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Investigating neutral and climate-linked morphological variation in human femora: A geometric morphometrics approach

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Abstract

This thesis aimed to differentiate climatic and ‘neutral’ morphological signatures in the human femur, allowing anthropologists to improve their interpretations of behaviour in the past. A dataset of geometric morphometric data and traditional linear measurements for eleven globally distributed hunter-gatherer groups, measures of distance from an estimated African Origin, and a set of climatic variables were used to separate the relative effect of neutral demographic processes and climatic selection on femoral morphology. Within-population shape variance was not significantly predicted by any of the variables tested. Adherence to Bergmann’s rule was identified in the linear measurements on the individual and population level, while within-population variance in femoral length was found to be significantly associated with maximum temperature. These results suggest that climatic selection may have overwritten any neutral signatures. Future research should expand the sample to clarify if the interesting but non-significant patterns identified represent real relationships.

Keywords: Hunter-Gatherers, Femoral Morphology, Neutral Theory, Climatic Selection

Summary for Lay Audiences

The femur is important for inferring the activities/behaviours of past peoples. However, it is impacted by a complex set of influences. This research aimed to differentiate climatic and 'neutral' morphological signatures on an element commonly used to infer behaviour in the past, allowing anthropologists to improve their interpretations. Distributions of neutral traits, those traits which have little to no effect on an individual's suitability to their environment, are shaped by evolutionary processes other than natural selection. Once such process is represented in the Out-of-Africa (OoA) model, the idea that serial founder effects (a type of genetic drift) produce a gradient of decreasing within-population variation in human traits (genetic, morphological, etc.) with increasing distance from Africa

In the following study, the morphology of the femur was examined via linear measurements and 3D models from eleven hunter-gatherer groups. Geometric Morphometrics (GM), the study of shape via landmarking, was used to quantify within-population shape variation. Correlation and regression analyses were used to determine the direction and strength of relationships between these measurements, measures of distance from an estimated origin in Africa, and climatic variables (including temperature, precipitation, and net primary productivity).

This thesis did not identify a statistically significant relationship between distance from Africa or the climate variables, and within-population shape variation, for any part of the femur. However, the small sample size may have impacted these results. For the linear measurements, adherence to Bergmann's rule, that as temperature decreases, an animal's body size will increase to deal with temperature stress, was identified on the individual and population level. Within-population variance in femoral length was found to be significantly associated with maximum temperature. These results suggest that a neutral signal is not evident in femoral morphology, or that one could not be identified using the methods employed here. Instead, climate has an influence on femoral shape, potentially overwriting any neutral signals. Ultimately, femoral morphology is the result of a complex set of influences, including genetics, plasticity, population adaptation and more. Future research should focus on expanding the number of populations in the GM sample to clarify if the patterns identified represent real relationships.

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1. Introduction

Global patterns of skeletal morphological variation have been widely studied in biological anthropology to understand the genetic and environmental factors that have shaped the evolution of our species (Weaver, 2018). Limb bones are widely considered to also reflect the lifetime experiences of individuals, specifically regularly experienced physical loading produced by repeated behaviours (e.g., Stock, 2006; Stock & Pfeiffer, 2001). Thus, information obtainable from the skeleton, and limb bones in particular, is dual faceted. The morphology of the skeleton is impacted by events occurring during an individual's lifetime, but also by events which occur before their birth, including those occurring on evolutionary timescales.

Through the study of digital models of femora from archaeological hunter-gatherers, this research aims to differentiate climatic and 'neutral' morphological signatures on an element commonly used to infer behaviour in the past, allowing anthropologists to improve their interpretations. More generally, this thesis seeks to piece apart the multiple influences on the femur to better understand the roles of different processes in producing femoral morphological variation.

1.1. Project Context

Skeletal morphology is influenced by a variety of factors, including climate, nutrition, loading environment/behaviour, and genetics. However, in many cases, it is not known how much variability a specific factor is responsible for, or how the factors relate to one another. Due in part to this complexity, most studies approach the skeleton with a focus on a specific influence or set of related influences, while only considering others as an aside or as a potential ‘alternative’ source of variation.

A topic that is seldom considered in Anthropological studies of morphology is the potential for neutral variation. Neutral traits are those traits with little to no effect on an individual’s suitability to their environment and as a result their distributions are shaped by evolutionary processes other than natural selection (e.g., genetic drift). Adaptationist explanations for morphological variation in the skeleton have been, and continue to be, dominant within the discipline of biological anthropology, and beyond, leading neutral processes to be minimally considered as drivers of variation (Gould & Lewontin, 1979; Schroeder & Ackermann, 2023). However, the application of neutral models to the evolution of craniodental and pelvic traits has identified that global variation in these elements strongly matches patterns that have been reported for neutral genetic traits, suggesting that morphological variation in these elements is not solely shaped by adaptative processes (Betti et al., 2009, 2010, 2013; Harvati & Weaver, 2006; Relethford, 1994). Postcranial elements other than the pelvis have received limited attention regarding identification of neutral genetic processes, despite the importance of these elements for interpreting behaviour and lifeways in the past.

In contrast, the impact of climate on body size and shape, and by extension, skeletal variation, has been widely studied. Historically, the relationship of climate to adult body proportion and size has been understood via Bergmann and Allen’s rules (James, 2018). Whether or not these ecogeographic ‘rules’ can be wholly explained as adaptations is debated (Serrat et al., 2008) but nonetheless, the patterns they suggest have been recurrently found in our species (Katzmarzyk & Leonard, 1998). When discussing these patterns using archaeological samples, analyses often include investigating the femur and its dimensions, usually comparing linear measurements between populations. What shapes variability in femoral dimensions and shape within populations is less well understood.

The current lack of focus on neutral femoral variation has implications for understanding behaviour in the past, as quantifying neutral variation in these elements, if present, would provide a baseline on which to test hypotheses about past activity. Additionally, gaining a better understanding of climatic impacts on variability would serve to further piece apart the complexity of factors acting on this element, especially given that studies often use levels of variability to investigate the potential impacts of neutral process.

1.2. Project Aims and Research Questions

Neutral morphological variation in long bones, and the femur especially, lacks detailed study and subsequent understanding. As such, this research focuses on clarifying the impacts of different sources of variation in human femoral morphology. Identifying the magnitude of neutral and climatic variation on the femur will provide an opportunity to clarify the effects of adaptive processes on this element, serving to fortify interpretations based on its morphology.

In this project, neutral variation will be identified through correspondence with serial founder effect models. Specifically, this research assesses fit of patterns of within-population variation in femoral morphology with an Out of Africa (OoA) expansion model and with a variety of climate variables. To do so, this study draws on a collection of 3D laser scans of groups of archaeological hunter-gatherer remains collected by current and former P.A.V.E. Lab members (P.I - Dr. Jay Stock, Members - Dr. Pere Ibáñez-Gimeno, Dr. Laura Buck, and Dr. Thomas G. Davies). To assess correspondence with current understandings of directional selection’s impacts on body size and stature, fit to ecogeographic ‘rules,’ and to further clarify the impact of climate, linear measurements of femora of the same archaeological groups are also analyzed. Shape variation within these groups is quantified via Geometric Morphometrics (GM) and the relationships of within-population shape variation with climatic variables and geographic distance from an African origin of expansion is examined.

The following overarching query has guided this research: to what degree does the human femur display adaptive and non-adaptive signals? The following questions have further clarified the approach and are the basis of this thesis.

1. How does directional and/or stabilizing selection interact with femoral morphology to produce variation in femoral length and femoral head diameter (as reflections of body size and stature)?
    a. Does examining within-population variance in femoral length and head diameter identify any patterns? Do these suggest a significant climatic or neutral influence?
2. Is some human femoral morphological variation a product of neutral genetic processes?
    a. Does this manifest as a linear relationship between distance from an African origin of expansion and within-population variation, as has been demonstrated in studies of other elements (e.g., Betti et al., 2009, 2012, 2013; von Cramon-Taubadel & Lycett, 2008)?
    b. Given proposed variable levels of plasticity for different long-bone sections in response to activity (Pearson & Lieberman, 2004), and the potential impact of climate on the proximal femur from its association with the pelvis where shape is understood to be climatically driven (Holliday & Hilton, 2010; Kurki, 2013), is the signal of Out of Africa serial founder events stronger in particular regions of the femur?

3. Will the impact of climate-based variation overwrite any non-adaptive signal in femoral morphological variability, as has been suggested in previous studies (Betti et al., 2012)?
    a. Does this manifest as a linear relationship between climatic variables and within-population variation?
    b. As above, is the association of climate to morphological variability stronger in particular regions of the femur?
4. What might be the cause of within-population variation left unexplained by neutral variation and climatic factors?

1.3. Organization of Thesis

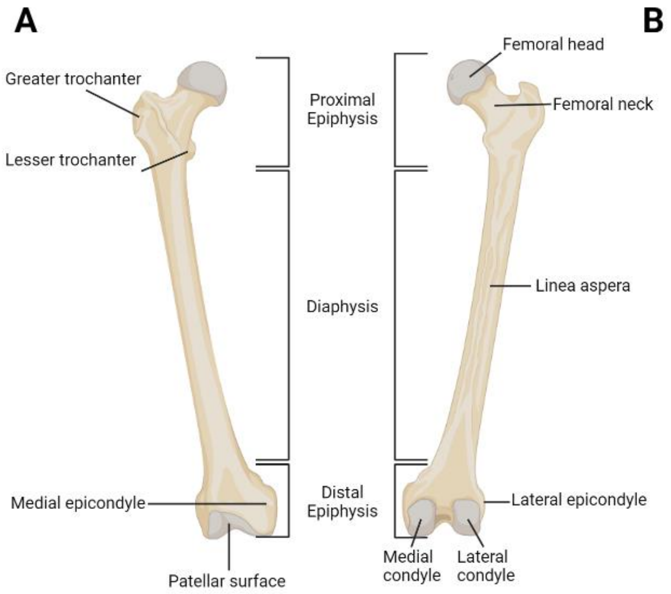
Chapter 2 provides specific research context, expanding upon the significance of the human femur, the potential influences of behaviour and environment on long bone morphology, and a description of neutral theory and its application to human morphology. This chapter also discusses research which has attempted to differentiate mechanisms of long bone morphological variation. Chapter 3 provides background and contextual information for each of the archaeological populations of hunter-gatherers included in this thesis, including information on ecology, lifeways, excavation, and curation history. The second section of this chapter discusses some ethical dimensions of this thesis. It engages with literature on institutional collections of human remains and digital data ethics. Chapter 4 addresses background information on Geometric Morphometrics and modular approaches to studying morphology. This chapter reviews the data collection protocols used to derive shape, size, climate, and distance data for the populations studied, and the statistical analyses conducted to test for the association of morphology and neutral and environmental factors. Chapter 5 presents the results of shape, climate, and distance variable generation. This is followed by the results of simple and multiple linear regressions investigating the relationships between phenotypic variance, climate, and OoA distance, as well as correlations and simple linear regressions of linear dimensions, linear measurement variance, and climatic variables. Chapter 6 addresses the research questions based on results presented in Chapter 5. The potential roles of neutral and selective pressures in shaping femoral morphological variability are highlighted. Chapter 7 summarizes the research findings, addresses potential limitations, and outlines areas for future research.

2. Literature Review

2.1. The Femur

The femur is the major bone in the human lower limb and is an element of significant research focus for a variety of reasons. Much interest comes from its interaction with the pelvis to form the hip joint and with the tibia to form the knee joint, and those joint's roles in the generation and transmission of forces associated with human locomotion (Büchler et al., 2018). The evolution of bipedalism has also fostered interest in the femur's variable morphology across time and between hominin species (e.g., Stern & Susman, 1983; Tardieu, 2010). In addition, the overall dimensions of the femur, in particular length, may play a role in locomotor energetics and thermoregulation, which may explain some biogeographic variation in human phenotype (e.g., Kozma et al., 2018; Pontzer, 2007). Figure 2.1 indicates key anatomical features of the femur.

Figure 2.1: Key Anatomical Features of the Mature Femur.



Note: A: Anterior view. B: Posterior view. Created with BioRender.com

Importantly, the analysis of long bone morphology can allow anthropologists to interpret the lived experiences of individuals from their skeletal remains. Long bones alter their size, shape, and properties through modeling and remodeling processes, especially in response to the *in vivo* loading environment. This is possible because bone exhibits plasticity. Broadly speaking, plasticity refers to an organism's ability to change aspects of phenotype in response to the environment (Stearns, 1989). Plasticity is contrasted by developmental constraint, bone's inability to respond to its environment due to physical, mechanical, or structural limitations. The morphological variation these processes produce can then be used to interpret the lived experiences of individuals from their skeletal remains. As the femur is the only bone in the proximal lower limb, it bears 100% of the load from most activities involving the legs. This in some ways makes loading easier to interpret, and as such the femur is one of the most commonly studied elements in biomechanical analyses.

2.2. Behavioural Influences on Long Bone Morphology

Skeletal remains are relied upon to make inferences about a vast array of aspects of the human experience, using a variety of methods. Bone shape may be useful to discuss behaviour, taxonomy, and life history, among other topics. As they are involved in the support of body mass, locomotion, and manipulation, long bones and their morphology are often used to reconstruct activity in the past (Ruff, 2018). That bone morphology reflects, in part, *in vivo* mechanical loading history is central to anthropologists' ability to infer past activity from human skeletal remains.

2.2.1. Boney Response to Activity.

The concept of bone functional adaptation proposes that bone tissue, when faced with increased strain through increased muscle activity or body size, deposits bone to reduce strain and return it to optimal levels (Ruff et al., 2006; Ruff, 2018). Conversely, decreased strain, through inactivity, including paralysis and spaceflight, causes resorption of bone to restore optimal strain levels (Ruff et al., 2006; Ruff, 2018). A bone's shape thus becomes tailored to the mechanical stresses it regularly endures, regarding both the magnitude and type of mechanical force applied, through bone cell action (Chen et al., 2010). On a cellular level, functional adaptation involves the responses of osteoblasts, osteoclasts, and osteocytes. When mechanical load is applied to bone, osteocytes (mature bone cells) are subjected to hydrostatic pressure due to fluid flow in the lacuno-canalicular network (Chen et al., 2010; Wallace et al., 2017). In response to this pressure, osteocytes signal other bone cell types to either deposit (osteoblasts) or resorb (osteoclasts) bone.

The principle of bone functional adaptation builds upon an early observation by Julian Wolff (Wolff, 1892/1986). Wolff suggested that trabecular bone modeling and remodeling processes produce patterns via changes in mechanical stress applied to bone, which could be explained via mathematical laws (Wolff, 1892/1986). Often referred to as Wolff's 'law,' and presented as a more general statement, Wolff's observation has been criticized, and demonstrated to not accurately reflect boney response to mechanical loading (see Pearson & Lieberman, 2004 for discussion). However, the observation that bone responds in some way to mechanical loading has been shown to be true (as reflected in the concept of bone functional adaptation).

Elaborating upon this principle, Harold Frost (2003) proposed the 'mechanostat' hypothesis which suggests that, if a bone is regularly subjected to a certain threshold of nontraumatic strain (i.e., mechanical stress that will not cause a fracture) bone mass will be increased. Conversely, if bone is loaded below this threshold bone mass is decreased via resorption. Additional complexity is added to the model when factors like sex/age/genetic variation in response to strain and in the target strain threshold are considered (Laurent et al., 2014; Ruff et al., 2006; Ruff, 2018; Wallace et al., 2012, 2017). However, generally speaking, this body of theory suggests that an element's mechanical performance is tailored to the *in vivo* loading conditions that are regularly experienced. Consequently, differences in mechanical loading regimes can be interpreted from differences in bone morphology, and thus, bone morphology can signal differences in activity patterns (Ruff, 2018).

Of note, many scholars have argued that this process is more complex than the simple picture presented above (e.g., Pearson & Lieberman, 2004; Ruff et al., 2006). Most significantly, as functional adaptation is a part of 'plasticity', it needs to be understood relative to constraints on morphology (discussed further in section 2.2.3.).

2.2.2. Interpreting Habitual Activity via Long Bone Morphology.

Long bones (like the femur) are often the elements used to analyze behaviour via skeletal morphology. The following discussion reviews traits that may be analyzed through surface morphology and are thus available via surface models. Other traits are known to reflect activity (like trabecular architecture and organization: Doershuk et al., 2019; Saers et al., 2019; Scherf et al., 2016), but these require analysis of internal attributes of bone, which is not approached in the current thesis. As such, while not an exhaustive discussion, this section does cover most external femoral traits that have been associated with activity.

Past activity is often inferred by analyzing the cross-sectional geometry (CSG) of long bone shafts (diaphyses). Biomechanical principles originally derived in the engineering field are used to quantify and compare levels of robusticity, the “strengthening or structural buttressing” of skeletal elements in response to their environments (Ruff et al., 1993, p. 21-22). When used to interpret activity from bone morphology, long bone diaphyses are conceptualized and analyzed as engineered beams (Ruff, 2018). Distributing bone tissue further from the neutral or bending axis increases that bone's resistance to loading, such that a bone with tissues that are further distributed will be stronger (more robust) along that axis. A more robust bone can be presumed to have experienced and adapted to higher loading conditions than a more gracile one. The distribution of buttressing in the cross-section of the bone can be used to calculate strength in particular directions, allowing one to infer attributes of commonly experienced strain.

A variety of methods can be used to derive cross-sections, including physical sectioning, periosteal molding, or by digitally sectioning the products of computed tomography (CT), biplanar radiography, or three-dimensional laser scanning (Davies et al., 2012). Surface scans may be used to create solid sections (based on only the periosteal contour - lacking the medullary cavity) which have been shown to produce CSG properties that are highly comparable to true sections in adult bones (Macintosh et al., 2013). Different CSG properties act as measures of resistance to different types of loadings (e.g., axial compression and tension, bending, torsion) or combinations of loadings (Ruff, 2018). Commonly, calculated bending strengths between populations are compared to discuss relative levels of activity (Ruff, 2018).

Many studies have used diaphyseal morphology and robusticity to make inferences about habitual activity in the past, in both archaeological and fossil remains (e.g., Macintosh et al., 2017; Ruff et al., 1993; Ruff & Hayes, 1983; Stock & Pfeiffer, 2001; Stock, 2006; Stock et al., 2011; Stock & Pfeiffer, 2004; Trinkaus et al., 1999). Most of these studies include the femur as an element of interest. Anthropologists can compare diaphyseal CSG property values between populations, hominins, individuals, and skeletal elements to infer relative differences in the magnitude of loading experienced. From this, inferences about activity levels, which may include reconstructing mobility patterns (e.g., marine vs terrestrial subsistence strategies), can be made (e.g., Stock & Pfeiffer, 2001; Stock, 2006). Analyzing the effects of loading on living athletes and controls, and comparing them to archaeological populations, has further clarified the effects of different activity patterns on long bone shaft geometry (e.g., Macintosh et al., 2017; Nadell & Shaw, 2016; Nikander et al., 2006; Shaw & Stock, 2009a, 2009b).

Another common aspect of long bone morphology discussed with reference to activity is anteroposterior shaft curvature, specifically of the femur and tibia, the main weight-bearing bones of the lower limb. There is an established relationship between curvature and activity, in that increased curvature is associated with increased activity levels (De Groote, 2008, 2011; Shackelford & Trinkaus, 2002). This association is counter intuitive given the associations between CSG property values and activity. Rather than protect against nonoptimal strain as previously discussed changes in cross-sectional geometry do, increased longitudinal bone curvature produces increased levels of strain (De Groote, 2011; Macintosh et al., 2015). Some explanations for why increased curvature could be a benefit despite it producing increased strain include increased predictability of bending strains and material failure, the translation of bending stress to axial stress (which bone is better equipped to handle), and increased potential for muscle packing (De Groote, 2011; Macintosh et al., 2015). Whichever explanation, or combination of explanations, is most accurate, long bone curvature has been positively associated with activity levels, though there are additional factors that influence curvature and could hold some responsibility for this association.

De Groote (2011) showed that Neanderthals display increased femoral curvature relative to early modern humans and inferred that this is a result of Neanderthals' higher activity levels. However, the difference in curvature between modern humans and Neanderthals may not be explained by lifetime behaviour alone. De Groote (2011) identified increased curvature as a potential autapomorphy of Neanderthals, or low curvature as a derived modern human trait, signaling a potential genetic influence on curvature. Similarly, while Bruns et al. (2002) found a significant decrease in femoral curvature in late 20th century Scottish individuals relative to medieval ones, they too suggested that functional factors (a decrease in activity with urbanization) may not be solely responsible, citing nutritional factors as a potential source of the observed variation.

An additional trait to consider is variation in femoral neck-shaft angle (NSA). This refers to the medial inclination of the proximal femur, where declination has been linked to increased physical activity during life (Anderson & Trinkaus, 1998; Child & Cowgill, 2017; Trinkaus, 1993). As an example, in their study exploring the link between femoral NSA and climate-induced body proportions in juveniles, Child and Cowgill (2017) found that population differences in NSA were variable throughout development, while differences in relative body mass were constant. The authors proposed that, regardless of body proportion, the declination of the femoral NSA is similar between populations with similar ambulatory and habitual behaviour patterns. However, as with other studies discussed, Child and Cowgill (2017) suggested that nutrition, hormones, and/or ecogeographic variables likely also play a role in neck-shaft angle variability.

2.2.3. Plasticity and Constraint.

Manifestation of lived experience in the morphology of skeletal elements is more complex than the picture painted above in the discussion of Wolff's Law and the theories of functional adaptation which followed. That some elements, and some regions of elements, are more plastic, while others are more canalized (directed or fixed genetically), is a key concept driving the approach of the current thesis. Plasticity refers to the ability to alter phenotype in response to the environment, while constraint (or canalization) refers to the inability to do so. Specifically, constraint refers to a bone's inability to respond to its environment due to physical, mechanical, or structural limitations. More plastic elements and regions are understood to reflect lifetime experiences, which may include thermal/altitudinal, nutritional, and biomechanical stressors. Conversely, more canalized regions and elements are understood to reflect phylogeny and genetic processes.

Within a single element, long bone epiphyses are understood to be more constrained, while diaphyses appear more phenotypically plastic (e.g., Lazenby et al., 2008; Nadell & Shaw, 2016; Ruff et al., 1993; Ruff & Runestad, 1992). However, there appears to be variation in the plasticity of diaphyseal regions. For example, in a study examining plasticity and constraint along humeral, radial, and tibial diaphyses of living athletes and controls, Nadell and Shaw (2016) found that the distal metaphysis appears to be more constrained by safety factors compared to midshafts and proximal sections. As such the mid and proximal diaphysis may display greater plasticity to habitual loading (Nadell & Shaw, 2016).

In terms of broad patterns within the limbs, it is suggested that mass is more readily deposited at the proximal limb segments (Hildebrand & Goslow, 2001; Nadell & Shaw, 2016; Pearson & Lieberman, 2004). This lessened constraint on tissue economy may produce more obvious signs of activity, hence the femur's frequent discussion in studies of past activity through the skeleton (Stock & Pfeiffer, 2001; Stock & Pfeiffer, 2004). However, in the lower limb, some research has suggested the tibial mid-diaphysis may show the clearest reflections of human mobility (Davies & Stock, 2014; Macintosh et al., 2014/2015; Stock, 2006).

2.3. Environmental Influences on Long Bone Morphology

Multiple studies of activity in the past have suggested that some of the long bone morphological variation observed which appears to be tied to activity may be the result of other factors. In particular, the physical environment an individual and their ancestors lived in, and the nonmechanical stresses those environments engendered, influences the shape and size of their long bones. To begin, Bergmann and Allen’s rules are well established, though sometimes contested, theories surrounding climatic influences on body size and proportion, which have been applied to explain patterns of variation in long bone morphology.

2.3.1. Bergmann and Allen’s Ecogeographic “Rules.”

Bergmann (1848) and Allen’s (1877) rules attempt to explain the relationship of climate with adult body proportion and size. Bergmann’s rule focuses on body size and states that, in a species with a large range of geographic dispersal (like humans), those in colder regions will exhibit larger body sizes, while those in warmer regions will be smaller (James, 2018).

Allen’s rule relates to body proportions and suggests that, in colder climates, arms, legs and other appendages will be shorter relative to those in warmer climates. Both principles are understood to reflect the body’s ability to dissipate or conserve heat to maintain homeostasis. In colder climates, a larger body mass with shorter limbs lowers the body’s’ surface area to volume ratio, increasing heat conservation. In warmer climates, a higher surface area to volume ratio increases heat dissipation.

Adherence to these principles has been demonstrated in numerous warm-blooded species, including being reflected in human linear growth patterns (James, 2018). In humans, it has been suggested that Allen's rule is reflected in the relative lengths of the distal and proximal limb segments (crural and brachial indices), where those in colder climates are expected to display relatively shorter distal segments (Katzmarzyk & Leonard, 1998). Adherence to Bergmann's rule has been repeatedly demonstrated in humans, though it is somewhat confounded by cultural/dietary variation in modern populations (e.g., Fukase et al., 2012; Katzmarzyk & Leonard, 1998). As an example, Fukase et al. (2012) found inter-regional differences in body size indicators in their samples of Jomon foragers that correlated with latitude. This produced a north-south geographical cline in body size (indicated by femoral head diameter and skeletal limb length) which corresponds to the patterns proposed by Bergmann's rule. Contrary to Allen's rule, however, no significant differences in intralimb proportions were found in this sample, suggesting, as others have, that reappraisal of Allen's rule may be necessary (Fukase et al., 2012). This lack of agreement with Allen's rule may be due to the increased climatic-driven plasticity of the tibia relative to other elements, which may in turn impact intralimb proportions.

2.3.2. Complicating Factors.

Complicating the conceptualization of environmental impacts on bone shape and size, the magnitude of environmental impacts among skeletal elements is thought to be variable. It appears that elements have different sensitivities to environmental stresses, which may include thermal stress, physical stress, nutritional stress etc. Distal elements are more impacted by stress (dietary or thermoregulatory) than proximal elements, while central body regions (the head and thorax) appear to show no, or significantly less, sensitivity to stress (Betti et al., 2015; Payne et al., 2018; Pomeroy et al., 2012). It has been proposed that this is a product of preserving the growth of functional regions (like the head/brain) at the expense of less-functional regions (like zeugopod (distal) elements), linked to the thrifty phenotype hypothesis (Payne et al., 2018; Pomeroy et al., 2012). In the face of environmental stress, energy that would otherwise be devoted to growing the zeugopod elements is instead reallocated to more 'important' regions. This has been reflected in studies of population-level variation in limb segment length, where the greatest differences between lower and higher stressed populations are found in the distal segments of the limbs (the tibia or ulna; Payne et al., 2018; Pomeroy et al., 2012). It is this lifetime-sensitive variability that may be responsible for the poor-fit of Allen's rule in some studies (like Fukase et al., 2012).

The pattern of environmental-stress linked differences manifesting in distal regions does not appear to extend to the feet, specifically the first metatarsal, which may need to maintain a particular morphology to allow for efficient bipedal locomotion, and whose morphology is thus more constrained (Betti et al., 2015). Whether the pattern extends to the hands is unclear, with some studies reporting shorter and stockier first metacarpals in populations from cold regions (Betti et al., 2015), and others finding no interpopulation differences in hand width (Payne et al., 2018).

There is further discussion surrounding whether ecogeographic patterns can be wholly explained as adaptations that are passed down genetically, as they appear to be impacted by a secondary growth response to temperature in homeothermic mammals (Serrat et al., 2008). Serrat et al. (2008) found that *in vivo* extremity temperature was a good predictor of extremity growth; mice in warm rearing environments had significantly longer ears, limbs, and tails than those raised in colder environments, as Allen's rule would suggest. As for the mechanism producing this variation, metatarsal organ culture results showed that total accrued growth was related to changes in chondrocyte proliferation and extracellular matrix volume that were correlated with tissue temperature (Serrat et al., 2008). At warmer temperatures, the researchers identified higher rates of mitosis and increased matrix volume (Serrat et al., 2008). The mineralized diaphyses between metatarsals in different temperatures did not differ in length (Serrat et al., 2008). Instead, a difference in length was generated on the cartilaginous ends of the bones (Serrat et al., 2008). These results suggest that environmental temperature has a direct effect on cartilage growth which in turn, being the precursor to bone, impacts final element length. The authors suggest that ecogeographic rules cannot be wholly explained as adaptations, but rather, are impacted by a secondary growth response, in addition to potential genetic effects (Serrat et al., 2008). These findings highlight the need to consider complexity, rather than subscribing to simple adaptationist explanations that have previously been used to explain ecogeographical patterns.

Roseman and Auerbach (2015) have similarly argued that adaptive hypotheses about ecogeography are relied upon too heavily to explain patterns of variation, and potential alternative explanations are often neglected. They suggest that, when discussing variation in postcranial morphology, population structure/history may account for a sizable portion of observed variance (Roseman & Auerbach, 2015). It is the potential impact of neutral processes on the femur that the current research seeks to better understand. As the proximal segment of the leg, it may be that environmental stress has a lower impact on femoral morphology. However, the shape/size of the pelvis is known to vary geographically, interpreted to reflect the ecogeographic rules about thermoregulation addressed above (Holliday & Hilton, 2010; Kurki, 2013). As the pelvis articulates with the proximal femur, this may impart influence on this region of the element, increasing the magnitude of climate-related impacts on this region's shape. Due to the integration of the femur with the pelvis, it may be that climatic/environmental effects are especially pronounced in the proximal region, obscuring neutral variation. This complexity is what prompted the division of the femur into multiple modules and the separate investigation of each's morphological variation in this project (as discussed in section 4.1.2).

2.4. Combating the Adaptationist Programme: Neutral Theory

Explanations for patterns of variation in skeletal morphology have typically focused on adaptive accounts (Gould & Lewontin, 1979; Weaver, 2018). Suggestions for the origins of traits often assume the 'adaptationist programme' by default, arguing that the trait under study must be an adaptation, the result of natural selection, rather than a consequence of some other mechanism (Smith, 2016). Neutral theory proposes that evolution can occur in the absence of a selective force, and that most variation results from genetic drift, supplemented by mutation and gene flow, as opposed to natural selection (Weaver, 2018).

The first coherent theories of Neutral Evolution (or the Stochastic Theory of Evolution) were proposed by Motoo Kimura in 1968 and independently by Jack Lester King and Thomas H. Jukes in 1969 (Jensen et al., 2019). Kimura expanded the concept in *The Neutral Theory of Molecular Evolution* (1983). This body of theory suggested that most *de novo* mutations (a genetic alteration present for the first time in an individual because of a mutation in a germ cell of one of the parents) are either sufficiently deleterious in effect to be unlikely to become fixed in the population or are selectively neutral and become fixed as a result of genetic drift (Kimura, 1968, 1983; King & Jukes, 1969). These early theories proposed that the positive or negative selection proposed by Darwinian evolution was too simplistic to explain patterns of genetic variation (Kimura, 1983).

Kimura suggested that genetic drift, a change in allele frequency within a population because of random chance, may look like Darwinian evolution, as it may appear that selection is acting on certain traits as variation is lost, but is in fact a ‘neutral’ process (1983). The introduction of neutral theory led to genetic drift being considered much more seriously as an evolutionary mechanism, increasing interest in a stochastic evolutionary theory (Jenson et al., 2019). Gene flow, the movement of alleles in or out of a population, was later appended into neutral genetic theory (Kimura & Maruyama, 1971) and neutral models of phenotypic evolution followed in the 1970s and 1980s (e.g., Lande, 1976; Lynch & Hill, 1986; Turelli et al., 1988). While neutral theory has had critics in the 50+ years since its initial formulation (e.g., Gillespie, 1991; Hahn, 2008; Kern & Hahn, 2018), this framework remains the basis of modern evolutionary genomics (Jensen et al., 2019).

2.4.1. Application of Neutral Theory to Human Morphology.

The decline of the ‘adaptationist paradigm’ in the study of morphology (resulting in the frequent decoupling of form and function) seems to have begun considerably before the first studies applying neutral theory to human morphology. Gould and Lewontin’s influential ‘spandrels’ paper (1979) is an early example of morphologists questioning the immediate assumption that morphology represents adaptation as defined as heritable variation (Pearson and Lieberman, 2004). In the early 2000s neutral models of evolution became widespread tools in the study of the human physical form (reviewed by Roseman & Weaver, 2007; von Cramon-Taubadel & Weaver, 2009), though initial applications began in the 1980’s and 1990’s (e.g., Lynch, 1989; Relethford, 1994). Weaver (2018) suggests that these models allow us to link morphology to population history and structure, reconstruct evolutionary relationships, and provide an understanding of the baseline on which adaptation acts. In addition, the application of neutral theory causes us to consider more seriously the role of random chance in our species' evolution.

2.5. Differentiating Mechanisms of Long Bone Morphological Variation

Many studies have attempted to differentiate mechanisms of long bone morphological variation. These studies attempt to disentangle the complexity brought about by the interactions of multiple factors on the human skeleton (like activity, climate, and neutral genetic processes). To be best able to interpret variation, the relative importance of these factors needs to be better understood. As examples, the following sections discuss two papers that have aimed to clarify the impacts of activity and climate on long bones and then review studies which have attempted to identify neutral variation in other skeletal elements, focusing on those which apply a similar methodology to this thesis. Finally, the limited number of studies which have considered neutral variation in the femur are outlined.

2.5.1. Studies of Activity and Climatic-Based Variation.

Pearson (2000) highlighted the importance of considering both climatic adaptation and lifestyle (behaviour) when comparing robusticity between hominin species. As addressed above, changes in robusticity have typically been interpreted as adaptive changes related to levels of activity. It has been proposed that the more complex culture of early modern humans produced a decrease in required physical exertion for survival, and a resultant decrease in robusticity compared to Neanderthals (Trinkaus, 1983). However, Pearson (2000) suggested that climatic adaptations are equally, if not more, important in influencing robusticity. They examined diaphyseal robusticity indices of recent skeletal samples for relationships with climate, lifestyle, and geographic region of origin, aiming to identify trends that could be applied to fossil populations. Most significant differences in robusticity were related to climate and region of origin, not lifestyle. Pearson (2000) applied the finding that individuals in colder regions displayed more robust bones to patterns in fossil populations. Neanderthals had high robusticity indices for the lower limb and humerus, and moderate to low indices for the upper limb, matching those results obtained for recent humans in cold climates. The Early Upper Paleolithic (EUP) modern humans were more gracile in almost all indices, suggesting to Pearson, long term habitation in a hot region, or recent emigration from one (2000). Robusticity increased in the human skeletons across time toward the Mesolithic, which Pearson interpreted as a gradual adaptation of our species to a cold European climate, rather than robust morphology being inherited from Neanderthals (2000). That environmental adaptation was equally, or more, important in influencing robusticity than activity suggests that climate may play a much larger role in long bone robusticity than previous explanations have suggested.

Stock (2006) investigated variation in long bone cross-sectional geometric properties in hunter-gatherers, focusing on the impacts of climate and habitual behaviour. Like Pearson (2000), this study considered the potential for multiple impacts on morphology, but also considered how we might disentangle the climate/activity complexity by identifying where signals were occurring on the bone, and with what strength. This study found that proximal and distal limb segment robusticity was correlated with both climate and mobility but that the strength of this association varied throughout the body (Stock, 2006). In particular, the correlations between climate and the polar second moment of area (*J*) increased from proximal to distal in the upper limb, but the opposite was true for the lower limb (Stock, 2006). For mobility, the strength of the relationship generally increased from proximal to distal in both the upper and lower limb (Stock, 2006). This suggests that, for the lower limb distal elements may be more strongly impacted by behaviour, and thus display a stronger signal of mobility while the proximal element (the femur) may be more impacted by climate. Importantly, this study also indicated that, despite these patterns, the femoral midshaft demonstrated the strongest correspondence with terrestrial mobility (Stock, 2006).

2.5.2. Identifying Neutral Variation.

When attempting to parse out the sources of morphological variation in the human skeleton, the potential impacts of neutral genetic process must be considered, in addition to the effects of behaviour and climate, to develop a complete understanding. Studies examining a neutral component of variation in skeletal morphology have generally done so in one of the following ways (Betti et al., 2013);

I) Examining the distribution of phenotypic variation at different demographic levels. Identifying neutral vs selected for traits based on their levels of within-population, geographic regional, and between population diversity (e.g., Relethford, 2002; Roseman & Weaver, 2004).

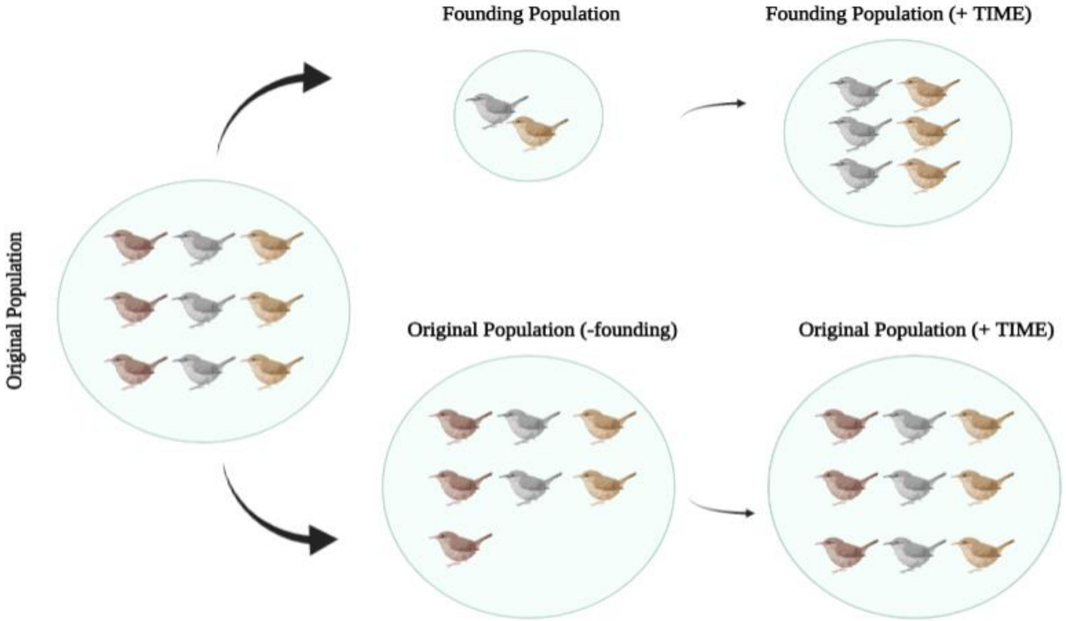
II) Comparing genetic and phenotypic distances directly, or indirectly by tracking agreement of morphological traits to an Isolation by Distance pattern (e.g., Harvati & Weaver, 2006; Relethford, 2004; Roseman, 2004; Smith, 2009; von Cramon-Taubadel, 2009).

III) Investigating preservation of serial founder event signals through agreement with an Out of Africa (OoA) model (e.g., Betti et al., 2009, 2012,2013; von Cramon-Taubadel & Lycett, 2008).

Ideally, genetic data would be used to help identify neutral variation, investigating if levels of phenotypic variation match levels of neutral genetic variation. However, if genetic data is absent (as was the case for this project as the groups included did not have good matches in the available open-source genetic datasets), the OoA method may be used which utilizes geographic distance as a proxy for genetic distance. Individuals further away geographically are assumed to be further away genetically. A limitation of this method is that it does not directly consider other factors, like gene flow, where population history beyond serial founder effects may impact levels of variability. Gene flow could increase or decrease variation in a founding population without movement toward or away from the original group. Apportionment of variance could be used to examine the effects of gene flow, looking at if geographically closer populations more closely resemble each other than those that are further away. While it would be ideal to combine the two methods, as others have done (e.g., Betti et al., 2013), this is beyond the scope of the current project. Focusing on foragers, however, helps control for this limitation as their distribution is not confounded by the major global patterns of population movement and migration that followed agriculture.

