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Human Pelvis and Long Bones Reveal Differential Preservation of Ancient Population History and Migration Out of Africa

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Abstract

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Keywords

Serial Founder Effect, Out Of Africa, Anatomically Modern Humans, Pelvis

Cover Page Footnote

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Human Pelvis and Long Bones Reveal Differential Preservation of Ancient Population History and Migration Out of Africa

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Abstract One of the main events in the history of our species has been our expansion out of Africa. A clear signature of this expansion has been found on global patterns of neutral genetic variation, whereby a serial founder effect accompanied the colonization of new regions, in turn creating a within-population decrease in neutral genetic diversity with increasing distance from Africa. This same distinctive pattern has also been described for cranial and dental morphological variation in human populations distributed across the globe. Here, we used a data set of postcranial linear measurements for 30 globally distributed human populations, and a climatic data set of minimum annual temperature, maximum annual temperature, and precipitation in order to separate for the first time the relative effect of neutral demographic processes and climatic selection on four long (limb) bones (femur, tibia, radius, and humerus) versus the pelvic bones of the human appendicular skeleton. We implemented a stepwise regression procedure in which phenotypic variance is assumed to be affected by the iterative founder events that accompanied human expansion from Africa, as well as by climate. This model included, as independent factors, geographic distance from central Africa, the three climatic variables, and all possible interactions between the three climatic variables. We excluded all nonsignificant factors by backward stepwise elimination with the aim of identifying the minimal model significantly explaining variation in the phenotypic data. Our results indicate a sharp difference in the way the pelvis and the limb bones reflect the neutral signature of the out-of-Africa expansion. Consistent with previous analyses of the cranium and dentition, pelvic shape variation shows a significant within-population decrease with increasing distance from Africa. However, no such pattern could be found in the long bones. Rather, in the case of both the tibia and the femur, a significant relationship between population-level variance and minimum temperature was demonstrated. Hence, in the case of these limb bones, it is probable that the effects of climatic selection have obliterated the demographic signature of human

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dispersal from Africa. Our finding that pelvic variation exhibits the neutral effects of demographic history suggests that consideration of this skeletal element might be used to shed light on factors of human population history, just as the cranium has done.

In recent years, the application of a population genetic approach has revealed that neutral evolutionary processes (i.e., drift and migration) can leave a strong signature on human phenotypic traits (e.g., Betti et al., 2009, 2010; Harvati and Weaver 2006a, 2006b; Manica et al. 2007; Relethford 1994, 2002, 2004; Roseman 2004; Roseman and Weaver 2004, 2007; Smith 2009, 2011; Strauss and Hubbe 2010; von Cramon-Taubadel and Lycett 2008; von Cramon-Taubadel 2009a, 2009b, 2011; von Cramon-Taubadel and Weaver 2009). Cranial shape variation in different human populations, in particular, tends to reflect the underlying neutral genetic pattern, to the point that cranial morphology can be used effectively to test for past demographic events, such as past migrations and the colonization of new regions (e.g., González-José et al. 2001, 2002, 2007; Hubbe et al. 2010, 2011; Manica et al. 2007; Pinhasi and von Cramon-Taubadel 2009; von Cramon-Taubadel and Pinhasi 2011).

One of the main events in the history of our species (*Homo sapiens*) has been the expansion out of the African continent, where the human species originated around 200,000 years ago, and the colonization of other continents occurred from at least 60,000 years ago (Cann et al. 1987; Ingman et al. 2000; Thomson et al. 2000). A very clear signature of the Out-of-Africa (OoA) expansion has been found on global patterns of neutral genetic variation, whereby an iterative founder effect that accompanied the colonization of new regions by peripheral populations generated a gradual decrease in genetic diversity with increasing distance from the African point(s) of origin (Liu et al. 2006; Prugnolle et al. 2005; Ramachandran et al. 2005). Notably, this genetic pattern is compatible with both single and multiple dispersals (e.g., Rasmussen et al. 2011) of populations from Africa, since the same basic relationship (i.e., between geographic distance from Africa and reduced within-group genetic variance) will be evinced regardless of how frequently any such dispersal(s) took place. Indeed, although recent genetic studies suggest that during this range expansion modern humans interbred with Neanderthals (*H. neanderthalensis*) and possibly other hominin species (Currat and Excoffier 2011; Green et al. 2010; Stoneking and Krause 2011), the limited amount of gene flow between these species, if any (Ghirotto et al. 2011a, 2011b; Hodgson et al. 2010), was evidently not enough to erase the OoA signature (Manica et al. 2007; Prugnolle et al. 2005; Ramachandran et al. 2005). Indeed, as Green et al. (2010: 721) put it, their analysis of the Neanderthal genome “continues to support the view that the vast majority of genetic variants that exist at appreciable frequencies outside Africa came from Africa with the spread of anatomically modern humans”.

