RIGHTING TIBIAL RETROVERSION: A FUNCTIONAL AND ONTOGENETIC ANALYSIS

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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

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DEDICATION

I owe my sincerest gratitude to my family: Gaby, Erika, and Cyrus. Thank you for your support and understanding, without which, I wouldn't've had the time or courage to earn this degree. A huge thank you to my parents, Faye and Joe, who told me I could be anything I wanted to be, and now I've tried them all.

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ABSTRACT

Tibial retroversion, or the posterior angulation of the tibial plateau relative to the diaphysis, has been tentatively linked to several behaviors in anthropological literature. While a large body of work, dating as far back as the late 1800's, has linked this morphology to squatting postures, this association is primarily from comparative studies of human groups as opposed to more controlled studies in populations knowns to squat. Other scholars have suggested that retroversion is related to overall robusticity or more explicitly, extensor muscle moment arm development.

This research attempts to clarify the underlying etiology of tibial retroversion by analyzing it in an explicitly ontogenetic and functional perspective. First, this analysis explored age and population-level variation in tibial retroversion. Second, the relationship between tibial retroversion and long bone strength via cross-sectional geometric properties was evaluated. This study used a large cross-sectional sample of immature modern human remains from seven historical and archaeological osteology collections that vary in origin and activity patterns. Results of this analysis indicate that there is no relationship between tibial retroversion and age after the first six months of life, while populations and subsistence strategies differ in their magnitude of retroversion. In addition, there is no relationship between tibial retroversion and size-standardized cross-sectional geometric properties, implying that variation in this feature is not purely a function of loading and activity levels. The lack of association with age and robusticity suggests that additional research is needed to shed light on whether this morphology is associated with squatting or other functional correlates.

Tibial retroversion, or the posteroinferior angulation of the tibial plateau relative to the diaphysis, has been described in the anthropological literature since the 1800s, but its functional etiology currently remains unclear. Some of the earliest discussions of this morphology date to descriptions of Neanderthal paleobiology which established spurious linkages between retroversion of the tibial plateau and a bent-knee or “ape-like” gait (Testut, 1889; Boule, 1911). However, much of the contemporary anthropological literature focuses on purported relationships between tibial retroversion and habitual squatting posture (Aitken, 1905; Angel, 1945; Boulle, 2001; Charles, 1893, 1894; Kate & Robert, 1965; Lisowski et al., 1957; Straus & Cave, 1957; Swati et al., 2015; Turner, 1895; Wood, 1920). In addition, more recent studies have suggested that generalized levels of activity and robusticity might be an underlying causal factor in the production of this morphology (Trinkaus & Rhoads, 1999). Outside of anthropology, clinical research has explored aspects of tibial retroversion or “tibial slope,” but has primarily tied this morphology to knee injury risk levels and anterior and posterior cruciate ligament reconstruction. Given the array of competing functional explanations, a broad analysis focusing on clarification of the underlying causes of proximal tibial shape may be valuable. Here, we use a large, geographically diverse sample of immature skeletal remains to explore the development of tibial retroversion in a functional and ontogenetic framework to elucidate the ultimate causes of tibial retroversion.

The basic developmental principles leading to the production of retroverted tibiae are broadly understood. The Heuter-Volkmann Law (Volkman, 1862) proposed that mechanical compression of the epiphyseal plate during skeletal immaturity slows growth. Given this, it follows that during fetal development in utero, the flexed position of the human leg exerts pressure on the posterior tibial plateau, repressing growth in that region (Charles, 1893, 1894; Huard & Montagne, 1950, 1953; Lustig, 1915; Retzius, 1900). Subsequently, early literature proposed that population differences in tibial retroversion occur when this fetal morphology is or is not maintained into adulthood in specific populations (Aitken, 1905).

Later research would elaborate on the specific hypothesized functional environments that could lead to maintained retroversion. Given high levels of tibial retroversion in great apes, early literature suggested that high human tibial retroversion might be indicative of a bent-knee gait similar to that of apes when walking bipedally (Collignon, 1880). This morphology was also observed in adult remains of the Spy Neanderthals, and though no conclusion was drawn about gait at that time, it was decided that this was a distinct feature differentiating "Quarternary man" and the modern human (Fraipont & Lohest, 1887). Finally, Boule's (1911) seminal description of La Chapelle-aux-Saints suggested tibial retroversion in Neanderthals resulted in a bent-knee gait, which was part of a larger picture of Neandertals as primitive and ape-like (Boule, 1911). It was later noted that while there is significant retroversion in Neanderthal tibiae, its magnitude was equal to what was found in modern humans whose lifestyles involved frequent bending of the knee (Straus, 1927). After further research was conducted on Neanderthal tibiae from Spy, La Chapelle-aux-Saints, and La Ferrassie, many of Boule's interpretations of Neanderthal anatomy were discredited (Straus & Cave, 1957).

