Covariation between human pelvis shape, stature, and head size alleviates the obstetric dilemma

Barbara Fischer[a,b,1] and Philipp Mitteroecker[b]

[a]Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, NO-0316 Oslo, Norway; and [b]Department of Theoretical Biology, University of Vienna, 1090 Vienna, Austria

Edited by Robert G. Tague, Louisiana State University, Baton Rouge, Louisiana, and accepted by the Editorial Board March 25, 2015 (received for review October 24, 2014)

Compared with other primates, childbirth is remarkably difficult in humans because the head of a human neonate is large relative to the birth-relevant dimensions of the maternal pelvis. It seems puzzling that females have not evolved wider pelvises despite the high maternal mortality and morbidity risk connected to childbirth. Despite this seeming lack of change in average pelvic morphology, we show that humans have evolved a complex link between pelvis shape, stature, and head circumference that was not recognized before. The identified covariance patterns contribute to ameliorate the "obstetric dilemma." Females with a large head, who are likely to give birth to neonates with a large head, possess birth canals that are shaped to better accommodate large-headed neonates. Short females with an increased risk of cephalopelvic mismatch possess a rounder inlet, which is beneficial for obstetrics. We suggest that these covariances have evolved by the strong correlational selection resulting from childbirth. Although males are not subject to obstetric selection, they also show part of these association patterns, indicating a genetic–developmental origin of integration.

pelvis | evolution | morphometrics | correlational selection | obstetric dilemma

Childbirth is remarkably difficult in humans because of the tight fit of the human neonate through the maternal birth canal (1, 2). Obstructed labor occurs in 3–6% of all births and is thought to be globally responsible for 8% of all maternal deaths today (3–5). The most frequent cause of obstructed labor is cephalopelvic disproportion—a mismatch between the fetal head and the mother's pelvis (5). Without effective medical intervention, maternal mortality due to childbirth is estimated to be 1.5% (6), but many more women experience acute or chronic morbidity and develop lasting disabilities as a consequence of obstructed labor (4, 7). In evolutionary terms, there have been incredible fitness costs associated with childbirth in humans throughout modern human evolution, yet the birth canal has not become sufficiently wider.

This "obstetric dilemma" (8) is considered to be a consequence of the conflicting demands on the human pelvis imposed by bipedal locomotion and a large brain size. The shape of the human pelvis is assumed to be a compromise solution. Human pelvises are shaped for upright walking, but at the same time, they must remain wide enough for giving birth to large-headed neonates (1, 2, 9–12). Upright walking evolved at least 4–5 million years ago and required major skeletal adjustments (9, 13, 14). Only in the late Pleistocene (600,000–150,000 B.P.) did a major increase in brain size evolve (13), and the increasingly large-headed neonates had to be delivered through a pelvis that had earlier been adapted to bipedalism. The obstetric dilemma might further be aggravated by a higher infant survival rate for heavier neonates (15), implying that a higher birth weight is favored by selection. However, a recent study showed that neonatal size and human gestation length are limited not only by pelvic dimensions but also by maternal metabolic capacity (16). Phenotypic plasticity of pelvic dimensions and head size in response to changes in nutrition, poor food availability, and infectious disease burden, among others, might influence the severity of the obstetric dilemma (17–19).

Despite the effect of environmental factors, pelvic dimensions are highly heritable in human populations (most pelvic traits have heritabilities in the range of 0.5–0.8) (20) (*SI Text* and Table S1). It has further been claimed that low levels of integration in the pelvis enable high evolvability (14, 21, 22), yet pelvis shape has seemingly not sufficiently responded to the strong selection pressure imposed by childbirth. Despite insufficient change in average pelvic morphology, selection might have shaped the covariation between pelvic morphology and other body dimensions to ameliorate the consequences of pelvic constraints on childbirth. Cephalopelvic disproportion is determined by the mother's pelvic dimensions relative to the size of the fetal head, implying that pelvis and head are subject to correlational selection. A twin study (23) reported a heritability of 0.73 for intracranial volume, despite the apparent plasticity in head shape due to cranial deformations during birth (resulting in a heritability of 0.14 for neonatal head circumference but of 0.90 for head circumference of infants aged 4–5 mo) (24) (*SI Text* and Table S1). Because of the considerable heritabilities for head size and pelvic dimensions, we predict that females with a larger head have evolved a birth canal that can better accommodate large-headed neonates, compared with females with a smaller head, who are likely to give birth to children with smaller heads.

Similarly, the risk of birth complications increases if the father is much taller than the mother (25). A short woman with a small pelvis might give birth to a large neonate with a large head, inherited from a much taller father. As this suggests, shorter women, on average, have harder births than taller women (25–30).