This same distinctive pattern has also been described for cranial and dental morphological variation, giving additional evidence that some skeletal traits vary according to a null model of neutral evolution (Betti et al. 2009;

Hanihara 2008; Manica et al. 2007; von Cramon-Taubadel and Lycett 2008). The presence of a neutral signal in craniodental traits may be seen as largely unexpected, since many studies had previously focused on the effects of selective pressures and developmental plasticity in creating cranial shape variation (e.g., Beals 1972; Beals et al. 1983, 1984; Franciscus and Long 1991).

Climate, in particular, has always been considered a powerful factor in shaping skeletal morphology, especially in the case of the postcranium. Allen's (1877) and Bergmann's (1847) rules offer specific predictions on how body proportions should change under strong climatic selection. Following Allen's (1877) rule, animals living in cold climates tend to have relatively shorter extremities than similar species or subspecies in warmer climates, in order to reduce the dissipation of heat. It has been suggested that Allen's rule has affected human populations in this manner, with populations living in cold regions exhibiting relatively shorter limb bones in respect to overall stature, versus relatively longer limbs in warm (equatorial) climates (Holliday and Hilton 2010). Conversely, Bergmann's (1847) rule states that populations living in cold regions tend to have higher body mass (i.e., increased volume), which can be achieved by an increase in absolute size. In line with Bergmann's rule, it has previously been shown that Inuit and other arctic populations have a higher body mass, larger trunks and pelvic regions in respect to most populations living near the equator (Holliday 1997; Ruff 1993, 1994). In summary, Allen's rule may be considered a change in overall body shape in the absence of an increase or decrease in the mass (volume) of an individual, while Bergmann's rule is related to an increase or decrease in absolute body mass (volume) without necessarily changing body shape.

In this study, we use a freely available data set of postcranial linear measurements (Goldman Data set — <http://web.utk.edu/~auerbach/GOLD.htm>; Auerbach and Ruff 2006) in order to separate, for the first time, the relative effect of neutral demographic processes and climatic selection on the long (limb) bones and the pelvic bones of the human appendicular skeleton. The original data set has been expanded to include six additional sub-Saharan African populations in order to adequately account for the high intracontinental variability expected in sub-Saharan African populations (e.g., Henn et al. 2011; Jorde et al. 1997, 2000). The OoA demographic (population history) signature will be used as an indicator of neutral evolution, given the very distinctive pattern and clear predictions associated with it. Hence, using this model as a null hypothesis, two specific predictions can be made depending on the level of selection acting on the different anatomical regions:

- (1) If phenotypic variation is largely neutral, then — in a manner similar to the human cranium — within-population postcranial variation should show a significant fit to the OoA (serial founder effect) model and exhibit no significant correlation with climate.
- (2) Conversely, if climatic selection has annihilated the underlying neutral signature, then postcranial phenotypic variation will not show a significant