The OoA model explains patterns of human genetic variation as the result of serial founder effects (a type of genetic drift). A founder event lowers effective population size and produces lower genetic diversity (heterozygosity; Weaver, 2018; Figure 2.2).

Figure 2.2: Founder Effect.



Note: Showing reduced genetic diversity (depicted as phenotypic diversity (feather colour)) when a subset of a larger population establishes a new population. Repeated (serial) founding events involve smaller and smaller effective population sizes, producing a pattern of lower diversity with increased geographic distance from the original (source) population. Created with BioRender.com

Serial founder events result in repeatedly decreased population sizes and heterozygosity in the subsequent founding populations, as it takes time for the variation that is lost to replenish via mutation and for effective population size to return to that seen in the original population. Thus, if a trait is evolving neutrally (i.e., not being selected for or against), within-population variance will decrease with increasing distance from the origin of the first founder event (Weaver, 2018). The OoA model applies this specifically to human evolution, where an African origin, or set of origins, is supported by archaeological and genetic data (Bandelt et al., 2006; Hublin et al., 2017). While all evidence points to an Africa as the origin of our species, recent debates about the roots of modern humans and pan-African ‘structured’ populations (see Scerri, 2023; Scerri et al., 2018, 2019 for discussion) make point estimates of origin less certain. This has implications for inferring neutral distances, as physical distance calculations require defined geographic points. However, this research will follow earlier studies which have used an estimated point of origin in central sub-Saharan Africa (e.g., Betti & Manica 2018; Betti et al., 2009; Betti et al., 2013;Von Cramon-Taubadel & Lycett, 2008). This region is often chosen as an origin for projects using an OoA model due to studies which routinely identify groups in this location as having the highest levels of genetic diversity in living human groups (e.g., Li et al., 2008; Schlebusch et al., 2020; Tishkoff et al., 2009).

Modeling serial founder effects as a major influence on human diversity leads to the prediction that human diversity will decrease with increasing distance from Africa. This has been supported via genetic data where, with increasing distance from an African point(s) of origin, within-population genetic diversity has been found to decrease (Li et al., 2008; Prugnolle et al., 2005; Ramachandran et al., 2005). Within-population morphological diversity of the cranium, dentition, and pelvis has been shown to demonstrate the same pattern.

Using linear measurements of 4666 skulls, Manica et al. (2007) examined the fit of craniometric traits to an OoA model, finding that a decrease in phenotypic variability occurs with increased distance from Africa. Manica et al. (2007) suggests that distance from Africa accounted for 19-25% of heritable variation in craniometric traits in their study, further emphasizing a neutral source of variation for these traits. Von Cramon-Taubadel & Lycett (2008) similarly examined patterns of craniometric variation and found that up to 26% of global within-population variation of these traits can be explained by geographic distance from sub-Saharan Africa. Supporting these earlier studies, Betti et al. (2009) suggested that climate plays a minimal role in determining human within-population cranial diversity and that distance from sub-Saharan Africa is the main predictor. For non-metric dental traits, Hanihara (2008) found support for OoA founder effect being a major driver of trait variation patterning. Patterns of human pelvic variation have also been shown to demonstrate fit to an OoA model as well. Exploring potential neutral variation in the human pelvis, Betti et al. (2013) found that, with both male and female os coxae, morphological variation demonstrated a fit with the OoA model, phenotypic diversity declined with increasing distance from sub-Saharan Africa. These studies suggest that morphological variation in these elements may reflect population history, rather than being solely a product of adaptation via natural selection as has previously been suggested.

2.5.3. Studies of Neutral Variation in the Femur.

The OoA model, and the serial founder effect framework, would suggest that, if the femur has evolved neutrally, the same pattern of decreasing variability with increased distance from an African point of origin found in previous studies of genetic variation and morphological diversity of the cranium, dentition, and pelvis should appear for human femoral morphological variation. However, potential neutral variation in long bones has received limited attention, perhaps due to the likelihood that the environmental and behavioural effects discussed previously would obscure a neutral signal. Discussing this, Roseman and Auerbach (2015) found that patterns of femoral length variation best fit regression models that included both a population structure and latitude (environmental) term, suggesting multiple forces are at play in this element. They suggested that, when discussing among-group variation in postcranial morphology, multiple factors should be considered and that population structure/history may account for a sizable portion of observed variance (Roseman and Auerbach, 2015).

Betti et al. (2012) appears to be the only study that explicitly addresses femoral shape and the OoA model. Betti et al. (2012) found that within-population femoral shape variance, calculated from size-adjusted linear measurements, was best explained by climatic variables, minimum temperature specifically, and that it did not correlate with geographic distance from Africa. They suggest that the effects of climatic selection may have obliterated the effects of population history (i.e., OoA dispersal signature) in this element (Betti et al., 2012). However, they also propose that higher resolution methods of quantifying shape might identify non-adaptive signals that went undetected in their study (Betti et al., 2012).

3. Group Descriptions and Ethical Dimensions

3.1. Study Groups Background

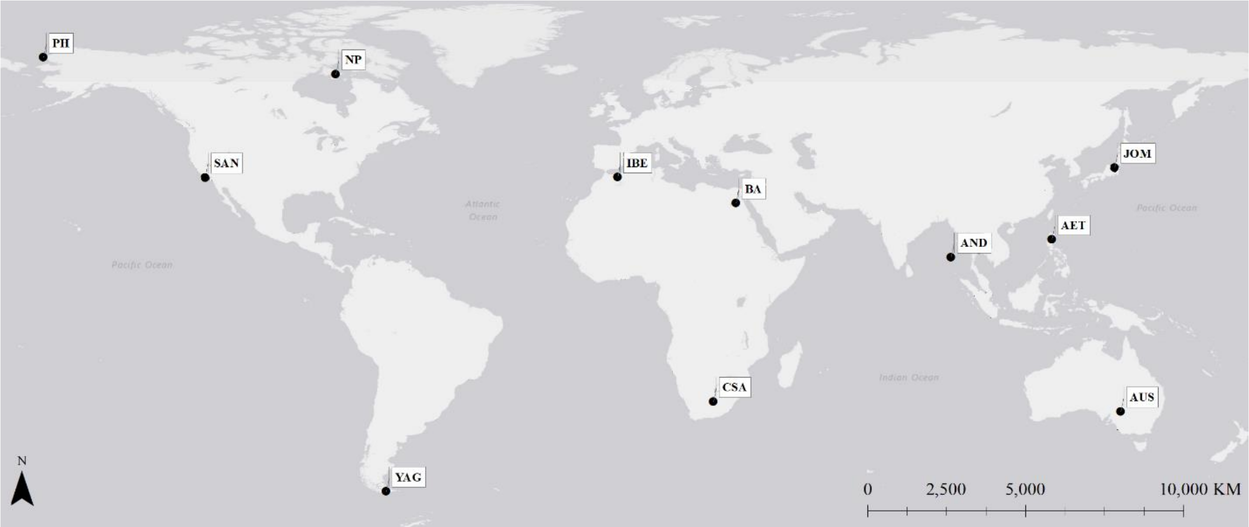
Eleven archaeological groups of hunter-gatherer/forager or early non-intensive agriculturalists (horticulturalists) are included in this project (Table 3.1). These groups were primarily chosen for their widespread geographic distribution (Figure 3.1), which is required to carry out a project looking to identify global patterns in variation. Additionally, hunter-gatherer/forager groups are considered particularly well-suited for studies of skeletal morphology due to suggested lower task specialization when compared to agricultural populations, and life-long participation in subsistence activities (Stock & Pfeiffer, 2001). In comparison to agricultural and industrial populations, it can also be more confidently assumed that hunter-gather-forager groups are relatively genetically homogenous and have been long-time inhabitants of their respective environments (Stock, 2002).

Related to this point, for this project, groups are characterized based on where they were excavated (i.e., where the individuals died). It is important that this is somewhat representative of where they were born, and where they resided throughout their lifetimes, as the relative order of the group’s distances from Africa must remain consistent across the lifespan (i.e., the location recorded for remains is not so far away from the place of birth that it would cause a group's relative position to swap with another’s). Despite some hunter-gatherer groups being highly mobile, travel across such a significant distance (intercontinental) within the lifespan of an individual is unlikely to occur.

Table 3.1: Study Populations General Information.

Population	**Date Range**	**Location(s)**
Aeta (AET)	Likely historic (Stock, 2013)	Luzon, Philippines
Andaman Islands (AND)	Protohistoric c. 1860 – 1900 CE (Stock & Pfeiffer, 2001; Stock, 2006)	Great and Little Andaman Island
Indigenous Australian (AUS)	Early phases of colonial occupation (Auerbach & Ruff, 2004)	Australia (various)
Predynastic Egyptian (BA)	5000 – 4000 BCE (Starling & Stock, 2007)	Badari, Egypt
Central South Africa (CSA)	1 000 – 200 yBP (Cameron, 2016)	South Africa (Reit River Sites)
Iberomaurusian (IBE)	c. 18 000 – 10 000 yBP (Kefi et al., 2018; Mariotti et al., 2009)	Taforalt, Morocco and Afalou, Algeria
Jomon (JOM)	4 000 – 2 500 yBP (Temple et al., 2008)	Japan (various)
Sadlermiut (NP)	1400 - 1900 CE (Merbs, 2018)	Native Point, Canada
Tigara (PH)	800 – 300 yBP (Hilton et al., 2014)	Point Hope, USA
Chumash (SAN)	4 200 – 3 500 yBP (Glassow, 1977); Early Period (Kennett, 2005)	Santa Cruz Island, USA
Yahgan (YAH)	Protohistoric est. 1880 (Stock, 2006)	Tierra Del Fuego, Chile

Figure 3.1: Geographic Distribution of Study Groups.



Note: Created with arcgis.com. Base map (adapted) credit - Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community.

The terms ‘hunter-gatherer,’ and ‘forager,’ are difficult to tightly define. Hunter-gatherers are often defined as groups who do not rely primarily on domesticated sources of subsistence that typically can be considered band societies of small, flexible groups with egalitarian socio-political relations (Kelly, 2013). This is a broader definition than what has been previously been proposed as Anthropology has moved beyond the idea that there is an “essential core of the foraging lifeway” and instead acknowledges the considerable variation within this broad category, including varying levels of sedentism vs mobility and significant differences in subsistence strategy (e.g., terrestrial vs marine; Kelly, 2013, p.2). For example, this thesis discusses groups which have a variety of subsistence strategies. Some are likely fully or mostly terrestrially based (e.g., central Australian), while others have significant marine food component (e.g., Point Hope), and others may have included some small-scale horticulture or animal husbandry (e.g., Central South Africa, Jomon, Badari).

The inclusion of three groups (the Badari, Jomon, and Central South African groups) in a study of hunter-gatherers could be considered controversial as they may have practiced some forms of incipient agriculture. However, the Egyptian Badari, while dating around the beginnings of agriculture in the Nile Basin, are identified as semi-nomadic pastoralists, which does not set them apart from the other groups in terms of mobility and activity (Hassan, 1988). For the Jomon foragers, while some regions in the Late-Final Jomon periods may have practiced forms of non-intensive agriculture, most appear to have maintained a recognizable hunter-gatherer lifeway (Imamura, 1996). Studies of morphological variation in this population identify the Jomon group (regardless of time period) as hunter-gatherer-fishers (Imamura, 1996). Finally, the Central South African group likely practiced a mixed foraging-herding subsistence strategy, associated with high mobility (Cameron, 2016).

Below background and contextual information on the groups included in this study is presented, including the location(s) and date(s) for the sites where the skeletal collections originated from, and available information about their excavation and curation. A brief discussion of activities and climate associated with the lifeways of each group is provided when information was available. Groups are presented in alphabetical order by name code.

3.1.1. Aeta (Philippines): AET

This group of remains curated at the Musée de l'Homme originates from southern Luzon, and based on the provenance of the collection, most likely represents Aeta foragers (also referred to as Agta, Ayta, or Dumagat; Peterson, 1978). However, this attribution is uncertain, especially given that the terms Aeta, Agta or Ayta may refer to any number of current communities (Stock, 2013). The remains likely date to the historic period (Stock, 2013).

The Philippian archipelago consists of over 7000 largely mountainous islands with long, but narrow, coastlines, and areas of lowland swamp and lakes (Kroeber, 1943). Luzon, the largest of the islands, has a hot tropical climate, is densely forested, and sees rain year-round, though the winter typically receives the highest rainfall (Kroeber, 1943). Given the nonspecific identification of the individuals, it is not possible to discuss specific subsistence activities, as these appear to vary significantly by location and community (Kroeber, 1943). However, generally speaking, pre- and near-contact Aeta are understood to be hunter-gatherers who lived in small, but multi-household, camps and utilized local flora and fauna like fish, boar, deer, shellfish and roots/tubers (Peterson, 1978).

The Aeta foragers and Indigenous Andamanese share a distinct phenotype that is typical of forager populations living in tropical rainforests, with the key characteristic being their especially small body size (Roberts et al., 2016; Stock, 2013). Tropical rainforest environments share high precipitation and temperature, which, in addition to their plant-species compositions, produce unique selective pressures (Roberts et al., 2016). Measurements correlated with stature and body mass are very low for both the Aeta forager and Indigenous Andamanese populations when compared to other, non-tropical rainforest, hunter-gatherer groups, suggesting significantly short stature and small body size (Stock, 2013). Why this phenotype is strongly associated with tropical rainforest environments is a subject of debate, with food limitation, warm-moist environments, potential life history trade-offs for earlier reproduction, or a combination of these factors being proposed as potential drivers (Perry & Dominy, 2009).

3.1.2. Andaman Islands: AND

The Andaman Islands group is dated to the time period immediately following European settlement of the islands in 1858 (contact in 1789; Myka, 1993). The skeletal collection used in this thesis is curated at the Natural History Museum, London and includes individuals from across Great and Little Andaman (Stock & Pfeiffer, 2001). Despite tribal divisions being noted at the time of British settlement (broadly Great Andamanese, the Onge, and the Jarawa), the groups are considered morphologically homogeneous (Cappieri, 1974 as cited in Stock & Pfeiffer, 2001; Stock & Migliano, 2009). Most individuals included in this thesis are identified as having Great Andamanese or Onge tribal affiliations.

The Andaman Islands consists of 325 islands running 338km north to south, with a total land area of 4692 square kilometers (Myka, 1993). The islands are hilly and, under natural conditions, densely forested by tropical vegetation (Myka, 1993). The climate is warm and moist with a prominent rainy season, being impacted by both the South-West and North-East monsoons (Radcliffe-Brown, 1922). Ethnographic literature suggests that pre-contact Indigenous Andamanese exploited both terrestrial (e.g., fruits, yams, wild pigs, and honey) and marine resources (e.g., fish, dugong, sea turtle; Stock and Pfeiffer, 2001; Myka, 1993). There appears to have been a recognized distinction in lifeway between coastal and inland Andamanese communities (Myka, 1993), though it is not known which specific areas the individuals in the study group may have resided in. Mobility is believed to have been generally restricted within the islands, with limited large-scale terrestrial tribal mobility (Stock and Pfeiffer, 2001). However, high marine mobility is suggested by ethnographic reports (Myka, 1993; Radcliffe-Brown, 1922) and supported via analysis of skeletal markers (Stock and Pfeiffer, 2001). This would have included swimming and the use of watercraft (Radcliffe-Brown, 1922; Stock and Pfeiffer, 2001).

3.1.3. Indigenous Australian: AUS

The group of Indigenous Australians included in this thesis is comprised of individual or small groups of remains dating to the early phases of colonial occupation. The remains are housed in the Natural History Museum, London and in the Duckworth Collection at the University of Cambridge. A variety of regions in Australia are represented (6 attributed only to Australia, 2 North Australia, 2 West Australia, 2 New South Wales, 4 South Australia). Precise provenience information past the state level is not available.

Australia displays a wide variety of climatic zones varying from hot, desert environments to wet, moderate ones. As most individuals identified to the state level originated from the area of New South Wales or South Australia, a coordinate in this region is used to approximate climate. This region would experience a more moderate, wet, climate in comparison to North Australia, but would be drier and hotter than more coastal locations, serving as a climatic middle ground. Indigenous Australians vary widely in cultural practice and identity, both at present and in the past. In terms of broad, regional variation; in past Indigenous Australian groups, Western Desert populations appear to have been the most mobile, due to the need to range long distances to acquire resources, while populations in Southern Australia tended to be less mobile (sometimes termed semi-sedentary; Carlson et al., 2007). Mobility in northern populations was likely based on exploitation pattern (inland vs coastal; Carlson et al., 2007). Resource availability and type would have varied widely, as would the tools and technology regularly used in subsistence activities.

3.1.4. Predynastic Egyptian (Badari): BA

The Egyptian Badari group dates to between 5000 - 4000 BC, placing it in the Neolithic/Predynastic period (Starling & Stock, 2007). The site (el-Badari) was first excavated in 1922 by Guy Brunton and Gertrude Caton-Thompson (Brunton & Caton-Thompson, 1928). The remains are currently housed in the Duckworth Collection at the University of Cambridge.

The Badari civilization is connected to the current earliest definitive food-processing sites in the Nile valley (Arkell & Ucko, 1965). However, a lack of evidence for permanent dwellings at the site of el-Badari suggests the community lived as semi-nomadic pastoralists, rather than intensive agriculturalists (Hassan, 1988). Starling and Stock (2007) demonstrated high levels of linear enamel hypoplasia in this ‘proto-agricultural population’, in keeping with predictions about increased nonspecific stress with the advent of agriculture. Analysis of femoral cross-sectional areas of the el-Badari vs. other Nile Basin communities suggests greater mobility/activity among the Badari, compared to agricultural groups (Stock et al., 2011). However, as with this project, the small sample size of the Badari skeletal collection limited the statistical robustness of these results (Stock et al., 2011). Given their location, climate experienced by the Badari would have been warm-hot-dry, typically associated with tropically adapted, narrow-bodied phenotypes.

3.1.5. Central South African: CSA

The Central South African group is from sites excavated along the Orange River and its main tributaries. The majority of individuals come from sites at Koffiefontein, while the remainder come from Jacobsdal, Blaauheuwel, Vlakfontein and Rooipad. Most of the sites are located along the Riet River and were occupied from 1000 - 200 yBP (Cameron, 2016). Remains are curated at three South African museums; the National Museum Bloemfontein (seven individuals), the National Museum Kimberly (ten individuals) and the Raymond Dart Collection at the University of the Witwatersrand (three individuals).

The climate of South Africa's central interior is semiarid, with irregular summer rainfall often resulting in drought conditions (Cameron, 2016). The Orange River and its tributaries provide much-needed fresh water, such that travel away from river valleys was likely limited in the past (Maggs, 1971). Plant life in prehistory was predominantly grasses, bushes, and underground storage organs (Cameron, 2016; Thornton-Barnett, 2013). Game animals included medium-small ungulates, birds and riverine fish, and, before the historic era, hippopotami, rhinoceroses, and buffalo (Morris & Beaumont, 1991).

The archaeology of the Riet River sites suggests a mix of wild and domesticated animals, as well as gathered foods, was consumed (Maggs, 1971). Some research suggests domesticated animals made up a considerably small portion of the diet (Humphreys, 1972), which has been supported by isotopic analysis (Masemula, 2015). As such, subsistence in these groups likely involved both foraging and herding. Biomechanical properties displayed by archaeological Southern African hunter-gatherer populations have been interpreted to indicate high degrees of terrestrial mobility (Stock & Pfeiffer, 2001). Cameron (2016) found that individuals from the central interior (the group in this thesis) frequently displayed higher cross-sectional geometric properties when compared to other hunter-gatherer populations, suggesting high levels of mobility in this group, though lower mobility than that exhibited by those in the Cape Coast region. Cameron (2016) suggested that high mobility in the Central interior may be due to sparse and unreliable resources.

3.1.6. Iberomaurusian (Taforalt & Afalou): IBE

The Iberomaurusian group consists of individuals from two sites, Taforalt, Morocco and Afalou, Algeria. Taforalt has been dated to 18 000 - 10 800 yBP, while Afalou is younger, at 15 000 - 11 000 yBP (Kefi et al., 2018; Mariotti et al., 2009). The Iberomaurusian necropolis of Taforalt was first excavated in the 1944 while Afalou was first excavated from 1928 to 1930 (Kefi et al., 2018; Mariotti et al., 2009). The remains are curated at the Institut de Paléontologie Humaine, in Paris France.

The term Iberomaurusian refers to a series of blade-based industries in the, mainly coastal, Maghreb (Mariotti et al., 2009). Additional names used are Epipaleolithic and late Upper Paleolithic, though Iberomaurusian appears to be the favored term (Mariotti et al., 2009). Botanical and faunal data suggests the climate of the region around Taforalt was similar to that seen today, though mild climatic oscillations are likely for the Epipalaeolithic period (Mariotti et al., 2009). Both sites are in a Mediterranean ecoregion that displays dry summers, rainy winters and is populated by Mediterranean forests, woodlands, and scrub. Hunter-gatherer economies including shellfish exploitation, and seasonal mobility, are typically ascribed to Iberomaurusian sites (Mariotti et al., 2009).

3.1.7. Jomon Foragers: JOM

The Jomon foragers in this thesis come from a variety of sites which date to between 6000 to 2000 BP, with the majority dated to the late/final phase of the Jomon Period (~4000 - 2500 BP; Mizoguchi & Dodo, 2001; Temple, 2018; Temple et al., 2008; Temple & Matsumura, 2011). The sites are located in Japan, on Hokkaido (Kotan-Onsen), Northern Honshu (Ebishima), Mid-Honshu (Yoshigo, Wakaumi, & Ono), Southern-Honshu (Tsukumo) and Kyushu (Goryo, Todoroki, & Yamaga; Buck et al., 2019). Remains are curated at the National Museum of Nature and Science in Tokyo, Kyoto University, Sapporo Medical University, and Kyushu University.

The Jomon culture is regarded as one of the longest continuous phases of complex hunter-gatherer populations in prehistory, named after the pottery they produced (chord-impressed, linear applique; Imamura, 1996; Temple, 2018). The Late Jomon period (4300 - 3300 BP) saw the division of Japan into two cultural areas (northeastern and southwestern), distinguished by pottery type (Habu, 2014; Imamura, 1996). It is suggested that populations in the two areas differed in their subsistence patterns, with northeastern populations engaging in hunting, fishing, and chestnut processing and southwestern populations depending more on plant foods, potentially representing early agriculture/horticulture (Imamura, 1996). The Final Jomon period (3300-2400 BP) is followed by the Yayoi period, the arrival of full-scale agriculture (Habu, 2014; Imamura, 1996)

Due to the north-south orientation of Japan, a variety of climatic zones occur, from a cool zone in Hokkaido, to a subtropical environment in Okinawa (Imamura, 1996). Precipitation is high across the country due to elevated levels of air bound moisture drawn from the surrounding seas and ocean (Imamura, 1996). The transition from the Middle Jomon to Late-Final Jomon period is marked by a sustained cooling between 4100 - 2300 BP, which culminated in a decline in temperature of about two to three degrees Celsius (Temple, 2018). Temple (2018) has suggested that the potential consequences of this climatic change were mediated through flexibility in both diet and mobility, with minimal indications of increased skeletal indicators of stress (relative to the Middle Jomon) visible on skeletons dated to this transition.

3.1.8. Sadlermiut (Native Point): NP

The Native Point site (KkHh-1) is a Sadlermiut (also Sagdlirmiut or Sallirmiut) site located on southeastern Southampton Island in Hudson's Bay, Nunavut (Merbs, 2018). Also referred to as the Tunirmiut site (a name given to the Sadlermiut community at Native Point by contemporary Inuit populations), Native Point was initially excavated between 1954 and 1955 by Henry B. Collins, and again by William S. Laughlin and Charles Merbs in 1959 (Merbs, 2018). Remains uncovered by these, and subsequent, excavations are caretaken by the Inuit Heritage Trust, and housed at the Canadian Museum of History in Gatineau, Québec. The referent used in this thesis is 'NP' though the referent 'CNP' may also be seen in the literature, which refers specifically to those remains excavated by Collins (Merbs, 2018). The group in this thesis is thought to represent an occupation period from the early 1400s to 1903, a time period before and during early European contact (Holland, 2007; Merbs, 1983). During the winter of 1902-03, an epidemic (possibly dysentery) introduced by Europeans led to the collapse of the Sadlermiut population at Native Point (Merbs, 1983, 2018; Symchych, 2016).

Given their location in Northern Hudson's Bay, the Sadlermiut would have been exposed to a cold, arctic tundra environment. As a result, alongside the Point Hope population, they have often been included in discussions of adaptations to cold stress (e.g., Holland, 2007; Symchych, 2016). Intensive marine resource exploitation is supported by archaeological findings; kayak rests and lances, and zooarchaeological remains of seal, fish, walrus, and whales have been associated with the Native Point site (Holland, 2007; Merbs, 2018). Degenerative joint disease, likely related to hunting, transportation, and scraping activities, appears on Sadlermiut remains at a fairly high rate, as do indications of traumatic injury (Merbs, 1983, 2018).

The distinct culture and technology of Sadlermiut, compared to contemporary mainland Inuit populations (e.g., Aivillingmiut and Igloolingmiut), is thought to have resulted from their relative isolation on Southampton Island, and nearby Walrus, Bencas, and Coats Islands (Merbs, 2018). Unique aspects include the use of chert to form flaked blade tools (as opposed to slate), limestone lamps (instead of soapstone), an exclusive style of harpoon head, and a polar bear mandible scraper (Merbs, 2018). Due to the distinct differences between the Sadlermiut and contemporary populations, genetic affiliations have been a longstanding point of interest. Previously, the Sadlermiut have been suggested to be descendants of the Dorset culture (e.g., Hayes et al., 2005). However, more recent genetic research suggests that the Sadlermiut may represent a long-isolated Thule population (Raghavan et al., 2014).

3.1.9. Tigara (Point Hope): PH

The Point Hope site (or Tikiġaq, “finger” in Iñupiat) is located on the northwest coast of Alaska (Hilton et al., 2014). The site is comprised of four cultural periods; Tigara (800 - 300 yBP), Birnirk (1500 - 1000 yBP), Ipiutak (2100 - 1500 yBP), and Norton (3000 - 2000 yBP; Auerbach, 2008; Larsen & Rainey, 1948). According to Collins (1984) via Hilton et al. (2014), while Point Hope likely does not represent a linear ancestor-descendant sequence, the site is one of the oldest known continuously occupied sites in North America. The group included in this project consists only of individuals from the Tigara period. The Point Hope material was excavated in the first half of the 19th century (1939-1941) by Helge Larsen and Froeligh Rainey (Hilton et al., 2014). These excavations uncovered around 10,000 artifacts and 500 skeletons, many of which are housed at the American Museum of Natural History, in New York (Larsen & Rainey, 1948).

Point Hope is located 200km north of the Arctic Circle and, unsurprisingly, individuals from this site are often included in discussions of adaptations to cold stress (Holliday & Hilton, 2010). Across time periods, individuals from the Point Hope site are described as possessing cold-adapted body proportions, tending to be shorter and heavier than those individuals adapted to warmer climes (Cowgill, 2014; Holliday & Hilton, 2010).

Subsistence in the Tigara period was focused on marine resource exploitation, with associated archaeological material (e.g., harpoons and flotation devices) and zooarchaeological remains (walrus, seal, and whale bone) frequently found within layers dated to this period (Cowgill, 2014; Dabbs, 2011). Compared to the earlier Ipiutak period, individuals in the Tigara period appeared to have experienced short-term acute stress (as opposed to chronic stresses), potentially related to resource shortages and trauma risk associated with bowhead whale hunting (Dabbs, 2011, p. 100).

3.1.10. Chumash (SCrI-3 Santa Cruz): SAN

The prehistoric Chumash group, curated at the Natural History Museum in London, consists of remains excavated from the SCrI-3 site on the western tip of Santa Cruz Island (Nelson, 1992). SCrI-3 was originally excavated in 1927 by Ronald Olson (Nelson, 1989). Walker (1986) suggests a time range of 5 000 - 4 000 BP for the site, while Glasgow (1977) suggests a range of 4,200 to 3,500 B.P. Both dates are based on comparative chronology of artifacts (Nelson, 1989). Regardless, the remains fall into the latter end of the Early Period (Kennett, 2005).

The Santa Barbara Channel experiences the cool, wet winters, and warm, dry summers typical of a mild Mediterranean climate (Kennett, 2005). There is some variation in climate between the islands themselves, due to ocean currents and variable topographic relief (Kennett, 2005). Santa Cruz is the largest of the Northern Channel Islands at 249 km^2 and, due to this large size, displays the greatest current floral diversity (Kennett, 2005). Compared to precontact mainland Chumash, Island Chumash relied more heavily on marine resources, with long coastlines and extensive kelp forests providing ample opportunity for fish, shellfish, and sea mammal exploitation (Kennett, 2005). Early Period subsistence appears to have combined terrestrial and marine resources (Kennett, 2005; Walker, 1986).

3.1.11. Yahgan (Tierra Del Fuego): YAH

The Yahgan (or Yagán, Yaghan, Yámana, or Yamana) group is the southernmost group included in this thesis. The remains represent protohistoric Yahgan foragers from the southern islands and south shore of Tierra del Fuego (Lothrop, 1928). The collection is housed at the Sapienza University of Rome and the Museum of Anthropology and Ethnology at the University of Florence and date to the end of the 19th Century (1880s; Stock, 2006).

Located at the southern tip of South America, the climate in the territory of the Yahgan is cold, windy and wet, with a mountainous landscape (Lothrop, 1928). Relying heavily on marine resources such as fur seals, sea lions, sea birds (e.g., Magellanic penguins), and shellfish, precontact Yahgan peoples utilized bark (beech) canoes (Lothrop, 1928; Yesner et al., 2003). Women are described as being particularly adept paddlers, where men primarily acted as hunters/fishers during marine activities, only paddling on long journeys (Bridges, 1948). This high marine mobility is reflected in the especially robust upper limb bones of Yahgan women when compared to other archaeological hunter-gatherer groups (Stock, 2002). Other primary activities, mainly done by women, included gathering shellfish and diving for sea urchins

(Garson, 1886). All demographics are identified as expert swimmers in the ethnographic literature (Garson, 1886). However, isotopic evidence suggests that precontact Yahgan may have been more reliant on terrestrial resources (like guanaco, a camelid) than ethnographic accounts indicate (Yesner et al., 2003). This discrepancy might be explained by European contact, as encroachment of European settlers and ranchers likely altered the availability of terrestrial species (Yesner et al., 2003). Much of the information we have about Yahgan lifeways comes from the writings of missionaries (e.g., Rev. Thomas Bridges; Bridges, 1886 via Lothrop, 1928). Lucas Bridges wrote extensively on the Indigenous Peoples of Tierra del Fuego in his ethnography *Uttermost Part of the World*, discussing his family's experiences and the effects of colonization by Europeans on local Indigenous communities (Bridges, 1948).

3.2. Ethical Dimensions

This current project relies upon archaeological collections of human remains, in digital formats. As such, the proceeding subsections discuss the ethical considerations that come alongside working with institutional collections of human remains and includes a specific discussion of digital data ethics issues pertaining to digitized remains.

3.2.1. Institutional Collections of Human Remains.

The digital models in this project were created from archaeological human remains housed in institutional collections (skeletal collections in museums and university labs/departmental collections). When studying bioarchaeological collections, the circumstances of the amalgamation of the collection, and those which make the remains available for continued study, should be deeply considered. This is especially the case where ancestors of living Indigenous Peoples may be involved. While biological anthropology has taken strides to recognize its dark and often racist past (for review and examples see de la Cova, 2019; Watkins, 2018; Zuckerman & Armelagos, 2011), despite our best efforts, the questions we ask, the approaches we take, and the conclusions we reach will always be impacted by the socio-political context of the discipline in which they are made and the points of view of those who make them. The hope is that reflection on the obvious biases in the history of the discipline will ensure current and future research is conducted in an ethical manner.

Related to this, Mant et al. argue that "complicating, problematizing, and questioning what we think we know about past lives demonstrates our respect to the individuals whose remains we have the privilege of studying," (2021, p.1). Grappling with how remains come to be in collections and why they continue to be accessible to researchers is a topic in the same vein. That I am able to work with digital models and data generated from these collections is a privilege and one cannot ignore the history that led to their creation and the potentially problematic nature of their continued study. A poignant example of researchers acknowledging, and problematizing, the circumstances in which collections have been amassed is the discussion surrounding the key American anatomical collections on which biological anthropology's main methods have been built (e.g., de la Cova, 2019; Lans, 2021; Mant et al., 2021; Watkins, 2018). Class, race, and structural violence historically influenced whose bodies were anatomized and as a result, influenced whose remains ended up in skeletal collections (de la Cova, 2019). Thus, many of the foundational anatomical collections for North American biological anthropology are predominantly comprised of marginalized individuals. For example, the Robert. J. Terry collection contains a high frequency of African American individuals (de la Cova, 2019) and the Huntington Collection consists primarily of the unclaimed dead and those who had low socio-economic status (Lans, 2021).

The amassment of collections of archaeological remains has occurred under the influence of similar socio-political biases. Radically for his time, where critical reflection on the history of the discipline was uncommon, Trigger (1984, p. 356) observed that “the nature of archaeological research is shaped to a significant degree by the roles that particular nation states play, economically, politically, and culturally, as interdependent parts of the modern world-system.” Trigger argues that social contexts generate distinctive archaeologies, where the questions asked, and methods used, are impacted by socio-political factors. Excavations of communities in the archaeological record, and much of the bioarchaeological study of the resulting collections, including my own, has been undertaken by those belonging to a colonising population who have limited ties to the past they attempt to understand or the individuals they study (Trigger, 1984). Highlighting the colonial foundations of museum collections in particular, Hicks (2020), states that institutions built on anthropological material culture research are not filled with objects that have been given, but rather, objects which have been taken. Material culture in these collections was stolen by colonial and/or imperial powers without the consent of the communities who made/used the objects or their descendants (Hicks, 2020). Stolen material culture could then be used to support national, colonial, and/or imperial ideologies at the detriment of the archaeological communities' descendants. As a result of particular socio-political biases and agendas taking precedent, the formation of archaeological collections, including those containing human remains, has involved problematic collection practices (e.g., stealing from burial places without consent) and was often done to support racist projects and ideas (Athreya & Ackermann, 2019). The ethnographic records of communities from which the remains were gathered also contain markers of colonial ideologies, most obviously signalled through what we now acknowledge as racist and demeaning language used to describe Indigenous Peoples and their lifeways. This was evident in many of the older ethnographies used to write the group descriptions in this thesis.

For some, the necessary action is to repatriate institutional collections to descendent communities, as their retainment is seen as a continuation of, and support for, the ideologies that built the collections in the first place (Meloche et al., 2020). Conversations around the return of ancestral human remains and cultural belongings held in institutional collections are commonplace today, with many seeking to find collaborative solutions which honour ancestors and descendant communities while allowing scientific research to continue (see Meloche et al., 2020 for case studies/discussion of best practices). For some, digital representations of these remains offer opportunities to continue research while supporting repatriation, while others include them in calls for repatriation. However, descendent communities are often difficult to define and are sometimes in opposition to one another. In some contexts, ancestor-descendant relationships are established culturally, others geographically, and others genetically. To my knowledge, there are no current repatriation requests, or ongoing conversations which would prevent further study, involving any of the digitized remains or specific collections used in this thesis.

3.2.2. Digital Data Ethics.

Three dimensional (3D) digitized remains in bioarchaeology mainly refers to digital representations generated via photogrammetry, structured light scanning, laser scanning, or computed tomography (CT; Spake et al., 2020). The benefits of studying digital human remains over physical ones are numerous and may include; reduced handling of fragile physical remains, more advanced statistical analyses of shape, the creation of precise digital records in advance of repatriation or destructive analyses, and increased potential for collection sharing between researchers and institutions (Errickson et al., 2017; Spake et al., 2020). While digitizations can be conceptualized as simple lines of code, human remains may maintain cultural significance in digital formats (Alves-Cardoso & Campanacho, 2022; Harries et al., 2018). As a result of digital images of human remains potentially maintaining cultural significance and the increased potential for rapid data sharing there are unique ethical considerations to reflect upon.

Hirst et al. (2018) reported that 3D digital representations of human remains are a significant ethical gray area; specific best practices were absent from formalized ethical codes in Anthropology and Archaeology when the authors reviewed them prior to 2018. As shown below in a review the ethical codes of some of the main biological anthropology associations in North America and the United Kingdom (the Canadian Association for Biological Anthropology (CABA), the American Association of Biological Anthropologists (AABA) and the British Association of Biological Anthropology and Osteoarchaeology (BABAO)), this observation largely holds true.

Canadian Association for Biological Anthropology: CABA's code of ethics, updated in 2019, does not directly address 3D digital remains (Canadian Association for Biological Anthropology, 2019). This document refers to the Tri-Council Policy Statement: Ethical Conduct for Research Involving Humans (TCPS 2) which does not clearly address ethical considerations specific to this data type either, as they are not physical remains of human beings and archaeological remains typically fall under the TCPS 2 definition of anonymous human biological material as "the materials never had identifiers attached to them, and risk of identification of individuals is low or very low" (Canadian Institutes of Health Research, Natural Sciences and Engineering Research Council of Canada, and Social Sciences and Humanities Research Council, 2018, p. 166).

American Association of Biological Anthropologists: AABA's Code of Ethics entered formal documentation in 2003 and has remained unchanged in the intervening years (Turner et al., 2018). As a result, no discussion of digital human remains is included in the code (American Association of Biological Anthropologists, 2003). However, the results of a survey which included questions about ethical concerns suggested that data sharing and the display/sharing of digital images, which may include 3D digitizations, was a main concern of AABA members. A 2019 meeting of the AABA ad hoc committee on data access and data sharing published a set of suggestions, which largely focus on increasing and normalizing data sharing (Turner & Mulligan, 2019). Of note, the commentary has been criticized for its lack of engagement with Indigenous data sovereignty (Tsosie et al., 2021). Due to the interest in digital data ethics signaled by the ad hoc committee and by the survey results, it seems likely that the coming updates to the AABA ethical code will include discussions of digitized remains and their distribution.

British Association of Biological Anthropology and Osteoarchaeology: Finally, BABAO has produced recommendations on the ethics of digital imaging of human remains (both 2D and 3D) following a 2016 panel discussion (Hassett et al., 2018). This document primarily discusses the value of these forms of documentation, and ethical issues involved in sharing and displaying the resulting images/data (British Association of Biological Anthropology and Osteoarchaeology, 2019). Consent of descendant communities or other stakeholders is not addressed in the final report, though some conversation is documented in the transcript of the panel's discussion (Hassett et al., 2018).

The dearth of clear guidelines about 3D digitization of human remains in updated ethical codes is surprising given that many researchers have identified this as an area where unique ethical considerations are evident (e.g., Hirst et al., 2018; Spake et al., 2020). However, given the variety of contexts and national and jurisdictional boundaries potentially surrounding collections of digital human remains, the creation of universal guidelines would be difficult. Despite this, and while the existing codes allow one to make general statements about treating human remains, in any format, with respect and care, there is value in discussing the ethical issues specific to digital remains, especially data sharing and ownership.

3.2.2.1. Data Sharing and Ownership.

With increasing calls for open data access in the sciences broadly (Faniel et al., 2018), and a frequent argument for data sharing being essential in Biological Anthropology (e.g., Turner & Mulligan, 2019), digitized human remains have the potential to answer global questions through shared data, limiting the need to repeatedly handle physical remains. However, there are a variety of views on the ethics of sharing and displaying images of human remains (Harries et al., 2018). While some view images as removed from the physical remains themselves, and even more so from the person they were in life, there are complex and variable ideas around photographs of remains (Harries et al., 2018). 3D digitizations may also elicit strong and varied responses.