Following in part from these early interpretations, the most accepted and abundant anthropological literature on tibial retroversion in modern humans has focused on documenting its association with habitual squatting. In 1889, it was suggested that this posture resulted in extreme force on the posterior portion of the tibial plateau, causing the posterior plateau slant (Thomson, 1889), and in fact, early literature on Neanderthals suggested that they likely squatted often (Charles, 1893, Klaatch, 1900). However, at that time, the link between retroverted tibial anatomy and habitual squatting was not very strong. Early research compared global populations and concluded that, because indigenous populations from the Americas, Asia, and Australia displayed more retroversion than those from Africa and Europe, squatting was a likely cause (Thomson, 1889, 1890). Additional research supported this interpretation using further population-level comparisons (Charles, 1894). When comparing a South Asian population to a European one, Charles (1894) found that individuals from India had more retroverted tibiae than those from Europe, but that infants had the same degree as adults, which would suggest potential non-functional causes. Other researchers, too, noted that retroversion was not unheard of in European populations, but was more common in the indigenous people of Mexico and Asia (Aitken, 1905; Hrdlicka, 1898). The link between retroversion and squatting gained traction when the above studies were cited by other researchers and bolstered by additional comparative studies of human populations, albeit ones with no stronger demonstrable links to squatting behavior (Cameron, 1934; Huard & Montagne, 1950, 1953; Kate & Robert, 1965; Klaatsch, 1900; Morgenthaler, 1955; Olivier, 1960; Wood, 1920).

More recent work has suggested, however, that the link between tibial retroversion and habitual squatting may be related to other causal factors. In his analysis, Trinkaus (1975) noted that squatting facets and tibial retroversion remain uncorrelated in recent populations, suggesting that the presence of tibial retroversion alone may not be indicative of habitual squatting. Trinkaus further posits that high ground reaction forces and thigh musculature activity when the knee is partially flexed may be sufficient to produce retroverted morphology in the tibial plateau (Trinkaus, 1975). Additional work in this area found that all Late Pleistocene specimens had relatively high levels of tibial retroversion and suggested that retroversion was related to extensor muscle moment arm development during growth (Trinkaus & Rhoads, 1999). Taken together, these lines of evidence may indicate that retroversion is related to overall activity and robusticity levels, which may be higher in non-industrial populations who are also more likely to engage in habitual squatting postures.

Additional comparative work has been conducted in clinical studies, where the angle of the tibial plateau is most widely referred to as "tibial slope" (or occasionally "caudal slope") and is discussed most frequently in the context of anterior and posterior cruciate ligament damage and reconstruction. Comparative clinical studies, however, have established that females tend to have a greater tibial slope than males (Brandon et al., 2006; Dare et al., 2015; Haddad et al., 2012; Hashemi et al., 2008; Hudek et al., 2011; Todd et al., 2010; Weinberg et al., 2017, but see de Boer et al., 2009; Schatka et al., 2018 for an alternate view), which may be related to the greater anterior cruciate ligament tears among females. This important finding may suggest a non-functional cause for variation in this feature and implies that squatting may not be the primary causal factor. In addition, tibial slope has also been studied in different ancestral groups, though not as comprehensively as sex, so the results are less conclusive. Some researchers have found statistically significant differences comparing individuals of Asian, European, and African descent (finding that Asians have a higher mean angle compared to both other groups), corroborating anthropological literature (Haddad et al., 2012; Pangaud et al., 2020), while others have found that those of African descent have a higher mean angle than those with European ancestry, which contradicts anthropological literature (de Boer et al., 2009; Weinberg et al., 2017). Additional studies have compared Chinese tibiae with Europeans and report a one-degree difference of slope (Yue et al., 2011). Ultimately, while the medical literature is more interested in whether the population differences translate into clinically significant differences in treatment outcomes, the patterns documented are potentially useful for understanding the links between this morphology and behavior.

Considering these factors detailed above, the link between tibial retroversion, activity, and squatting is not as well established as has been previously suggested. While differences between urban and non-industrial populations have been documented, squatting is only one of several factors, including overall levels of physical activity, that could be responsible for the posterior tilt of the tibial plateau in some human groups. While it is impossible to directly test this link with skeletal data alone, this analysis will explore two separate but related questions in a large and diverse sample of immature individuals. First, we evaluate if there is a relationship between age and tibial retroversion during growth in different populations and different subsistence strategies, as researchers have purported that retroversion decreases from infancy to adulthood unless a population habitually squats (LeVeau & Bernhardt, 1984; Retzius, 1900; Titze, 1951). This might suggest that we will see not only differences between populations, but that samples from industrial and/or urban backgrounds would show decreased tibial retroversion relative to agriculturalists and particularly foraging groups. In addition, if a retroverted tibial plateau is associated with specific behaviors, we would expect to see its morphology change with age due to increased loading during growth. Alternatively, if populations and subsistence strategies differ in their degree of retroversion but these differences remain relatively stable throughout ontogeny, this may suggest other non-functional causes. Second, the relationship between tibial retroversion and overall activity levels was investigated by evaluating the correlation between tibial retroversion and cross-sectional geometry, which quantifies bone mass and distribution in order to evaluate bone loading during life. A strong correlation between these two variables would suggest the overall activity levels may be a predictor of tibial retroversion.