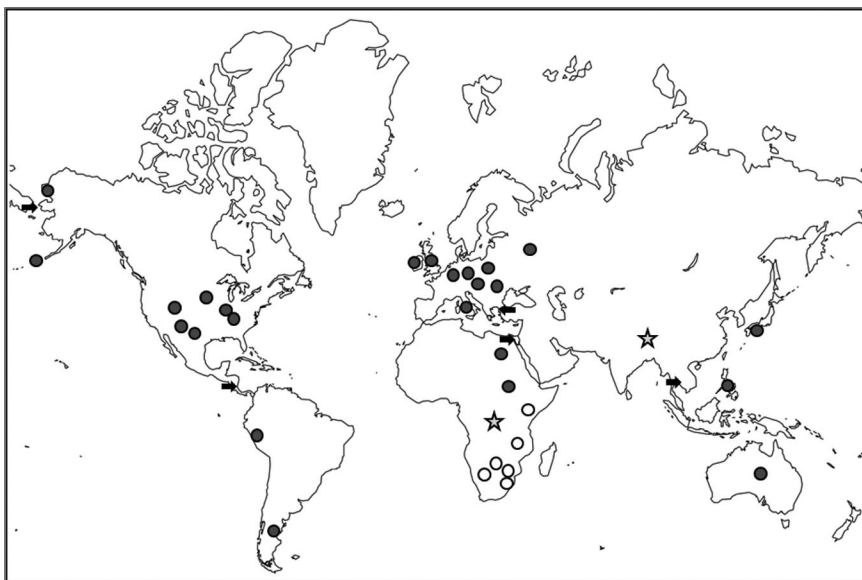


Figure 1. Distribution of the population samples from the Goldman data set (solid circles), and the newly collected African samples (open circles). Points used as starting points for calculation of geographic distances used in the analyses are represented by stars, while compulsory waypoints are indicated as black arrows.

fit to the OoA model, but will rather exhibit a significant relationship with climate.

Materials and Methods

From the original data in the Goldman data set, only populations with complete data from at least 15 individuals were selected for inclusion in the analyses (Figure 1, Table 1). In order to avoid the potentially confounding effects of sexual dimorphism, the analyses were restricted to male individuals because of the much larger sample size available. Measurements were chosen preferably from the left side, using the right side only in cases where the left presented missing data. The data set thus comprised measurements for the pelvis, femur, tibia, humerus, and radius.

In addition to the 24 population samples collated from the Goldman data set, an additional six sub-Saharan samples were added by collecting primary data (LB) housed at the National Museum of Kenya (Nairobi, Kenya) and the University of Witwatersrand (Johannesburg, South Africa) (see Table 1). These additional samples were chosen in order to maximize the geographic coverage of sub-Saharan Africans close to the putative origin as described in previous studies of molecular variation (e.g., Manica et al. 2007). The same measurements as used in the Goldman database (see Table 2) were collected on each of the five anatomical regions according to the protocol described by Auerbach and Ruff

Table 1. Names, Geographic Co-Ordinates, Climatic Data, and Sample Sizes for Each of the 30 Populations Assessed^a

Population		Geographic Co-ordinates		Climatic Variables			Anatomical Regions (sample sizes)				
Location	Note	Lat.	Long.	Min Temp (°C)	Max Temp (°C)	Precipitation (mm/year)	Pelvis (n)	Humerus (n)	Radius (n)	Femur (n)	Tibia (n)
Aleutian Islands	Agatu	52.5	-174.83	-2.5	12.8	1355	31	53	49	55	54
Argentina	Patagonia	-41.75	-69	-6.2	22.6	187	15	21	21	21	19
Arizona	Canyon Muerto	36.13	-109.48	-8.6	32.1	247	16	22	22	23	22
Australia	Australians	-25.27	133.77	4.3	37	133.77	20	28	27	29	29
Austria		47.52	14.55	-10.1	17	1361	59	103	104	102	100
Belgium		50.5	4.47	-1.1	22.4	853	18	34	34	32	35
*Botswana	Tswana	-22.05	23.92	5	33.2	362	33	33	32	33	33
Egypt	Dynastic Egypt	30.03	31.22	6.9	34.9	17	47	79	77	80	78
England		52	-0.73	0	21.9	618	16	71	69	71	71
Germany		51.15	10.45	-3.4	22.3	584	47	67	67	67	64
Hungary		47.15	19.5	-4.1	26.8	532	22	26	25	26	25
Illinois	Native Americans	40.62	-89.38	-9.9	30.1	954	24	42	42	42	40
Ireland		53.4	-8.25	1.6	18.8	984	20	23	23	23	22
Italy		41.88	12.42	3.8	30	771	30	47	47	47	47
Japan		36.2	138.25	-7.9	28.1	1201	29	45	49	48	48
*Kalahari desert	Khoe-San	-25	21	1.5	34.9	261	19	21	20	21	19
Kentucky	Indian Knoll	37.83	-84.27	-5.1	30.4	1177	25	61	61	60	60
*Kenya	Mainly Kikuyu	1	38	15.6	33.9	461	33	34	32	34	34
*Malawi		-13.25	34.3	14.7	32.2	1147	32	32	32	31	30
New Mexico	Hawikuh	34.97	-105.02	-6.6	32.4	344	26	73	69	73	73
Peru	Ancon necropolis	-12.77	-74.62	-1.5	18.4	855	17	29	29	29	29
Philippine Islands	"Negritos"	12.87	121.77	22.6	32.6	2214	15	29	29	30	31
Pont Hope, Alaska	Ipiutak and Tigara	68.33	-166.8	-26.7	10.3	238	34	76	79	77	76
Poland		51.92	19.13	-7	24.6	537	24	25	25	25	25
Russia		55.75	37.62	-12.3	23.1	678	28	36	36	36	36
South Dakota	Arikara	43.95	-100.07	-15	32.4	469	29	56	59	59	59
Sudan	Nubia	12.85	30.22	14	38.7	386	30	51	52	52	53
*Swaziland	Swazi	-26.52	31.47	8.1	29.3	724	36	39	39	39	36
Utah	Cliff Dwellers	40.32	-111.62	-8.5	32.5	378	21	34	32	33	31
*Venda, S. Africa	Venda	22.33	30.17	9.8	32.5	387	28	28	26	29	27