Significance

Because of the tight fit of the large human neonate through the narrow maternal birth canal, childbirth is remarkably difficult. In this study we show that the dimensions of head, stature, and pelvis in a human body are linked in a complex way that was not recognized before and that contributes to ameliorate this tight fit. We show that females with a large head possess a birth canal that can better accommodate large-headed neonates. Because mothers with large heads usually give birth to neonates with large heads, the detected pattern of covariation contributes to ease childbirth and has likely evolved in response to strong selection.

Author contributions: B.F. designed research; B.F. performed research; B.F. and P.M. analyzed data; and B.F. and P.M. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. R.G.T. is a guest editor invited by the Editorial Board.

Data deposition: The data reported in this paper have been deposited in the Dryad Digital Repository, www.datadryad.org (DOI no. 10.5061/dryad.2d728).

[1]To whom correspondence should be addressed. Email: barbara.fischer@ibv.uio.no.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1420325112/-/DCSupplemental.

ANTHROPOLOGY

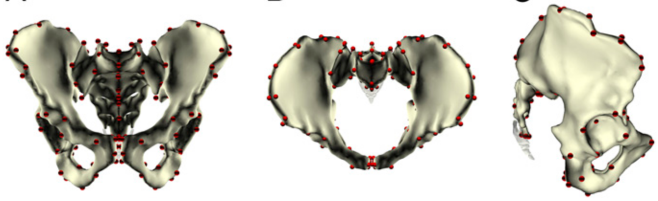

Fig. 1. Pelvic landmarks. The full set of 126 3D pelvic landmarks measured on each pelvis, shown as red spheres on the mean pelvis shape, are shown in (*A*) anterior, (*B*) superior, and (*C*) lateral view. The mean pelvis shape was computed as the average shape of all individuals in our dataset.

Given the high heritability of stature (24, 31, 32), we therefore also predict that the stronger obstetric selection pressure on shorter women has led to a pelvis with a birth canal that is more shaped toward obstetric demands in comparison with taller women.

We suggest that the optimal compromise between a large birth canal and a narrow pelvis is not uniform across a population but rather depends on both head size and stature. Hence, correlated variation between pelvic form, head size, and stature would reduce cases of obstructed labor and increase the human population's mean fitness. The joint selection regimes might have led to an adaptive integration (covariation) between pelvis shape, head circumference, and stature within human populations. To detect such integration patterns within the human body, we assess the covariation between human pelvis shape, head circumference, and stature in males and females by applying geometric morphometrics to fine-resolution 3D landmark data (Fig. 1 and Table S2) from 99 human skeletons.

Results

On average, females had a broader and flatter pelvis with a wider and shallower pelvic cavity than males (Fig. 2; see Table S3 for summary statistics of pelvic measurements in males and females).

As head circumference and stature were correlated ($r = 0.45$ in females and $r = 0.49$ in males; see also ref. 33), the direct effects of head circumference and stature on pelvis shape, independent of each other, were computed by regressing pelvis shape on both variables (multivariate multiple regression of Procrustes shape coordinates on stature and head circumference). Summary statistics for head circumference and stature are given in Table 1. Pelvis shape was significantly associated with stature in both sexes and with head circumference in females (Table 2). Fig. 3 illustrates the regression results by 3D reconstructions of average pelvis shapes for short and tall persons, respectively. Taller individuals had, on average, a relatively higher and narrower pelvis with a more oval pelvic inlet and a more forward projecting symphysis than shorter individuals. In males the sacrum and the pubic symphysis increased in relative length with increasing stature. This effect was only weakly present in females. Similarly, Fig. 4 illustrates the regression results for persons with large and small heads. Females with a large head had, on average, a relatively shorter sacrum that projects outwards from the birth canal. This association was not present in males. In both sexes, however, the pelvic inlet tended to be more circular in individuals with larger heads and more oval in individuals with smaller heads. The visual results from the 3D reconstructions (Figs. 3 and 4) were confirmed by regressions of selected pelvis measures (sacral length, sacral angle, anteroposterior diameter of the outlet, and inlet shape) on stature and head circumference (Table 3).

The magnitude of pelvic shape change (in units of Procrustes distance) connected to stature and head circumference was only slightly larger for females than for males (Table 2), but the pattern of shape change differed between the sexes. The pelvic shape change associated with stature differed significantly between males and females ($P < 0.001$ for a test of the angle between the vectors of regression coefficients), as did the shape pattern associated with head circumference ($P < 0.001$). The correlation of stature with the pelvic shape scores (as a measure of the strength of association) was similar in both sexes (Table 2 and Fig. 5), whereas the corresponding correlation for head circumference was larger for females than for males (Table 2 and Fig. 5).

