de Ruiter DJ, Berger LR. 2011 A partial pelvis of *Australopithecus sediba*. *Science* **333**, 1407-1411. (doi:10.1126/science.1202521).
- [77] Marchal F. 2000 A new morphometric analysis of the hominid pelvic bone. *J. Hum. Evol.* **38**, 347-365.
- [78] Arsuaga J-L, Lorenzo C, Carretero J-M, Gracia A, Martinez I, Garcia N, Bermudez de Castro J-M, Carbonell E. 1999 A complete human pelvis from the Middle Pleistocene of Spain. *Nature* **399**, 255-258.
- [79] Bonmatí A, Gómez-Olivencia A, Arsuaga J-L, Carretero JM, Gracia A, Martínez I, Lorenzo C, Bermudez de Castro JM, Carbonell E. 2010 Middle Pleistocene lower back and pelvis from an aged human individual from the Sima de los Huesos site, Spain. *Proc. Natl. Acad. Sci. U. S. A.* **107**, 18386-18391. (doi:10.1073/pnas.1012131107).
- [80] Tague RG, Lovejoy CO. 1986 The obstetric pelvis of A.L. 288-1 (Lucy). *J. Hum. Evol.* **15**, 237-255.

Table and figure captions

Table 1. Skeletal samples included in the study. $N_{\text{body size}}$ 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).

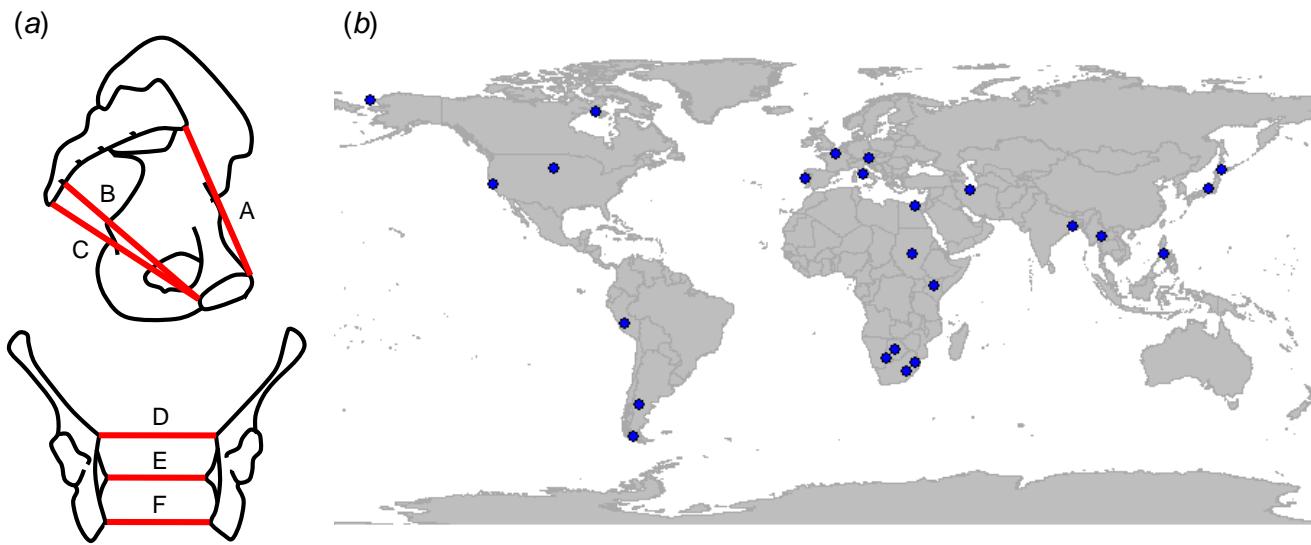
Figure 3. 3D plot of population averages for the inlet, midplane and outlet indices (*a*) and coefficient of variation for various postcranial indices and measurements (*b*). Populations from four geographic regions are highlighted in different colours in panel (*a*) (Africa = green, Asia = yellow, Europe 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.