Given their potential cultural significance, the sharing of digital human remains between researchers and research groups requires careful consideration. If physical remains with known descendant communities are not shared without express consent, it seems logical that the same be applied to digitized remains. However, from a legal standpoint, with regard to copyright law, intellectual property law, and questions of ownership, who has a right to share digitized remains are complicated (Hirst et al., 2018; Spake et al., 2020). Consensus regarding whether the data belongs to the institution who holds the physical remains, the researcher who took the scans, or the descendant community (if known) is lacking (Hirst et al., 2018). According to Spake et al. (2020), under international intellectual copyright law, it would be possible for a researcher to claim authorship of digitized human remains, due to the decisions that go into manipulating the scans into a final model. Without prior agreement, a researcher could claim authorship of a model, even if the project itself is conducted for a descendant community, and copyright law would not automatically support descendant community control (Hollowell & Nicholas, 2008; Spake et al., 2020).

This conversation around data ownership is important given the colonial history of Anthropology, which many are attempting to correct and make amends for. Tsosie et al., (2021) argue that "addressing problems of colonialism will ultimately not entail whether open data practices are implicitly and universally decolonial, but whether Indigenous peoples have shared governance over the afterlives of data generated about and affecting them," (p.2). Additional consideration is needed in cases where physical remains are repatriated, as it could be argued that digital models should be included in that process if desired by the descendant community. Data sharing may complicate the repatriation process if digital data repatriation is desired, or, if digital data is not considered culturally significant, it may provide opportunities for future collaboration and study after the repatriation of the physical remains they represent.

Currently, it is the responsibility of curating institutions to ensure approved research fits within local rules and ethical guidelines, and that these rules are adhered to with regards to future use of digital data. Typically, the institution maintains copies of digital data, and does not allow data sharing beyond the projects for which they were collected. This should ensure they are not used for anything beyond the agreed upon purposes or made public. For the current study, all analyses and 3D scans were approved by curators in accordance with all relevant regulations, including permission from Indigenous claimant communities where applicable.

4. Methods

4.1. Methodological Background

4.1.1. Three Dimensional Geometric Morphometrics.

Geometric Morphometrics (GM) is a methodology which uses cartesian geometric coordinates to mathematically describe structures. Expanding upon traditional morphometrics (which examines linear dimensions in bivariate space), GM maintains geometric relationships among data in 3D space and permits the removal of the confounding influence of size variation, allowing for more accurate depiction and analysis of shape.

Biological anthropologists have used three-dimensional GM to examine a broad range of skeletal elements, samples, and processes, to explore diverse questions about sources of morphological diversity (e.g., Betti et al., 2013; De Groote, 2011; Smith et al., 2013, p. 20; Terhune et al., 2013; Waltenberger et al., 2021). Differences in shape may signify variation in growth and development processes and the functions of biological parts, and inform us about selective pressures and different responses to them (Zelditch et al., 2012, p.1). GM has previously been applied to investigate neutral morphological variation in the cranium and pelvis (Betti et al., 2013; Galland & Friess, 2016; Harvati & Weaver, 2006; Smith, 2009), but not to the same questions pertaining to the femur. This is significant as, by accounting for more subtle variation in shape, GM provides a more complete representation of shape than linear measurements and allows for a more detailed discussion and exploration of the potential mechanisms behind shape variation (Betti et al., 2012; Slice, 2007). The lack of GM studies examining neutral femoral variation means that subtler manifestations of neutrality may go undetected, hence the application of this method in the current study.

For most applications, GM involves digitizing Cartesian coordinate-based landmarks to capture the morphology of a set of specimens. Landmarks are chosen based on homology (points on one individual correspond to the same point on all other specimens), adequate coverage of form, repeatability/replicability, and consistency of relative position (i.e., landmarks do not switch positions relative to one another; Zelditch et al., 2012). Following Bookstein (1992), landmarks can be defined as one of three types:

I. Locally defined points tied to the discrete juxtaposition of tissues (e.g., a foramen).

III. Locally defined points which refer to geometric constructs (e.g., maximum point of curvature of the orbit).

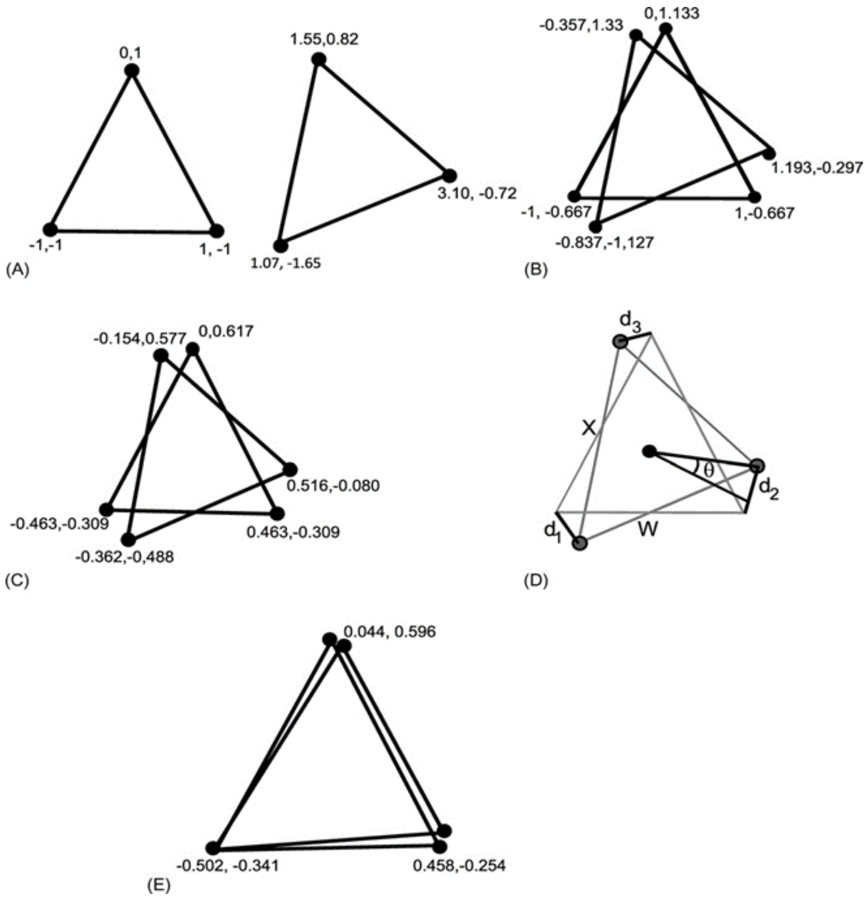
III. Points which are geometrically defined in relation to the whole structure, which generally are extreme points (e.g., the most distal point of the humerus).

Bookstein (1992) argues that type I landmarks are the most informative as they are surrounded by tissues on all sides, and thus capture information about forces in all directions. However, others (e.g., Zelditch et al., 2012) argue that type II landmarks can be just as informative, especially about biological processes that involve the deposition of bone at the margins of an element, like biomechanical and developmental processes.

The idea of a fixed, point landmark has often been too stringent to allow for effective analysis of biological shapes, which frequently involve structures lacking in discrete landmarks (Gunz et al., 2005). If a shape has complex curves with few definable landmarks, or if identifying landmarks would prove difficult due to specimens varying widely in morphology, semilandmarks may be employed (Adams et al., 2013; Slice, 2007). Semilandmarks are geometrically homologous landmarks, constrained by anatomical landmarks, which represent the underlying topology of an object (Bookstein, 1997; Rolfe et al., 2021). Rather than being tied to a specific locus, these landmarks sample the curve between two or more fixed landmarks, sliding along that curve to best capture its shape and minimize bending energy. Applying semilandmarks has the potential to vastly increase the shape data that can be derived from difficult-to-landmark regions like long bone shafts. Initially, a lack of software limited the use of semilandmarks (Slice, 2007). This issue has since been resolved as there are now a variety of software packages capable of generating and interpreting semilandmarks. Semilandmark application has received some critiques, as this landmark type has only one meaningful direction of change due to being anchored by fixed points (Bookstein, 1992). However, the application of semilandmarks allows for the description of regions which would otherwise have sparse or no definable landmarks, leading many researchers to view them as a valid, and valuable, methodological tool (Zelditch et al., 2012).

In the process of GM data collection, once landmarks and semilandmarks are generated, their coordinates are subjected to a preprocessing step which standardizes the landmark coordinates to remove size, orientation, and positional data. This typically takes the form of Generalized Procrustes Analysis (GPA). This is a three-step process. The first step translates the centers of each landmark configuration to the origin, removing positional variation. The second scales the landmark configurations to the same centroid size. Finally, the third step rotates the configurations to reduce the summed squared distances between homologous landmarks, removing orientation variation (Zelditch et al., 2012, Figure 4.1).

Figure 4.1: Process of Procrustes Superimposition.



Note: A) data collected; B) centered configurations; C) centered and scaled configurations; D) calculation of angle of rotation; E) centered, scaled, and rotated configurations in their ideal alignment. Zelditch et al. (2012, p.63, Figure 3.9).

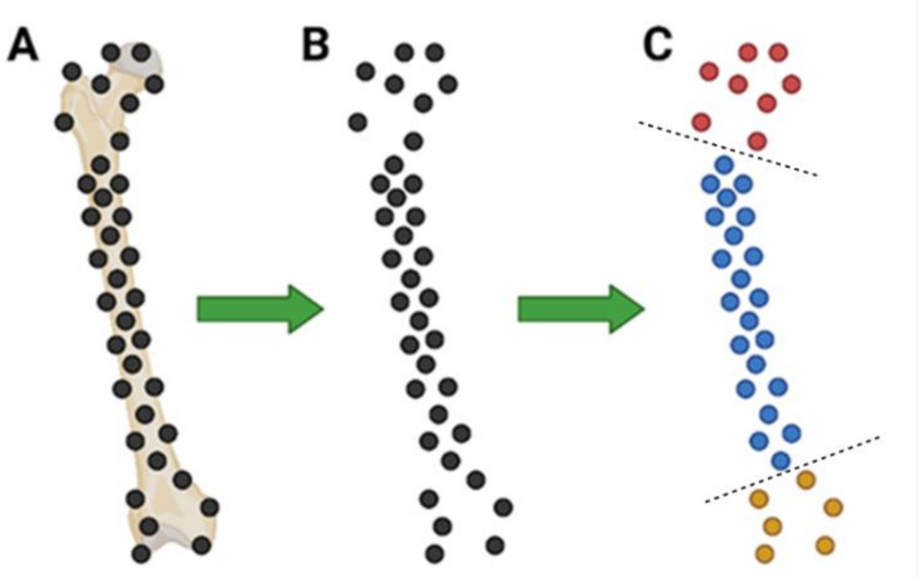
This process yields Procrustes coordinates which contain only shape information (Slice, 2007). The differences in landmark coordinate values are reflections of difference in shape as the landmark configurations enter a common coordinate system. These coordinates can in turn be subjected to multivariate statistical analyses, typically a Principal Component Analysis (PCA) or a Canonical Variates Analysis (CVA), to generate new variables which summarize the shape variation present within the sample. The variables produced by these dimension reductions can then be used to analyze the relative impacts of various factors on shape via further statistical analyses.

4.1.2. A Modular Approach to Capturing Shape.

Interpretations of postcranial morphology, in discussions of evolution, can be divided into two broad categories: particulate or integrative models (Churchill, 1996). Those suggesting evolution operates in a particulate manner argue that changes in specific morphological traits inform us about microevolutionary processes (like changes in behaviour) that impact isolated regions of the skeleton and skeletal elements (Churchill, 1996). This is related to Neo-Darwinian perspectives and suggests evolution in the postcranial skeleton is largely mosaic, where traits are influenced differently by genetic evolution and developmental plasticity (Churchill, 1996). In contrast, the integrative perspective argues that changes in specific traits are correlated to overall changes in body form (Churchill, 1996). The integration of functional systems constrains and directs evolution in this framework (Churchill, 1996). Comparing traits between groups/species indicates change in overall body form, influenced by factors like growth patterns and climatic adaptation (Churchill, 1996).

Due to the likelihood that a multitude of factors influence shape variation in the femur, this research exists between these two perspectives, dividing the femur into discrete sections (Figure 4.2), but also considering their integration. This provides an opportunity to examine the potential impacts of climatic and neutral processes in different regions of the femur, but also to consider how the sections interact with one another. The femur's integration with the rest of the body, especially the pelvis, is likely to impact where signals are most evident, with climatic signals potentially stronger at the proximal end. Further, the three modules represent different functional regions of the bone, the mechanics at the hip (proximal) and knee (distal), and the transfer of load between these joints (diaphysis). As a part of a larger biological system, both within the musculoskeletal system and the body as a whole, it would be inappropriate to conceptualize the femur as an isolated element, but the potential for particulate impacts of different processes at specific regions should also be considered. By treating the femur as a whole element *and* as three distinct modules, the research methodology in this thesis has the potential to differentiate influences on morphology that may otherwise go undetected as they only act on particular regions or would be covered by stronger signals of other influences which span the entire element. This treatment of the femur allowed the research questions about variable influences at different sections of the element to be addressed.

Figure 4.2: Simplified Landmarking Scheme.



Note: These are not the landmarks applied in this thesis, rather this figure is provided as an example landmarking scheme. A) capturing femoral morphology via landmarking B) full-landmark set C) modular landmarks (red - proximal region, blue - diaphyseal region, yellow - distal region). This project intends to look at neutral and environmental signals in the morphology of the whole femur (B) and in each of the modules, proximal, diaphyseal, and distal (C). Image created in Biorender.com.

4.2. Data Collection

This project required 3 types of data: shape data which captured the morphological variation present in globally distributed groups of humans, climate data for the regions those populations lived in, and the distances of those groups from an estimated human origin in Africa.

4.2.1. Shape Data.

Shape data collection involved; scanning physical remains and producing digital models from those scans, selecting an appropriate sample from the repository of scans, preparing those scans for landmarking, fixed and semilandmarking, landmark processing, and quantification of within-population variation. Replicability of the landmarking process was assessed and linear measurements were also obtained.

4.2.1.1. Scanning and Model Creation.

This project relied on digital models generated from laser surface scans of archaeological human femora. Three-dimensional femoral surface scans were collected by previous PAVE lab researchers (Dr. Pere Ibáñez-Gimeno, Dr. Thomas G. Davies, and Dr. Laura Buck), using a consistent methodology (see Davies et al., 2012 for description). After the surface scans for each individual were acquired, they were processed into a single model by trimming unwanted data/scanning artifacts, aligning scan faces, and fusing scans into a single mesh/model. This produced virtual surface models defining the periosteal boundary of the element, capturing surface morphology.

4.2.1.2. Sample Selection.

All available models for each location group were assessed for preservation of landmark regions. Common reasons for removal from the sample at this stage included incomplete/fractured diaphysis, damage to the epicondylar regions or femoral head, and large scanning errors (voids in the model). For models that contained multiple bones, the femur was isolated using the 3D visualization and editing software MeshMixer 3.5 by Autodesk.

The number of available scans (~500) vastly outnumbered what would be feasible for a Master's project, even after those models with poor preservation were removed. As the questions approached by this project concern global patterning, it was decided to focus on landmarking individuals from as many groups as possible, rather than to landmark a greater number of individuals from a smaller number of groups. A maximum of 20 models for each group was selected. All individuals were adults. Individuals estimated as male, female, or indeterminate/unrecorded were included in this study, as using only individuals of a single sex would have severely reduced available the sample size and within-sample variation. Aiming to control for sexual dimorphism, and to allow for additional statistical analysis identifying sex-specific differences in variability, as equal a sex distribution as possible within each group was aimed for. Sex was estimated by previous researchers (Dr. Stock, Dr. Ibáñez-Gimeno, and Dr. Davies) based on standard techniques described by Buikstra & Ubelaker (1994). In total, 172 models were selected for preparation and landmarking (Table 4.1).

Table 4.1: Sample Breakdown by Population and Sex.

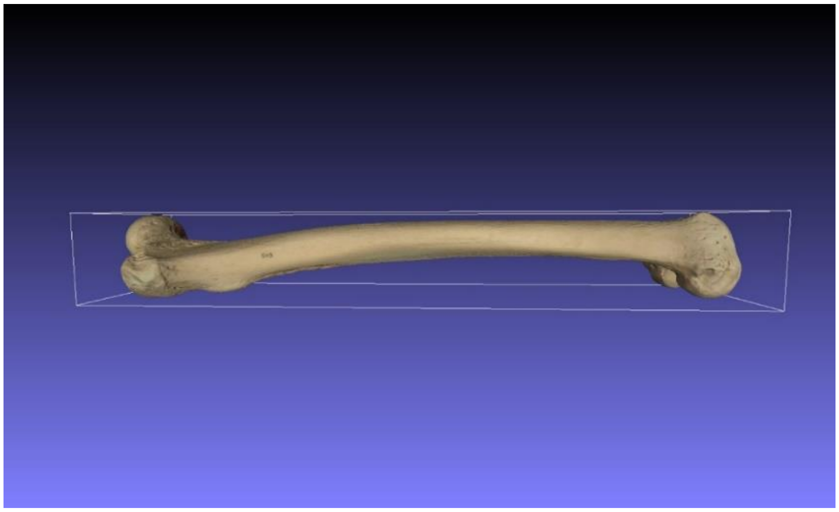
Population	**Code**	**Sample Size**	**F**	**M**	**U**
Aeta Foragers	AET	16	7	7	2
Andaman Islands	AND	16	10	6	0
Indigenous Australian	AUS	14	1	5	8
Predynastic Egyptian	BA	6	3	1	2
Central South Africa	CSA	19	11	8	0
Iberomaurusian	IBE	11	2	4	5
Jomon	JOM	17	5	11	1
Sadlermiut	NP	19	7	10	2
Tigara	PH	18	8	7	3
Chumash	SAN	18	3	5	10
Yahgan	YAH	18	9	7	2
	Total	172	66	71	35

Note: F – female, M – male, U – undetermined/unrecorded.

4.2.1.3. Preparation in MeshLab and MeshMixer.

Femoral models were translated into a common alignment in the 3D processing and editing software MeshLab (by Cignoni et al., 2008). Femoral condyles were rotated to lie flat on the minimum (distal) surface of the mesh bounding box, with the most posterior points of the condyles against the posterior surface of the bounding box (Figure 4.3). This does not directly mimic the alignment achieved with an osteometric board. Rather, it was the most easily repeatable alignment across all programs used in the landmarking process.

Figure 4.3: Femoral Alignment.



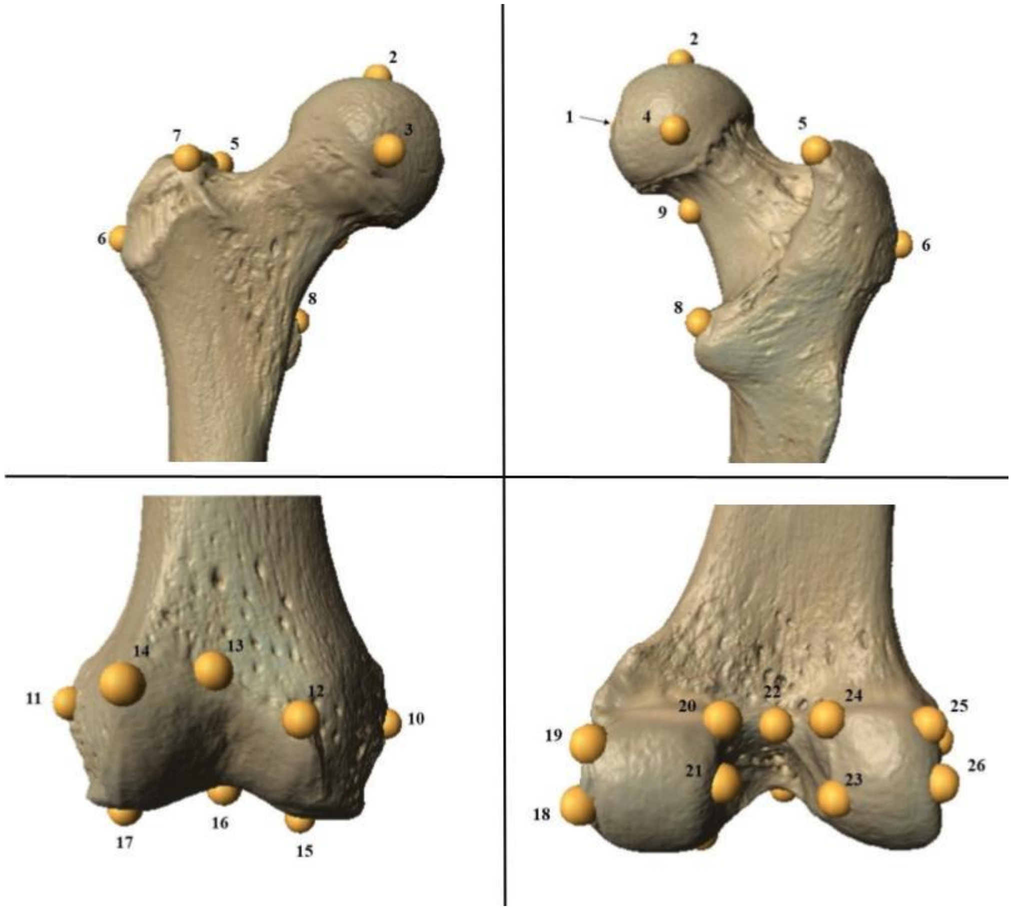
Note: Visualized in MeshLab (by Cignoni et al., 2008).

To provide repeatable anchor points for semilandmark curve and patch placement in later steps (4.2.1.4), planar sections at 15% and 80% of total element length were created using geometric measures computed from the bounding box. These sections were then traced onto the model. The midpoints along each line on the anterior and posterior surfaces were marked for ease of semilandmark curve placement. Landmarks and semilandmarks were preferentially placed on right sided femora as these were more numerous in the collection than left sided elements. Where right sides were absent or in poor condition, left-sided bones were mirrored in MeshMixer 3.5 prior to landmarking to create right sided femora. When this step was required, subsequent re-alignment into the position outlined above was performed prior to landmarking.

4.2.1.4. Landmarking.

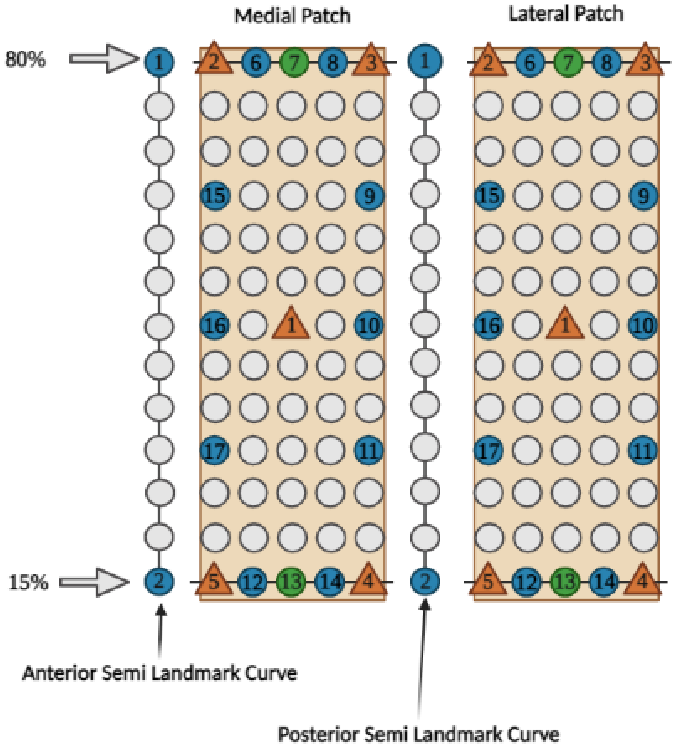
A series of fixed landmarks were laid on the surface of the models using Stratovan Checkpoint (Stratovan Corporation, 2018). Figure 4.4 visualizes the fixed landmark locations on the distal and proximal ends of the femur. Table A1 describes the types and positions of the fixed landmarks. The sample size of this project (n = 172) was more than three times larger than the number of fixed landmarks used (n = 27), suggesting that the sample size is adequate. Guidelines surrounding sample size to semilandmark ratio are still debated (Bardua et al., 2019).

Figure 4.4: Fixed Landmarks.



Due to the relatively featureless nature of the femoral diaphysis, semilandmarks were employed to capture shape in this region. There are a variety of methods for projecting and sliding semilandmarks, which vary widely in their coding and computational requirements. For this project, a landmark-driven geometric approach was applied, rather than the more complex, and less user-guided, algorithmically sampled methods which produce pseudo-landmarks (Rolfe et al., 2021). Specifically, to capture the shape of the femoral shaft (diaphysis) both semilandmark curves and patches were employed. Semilandmark curves consist of a series of sliding semilandmarks generated between two set points, essentially creating a line of landmarks along a curved surface. In this thesis the term ‘patch’ refers to a template of semilandmarks (usually a rectangle) which are warped (by placing leading points) onto the specimen, covering a wider area than a single line. This is the term used in the Stratovan software used for the landmarking process. Two semilandmark curves consisting of 13 semilandmarks each were run between the lines indicating 80% and 15% total element length, one on the midpoint of the anterior surface and one on the midpoint of the posterior surface. This captured the anterior and posterior curvature of the femur in a similar way to established methods (e.g., De Groote, 2011). These curves were used to orient two 5 by 13 semilandmark patches, one placed on the medial surface and one on the lateral, which extend from the level of 80% to 15% total element length. Together these steps created a wrap of semilandmarks around the diaphysis (Figure 4.5).

Figure 4.5: Semilandmark Placement Procedure.



Note: Patches were wrapped around the diaphysis such that each longitudinal edge met one of the semilandmark curves to form a pseudo-cylinder of points that captured the shape of the diaphysis. Orange triangles were moved next to the corresponding point on the curves in the initial step. Point 1 was placed at the midpoint of the lateral or medial side (such that connectors make an arc) using the 7th semilandmark on either curve as a guide. Green points (7 & 13) were placed midway along the respective %bone-length section with other points (6 & 8, or 12 & 14) placed between the orange and green points. For the lateral patch on individuals with pronounced linea aspera, point 10 needed to be manually placed closer to the posterior semilandmark curve so that the patch edge captured the lateral aspect of this feature. Figure created with Biorender.com.

Through this process, 156 semi-landmarks were produced which captured the shape of the diaphysis. As the semi-landmarks were distributed equally across the curve or surface they sampled, the shape of the diaphysis was captured at approximately 5% intervals between 80 and 15% of total length. Some models showed 50% length indicators left by previous researchers on the physical remains. In all cases, this line corresponded to the 50% semi landmark section, providing additional validation for the orientation used and the resultant landmark placements.

4.2.1.5. Semi Landmark Sliding and Generalized Procrustes Analysis.

The literature suggests that uncertainty is always introduced when digitizing semilandmarks (Schlager, 2017). In this thesis, noise in the data generated by a lack of homology was reduced by allowing semilandmarks to slide. Sliding moves semilandmarks along their respective surfaces aiming to bring them into an ‘optimal’ position that maximizes correspondence across all semilandmarks (Bardua et al., 2019). Using the package *Morpho*, semilandmarks were slid into their most homologous positions by minimizing bending energy between specimens, following protocol laid out by Schlager (2017). After the semilandmarks were slid, Generalized Procrustes Analysis (GPA) was used to remove size and orientation data from the landmark configurations. The *gpagan* function from *geomorph* (Adams et al., 2022; Baken et al., 2021) was used to perform the GPA, producing Procrustes Coordinates for each individual. The *gpagan* function also performs a Principal Component Analysis (PCA) including all individuals and landmarks, using the Procrustes Coordinates. PCA is a method of dimension reduction which transforms sets of variables into new variables called Principal Components (PCs; Klingenberg, 2016). These PCs describe the axes of variation within the sample (Klingenberg, 2016). Each individual receives a PC score on each PC, detailing where they fall along these axes. These PC scores can then be used as new variables in further statistical analyses, in this case, to quantify within-population variation.

This process was conducted for all four landmark sets (whole landmark set, proximal landmarks, diaphyseal landmarks, and distal landmarks), for the full population groups, and for the male, and female subsamples where at least seven individuals were available. The inclusion cut-off, of minimum seven individuals, was chosen in an attempt to include the greatest number of groups while aiming to maintain some statistical robusticity. Groups with a sufficient female sample size were AET, AND, CSA, NP, PH, and YAH. Groups with a sufficient male sample size were AET, CSA, JOM, NP, PH, and YAH.

4.2.1.6. Quantifying Within Population Variation.

Within-population variation for all 4 landmark sets (whole landmark set, proximal landmarks, diaphyseal landmarks, and distal landmarks) was calculated following previous studies which have used the trace (the sum along the diagonal) of the variance-covariance matrix of the PC scores for each population (Betti et al., 2013; Franklin et al., 2010). This summed each PC's variance within that population/sex subset, calculating total intrapopulation shape variance. A maximum of 12 intrapopulation shape variables for each group were produced (Table 4.2).

Table 4.2: Within-Population Morphological Diversity Variables.

Variable	Definition	Variable	Definition
wvw	Full landmark configuration variation within whole sample	*svw*	Diaphyseal landmark configuration variation within whole sample
wvf	Full landmark configuration variation within female subsample	*svf*	Diaphyseal landmark configuration variation within female subsample
wvm	Full landmark configuration variation within male subsample	*svm*	Diaphyseal landmark configuration variation within male subsample
pvw	Proximal landmark configuration variation within whole sample	*dvw*	Distal landmark configuration variation within whole sample
pvf	Proximal landmark configuration variation within female subsample	*dvf*	Distal landmark configuration variation within female subsample
pvm	Proximal landmark configuration variation within male subsample	*dvm*	Distal landmark configuration variation within male subsample

4.2.1.7. Replicability.

Landmark placement error measurements were conducted on thirty-three individuals (three from each group) via two methods. The first examined the deviation of each landmark and semi-landmark in the two trial placements and the second used a Procrustes ANOVA to examine the significance of error-driven variation versus biological variation.

Deviation was calculated using Equation 1, which compares the Euclidean coordinates in 3D space (x, y, z) between two trials, determining the deviation between them. Following Lewton (2012, 2015), an average deviation below 1.00 mm was considered minimal (Meyers, 2018).

$$\mathrm{d} = \sqrt{(x1 - x2)^2 + (y1 - y2)^2 + (z1 - z2)^2}$$

Equation 1: Calculation of average deviation of a landmark between trial 1 and trial 2 (Lewton, 2012, 2015).

Fixed-landmark error was also calculated via a Procrustes ANOVA conducted in MorphoJ (Klingenberg, 2011). The values generated by this test can be used to examine the ratio of measurement error to biological variation (Klingenberg, 2015). A high ratio indicates that measurement error makes up a negligible amount of variation, whereas a low ratio would suggest that replication and measurement error reduction are necessary (Klingenberg, 2015). Most studies suggest that if the mean square for individual variation exceeds that for the measurement error; error is negligible (e.g., Benítez et al., 2014; Ito et al., 2015). Results of these checks are presented in 5.2.1, which indicate error in this study is insignificant.

4.2.2. Linear Measurement Data.

To assess fit to general ecogeographic trends, to clarify the impact of climate on femoral morphology, analysis of linear femoral dimensions was conducted. Measurements of maximum femoral length and femoral head diameter from the same archaeological groups were assessed. Most linear data was collected by Drs. Stock, Davies, Cameron, and Ibáñez-Gimeno. Data for the Chumash group was obtained from a freely available data set of postcranial linear measurements (Goldman Data set — http://web.utk.edu/~auerbach/GOLD.htm; Auerbach & Ruff, 2006). Only individuals with both femoral length and femoral head diameter measurements were included. Measurements were chosen preferably from the left side, using the right side only in cases where the left presented missing data. While there is some cross-over between the scanned individuals, and those for which linear measurements were available, the GM and linear data samples are not identical (Table 4.3). Sample size per-group was restricted to 35 to maintain some consistency in sample size across the populations (Table A2). No linear measurements for female Santa-Cruz Chumash individuals were available.

Table 4.3: GM and Linear Measurements Sample Sizes and Cross-Over.

Sample	**N**	**M**	**F**	**U**
GM	172	71	66	35
Linear Data	252	103	84	65
Both	118	51	50	17

Note: Sample size (N), male sample size (M), female sample size (F), indeterminate/unrecorded sex (U).

4.2.3. Climate Data.

To assess the impact of climate on femoral morphological variability in this project, a global dataset covering, at minimum, the last 20 000 years was needed. This required the use of climate modeling data, which uses computational models that represent the atmosphere, ocean, sea ice, and land surface to simulate climatic conditions in the past (Valdes et al., 2017).

4.2.3.1. Beyer et al. (2020) Reconstruction and pastclim.

Beyer et al. (2020) have generated a high-resolution terrestrial climate, bioclimate, and vegetation dataset for the last 120 000 years. Combining the medium-resolution HadCM3 (Singarayer & Valdes, 2010) general circulation model simulations for the last 120 000 years and high resolution HadAM3H (Valdes et al., 2017) simulations for the last 21 000, this dataset allows for high resolution spatial analysis of climate across a wide timespan (Beyer et al., 2020). The Beyer et al. (2020) dataset contains 19 bias corrected bioclimatic variables and three vegetation variables at a resolution of 0.5° longitude × 0.5° latitude.

4.2.3.2. Extracting Variables for Location and Time.

Climate reconstructions are stored in formats (generally netCDF) which are difficult to manage and are often exceedingly large (Leonardi et al., 2022). The R package *pastclim* (Leonardi et al., 2022) facilitates the use of the Beyer et al. (2020) dataset, allowing climatic variables to be quickly generated for specific areas of interest in any time period within the last 120 000 years. Coordinates recorded for each sample were rounded to the nearest whole degree and dates BP were rounded to the nearest thousand years to meet the requirements of the *pastclim* package (Table 4.4).

Table 4.4: Dates and Coordinates for pastclim Climate Variable Derivation.

Group	**Date**	***pastclim* Coordinates**	**Raw Coordinates**
AET	0	17° N, 121° E	16.5662° N, 121.2626° E
AND	0	12° N, 93° E	11.6234° N, 92.7265° E
AUS	0	32° S, 140 E	32.2679° S, 140.1386° E
BA	-7 000	27° N, 31° E	27.0 ° N, 31.4167° E
IBE	-16 000	35° N, 2° W	34.8106° N, 2.4083° W
JOM	-3 000	36° N, 140° E	35.6762° N, 139.6503° E
CSA	-1 000	29°S, 25°E	29.3969°S, 24.9940°E
NP	-1 000	64°N, 82°W	63.6939°N, 82.4176°W
PH	-1 000	68°N, 166°W	68.3489°N, 166.7397°W
SAN	-4 000	34°N, 120°W	33.9926°N, 119.679°W
YAH	0	55°S, 68°W	55.0483°S, 68.1478°W

Note: Under date, 0 means modern data is used by *pastclim.*

The variables extracted are found in Table 4.5. When discussing the impacts of climate on the human body, temperature is the most commonly used variable, as it links to the ecogeographic rules discussed in the literature review that have shaped our understanding of climatic adaptation in the skeleton. Studies investigating potential neutral variation have also used precipitation as a variable to assess climate-linked variation (e.g., Betti et al., 2010, 2014). Minimums and maximums were used for both the temperature and precipitation variables instead of averages, based on the assumption that morphology would be more driven by extremes than averages. Temperature Seasonality is a measure of temperature change per year which uses the standard deviation of the mean monthly temperature x 100 (O’Donnel & Ignizio, 2012). A larger standard deviation indicates greater variability/seasonality in temperature. Net Primary Productivity (NPP) is a measure of plant growth which is equal to the amount of carbon taken up by vegetation through photosynthesis, minus the carbon lost to respiration (Chapin & Eviner, 2014). This variable essentially acts as a measure of the amount of energy stored in an ecosystem and broadly identifies the amount of resources available to the groups in this thesis. NPP and precipitation are intrinsically linked as plant growth and productivity is contingent up water availability, alongside temperature, soil nutrients, and soil texture (Moran, 2022a). NPP and precipitation variables were included to look at if resource availability, as determined by climate, may be linked to variation in morphology, body size, and/or stature.

Table 4.5: Variables Extracted from pastclim.

pastclim term **(thesis term)**	**Variable**	**Units Returned**
bio04 (Season)	Temperature Seasonality	°C
bio05 (MinTemp)	Minimum Annual Temperature	°C
bio06 (MaxTemp)	Maximum Annual Temperature	°C
bio13 (MaxPrecip)	Precipitation of Wettest Month	mm month^{-1}
bio14 (MinPrecip)	Precipitation of Driest Month	mm month^{-1}
npp (npp)	Annual Net Primary Productivity	gC m^{-2} year^{-1}

4.2.4. Distance from Origin Calculation.

Distance from an estimated 'Origin' Point (22.3°S, 20.0°E), in central Sub-Saharan Africa was calculated using least cost path (LCP) analysis, conducted in ArcMap 10.8.2. This location, on the border of Namibia and Botswana, was chosen following studies which have identified groups in this region (Khoe-Sān populations) as having the greatest levels of genetic diversity (e.g., Li et al., 2008; Schlebusch et al., 2020; Tishkoff et al., 2009). The LCP is used to calculate a geographic distance to be used as a proxy for genetic distance. The ‘routes’ generated likely do not reflect actual movement but rather are used to generate a value for distance from the estimated origin and thus serve as a reasonable proxy for genetic distances.

LCP analysis identifies the 'cheapest' route between two points, as calculated on a friction surface (Wheatley & Gillings, 2002). The path that accumulates the lowest cost from the origin to destination is identified, with slope being the most common factor used to generate the cost surface, in addition to geographic distance (Beyin et al., 2019). Additional variables could be considered, including those which attempt to take into account the unpredictability of human nature and agency, which are generally not reflected in LCP analysis (Gustas & Supernant, 2019). However, as the least cost paths were not the ultimate analysis of this thesis and were instead a tool used to approximate distance from an African origin of expansion, emphasis was placed on conducting as simple a calculation as possible, while following previous studies. The same logic was applied when selecting the elevation models to be used. For simplicity, the distance data was not chronologically situated, and instead contemporary topographic data was used. Sea level change across time may have influenced land available for terrestrial travel and should be considered if a precise route is the object of analysis. Given the coarser needs of this project, not accounting for these factors is unlikely to have had a significant impact on the distances generated.