Discussion

The human pelvis must serve two conflicting purposes: childbirth and bipedal locomotion. Pelvic morphology is therefore exposed to different selection pressures in males and females, which led to the well-known sexual dimorphism in human pelvis shape (34–36) that was also confirmed in our study (Fig. 2). The risk of cephalopelvic disproportion—and hence the strength of obstetric selection—is associated with the mother's stature (25–30) and the newborn's head size, which in turn is genetically correlated with the head size of the mother (23). The optimal compromise solution for pelvis shape may thus not be uniform within a population but may rather depend on stature and head size. Integration of pelvis shape with stature and head size would therefore reduce the frequency of obstructed labor and increase

Table 1. Summary statistics for stature and head circumference, separately for males and females

	Females, mm		Males, mm	
Measure	Mean	SD	Mean	SD
Stature	1,595.7	65.8	1,731.2	76.8
Head circumference	532.2	23.1	552.4	18.9

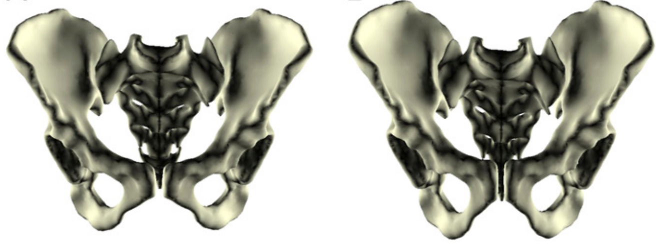

Fig. 2. Sexual dimorphism in the human pelvis. (*A*) The average female pelvis shape and (*B*) the average male pelvis shape in the sample, in frontal view. The differences between these two average shapes illustrate well-known patterns of sexual dimorphism in the human pelvis. Females have a broader and flatter pelvis, a wider and shallower pelvic cavity, a wider subpubic angle, and smaller acetabula than males.

Table 2. Results of the regression of pelvis shape on stature and head circumference, separately for females and males

	Stature			Head circumference		
Sex	Cor.	Procr.	*P* value	Cor.	Procr.	*P* value
Females	0.50	0.038	<0.001	0.67	0.030	<0.001
Males	0.53	0.031	<0.001	0.53	0.028	0.19

Shown are the following: correlation (Cor.) between the regression scores and the two variables (indicating the strength of the association), magnitude of shape effects in units of Procrustes distance (Procr.) associated with the two variables (measured as the norm of the vector of regression coefficients multiplied by 2 SDs of stature/head circumference), and the *P* value of the null hypothesis of no association between pelvis shape and stature/head circumference.

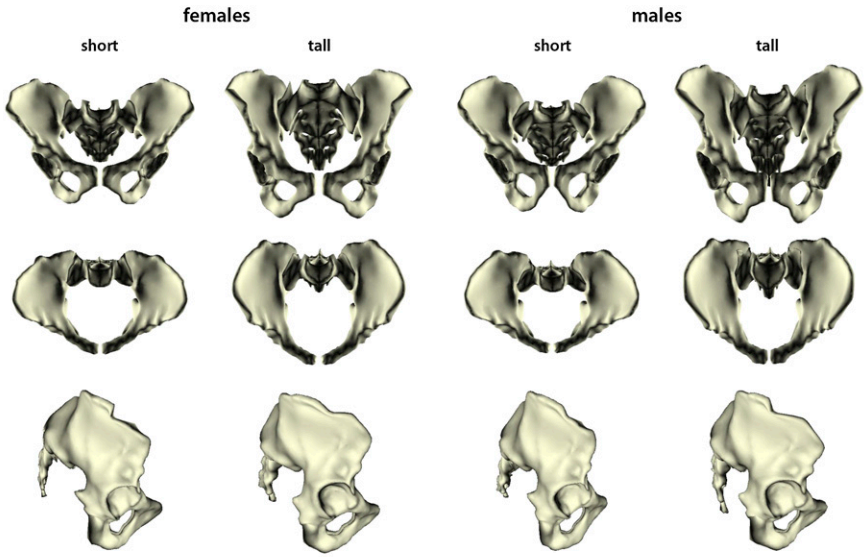

Fig. 3. Association between pelvis shape and stature, illustrated by average pelvis shapes for individuals with short and tall stature, separately for females and males. The shape differences shown here correspond to the partial linear regression coefficients for stature from the shape regressions. Hence, they represent the association of pelvis shape with stature, independent of head circumference. Each of these pelvis shapes is shown in anterior, superior, and lateral view (*Top*, *Middle*, and *Bottom*, respectively). The magnitude of the displayed shape differences corresponds to a deviation of $\pm$40 cm in stature from the sample average, which is approximately a twofold extrapolation of the actually occurring variation. On average, taller persons have a taller and narrower pelvis with longer ilial blades and a shorter relative distance between the acetabula compared with shorter persons. Taller persons also have a more oval pelvic cavity with an outward-projecting pubic symphysis, whereas short persons have a rounder pelvic cavity. The relative height of the sacrum and the symphysis increases with stature in males. This effect is weakly present in females.

