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Are human hands and feet affected by climate? A test of Allen's Rule.

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Abstract

Objectives

In recent years, several studies have shown that populations from cold, high-latitude regions tend to have relatively shorter limbs than populations from tropical regions, with most of the difference due to the relative length of the zeugopods (i.e. radius, ulna, tibia, fibula). This pattern has been explained either as the consequence of long-term climatic selection or of phenotypic plasticity, with temperature having a direct effect on bone growth during development. The aims of this study were to test whether this pattern of intra-limb proportions extended to the bones of the hands and feet, and to determine whether the pattern remained significant after taking into account the effects of neutral evolutionary processes related to population history.

Materials and Methods

Measurements of the limb bones, including the first metatarsal and metacarpal, were collected for 393 individuals from 10 globally distributed human populations. The relationship between intra-limb indices and minimum temperature was tested using generalized least squares regression, correcting for spatial autocorrelation.

Results

The results confirmed previous observations of a temperature-related gradient in intra-limb proportions, even accounting for population history. This pattern extends to the hands, with populations from cold regions displaying a relatively shorter and stockier first metacarpal; however, the first metatarsal appears to be wider but not shorter in cold-adapted populations.

Discussion

The results suggest that climatic adaptation played a role in shaping variation in limb proportions between human populations. The different patterns shown by the hands and feet might be due to the presence of evolutionary constraints on the foot to maintain efficient bipedal locomotion.

Studies from across anthropology and human biology have long suggested a causal relationship between climate and human body size and its proportions (Ridgeway, 1908; Roberts, 1953; Schreider, 1964). Human groups living in cold climatic conditions appear to have larger overall body mass (e.g., Roberts, 1953; Ruff, 1994; Katzmarzyk and Leonard, 1998; Leonard and Katzmarzyk, 2010) conforming to the basic predictions of Bergmann's ecogeographic "rule" (Bergmann, 1847). When average body dimensions are compared among populations from different geographic areas, people living in cold, high-latitude regions appear to have wider hips (Ruff, 1993, 1994, 1995; Holliday, 1997b; Weaver and Hublin, 2009; Holliday and Hilton, 2010) and relatively shorter arms and legs in respect to populations from hot, tropical regions (Coon, 1962; Roberts, 1978; Trinkaus, 1981; Ruff, 1994, 2002; Holliday, 1997a,b, 1999, 2002; Tilkens et al., 2007; Holliday and Hilton, 2010). A similar pattern had been previously described in other endothermic animals and is often referred to as Allen's (1877) rule, whereupon comparison of closely related species or subspecies shows that high-latitude species tend to display shorter appendages, including ears and tail, than low latitude ones (e.g., Niles, 1973; Lindsay, 1987; Rasmussen, 1994; Fooden and Albrecht, 1999; Nudds and Oswald, 2007).

This pattern of geographic variation in body proportions has often been explained as the result of climate-related adaptation. At parity of volume, more elongated shapes have a higher surface-to-volume ratio. As body heat in endotherms is generated internally and dissipated at the surface, a high surface-to-volume ratio would facilitate heat dissipation, therefore being adaptive in hot climates; on the other hand, a low ratio, as resulting from shorter and stockier extremities, would promote heat retention and have adaptive value in cold climates. What is less clear, however, is to what extent this adaptation is the result of long-term genetic selection or environmentally-mediated plasticity. This later explanation is underpinned by studies showing the short-term effects of environmental factors such as nutrition, stress and altitude in regulating childhood limb proportions when genetically-similar populations are compared (e.g., Stinson and Frisancho, 1978; Pomeroy et al., 2012, 2013).

Regardless of the underlying mechanism, when this adaptive rationale is applied to humans, the more elongated body and longer limbs of tropical populations can be interpreted as an adaptation to more efficient heat dissipation, while the more compact body shape of high-latitude populations could be advantageous by retaining more metabolic heat in cold climates. Interestingly, the reduction in relative limb length in high-latitude populations is not achieved by a general shortening of all limb bones; instead, a reduction in the length of the zeugopods (i.e. radius, ulna, tibia and fibula) seems to be largely responsible for the difference (Trinkaus, 1981; Ruff and Walker, 1993; Ruff, 1994; Ahlström, 1997; Holliday and Ruff, 2001; Béguelin, 2011; Pomeroy et al., 2012, 2013; but see Porter, 1999).

Experimental evidence for the link between human body proportions and efficiency in heat dissipation was described in a study by Tilkens and colleagues (2007). They compared resting metabolic rate in individuals of various relative limb lengths under different temperatures. The predictions of the study were that, if longer-limbed individuals were more efficient in dissipating heat than shorter-limbed ones, they would show a larger increase in resting metabolic rate following a drop in ambient temperature in order to maintain stable body temperature. The results showed a significant correlation between resting metabolic rate and body proportions, therefore supporting the causal relationship underlying Allen’s rule (Tilkens et al., 2007).

Differences in body proportions between populations have been shown to appear early in life. For example, differences in body proportions between Inuit and Aleut on one side, and lower latitude populations on the other side, appear very early in childhood (Y’Edynak, 1976); the same seems to be true for Australian aboriginal body proportions (Eveleth and Tanner, 1976) and limb proportions in prehistoric Japanese from the Jomon period (Temple et al., 2011). Moreover, differences in limb proportions and relative pelvic width between African-American and European-American groups were shown to appear during early fetal development (Schultz, 1923, 1926), and the difference in crural index (tibial length / femoral length) between South Africans and Europeans seems to persist from birth through adulthood (Frelat and Mittereocker, 2011). Finally, a larger comparative study of body size and shape in populations from different continents recently confirmed that population differences in both bi-iliac breadth and intra-limb proportions, and their correlation with climate, are already present in immature individuals and persist throughout growth (Cowgill et al., 2012). The results of such studies imply a strong genetic component of climatic adaptation, suggesting the action of natural selection (Holliday, 1997a).