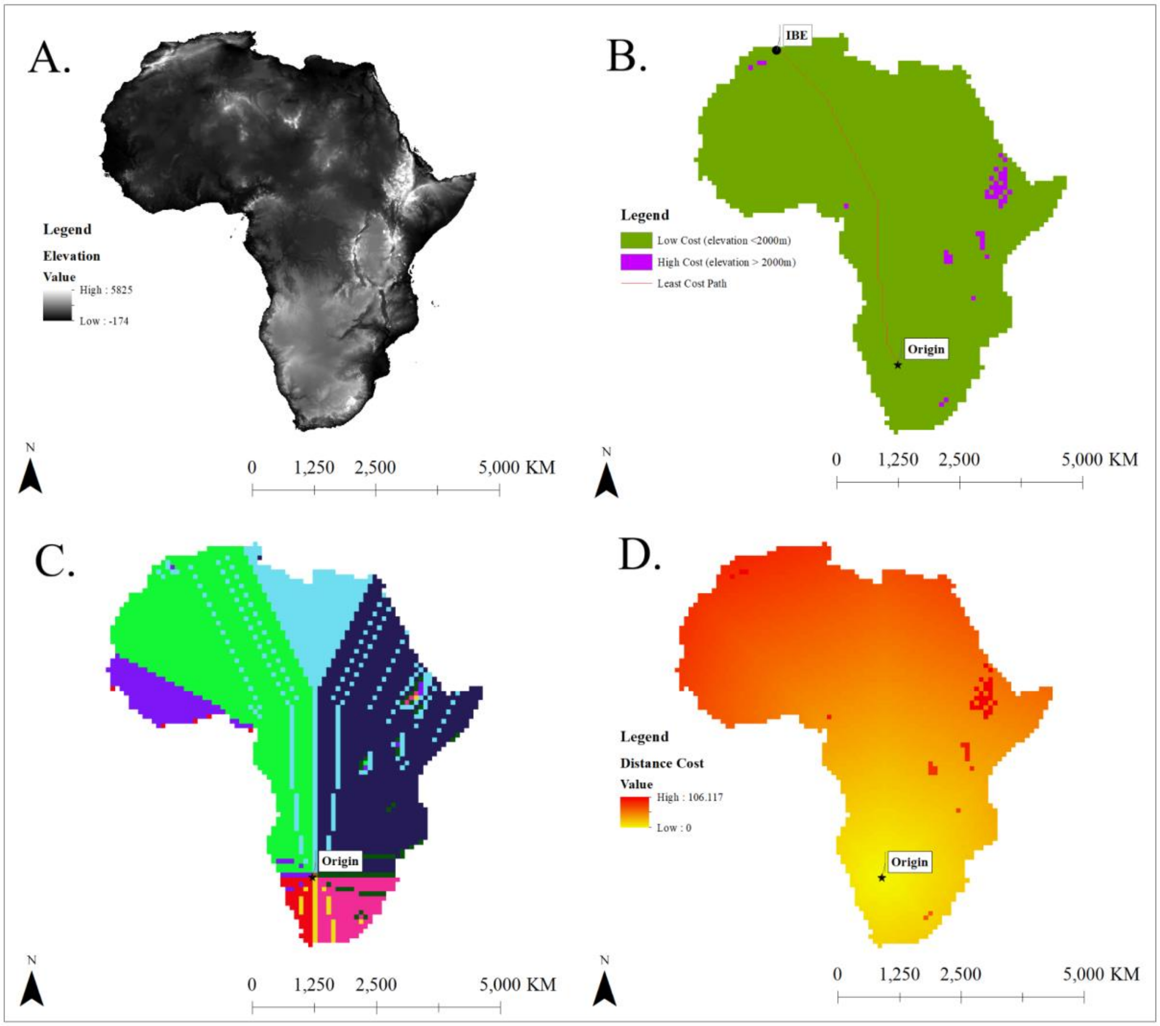
An elevation raster was created using the GTOPO30 digital elevation model (DEM) developed by the U.S. Geological Survey's Center for Earth Resources Observation and Science (EROS, 1997). This DEM has a resolution of 30-arc seconds and was resampled to 100 times coarser resolution, producing 92km by 92km cells (0.833333 by 0.833333 decimal degrees). This resampling was deemed necessary to limit the processing resources required to merge the 21 DEM files needed to cover the study area and to conduct the LCP analyses. This resampled DEM was reclassified into two interval values, with areas of mean altitude over 2000m possessing higher movement cost, following Manica et al. (2007). Also following this work, specific land bridges were assumed - connection between Africa and Eurasia via the Levant, connection of Eurasia to North America via the Bering Strait, and connection between the Malaysian Peninsula to Melanesia and Oceania (Manica et al., 2007; Table 4.6).

Table 4.6: Obligatory Waypoints Imposed in this Study.

Waypoints	*Coordinates*
Sinai Peninsula, Egypt (any route out of Africa)	30.02N, 32.56E
Bering Strait (routes to the Americas)	65.38N, 167.31W
Panama (routes to South America)	8.92 N, 80.19W

After the reclassification, the Cost Distance tool was used to determine the cumulative cost from the Origin Point to all other cells in the extent of the study area. At the same time a cost direction layer was generated (showing the direction of least cost back to the origin from each cell). Then the Cost Path as Polyline tool was used to generate the most probable least cost path for each destination point based on the cost direction and cost distance layers (Figure 4.6).

Figure 4.6: Example of LCP Process using the Origin and Iberomaurusian Coordinates.



Note: The GTOPO30 DEM (A.) was resampled to a coarser resolution and reclassified into areas with elevation above (purple) and below (green) 2000m (B.). The LCP process combined data shown in C. (cost direction) and D. (cost distance) to produce the final Least Cost Path, in red on B., between the estimated African Origin of expansion, and the destination (IBE). The cost direction layer (or backlink raster) shows, for each pixel, the direction to take to follow the LCP back to the origin. A change in colour indicates a change in direction to the next cell on the lowest accumulated path The length of this polyline is then calculated (in KM) to produce the distance from the origin variable.

4.3. Statistical Analyses

Statistical analyses were conducted in R version 4.2.1 via Rstudio (R Core Team, 2021; RStudio Team, 2021). An alpha level of $p < 0.05$ was considered significant for all tests administered.

4.3.1. Linear Measurement Analyses.

Analysis of the linear measurement data was used to assess fit to general ecogeographic trends, to clarify the impact of climate on femoral morphology. Correlation analyses of femoral length and head diameter with the climatic variables were performed, followed by simple linear regression analyses. To examine population level effects, these analyses were repeated on the population means for each measurement variable. For both individual and population effects we expected to find patterns which support known ecogeographic rules. This included the predictions that we would observe increased femoral head diameter (body size) with decreasing temperature and increasing latitude and increasing femoral length with increasing temperature and decreasing latitude, as an indication of increasing stature.

Variance for each measurement for each population was calculated and used to examine relationships between within-population variance and climate (either varxfld (variance in femoral length) or varxfhd (variance in femoral head diameter)). To remove the potentially confounding influence of size, the analyses were re-conducted using coefficients of variation (CV = $\left(\frac{\sigma}{\mu}\right) \times 100$). What patterns to expect for linear variability and climate was unclear. However, we expected that adjusting for size (variance vs coefficient of variation) would have a significant effect on the relationships identified with climate.

4.3.2. Analyses of Within-Population Variability in Shape.

To evaluate predictions about the impacts of neutral factors and climate on within-population femoral morphological variability, a series of regression analyses were conducted. First, to identify any potential signatures of serial founder effects, simple linear regression analyses were implemented, where within-population phenotypic variance was dependent on geographic distance from the origin of expansion (following Betti et al., 2012/2013). If population history has significantly shaped femoral variation, we expected to see a decrease in within-population variance with distance from Africa, reflecting the neutral pattern seen in genetic diversity. If other factors (e.g., local adaptation, or phenotypic plasticity related to diet, temperature, activity) are more influential, we expected that the neutral pattern would be erased/overwritten which would result in no pattern, or potentially a pattern of increasing variability with increasing distance, to appear. The analyses were conducted for each landmark module, and for each sex subsample.

The impact of the *pastclim* derived climatic and bioclimatic variables on within-population phenotypic variance was assessed via multiple regression analysis and repeated for each of the landmark modules and subsamples. Expected patterns for phenotypic variability and climate are more ambiguous. However, we expected some relationship between climatic and phenotypic variability in the femur to be identified based on the results of previous research (Betti et al., 2012). Specifically, Betti et al. (2012) found a significant predictive relationship between minimum temperature and within-population phenotypic diversity in this element.

The best minimal model for each shape module variable was selected following a stepwise procedure using the *Drop1* function in R (https://rdrr.io/cran/VGAM/man/drop1.html). These analyses began with full models that included all climatic and bioclimatic variables as independent factors. Backward stepwise elimination was then performed, excluding single factors sequentially based on the relative increase/decrease of the Akaike Information Criterion (AIC; Akaike, 1973). The analyses were conducted for each landmark module, and for each sex subsample.

Importantly, all tests using the GM data were likely to have low statistical power due to low sample sizes, as the original sample of 172 individuals was reduced to 11 populations (or 6 in the analyses of single-sex data; see section 6.1 for more discussion). As a result of small sample sizes, and resultingly non-significant or borderline p-values, the analyses of the coefficient of determination (R^2) were especially relevant. There are different guidelines for thresholds of R^2 in different academic fields. Due to the complex and multivariate nature of human biological variation, where there are thought to be small additive effects from many different influences, a fairly low R^2 could be considered as having significant explanatory power and reveal meaningful associations. If the goal of the research is not to produce predictions, but rather to identify if specific variables have a significant effect, a low R^2 may still identify relevant and interesting patterns, especially if significance is detected (Ozili, 2022). As a result, any model built off the GM data with a R^2 over 0.25 and a p-value nearing significance (~0.1) was considered in more detail.

5. Results

5.1. Sample

The summary statistics for the study samples are presented in Tables A2-A3 in the Appendix.

5.2. Shape Data

5.2.1. Rates of Landmark Error.

Two landmark trials of thirty-three individuals were used to assess error in the landmarking process via two methods, calculation of deviation in landmark placement and a Procrustes ANOVA. The first assessed raw consistency in landmark placement while the second assessed the relative size of biological variation versus error-initiated variation.

The first method identified average deviation between the first and second landmark iterations to be 1.55mm when including the whole landmark configuration. For the modules, the proximal landmark configuration average deviation was 1.75mm, the distal landmark configuration average deviation was 1.78mm, and the metaphyseal semilandmark configuration average deviation was 1.51mm. Landmarks which deviated over 1.0mm (the limit proposed by Lewton (2015) to consider deviation minimal) did not appear to be concentrated in a particular region (Appendix Table A4). Some landmark deviation is to be expected given that this thesis primarily used type II landmarks which are harder to define and consistently locate than type I (refer to section 4.1.1. for definitions). Additionally, the deviation of the semi-landmarks after the sliding procedure was likely lower than what is reported here, as the measures of deviation were calculated on the un-slid coordinates.

The second method utilizing Klingenberg's (2015) Procrustes ANOVAs to evaluate the significance of variation caused by error against actual shape variation was conducted in MorphoJ (Klingenberg, 2011). Only the fixed landmarks were assessed as MorphoJ lacks the ability to process semilandmarks. Fixed landmark placement error was found to be insignificant compared to individual shape variation (Table 5.1).

Table 5.1: Repeatability of Measurements, Procrustes ANOVA.

Effect	Procrustes sums of squares	Procrustes mean squares	*df*	*F*	*P value*
Individual	0.0546	0.0000031670	17248	10.91	<.0001
Measurement Error	0.0051	0.0000002903	17787		

Note: Shape variation (Individual) and Error variation (Measurement Error). N = 33.

The mean square for individual variation exceeded that for measurement error. This suggested that the amount of variation caused by landmark placement error was considerably smaller than variation caused by biological difference. This suggested that the measures of population level shape variation, obtained from PCs derived from configurations using these landmarks, were unlikely to be significantly impacted by the error in landmark placement identified by the first method. The landmarks used in this study can thus be considered fairly repeatable and reliable.

5.2.2. Within-Population Morphological Variation.

The trace of the variance-covariance matrix of the PC scores for each population derived from the landmarked femora were used to calculate four within-population morphological variation variables for each sample group. Where appropriate sample sizes were available, up to an additional eight variables were calculated based on the variation in the female and male subsamples. Within-population variation was uncorrelated with sample size. All PCs generated were used to calculate the phenotypic variability variables. Appendix Table A5 outlines the number of PCs used in each calculation and the within-population phenotypic variability values for each sample group.

5.3. Climate Variables

As discussed in 4.2.3.2, *pastclim* was used to produce six climatic/bioclimatic variables for each population, Temperature Seasonality (Season), Maximum Annual Temperature (MaxTemp), Minimal Annual Temperature (MinTemp), Precipitation of Wettest Month (MaxPrecip), Precipitation of Driest Month (MinPrecip), and Annual Net Primary Productivity (NPP). The values derived corresponded to expectations based on current climatic conditions and background literature (Table 5.2).

Table 5.2: Climate Variables Derived from pastclim.

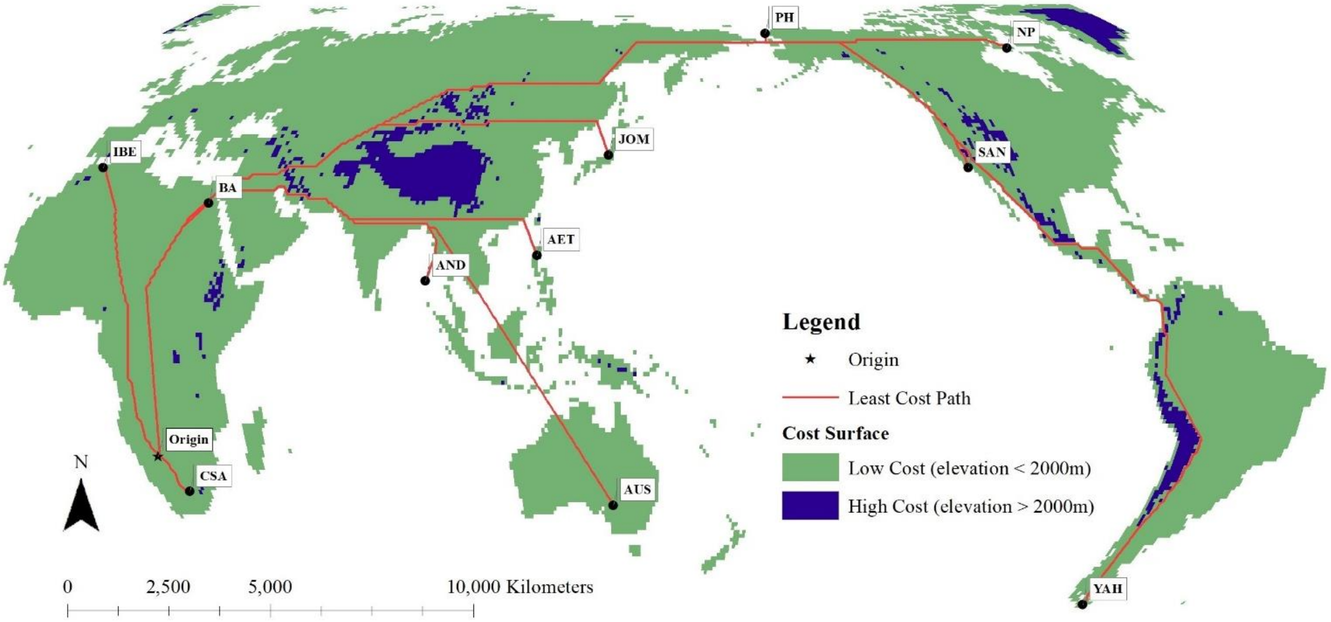
Group	*Season*	*MaxTemp*	*MinTemp*	*MaxPrecip*	*MinPrecip*	*NPP*
AET	107.857	30.150	15.793	581.583	60.410	1514
AND	59.569	32.753	22.138	538.328	14.317	1658
AUS	569.353	33.097	2.650	23.343	11.243	307
BA	744.161	38.748	2.926	4.615	0.000	46
CSA	581.143	32.160	-0.664	76.226	7.271	441
IBE	566.490	29.473	0.259	84.234	5.770	213
JOM	810.388	29.177	-2.400	187.720	57.857	791
NP	1370.057	13.242	-32.201	45.809	10.507	193
PH	1274.674	10.870	-31.278	40.888	4.419	164
SAN	338.120	25.173	4.995	87.945	0.000	365
YAH	274.099	13.797	-1.670	78.120	40.710	412

Note: Units - MaxTemp in °C, MinTemp in °C, MaxPrecip –in mm, MinPrecip –in mm, npp – in gC m^{-2}.

5.4. Distance from The Origin

Distance from an African origin was used as a proxy for genetic distance in the analyses examining potential Out of Africa signals in this thesis. A hypothetical origin at 22.3°S, 20.0°E was selected based on genetic research (see section 4.2.4.). Least Cost Path analysis conducted in ArcMap 10.8.2 generated polylines between this estimated origin to each of the group locations, avoiding areas with an altitude greater than 2,000 m and including mandatory waypoints (Figure 5.1). The distances derived from these polylines, identifying an approximate distance from the selected origin to the group location, are reported in Table 5.3.

Figure 5.1: Results of Least Cost Path Analysis.



Note: Red lines indicate the least cost path between each group location (black dots) and the hypothetical origin at 22.3°S, 20.0°E (black star). Base map credit: resampled and reclassified GTOPO30 DEM.

Table 5.3: Distance from Origin (22.3°S, 20.0°E) to Group Locations.

group	*Distance (km)*	*group*	*Distance (km)*
CSA	1’023.7	**AUS**	21’548.7
BA	5’941.3	**PH**	25’193.0
IBE	7’312.7	**SAN**	32’166.7
AND	14’645.4	**NP**	34’424.3
AET	16’924.0	**YAH**	45’800.6
JOM	20’839.8		

Note: Results are presented from nearest to furthest distance from the hypothetical origin.

5.5. Analyses of Linear Measurements

Correlation and regression analyses were used to determine whether previously established relationships of climate with stature and body mass could be identified in this sample, to test the general validity of analyses based on data derived from the LCP process and climate models, and determine if this relationship is predictive between the climatic/distance variables and traditional Euclidean measurements. Femoral length functioned as a proxy for stature while femoral head diameter acted as a proxy for body mass. Latitude was added into the analyses as it is one of the most common variables used in studies examining ecogeographic rules in body size and shape. To be able to directly compare the results derived from the GM data to the linear data, within-population variance in the linear measurements and coefficients of variation for the linear measurements were calculated and their relationships to the climate and distance variables were also explored.

5.5.1. Correlation Analyses of Linear Measurements.

5.5.1.1. Correlation Analyses of Individual Linear Measurement Data.

Correlation analysis was used to identify if there is a relationship between femoral length, femoral head diameter, and the climatic/distance variables. Normal distribution was evaluated using Shapiro-Wilk tests (Appendix Tables A6-A8). All were non-normally distributed, other than Male maximum femoral length, resulting in the use of Spearman Rank Correlation analyses. Results of the Spearman correlations are shown in Table 5.4.

Table 5.4: Correlations with Maximum Femoral Length and Femoral Head Diameter.

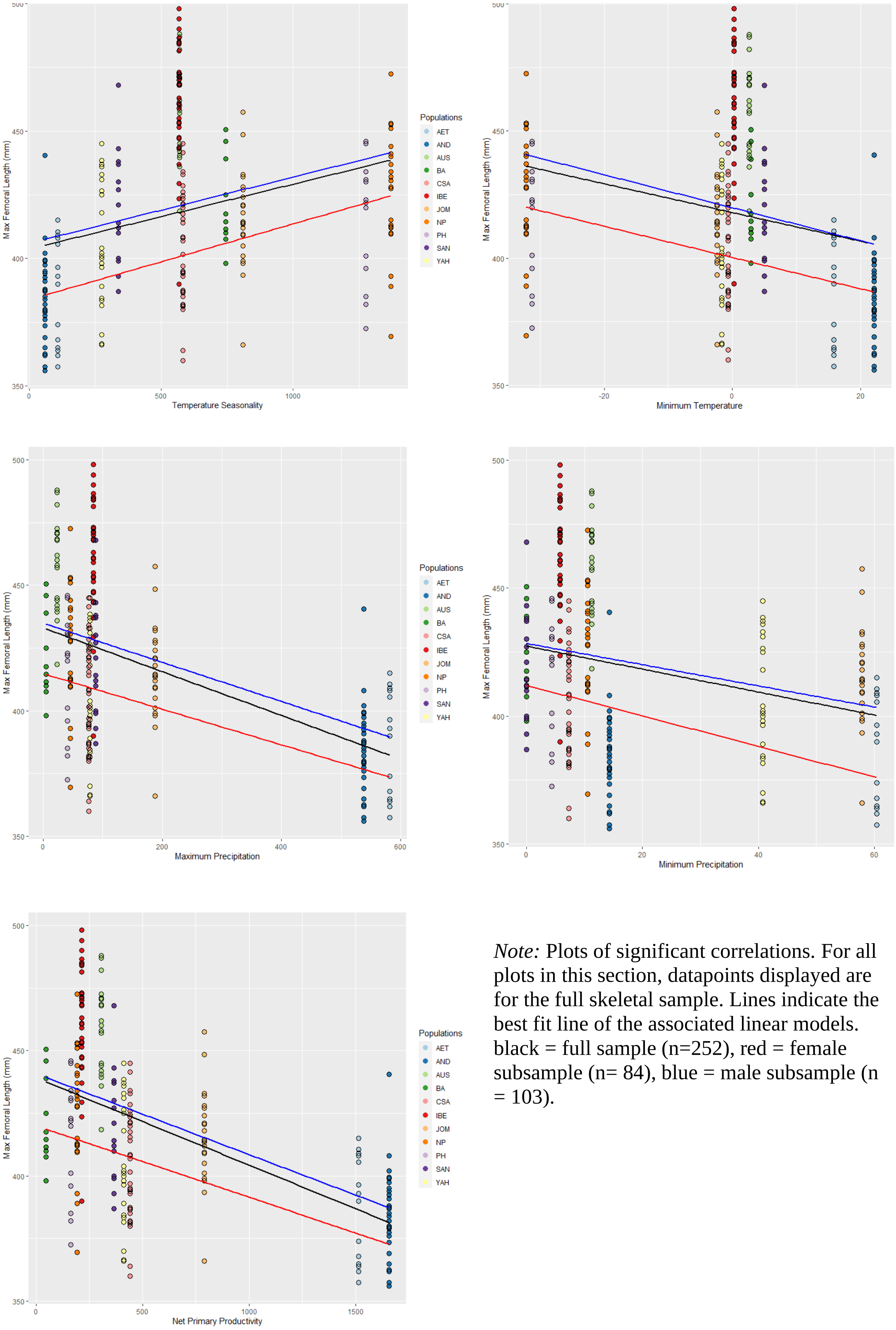
	Wxfln	*Wxfhd*	*Fxfln*	*Fxfhd*	*Mxfln*	*Mxfhd*
Season	0.29**	0.44**	0.40**	0.55**	0.36**	0.55**
MaxTemp	0.02	-0.35**	-0.03	-0.40**	-0.13	-0.48**
MinTemp	-0.25**	-0.47**	-0.33**	-0.54**	-0.35**	-0.59**
MaxPrecip	-0.50**	-0.45**	-0.47**	-0.48**	-0.51**	-0.48**
MinPrecip	-0.28**	-0.12*	-0.35**	-0.20	-0.26**	-0.10
NPP	-0.54**	-0.52**	-0.51**	-0.50**	-0.58**	-0.56**
Distance	-0.07	0.20*	-0.13	0.23*	-0.05	0.24*

Note: Reporting ρ and significance level *p<0.05 **p<0.01

Note: Variables - Maximum Femoral Length (Wxfln), Female Maximum Femoral Length (Fxfln), Male Maximum Femoral Length (Mxfln), Maximum Femoral Head Diameter (Wxfhd), Female Femoral Head Diameter (Fxfhd), Male Femoral Head Diameter (Mxfhd), Temperature Seasonality (Season), Maximum Annual Temperature (Max Temp), Minimal Annual Temperature (Min Temp), Precipitation of Wettest Month (Max Precip), Precipitation of Driest Month (Min Precip), Annual Net Primary Productivity (NPP), and Distance (in km) from Hypothetical African Origin..

All bivariate pairings including femoral length (whole sample, female, and male), other than those with MaxTemp and OoA Distance, were statistically significant. Temperature Seasonality displayed positive correlations, while all other significant correlations were negative (Figure 5.2). Generally, the single sex samples displayed stronger correlations than the full sample (combined male and female, plus undetermined/unrecorded). This was expected given the likelihood of a bimodal distribution of the measurements when combining sexes. For all three samples, the strength of the significant correlations varied from suggesting a weak correlation (MinTemp) to a moderate correlation (NPP).

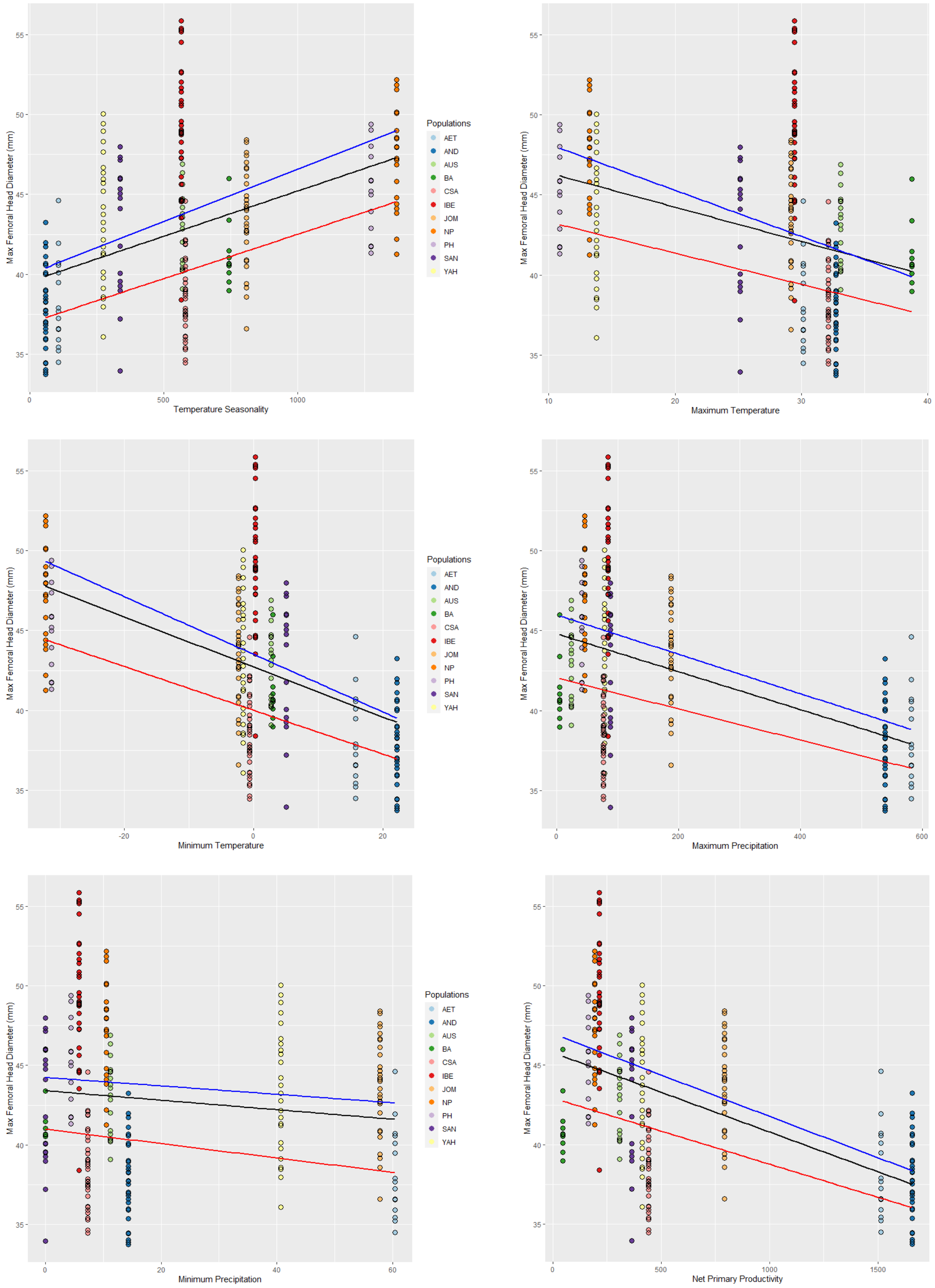
Figure 5.2:Maximum Femoral Length Plotted Against Climatic Variables.



Note: Plots of significant correlations. For all plots in this section, datapoints displayed are for the full skeletal sample. Lines indicate the best fit line of the associated linear models. black = full sample (n=252), red = female subsample (n= 84), blue = male subsample (n = 103).

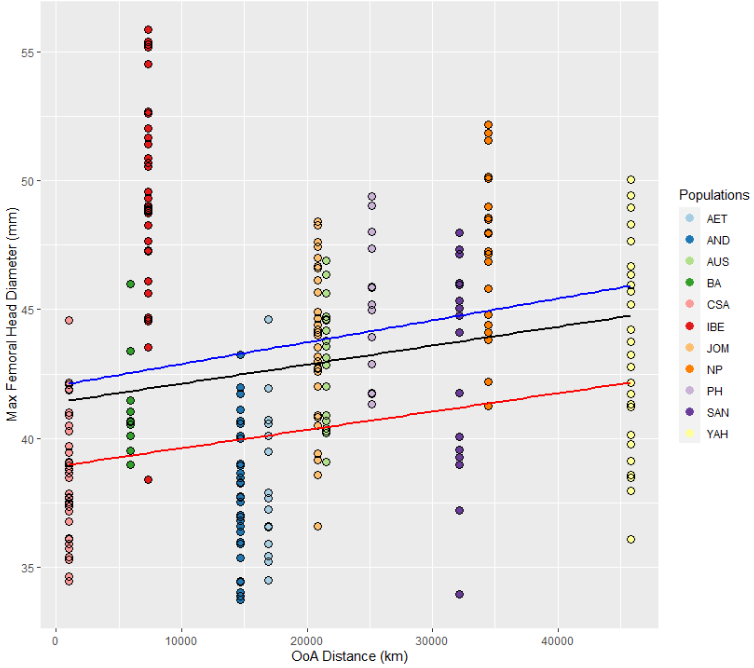
All bivariate pairings including femoral head diameter were found to be statistically significant (Table 5.4). The null hypothesis, that the ranks of one variable do not co-vary with the ranks of the other, was rejected in all Spearman’s tests. Temperature seasonality and OoA distance were found to have a positive correlation with xfhd (whole sample, female subsample, and male subsample), while all other variables had a negative correlation (Figures 5.3-5.4). The strength/effect size of the correlations varied from non/negligible correlation (MinPrecip) to moderate correlation (NPP). As with femoral length, the single sex samples generally displayed stronger correlations than the full sample.

Figure 5.3:Maximum Femoral Head Diameter Plotted Against Climate Variables.



Note: Plots of significant correlations. For all plots in this section, datapoints displayed are for the full skeletal sample. Lines indicates the best fit line of the associated linear models. black = full sample (n=252), red = female subsample (n= 84), blue = male subsample (n = 103).

Figure 5.4: Maximum Femoral Head Diameter Plotted Against OoA Distance.



To examine the relationship of latitude to the linear femoral measurements, and by extension, body mass and stature, absolute difference in latitude from the equator was calculated and correlation analyses between femoral head diameter, femoral length, and this variable were conducted. This was done as it is expected that the relationship of latitude to the linear measurements should be parabolic rather than linear (smaller body size and shorter limbs at the equator, larger body sizes with longer limbs further away).

Across all sample groups, femoral length and absolute latitude had a significant weak-moderate correlation (Table 5.5; Figure 5.5), while the correlation detected between absolute latitude and femoral head diameter was also significant and moderate-strong in strength (Table

5.5; Figure 5.6). As expected, absolute latitude consistently produced stronger correlations with the linear measurements than did latitude (Table 5.5).

Table 5.5: Correlation Analyses of Linear Measurements and Absolute Latitude.

	Wxfln	Wxfhd	Fxfln	Fxfhd	Mxfln	Mxfhd
Absolute Latitude	0.23**	0.50**	0.25*	0.55**	0.34**	0.61**
Latitude	0.17**	0.37**	0.28**	0.50**	0.21*	0.36**

Note: Reporting ρ and significance level *p<0.05 **p<0.01 Variables - Maximum Femoral Length (Wxfln), Female Maximum Femoral Length (Fxfln), Male Maximum Femoral Length (Mxfln), Maximum Femoral Head Diameter (Wxfhd), Female Femoral Head Diameter (Fxfhd), Male Femoral Head Diameter (Mxfhd).

Figure 5.5: Maximum Femoral Length Plotted Against Absolute Latitude

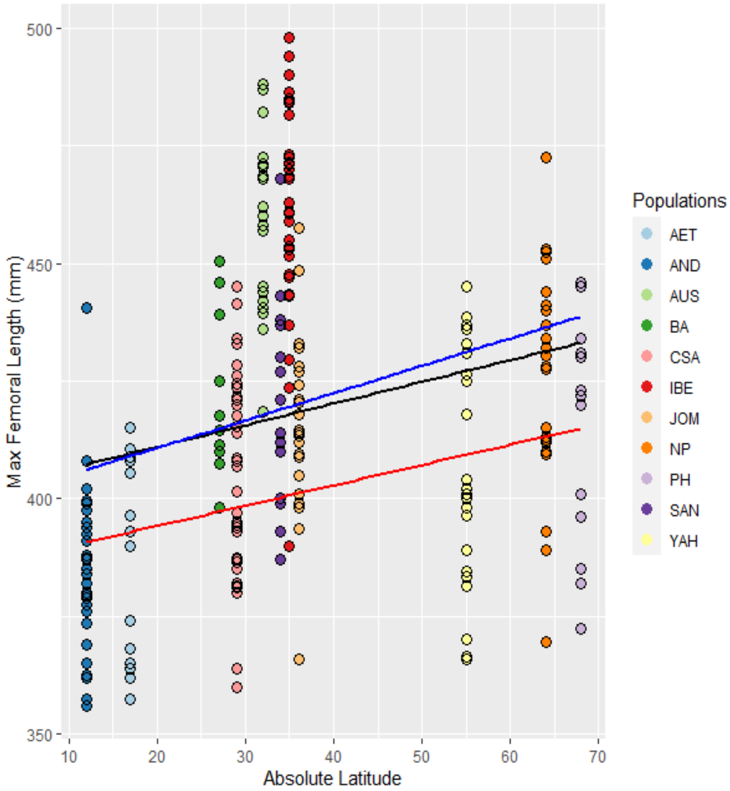
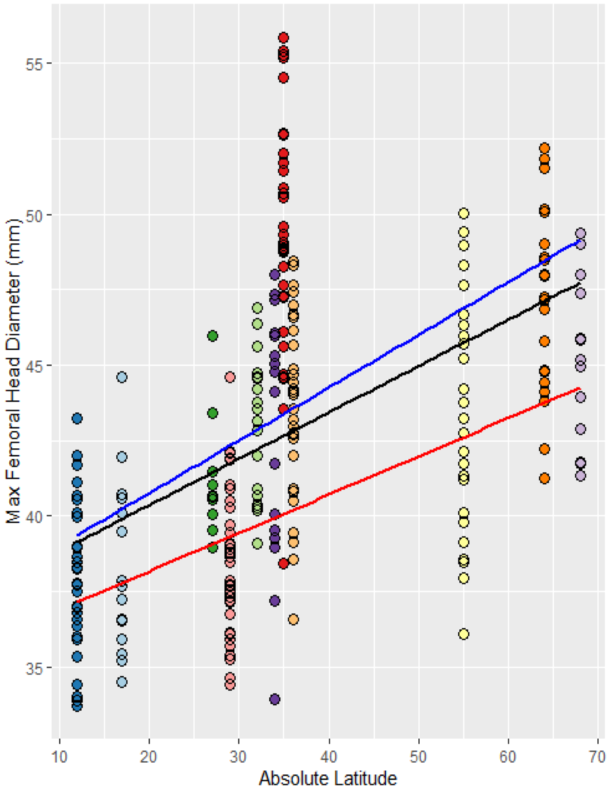


Figure 5.6: Maximum Femoral Head Diameter Plotted Against Absolute Latitude



5.7.1.2. Correlation Analyses of Linear Measurement Group Means.

To examine the influence of climate at the population level, the relationships between the group means presented in Table A3 and the climatic variables were assessed via correlation analyses. Normality was assessed via Shapiro-Wilk tests (Table A9), and a mix of Spearman Rank Correlations and Pearson's Correlations were used. The results are presented in Table 5.6.

Table 5.6: Correlations with Mean Maximum Femoral Length and Mean Maximum Femoral Head Diameter.

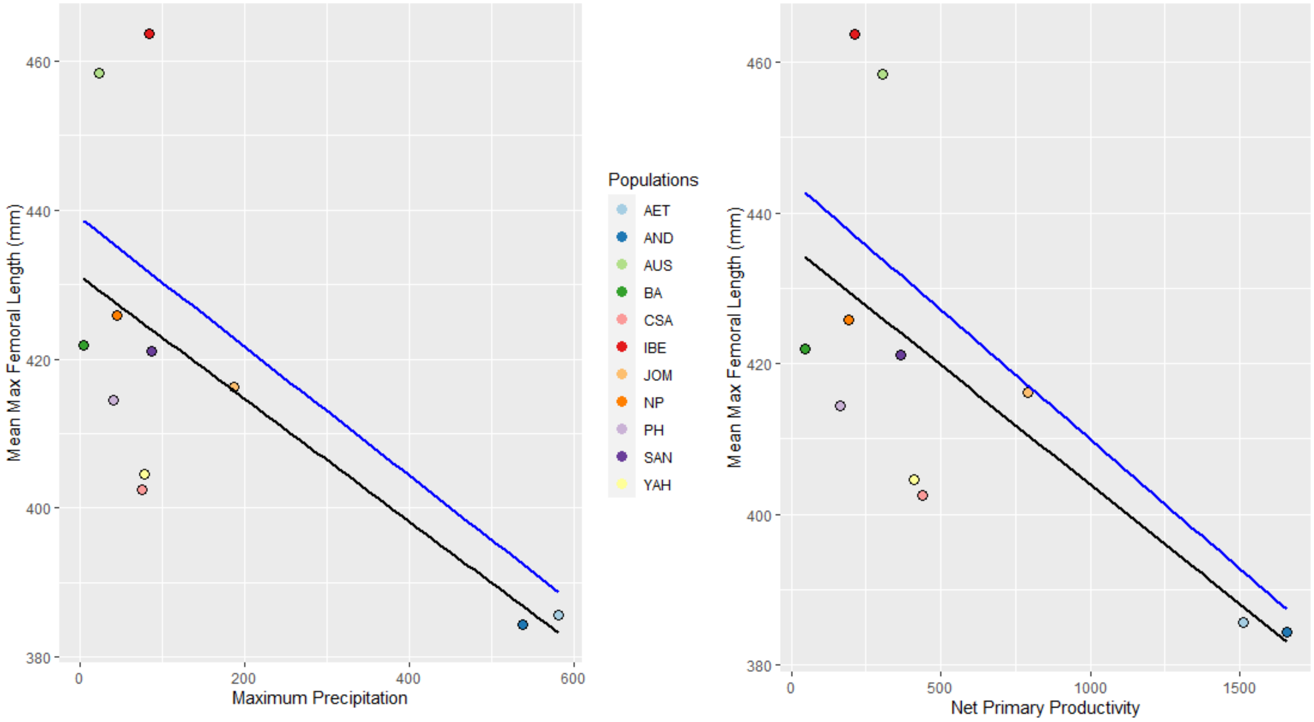
	Wxflnmean	*Wxfhdmean*	*Fxflnmean*	*Fxfhdmean*	*Mxflnmean*	*Mxfhdmean*
Season	0.36	0.60*	0.37	0.58	0.36	0.65*
MaxTemp	0.06	-0.50	0.13	-0.32	0.08	-0.51
MinTemp†	-0.29	-0.65*	-0.26	†0.56	-0.29	-0.70*
MaxPrecip†	-0.66*	-0.60	-0.59	-0.55	-0.63*	-0.51
MinPrecip†	-0.42	-0.24	-0.46	-0.30	-0.40	-0.15
NPP†	-0.68*	-0.65*	-0.61	-0.62	-0.67*	-0.58
Distance	-0.06	0.31	-0.23	0.09	-0.13	0.22
Latitude	0.09	0.43	0.18	0.50	-0.03	0.33
Absolute Latitude	0.25	0.68*	0.17	0.53	0.25	0.70*

Note: Reporting *ρ* and significance level *p<0.05 **p<0.01. † indicates a nonparametric Spearman's correlation was used and *ρ* is reported. Otherwise, Pearson's correlation was used, and *r* is reported.

Note: Variables - Maximum Femoral Length (Wxfln), Female Maximum Femoral Length (Fxfln), Male Maximum Femoral Length (Mxfln), Maximum Femoral Head Diameter (Wxfhd), Female Femoral Head Diameter (Fxfhd), Male Femoral Head Diameter (Mxfhd), Temperature Seasonality (Season), Maximum Annual Temperature (Max Temp), Minimal Annual Temperature (Min Temp), Precipitation of Wettest Month (Max Precip), Precipitation of Driest Month (Min Precip), Annual Net Primary Productivity (NPP), Distance (in km) from Hypothetical African Origin, and Latitude.

Maximum precipitation and net primary productivity were found to display statistically significant strong negative correlations with mean femoral length in the whole sample and the male subsample (Table 5.6, Figure 5.7). No significant correlations were found between mean female femoral length and any of the variables assessed.