the population's mean fitness. Accordingly, we hypothesized that correlational selection has produced patterns of covariance between pelvis shape and other body dimensions. Earlier studies based on smaller sets of linear measurements could not clearly demonstrate such patterns (37–40).

Here we showed that the shape of the human pelvis is indeed associated with body height and head circumference. Both in males and females, persons with a smaller head have, on average, a more oval pelvic inlet (a larger ratio of anteroposterior diameter to transverse diameter), whereas persons with a larger head have a rounder pelvic inlet. Similarly, taller persons tend to have a more oval pelvic inlet and shorter persons a rounder pelvic inlet. This link between inlet shape and stature has been identified in several other studies (37, 41–43). The obstetric

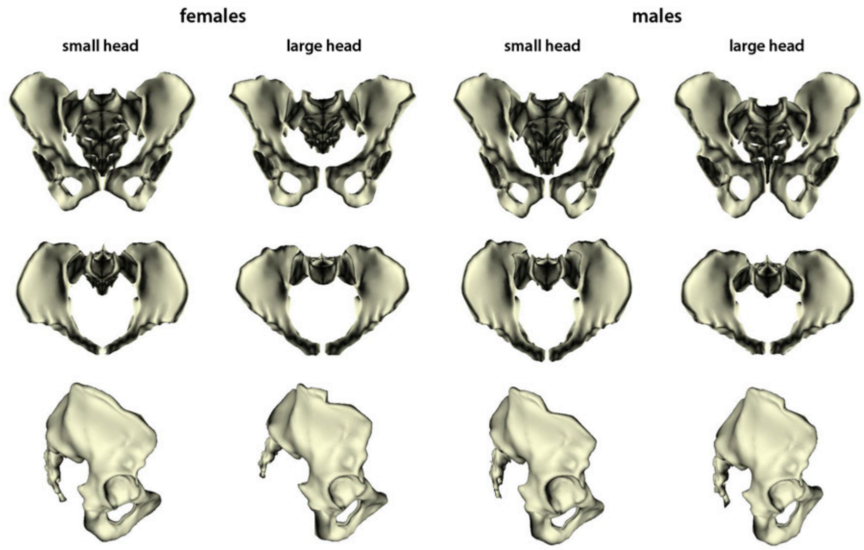

Fig. 4. Association between pelvis shape and head circumference, illustrated by average pelvis shapes for individuals with small and large head circumference, separately for females and males. These shape differences correspond to the partial linear regression coefficients for head circumference from the shape regressions. Hence, they represent the association of pelvis shape with head circumference, independent of stature. Each of these pelvis shapes is shown in anterior, superior, and lateral view (*Top*, *Middle*, and *Bottom*, respectively). The magnitude of the displayed shape differences corresponds to a deviation of $\pm$10 cm in head circumference from the sample average, which is approximately a twofold extrapolation of the actually occurring variation. Both in males and females, a round pelvic cavity is associated with a large head, whereas an oval pelvic cavity is associated with a small head. On average, females—but not males—with a large head have a shortened sacrum projecting outward from the birth canal.

Table 3. Summary statistics for sacral length, inlet shape, sacral angle, and anteroposterior diameter of the outlet, together with associations between these variables and head circumference and stature, separately for males and females

	Females				Males			
Measure	Mean	SD	Slope head	Slope stature	Mean	SD	Slope head	Slope stature
Sacral length	104.8	12.3	−0.0162	0.1073	112.5	14.3	−0.0582	0.0792
Sacral angle	78.8	8.3	0.1414	−0.0359	79.4	8.8	−0.0025	−0.0112
Inlet shape	1.11	0.13	0.0010	−0.0004	1.15	0.11	0.0016	−0.0004
Antero-posterior diameter of the outlet	118.3	10.4	0.1781	0.0492	111.0	7.6	−0.0598	0.0285