Although directional selection and the resulting genetic variation between populations has long been the favored explanation for latitudinal differences in relative limb proportions, several studies have also highlighted a direct effect of temperature on skeletal growth in non-human endotherms raised in experimental conditions, which for the limbs matches the prediction of Allen's rule (Ashoub, 1958; Lee et al., 1969; Weaver and Ingram, 1969; Riesenfeld 1973; Al-Hilli and Wright, 1983; Rae et al., 2006; Serrat et al., 2008, 2009; Serrat, 2013). Serrat (2013) and Serrat et al. (2008), for example, showed that temperature has a direct effect on limb bone growth in mice, particularly accentuated during the early postnatal development. Their results suggest a direct negative influence of low environmental temperature on cartilage growth, which, as a precursor of bone, in turn affects bone elongation in animal limbs.

Despite the evidence of population differences in body and limb proportions at early developmental stages, which suggests a genetic basis, phenotypic plasticity could still be a contributing factor. A recent study found significantly different body proportions between highland and lowland Peruvian populations present throughout ontogeny (Pomeroy et al., 2012). The two populations are expected to be genetically close, so the differences are possibly due to early exposure to different environmental conditions such as temperature and diet. Separating the effects of climate on skeletal morphology through plastic reactions from the long-term effects of directional natural selection is extremely difficult, and the question of how these factors interact in shaping human morphology is still a matter of some debate (Bogin and Rios, 2003; Wells, 2012, Serrat, 2013).

Irrespective of the causal mechanism, however, we might expect that the pattern of shorter, more compact limb bones in cold regions be extended to the bones of the hands and feet. Indeed, if the differences in limb proportions are partly due to low temperature during bone development, we would expect the pattern to be particularly accentuated at the end of the extremities, which are further away from the core of the body and more susceptible to the effects of environmental temperature. The accentuated shortening of the zeugopods with respect to the stylopods (i.e. humerus and femur), as reported for high-latitude and high-altitude populations (e.g., Trinkaus, 1981; Ruff and Walker, 1993; Ruff, 1994; Pomeroy et al., 2012, 2013), seems to support this hypothesis. In addition, given that the autopods (hands and feet) are serial homologues, with a common genetic and developmental architecture (e.g. Reno et al., 2008; Rolian et al., 2010; Young et al., 2010), it might be expected that they exhibit the same pattern of association with temperature variation.

There has been limited research on the effect of climate on human and hominin hands and feet. Previous research has shown that climate correlates with the thickness of long bone diaphyses relative to length as well as the size of their articular regions relative to length (Schwidetzky, 1979; Collier, 1989; Ruff, 1994; Pearson, 2000; Pearson and Millones, 2005). The bones of people from cold climates tend to be proportionately thicker and have proportionately larger epiphyses than those of people from warm climates. Stockier, more robust bones can also be interpreted as the result of Allen's rule, as an increase in thickness would have a similar effect on the surface-to-volume ratio to a decrease in length. Pearson (2000) found that this pattern is also valid for the diaphyses of the first metatarsal and third metacarpal, but not the shaft of the first metacarpal, and Pearson and Busby (2006) showed that the stout first metatarsals of Neanderthals resembled those of Holocene populations from cold regions. A comparative study of the shape of the second metacarpal in Inuit and European-American populations also revealed significant differences between the two samples, the Inuit metacarpal being shorter and wider than in European-Americans (Lazenby and Smashnuk, 1999). The results are suggestive, but the limited scope of the study (based on only two populations) makes it impossible to evaluate if this difference in shape is due to climate, or whether it is simply due to neutral genetic differences accumulated after the two populations diverged during the expansion of humans out of Africa (Henn et al., 2012).

Human populations that live in geographic proximity tend to experience similar climatic conditions as well as a shared population history, the latter resulting in genetic and consequently phenotypic similarity. In a comparable fashion, populations from distant geographic regions tend to be genetically more dissimilar as well as often experiencing different climates (Roseman and Auerbach, 2015). The collinearity between genetic distance and climatic distance, due to the relationship of both variables with geographic distance, can have a confounding effect, leading to a spurious correlation between phenotypic characteristics, which are directly affected by underlying genetic differences, and climate (von Cramon-Taubadel, 2014; Roseman and Auerbach, 2015). To avoid this problem when testing for the effects of climate on the phenotype, it is essential to take into account the pattern of similarity between populations due to shared population history, as expected under a neutral model of genetic and phenotypic evolution (e.g., see Roseman, 2004). Unfortunately, previous tests of the validity of Allen’s rule in humans have not accounted for the underlying neutral pattern of variation, leaving open the question of how much of the suggested signature of climatic adaptation is indeed due to climate as opposed to neutral demographic processes.

Given the foregoing, the aims of this study are two-fold:

1) To re-evaluate the effects of climate on human variation in limb proportions, while taking into account the underlying neutral pattern due to past population history;

2) If the pattern of climate-related variation in limb proportion is confirmed, with lower crural (tibial length / femoral length) and brachial (radial length / humeral length) indices in high-latitude populations, to test if such pattern extends to the hands and feet.