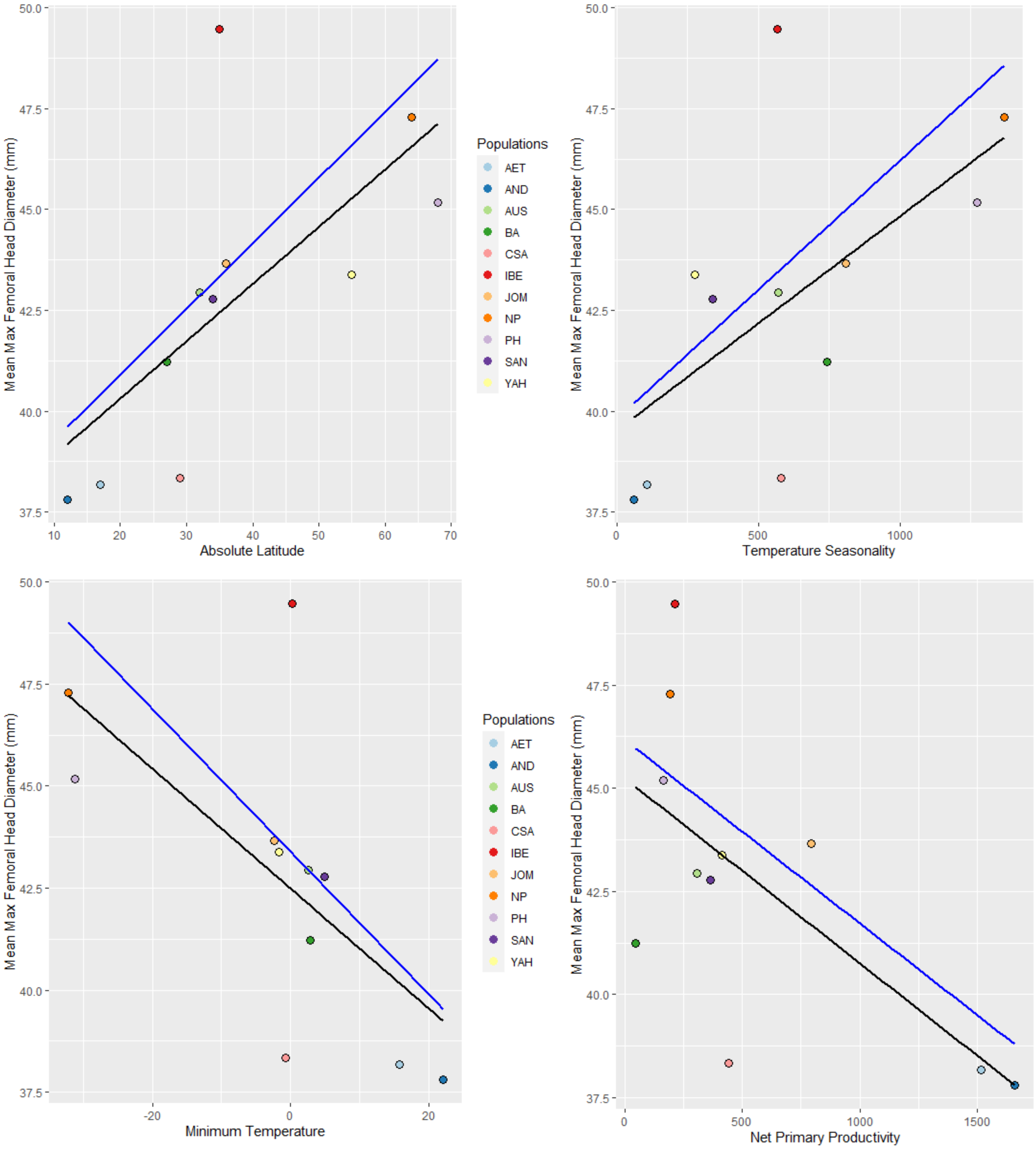
Figure 5.7: Mean Maximum Femoral Length Plotted Against Maximum Precipitation and Net Primary Productivity.



Note: Lines indicate the best fit line of the associated linear models. black = full sample, blue = male subsample. Datapoints are for the full sample.

Significant correlations were found between mean maximum femoral head diameter and temperature seasonality, absolute latitude, net primary productivity, and minimum temperature in the whole sample and the male subsample (Table 5.6). Absolute latitude and temperature seasonality displayed strong positive correlations with mean maximum femoral head diameter, while net primary productivity and minimum temperature displayed strong negative correlations with mean maximum femoral head diameter (Figure 5.8). No significant correlations were found between mean female femoral head diameter and any of the variables assessed.

Figure 5.8: Mean Maximum Femoral Head Diameter Plotted Against Absolute Latitude, Temperature Seasonality, Minimum Temperature and Net Primary Productivity.



Note: Lines indicate the best fit line of the associated linear models. black = full sample, blue = male subsample.

5.5.2. Correlation Analyses of Linear Measurement Variance.

Correlation analysis was used to identify if a relationship between within-population variability in femoral length and femoral head diameter, and the climatic/distance variables exists. The variance of each measurement for each population was calculated and used as the within-population variability measure. To adjust for size, the analyses were also conducted using coefficients of variation (CV = $\left(\frac{\sigma}{\mu}\right) \times 100$). Due to some variables being non-normally distributed (Appendix Table A9), both Pearson's and Spearman's correlations were used – with the results from the appropriate test being reported in Tables 5.7 and 5.8. As the impact of climate on shape variability was only explored in the whole sample, only the sex-pooled data was used in this set of analyses.

Table 5.7: Correlations with Within Population Variance in Maximum Femoral Length and Femoral Head Diameter.

	varxfln	*varxfhd*
Season	0.39	-0.23
MaxTemp	-0.79**	-0.43
MinTemp†	-0.66*	-0.01
MaxPrecip†	-0.39	-0.08
MinPrecip†	-0.19	0.13
NPP†	-0.46	-0.11
Distance	0.40	0.57
Latitude	0.08	0.01
Absolute Latitude	0.75**	0.26

Note: Variance of femoral length (varxfln) and variance of femoral head diameter (varxfhd). Reporting correlation coefficient and significance level *p<0.05 **p<0.01.† nonparametric Spearman's correlation analysis, ρ is reported. Otherwise, Pearson's correlation analysis , r is reported.

Only within-population variance in femoral length (varxfln) had statistically significant correlations with any of the variables. The significant correlations were with maximum annual temperature, minimum annual temperature, and absolute latitude (MaxTemp, MinTemp, Absolute Latitude). A strong negative correlation was found between within-population variance in femoral length and maximum annual temperature (*r* = -0.79). A strong positive correlation was found between within-population variance in femoral length and absolute latitude (*r* = 0.75). A slightly weaker, but still strong, negative correlation was found between within-population variance in femoral length and minimum annual temperature (*ρ* =-0.66).

Coefficients of variation were used to remove the influence of size and the analyses were repeated. This returned only one statistically significant correlation, that between the coefficient of variation (CV) for maximum femoral length and maximum temperature (Table 5.8). The correlation was strong and negative. Of note, the p-value for the correlation between absolute latitude and the coefficient of variation (CV) for maximum femoral length was close to significance (p = 0.0515, *r* = 0.60, strong positive correlation).

Table 5.8: Correlations with Population Level Coefficients of Variation for Maximum Femoral Length and Femoral Head Diameter.

	CVxfln	*CVxfhd*
Season	0.20	-0.46
MaxTemp	-0.77**	-0.34
MinTemp†	-0.50	-0.34
MaxPrecip†	-0.10	0.21
MinPrecip†	-0.01	0.22
NPP†	-0.16	0.20
Distance	0.40	0.53
Latitude	0.00	-0.11
Absolute Latitude	0.60	0.04

Note: Reporting correlation coefficient and significance level *p<0.05 **p<0.01.† indicates a nonparametric Spearman's correlation analysis was used and *ρ* is reported. Otherwise, Pearson's correlation analysis was used, and *r* is reported. Coefficient of variation for femoral length (CVxfln) and Coefficient of variation for femoral head diameter (VCxfhd).

5.5.3. Regression Analyses of Linear Data.

To clarify the direction and magnitude of the relationships between femoral length, femoral head diameter, and the climate and distance variables, simple linear regressions were performed. The regression lines generated on the plots presented in the previous sections appear to be comparable between the whole, and sex-separated samples. As such, only relationships in the whole sample were tested. When non-normality of residuals was identified for a model (Tables 5.9 – 5.11, N. Dist column, Appendix Table A6), a variety of approaches were tried to reduce or remove skewness. In some cases, a normal distribution could not be imposed via any of the methods attempted. These results must be interpreted with that context in mind.

Table 5.9: Femoral Length (Wxfln) Regression Results.

Model	*p-value*	*R^2*	*SRE*	*f*	*B_2*	*N. Dist*
xfln ~ season	**<0.01**	0.08618	31.92	23.58	0.0255	N
logxfln ~logseason	**<0.01**	0.2108	0.03064	66.78	0.0385	Y
xfln ~ maxtemp	0.774	0.0003	33.39	0.08267	0.0747	N
xfln ~ mintemp	**<0.01**	0.0636	32.32	16.98	-0.5652	N
xfln ~ maxprecip	**<0.01**	0.2475	28.97	82.23	-0.0873	Y
xfln ~ minprecip	**<0.01**	0.07878	32.05	21.38	-0.4482	N
xfln ~ npp	**<0.01**	0.2946	28.05	104.4	-0.0348	Y
xfln ~ distance	0.2799	0.004	33.32	1.173	-0.0002	N
xfln ~ latitude	**<0.01**	0.0276	32.93	7.095	0.1471	N
xfln ~ absolute latitude	**<0.01**	0.05063	32.54	13.33	0.4618	N
logxfln ~ logabsolute latitude	**<0.01**	0.1261	0.03224	36.06	0.0562	N

Note: N. Dist = normal distribution, yes (Y) or no (N). If model includes 'log' – data was logarithmically transformed. Significant p-values bolded. P-values are for the regression model.

Table 5.10: Femoral Head Diameter (Wxfhd) Regression Results.

Model	*p-value*	*R^2*	*SRE*	*f*	*B_2*	*N. Dist*
xfhd ~ season	**<0.01**	0.1898	4.512	58.56	0.0057	N
logxfhd ~ logseason	**<0.01**	0.2451	0.04394	81.17	0.0609	Y
xfhd ~ maxtemp	**<0.01**	0.1208	4.7	34.35	-0.2143	N
logxfhd ~ logmaxtemp	**<0.01**	0.1128	0.04763	31.78	-0.1018	N
xfhd ~ mintemp	**<0.01**	0.2169	4.436	69.23	-0.5652	N
xfhd ~ MaxPrecip	**<0.01**	0.2022	4.477	63.38	-0.0118	Y
xfhd ~ minprecip	**0.048**	0.01557	4.973	3.954	-0.0299	N
xfhd ~ npp	**<0.01**	0.2706	4.281	92.75	-0.0050	Y
xfhd ~ distance	**<0.01**	0.03926	4.913	10.22	0.00007	N
logxfhd ~ logdistance	**<0.01**	0.08071	0.04849	21.95	0.0283	Y
xfhd ~ latitude	**<0.01**	0.1401	4.648	40.74	0.0498	N
xfhd ~ absolute latitude	**<0.01**	0.2489	4.344	82.83	0.1537	N
logxfhd ~ logabsolute latitude	**<0.01**	0.3084	0.04205	111.5	0.1289	Y

Note: N. Dist = normal distribution, yes (Y) or no (N). If model includes 'log' – data was logarithmically transformed. Significant p-values bolded. P-values are for the regression model.

As would be expected given the correlation analyses, for maximum femoral length, all variables but maximum temperature and distance were identified as significant predictors. As seasonality, latitude, and absolute latitude increased across the sample, maximum femoral length also increased (Figures 5.2 & 5.5). For minimum temperature, maximum precipitation, minimum precipitation, and net primary productivity, as the values increased, maximum femoral length decreased (Figure 5.2). However, the R^2 values were fairly low across all variables.

For femoral head diameter, all variables were identified as significant predictors. As was the case with maximum femoral length, as seasonality and absolute latitude increased across the sample, so did max femoral head diameter (Figure 5.3 & 5.6). Distance from the approximated origin in Africa also had a positive relationship with femoral head diameter (Figure 5.4). For maximum and minimum temperature, maximum and minimum precipitation, and net primary productivity, as the values increased, femoral head diameter decreased (Figure 5.3). As with maximum length however, R^2 values were fairly low across all variables, though not negligible given the data type.

These analyses were repeated for the pairs of mean measurements and climatic variables which had significant correlations (Table 5.11).

Table 5.11: Mean Linear Measurement Regression Results.

Model	*p-value*	*R^2*	*SRE*	*f*	*B_2*	*N. Dist*
meanxfln ~maxprecip	**0.02606**	0.4401	19.99	7.074	-0.0824	Y
meanxfln ~ npp	**0.02056**	0.4664	19.51	7.865	-0.0317	N
logmeanxfln ~ npp	**0.01597**	0.4932	0.01951	8.759	-0.00003	Y
meanxfhd ~ season	**0.0488**	0.3655	3.141	5.185	0.0053	Y
meanxfhd ~ npp	**0.02881**	0.4287	2.981	6.753	-0.0045	Y
meanxfhd ~ mintemp	**0.02966**	0.4553	2.99	6.66	-0.1466	Y
meanxfhd ~ absolute latitude	**0.02079**	0.4652	2.884	7.828	0.1417	N
logmeanxfhd ~ logabsolute latitude	**0.0073**	0.5686	0.02623	11.86	0.1253	Y

Note: N. Dist = normal distribution, yes (Y) or no (N). If model includes 'log' – data was logarithmically transformed. Significant p-values bolded. P-values are for the regression model.

For mean maximum femoral length, maximum monthly precipitation was identified as a significant predictor. As minimum precipitation increased maximum femoral length decreased (Figure 5.7). Net primary productivity was also identified as a significant predictor with a negative slope (Figure 5.7), but the residuals were non-normally distributed. Logging mean-femoral length and rerunning the analysis produced a significant result and normally distributed residuals. This suggested that, as net primary productivity increased, femoral length decreased (Figure 5.9). All three regression analyses produced fairly high R^2 suggesting a large amount of explanatory power.

Temperature seasonality and absolute latitude had significant, predictive relationships with mean femoral head diameter. As seasonality increased, so did mean femoral head diameter (Figure 5.8). The residuals for meanxfhd ~ absolute latitude were non-normally distributed, which was addressed by logging both variables. The results suggested that the further from the equator, the larger mean femoral head diameter tend to be (Figure 5.10). Net primary productivity and minimum temperature both displayed a significant predictive relationship with mean maximum femoral head diameter and both models had a negative slope. This suggested that, as net primary productivity and minimum temperature increased, mean femoral head diameter decreased (Figure 5.8).

Figure 5.9: Logged Mean Maximum Femoral Length Plotted Against Net Primary Productivity.

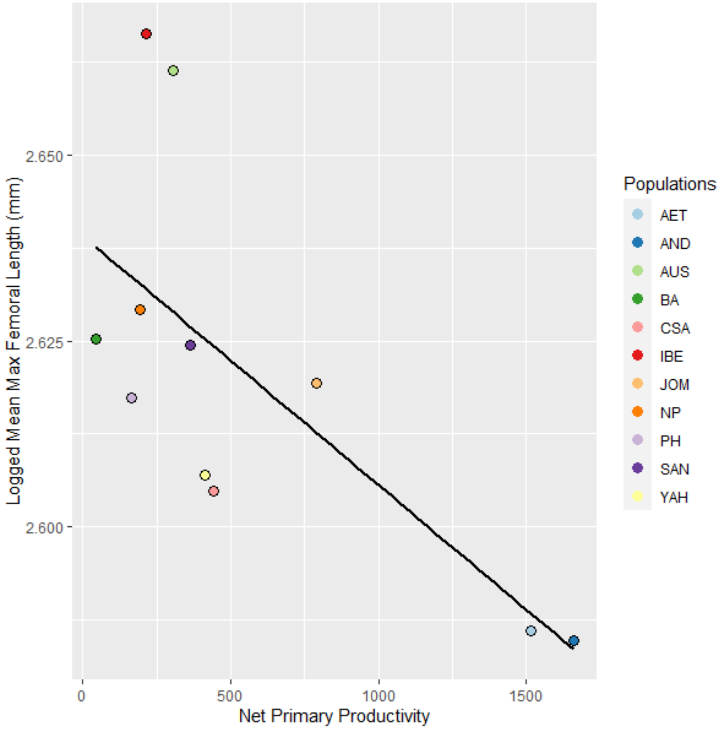
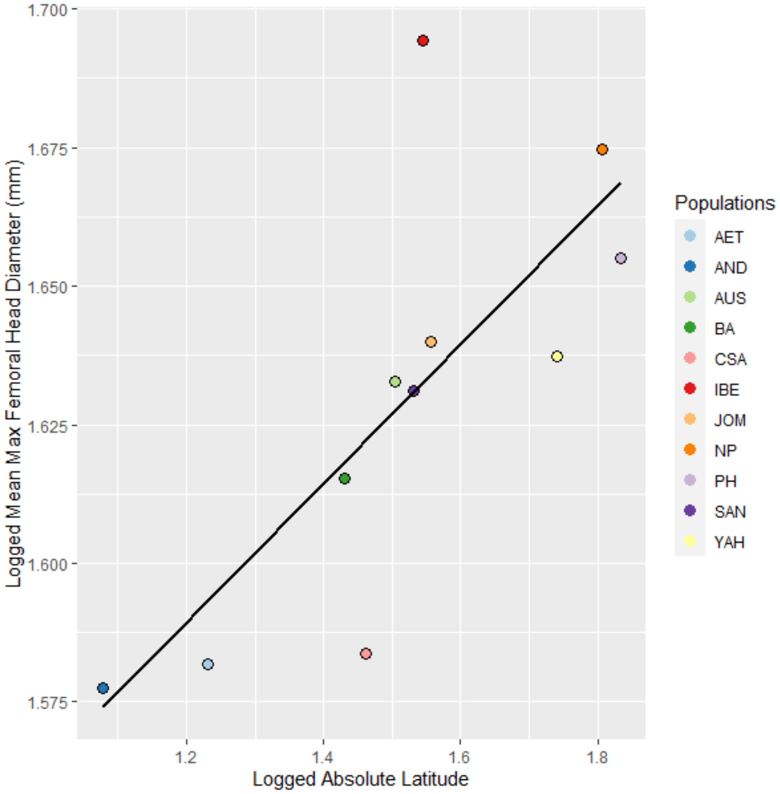


Figure 5.10: Logged Mean Maximum Femoral Head Diameter Plotted Against Logged Absolute Latitude.



5.5.4. Regression Analyses of Variance of Linear Data.

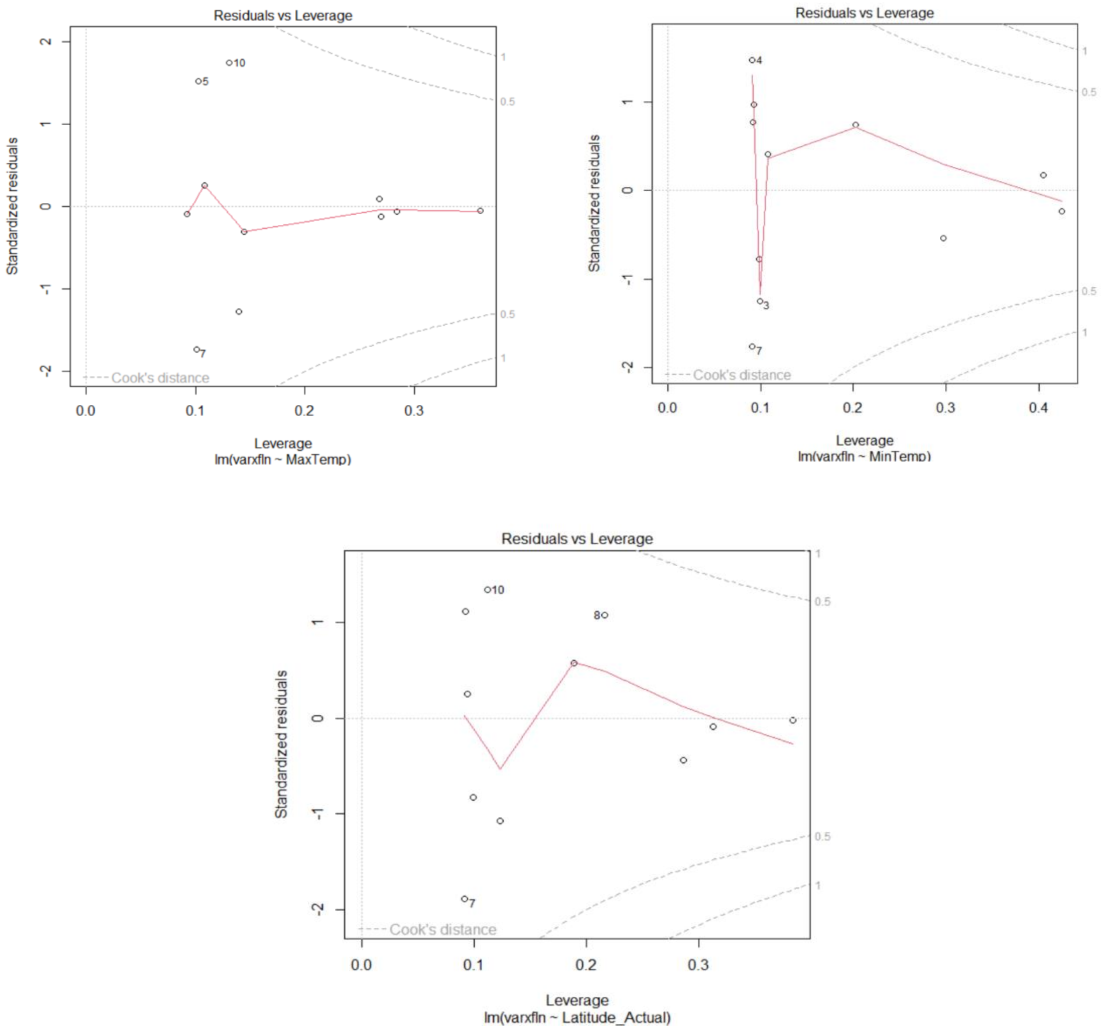
Simple linear regressions were used to clarify the direction and magnitude of the three significant relationships (variance in femoral length with maximum and minimum annual temperature and absolute latitude) found by the correlation analyses of within population variance in linear measurements and climate. All three variables were identified as significant predictors of variance in femoral length (Table 5.12). The residuals of each model were normally distributed (Table A9) and no highly influential points were identified via residuals/leverage plots (Figure 5.11).

Table 5.12: Within-Population Variance in Femoral Length (varxfln) Regression Results.

Model	*p-value*	R^2	*SRE*	*F*	B_2
varxfln ~ maxtemp	**0.00355****	0.6298	76.81	15.31	-10.152
varxfln ~ mintemp	**0.02681***	0.4369	94.73	6.982	-4.756
varxfln ~ absolute latitude	**0.00782****	0.5629	83.47	11.59	4.991

Note: * signficance at *$p<0.05$ ** significance at $p<0.01$

Figure 5.11: Residuals vs Leverage Plots for Femoral Length Variance and Max/Min Temperature and Latitude Regression Models.



Note: No datapoints fell outside the 0.5 or 1 cooks distance lines. This suggested that no highly influential datapoints were present, despite the small sample size.

Examining the plots, as distance from the equator increased, variance increased (Figure 5.12). As maximum and minimum annual temperature values increased, variance in maximum femoral length decreased (Figure 5.13-5.14). Essentially these all suggested that, as temperature increased (hotter temperatures closer to the equator), variance in length decreased.

Figure 5.12: Within-Population Variance in Maximum Femoral Length Plotted Against Absolute Latitude.

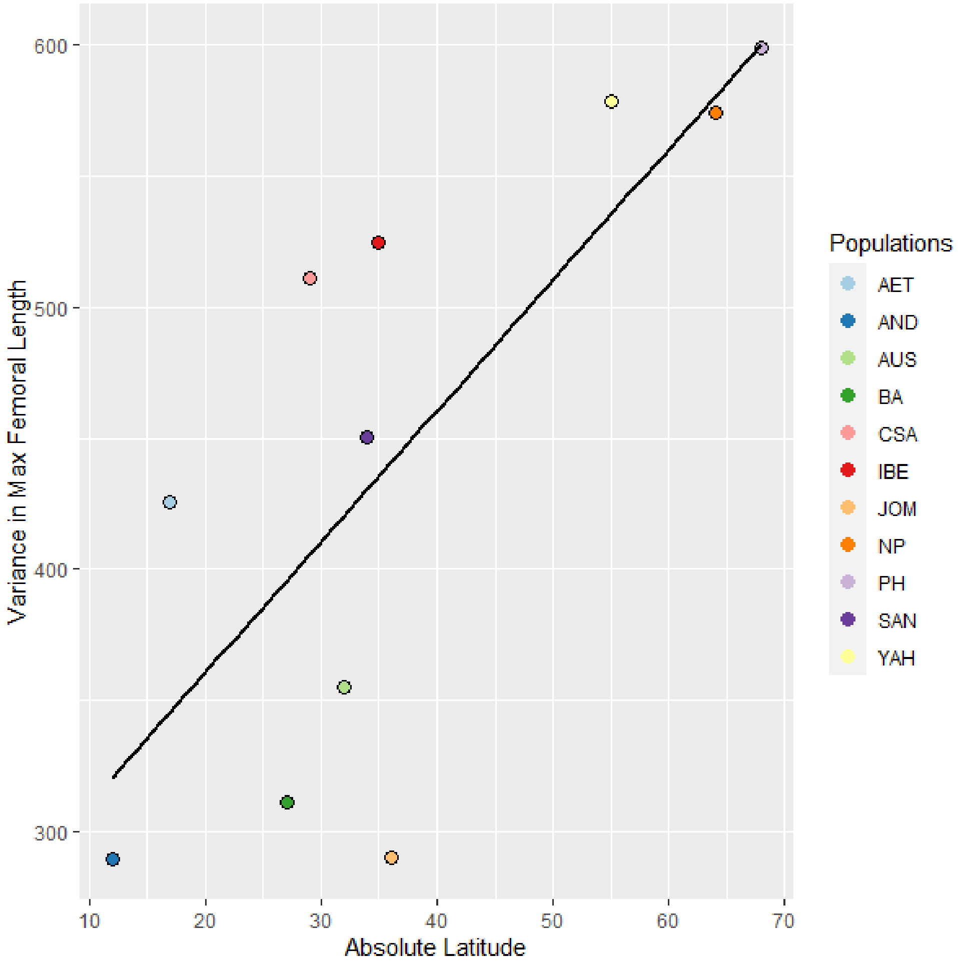


Figure 5.14: Within-Population Variance in Maximum Femoral Length Plotted Against Maximum Annual Temperature.

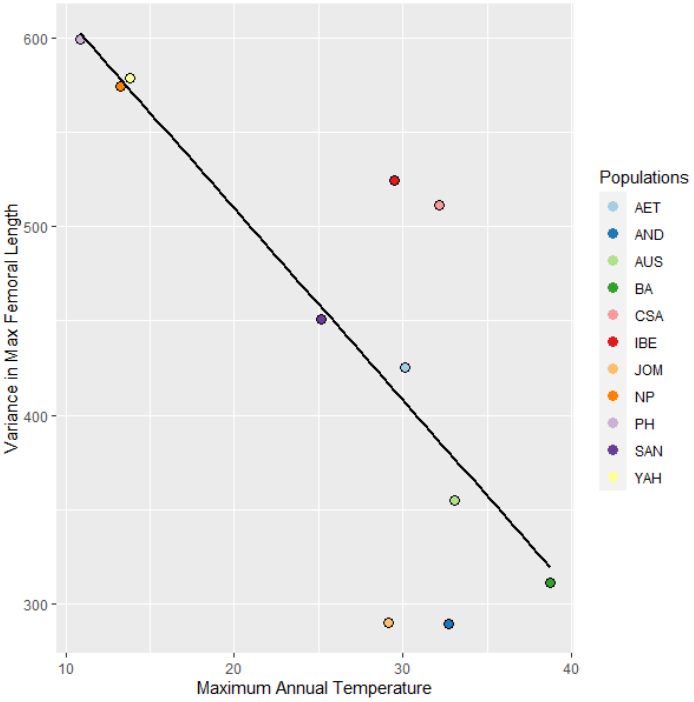
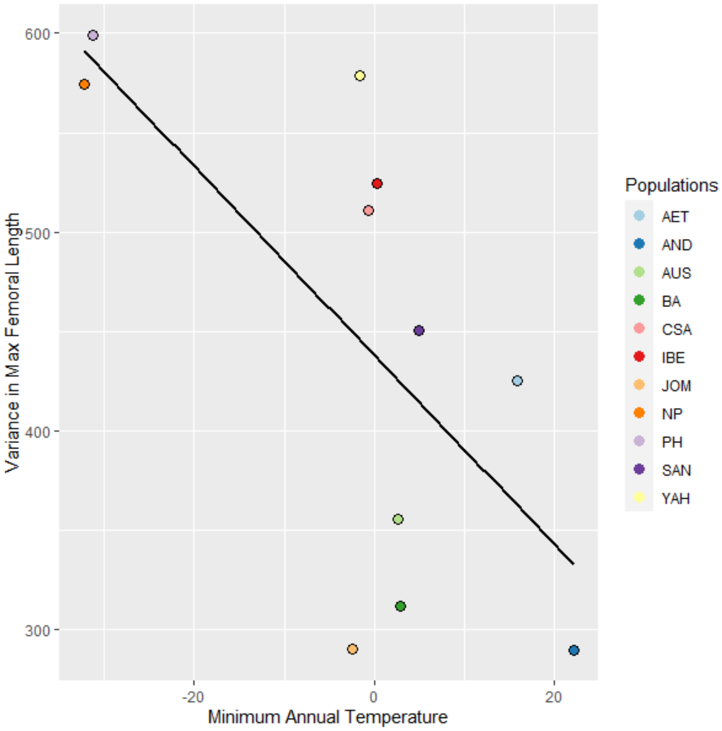


Figure 5.13: Within-Population Variance in Maximum Femoral Length Plotted Against Minimum Annual Temperature.

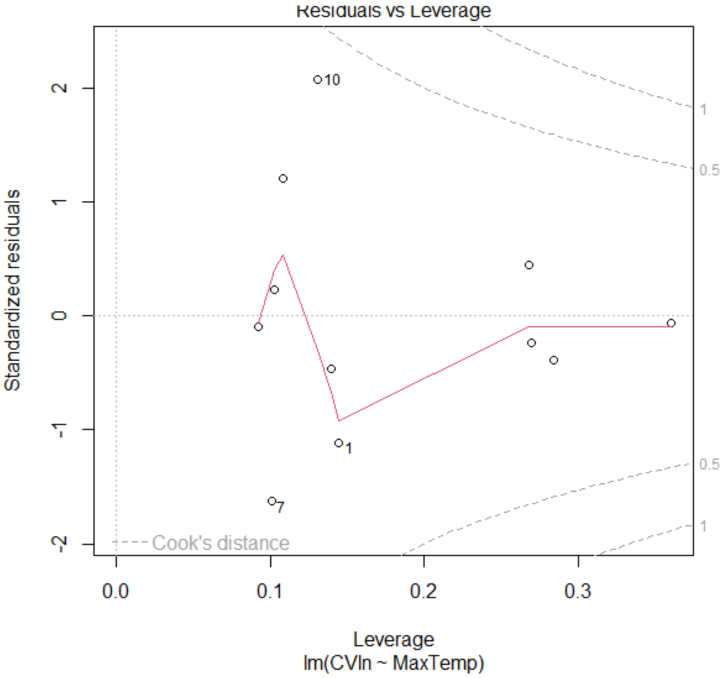


Regression analysis was also conducted on the coefficients of variation, which functioned as a size adjusted measure of variance. Specifically, the relationship of femoral length with maximum temperature as the independent variable was assessed as this pair displayed a significant correlation in the previous analyses. Maximum temperature was identified as a significant predictor of variability in femoral length, after controlling for body size (Table 5.13). The residuals were normally distributed (Table A9) and no highly influential datapoints were identified (Figure 5.15).

Table 5.13:Body-Size Adjusted Within-Population Variance in Femoral Length (CVxfln) Regression Results.

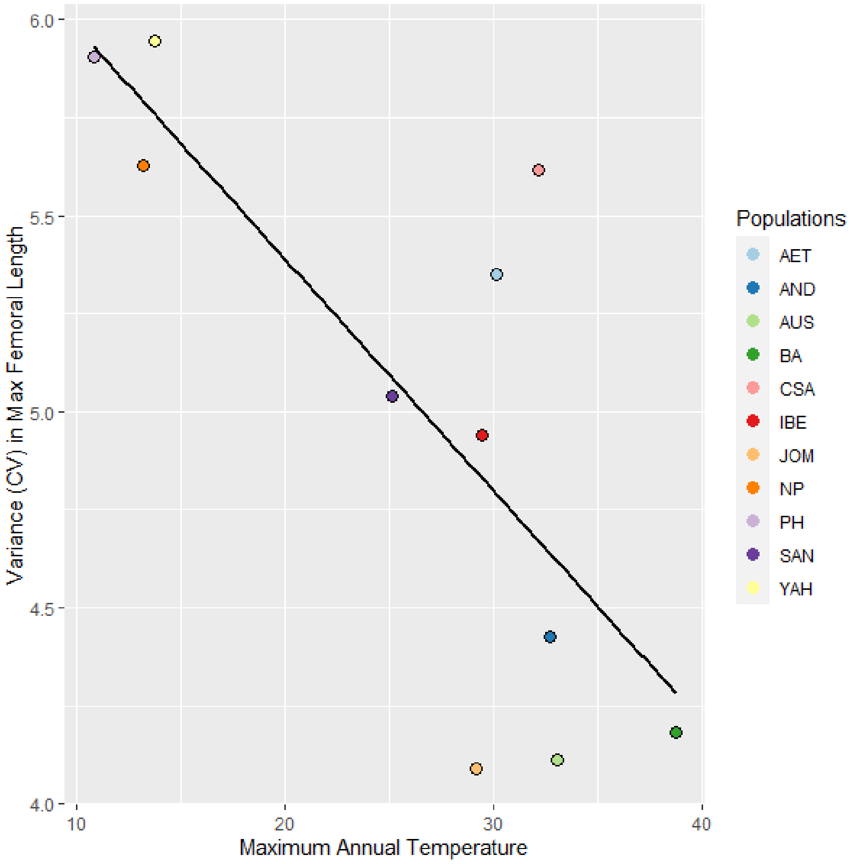
Model	*p-value*	R^2	*SRE*	*f*	B_1
CVxfln ~ MaxTemp	**0.006035**	0.586	0.4902	12.74	-0.059

Figure 5.15: Residuals vs Leverage Plot for Coefficient of Variation for Femoral Length and Maximum Temperature Regression Model.



This suggested that, as temperature increased within-population variation in length decreased, even when the data was size adjusted (Figure 5.16).

Figure 5.16: Coefficient of Variation in Maximum Femoral Length Plotted Against Maximum Annual Temperature.



5.6. Within-Population Morphological Shape Variation (3D GM) and Distance from Origin

This theses' research directives included questions about the drivers of within-population femoral morphological variation. Having demonstrated that patterns can be detected in linear metric data, this thesis also asked if a neutral signal could be detected in within-population shape variation using landmark based 3D GM. Under an OoA model of neutral evolution, one would expect morphological variation to decrease with increased distance from an approximated human origin of expansion in Africa. To address whether a neutral signal is present in femoral morphology, the relationship between within-population morphological variation and geographic distance from the origin was examined via regression analyses. The traces of the variance-covariance matrix of the PC scores for each population (summing each PC's variance) were used as measures of within-population femoral variation.

Table 5.14 shows the results of the simple regression analyses of phenotypic shape variance and distance from the inferred origin. For all tests administered, the validity of the model was assessed by inspecting the residuals. All passed the assumption of normality, assessed via Shapiro-Wilk tests (Table A10).

Table 5.14: Results from Phenotypic Variability ~ OoA Distance Regressions.

Model	R^2	*P-value*	B_2
wvw ~ distance	0.001148	0.9212	-1.694e-10
wvf ~ distance	0.00608	0.8833	-3.488e-10
wvm~ distance	0.1581	0.4351	2.801e-09
pvw ~ distance	0.2847	0.09095	-4.507e-08
pvf ~ distance	0.3958	0.1808	-4.947e-08
pvm ~ distance	0.02822	0.7504	-1.111e-08
dvw ~ distance	0.0426	0.5426	-1.655e-08
dvf ~ distance	0.005863	0.8854	-6.177e-09
dvm ~ distance	0.3954	0.1811	-5.883e-08
svw ~ distance	0.004959	0.837	3.856e-10
svf ~ distance	0.1208	0.4996	1.420e-09
svm ~ distance	0.4147	0.1676	4.730e-09

Note: Reporting within-population variation for all 4 landmarks sets (whole landmark set, proximal landmarks, diaphyseal(shaft) landmarks, and distal landmarks) for the sex-pooled and sex-divided samples. First two letters in the variable codes correspond to the landmark configuration analyzed (whole (wv), proximal (pv), distal (dv), diaphyseal/shaft(sv) landmark configuration), last letter corresponds to the sample used (whole sample (w), female sample (f), male sample (m)). E.g., wvw (within population variability of whole landmark set, sex pooled sample).

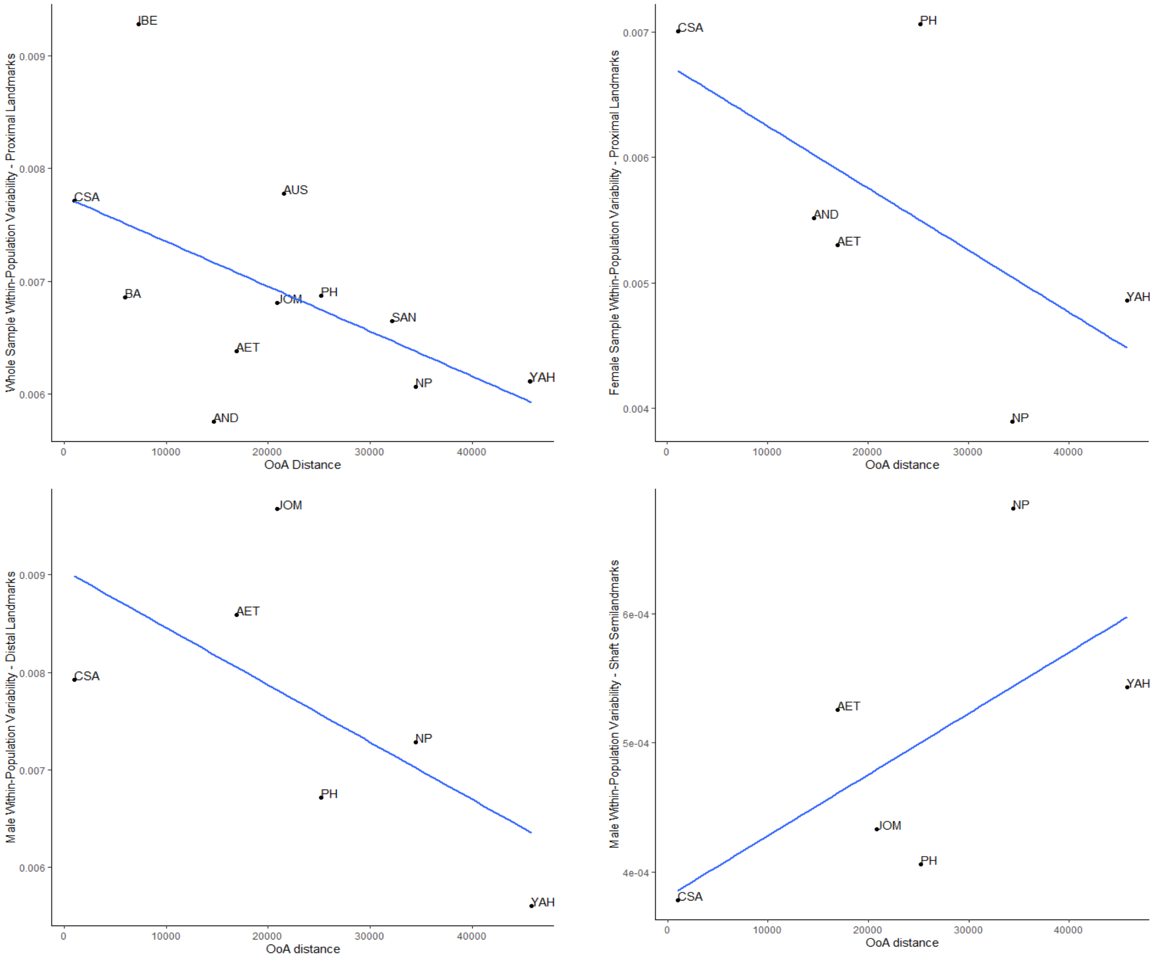
No models produced significant p-values. This would suggest that distance from an estimated origin in Africa is not a significant predictor of femoral morphological variation. However, as distilling the shape data to population level resulted in low sample sizes, and likely underpowered analyses, it is relevant to discuss the R^2 values despite the lack of significant p-values as they may indicate interesting patterns which should be re-examined. As addressed in the methods chapter (section 4.3.1.), due to the complex and multivariate nature of human biological variation, lower R^2s can be considered to indicate more significant explanatory power. In this case, R^2s around 0.25 are considered relevant for discussion, with anything around 0.4 being considered to have fairly high explanatory power.