Sacral length is defined as in Table S3. Sacral angle is the angle at the promontorium between (*i*) the anteroposterior diameter of the inlet and (*ii*) the sacral length, both as in Table S3. Inlet shape is the ratio of anteroposterior diameter to transverse diameter of the inlet; both distances are defined as in Table S3. Anteroposterior diameter of the outlet is as in Table S3. Slope head and slope stature are the partial regression coefficients from the regressions of the measures on head circumference and stature. They describe the corresponding amount of change for one unit of change in head circumference or stature, respectively. Inlet shape is dimensionless, sacral angle is in degrees, and all other measurements are in millimeters. Sacral length increases with stature in both females and males but decreases with head size. The sacral angle increases substantially with head size in females but decreases slightly in males. The anteroposterior diameter of the outlet increases with head size in females but not in males, confirming that the sacrum projects outwards in large-headed females. The regression slopes for inlet shape confirm that the inlet becomes more oval with increasing stature and rounder with increasing head size in females and males.

literature reports that a pelvis with a round inlet—referred to as a "gynecoid" pelvis—is superior to other pelvis shapes in accommodating the head of the fetus during childbirth (44–46).

Although the association of stature and head size with overall inlet shape is similarly present in both males and females, we also found highly sex-specific patterns. In females, the sacrum tilts outwards with increasing head circumference, thus enlarging the birth canal in large-headed females. This does not occur in males. It has been reported that the sacral inclination has an important effect on lower pelvic capacity during childbirth (44, 45) and that women who required an emergency Cesarean section had a more narrow pelvic outlet (i.e., an inward-projecting sacrum) than a control group (47).

Around these average patterns that we detected, pertinent individual variation is present (Fig. 5 and Table 3). Also, the individual risk of obstructed labor is influenced by numerous other factors, many of which are environmental (18). However, as long as the average risk of cephalopelvic mismatch in a population is statistically associated with stature and head size and as long as enough independent genetic variation for these traits is present, the population is expected to evolve an adaptive covariance pattern (48). We therefore suggest that the apparently adaptive covariance patterns, which we identified, have originated from the correlational selection on pelvis and head dimensions during the birth process.

Correlational selection can lead to linkage disequilibrium—the nonrandom association of genes underlying the coselected traits—and hence to the phenotypic integration of these traits (48–50). It has also been proposed that correlational selection can lead to integration at a developmental–genetic level by the evolution of genes with adaptive pleiotropic effects on the traits (51, 52) or by the joint inheritance of beneficial gene combinations due to genetic linkage (physical proximity at the chromosomes) (53). We cannot directly assess from our data at which level pelvis shape is integrated with stature and head size. However, the presence of the same integration pattern of overall inlet shape with head circumference and stature in both males and females—even though the obstetric demands only exist in females—indicates integration at the genetic level (linkage or pleiotropy). The origin of female-specific integration patterns remains unclear; its analysis would require fine-scale genetic association studies.

To conclude, we found pervasive integration of pelvis shape, including the shape of the inlet, with stature and head circumference. The female integration, which we detected, is evidently advantageous for childbirth; it matches the patterns reported in the gynecological literature. Despite individual variation around this average association pattern and considerable phenotypic plasticity of neonatal head size and maternal pelvis form, this integration may have helped to alleviate the obstetric dilemma. The fit of the human fetus through the maternal birth canal is so tight that evolutionary change of pelvis shape, of the extent of the associations detected here, is relevant for obstetrics and is likely to have reduced rates of maternal mortality in humans.

Materials and Methods

The data used in this analysis stem from a large dataset compiled by Herbert Reynolds et al. (54) in 1982 in a study for the Federal Aviation Administration (Washington, DC). Their original aim was to develop a geometric model of human pelvic morphology to improve crash test devices and ultimately vehicle safety. We are grateful to Reynolds et al. for sharing these data. The measured skeletons are part of the Hamann–Todd collection at the Cleveland Museum of Natural History. Before skeletonization of the human bodies, which were acquired between 1919 and 1939 to the collection, a complete series of anthropometric measurements were taken. Of these measurements, we used head circumference and stature. From nearly 3,000