a. Only male specimens were used. Starred (*) samples indicate the additional samples collected from six sub-Saharan African populations for the purposes of the current study. All other samples were collated from the Goldman database (<http://web.utk.edu/~auerbach/GOLD.htm>). Climatic data were collated from the published WORLDCLIM database (Hijmans et al. 2005).

Table 2. Linear Measurements Used to Estimate Within-Population Variance for Each of the Five Anatomical Regions

<i>Measurements</i>	
<i>Humerus</i>	<i>Femur</i>
- Maximum Length	- Maximum Length
- Epicondylar Breadth	- Bicondylar Length
- Head Diameter	- Epicondylar Mediolateral Breadth
- 50% Diaphyseal Mediolateral Diameter	- Distal Articular (Bicondylar) Mediolateral Breadth
- 50% Diaphyseal Anteroposterior Diameter	- Head Anteroposterior Diameter
	- 50% Diaphyseal Mediolateral Diameter
	- 50% Diaphyseal Anteroposterior Diameter
<i>Tibia</i>	
- Maximum Length	
- Plateau Mediolateral (Bicondylar) Breadth	<i>Pelvis</i>
- 50% Diaphyseal Mediolateral Diameter	- Bi-iliac Breadth
- 50% Diaphyseal Anteroposterior Diameter	- Maximum Iliac Blade Length
	- Maximum Acetabular Height
<i>Radius</i>	
- Maximum Length	
- 50% Diaphyseal Mediolateral Diameter	
- 50% Diaphyseal Anteroposterior Diameter	

(2004, 2006). Given that population within-group variances were calculated using each individual population sample (i.e., from a single observer), inter-observer error is unlikely to affect the results of the analysis. Moreover, the effect of inter-observer differences was also tested by performing a post-hoc analysis of just the Goldman data set minus the new sub-Saharan samples.

All measurements (Table 2) were size-adjusted by dividing each measurement by the geometric mean of all measurements of the same bone (Jungers et al. 1995). This method equalizes the volumes of all specimens (i.e., isometrically scales each specimen to the same size) while maintaining overall shape information (Falsetti et al. 1993; Jungers et al. 1995). Individual within-population variances were calculated as the average of the trace of the variance-covariance matrix, following the Relethford and Blangero (1990) model for quantitative traits. The Relethford-Blangero estimator of population genetic affinities based on quantitative traits assumes an equal and additive model of inheritance. Multivariate covariance matrices were calculated under the assumption that population phenotypic variances are proportional to genetic variances. All within-population variances were calculated under the assumption of complete heritability $h^2 = 1$ given the lack of appropriate population-specific heritability estimates for the anatomical regions under consideration here.