The R^2 values suggested that geographic distance from an estimated origin in Africa does not explain a large amount of femoral shape variance across all sex-samples when the whole landmark configuration is used (wvw, wvf, wvm). However, both proximal shape variability in the whole sample ($R^2 = 0.285$) and the female subset ($R^2 = 0.396$) may be somewhat predictable from OoA Distance (Figure 26). The same was true for distal shape variability in the male subsamples (R2 =0.395; Figure 26). As would be expected under a neutral model, there was a pattern of decreasing variability with increasing distance when looking at these variables. Additionally, the model of proximal variation in the whole sample and OoA distance was near statistical significance ($p = 0.091$) despite the small sample size.

Svm~Distance had the largest R^2 at 0.415, suggesting that distance had a relatively strong relationship with within-population diaphyseal shaft variability in males. However, the relationship was the opposite of what would be expected under a neutral OoA model (Figure

5.17). Morphological variability in the male diaphysis appeared to increase with increasing distance from an African origin.

Figure 5.17:Plots of Within-Population Phenotypic Variability and OoA Distance



Note: Plotting variables where regression $R^2 > 0.25$.

With small sample sizes, it is very possible to produce a high R^2 by chance. However, if this was the case, and the R^2 were simple reflections of noise in the data or indicative of absence of a pattern, one would expect about a 50/50 split in the direction of the relationships. That the majority (8/12) of the slopes (B_2, Table 5.14) were negative (indicating that variability decreased with increasing distance) suggests an overall pattern that matches the neutral expectation in the whole, proximal, and distal regions. The opposite appeared to be true for the shaft, where predictive models using OoA distance all possessed positive slopes. In almost all cases, pvm and wvm being the exception, the R^2s returned were higher and the p-values were lower for the landmark modules compared to the whole landmark set (Table 5.14). This may highlight the relevance of a modular conception of femoral shape.

5.7. Within-Population Morphological Variation (3D GM) and Climate

The next set of analyses addressed the potential role of climate in shaping within-population femoral morphological variability via regression analyses. The relationship of the climatic variables (Season, MaxTemp, MinTemp, MaxPrecip, MinPrecip, NPP) to within-population phenotypic variability (wvw, pvw, dvw, svw) were examined. Table 5.15 displays the results of the stepwise regression analysis of phenotypic shape variance and climate variables for the sex-pooled sample. The sex-separated subsamples were not analyzed due to the limited sample size, where the number of groups (individual data points) were equal to the number of variables in the multiple regression.

Table 5.15: Results of Phenotypic Variance and Climate Variables Multiple Regressions.

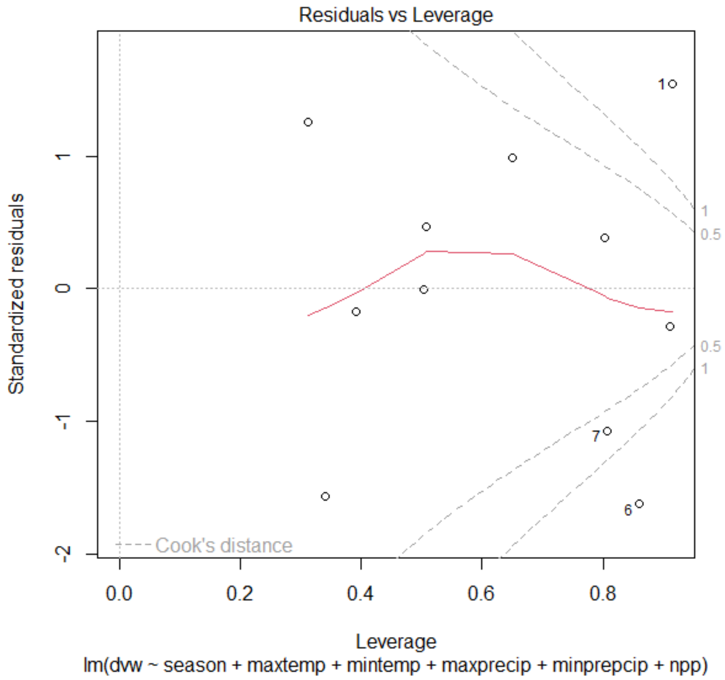
Minimal Model	*Adjusted R^2 (Multiple R^2)*	*P-value*
wvw ~ climate variables	0.2504 (0.7002)	0.348
pvw ~ climate variables	0.1939 (0.5224)	0.6531
dvw ~ climate variables	0.6556 (0.8622)	0.09405
svw ~ climate variables	0.2496 (0.6999)	0.3486

Note: In all cases no statistically significant factors were found. As such, the values for the full model (which included all climate variables) are presented. The first two letters in the variable codes correspond to the landmark configuration analyzed (whole landmark set (wv), proximal landmarks (pv), diaphyseal (shaft) landmarks (sv), and distal landmarks whole (dv)).

No combination of climatic variables was found to be a significant predictor of any measure of within-population femoral variability in terms of p-value. However, as with the distance regressions, these analyses are likely underpowered due to the sample size. Thus, the R^2 values are worth discussing, particularly that for distal variability, as this model was near significance at alpha 0.05 level (p-value = 0.094). The models for whole landmark configuration variability (wvw) and shaft semi-landmark variability (svw) produced moderate R^2 values, which suggested a fairly strong relationship between climatic factors and these measures of variability. The model predicting distal landmark variability (dvw) had a very high R^2 (0.66) suggesting that a large amount of variation in shape variability in this region may be linked to climatic factors.

However, a Cook's distance plot of the dvw ~ climate model identifies two highly influential data points, suggesting that more analysis is required (Figure 5.18).

Figure 5.18: Residuals vs Leverage Plot of dvw ~ climate variables Multiple Regression



Note: The presence of highlight influential points (those outside the 0.5 or 1 Cook's distance lines) may suggest that the model specified does not provide a good fit to the data. Point 1: AET, Point 6: JOM.

The regression analysis was re-run with these two points (AET and JOM) removed. The model was significant (p-value 0.03034) with a high R^2 (Adjusted 0.9591, Multiple 0.9898; Table 5.16). Seasonality, Minimum Temperature, Maximum Precipitation and Net Primary Productivity were identified as part of the minimal model.

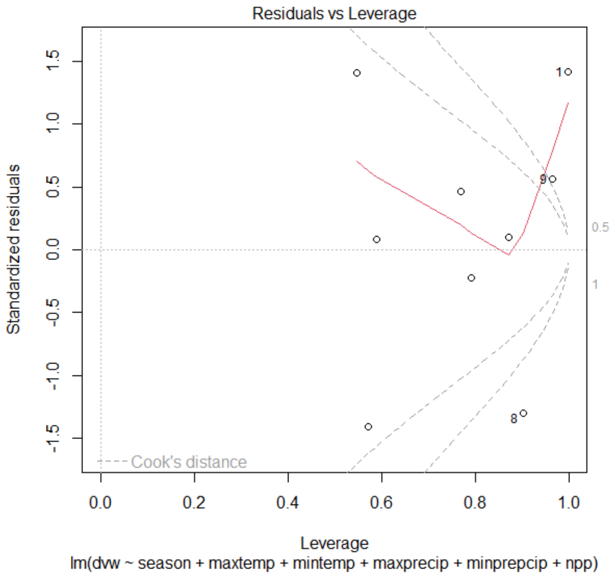
Table 5.16: Variable Loadings for dvw ~ climate Multiple Regression with AET and JOM removed

Variable	*Coefficient*	*t value*	*p value*
Intercept	6.261e-03	10.076	0.00971 **
Season	9.485e-06	4.835	0.04021 *
Max Temp	-1.203e-04	-2.495	0.13005
Min Temp	3.248e-04	4.658	0.04312 *
Max Precip	-2.496e-05	-7.232	0.01859 *
Min Precip	3.474e-05	3.499	0.07285
NPP	6.880e-06	6.268	0.02452*

Note: *Sig at 0.05 **sig at 0.01

The residuals were normally distributed (Shapiro-Wilk test p = 0.3294). However, again, highly influential datapoints were identified (AND, SAN; Figure 5.19). Thus the ‘pattern’ identified and the high R^2 may be: representative of statistical noise; an artifact of the small sample size; or illustrative of underlying non-linear relationships.

Figure 5.19: Residuals vs Leverage Plot of dvw ~ climate variables Multiple Regression with JOM and AET Removed



Note: Point 1: AND, Point 8: SAN.

As with the distance tests, in almost all cases, pvw being the exception, the R^2 returned was higher, and the p-value was lower, for the landmark modules than the whole landmark set. This again may highlight the relevance of a modular conception of the femur.

6. Discussion

This thesis sought to explore climatic and ‘neutral’ morphological signatures in the human femur. The results demonstrate a significant impact of climate for the linear Euclidean data. For the GM data, within-population shape variance is not significantly predicted by any of the variables tested, including Out of Africa distance. This provides some evidence that climatic selection may have overwritten any signatures of neutral processes present in this element.

6.1. The Limitation of Low Statistical Power

While unconventional, it is relevant to begin the discussion section of this thesis by highlighting a limitation that likely impacted the statistical analyses conducted, as this significantly impacts how the results are interpreted.

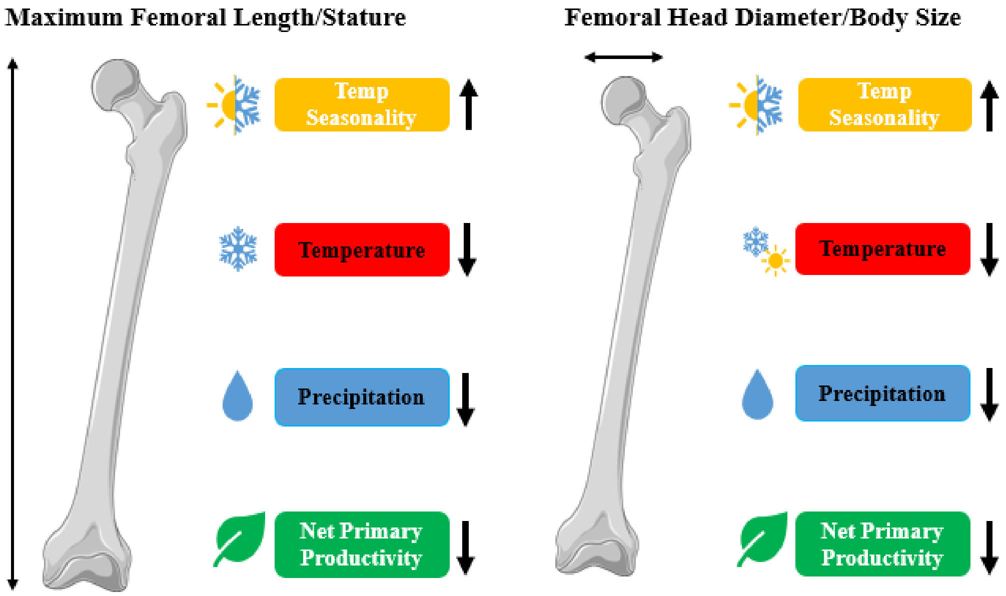
The largest issue facing this thesis is the low statistical power of its analyses. Statistical power refers to the probability of a hypothesis test finding an effect if there is one to be found (Carlson, 2017). Specifically, the low power of these analyses increases the risk of committing type II (β) error, producing a false negative. Type II error may be reduced by lowering the significance level threshold (e.g., 0.1 rather than 0.05) but this has the effect of increasing the likelihood of type I error (a false positive), leading to a standard p-value being chosen for this thesis (0.05). In archaeology, the consequences of error in statistical testing does not tend to have life or death consequences, as opposed to disciplines like medicine (Carlson, 2017). Instead, the consequence of type II error tends to be that we fail to recognize interesting patterns by ignoring results which lack statistical significance. In many cases, failure to find statistically significant patterns may be a problem of sample size (Carlson, 2017). In this thesis, while the original sample size of 174 for the GM data may not appear small, because the questions asked concern within-population variability, sample size reduced to 11, and then again to 6 for the sex-divided samples. This reduction in sample size leads to a decrease in the statistical power of the tests used to analyse the GM data and an increased likelihood of type II error. The tests in this thesis with low statistical power, specifically those analyzing the GM data, while being unlikely to produce statistically significant results may be able to identify potential patterns worth revisiting with more robust samples with more statistical power.

6.2. Potential Directional Selection Acting on Femoral Morphology: Linear Measurements

This thesis posed the question: how does directional selection (specifically climatic influence) interact with femoral morphology to produce variation in femoral length and femoral head diameter? The use of these particular measurements allows for discussion of patterns in body size and stature. Individual and population level effects were identified using individual measurements and group means. To be able to speak more directly to Bergman and Allen’s rules, relationships between latitude and the linear measurements were also examined.

At the individual level, maximum femoral length appears to be impacted by temperature (seasonality and minimum), precipitation, and net primary productivity (Figure 6.1). Individuals in environments with more seasonal variability in temperature display longer femora, while those in warmer, wetter and/or more vegetated regions display shorter femora. The same effects are found for femoral head breath (Figure 6.1). Latitude and absolute latitude appear to have a positive relationship with both measurements, though the relationship with absolute latitude is stronger (individuals further from the equator have longer femora with larger femoral heads). These relationships were consistent across the sex-subsamples.

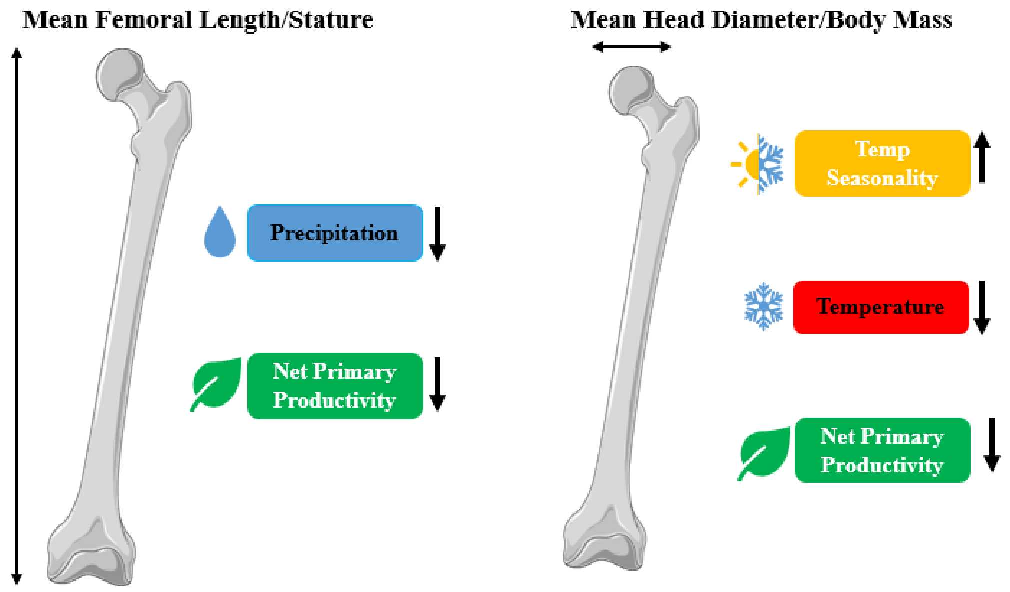
Figure 6.1: Individual Level Impacts of Climate Variables on Linear Measurements.



Note: Inferred effects of climatic variables on femoral measurements on the level of the individual. Temperature (either increased minimum or both increased minimum and increased maximum – overall increase in temperature), precipitation (increased minimum and increased maximum). Figure partly generated using Servier Medical Art, provided by Servier, licensed under a Creative Commons Attribution 3.0 unported license.

At the population level, mean femoral length appears to be impacted by precipitation and net primary productivity (Figure 6.2). Groups in drier and/or less vegetative regions have longer average femoral lengths. For mean femoral head diameter, temperature and net primary productivity have a significant impact (Figure 6.2). Groups in regions displaying more seasonal variability in temperature had larger femoral heads on average. Groups in colder and/or less vegetative regions also displayed larger mean femoral heads. Mean femoral head diameter also appears to be linked to absolute latitude, where groups further from the equator display larger femoral heads on average. These results only applied to the whole sample and the male subset as no significant correlations were found between the female measurements or means and any variables. The female sub-sample contains one fewer population (Chumash) which may have produced this result. It may also be that there is increased constraint on female phenotypic variation tied to reproductive, and/or other, processes.

Figure 6.2: Population Level Impacts of Climate Variables on Linear Measurements.



Note: Inferred effects of climatic variables on femoral measurements at the population level. Temperature (either increased minimum or both increased minimum and increased maximum – overall increase in temperature), precipitation (increased minimum and increased maximum). Figure partly generated using Servier Medical Art, provided by Servier, licensed under a Creative Commons Attribution 3.0 unported license.

The results that mean femoral length is related to precipitation and net primary productivity is likely the product of the inclusion of two small bodied/tropical rainforest forager groups, the Andaman Islanders and Aeta foragers. In the plots of these relationships (Figure 5.9), these groups can be seen isolated in the bottom right corner. As noted the two groups are at the extreme small end of body size, and their environments are densely forested and experience high levels of precipitation. It is possible there would not be a relationship between mean femoral length and these variables if these groups were removed, as this trend may be a signal of phenotypes which are adaptive in specific environments. There are multiple hypotheses as to why a small-bodied phenotype is strongly associated with tropical rainforest environments, including adaptive hypotheses surrounding coping with food limitation, warm-moist environments, potential life history trade-offs for earlier reproduction, or a combination of these (Perry & Dominy, 2009). The association of high NPP with small body types may seem counterintuitive, as one might assume higher biodiversity/availability of plant matter would lead to an abundance of nutrients and therefore increased growth. However, the energy in these ecosystems is largely taken up by system maintenance, leaving less net productivity for humans and other high-level consumers (Moran, 2022c). Thermoregulation is an additional energetic challenge in these environments as high humidity decreases the effectiveness of evaporative cooling while temperatures remain high (Roberts et al., 2016). This may lead to favouring of small body sizes to reduce metabolic heat generation (Roberts et al., 2016).

6.2.1. Fit with Bergmann and Allen's Ecogeographic Rules.

The results of this thesis could extend to discuss ecogeographic patterns in body mass and stature as femoral length corresponds to stature (e.g., Bass, 2005), while femoral head diameter is closely related to body mass (e.g., Grine et al., 1995, McHenry, 1992, Ruff et al., 1991). The results fit with some of the predictions generated from Bergmann's rule, but not Allen's.

To review, under Bergmann's rule, one would expect, in a species with a large range of geographic dispersal, that those in colder regions will exhibit larger body sizes, while those in warmer regions will be smaller (James, 2018). If present this pattern could manifest in both the femoral length and femoral head diameter data. This thesis found that, on both an individual and population level, climate appears to be a driving force in shaping body size and stature, proxied from femoral head diameter and length. In accordance with Bergmann's rule, femoral heads (and by extension, body masses) are larger in colder environments. These environments tend to also display more seasonal variation in temperature and low net primary productivity, which were also found to be related to femoral head diameter. Individuals in colder environments also displayed the longest femora, and by extension the tallest statures, though population means in femoral length were not found to be related to temperature in this study. Unsurprisingly given that it is closely tied to temperature, latitudinally the further from the equator (0°) a population or individual is, the larger their femoral heads and femoral lengths tend to be.

The pattern presented by Bergmann’s rule, of increasing body size with decreasing temperature, is understood to reflect changing surface-area to volume ratios in response to thermoregulatory challenges. An individual with a larger body mass will conserve heat better than an individual of the same stature with a smaller body mass. In hot environments, a smaller body mass is more advantageous to increase heat dissipation. Femoral head diameter (indicative of body mass) increasing with decreasing temperature and increased distance from the equator is likely a reflection of this principle.

That those individuals in the hottest regions in this thesis, those in tropical forests, display the smallest statures, and likely the smallest surface area to volume ratios as a result, is not wholly unexpected. It has been suggested that, in climates where temperatures are very high, thermoregulatory challenges are likely to impact body proportions in ways such that the pattern varies from the expected increase in stature with increasing temperature. In these environments, heat gain via convection and radiation from a taller body can outweigh the advantages which come from greater surface area (Bar-Or et al., 1969). In these cases, a more compact build may be favourable (Bar-Or et al., 1969; Hanna & Brown, 1983). As discussed, the small mean body sizes of the Aeta Forager and Andaman Islander groups, who would be especially subject to this kind of temperature stress (Perry & Dominy, 2009), likely weigh heavily in this result.

Both selection and plasticity may have a role in shaping patterns of femoral length and head diameter. Selective pressure on the individual and/or population level in general accordance with Bergmann’s rule does produce the clinal variation in body size and stature, and femoral length and head diameter, observed in this thesis. It is also possible that climatic (specifically temperature) impacts effect femoral measurements during the lifetime, through some secondary growth mechanism. However, the results of this thesis are the opposite of what would be expected given previous studies of mice which found reduced chondrocyte proliferation and extracellular matrix volume in lower temperatures, producing an overall reduction in bone length (Serrat et al., 2008). Nevertheless, direct effects of *in-vivo* temperature on growth of limb bones during the growth period is a potential mechanism that could impact stature and femoral length.

Allen’s rule (1877) is unlikely to directly apply to this thesis as femur length alone provides an incomplete indication of lower limb length without inclusion of the tibia. Studies of the impact of climatic stress on long bone measurements have found that the magnitude of environmental impacts among skeletal elements is variable (Betti et al., 2015; Payne et al., 2018; Pomeroy et al., 2012). In the lower limb, the tibia is thought to be more impacted by stress than the femur, such that overall reductions in limb length with stress may be mainly caused by a reduction in tibial length while femoral length is preserved (Payne et al., 2018; Pomeroy et al., 2012). If a decrease in lower limb length is occurring with decreasing temperature, this previous research suggests that the reduction is primarily driven by variation in tibial length. If the femur is less responsive to climatic stress, a decrease in limb length could occur without a change in femoral length, resulting in a poor fit of the femur as a proxy for overall lower limb length without also considering tibial length, and the absence of the patterns expected under Allen’s rule. This is a potential explanation for why the expected patterns under Allen's rule are not reflected in the results of this thesis' analysis of femoral length.

6.3. What Shapes Within-Population Variance in Femoral Linear Measurements?

To provide a comparison to the GM derived-shape data, this thesis also asked if the amount of variation in linear femoral measurements within a population is shaped significantly by climatic or neutral influences. Size-adjusted and non-size adjusted variables were used.

No significant predictors for variability in femoral head diameter variation were found. However, climatic factors, specifically minimum temperature and maximum temperature, and absolute latitude had significant, predictive relationships with femoral length variance. This suggests that temperature may have a significant role in shaping variability in femoral length, and by extension, within-population variability in stature. The groups existing in the coldest environments displayed the largest variances in femoral length.

These results are in line with research by Betti et al. (2012) which found that minimum temperature was predictive of femoral phenotypic variability. Betti et al. (2012) included measures of femoral length (maximum length and bicondylar length) and anteroposterior head diameter in the calculation of phenotypic variability alongside four other femoral measurements. However, Betti et al. (2012) performed their analysis on size-adjusted data, making it more analogous to this thesis' analysis of coefficient of variation data.

When the measure of variability is size adjusted, the relationships between variability and climatic factors become less strong and the relationships with femoral length and minimum temperature and absolute latitude become non-significant. However, maximum temperature did display a significant predictive relationship with size-adjusted variability in maximum length (represented by coefficients of variation). Like with the variance data, those populations at higher temperatures exhibited lower levels of variability in femoral length. In-keeping with Betti et al. (2012), when femoral measurements are size-standardized, temperature is suggested to influence femoral variability. In this case, increased maximum temperature has a limiting impact on femoral length variability, and by extension, stature.

A potential explanation for why decreased variability in femoral length may occur with increased temperature is that there is some interaction between cultural buffers against temperature stress and stabilizing selection. It may be that, due to the limited potential for cultural adaptation to heat stress, populations in warmer climates experience increased stabilizing selection on height when compared to populations in colder environments (which are more able to culturally buffer themselves from the environment, limiting thermoregulatory stress).

Human adaptive techniques to temperature stress typically fall under either material cultural adjustments or behavioural adaptations (Hanna & Brown, 1983). Behavioural adaptations often entail avoiding times/areas which exhibit the most extreme temperatures (heat or cold; Hanna & Brown, 1983). Material culture adjustments aim to establish a favorable microclimate to counter the potential of heat gain or loss (as a current example, the use of air conditioning and interior heating; Hanna & Brown, 1983). Material cultural adjustments and behavioural adaptations to temperature stress in hunter-gatherers in cold environments (like those of the Native Point and Point Hope groups) are well documented (see Frisancho (1993) for examples). Here the main concern is heat loss reducing skin temperature, and eventually, internal body temperature. The most effective strategy to avoiding cold stress is to insulate the body (Moran, 2022b). In groups like those in this thesis, this is often done using thick, tailored clothing and insulated housing (Ocobock et al., 2021). Behaviourally, cold-stressed groups may increase heat production via increased activity (Ocobock et al., 2021). To emphasize the importance of this topic, behavioural and technological adaptation to cold habitats have been identified as key factors in our species ability to expand into diverse ecological regions (Buck et al., 2018).

Hot-dry climates (like those of the Australian and Egyptian Badari groups) are characterized by extreme hot deserts, but often display cool nights that may yield additional, cold related thermoregulatory challenges (Hanna & Brown, 1983; Frisancho, 1993). The major concerns are radiation, convection, and conductive heat gain, which can be mediated by housing and clothing, in addition to behavioural adaptations centered on avoiding periods of extreme heat (e.g., mid-day). Night-time cold stress is often mediated through the use of strategies like windbreaks, fire, and kleptothermic sleeping arrangements (Frisancho, 1993). Hot-wet environments (like those of the Aeta foragers and Andaman Islanders) offer less potential for the application of human adaptive techniques when compared to hot-dry or cold environments (Hanna & Brown, 1983). In these environments evaporative cooling has reduced effectiveness due to increased humidity, while solar radiation is less of an issue (Perry & Dominy, 2009; Roberts et al., 2016). To mediate this culturally, houses with high ventilation are often used, which may include elevated platforms. Clothing is typically ineffective in decreasing heat gain in hot-wet environments; the most effective strategy is to wear none at all.

It has been argued that the ability to control the temperature of our environment, by creating a favourable microenvironment, removes the stimulus to adapt and that humans possess greater means of culturally adapting to cold rather than heat (Tipton et al., 2008). As reflected above, it is easier to culturally modify yourself and your environment to stay warm than to cool yourself or your environment, especially in hunter-gatherer groups. If heat stress cannot be effectively mediated by the mechanisms described above, natural selection may act upon the body, and if a particular stature is more advantageous in a specific climate, the mean should shift towards that height and the range of statures within the populations should reduce. If this is true, we would expect the range of statures within a population to be associated with temperature, and for those in the hottest regions to display the most limited variability in stature, as was found in this thesis for both variance and CV of femoral length. The potential association of within-population variance in stature and temperature appears to be unstudied, offering an interesting avenue for continued research.

6.4. Evidence for a Neutral Signal in Femoral Variability in Shape

Adaptationist explanations for morphological variation in the skeleton are dominant within the discipline of biological anthropology (Athreya & Ackermann, 2019), and beyond, such that neutral processes tend to be minimally considered as potential drivers of variation (Gould & Lewontin, 1979; Weaver, 2018). Studies of the skull (Betti et al., 2009; Mancia et al, 2007; Von Cramon-Taubadel & Lycett, 2008), dental traits (Hanihara, 2008), and the pelvis (Betti et al., 2013) have found adherence to models of serial founder effects in patterns of diversity, such that within-population variation decreases with increased distance from Africa. This suggests that there is a significant neutral component to the morphology of these elements. To assess whether a neutral signal is preserved in the femur, this thesis asked if there is a similar linear relationship to those found by these previous studies between distance from an African origin of expansion and femoral within-population morphological variation.

This thesis did not find significant evidence for an Out of Africa signal. No statistically significant relationships were found between distance from the estimated origin in Africa and any of the within-population shape variability measures. Femoral shape does not show a significant decrease in within-population variation with increasing distance from Africa. That a neutral signal of demographic history in femoral morphology was not identified is consistent with previous research based on linear measurements (Betti et al., 2012).

However, there is potential that the absence of significant results is the product of the underpowered nature of the analyses. Potential patterns emerge when looking at the coefficients of determination and slopes. Though the regressions did not produce a significant p-value, proximal shape variability in the whole sample and female subset and distal variability in the male subset had relatively high R^2 and slopes which indicate a pattern of decreasing within-population variability with increasing distance from Africa, as would be expected under a neutral model. That all measures of proximal and distal variability, and nearly all measures of whole femur variability, possessed negative slopes further indicates the need to repeat these analyses on a larger sample size which includes more populations.

This thesis identified some potential sex-specific differences in the GM results, specifically that female <u>proximal</u> variability potentially patterns with OoA distance while male variability does not, and that male <u>distal</u> variability may pattern with OoA distance, while female variability does not. A potential adaptive explanation could be that, due to constraints on pelvic morphology imposed by childbirth, the female proximal femur has limited ability to respond to the environment, therefore maintaining evolutionary signals more than the male proximal femur (where the pelvis is not under these constraints). Potential differences in hip joint variability between sexes appears to be unstudied. If the constraints placed on the female pelvis does impact proximal femoral variability, I would expect a similar decrease in variability to be present on the other surface of the joint, the acetabulum.

A final interesting pattern coming out of the shape and distance analyses is that shaft variability consistently displayed a negative relationship with OoA distance (populations further from Africa appear to display more variation in shaft shape). Additionally, male shaft variability displayed a relatively high coefficient of determination with OoA distance. As discussed in the literature review, long bone diaphyses are responsive to mechanical loading (Ruff et al., 2006; Ruff, 2018), and therefore, femoral diaphyseal shape may be reflective of activity (Stock, 2006; Stock & Buck, 2010; Stock & Pfeiffer, 2001/2004). It may be that the patterns in shaft variability are a product of differences in consistency of mobility/activity between individuals, with some populations having individuals participate equally in the same activities, while other groups may display significant variation in levels and types of activity between individuals. Groups which participate in consistent activities between individuals might have low variability in diaphyseal shape, while those with high variation in individual activity level might display higher variability. Data on within-population variability in activity was not collected in this thesis but it may be that increased environmental diversity could be associated with increased individual level diversification of activity patterns, which may in turn produce increased within-population variation in shaft morphology.

6.5. Evidence for Climate Linked Femoral Variability in Shape

It has been previously suggested that the absence of a neutral signal in within-population variability in long bone morphology could be the result of overwriting by climate-based selective processes (Betti et al., 2012). To assess if this may be true for this thesis, associations of climatic variables and within-population variability measures were tested for. As with the previous analysis of within-population variability and OoA distance, no significant results were returned. No combination of climatic variables was found to be a significant predictor of any measure of within-population femoral variability in the whole sample.

A previous study using linear measurements found that minimum temperature was predictive of femoral phenotypic variability (Betti et al., 2012). That this thesis did not return equivalent results may be due to the use of Geometric Morphometrics instead of linear measurements. Additionally, the use of GM likely captured a more refined depiction of shape, potentially adding noise or increased complexity to the data, preventing climatic relationships from being conclusively identified. Size is likely highly related to climate. Betti et al. (2012) size-adjusted their measurements by dividing each measurement by the geometric mean of all measurements of the same bone. During the GM process Procrustes superimposition similarly removes size variation by scaling landmark configurations to centroid size 1. It is possible that the Procrustes superimposition more thoroughly removes size variation than other methods, thus weakening any potential relationship of climate with shape. Subtle variation in GM data may correspond to thermoregulatory-linked changes, but likely as a secondary consequence of variation in size or proportion. That size and climatic factors are related was reflected in the linear analyses where femoral head diameter was significantly related to all climate variables tested and femoral length to most variables. Variability in femoral length was also impacted by temperature. This suggests that femoral shape, without size, may not be impacted by climatic factors enough to produce an identifiable signal.

6.6. The Relevancy of a Modular Approach

Both the neutral and climate variation research questions asked if signals were stronger in particular regions of the femur. While this is inconclusive given the non-significant nature of the results, there does appear to be differences in variability across the modules. For example, populations with the most variation in proximal module shape do not necessarily have the most distal or whole module variability.

The modular approach was able to identify patterns that would have gone undetected if only whole bone shape was considered. Patterns appear in the modular data which do not appear in the whole bone. For example, whole landmark femoral shape variability appeared to have a negative relationship with OoA distance, while shaft variability appeared to be positively associated with the same variable. This is unsurprising given research that suggests varying levels of constraint and plasticity along long bones, and that the likelihood of bone alteration may also vary based on the factor involved (e.g., Nadell & Shaw, 2016; Pearson & Lieberman, 2004; Ruff et al., 2006). It may be relevant to apply similar approaches which treat the femur as both modular *and* as a whole element in future studies, as it may lend itself to piecing apart the complex factors influencing morphology.

6.7. What May be Producing Unexplained Variation?

The final question this thesis asks is: What might be the cause of variation left unexplained by neutral, OoA-linked, processes and climatic factors?

This study improves upon previous research by restricting the sample to include only hunter-gatherers, removing confounding variables which come about from mixing groups with highly variable subsistence strategies (e.g., agriculturalists, hunter-gatherers, and industrial populations). However, there is significant variation in the activities and intensity of mobility seen in the lifeways of hunter-gatherers (Kelly, 2013). Differing population activity patterns, and the subsequent remodeling of bone in response to loading, could have contributed to erasing evidence of climatic signals on the femur that would otherwise have been identifiable (Stock, 2006; Stock and Pfeiffer, 2001). Similarly, activity could also have prevented the effects of demographic history (i.e., a neutral signal) from being readily identifiable in the femur, whereas activity would likely have a limited role in shaping some of the elements where a neutral signal has been identified (e.g., the skull).

Neutral processes, which would not manifest as decreasing variability with increasing distance from Africa, may also impact femoral shape. For example, gene flow (the movement of genes in or out of a population) may increase or decrease variation without groups moving geographically (Weaver, 2018). Novel genetic mutations may also produce or reduce variation in a trait (Weaver, 2018). These other neutral processes may produce patterns that would not be identified via the methods applied in this study. Other studies (e.g., Betti et al., 2013) have examined the potential impact of gene flow by examining apportionment of variance. If the relative apportionment of within- and between-population phenotypic variance at differing levels is like those for neutral genetic markers, this might suggest that global patterns of variation can be attributed to neutral evolutionary processes (Betti et al., 2013). This would be relevant to explore in future studies.

7. Conclusion

This study aimed to differentiate climatic and ‘neutral’ morphological signatures in the human femur, as this element is impacted by a complex set of influences and is important to anthropological research. This was achieved by examining morphological variation, derived from geometric morphometric data and traditional linear measurements, in human femora from a globally distributed sample of archaeological hunter-gatherers. Searching for signals of selective and neutral processes, statistical analyses were used to determine the associations of measures of within-population phenotypic diversity and individual/group linear dimensions to measures of distance from an estimated origin in Africa and climatic variables.

7.1. Findings and Contributions

Analysis of the linear data produced statistically significant results. On the individual-level, femoral head diameter was found to be negatively impacted by temperature, precipitation, and net primary productivity. Absolute latitude and temperature seasonality had a positive association with femoral head diameter. Individuals further from the equator displayed larger femoral heads. There were also significant positive associations between mean femoral head diameter, temperature seasonality and absolute latitude, and negative associations of mean femoral head diameter to net primary productivity and temperature, though only in the whole sample and the male subsample. These results suggest adherence to Bergmann’s rule (1848). As temperature decreases (or absolute latitude increases), body mass increases, likely to reduce surface area to volume ratios to as a form of adaptive compensation to thermal stress.

On the individual-level, as with femoral head diameter, femoral length was found to be negatively impacted by temperature, precipitation, and net primary productivity, and positively associated with temperature seasonality and latitude. This may again be a reflection of Bergmann's rule, at least on the individual level. Mean femoral length had a negative association with precipitation and net primary productivity. However, it was argued that these relationships are likely a product of the inclusion of two small bodied/tropical rainforest forager groups, the Andaman Islanders and Aeta foragers. Strong climate-based selection for small body size among these groups may have overwritten any other more subtle variation that might be found among the other populations. It was also argued that Allen's rule could not be directly applied to this data as the tibia, which is likely more impacted by climatic stress, was not included, making assumptions about limb length speculative.

Within-population variance in femoral length was found to be significantly associated with maximum temperature, even when measurements were size corrected via the use of coefficients of variation. This was suggested to be a product of technological and behavioural adaptations being less-effective in hot climates (especially hot-wet environments), increasing stabilizing selection acting on these populations compared to those in colder environments, and limiting the range of stature within the populations as a result.

This thesis did not identify a statistically significant relationship between distance from an estimated African origin and within-population shape variation. This was true for the whole bone and for each of the modules. However, an overall pattern of decreasing within-population variation with increasing OoA distance was identified in the whole femur and the proximal and distal modules. The converse pattern was identified for diaphyseal within-population variation.

Sex-specific patterns, with female proximal variation and male distal variation being close to significance and possessing relatively high coefficients of determination, were also identified.

For within-population variation and climate, no statistically significant relationships were identified. This was unexpected given previous research which had found a significant relationship between femoral within-population variance and minimum temperature (Betti et al., 2012). However, the difference may be a product of the methodologies employed as this thesis used GM data, while Betti et al.'s study utilized size-adjusted linear measurements (2012). Overall, these results suggested that a neutral signal is not evident in femoral morphology, or one could not be identified with the methods employed. Instead, given the results of the linear data analysis, it may be that the influence of climatic factors has overwritten any neutral signals.

Ultimately, femoral morphology is the result of a complex set of influences, including genetics, plasticity, population adaptation, and more. Despite not finding concrete evidence for a neutral signal, this thesis contributes to a growing body of research aiming to unseat the automatic assumption that adaptation by natural selection is the primary, or most important, driver of variation in morphology, emphasizing the importance of considering neutral non-selective processes and embracing complexity. In addition, it identified interesting patterns that may indicate a weak neutral signal, which should be explored with a more robust set of groups. Another contribution this thesis makes is the application of a modular geometric morphometrics approach to long bone morphology. This methodology may be useful in future studies aiming to parse out the impacts of various factors at different regions.