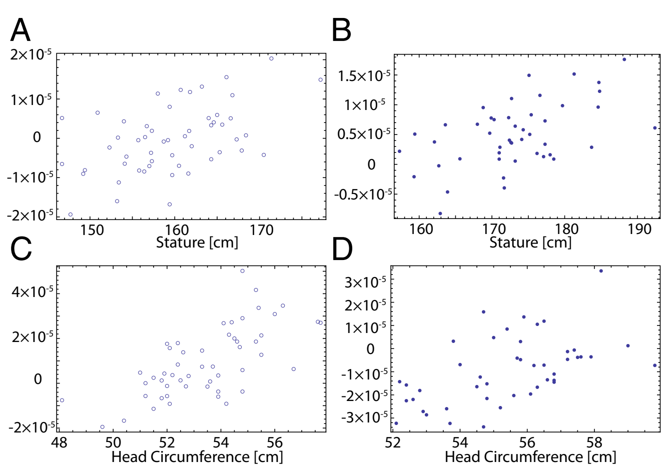

Fig. 5. Shape regression scores. Shown is a scatterplot of stature versus the regression scores from the regression of pelvic shape on stature (with head circumference as covariate). As these scores are projections of the individual pelvis shapes on the corresponding vector of regression coefficients (linear combination of the shape variables weighted by their covariance with stature), they are the shape scores with maximum covariance with stature. The scatterplots are computed separately for (*A*) females and (*B*) males. Similar scatterplots of head circumference versus the corresponding regressions scores are shown in *C* and *D* for females and males. Open circles represent female pelvises, and filled circles represent male pelvises.

available skeletal specimens at the Hamann–Todd collection, the study sample of Reynolds et al. was selected to match the body weight and size distribution of the US population. Only adult specimens, 18–55 y old at time of death, were used. The pelvises were reassembled, and 3D landmark coordinates were recorded on each of the articulated pelvises using a Hewlett Packard digitizer (54).

We performed a geometric morphometric shape analysis of the 99 human pelvises of US American Whites (46 males and 53 females). We selected 71 of the landmarks measured by Reynolds et al., based on the quality of their definition and on the availability in the sample. In several individuals, some landmarks were still missing (3.7% of all landmarks in all individuals). These missing landmarks were reconstructed by thin-plate spline interpolation using the sample mean shape as a reference (55, 56).

Because most landmarks were measured on the left hemipelvis only, we mirrored all unpaired landmarks across the midplane and thereby restored the data for the right hemipelvis. The midplane was estimated as a least-squares fitted plane to the unpaired midlandmarks (55). This resulted in configurations of 126 3D landmarks per pelvis (Fig. 1). We computed a Generalized Procrustes Analysis of these configurations to remove variation in overall size, position, and orientation (55, 57).

Based on the resulting Procrustes shape coordinates, we computed the average female and male pelvis shapes. To determine to which extent the two variables of head circumference and stature account for differences in pelvis shape, we regressed the Procrustes shape coordinates on the two variables (multivariate multiple regression), separately for males and females. These "shape regressions" yield vectors of regression coefficients that describe how all of the pelvic shape dimensions change together in response to one unit change of stature or head circumference. The resulting pattern of shape change was visualized by adding a multiple of the vector of regression coefficients to the mean shapes for each sex. In this way we produced extrapolations for pelvis shapes of females and males with large and small body height or head circumference. To test for the statistical significance of the shape regressions, we performed permutation tests for the regressions with explained variance as a test statistic and with 5,000 random permutations (Table 2). As a goodness-of-fit estimate for the shape regressions, we computed correlations and scatterplots between head circumference and the corresponding regression scores (projections of the individual pelvis shapes on the vector of regression coefficients) and did the same for stature (Table 2 and Fig. 5). To evaluate the magnitude of shape change (summed over all landmarks) that is associated with stature and head circumference, we computed the norm of the corresponding regression coefficient vectors, multiplied by 2 SDs (pooled within both sexes), of stature or head circumference, respectively (Table 2). This corresponds to the amount of shape change (in units of Procrustes distance) associated with 2 SDs of stature and head circumference. These analyses were computed for females and males separately (Table 2). To test whether the pattern of associated shape change differs between males and females, we performed permutation tests with the angle between the female and male regression vectors as the test statistic and with 5,000 random permutations.

To visualize group differences and regression results, we used a 3D surface model of an articulated pelvis (www.turbosquid.com, product ID 710664, Oormi Creations), on which we also measured the 126 3D landmarks using the software Amira (version 5.4.5, FEI Visualization Sciences Group). We deformed this surface model to the target landmark configurations using the thin-plate spline interpolation algorithm (55, 56, 58, 59).

The surface models in Figs. 3 and 4 are visualizations of the regression coefficients and therefore represent the effect sizes of the association of pelvis shape with stature and head circumference for the two sexes. The magnitude of the associated shape change is expressed by the Procrustes distance reported in Table 2. The strength of the association is reflected by the correlation of stature and head circumference with the corresponding regression scores, tested against the null hypothesis of no association by the permutation tests (Table 2 and Fig. 5).

All morphometric and statistical analyses were performed with Mathematica 8 (Wolfram Research, Inc.).