Materials and Methods

Measurements of the limb bones were collected by LB and OP for 393 individuals from a geographically and climatically diverse set of human populations (Table 1, Figure 1). The measurements included the maximum length of the femur, tibia, humerus and radius, as well as the breadth of the distal epiphysis and the maximum length of the first metacarpal and of the first metatarsal (see Table S1 for the populations' mean and standard deviation). Unilateral data were collected preferentially for the left limb, except in cases where the right limb showed better preservation. The measurements were used to calculate a series of indices, which are informative of limb proportions and metapodial shape (Table 2, Table S2). Crural and brachial indices were calculated in order to verify previous suggestions that high-latitude populations tend to have relatively shorter zeugopods than tropical populations. To evaluate if this pattern extended to the feet, we computed the length of the first metatarsal relative to the maximum length of the femur and the tibia (Foot Index 1 and Foot Index 2). Similar indices were calculated for the first metacarpal, in respect to the humerus and radius (Hand Index 1 and Hand Index 2). Finally, to evaluate if climate had an effect on the general shape of the metapodials, the ratio between epiphyseal breadth and maximum length was calculated for the first metatarsal and the first metacarpal.

Adult individuals of both sexes were included in the study and analyzed together. Males tend to have bigger bones than females, due to body size sexual dimorphism and higher male robusticity. However, by using indices we effectively standardize the measurements by size, making males and females more directly comparable. Sexual dimorphism in robusticity might still have an impact on the shape of the metapodials, where breadth and length are compared. Moreover, it is possible that the two sexes show slightly different limb proportions (Trinkaus, 1981; Aiello and Dean, 1990; Ruff, 1994). Although we do not expect these differences to be stronger than between-population differences, their effect on the analyses could increase the amount of noise and partially obscure the general pattern. In order to account for this possibility, we have repeated the analyses for the male and female dataset separately.

The analyses were run on modern human data (Table 1). Due to incomplete preservation of some of the skeletons, especially in the archeological samples, missing data meant that the sample size for the various indices was lower than the total number of studied individuals. The minimum sample size in the different analyses was seven individuals in the combined sex dataset (Fuegians).

To test for the effects of climate, the average minimum temperature of the coldest month for all populations was obtained from WorldClim (www.worldclim.org, Hijmans et al. 2005) as interpolated GIS layers at 30arc-second definition (*ca.* 1 km). Minimum temperature was chosen as a general indicator of climate for two reasons: Allen's rule specifically addresses the effects of temperature on body proportions, and minimum temperature consistently showed a stronger effect than maximum temperature in previous analyses of human skeletal variation (Betti et al. 2010, 2014). Population averages for the various indices were regressed on minimum temperature, to test for a relationship between climate and limb proportions. The regression was computed by Generalized Least Square analysis (GLS, function *gls* in library *nlme*), using the R software version 3.1.1 (R Core Team, 2014).

Geographically closer populations tend to be genetically more similar to each other (e.g., Relethford 2004b; Ramachandran et al., 2005; Liu et al., 2006), due to shared population history and gene flow, and we can expect that this genetic similarity will be reflected in phenotypic similarity. To account for this underlying similarity pattern, which could have a confounding effect on the analyses, spatial autocorrelation was explicitly included in the regression model (as in Betti et al., 2014). Pair-wise geographic distances between populations were calculated using great circle distances, based on the haversine (Sinnott, 1984), using waypoints to avoid long-distance sea-crossings (Betti et al., 2012). The GLS algorithm can calculate pair-wise geographical distances from spatial coordinate data, computing Euclidean distances between coordinate points. However, overland distances between human populations, corresponding to likely routes of expansion and migration, are effectively non-Euclidean distances. To overcome this problem, Multi Dimensional Scaling (MDS) was applied to the original matrix of overland geographic distance, in order to extract a number of orthogonal axes to be used as new spatial coordinate axes. Four MDS axes were selected and used as spatial coordinates for the GLS analysis. A Mantel test confirmed that original and new distances, calculated from the MDS variables, were highly correlated ($r = 0.999$, $p < 0.001$). Different autocorrelation structures were fitted to the data within the GLS model, and an ANOVA test was carried out to test the significance of the contribution of each spatial autocorrelation structure to the model. When adding a significant improvement, the structure associated with the largest decrease in AIC (Akaike Information Criterion; Akaike, 1973) was chosen for the analyses. In the absence of a significant effect of spatial autocorrelation, the model would become a simple regression.

Results

The results show that the crural and brachial indices vary according to temperature in modern human populations (Figure 2, Table 3). Confirming the results of previous studies, high-latitude populations tend to have a shorter tibia and radius in respect to the proximal limb bones. This pattern is still valid even after taking into account spatial autocorrelation due to past population history.

There is some evidence that males tend to have a higher brachial index than females (Trinkaus, 1981; Aiello and Dean, 1990; Ruff, 1994). Sexual dimorphism could have, in principle, a confounding effect on these analyses, especially as the proportion of males and females is not the same in all population samples. However, repeating the analyses on male and female individuals returned comparable results (Tables S3 and S4).

A similar effect of climate appears to extend to the hands, but not the feet. The first metacarpal is relatively shorter in populations inhabiting cold regions in respect to tropical populations, when compared to humeral length (Hand Index 1). However, no significant difference can be detected when metacarpal length is computed relative to radial length (Hand Index 2). The results suggest that the length of the first metacarpal is affected by climate in the same way as the radius, but its more peripheral position is not reflected in a more extreme reduction in length in respect to the radius. The length of the first metatarsal, on the other hand, does not appear to be significantly affected by climate (Figure 3, Table 3).