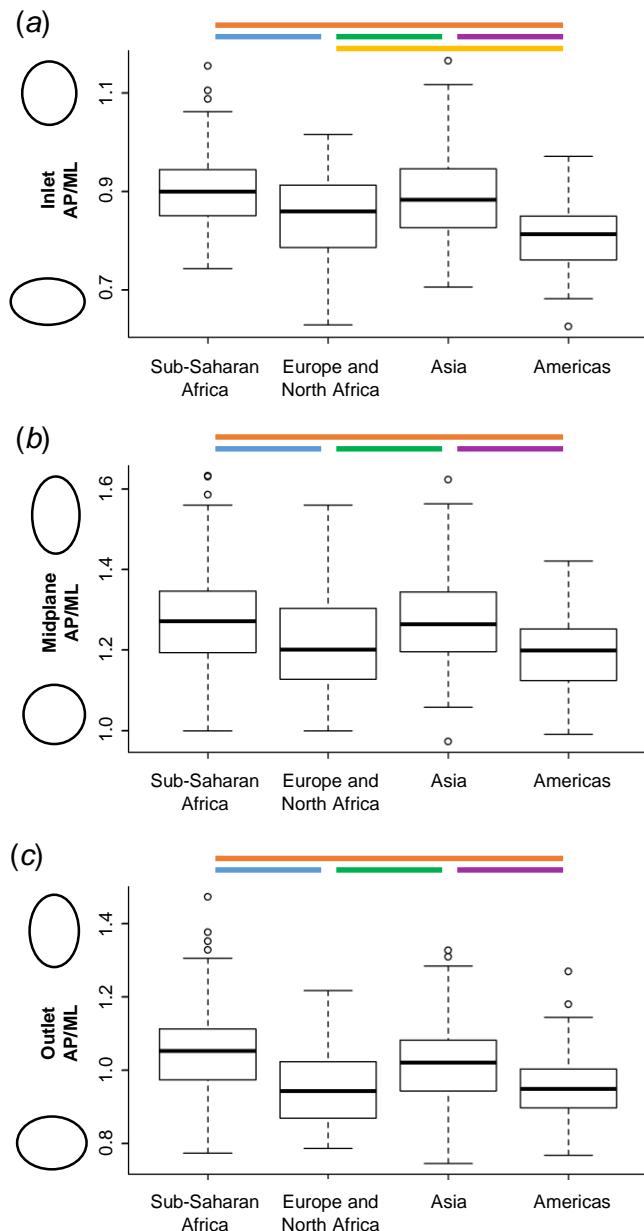
Figure 4: Graphical representation of the key results. (a) plot of within-population phenotypic distance and geographic distance from central sub-Saharan Africa; (b) plot of between-population phenotypic distance and genetic distance; (c) plot of the population average inlet index against minimum temperature; (d) plot of the residuals of the regression of canal size on body mass, against body mass.

Tables

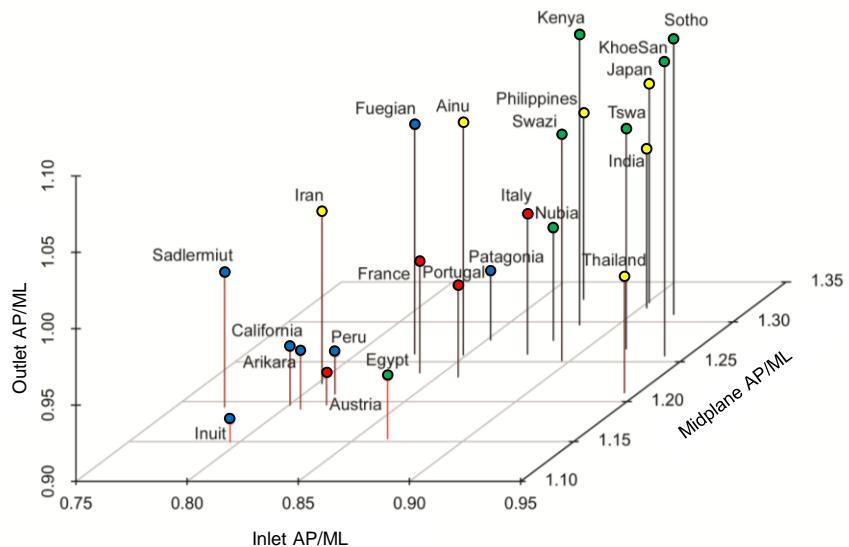
Table 1. Skeletal samples included in the study. N_{body size} is the number of individuals for whom it was possible to estimate body size based on the size of the acetabulum.

Region	N _{tot}	N _{body size}
<i>Africa</i>		
Botswana, Tswana	18	18
Kenya, Kykuyu	21	21
Lesotho, Sotho	21	21
Nubia	17	16
South Africa, Khoe-San	12	12
Swaziland	16	16
<i>Europe/North Africa</i>		
Austria	13	13
Egypt dynastic	9	9
France	15	15
Italy	6	6
Portugal	25	25
<i>Asia</i>		
Ainu, Japan	13	3
India	11	6
Iran (Iron Age)	11	11
Japan	21	21
Philippines, 'negritos'	8	8
Thailand	21	20
<i>America</i>		
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)