7.2. Limitations and Recommendations

This research faced a number of limitations with statistical power and patchy coverage being the most evident. As discussed, while the original sample size of 174 for the GM data may not appear small, because the questions asked concern within-population variability, sample size reduced to 11, and then again to 6 for the sex-divided samples. This reduction in sample size leads to a decrease in the statistical power of the tests used to analyse the GM data and an increased likelihood of type II error. There was potential that basing interpretations solely on statistical significance would lead to failure to recognize interesting patterns (Carlson, 2017). To account for this in this thesis, emphasis was placed on investigating patterns in spite of non-statistically significant results.

A potentially more satisfactory solution would be to increase the number of groups under analysis, as this would increase the statistical power of the analyses, decreasing the potential for type II error and instilling more confidence in the results produced. This would have the added benefits of filling in the regions that were not well covered in this thesis, specifically Europe and large parts of Asia, and allowing for sex-separated analysis of climatic impacts. It would be important to ensure the sample sizes of each individual group are large enough to accurately capture within-group variation and that confounding factors are adequately controlled for. This may mean including only groups with hunter-gatherer-forager lifeways and imposing a minimal number of individuals for inclusion, as was the case in this thesis.

Ideally, when including individuals from multiple sites in the same group, site specific coordinates could have been used for the analyses looking at individual-level effects of climate on linear measurements, as there may have been some interesting patterns identifiable there. For example, studies have examined similar samples of Jomon foragers and found that the group exhibits a north to south cline in body size (Fukase et al., 2012). If future studies apply a similar methodology to this thesis, this may be relevant information to collect and analyse. This was not possible in the current project as, in most cases, specific sites for individuals were unknown.

While identified as negligible in this thesis via the Procrustes ANOVA, a final area which may be improved in future research is the introduction of error during the landmarking process. Some measurement error is inevitable, but it could be reduced with practice as this would build familiarity with the landmarking protocol. A potential suggestion would be to conduct two full landmark trials for each individual and take the average of the two as the final configuration.

7.3. Future Research

The results of this thesis open a number of interesting avenues for future research. As already mentioned, it would be prudent to increase the number of groups included and rerun the GM analyses with the aim of increasing statistical power, potentially producing statistically significant results in addition to investigating the interesting patterns already identified.

There is also a wealth of potential applications of the GM data itself. Though not analysed in this project, the individual PC scores used to calculate the within-population variation variables could be analysed to examine how shape differs in relation to climatic variables and/or neutral distances. Mean PC scores (capturing average shape in the population) could also be used to look at population-level effects. The GM data could be used to consider the impacts of neutral processes outside of OoA serial founder effects. For example, one could examine the relative apportionment of within- and between-population morphological variance at differing geographic levels to see if it patterns in a comparable way to neutral genetic markers (as Betti et al., 2013 did for the pelvis).

For the linear data, one of the results that deserves further exploration is the relationship of within-population variation in femoral length (as a proxy for stature) and temperature. Any potential association of stature variance and temperature appears to be unstudied. It would be interesting to determine if this pattern persists in a larger sample, and if behavioural and technological adaptation buffering temperature stress, or a lack of effectiveness increasing stabilizing selection, could be a driving factor. As with the GM data, expanding this research would involve increasing the number of groups. However, because linear measurement is more common in anthropological research than digitization, this would likely prove a much easier task than collecting more digital models.

8. References

Adams, D. C., Collyer, M. L., Kaliontzopoulou, A., & Baken, E. K. (2022). Geomorph: Software for geometric morphometric analyses. (R package version 4.0.4.). https://cran.r-project.org/package=geomorph.

Adams, D. C., Rohlf, F. J., & Slice, D. E. (2013). A field comes of age: Geometric morphometrics in the 21st century. *Hystrix, the Italian Journal of Mammalogy, 24*(1). https://doi.org/10.4404/hystrix-24.1-6283

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In B. Petrov N. & F. Caski (Eds.), In *Second International Symposium on Information Theory* (pp. 267–281).

Allen, J. A. (1877). The influence of physical conditions in the genesis of species. *Radic Rev, 1,* 108–140.

Alves-Cardoso, F., & Campanacho, V. (2022). To Replicate, or Not to Replicate? The Creation, Use, and Dissemination of 3D Models of Human Remains: A Case Study from Portugal. *Heritage, 5*, 1637–1658. https://doi.org/10.3390/ heritage5030085

American Association of Biological Anthropologists. (2003). Code of Ethics of the American Association of Physical Anthropologists. https://physanth.org/documents/3/ethics.pdf

American Association of Biological Anthropologists. (2019). Assessing the Ethics Needs & Interests of the AAPA Membership Survey. https://physanth.org/documents/206/AAPA_Ethics_Survey_Report_Jan_2019.pdf

Anderson, J. Y., & Trinkaus, E. (1998). Patterns of sexual, bilateral and interpopulational variation in human femoral neck-shaft angles. *Journal of Anatomy, 192*(2), 279–285. https://doi.org/10.1046/j.1469-7580.1998.19220279.x

Arkell, A. J., & Ucko, P. J. (1965). Review of Predynastic development in the Nile Valley. *Current Anthropology, 6*(2), 145–166. https://doi.org/10.1086/200578

Athreya, S., & Ackermann, R. R. (2019). Colonialism and narratives of human origins in Asia and Africa. In *Interrogating Human Origins*. Routledge.

Auerbach, B. M. (2008). Human skeletal variation in the New World during the Holocene: Effects of climate and subsistence across geography and time - Part I [Ph.D., The Johns Hopkins University]. In ProQuest Dissertations and Theses. https://search.proquest.com/docview/304614898/abstract/CF1F9356D9DC4BE2PQ/1

Auerbach, B. M., & Ruff, C. B. (2004). Human body mass estimation: A comparison of morphometric and mechanical methods. *American Journal of Physical Anthropology, 125*(4), 331–342. https://doi.org/10.1002/ajpa.20032

Auerbach, B. M., & Ruff, C. B. (2006). Limb bone bilateral asymmetry: Variability and commonality among modern humans. *Journal of Human Evolution, 50*(2), 203–218. https://doi.org/10.1016/j.jhevol.2005.09.004

Baken, E. K., Collyer, M. L., Kaliontzopoulou, A., & Adams, D. C. (2021). geomorph v4.0 and gmShiny: Enhanced analytics and a new graphical interface for a comprehensive morphometric experience. *Methods in Ecology and Evolution, 12,* 2355-2363.

Bandelt, H.-J., Kong, Q.-P., Richards, M., & Macaulay, V. (2006). Estimation of Mutation Rates and Coalescence Times: Some Caveats. In H.-J. Bandelt, V. Macaulay, & M. Richards (Eds.), *Human Mitochondrial DNA and the Evolution of Homo sapiens* (pp. 47–90). Springer. https://doi.org/10.1007/3-540-31789-9_4

Bar-Or, O., Lundegren., H. M, & Buskirk, E. R. (1969). Heat tolerance of exercising obese and lean women. *Journal of Applied Physiology*, *26*(4). https://doi.org/10.1152/jappl.1969.26.4.403

Bardua, C., Felice, R. N., Watanabe, A., Fabre, A. C., & Goswami, A. (2019). A Practical Guide to Sliding and Surface Semilandmarks in Morphometric Analyses. *Integrative Organismal Biology*, *1*(1), obz016. https://doi.org/10.1093/iob/obz016

Bass, W. M. (2005). *Human Osteology: A Laboratory and Field Manual* (5th ed. edition). Missouri Archaeological Society.

Benítez, H. A., Püschel, T., Lemic, D., Čačija, M., Kozina, A., & Bažok, R. (2014). Ecomorphological Variation of the Wireworm Cephalic Capsule: Studying the Interaction of Environment and Geometric Shape. *PLOS ONE, 9*(7), e102059. https://doi.org/10.1371/journal.pone.0102059

Bergmann, C. (1848). *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Größe*. Göttingen: Vandenhoeck und Ruprecht. http://archive.org/details/bub_gb_EHo-AAAAcAAJ

Betti, L., Balloux, F., Amos, W., Hanihara, T., & Manica, A. (2009). Distance from Africa, not climate, explains within-population phenotypic diversity in humans. *Proceedings of the Royal Society B: Biological Sciences, 276*(1658), 809–814. https://doi.org/10.1098/rspb.2008.1563

Betti, L., Balloux, F., Hanihara, T., & Manica, A. (2010). The relative role of drift and selection in shaping the human skull. *American Journal of Physical Anthropology, 141*(1), 76–82. https://doi.org/10.1002/ajpa.21115

Betti, L., & Manica, A. (2018). Human variation in the shape of the birth canal is significant and geographically structured. *Proceedings of the Royal Society B: Biological Sciences, 285*(1889), 20181807. https://doi.org/10.1098/rspb.2018.1807

Betti, L., Von Cramon-Taubadel, N., & Lycett, S. J. (2012). Human Pelvis and Long Bones Reveal Differential Preservation of Ancient Population History and Migration Out of Africa. *Human Biology, 84*(2), 139–152. https://doi.org/10.3378/027.084.0203

Betti, L., von Cramon-Taubadel, N., Manica, A., & Lycett, S. J. (2013). Global Geometric Morphometric Analyses of the Human Pelvis Reveal Substantial Neutral Population History Effects, Even across Sexes. *PLoS ONE, 8*(2), e55909. https://doi.org/10.1371/journal.pone.0055909

Betti, L., von Cramon-Taubadel, N., Manica, A., & Lycett, S. J. (2014). The interaction of neutral evolutionary processes with climatically-driven adaptive changes in the 3D shape of the human os coxae. *Journal of Human Evolution, 73*, 64–74. https://doi.org/10.1016/j.jhevol.2014.02.021

Betti, L., Lycett, S. J., von Cramon-Taubadel, N., & Pearson, O. M. (2015). Are human hands and feet affected by climate? A test of Allen's rule. *American Journal of Physical Anthropology, 158*(1), 132–140. https://doi.org/10.1002/ajpa.22774

Beyer, R. M., Krapp, M., & Manica, A. (2020). High-resolution terrestrial climate, bioclimate and vegetation for the last 120,000 years. *Scientific Data, 7*(1), 236. https://doi.org/10.1038/s41597-020-0552-1

Beyin, A., Hall, J., & Day, C. A. (2019). A Least Cost Path Model for hominin dispersal routes out of the East African Rift region (Ethiopia) into the Levant. *Journal of Archaeological Science: Reports, 23*, 763–772. https://doi.org/10.1016/j.jasrep.2018.11.024

Bookstein, F. L. (1992). *Morphometric Tools for Landmark Data: Geometry and Biology*. Cambridge University Press. https://doi.org/10.1017/CBO9780511573064

Bookstein, F. L. (1997). Landmark methods for forms without landmarks: Morphometrics of group differences in outline shape. *Medical Image Analysis, 1*(3), 225–243. https://doi.org/10.1016/S1361-8415(97)85012-8

Bridges, L. E. (1948). *Uttermost Part of the Earth*. Hodder & Stoughton.

British Association of Biological Anthropology and Osteoarchaeology. (2019). BABAO recommendations on the ethical issues surrounding 2D and 3D digital imaging of human remains. https://www.babao.org.uk/assets/Uploads/BABAO-Digital-imaging-code-2019.pdf

Bruns, W., Bruce, M., Prescott, G., & Maffulli, N. (2002). Temporal trends in femoral curvature and length in medieval and modern Scotland. *American Journal of Physical Anthropology, 119*(3), 224–230. https://doi.org/10.1002/ajpa.10113

Brunton, G., & Caton-Thompson, G. (1928). *The Badarian civilisation and predynastic remains near Badari*. British School of Archaeology in Egypt.

Büchler, L., Tannast, M., Siebenrock, K. A., & Schwab, J. M. (2018). Biomechanics of the Hip. In K. A. Egol & P. Leucht (Eds.), *Proximal Femur Fractures* (pp. 9–15). Springer International Publishing. https://doi.org/10.1007/978-3-319-64904-7_2

Buck, L. T., De Groote, I., Hamada, Y., Hassett, B. R., Ito, T., & Stock, J. T. (2019). Evidence of different climatic adaptation strategies in humans and non-human primates. *Scientific Reports*, *9*(1), 11025. https://doi.org/10.1038/s41598-019-47202-8

Buck, L. T., De Groote, I., Hamada, Y., & Stock, J. T. (2018). Humans preserve non-human primate pattern of climatic adaptation. *Quaternary Science Reviews*, *192*, 149–166. https://doi.org/10.1016/j.quascirev.2018.05.032

Buikstra, J. E., & Ubelaker, D. H. (1994). *Standards for Data Collection from Human Skeletal Remains* (Spi edition). Arkansas Archeological Survey.

Cameron, M. E. (2016). *Behaviour, Biology, and Ecology: Investigating the Impact of Ecological Constraints on Prehistoric Southern African Skeletal Phenotypes* [PhD]. University of Cambridge.

Canadian Association for Biological Anthropology. (2019). Code of Ethics. https://caba-acab.net/sites/default/files/basic-page/capa-acap_code_of_ethics_-_jan_2019.pdf

Canadian Institutes of Health Research, Natural Sciences and Engineering Research Council of Canada, and Social Sciences and Humanities Research Council. (2018). Tri-Council Policy Statement: Ethical Conduct for Research Involving Humans. https://ethics.gc.ca/eng/documents/tcps2-2018-en-interactive-final.pdf

Carlson, D. L. (2017). *Quantitative Methods in Archaeology Using R*. Cambridge University Press.

Carlson, K. J., Grine, F. E., & Pearson, O. M. (2007). Robusticity and sexual dimorphism in the postcranium of modern hunter-gatherers from Australia. *American Journal of Physical Anthropology*, *134*(1), 9–23. https://doi.org/10.1002/ajpa.20617

Chapin, F. S., & Eviner, V. T. (2014). 10.6—Biogeochemical Interactions Governing Terrestrial Net Primary Production. In H. D. Holland & K. K. Turekian (Eds.), *Treatise on Geochemistry* (Second Edition) (pp. 189–216). Elsevier. https://doi.org/10.1016/B978-0-08-095975-7.00806-8

Chen, J.H., Liu, C., You, L., & Simmons, C. A. (2010). Boning up on Wolff's Law: Mechanical regulation of the cells that make and maintain bone. *Journal of Biomechanics*, *43*(1), 108–118. https://doi.org/10.1016/j.jbiomech.2009.09.016

Child, S. L., & Cowgill, L. W. (2017). Femoral neck-shaft angle and climate-induced body proportions. *American Journal of Physical Anthropology*, *164*(4), 720–735. https://doi.org/10.1002/ajpa.23311

Churchill, S. E. (1996). Particulate versus integrated evolution of the upper body in late pleistocene humans: A test of two models. *American Journal of Physical Anthropology, 100*(4), 559–583. https://doi.org/10.1002/(SICI)1096-8644(199608)100:4<559::AID-AJPA9>3.0.CO;2-L

Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F., & Ranzuglia, G. (2008). MeshLab: An Open-Source Mesh Processing Tool. 8.

Collins, H. B. (1984). History of research before 1945. In W. C. Sturtevant & D. Damas (Eds.), *Handbook of North American Indians* (Vol. 5, pp. 8–16). Smithsonian Institution Press.

Cowgill, L. W. (2014). Postcranial growth and development of immature skeletons from Point Hope, Alaska. In C. E. Hilton, B. M. Auerbach, & L. W. Cowgill (Eds.), *The Foragers of Point Hope* (pp. 212–232). Cambridge University Press. https://doi.org/10.1017/CBO9781139136785.014

Dabbs, G. R. (2011). Health status among prehistoric Eskimos from Point Hope, Alaska. *American Journal of Physical Anthropology, 146*(1), 94–103. https://doi.org/10.1002/ajpa.21556

Davies, T. G., & Stock, J. T. (2014). Human Variation in the Periosteal Geometry of the Lower Limb: Signatures of Behaviour Among Human Holocene Populations. In K. J. Carlson & D. Marchi (Eds.), *Reconstructing Mobility: Environmental, Behavioral, and Morphological Determinants* (pp. 67–90). Springer US. https://doi.org/10.1007/978-1-4899-7460-0_5

Davies, T., Shaw, C., & Stock, J. (2012). A test of a new method and software for the rapid estimation of cross-sectional geometric properties of long bone diaphyses from 3D laser surface scans. *Archaeological and Anthropological Sciences, 4*, 277–290. https://doi.org/10.1007/s12520-012-0101-8

De Groote, I. (2008). *A comprehensive analysis of long bone curvature in Neanderthals and Modern Humans using 3D morphometrics* [PhD]. University College London.

De Groote, I. (2011). Femoral curvature in Neanderthals and modern humans: A 3D geometric morphometric analysis. *Journal of Human Evolution, 60*(5), 540–548. https://doi.org/10.1016/j.jhevol.2010.09.009

de la Cova, C. (2019). Marginalized bodies and the construction of the Robert J. Terry anatomical skeletal collection. In M. Mant & A. J. Holland (Eds.), *Bioarchaeology of Marginalized People* (pp. 133–155). Elsevier. https://doi.org/10.1016/B978-0-12-815224-9.00007-5

Doershuk, L. J., Saers, J. P. P., Shaw, C. N., Jashashvili, T., Carlson, K. J., Stock, J. T., & Ryan, T. M. (2019). Complex variation of trabecular bone structure in the proximal humerus and femur of five modern human populations. *American Journal of Physical Anthropology, 168*(1), 104–118. https://doi.org/10.1002/ajpa.23725

Earth Resources Observation and Science Center/U.S. Geological Survey/U.S. Department of the Interior. (1997). *USGS 30 ARC-second Global Elevation Data, GTOPO30*. [Data Set]. https://doi.org/10.5065/A1Z4-EE71.

Errickson, D., Grueso, I., Griffith, S. J., Setchell, J. M., Thompson, T. J. U., Thompson, C. E. L., & Gowland, R. L. (2017). Towards a Best Practice for the Use of Active Non-contact Surface Scanning to Record Human Skeletal Remains from Archaeological Contexts. *International Journal of Osteoarchaeology, 27*(4), 650–661. https://doi.org/10.1002/oa.2587

Faniel, I. M., Austin, A., Kansa, E., Kansa, S. W., France, P., Jacobs, J., Boytner, R., & Yakel, E. (2018). Beyond the Archive: Bridging Data Creation and Reuse in Archaeology. *Advances in Archaeological Practice*, *6*(2), 105–116. https://doi.org/10.1017/aap.2018.2

Franklin, D., Cardini, A., & Oxnard, C. E. (2010). A geometric morphometric approach to the quantification of population variation in sub-Saharan African crania. *American Journal of Human Biology*, *22*(1), 23–35. https://doi.org/10.1002/ajhb.20908

Frisancho, A. R. (1993). *Human Adaptation and Accommodation*. University of Michigan.

Frost, H. M. (2003). Bone's mechanostat: A 2003 update. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology, 275A*(2), 1081–1101. https://doi.org/10.1002/ar.a.10119

Fukase, H., Wakebe, T., Tsurumoto, T., Saiki, K., Fujita, M., & Ishida, H. (2012). Geographic variation in body form of prehistoric Jomon males in the Japanese archipelago: Its ecogeographic implications. *American Journal of Physical Anthropology*, *149*(1), 125–135. https://doi.org/10.1002/ajpa.22112

Galland, M., & Friess, M. (2016). A three-dimensional geometric morphometrics view of the cranial shape variation and population history in the New World. *American Journal of Human Biology, 28*(5), 646–661. https://doi.org/10.1002/ajhb.22845

Garson, J. G. (1886). On the Inhabitants of Tierra del Fuego. *The Journal of the Anthropological Institute of Great Britain and Ireland, 15*, 141–160. https://doi.org/10.2307/2841569

Gillespie, J. H. (1991). *The causes of molecular evolution*. Oxford University Press.

Glassow, M. A. (1977). Archaeological Overview of the Northern Channel Islands California Including Santa Barbara Island. Western Archaeological Center National Park Service.

Gould, S. J., & Lewontin, R. C. (1979). The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme. *Proceedings of the Royal Society of London. Series B, Biological Sciences, 205*(1161), 581–598.

Grine, F. E., Jungers, W. L., Tobias, P. V., & Pearson, O. M. (1995). Fossil Homo femur from Berg Aukas, northern Namibia. *American Journal of Physical Anthropology*, *97*(2), 151–185. https://doi.org/10.1002/ajpa.1330970207

Gunz, P., Mitteroecker, P., & Bookstein, F. L. (2005). Semilandmarks in Three Dimensions. In D. E. Slice (Ed.), *Modern Morphometrics in Physical Anthropology* (pp. 73–98). Springer US. https://doi.org/10.1007/0-387-27614-9_3

Gustas, R., & Supernant, K. (2019). Coastal migration into the Americas and least cost path analysis. *Journal of Anthropological Archaeology*, *54*, 192–206. https://doi.org/10.1016/j.jaa.2019.04.006

Habu, J. (2014). Early sedentism in East Asia: From Late Paleolithic to early agricultural societies in Insular East Asia. In C. Renfrew & P. Bahn (Eds.), *The Cambridge World Prehistory* (pp. 724–741). Cambridge University Press.

Hahn, M. W. (2008). Toward a Selection Theory of Molecular Evolution. *Evolution*, *62*(2), 255–265. https://doi.org/10.1111/j.1558-5646.2007.00308.x

Hanihara, T. (2008). Morphological variation of major human populations based on nonmetric dental traits. *American Journal of Physical Anthropology*, *136*(2), 169–182. https://doi.org/10.1002/ajpa.20792

Hanna, J. M., & Brown, D. E. (1983). Human Heat Tolerance: An Anthropological Perspective. *Annual Review of Anthropology*, *12*(1), 259–284. https://doi.org/10.1146/annurev.an.12.100183.001355

Harries, J., Fibiger, L., Smith, J., Adler, T., & Szöke, A. (2018). Exposure: The ethics of making, sharing and displaying photographs of human remains. *Human Remains and Violence: An Interdisciplinary Journal*, *4*(1), 3–24. https://doi.org/10.7227/HRV.4.1.2

Harvati, K., & Weaver, T. D. (2006). Human cranial anatomy and the differential preservation of population history and climate signatures. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology*, *288A*(12), 1225–1233. https://doi.org/10.1002/ar.a.20395

Hassan, F. A. (1988). The Predynastic of Egypt. *Journal of World Prehistory*, *2*(2), 135–185. https://doi.org/10.1007/BF00975416

Hassett, B. R., Rando, C., Bocaege, E., Alfonso Durruty, M., Hirst, C., Smith, S., Ferreira Ulguim, P., White, S., & Wilson, A. (2018). Transcript of WAC 8 Digital Bioarchaeological Ethics Panel Discussion, 29 August 2016 and Resolution on Ethical Use of Digital Bioarchaeological Data. *Archaeologies*, *14*(2), 317–337. https://doi.org/10.1007/s11759-018-9343-0

Hayes, M. G., Coltrain, J., & O'Rourke, D. H. (2005). Molecular archaeology of the Dorset, Thule and Sadlermiut. In P. D. Sutherland (Ed.), *Contributions to the Study of the Dorset Palaeo-Eskimos* (pp. 11–32). University of Ottawa Press. https://muse.jhu.edu/book/65398

Hicks, D. (2020). *The Brutish Museums The Benin Bronzes, Colonial Violence and Cultural Restitution*. Pluto Press, London UK.

Hildebrand, M., & Goslow, G. E. (2001). *Analysis of vertebrate structure* / Milton Hildebrand, G.E. Goslow, Jr. ; Prinicple illustrator, Viola Hildebrand. (5th ed.). Wiley.

Hilton, C. E., Auerbach, B. M., & Cowgill, L. W. (2014). Introduction: Humans on the edge of the Alaskan Arctic. In C. E. Hilton, B. M. Auerbach, & L. W. Cowgill (Eds.), *The Foragers of Point Hope* (pp. 1–8). Cambridge University Press. https://doi.org/10.1017/CBO9781139136785.004

Hirst, C. S., White, S., & Smith, S. E. (2018). Standardisation in 3D Geometric Morphometrics: Ethics, Ownership, and Methods. *Archaeologies, 14*(2), 272–298. https://doi.org/10.1007/s11759-018-9349-7

Holland, E. J. (2007). *Ethnographic data to understand Sadlermiut childhood* [Masters thesis]. University of Manitoba.

Holliday, T. W., & Hilton, C. E. (2010). Body proportions of circumpolar peoples as evidenced from skeletal data: Ipiutak and Tigara (Point Hope) versus Kodiak Island Inuit. *American Journal of Physical Anthropology, 142*(2), 287–302. https://doi.org/10.1002/ajpa.21226

Hollowell, J., & Nicholas, G. (2008). Intellectual Property Issues in Archaeological Publication: Some Questions to Consider. *Archaeologies, 4*(2), 208–217. https://doi.org/10.1007/s11759-008-9073-9

Hublin, J.J., Ben-Ncer, A., Bailey, S. E., Freidline, S. E., Neubauer, S., Skinner, M. M., Bergmann, I., Le Cabec, A., Benazzi, S., Harvati, K., & Gunz, P. (2017). New fossils from Jebel Irhoud, Morocco and the pan-African origin of Homo sapiens. *Nature (London), 546*(7657), 289–292. https://doi.org/10.1038/nature22336

Humphreys, A. J. B. (1972). *The type R settlements in the context of the later prehistory and early history of the Riet River Valley* [MA Thesis]. University of Cape Town.

Imamura, K. (1996). *Prehistoric Japan: New Perspectives on Insular East Asia*. University of Hawaii Press.

Ito, T., Nishimura, T. D., Hamada, Y., & Takai, M. (2015). Contribution of the maxillary sinus to the modularity and variability of nasal cavity shape in Japanese macaques. *Primates; Journal of Primatology*, *56*(1), 11–19. https://doi.org/10.1007/s10329-014-0440-4

James, G. D. (2018). Bergmann's and Allen's Rules. In *The International Encyclopedia of Biological Anthropology* (pp. 1–3). American Cancer Society. https://doi.org/10.1002/9781118584538.ieba0048

Jensen, J. D., Payseur, B. A., Stephan, W., Aquadro, C. F., Lynch, M., Charlesworth, D., & Charlesworth, B. (2019). The importance of the Neutral Theory in 1968 and 50 years on: A response to Kern and Hahn 2018. Evolution; International Journal of Organic *Evolution, 73*(1), 111–114. https://doi.org/10.1111/evo.13650

Katzmarzyk, P. T., & Leonard, W. R. (1998). Climatic influences on human body size and proportions: Ecological adaptations and secular trends. *American Journal of Physical Anthropology, 106*(4), 483–503. https://doi.org/10.1002/(SICI)1096-8644(199808)106:4<483::AID-AJPA4>3.0.CO;2-K

Kefi, R., Hechmi, M., Naouali, C., Jmel, H., Hsouna, S., Bouzaid, E., Abdelhak, S., Beraud-Colomb, E., & Stevanovitch, A. (2018). On the origin of Iberomaurusians: New data based on ancient mitochondrial DNA and phylogenetic analysis of Afalou and Taforalt populations. *Mitochondrial DNA Part A, 29*(1), 147–157. https://doi.org/10.1080/24701394.2016.1258406

Kelly, R. L. (2013). *The Lifeways of Hunter-Gatherers: The Foraging Spectrum*. Cambridge University Press. http://ebookcentral.proquest.com/lib/uvic/detail.action?docID=1139695

Kennett, D. J. (2005). *The Island Chumash: Behavioral Ecology of a Maritime Society*. Berkley and Los Angeles: The University of California Press.

Kern, A. D., & Hahn, M. W. (2018). The Neutral Theory in Light of Natural Selection. *Molecular Biology and Evolution, 35*(6), 1366–1371. https://doi.org/10.1093/molbev/msy092

Kimura, M. (1968). Evolutionary Rate at the Molecular Level. *Nature, 217*(5129), 624–626. https://doi.org/10.1038/217624a0

Kimura, M. (1983). *The Neutral Theory of Molecular Evolution*. Cambridge University Press.

Kimura, M., & Maruyama, T. (1971). Pattern of neutral polymorphism in a geographically structured population*. *Genetics Research, 18*(2), 125–131. https://doi.org/10.1017/S0016672300012520

King, J. L., & Jukes, T. H. (1969). Non-Darwinian Evolution. *Science, 164*(3881), 788–798. https://doi.org/10.1126/science.164.3881.788

Klingenberg, C. P. (2011). MorphoJ: An integrated software package for geometric morphometrics. *Molecular Ecology Resources, 11*(2), 353–357. https://doi.org/10.1111/j.1755-0998.2010.02924.x

Klingenberg, C. P. (2015). Analyzing Fluctuating Asymmetry with Geometric Morphometrics: Concepts, Methods, and Applications. *Symmetry, 7*(2), Article 2. https://doi.org/10.3390/sym7020843

Klingenberg, C. P. (2016). Size, shape, and form: Concepts of allometry in geometric morphometrics. *Development Genes and Evolution, 226*(3), 113–137. https://doi.org/10.1007/s00427-016-0539-2

Kozma, E. E., Webb, N. M., Harcourt-Smith, W. E. H., Raichlen, D. A., D’Août, K., Brown, M. H., Finestone, E. M., Ross, S. R., Aerts, P., & Pontzer, H. (2018). Hip extensor mechanics and the evolution of walking and climbing capabilities in humans, apes, and fossil hominins. *Proceedings of the National Academy of Sciences of the United States of America, 115*(16), 4134–4139. https://doi.org/10.1073/pnas.1715120115

Kroeber, A. (1943). *Peoples of the Philippines*. American Museum of Natural History.

Kurki, H. K. (2013). Bony pelvic canal size and shape in relation to body proportionality in humans. *American Journal of Physical Anthropology, 151*(1), 88–101. https://doi.org/10.1002/ajpa.22243

Lande, R. (1976). Natural Selection and Random Genetic Drift in Phenotypic Evolution. *Evolution, 30*(2), 314–334. https://doi.org/10.2307/2407703

Lans, A. M. (2021). Decolonize this collection: Integrating black feminism and art to re-examine human skeletal remains in museums. *Feminist Anthropology, 2*(1), 130–142. https://doi.org/10.1002/fea2.12027

Larsen, H. E., & Rainey, F. G. (1948). Ipiutak and the Arctic whale hunting culture. *Anthropological papers of the AMNH* ; v. 42. https://digitallibrary.amnh.org/handle/2246/65

Laurent, M., Antonio, L., Sinnesael, M., Dubois, V., Gielen, E., Classens, F., & Vanderschueren, D. (2014). Androgens and estrogens in skeletal sexual dimorphism. Asian Journal of *Andrology, 16*(2), 213–222. https://doi.org/10.4103/1008-682X.122356

Lazenby, R. A., Cooper, D. M. L., Angus, S., & Hallgrímsson, B. (2008). Articular constraint, handedness, and directional asymmetry in the human second metacarpal. *Journal of Human Evolution, 54*(6), 875–885. https://doi.org/10.1016/j.jhevol.2007.12.001

Leonardi, M., Hallett, E. Y., Beyer, R., Krapp, M., & Manica, A. (2022). pastclim: An R package to easily access and use paleoclimatic reconstructions. *BioRxiv,* 2022.05.18.492456. https://doi.org/10.1101/2022.05.18.492456

Lewton, K. L. (2012). Evolvability of the Primate Pelvic Girdle. *Evolutionary Biology, 39*(1), 126–139. https://doi.org/10.1007/s11692-011-9143-6

Lewton, K. L. (2015). Allometric scaling and locomotor function in the primate pelvis. American *Journal of Physical Anthropology, 156*(4), 511–530. https://doi.org/10.1002/ajpa.22696

Li, J. Z., Absher, D. M., Tang, H., Southwick, A. M., Casto, A. M., Ramachandran, S., Cann, H. M., Barsh, G. S., Feldman, M., Cavalli-Sforza, L. L., & Myers, R. M. (2008). Worldwide Human Relationships Inferred from Genome-Wide Patterns of Variation. *Science, 319*(5866), 1100–1104. https://doi.org/10.1126/science.1153717

Lothrop, S. K. (1928). *The Indians of Tierra del Fuego*. New York : Museum of the American Indian, Heye Foundation.

Lynch, M. (1989). Phylogenetic Hypotheses Under The Assumption of Neutral Quantitative-Genetic Variation. *Evolution; International Journal of Organic Evolution*, *43*(1), 1–17. https://doi.org/10.1111/j.1558-5646.1989.tb04203.x

Lynch, M., & Hill, W. G. (1986). Phenotypic Evolution by Neutral Mutation. *Evolution, 40*(5), 915–935. https://doi.org/10.2307/2408753

Macintosh, A. A., Pinhasi, R., & Stock, J. T. (2014). Lower limb skeletal biomechanics track long-term decline in mobility across ~6150 years of agriculture in Central Europe. *Journal of Archaeological Science*, *52*, 376–390. https://doi.org/10.1016/j.jas.2014.09.001

Macintosh, A. A., Davies, T. G., Pinhasi, R., & Stock, J. T. (2015). Declining tibial curvature parallels ~6150 years of decreasing mobility in central european agriculturalists. *American Journal of Physical Anthropology*, *157*(2), 260–275. https://doi.org/10.1002/ajpa.22710

Macintosh, A. A., Davies, T. G., Ryan, T. M., Shaw, C. N., & Stock, J. T. (2013). Periosteal versus true cross-sectional geometry: A comparison along humeral, femoral, and tibial diaphyses. *American Journal of Physical Anthropology*, *150*(3), 442–452. https://doi.org/10.1002/ajpa.22218

Macintosh, A. A., Pinhasi, R., & Stock, J. T. (2017). Prehistoric women's manual labor exceeded that of athletes through the first 5500 years of farming in Central Europe. *Science Advances*, *3*(11), eaao3893. https://doi.org/10.1126/sciadv.aao3893

Maggs, T. M. O. (1971). Pastoral Settlements on the Riet River. *The South African Archaeological Bulletin*, *26*(101/102), 37–63. https://doi.org/10.2307/3888527

Manica, A., Amos, B., Balloux, F., & Hanihara, T. (2007). The effect of ancient population bottlenecks on human phenotypic variation. *Nature, 448*(7151), 346–348. https://doi.org/10.1038/nature05951

Mant, M., de la Cova, C., & Brickley, M. B. (2021). Intersectionality and trauma analysis in bioarchaeology. *American Journal of Physical Anthropology, 174*(4), 583–594. https://doi.org/10.1002/ajpa.24226

Mariotti, V., Bonfiglioli, B., Facchini, F., Condemi, S., & Belcastro, M. G. (2009). Funerary practices of the Iberomaurusian population of Taforalt (Tafoughalt; Morocco, 11–12,000BP): New hypotheses based on a grave by grave skeletal inventory and evidence of deliberate human modification of the remains. *Journal of Human Evolution*, *56*(4), 340–354. https://doi.org/10.1016/j.jhevol.2009.01.001

Masemula, N. (2015). *An investigation of skeletons from Type-R settlements along the Riet and Orange Rivers, South Africa, using stable isotope analysis* [MA Thesis]. University of Cape Town.

McHenry, H. M. (1992). Body size and proportions in early hominids. *American Journal of Physical Anthropology*, *87*(4), 407–431. https://doi.org/10.1002/ajpa.1330870404

Meloche, C. H., Spake, L., & Nichols, K. L. (2020). *Working with and for ancestors: Collaboration in the care and study of ancestral remains.* Routledge, Taylor & Francis Group.

Merbs, C. F. (1983). Patterns of activity-induced pathology in a Canadian Inuit population. national museum of man mercury series, archaeological survey of Canada, Paper No.119. Ottawa: National Museums of Canada.

Merbs, C. F. (2018). The Discovery and Rapid Demise of the Sadlermiut. In C. M. Stojanowski & D. H. Temple (Eds.), *Hunter-Gatherer Adaptation and Resilience: A Bioarchaeological Perspective* (pp. 302–327). Cambridge University Press.

Meyers, J. L. (2018). *The relationship between proximal long bone shape and activity among four hunter-gatherer populations* [Master's thesis, University of Victoria]. University of Victoria ETD. https://dspace.library.uvic.ca//handle/1828/8460

Mizoguchi, Y., & Dodo, Y. (2001). Metric and Non-metric Characters of the Jomon Skulls from the Ebishima Shell-Mound in Northeastern Honshu, Japan. *Anthropological Science, 109*(1), 23–56. https://doi.org/10.1537/ase.109.23

Moran, E. F. (2022a). Fundamental Concepts and Methods. In *Human Adaptability* (4th ed.).

Routledge.

Moran, E. F. (2022b). Human Adaptability to Arctic Zones. In E. F. Moran, *Human Adaptability*

(4th ed., pp. 105–136). Routledge.

Moran, E. F. (2022c). Human Adaptability to the Humid Tropics. In E. F. Moran, *Human*

Adaptability (4th ed., pp. 219–247). Routledge.

Morris, D., & Beaumont, P. (1991). !Nawabdanas: Archaeological Sites at Renosterkop Kakamas District, Northern Cape. *The South African Archaeological Bulletin*, *46*(154), 115–124. https://doi.org/10.2307/3889090

Myka, F. P. (1993). *Decline of Indigenous Populations: The Case of the Andaman Islanders*. Rawat Publications.

Nadell, J. A., & Shaw, C. N. (2016). Phenotypic plasticity and constraint along the upper and lower limb diaphyses of *Homo sapiens*: PLASTICITY AND CONSTRAINT ALONG LIMBS. *American Journal of Physical Anthropology*, *159*(3), 410–422. https://doi.org/10.1002/ajpa.22889

Nelson, G. C. (1989). *Maxillary canine/third premolar transposition in a prehistoric population from Santa Cruz Island California*. Graduate Student Theses, Dissertations, & Professional Papers. https://scholarworks.umt.edu/etd/7311

Nelson, G. C. (1992). Maxillary canine/third premolar transposition in a prehistoric population from Santa Cruz Island, California. *American Journal of Physical Anthropology, 88*(2), 135–144. https://doi.org/10.1002/ajpa.1330880203

Nikander, R., Sievänen, H., Uusi-Rasi, K., Heinonen, A., & Kannus, P. (2006). Loading modalities and bone structures at nonweight-bearing upper extremity and weight-bearing lower extremity: A pQCT study of adult female athletes. *Bone, 39*(4), 886–894. https://doi.org/10.1016/j.bone.2006.04.005

Ocobock, C., Lacy, S., & Niclou, A. (2021). Between a rock and a cold place: Neanderthal biocultural cold adaptations. *Evolutionary Anthropology: Issues, News, and Reviews, 30*(4), 262–279. https://doi.org/10.1002/evan.21894

O’Donnel, M. S., & Ignizio, D. A. (2012). Bioclimatic predictors for supporting ecological applications in the conterminous United States. In Bioclimatic predictors for supporting ecological applications in the conterminous United States (USGS Numbered Series No. 691; Data Series, Vol. 691, p. 17). U.S. Geological Survey. https://doi.org/10.3133/ds691

Ozili, P. K. (2022). *The Acceptable R-Square in Empirical Modelling for Social Science Research* (SSRN Scholarly Paper No. 4128165). https://doi.org/10.2139/ssrn.4128165

Payne, S., Kumar BC, R., Pomeroy, E., Macintosh, A., & Stock, J. (2018). Thrifty phenotype versus cold adaptation: Trade-offs in upper limb proportions of Himalayan populations of Nepal. *Royal Society Open Science*, *5*(6), 172174. https://doi.org/10.1098/rsos.172174

Pearson, O. M. (2000). Activity, Climate, and Postcranial Robusticity: Implications for Modern Human Origins and Scenarios of Adaptive Change. *Current Anthropology*, *41*(4), 569–607. https://doi.org/10.1086/317382

Pearson, O. M., & Lieberman, D. E. (2004). The aging of Wolff’s “law”: Ontogeny and responses to mechanical loading in cortical bone. *American Journal of Physical Anthropology*, *125*(S39), 63–99. https://doi.org/10.1002/ajpa.20155

Perry, G. H., & Dominy, N. J. (2009). Evolution of the human pygmy phenotype. *Trends in Ecology & Evolution*, *24*(4), 218–225. https://doi.org/10.1016/j.tree.2008.11.008

Peterson, J. T. (1978). *The Ecology of Social Boundaries: Agta Foragers of the Philippines*. University of Illinois Press.