To test for the OoA signature, the geographic distances of each population sample from central sub-Saharan Africa (Betti et al. 2009; Manica et al. 2007) were calculated using great circle distances, based on the haversine (Sinnott 1984). In order to better approximate actual distances on the ground (i.e., limiting long-distance sea-crossings), five waypoints were imposed when calculating the distances. These geographic waypoints and their co-ordinates are listed in Table 3. In

Table 3. Origin Points Used to Calculate Great Circle Distances and Obligatory Waypoints Imposed in This Study

<i>Origins</i>	<i>Coordinates</i>
Central Africa (Democratic Republic of the Congo)	8S, 25E
Central Asia (Lhasa, Tibet, China)	29.63N, 91.13E
<i>Waypoints</i>	
Sinai Peninsula, Egypt (any route out of Africa)	30.07N, 33.7E
Istanbul, Turkey (routes connecting Africa and Europe)	41N, 29E
Thailand (routes to Australia)	16.13N, 98.35E
Bering Strait (routes to the Americas)	65.78N, 169.97W
Panama (routes to South America)	13.5N, 86.2W

order to compare phenotypic variability with climate, a climatic data set of average minimum and maximum temperature (°C) for the coldest and hottest month respectively, and annual average precipitation (mm/year) was collated from WORLDCLIM (Hijmans et al. 2005), as a set of global climatic GIS layers interpolating data from approximately 15,000 weather stations distributed worldwide (Table 2). Ideally, climatic data coeval to the population samples should be used for the analyses. Variation in climatic conditions during the time span covered by our samples, however, has been quite limited. Moreover, given the global nature of our sample, small regional temporal fluctuations in temperature will be minimal compared with the global differences in temperature between widely distributed populations. Indeed, the use of modern global climatic data of this nature is in line with recent equivalent analyses of human cranial variation (e.g., Betti et al. 2009, 2010; Harvati and Weaver 2006a, 2006b; Hubbe et al. 2009; Noback et al. 2011; Roseman 2004; von Cramon-Taubadel 2009, 2011).

In order to test the predictions, we implemented a stepwise regression procedure using the “Drop1” function (<http://stat.ethz.ch/R-manual/R-patched/library/stats/html/add1.html>) of the software R (R Development Core Team 2007). We started with a full linear model, in which phenotypic variance is assumed to be affected by the iterative founder events that accompanied the expansion of the species OoA, as well as by climate. This model included, as independent factors, geographic distance from Central Africa, minimum and maximum temperature, average precipitation, and all possible interactions between the three climatic variables. Starting from this model, we excluded all nonsignificant factors by backward stepwise elimination. The exclusion of single factors, sequentially, from the model was performed respecting the hierarchy of factors (interactions between factors were considered before excluding the factors themselves), and was determined by the relative increase/decrease of Akaike Information Criterion (AIC) (Akaike 1973) following the exclusion of a factor. Moreover, an ANOVA was performed at each step to confirm that the exclusion of the factor did not significantly decrease the

Table 4. Results of the Linear Models^a

<i>Skeletal Region</i>	<i>Minimal Model</i>	<i>R²</i>	<i>P-value</i>
Pelvis	PhVar~Dist	0.154	0.032
Humerus	n.a.	0.214	0.555
Tibia	PhVar~Tmin	0.163	0.027
Radius	n.a.	0.251	0.425
Femur	PhVar~Tmin	0.261	0.004

a. Statistically significant results are in bold ($\alpha = 0.05$). PhVar = Phenotypic Variance, Dist = Distance from Africa, $T_{\min}$ = Minimum Temperature. In the case of the humerus and radius, no significant factors were found so the values for the full model are presented.

accuracy of the model. In cases where no significant factor was found, the results of the full model regression are presented.

Results

Table 4 and Figure 2 show the results of the stepwise regression analysis. Notably, the results of the linear models show a very different pattern for the pelvis in respect to the limb bones. Pelvic shape variance is significantly correlated with geographic distance from Africa (i.e., minimal model = PhVar~Dist), following the same pattern expected under the neutral model, and in line with the previous results from genetic markers and craniodental traits. Conversely, the humerus, tibia, radius, and femur do not exhibit a fit to the geographic (OoA) model. Rather, within-population morphological diversity for both the femur and tibia significantly correlates with minimum temperature (i.e.,