Despite the different way in which climate seems to have affected relative metatarsal and metacarpal length, the shape of both bones follows the prediction of Allen's rule: the two metapodials are significantly stockier in populations from cold area in respect to warm areas (Figure 4, Table 3). The difference in metapodial robusticity in human populations could also be an indirect consequence of a general increase in body size and robusticity in cold environments, a pattern previously identified in human populations and usually referred to as Bergmann's (1847) rule (Roberts, 1978; Ruff, 1994; Holliday, 1997a, 1997b; Pearson, 2000). Both Allen's and Bergmann's rules stem from the same principle: both an isometric increase in body size and shorter, stockier extremities will reduce the surface-to-volume ratio of the body, and favor heat retention in cold environments.

When the two sexes are analyzed independently, the female dataset does not show a significant relationship between the length and shape of the metacarpal and temperature (Table S4). Given the fact that the female dataset is smaller than the male dataset and includes fewer populations, it is possible that this difference is simply due to the reduced and less representative female sample size.

To evaluate from a different angle the co-variation in length between the different bones, we calculated the variance, covariance, and correlation (i.e. standardized covariance) for the studied limb segments (Table 4; Tables S5 and S6 present sex-specific results). The results show that limb bone lengths tend to show the highest correlation with the homologous bone in the other limb, as opposed to other bones within the same limb. These results support the hypothesis that different evolutionary processes affect the various limb segments differently. The lowest correlation between homologous segments is the one between the two metapodials, in accordance with the different patterns identified in the climatic regression analyses.

Discussion

This study adds to the body of evidence of a temperature gradient in limb proportions in human populations. A correlation between crural and brachial indices and minimum temperature holds true even when taking into consideration the neutral pattern of variation due to past population history. Spatial autocorrelation is the natural outcome of gene flow and recent shared ancestry between geographically close populations, and it would be expressed though the genetic component of phenotypic variation. However, this study could only detect a significant spatial autocorrelation for the crural index. This finding is consistent with the findings of Roseman and Auerbach (2015) who also found that a model of population structure best described variation in global crural indices, while brachial indices were best related to a model that included both population structure and latitude.

This lack of spatial autocorrelation is surprising, as a number of recent studies have highlighted a significant and substantial signature of population history in cranial and pelvic global human variation (Relethford, 2004a,b; Roseman, 2004; Harvati and Weaver, 2006; Manica et al., 2007; von Cramon-Taubadel and Lycett, 2008; von Cramon-Taubadel, 2009, 2011a, 2014; Betti et al., 2009, 2010, 2013, 2014). However, the preservation of a neutral population history signature in a species' phenotypic variation can be affected by various processes (Roseman and Weaver, 2007), including strong diversifying natural selection acting on the populations, and substantial phenotypic plasticity (von Cramon-Taubadel 2011b, 2014). Both of these processes have been suggested to affect the limbs. An alternative explanation for the lack of a consistent pattern of spatial autocorrelation is that the small number of populations analyzed, and their scattered geographic distribution, make it difficult to identify and model the underlying neutral pattern. Although both explanations are possibly valid, other studies have revealed a weaker, if not absent, signature of past population history on limb bones, in contrast to the cranium and the pelvis, even when a larger number of populations was analyzed (Betti et al., 2012; von Cramon-Taubadel et al., 2013). This suggests that the effects of selection and developmental plasticity on the limbs are likely to contribute to the lack of a clear spatial autocorrelation pattern for many of the indices.

The role of climate in generating the described pattern is also supported by the fact that it extends to the hands and feet, affecting the shape of the metapodials and the relative length of the first metacarpal, in accordance with the predictions of Allen’s rule. Although the shortening of distal bones in cold regions extends to the metacarpal, the same is not true for the first metatarsal. On the other hand, the *shape* of the metatarsal, as for the metacarpal, is significantly stockier (i.e., relatively broader) in cold climates, suggesting that the preservation of the metatarsal length might be due to evolutionary constraints and not to the lack of climatic selective pressures. One possible explanation for the difference in the results for the metatarsal is the need to maintain a certain relative metatarsal length for efficient bipedalism. This would suggest a functional constraint on foot morphology not present (to the same extent) in the hand. Another possibility to consider is the effect of cultural buffering via the extensive use of footwear. While cold-dwelling populations no doubt also use insulating clothing on their hands in the form of gloves, the use of temperature-relevant footwear may have been more ubiquitous throughout human prehistory as a means of preventing debilitating tissue damage to feet during periods of seasonal or persistent low temperature. On the basis of trends in pedal phalange gracility it has been estimated that the use of human footwear dates back at least to the middle Upper Paleolithic (~40 kya) (Trinkaus and Shang, 2008).