ACKNOWLEDGMENTS. We thank Herbert Reynolds and coauthors for sharing the data. We also thank Kjetil Voje, Thomas Hansen, Mark Grabowski, Anna Mazzarella, Emiliano Trucchi, Regina Fuchs, Philipp Gunz, Fred Bookstein, and Horst Seidler for discussion and for reading and commenting on the manuscript. We would also like to thank editor Robert Tague and two anonymous reviewers for their comments, which helped us to improve the manuscript. B.F. was supported by the Norwegian Research Council.

1. Wittman AB, Wall LL (2007) The evolutionary origins of obstructed labor: Bipedalism, encephalization, and the human obstetric dilemma. *Obstet Gynecol Surv* 62(11):739–748.
2. Schultz AH (1969) *The Life of Primates* (Universe Books, New York).
3. Say L, et al. (2014) Global causes of maternal death: A WHO systematic analysis. *Lancet Glob Health* 2(6):e323–e333.
4. Murray CJL, Lopez AD, eds (1996) *The Global Burden of Disease. A Comprehensive Assessment of Mortality and Disability From Diseases, Injuries and Risk Factors in 1990 and Projected to 2020* (World Health Organization, Geneva, Switzerland).
5. Dolea C, AbouZhar C (2003) *Global Burden of Obstructed Labour in the Year 2000* (World Health Organisation, Geneva, Switzerland).
6. Van Lerberghe W, De Brouwere V (2001) Reducing maternal mortality in a context of poverty. *Safe Motherhood Strategies: A Review of the Evidence,* Studies in Health Services Organisation & Policy, eds De Brouwere V, Van Lerberghe W (ITG Press, Antwerp, Belgium), pp 1–5.
7. Neilson JP, Lavender T, Quenby S, Wray S (2003) Obstructed labour. *Br Med Bull* 67(1):191–204.
8. Washburn SL (1960) Tools and human evolution. *Sci Am* 203:63–75.
9. Lovejoy CO (2005) The natural history of human gait and posture. Part 1. Spine and pelvis. *Gait Posture* 21(1):95–112.
10. Rosenberg K, Trevathan W (1995) Bipedalism and human birth: The obstetrical dilemma revisited. *Evol Anthropol Issues News Rev* 4(5):161–168.
11. Krogman WM (1951) The scars of human evolution. *Sci Am* 185(6):54–57.
12. Kurki HK (2013) Bony pelvic canal size and shape in relation to body proportionality in humans. *Am J Phys Anthropol* 151(1):88–101.
13. Ruff CB, Trinkaus E, Holliday TW (1997) Body mass and encephalization in Pleistocene Homo. *Nature* 387(6629):173–176.
14. 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(5):1336–1356.
15. Alberman E (1991) Are our babies becoming bigger? *J R Soc Med* 84(5):257–260.
16. Dunsworth HM, Warrener AG, Deacon T, Ellison PT, Pontzer H (2012) Metabolic hypothesis for human altriciality. *Proc Natl Acad Sci USA* 109(38):15212–15216.
17. Thoms H (1947) The role of nutrition in pelvic variation. *Am J Obstet Gynecol* 54(1):62–73.
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 (Suppl 55):40–71.
19. Kelley JO, Angel JL (1987) Life stresses of slavery. *Am J Phys Anthropol* 74(2):199–211.
20. Sharma K (2002) Genetic basis of human female pelvic morphology: A twin study. *Am J Phys Anthropol* 117(4):327–333.
21. Grabowski MW (2012) Hominin obstetrics and the evolution of constraints. *Evol Biol* 40(1):57–75.
22. Lewton KL (2011) Evolvability of the primate pelvic girdle. *Evol Biol* 39(1):126–139.
23. Gilmore JH, et al. (2010) Genetic and environmental contributions to neonatal brain structure: A twin study. *Hum Brain Mapp* 31(8):1174–1182.
24. Smit DJA, et al. (2010) Heritability of head size in Dutch and Australian twin families at ages 0-50 years. *Twin Res Hum Genet* 13(4):370–380.
25. Stulp G, Verhulst S, Pollet TV, Nettle D, Buunk AP (2011) Parental height differences predict the need for an emergency caesarean section. *PLoS ONE* 6(6):e20497.
26. Baird D (1952) The cause and prevention of difficult labour. *Am J Obstet Gynecol* 63(6):1200–1212.
27. Bresler JB (1962) Maternal height and the prevalence of stillbirths. *Am J Phys Anthropol* 20(4):515–517.
28. Molloy WB (1969) Labor in short women. *Obstet Gynecol* 34(3):330–334.
29. Camilleri AP (1981) The obstetric significance of short stature. *Eur J Obstet Gynecol Reprod Biol* 12(6):347–356.
30. Dougherty CRS, Jones AD (1988) Obstetric management and outcome related to maternal characteristics. *Am J Obstet Gynecol* 158(3 Pt 1):470–474.
31. Galton F (1886) Regression towards mediocrity in hereditary stature. *J Anthropol Inst GB Ireland* 15:246–263.
32. Lango Allen H, et al. (2010) Hundreds of variants clustered in genomic loci and biological pathways affect human height. *Nature* 467(7317):832–838.
33. Geraedts EJ, et al. (2011) Association between head circumference and body size. *Horm Res Paediatr* 75(3):213–219.
34. Wood BA, Chamberlain AT (1986) The primate pelvis: Allometry or sexual dimorphism? *J Hum Evol* 15(4):257–263.
35. Arsuaga JL, Carretero JM (1994) Multivariate analysis of the sexual dimorphism of the hip bone in a modern human population and in early hominids. *Am J Phys Anthropol* 93(2):241–257.
36. LaVelle M (1995) Natural selection and developmental sexual variation in the human pelvis. *Am J Phys Anthropol* 98(1):59–72.
37. Tague RG (2000) Do big females have big pelves? *Am J Phys Anthropol* 112(3):377–393.
38. Tague RG (1992) Sexual dimorphism in the human bony pelvis, with a consideration of the Neandertal pelvis from Kebara Cave, Israel. *Am J Phys Anthropol* 88(1):1–21.
39. Kurki HK (2011) Pelvic dimorphism in relation to body size and body size dimorphism in humans. *J Hum Evol* 61(6):631–643.
40. 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(6):795–802.