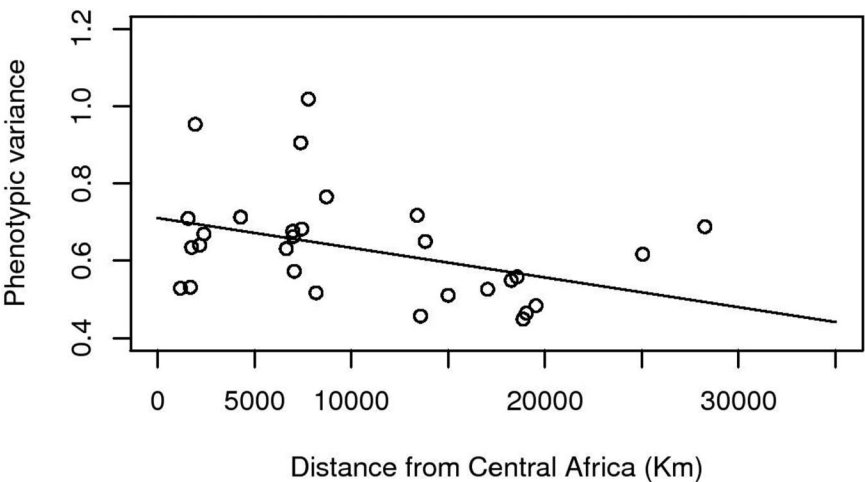


Figure 2. Linear regression of phenotypic within-population variance and geographic distance for the pelvis, with central Africa (8S, 25E) used as point of origin ($R^2 = 0.154$, $P = 0.032$).

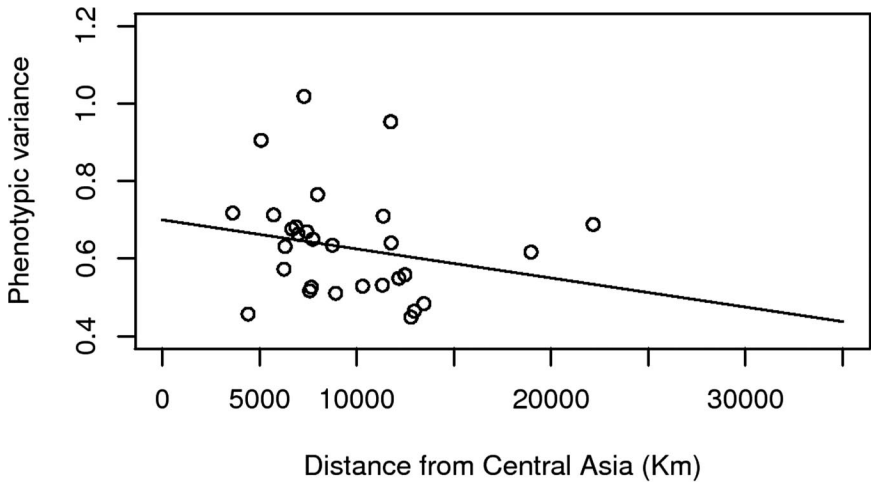


Figure 3. Linear regression of phenotypic within-population variance and geographic distance for the pelvis, with central Asia (29.63N, 91.13E) used as point of origin ($R^2 = 0.042$, $P = 0.28$).

minimal model = $\text{PhVar} \sim \text{Tmin}$). These results are consistent with the hypothesis that climatic selection has obliterated the effects of population history (i.e., OoA dispersal) in the case of these lower limb bones.

In order to further evaluate the robustness of our results, a number of post-hoc tests were undertaken. In the case of the pelvis (for comparison with the OoA model), we tested for a fit between geographic distance and a hypothetical point of origin in central Asia (see Figure 3, Table 3). No significant relationship was found ($R^2 = 0.042$; $P = 0.28$). We also repeated the OoA analysis for the pelvis using only populations included in the original Goldman data set, in order to corroborate that the results were not affected by the inclusion of the additional data from sub-Saharan Africa. This analysis provided results consistent with those of our primary analysis ($R^2 = 0.162$; $P = 0.05$). Additionally, we tested whether a significant relationship existed between population sample sizes for the pelvis and within-population variances; no such relationship was found ($R^2 = 0.00031$; $P = 0.93$).