It is interesting to note that the first metacarpal tends to be shorter in cold regions, but only relative to the humerus and not to the radius. In other words, the reduction in the length of the metacarpal in cold regions does not exceed the reduction of the radius, which means that the process that generated the temperature-related difference, be it directional selection or plasticity, is not stronger at the distal extremity of the limb. If temperature has a direct effect on bone elongation during development, as shown by Serrat and colleagues in their experimental studies (Serrat et al., 2008; Serrat, 2013), we would have expected that the hands and feet showed a particularly marked difference in length in opposite climates, being further away from the core of the body and more susceptible to the effects of environmental temperature. This is not the case. It is worth noting, however, that there is evidence that recent polar populations have evolved physiological adaptations that help the diffusion of body heat to the extremities, which could reduce the direct effect of low environmental temperature (see e.g., Frisancho, 1993). Brown and colleagues (1953) reported an increase in peripheral blood flow in Inuit individuals after exposure to low temperatures, interpreted as an adaptation against frostbite. Similarly, Hildes and colleagues (1961) found that a more efficient vasodilation in Inuit hunters increased heat flow to the hands in comparison to men of European ancestry. Our findings are also consistent with those of Pomeroy et al., (2012, 2013) whereby hand and foot size is protected from hypoxia during growth relative to the zeugopod, which they attribute to a response analogous to a “thrifty phenotype”. Therefore, while our results suggest that metacarpal dimensions are not being wholly protected from cold-mediated adaptation in the same way as the metatarsal, the overall reduction in metacarpal length in cold-adapted populations does not *exceed* that seen in the arm zeugopod.

It is also important to consider that the first metapodials might not be representative of the other bones of the hand and feet. This is particularly true for the first metatarsal, which differs remarkably is size and shape in respect to the other metatarsals, and has a more significant role in support and propulsion during bipedal locomotion.

Other indirect evidence for a causal relationship between climate and limb bone proportions comes from the fact that Neanderthals seem to fit the same trend as recent human populations, showing hyper-polar proportions for the lower limb (see also Holliday, 1997a,b; Weaver, 2003). The hyper-polar lower limb proportions of Neanderthals have been suggested to be the result of strong natural selection during glacial periods. However, temperatures in Europe during glacial peaks would likely have been less extreme than in polar regions inhabited currently by Inuit people. The lack of evidence for footwear and the ability to make fitting clothes (Trinkaus, 2005; Gilligan, 2008) could mean that Neanderthals had a lower level of cultural buffering in respect to later modern humans, resulting in a higher selective pressure (Ruff 1994). On the other hand, Paleolithic anatomically modern humans in Europe do not show a latitudinal pattern in limb proportions (Trinkaus, 1981;

Holliday, 1997a, 1999). The absence of climatic adaptation in these early European human populations has been attributed to their relatively recent migration into higher latitudes from warmer regions of Africa and the Near East, with limited time for natural selection to affect their body shape (Holliday and Falsetti, 1995; Holliday 1997a). The absence of a short-term variation in limb proportions with the colonization of colder, high-latitude regions might suggest a limited role of phenotypic plasticity in driving geographical variation in human populations, and better support long-term climatic adaptation through natural selection.

In summary, human limb bones proportions show a temperature-related gradient most likely due to long-term climatic adaptation (instead or in addition to developmental plasticity), even after accounting for past population history. This temperature gradient characterizes not only the relative length of the zeugopods, but it extends to the hands and partially the feet. The difference between the upper and lower limb extremities is surprising, as serially homologous structures would be expected to vary in a similar fashion (e.g. Lande 1979; Cheverud 1996; Rolian et al., 2010), and might be due to the presence of evolutionary constraints on the foot related to locomotory efficiency. Indeed, the lengths of the two metapodials show a lower correlation than other homologous limb segments, supporting the possibility that the two bones are shaped by different processes. More in-depth studies will be necessary to test this specific hypothesis in the future.

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Figure Legends

Fig. 1. Geographic location of the studied populations.

Fig. 2. Relationship between average crural (**A**; $R^2 = 0.553$, $P = 0.014$) and brachial (**B**; $R^2 = 0.585$, $P = 0.010$) indices and minimum temperature in modern human populations.

Fig. 3. Relationship between average Foot Index 1 (**A**; $R^2 = 0.082$, $P = 0.423$) and Hand Index 1 (**B**; $R^2 = 0.506$, $P = 0.021$) and minimum temperature in modern human populations.

Fig. 4. Relationship between average shape indices for the first metatarsal (**A**; $R^2 = 0.473$, $P = 0.028$) and metacarpal (**B**; $R^2 = 0.791$, $P < 0.001$) (Metatarsal 1 Index and Metacarpal 1 Index) and minimum temperature in modern human populations.