41. Holland EL, Cran GW, Elwood JH, Pinkerton JH, Thompson W (1982) Associations between pelvic anatomy, height and year of birth of men and women in Belfast. *Ann Hum Biol* 9(2):113–120.
42. Bernard RM (1952) The shape and size of the female pelvis. *Edinburgh Med J* 59(2): 1–15.
43. Ince JGH, Young M (1940) The bony pelvis and its influence on labour: A radiological and clinical study of 500 women. *Int J Obstet Gynaecol* 47(2):130–190.
44. 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(4):479–505.
45. Maharaj D (2010) Assessing cephalopelvic disproportion: Back to the basics. *Obstet Gynecol Surv* 65(6):387–395.
46. Stewart KS, Cowan DB, Philpott RH (1979) Pelvic dimensions and the outcome of trial labour in Shona and Zulu primigravidas. *S Afr Med J* 55(21):847–851.
47. Stålberg K, Bodestedt A, Lyrenäs S, Axelsson O (2006) A narrow pelvic outlet increases the risk for emergency cesarean section. *Acta Obstet Gynecol Scand* 85(7):821–824.
48. Sinervo B, Svensson E (2002) Correlational selection and the evolution of genomic architecture. *Heredity (Edinb)* 89(5):329–338.
49. Jones AG, Arnold SJ, Bürger R (2003) Stability of the G-matrix in a population experiencing pleiotropic mutation, stabilizing selection, and genetic drift. *Evolution* 57(8): 1747–1760.
50. Arnold SJ, Bürger R, Hohenlohe PA, Ajie BC, Jones AG (2008) Understanding the evolution and stability of the G-matrix. *Evolution* 62(10):2451–2461.
51. Wagner GP, Altenberg L (1996) Perspective: Complex adaptations and the evolution of evolvability. *Evolution* 50(3):967–976.
52. Pavlicev M, Cheverud JM, Wagner GP (2011) Evolution of adaptive phenotypic variation patterns by direct selection for evolvability. *Proc Biol Sci* 278(1713): 1903–1912.
53. Hurst LD (1999) The evolution of genomic anatomy. *Trends Ecol Evol* 14(3): 108–112.
54. Reynolds HM, Snow CC, Young JW (1982) *Spatial Geometry of the Human Pelvis*, memorandum report prepared for the U.S. Department of Transportation, Federal Aviation Administration, Office of Aviation Medicine (National Technical Information Service, Washington, DC).
55. Mitteroecker P, Gunz P (2009) Advances in geometric morphometrics. *Evol Biol* 36(2): 235–247.
56. Bookstein FL (1989) Principal warps: Thin-plate splines and the decomposition of deformations. *IEEE Trans Pattern Anal Mach Intell* 11(6):567–585.
57. Rohlf FJ, Slice D (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst Biol* 39(1):40–59.
58. Bookstein FL (1997) *Morphometric Tools for Landmark Data: Geometry and Biology*, reprint edition (Cambridge Univ Press, Cambridge, UK).
59. Klingenberg CP (2013) Visualizations in geometric morphometrics: How to read and how to make graphs showing shape changes. *Hystrix* 24(1):15–24.