Discussion

An OoA fit to a serial founder effect model has previously been shown for human genetic variation (Liu et al. 2006; Prugnolle et al. 2005; Ramachandran et al. 2005), craniodental variation (Hanihara 2008; Manica et al. 2007; von Cramon-Taubadel and Lycett 2008), and even linguistic variation (Atkinson 2011). Here, we assessed whether population-level variation in post-cranial elements of the human skeleton might also fit this model.

Our results indicate a sharp difference in the way the pelvis and the limb bones reflect the neutral signature of the OoA expansion. Consistent with

previous analyses of the cranium and dentition, pelvic shape shows a significant decrease in within-population variation with increasing distance from Africa. However, no such pattern could be found in the long bones. Rather, in the case of both the tibia and the femur, a significant relationship between population-level variance and minimum temperature was demonstrated. Hence, in the case of these lower limb bones, it is probable that the effects of climatic selection have obliterated the effects of population history (i.e., our dispersal OoA).

These results also indicate that climatic selection has had a stronger effect on the lower limb in respect to the upper limb, at least in terms of shape effects. One possible explanation could be that differing population activity patterns, and the subsequent remodeling responses of osseous tissue at a population level, may feasibly have contributed to erasing evidence of climatic selection on the upper limb that could otherwise have been present (e.g., Currey 1984; Ruff 1999; Stock) and Pfeiffer 2001; Stock 2006). Such factors could also, of course, provide an additional reason (i.e., to selection) as to why the effects of demographic history are not as readily detected in the long bones as they are in the pelvis.

The OoA signature appears less clear on the pelvis than on the cranium, where it has been shown that as much as 19–26% of within-population levels of variation may be explained by distance from sub-Saharan Africa (e.g., von Cramon-Taubadel and Lycett 2008). This may be due to methodological differences, such as the far lower number of pelvic measurements used; however, we cannot rule out the possibility that such differences might also reflect differing microevolutionary histories for the cranium versus the pelvis (i.e., they have been affected differentially by the evolutionary forces of drift, migration, selection, etc.). Indeed, while our results show a clear difference in the relative neutrality of the pelvis compared against the limb bones, our results should not be interpreted as implying that *no* climatic (or other) selection has acted on the human pelvis in different populations and regions, merely that the extent of such selection has not obliterated entirely the effects of population history. Moreover, we cannot assess the impact of directional versus stabilizing selection on the post-cranium, as directional selection can increase differences between populations, without necessarily affecting within-population diversity.

The results of our analyses are particularly striking when we consider that two out of the three pelvic measurements have previously been suggested to be under climatic selection. The diameter of the acetabulum varies accordingly to the femoral head diameter (Ruff 2010), which in turn relates closely to body mass (e.g., Grine et al. 1995; McHenry 1992; Ruff et al. 1991). According to Bergmann's (1847) rule, body mass should be higher in cold climates in respect to warm regions, and we could therefore expect femoral head diameter, and therefore acetabular diameter, to be affected by climate in a similar way. Bergmann's and Allen's rule have also been used to explain the global pattern of bi-iliac breadth, with larger hips and trunks in arctic regions and narrower bodies in tropical populations (Ruff 1994). However, it is worth reiterating that our

analyses used data scaled for the effects of overall isometric size (i.e., volumes were equalized). Hence, while raw pelvic dimensions may have been affected by selection for overall isometric size (i.e., according to Bergmann's rule), our results suggest that the effects of climate on pelvic shape variation have not been prevalent.

One of the limitations of our analysis is that it only included male specimens. An important future extension of this study is, therefore, to determine if the neutral pattern of variation we have found in males holds true in global patterns of human female pelvic morphology. This is important to determine, given the fundamental functional involvement of the pelvis in parturition, and hence potential obstetric constraints on morphological variation (e.g., Rosenberg and Trevathan 1997; Tague 1995; Weaver and Hublin 2009).

Our finding that human pelvic variation exhibits the neutral effects of demographic history, suggests that consideration of this skeletal element might be used to shed light on factors associated with population history, just as the human cranium has done (Roseman and Weaver 2007; von Cramon-Taubadel and Weaver 2009). Moreover, its potential role as an indicator of neutral demographic history may also be of import with regard to interpreting population history in fossil hominins, especially given that the available fossil sample of hominin pelvic remains has improved in recent years (Kibii et al. 2011; Lovejoy et al. 2009; Simpson et al. 2008).

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