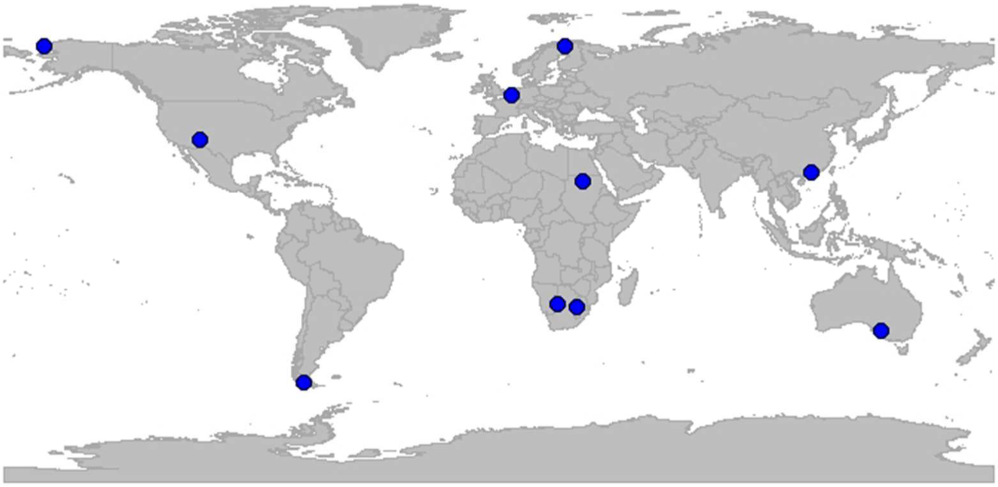

Fig. 1. Geographic location of the studied populations.
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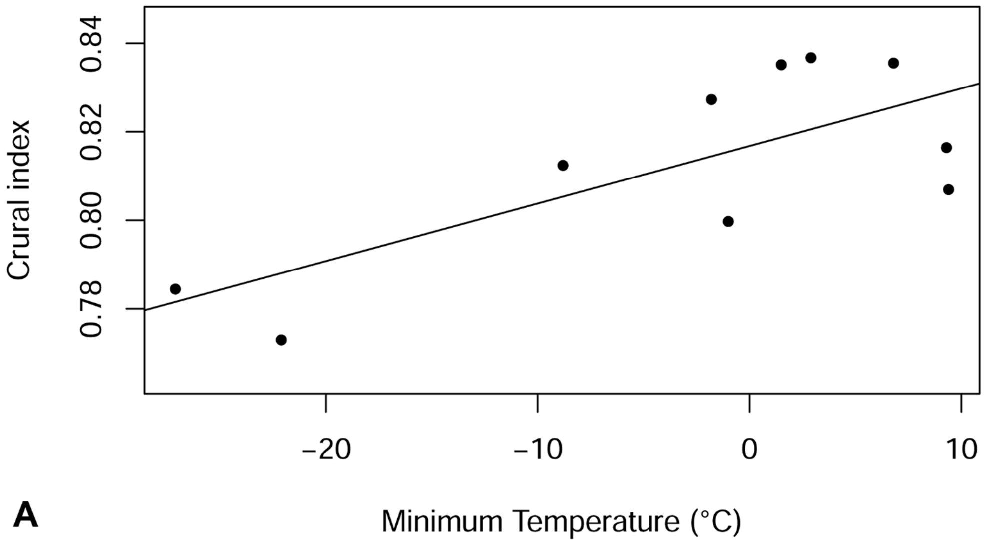

Fig. 2. Relationship between average crural (A; R2= 0.553, P = 0.014) and brachial (B; R2 = 0.585, P = 0.010) indices and minimum temperature in modern human populations.
140x76mm (300 x 300 DPI)

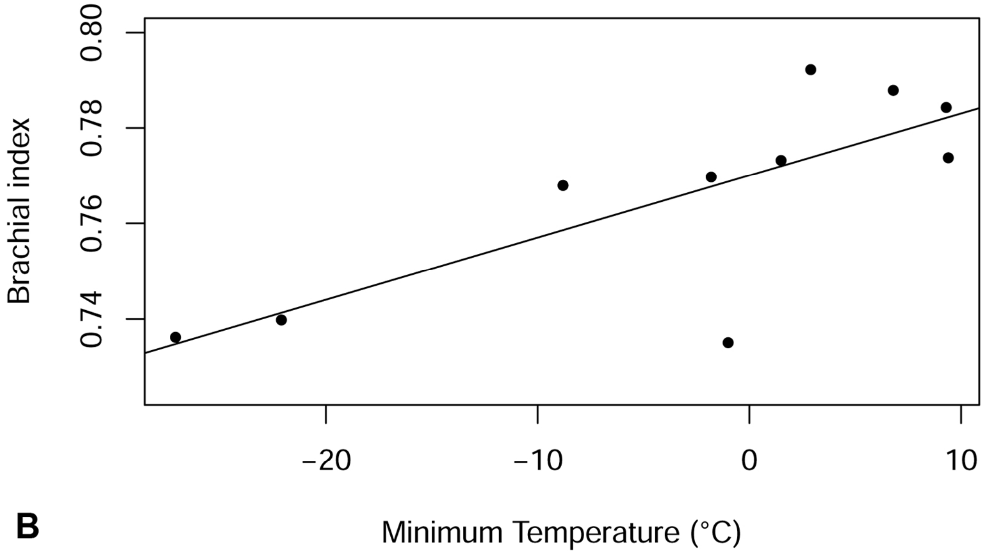

Fig. 2. Relationship between average crural (A; R2 = 0.553, P = 0.014) and brachial (B; R2 = 0.585, P = 0.010) indices and minimum temperature in modern human populations.
140x80mm (300 x 300 DPI)