Pomeroy, E., Stock, J. T., Stanojevic, S., Miranda, J. J., Cole, T. J., & Wells, J. C. K. (2012). Trade-Offs in Relative Limb Length among Peruvian Children: Extending the Thrifty

Phenotype Hypothesis to Limb Proportions. *PLoS ONE*, *7*(12), e51795. https://doi.org/10.1371/journal.pone.0051795

Pontzer, H. (2007). Effective limb length and the scaling of locomotor cost in terrestrial animals. *Journal of Experimental Biology*, *210*(10), 1752–1761. https://doi.org/10.1242/jeb.002246

Prugnolle, F., Manica, A., & Balloux, F. (2005). Geography predicts neutral genetic diversity of human populations. *Current Biology*, *15*(5), R159–R160. https://doi.org/10.1016/j.cub.2005.02.038

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Radcliffe-Brown, A. R. (1922). *The Andaman Islanders*. The Free Press.

Raghavan, M., DeGiorgio, M., Albrechtsen, A., Moltke, I., Skoglund, P., Korneliussen, T. S., Grønnow, B., Appelt, M., Gulløv, H. C., Friesen, T. M., Fitzhugh, W., Malmström, H., Rasmussen, S., Olsen, J., Melchior, L., Fuller, B. T., Fahrni, S. M., Stafford, T., Grimes, V., … Willerslev, E. (2014). The genetic prehistory of the New World Arctic. Science, 345(6200), 1255832. https://doi.org/10.1126/science.1255832

Ramachandran, S., Deshpande, O., Roseman, C. C., Rosenberg, N. A., Feldman, M. W., & Cavalli-Sforza, L. L. (2005). Support from the relationship of genetic and geographic distance in human populations for a serial founder effect originating in Africa. *Proceedings of the National Academy of Sciences*, *102*(44), 15942–15947. https://doi.org/10.1073/pnas.0507611102

Relethford, J. H. (1994). Craniometric variation among modern human populations. *American Journal of Physical Anthropology*, *95*(1), 53–62. https://doi.org/10.1002/ajpa.1330950105

Relethford, J. H. (2002). Apportionment of global human genetic diversity based on craniometrics and skin color. *American Journal of Physical Anthropology*, *118*(4), 393–398. https://doi.org/10.1002/ajpa.10079

Relethford, J. H. (2004). Boas and beyond: Migration and craniometric variation. *American Journal of Human Biology: The Official Journal of the Human Biology Council*, *16*(4), 379–386. https://doi.org/10.1002/ajhb.20045

Roberts, P., Boivin, N., Lee-Thorp, J., Petraglia, M., & Stock, J. (2016). Tropical forests and the genus Homo. *Evolutionary Anthropology: Issues, News, and Reviews*, *25*(6), 306–317. https://doi.org/10.1002/evan.21508

Rolfe, S., Pieper, S., Porto, A., Diamond, K., Winchester, J., Shan, S., Kirveslahti, H., Boyer, D., Summers, A., & Maga, A. M. (2021). SlicerMorph: An open and extensible platform to retrieve, visualize and analyse 3D morphology. *Methods in Ecology and Evolution*, *12*(10), 1816–1825. https://doi.org/10.1111/2041-210X.13669

Roseman, C. C. (2004). Detecting interregionally diversifying natural selection on modern human cranial form by using matched molecular and morphometric data. *Proceedings of the National Academy of Sciences*, *101*(35), 12824–12829. https://doi.org/10.1073/pnas.0402637101

Roseman, C. C., & Auerbach, B. M. (2015). Ecogeography, genetics, and the evolution of human body form. *Journal of Human Evolution*, *78*, 80–90. https://doi.org/10.1016/j.jhevol.2014.07.006

Roseman, C. C., & Weaver, T. D. (2004). Multivariate apportionment of global human craniometric diversity. *American Journal of Physical Anthropology*, *125*(3), 257–263. https://doi.org/10.1002/ajpa.10424

Roseman, C. C., & Weaver, T. D. (2007). Molecules versus morphology? Not for the human cranium. *BioEssays: News and Reviews in Molecular, Cellular and Developmental Biology*, *29*(12), 1185–1188. https://doi.org/10.1002/bies.20678

RStudio Team. (2021). RStudio: Integrated Development Environment for R [R]. RStudio, PBC. http://www.rstudio.com/

Ruff, C. B. (2018). Biomechanical Analyses of Archaeological Human Skeletons. In M. A. Katzenberg & A. L. Grauer (Eds.), *Biological Anthropology of the Human Skeleton* (pp. 189–224). John Wiley & Sons, Inc. https://doi.org/10.1002/9781119151647.ch6

Ruff, C. B., & Hayes, W. C. (1983). Cross-sectional geometry of Pecos Pueblo femora and tibiae—A biomechanical investigation: I. Method and general patterns of variation. *American Journal of Physical Anthropology*, *60*(3), 359–381. https://doi.org/10.1002/ajpa.1330600308

Ruff, C. B., Scott, W. W., & Liu, A. Y. (1991). Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *American Journal of Physical Anthropology*, *86*(3), 397–413. https://doi.org/10.1002/ajpa.1330860306

Ruff, C. B., Trinkaus, E., Walker, A., & Larsen, C. S. (1993). Postcranial robusticity in Homo. I: Temporal trends and mechanical interpretation. *American Journal of Physical Anthropology*, *91*(1), 21–53. https://doi.org/10.1002/ajpa.1330910103

Ruff, C., Holt, B., & Trinkaus, E. (2006). Who's afraid of the big bad Wolff?: "Wolff's law" and bone functional adaptation. *American Journal of Physical Anthropology*, *129*(4), 484–498. https://doi.org/10.1002/ajpa.20371

Saers, J. P. P., Ryan, T. M., & Stock, J. T. (2019). Trabecular bone functional adaptation and sexual dimorphism in the human foot. *American Journal of Physical Anthropology*, *168*(1), 154–169. https://doi.org/10.1002/ajpa.23732

Scerri, E. M. L. (2023). One species, many roots? *Nature Ecology & Evolution*, *7*(7), Article 7. https://doi.org/10.1038/s41559-023-02080-2

Scerri, E. M. L., Chikhi, L., & Thomas, M. G. (2019). Beyond multiregional and simple out-of-Africa models of human evolution. *Nature Ecology & Evolution*, *3*(10), Article 10. https://doi.org/10.1038/s41559-019-0992-1

Scerri, E. M. L., Thomas, M. G., Manica, A., Gunz, P., Stock, J. T., Stringer, C., Grove, M., Groucutt, H. S., Timmermann, A., Rightmire, G. P., d'Errico, F., Tryon, C. A., Drake, N. A., Brooks, A. S., Dennell, R. W., Durbin, R., Henn, B. M., Lee-Thorp, J., deMenocal, P., … Chikhi, L. (2018). Did Our Species Evolve in Subdivided Populations across Africa, and Why Does It Matter? *Trends in Ecology & Evolution*, *33*(8), 582–594. https://doi.org/10.1016/j.tree.2018.05.005

Scherf, H., Wahl, J., Hublin, J.-J., & Harvati, K. (2016). Patterns of activity adaptation in humeral trabecular bone in Neolithic humans and present-day people. *American Journal of Physical Anthropology*, *159*(1), 106–115. https://doi.org/10.1002/ajpa.22835

Schlager, S. (2017). Morpho and Rvcg—Shape analysis in R. In G. Zheng, S. Li, & G. Szekely (Eds.), *Statistical shape and deformation analysis* (pp. 217–256). Academic Press.

Schlebusch, C. M., Sjödin, P., Breton, G., Günther, T., Naidoo, T., Hollfelder, N., Sjöstrand, A. E., Xu, J., Gattepaille, L. M., Vicente, M., Scofield, D. G., Malmström, H., de Jongh, M., Lombard, M., Soodyall, H., & Jakobsson, M. (2020). Khoe-San Genomes Reveal Unique Variation and Confirm the Deepest Population Divergence in Homo sapiens. *Molecular Biology and Evolution*, *37*(10), 2944–2954. https://doi.org/10.1093/molbev/msaa140

Schroeder, L., & Ackermann, R. R. (2023). Moving beyond the adaptationist paradigm for human evolution, and why it matters. *Journal of Human Evolution*, *174*, 103296. https://doi.org/10.1016/j.jhevol.2022.103296

Serrat, M. A., King, D., & Lovejoy, C. O. (2008). Temperature regulates limb length in homeotherms by directly modulating cartilage growth. *Proceedings of the National Academy of Sciences*, *105*(49), 19348–19353. https://doi.org/10.1073/pnas.0803319105

Shackelford, L. L., & Trinkaus, E. (2002). Late Pleistocene human femoral diaphyseal curvature. *American Journal of Physical Anthropology*, *118*(4), 359–370. https://doi.org/10.1002/ajpa.10093

Shaw, C. N., & Stock, J. T. (2009a). Habitual throwing and swimming correspond with upper limb diaphyseal strength and shape in modern human athletes. *American Journal of Physical Anthropology*, *140*(1), 160–172. https://doi.org/10.1002/ajpa.21063

Shaw, C. N., & Stock, J. T. (2009b). Intensity, repetitiveness, and directionality of habitual adolescent mobility patterns influence the tibial diaphysis morphology of athletes. *American Journal of Physical Anthropology*, *140*(1), 149–159. https://doi.org/10.1002/ajpa.21064

Singarayer, J. S., & Valdes, P. J. (2010). High-latitude climate sensitivity to ice-sheet forcing over the last 120kyr. *Quaternary Science Reviews*, *29*(1), 43–55. https://doi.org/10.1016/j.quascirev.2009.10.011

Slice, D. E. (2007). Geometric Morphometrics. *Annual Review of Anthropology*, *36*(1), 261–281. https://doi.org/10.1146/annurev.anthro.34.081804.120613

Smith, H. F. (2009). Which cranial regions reflect molecular distances reliably in humans? Evidence from three-dimensional morphology. *American Journal of Human Biology*, *21*(1), 36–47. https://doi.org/10.1002/ajhb.20805

Smith, H. F., Ritzman, T., Otárola-Castillo, E., & Terhune, C. E. (2013). A 3-D geometric morphometric study of intraspecific variation in the ontogeny of the temporal bone in modern Homo sapiens. *Journal of Human Evolution*, *65*(5), 479–489. https://doi.org/10.1016/j.jhevol.2013.01.017

Smith, R. J. (2016). Explanations for adaptations, just-so stories, and limitations on evidence in evolutionary biology. *Evolutionary Anthropology: Issues, News, and Reviews*, *25*(6), 276–287. https://doi.org/10.1002/evan.21495

Spake, L., Nicholas, G., & Cardoso, H. (2020). The digital lives of Ancestors: Ethical and intellectual property considerations surrounding the 3-D recording of human remains. In C. H. Meloche, L. Spake, & K. L. Nichols (Eds.), *Working with and for Ancestors: Collaboration in the Care and Study of Ancestral Remains* (pp. 205–218). Routledge. https://doi.org/10.4324/9780367809317-21

Starling, A. P., & Stock, J. T. (2007). Dental indicators of health and stress in early Egyptian and Nubian agriculturalists: A difficult transition and gradual recovery. *American Journal of Physical Anthropology*, *134*(4), 520–528. https://doi.org/10.1002/ajpa.20700

Stearns, S. C. (1989). The Evolutionary Significance of Phenotypic Plasticity: Phenotypic sources of variation among organisms can be described by developmental switches and reaction norms. *BioScience*, *39*(7), 436–445. https://doi.org/10.2307/1311135

Stern, J. T., & Susman, R. L. (1983). The locomotor anatomy of Australopithecus afarensis. *American Journal of Physical Anthropology*, *60*(3), 279–317. https://doi.org/10.1002/ajpa.1330600302

Stock, J. T. (2002). *Climatic and behavioural influences on postcranial robusticity among Holocene foragers* [Ph.D., University of Toronto (Canada)]. https://tspace.library.utoronto.ca/bitstream/1807/119659/3/NQ74566_OCR.pdf

Stock, J. T. (2006). Hunter-gatherer postcranial robusticity relative to patterns of mobility, climatic adaptation, and selection for tissue economy. *American Journal of Physical Anthropology*, *131*(2), 194–204. https://doi.org/10.1002/ajpa.20398

Stock, J. T. (2013). The Skeletal Phenotype of "Negritos" from the Andaman Islands and Philippines Relative to Global Variation among Hunter-Gatherers. *Human Biology*, *85*(1–3), 67–94. https://doi.org/10.13110/humanbiology.85.1-3.0067

Stock, J. T., Bazaliiskii, V. I., Goriunova, O. I., Savel'ev, N. A., & Weber, A. W. (2011). 9. Skeletal Morphology, Climatic Adaptation, and Habitual Behavior among Mid-Holocene Cis-Baikal Populations. In *9. Skeletal Morphology, Climatic Adaptation, and Habitual Behavior among Mid-Holocene Cis-Baikal Populations* (pp. 193–216). University of Pennsylvania Press. https://doi.org/10.9783/9781934536391.193

Stock, J. T., & Buck, L. (2010). Canalization and plasticity in humans and primates: Implications for interpreting the fossil record. In *150 años después de Darwin: ¿evolución, futuro o crisis? Lecciones sobre evolución humana* (p. 91:101). INSTITUTO TOMÁS PASCUAL SANZ, CENIEH.

Stock, J. T., & Migliano, A. B. (2009). Stature, Mortality, and Life History among Indigenous Populations of the Andaman Islands, 1871–1986. *Current Anthropology*, *50*(5), 713–725. https://doi.org/10.1086/605429

Stock, J. T., & Pfeiffer, S. (2001). Linking structural variability in long bone diaphyses to habitual behaviors: Foragers from the southern African Later Stone Age and the Andaman Islands. *American Journal of Physical Anthropology*, *115*(4), 337–348. https://doi.org/10.1002/ajpa.1090

Stock, J. T., & Pfeiffer, S. K. (2004). Long bone robusticity and subsistence behaviour among Later Stone Age foragers of the forest and fynbos biomes of South Africa. *Journal of Archaeological Science*, *31*(7), 999–1013. https://doi.org/10.1016/j.jas.2003.12.012

Stratovan Corporation. (2018). Stratovan Checkpoint (Version 2018.09.07). https://www.stratovan.com/products/checkpoint

Supernant, K. (2020). Moving beyond collaborative practice. In C. H. Meloche, L. Spake, & K. L. Nichols (Eds.), *Working with and for Ancestors* (pp. 268–280). Routledge.

Symchych, N. (2016). *An Ecogeographic Study of Body Proportion Development in the Sadlermiut Inuit of Southampton Island, Nunavut* [Masters Thesis, University of Toronto]. TSpace.

Tardieu, C. (2010). Development of the human hind limb and its importance for the evolution of bipedalism. *Evolutionary Anthropology: Issues, News, and Reviews*, *19*(5), 174–186. https://doi.org/10.1002/evan.20276

Temple, D. H. (2018). Persistence of Time: Resilience and Adaptability in Prehistoric Jomon Hunter-Gatherers from the Inland Sea Region of Southwestern Honshu, Japan. In C. M. Stojanowski & D. H. Temple (Eds.), *Hunter-Gatherer Adaptation and Resilience: A Bioarchaeological Perspective* (pp. 85–109). Cambridge University Press. https://doi.org/10.1017/9781316941256.005

Temple, D. H., Auerbach, B. M., Nakatsukasa, M., Sciulli, P. W., & Larsen, C. S. (2008). Variation in limb proportions between Jomon foragers and Yayoi agriculturalists from prehistoric Japan. *American Journal of Physical Anthropology*, *137*(2), 164–174. https://doi.org/10.1002/ajpa.20853

Temple, D. H., & Matsumura, H. (2011). Do body proportions among Jomon foragers from Hokkaido conform to ecogeographic expectations? Evolutionary implications of body size and shape among northerly hunter-gatherers. *International Journal of Osteoarchaeology, 21*(3), 268–282. https://doi.org/10.1002/oa.1129

Terhune, C. E., Kimbel, W. H., & Lockwood, C. A. (2013). Postnatal temporal bone ontogeny in Pan, Gorilla, and Homo, and the implications for temporal bone ontogeny in Australopithecus afarensis. *American Journal of Physical Anthropology, 151*(4), 630–642. https://doi.org/10.1002/ajpa.22318

Thornton-Barnett, S. (2013). *Ancestral pharmacopoeias: A paleoethnobotanical assessment of plant use in the Western Free State, South Africa* [MA Thesis]. Texas State University.

Tipton, M., J., Pandolf, K., B., Sawka, M., N., Werner, J., & Taylor, N. A. S. (2008). Chapter 21: Physiological adaptation to hot and cold environments. In N. A. S. Taylor & H. Groeller (Eds.), *Physiological bases of human performance during work and exercise* (pp. 379–4000). Churchill Livingstone.

Tishkoff, S. A., Reed, F. A., Friedlaender, F. R., Ehret, C., Ranciaro, A., Froment, A., Hirbo, J. B., Awomoyi, A. A., Bodo, J.-M., Doumbo, O., Ibrahim, M., Juma, A. T., Kotze, M. J., Lema, G., Moore, J. H., Mortensen, H., Nyambo, T. B., Omar, S. A., Powell, K., … Williams, S. M. (2009). The Genetic Structure and History of Africans and African Americans. *Science, 324*(5930), 1035–1044. https://doi.org/10.1126/science.1172257

Trigger, B. G. (1984). Alternative Archaeologies: Nationalist, Colonialist, Imperialist. *Man, 19*(3), 355–370. https://doi.org/10.2307/2802176

Trinkaus, E. (1983). Neandertal postcrania and the adaptive shift to modern humans. In E. Trinkaus (Ed.), *The Mousterian Legacy: Human Biocultural Change in the Upper Pleistocene* (pp. 165–200, S164). British Archaeological Reports.

Trinkaus, E. (1993). Femoral neck-shaft angles of the Qafzeh-Skhul early modern humans, and activity levels among immature Near Eastern Middle Paleolithic hominids. *Journal of Human Evolution*, *25*(5), 393–416. https://doi.org/10.1006/jhev.1993.1058

Trinkaus, E., Stringer, C. B., Ruff, C. B., Hennessy, R. J., Roberts, M. B., & Parfitt, S. A. (1999). Diaphyseal cross-sectional geometry of the Boxgrove 1 Middle Pleistocene human tibia. *Journal of Human Evolution*, *37*(1), 1–25. https://doi.org/10.1006/jhev.1999.0295

Tsosie, K. S., Yracheta, J. M., Kolopenuk, J., & Smith, R. W. A. (2021). Indigenous data sovereignties and data sharing in biological anthropology. *American Journal of Physical Anthropology*, *174*(2), 183–186. https://doi.org/10.1002/ajpa.24184

Turelli, M., Gillespie, J. H., & Lande, R. (1988). Rate Tests for Selection on Quantitative Characters During Macroevolution and Microevolution. *Evolution*, *42*(5), 1085–1089. https://doi.org/10.2307/2408923

Turner, T. R., & Mulligan, C. J. (2019). Data sharing in biological anthropology: Guiding principles and best practices. *American Journal of Physical Anthropology*, *170*(1), 3–4. https://doi.org/10.1002/ajpa.23909

Turner, T. R., Wagner, J. K., & Cabana, G. S. (2018). Ethics in Biological Anthropology. *American Journal of Physical Anthropology*, *165*(4), 939–951. https://doi.org/10.1002/ajpa.23367

Valdes, P. J., Armstrong, E., Badger, M. P. S., Bradshaw, C. D., Bragg, F., Crucifix, M., Davies-Barnard, T., Day, J. J., Farnsworth, A., Gordon, C., Hopcroft, P. O., Kennedy, A. T., Lord, N. S., Lunt, D. J., Marzocchi, A., Parry, L. M., Pope, V., Roberts, W. H. G., Stone, E. J., … Williams, J. H. T. (2017). The BRIDGE HadCM3 family of climate models: HadCM3@Bristol v1.0. *Geoscientific Model Development*, *10*(10), 3715–3743. https://doi.org/10.5194/gmd-10-3715-2017

von Cramon-Taubadel, N. (2009). Congruence of individual cranial bone morphology and neutral molecular affinity patterns in modern humans. *American Journal of Physical Anthropology*, *140*(2), 205–215. https://doi.org/10.1002/ajpa.21041

von Cramon-Taubadel, N., & Lycett, S. J. (2008). Brief Communication: Human cranial variation fits iterative founder effect model with African origin. *American Journal of Physical Anthropology*, *136*(1), 108–113. https://doi.org/10.1002/ajpa.20775

von Cramon-Taubadel, N., & Weaver, T. D. (2009). Insights from a quantitative genetic approach to human morphological evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *18*(6), 237–240. https://doi.org/10.1002/evan.20233

Walker, P. L. (1986). Porotic hyperostosis in a marine-dependent California Indian population. *American Journal of Physical Anthropology*, *69*(3), 345–354. https://doi.org/10.1002/ajpa.1330690307

Wallace, I. J., Demes, B., & Judex, S. (2017). Ontogenetic and Genetic Influences on Bone's Responsiveness to Mechanical Signals. In C. J. Percival & J. T. Richtsmeier (Eds.), *Building Bones: Bone Formation and Development in Anthropology* (pp. 233–253). Cambridge University Press. https://doi.org/10.1017/9781316388907.011

Wallace, I. J., Tommasini, S. M., Judex, S., Garland, T., & Demes, B. (2012). Genetic variations and physical activity as determinants of limb bone morphology: An experimental approach using a mouse model. *American Journal of Physical Anthropology*, *148*(1), 24–35. https://doi.org/10.1002/ajpa.22028

Waltenberger, L., Pany-Kucera, D., Rebay-Salisbury, K., & Mitteroecker, P. (2021). The association of parturition scars and pelvic shape: A geometric morphometric study.

American Journal of Physical Anthropology, *174*(3), 519–531. https://doi.org/10.1002/ajpa.24196

Watkins, R. (2018). Anatomical Collections as the Anthropological Other: Some Considerations. In P. K. Stone (Ed.), *Bioarchaeological Analyses and Bodies: New Ways of Knowing Anatomical and Archaeological Skeletal Collections* (pp. 27–47). Springer International Publishing. https://doi.org/10.1007/978-3-319-71114-0_3

Weaver, T. D. (2018). Neutral theory and the evolution of human physical form: An introduction to models and applications. *Journal of Anthropological Science*, *96*, 7–26.

Wheatley, D., & Gillings, M. (2002). *Spatial Technology and Archaeology: The Archaeological Applications of GIS.* CRC Press. https://doi.org/10.1201/b12806

Wolff, J. (1986). *The law of bone remodelling*. Springer-Verlag, Berlin. (Original work published 1892).

Yesner, D. R., Torres, M. J. F., Guichon, R. A., & Borrero, L. A. (2003). Stable isotope analysis of human bone and ethnohistoric subsistence patterns in Tierra del Fuego. *Journal of Anthropological Archaeology*, *22*(3), 279–291. https://doi.org/10.1016/S0278-4165(03)00040-0

Zelditch, M., Swiderski, D., & Sheets, H. D. (2012). *Geometric morphometrics for biologists: A primer* (2nd ed.). Elsevier/Academic Press.

Zuckerman, M. K., & Armelagos, G. J. (2011). The Origins of Biocultural Dimensions in Bioarchaeology. In S. C. Agarwal & B. A. Glencross (Eds.), *Social Bioarchaeology* (pp. 13–43). Wiley-Blackwell. https://doi.org/10.1002/9781444390537.ch2

9. Appendix

Table A 1: Description of Fixed Landmark Locations.

Number	Definition	Epiphysis
1	Center of fovea capitis	Proximal
2	Most proximal point on the femoral head	Proximal
3	Most anterior point of the femoral head	Proximal
4	Most posterior point of the femoral head	Proximal
5	Most proximo-posterior point of greater trochanter	Proximal
6	Most lateral point of greater trochanter	Proximal
7	Most proximo-anterior point of great trochanter	Proximal
8	Tip of lesser trochanter	Proximal
9	Maximum point of constriction on ridge running from lesser trochanter to the femoral head	Proximal
10	Most medial point on the medial epicondyle	Distal
11	Most lateral point on the lateral epicondyle	Distal
12	Proximo-medial corner of the facet margin on the anterior aspect of the distal articular surface	Distal
13	Medio-lateral inflection of the anterior-proximal margin of the distal articular surface	Distal
14	Proximo-lateral corner of the facet margin on the anterior aspect of the distal articular surface	Distal
15	Most distal point of the medial condyle	Distal

16	Most distal inflection point of patellar grove	Distal
17	Most distal point of the lateral condyle	Distal
18	Most posterior point of the medial facet margin of the medial condyle	Distal
19	Proximo-medial corner of the facet margin on the posterior aspect of the medial condyle	Distal
20	Proximo-lateral corner of the facet margin on the posterior aspect of the medial condyle	Distal
21	Most posterior point of the lateral facet margin of the medial condyle	Distal
22	Most proximal point of the posterior aspect of the groove margin	Distal
23	Most posterior point of the medial facet margin of the lateral condyle	Distal
24	Proximo-medial corner of the facet margin on the posterior aspect of the lateral condyle	Distal
25	Proximo-lateral corner of the facet margin on the posterior aspect of the lateral condyle	Distal
26	Most posterior point of the lateral facet margin of the lateral condyle	Distal

Table A 2: Descriptive Statistics.

Group	*Model N (F/M/U)*	*Linear N (F/M/U)*	*distance (km)*	*season*	*max temp (°C)*
AET	16 (7/7/2)	16 (7/7/2)	16924	107.857	30.15
AND	16 (10/6/0)	31(15/16/0)	14645	59.569	32.753
AUS	14 (1/5/8)	19 (2/2/15)	21549	569.353	33.097
BA	6 (3/1/2)	10 (4/3/3)	5941	744.161	38.748
CSA	17 (5/11/1)	36(20/16/0)	1024	581.143	32.16
IBE	19 (11/8/0)	35(7/14/14)	7313	566.49	29.473
JOM	11 (2/4/5)	29 (4/6/19)	20840	810.388	29.177
NP	19 (7/10/2)	22(9/13/0)	34424	1370.057	13.242
PH	18 (8/7/3)	13(7/6/0)	25193	1274.674	10.87
SAN	18 (3/5/10)	16 (0/7/9)	32167	338.12	25.173
YAH	18 (9/7/2)	25(9/13/3)	45801	274.099	13.797

Group	*min temp (°C)*	*maxprecip (mm)*	*minprecip (mm)*	*npp*
AET	15.793	581.583	60.41	1514
AND	22.138	538.328	14.317	1658
AUS	2.65	23.343	11.243	307
BA	2.926	4.615	0	46
CSA	-0.664	76.226	7.271	441
IBE	0.259	84.234	5.77	213
JOM	-2.4	187.72	57.857	791
NP	-32.201	45.809	10.507	193
PH	-31.278	40.888	4.419	164
SAN	4.995	87.945	0	365
YAH	-1.67	78.12	40.71	412

Note: Reporting sample size, total and by sex, values for distance and climatic/bioclimatic variables. NPP units gC m−2 year−1. F = female, M = male, U = unknown.

Table A 3: Group Means ($\bar{x}$) of Linear Measurements, By Sex.

Group	xfln (mm)	xfhd (mm)	F xfln (mm)	F xfhd (mm)	M xfln (mm)	M xfhd (mm)
AET	385.6	38.18	369.6	36.45	397.7	40.08
AND	384.4	37.81	377.8	36.64	390.5	38.91
AUS	458.4	42.94	444.5	40.59	475.0	44.60
BA	421.9	41.23	409.2	40.19	445.2	42.96
CSA	402.5	38.34	397.8	37.40	408.4	39.53
IBE	463.7	49.47	469.8	49.30	469.1	50.48
JOM	416.2	43.65	411.2	42.50	409.3	43.45
NP	425.8	47.29	417.1	44.59	431.7	49.16
PH	414.4	45.18	402.8	43.11	428.0	47.59
SAN	421.1	42.78	N/A	N/A	403.1	38.67
YAH	404.6	43.39	381.4	39.86	419.6	45.31

Note: xfln (maximum femoral length, whole sample), xfhd (maximum femoral head diameter, whole sample), F (female subsample used), M (male subsample used).

Table A 4: Average Deviation (mm) by Landmark Number.

LM #	Dev.	*LM #*	Dev.	*LM #*	Dev.	*LM #*	Dev.	*LM #*	Dev.	*LM #*	Dev.	*LM #*	Dev.
1	0.7	*31*	1.1	*61*	1.1	*91*	1.7	*121*	1.5	*151*	2.3	*181*	1.7
2	1.5	*32*	1.1	*62*	1.3	*92*	1.3	*122*	1.5	*152*	1.4	*182*	1.2
3	1.6	*33*	1.1	*63*	1.3	*93*	1.2	*123*	1.6	*153*	1.7		
4	1.8	*34*	1.0	*64*	1.4	*94*	1.6	*124*	1.0	*154*	2.2		
5	2.0	*35*	1.0	*65*	1.6	*95*	1.9	*125*	1.6	*155*	2.5		
6	2.2	*36*	1.0	*66*	1.2	*96*	1.5	*126*	1.0	*156*	2.4		
7	2.1	*37*	0.9	*67*	1.5	*97*	1.2	*127*	1.2	*157*	1.4		
8	1.9	*38*	0.9	*68*	1.3	*98*	1.2	*128*	1.6	*158*	1.7		
9	2.2	*39*	0.8	*69*	1.6	*99*	1.4	*129*	1.3	*159*	2.1		
10	1.8	*40*	1.0	*70*	1.9	*100*	1.6	*130*	2.1	*160*	2.7		
11	1.7	*41*	1.0	*71*	1.5	*101*	1.2	*131*	1.3	*161*	2.2		
12	2.4	*42*	1.0	*72*	1.7	*102*	1.2	*132*	1.3	*162*	1.4		
13	2.4	*43*	1.0	*73*	1.4	*103*	1.3	*133*	1.7	*163*	1.7		
14	2.1	*44*	1.0	*74*	1.7	*104*	1.3	*134*	1.7	*164*	1.9		
15	1.6	*45*	1.1	*75*	2.1	*105*	1.3	*135*	2.2	*165*	2.4		
16	2.5	*46*	1.0	*76*	1.7	*106*	1.1	*136*	1.8	*166*	1.9		
17	1.8	*47*	0.8	*77*	1.7	*107*	1.2	*137*	1.3	*167*	1.3		
18	1.5	*48*	0.8	*78*	1.4	*108*	1.3	*138*	1.7	*168*	1.6		
19	1.6	*49*	0.7	*79*	1.8	*109*	1.2	*139*	1.8	*169*	1.8		
20	1.8	*50*	0.7	*80*	2.2	*110*	1.2	*140*	2.6	*170*	2.1		
21	1.6	*51*	0.8	*81*	1.8	*111*	1.1	*141*	2.0	*171*	1.5		
22	1.6	*52*	0.9	*82*	1.6	*112*	1.0	*142*	1.3	*172*	1.3		
23	1.5	*53*	1.3	*83*	1.4	*113*	1.4	*143*	1.7	*173*	1.5		
24	1.3	*54*	1.4	*84*	1.9	*114*	1.8	*144*	2.0	*174*	1.8		
25	1.6	*55*	1.4	*85*	2.2	*115*	1.3	*145*	2.7	*175*	2.0		
26	2.3	*56*	1.4	*86*	1.8	*116*	1.5	*146*	2.4	*176*	1.2		
27	1.0	*57*	1.3	*87*	1.5	*117*	1.0	*147*	1.4	*177*	1.2		
28	1.0	*58*	1.2	*88*	1.3	*118*	1.7	*148*	1.6	*178*	1.5		
29	1.1	*59*	1.1	*89*	1.8	*119*	1.3	*149*	2.1	*179*	2.4		
30	1.1	*60*	1.3	*90*	2.1	*120*	1.5	*150*	2.8	*180*	2.2		

Table A 5: Results of Within-Population Variance Calculation.

	wvw	*pvw*	*dvw*	*svw*	*wvf*	*pvf*	*dvf*	*svf*	*wvm*	*pvm*	*dvm*	*svm*
#PCs	171	20	44	171	51	20	44	51	49	19	43	49
AET	0.000590	0.0063798	0.00923	0.00047	0.000416	0.005299	0.007446	0.000296	0.0006295	0.005219	0.00859	0.000525
AND	0.000514	0.00575	0.00855	0.00040	0.000476	0.005516	0.007966	0.000351				
AUS	0.000651	0.00778	0.01047	0.00050								
BA	0.000700	0.00686	0.00986	0.00063								
IBE	0.000719	0.00928	0.00771	0.00060								
JOM	0.000679	0.00681	0.01031	0.00049					0.00060	0.006506	0.00968	0.000433
CSA	0.000601	0.00771	0.00908	0.00046	0.000582	0.007008	0.008792	0.000447	0.00053	0.008123	0.00793	0.000378
NP	0.000727	0.00606	0.00756	0.00061	0.000455	0.003891	0.006199	0.000411	0.00077	0.006949	0.00728	0.000681
PH	0.000566	0.00687	0.00735	0.00044	0.000584	0.007066	0.006333	0.000388	0.00045	0.005829	0.00672	0.000406
SAN	0.000625	0.00665	0.00829	0.00053								
YAH	0.000610	0.00610	0.00898	0.00053	0.0005437	0.004861	0.009329	0.000472	0.00061	0.007021	0.00560	0.000543

Note: Reporting number of PCs per shape variable and within-population variation (sum of trace of variance co-variance of pc scores). Grayed cells indicated no data collected (inappropriate sample size).

Table A 6: Tests of Normality - Linear Data Full Sample (Shapiro-Wilk).

Variable/Model	*W*	*Sig.*	*N*
xfln	0.981	0.001888*	252
xfhd	0.97889	0.0008426*	252
Season	0.8896	1.36e-12*	252
MaxTemp	0.78482	<2.2e-16*	252
MinTemp	0.80926	<2.2e-16*	252
MaxPrecip	0.66628	<2.2e-16*	252
MinPrecip	0.74924	<2.2e-16*	252
NPP	0.75585	<2.2e-16*	252
Distance	0.92339	4.098e-10*	252
Latitude	0.89137	1.777e-12*	252
Absolute Latitude	0.88976	1.392e-12	252
xfln~season	0.97502	0.0002054*	252
xfln~mintemp	0.97665	0.0003677*	252
xfln~maxprecip	0.99236	0.2189	252
xfln~minprecip	0.98366	0.005461*	252
xfln~npp	0.9911	0.1291	252
xfln~distance	0.98293	0.00406*	252
xfln ~ latitude	0.98013	0.00135*	252
xfln~ absolute latitude	0.97726	0.0004593*	252
logxfln~logseason	0.98986	0.07586	252
logxfln~maxtemp	0.98183	0.002617*	252
logxfln~log absolute latitude	0.98682	0.0204*	252
xfhd~season	0.96967	3.384e-05*	252
xfhd~maxtemp	0.97703	0.0004227*	252
xfhd~mintemp	0.97414	0.0001513*	252
xfhd~maxprecip	0.99176	0.1704	252
xfhd~minprecip	0.98069	0.001674*	252
xfhd~npp	0.99279	0.2608	252
xfhd~distance	0.97745	0.0004935*	252
xfhd~latitude	0.98769	0.02968*	252
xfhd~absolute latitude	0.97585	0.0002764*	252
logxfhd~logseason	0.99352	0.3472	252
logxfhd~logmaxtemp	0.98695	0.0216*	252
logxfhd~logdistance	0.9932	0.3072	252
logxfhd~logabsolute latitude	0.99379	0.3852	252

Note: *significance at α =0.05.

Table A 7: Tests of Normality – Linear Data Female Sample (Shapiro-Wilk).

Variable/Model	*W*	*Sig.*	*N*
xfln	0.92769	0.0001542*	84
xfhd	0.93522	0.0003807*	84
Season	0.86241	2.564e-07*	84
MaxTemp	0.75038	1.225e-10*	84
MinTemp	0.82751	1.713e-08*	84
MaxPrecip	0.66898	1.822e-12*	84
MinPrecip	0.72276	2.676e-11*	84
NPP	0.75061	1.24e-10*	84
Distance	0.88793	2.43e-06*	84
Latitude	0.90721	1.619e-05*	84
Absolute Latitude	0.87229	5.934e-07*	84

Note: *significance at α =0.05.

Table A 8: Tests of Normality -Linear Data Male Sample (Shapiro-Wilk).

Variable/Model	*W*	*Sig.*	*N*
xfln	0.97573	0.05488	103
xfhd	0.96821	0.01394*	103
Season	0.8623	2.432e-08*	103
MaxTemp	0.79208	9.338e-11*	103
MinTemp	0.82789	1.326e-09*	103
MaxPrecip	0.64663	2.172e-14*	103
MinPrecip	0.75133	6.462e-12*	103
NPP	0.72858	1.654e-12*	103
Distance	0.91118	3.696e-06*	103
Latitude	0.89547	6.37e-07*	103
Absolute Latitude	0.89377	5.31e-07	103

Note: *significance at α =0.05.

Table A 9: Tests of Normality – Linear Dimension Means and Variance (Shapiro-Wilk).

Variable/Model	*W*	*Sig.*	*N*
xflnmean	0.91752	0.2985	11
xfhdmean	0.94234	0.5484	11
Fxflnmean	0.9347	0.4957	10
Fxfhdmean	0.93162	0.464	10
Mxflnmean	0.92098	0.3269	11
Mxfhdmean	0.92835	0.3944	11
varxfln	0.89657	0.1678	11
varxfhd	0.90759	0.2283	11
CVxfln	0.89264	0.15	11
CVxfhd	0.95875	0.756	11
Season	0.9282	0.3929	11
MaxTemp	0.86583	0.06851	11
MinTemp	0.85259	0.04612*	11
MaxPrecip	0.68395	0.000291*	11
MinPrecip	0.77176	0.00403*	11
NPP	0.78007	0.005145*	11
Distance	0.97555	0.9364	11
Latitude	0.92117	0.3285	11
Absolute Latitude	0.91569	0.2844	11
Meanxfln~maxprecip	0.87137	0.08073	11
Meanxfln~npp	0.8484	0.049067*	11
logmeanxfln~npp	0.8553	0.05003	11
Meanxfhd~season	0.92414	0.3546	11
Meanxfhd~npp	0.96236	0.8007	11
Meanxfhd~mintemp	0.86707	0.07108	11
Meanxfhd~absolute latitude	0.82694	0.02128*	11
Logmeanxfhd ~logabsilute latitude	0.86486	0.06657	11
varxfln ~ MaxTemp	0.90256	0.1986	11
varxfln ~ MinTemp	0.97465	0.9293	11
varxfln ~ absolute latitude	0.96561	0.8391	11
CVxfln ~ MaxTemp	0.95844	0.7521	11

Note: For regression models (variable ~ variable), normality tests are performed on the residuals. *significance at α =0.05.

Table A 10: Tests of Normality – GM Tests (Shapiro-Wilk).

Variable/Model	*W*	*Sig.*	*N*
wvw ~ distance	0.97133	0.8996	11
pvw ~ distance	0.94668	0.6019	11
dvw ~ distance	0.94803	0.6189	11
svw ~ distance	0.94348	0.5623	11
wvf ~ distance	0.90275	0.3904	6
pvf ~ distance	0.94649	0.7118	6
dvf ~ distance	0.93965	0.6564	6
svf ~ distance	0.98632	0.9783	6
wvm~ distance	0.9885	0.9852	6
pvm ~ distance	0.97543	0.9267	6
dvm ~ distance	0.89239	0.3309	6
svm ~ distance	0.9298	0.5786	6
wvw ~ climate	0.92046	0.3225	11
pvw ~ climate	0.92581	0.3701	11
dvw ~ climate	0.98356	0.9827	11
svw ~ climate	0.82661	0.02107*	11

Note: For regression models (variable ~ variable), normality tests are performed on the residuals. *significance at $\alpha = 0.05$.

Curriculum Vitae

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