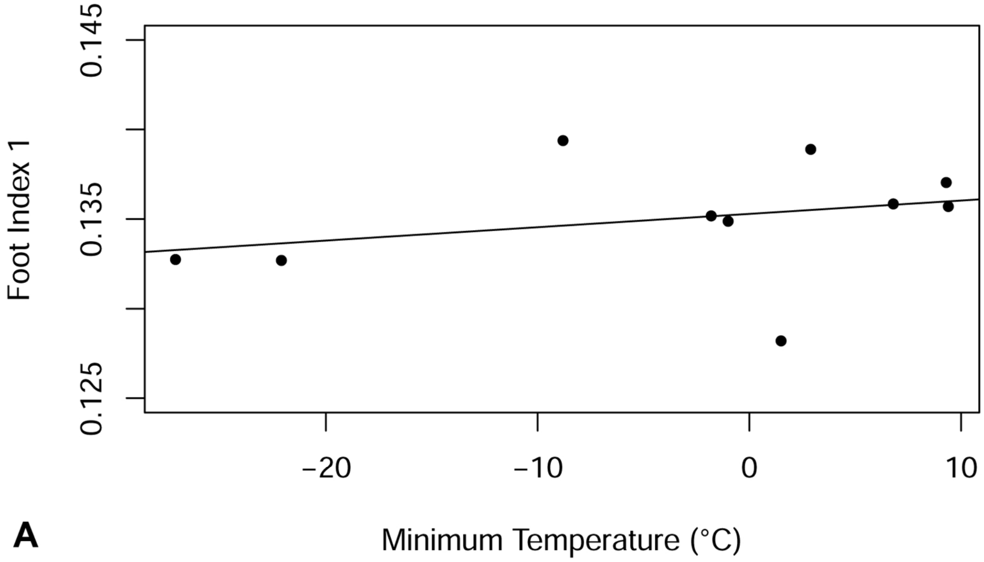

Fig. 3. Relationship between average Foot Index 1 (A; R2 = 0.082, P = 0.423) and Hand Index 1 (B; R2 = 0.506, P = 0.021) and minimum temperature in modern human populations.
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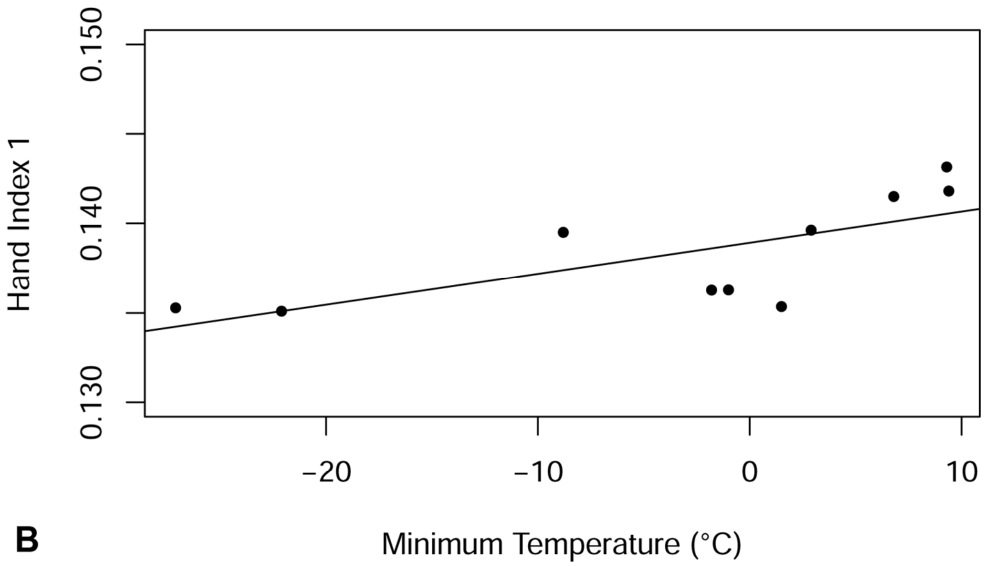

Fig. 3. Relationship between average Foot Index 1 (A; R2 = 0.082, P = 0.423) and Hand Index 1 (B; R2 = 0.506, P = 0.021) and minimum temperature in modern human populations.
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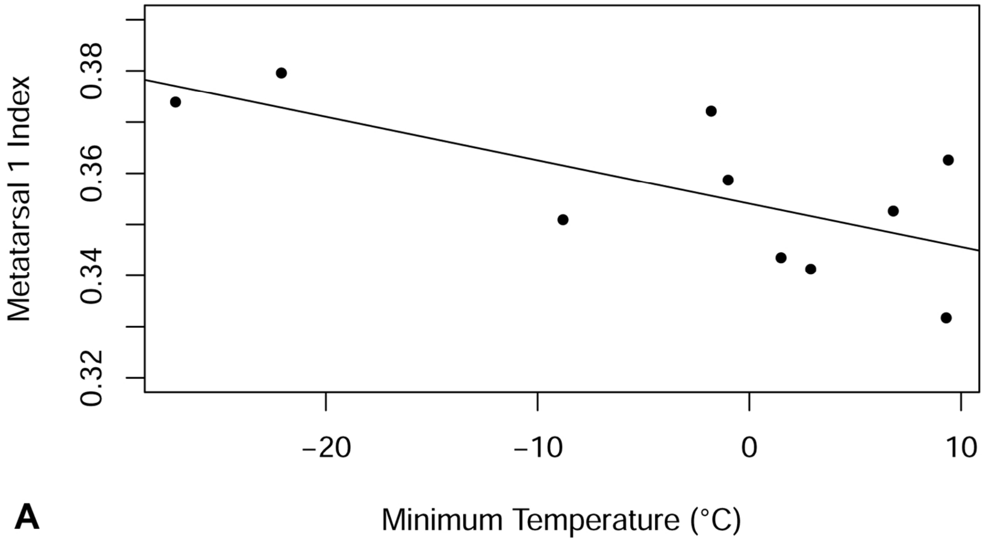
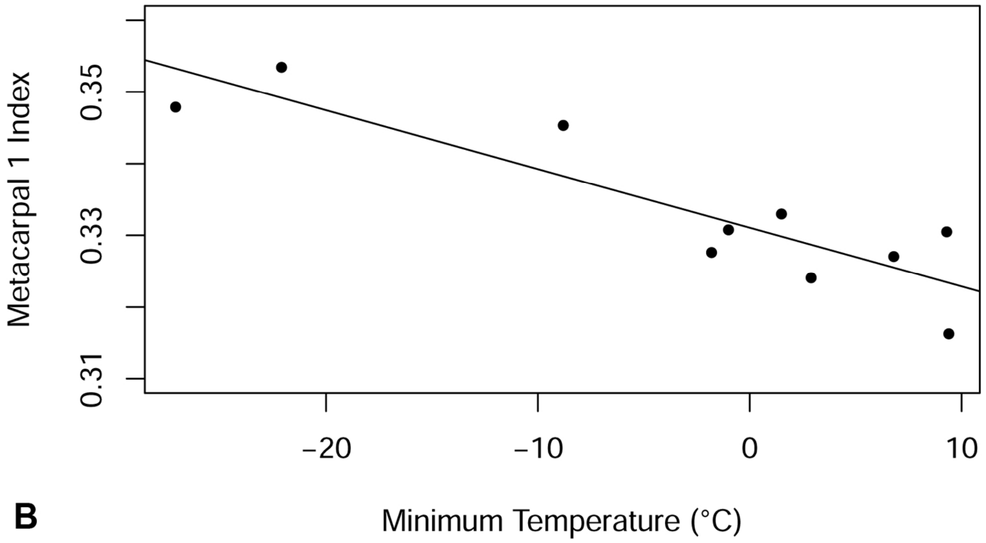


Fig. 4. Relationship between average shape indices for the first metatarsal (A; R2 = 0.473, P = 0.028) and metacarpal (B; R2 = 0.791, P < 0.001) (Metatarsal 1 Index and Metacarpal 1 Index) and minimum temperature in modern human populations.
140x75mm (300 x 300 DPI)



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140x75mm (300 x 300 DPI)

Tables

TABLE 1. Population samples and institutions where the material is curated. Tmin = average minimum temperature of the coldest month (°C).

Population	Latitude	Longitude	Tmin	Total sample size	Males	Females	Institution*
Australia	-34.9	138.6	6.8	23	17	6	DC, NMNH, AMNH, UO
South China	23.1	113.3	9.4	26	26		NMNH
Inupiat, Alaska	68.5	-165.5	-27.1	63	40	23	NMNH, AMNH
Zuni, New Mexico	34.9	-109	-8.8	25	8	17	DC
Khoisan	-25	21	1.5	38	22	16	SAM, UCT, DC
Saami	69	24	-22.1	50	26	24	UO
Nubia	19.6	30.4	9.3	50	27	23	DC
Fuegians	-53.5	-71.3	-1.8	10	6	4	IP, MFM, ME
European-Americans	50.8	4.5	-1	50	25	25	NMNM
Zulu	-26.2	28.1	2.9	58	31	27	DCUW

* AMNH = American Museum of Natural History, New York; DC= Duckworth Collection, Cambridge, UK; DCUW = Dart Collection of the University of the Witwatersrand, Johannesburg; IP = Instituto de la Patagonia, Punta Arenas; ME = Museo Etnográfico, Buenos Aires; MFM = Museo del Fin del Mundo, Ushuaia; NMNH = National Museum of Natural History, Washington, DC; SAM = South African Museum, Cape Town; UCT = University of Cape Town; UO = University of Oslo.

TABLE 2. Description of the indices used in the analyses. Mt1 = first metatarsal; Mc1 = first metacarpal.

Index	**Description**
Crural index	Maximum length of tibia/maximum length of femur
Foot index 1	Maximum length of Mt1/maximum length of femur
Foot index 2	Maximum length of Mt1/maximum length of tibia
Metatarsal 1 index	Maximum breadth of distal epiphysis/maximum length
Brachial index	Maximum length of radius/maximum length of humerus
Hand index 1	Maximum length of Mc1/maximum length of humerus
Hand index 2	Maximum length of Mc1/maximum length of radius
Metacarpal 1 index	Maximum breadth of distal epiphysis/maximum length

TABLE 3. Results of generalized linear models of the various indices on minimum temperature. R^2 and p-value are estimated after a simple linear regression analysis. Significant results in bold.

Index	**R^2**	**P-value**	**P-value ANOVA**[a]	**New p-value**[b]
Crural index	0.553	**0.014**	<0.001 CorGaus	**<0.001**
Foot index 1	0.082	0.423	n.s.	
Foot index 2	0.177	0.226	n.s.	
Metatarsal 1 index	0.473	**0.028**	n.s.	
Brachial index	0.585	**0.010**	n.s.	
Hand index 1	0.506	**0.021**	n.s.	
Hand index 2	0.092	0.394	n.s.	
Metacarpal 1 index	0.791	**<0.001**	n.s.	

[a] Results of ANOVA test comparing the simpler linear model with the generalized least square model that accounted for spatial autocorrelation (p-value ANOVA). A significant result ($\alpha \leq 0.05$) implies

that spatial autocorrelation is a significant factor in the model. The type of spatial autocorrelation is specified in the table (CorGaus = gaussian).

[b] New p-value obtained including spatial autocorrelation in the model.

TABLE 4. Variance (diagonal), covariance (upper triangle), and correlation (lower triangle, italic) values for the lengths of the studied bones. Mt1 = first metatarsal; Mc1 = first metacarpal.

	Femur	Tibia	Mt1	Humerus	Radius	Mc1
Femur	940.182	855.158	113.226	543.327	484.638	70.330
Tibia	*0.908*	943.104	118.058	489.998	512.644	72.196
Mt1	*0.770*	*0.802*	22.996	67.854	67.834	12.940
Humerus	*0.878*	*0.791*	*0.701*	407.367	310.693	45.343
Radius	*0.846*	*0.894*	*0.757*	*0.824*	348.777	45.992
Mc1	*0.687*	*0.705*	*0.809*	*0.673*	*0.738*	11.133