MATERIALS AND METHODS

Samples

This analysis explored age and population-level variation in tibial retroversion in a large sample of immature skeletons from seven groups of varying subsistence strategies, activity levels, and geographic locations ($N = 383$). Specific sample sizes and time periods are shown in Table 1, and additional details can be found in Cowgill (2010).

Table 1. Sample description, size, date, and location.

Sample	Original Location	Approx. Time Period	N	Sample location
California Amerindian	Northern California	500-4600 BP	61	Phoebe Hearst Museum at the University of California, Berkeley (Berkeley, CA)
Dart	Johannesburg, South Africa	20th century	55	School of Medicine, University of Witwatersrand (Johannesburg, South Africa)
Indian Knoll	Green River, Kentucky	4143-6415 BP	73	University of Kentucky, Lexington (Lexington, KY)
Kulubnarti	Batn el Hajar, Upper Nubia	Medieval (6th-14th century)	74	University of Colorado, Boulder (Boulder, CO)
Luis Lopes	Lisbon, Portugal	20th century	40	Bocage Museum (Lisbon, Portugal)
Mistihalj	Bosnia-Herzegovina	Medieval (15th century)	27	Peabody Museum at Harvard University (Cambridge, MA)
Point Hope	Point Hope, Alaska	300-2100 BP	41	American Museum of Natural History (New York, NY)

These samples were chosen to represent a probable diverse selection of lifeways and activity patterns as well as ancestral background. As such, these sampled populations vary in genetic background, daily activity levels, body proportions, and other intrinsic and extrinsic factors. Five of the seven samples are from nonurban, nonmechanized societies (Mistihalj, Kulubnarti, Indian Knoll, Point Hope, and California Amerindian), and of these, the latter three derive from semi-sedentary foraging populations, while the former are agriculturalists and pastoralists, respectively. In contrast, the Dart collection material is ethnically mixed, both urban and nonurban samples of Sub-Saharan Africans, and the Luis Lopes collection is composed of urban, 20th century Portuguese. For analyses of subsistence strategy, Point Hope, Indian Knoll, and California Amerindian are considered foragers, Mistihalj and Kulubnarti are grouped as agriculturalists, and Dart and Luis Lopes are categorized as urban.

Age at death was determined using lateral mandibular radiographs from associated dental material, when available. Crown and root dental formation standards following Liversidge and Molleson (2004) and Smith (1991) were used to assess developmental age for each individual. Each set of dentition was scored twice on two consecutive days, and individual teeth that produced different dental stage scores were evaluated a third time to resolve inconsistencies. When no dentition was directly associated with the postcranial remains, developmental age was predicted from within sample Least Squares regression of femoral, tibial, or humeral length on age for each comparative sample in order to maximize sample size (Cowgill, 2010). No attempt was made to determine sex due to the unreliability of sex estimation in immature samples. Specimens with obvious pathologies were excluded in the analyses.

Measurements

The measurement of tibial retroversion has been previously defined as the posterior angulation of the tibial plateau relative to the diaphysis. For this study, we followed the methods of Trinkaus (personal correspondence), measuring the angle of retroversion using a protractor and graph paper. Both fused and unfused tibiae were measured in a similar fashion. A small subset of the combined sample were early adolescents that had unfused tibiae, but the proximal epiphyses were present (N=8). These individuals had tibial retroversion measured on both fused and unfused tibial plateaus. Differences between the unfused and fused measurements ranged from 2º to 4º, with a mean of 3º.

Tibial cortical area (CA), I_{max}/I_{min}, and polar second moment of area (J) were collected at 50% of tibial metaphyseal length. Cortical area can be interpreted as a measure of bone strength under compression, I_{max}/I_{min} is a ratio of maximum to minimum bending strength and is an indicator of bone shape, and the polar second moment of area is a proxy for the overall torsional rigidity of a bone (Ruff, 2018). Cross-sectional properties were reconstructed using a method similar to O'Neill and Ruff's (2004) "latex cast method" using silicone molding putty and anteroposterior and mediolateral radiographs. The external surface of the diaphysis was molded with Cuttersil Putty Plus silicone molding putty. Anterior, posterior, medial, and lateral cortical bone widths were measured with digital calipers, and measurements were corrected for parallax distortion by comparing external breadth measured on the radiograph with external breadth measured on the element itself at each section level. Once corrected for parallax, the four cortical bone measurements were plotted onto the two-dimensional copy of the original mold, and the endosteal contours were interpolated by using the subperiosteal outline as a guide. The resultant sections were enlarged on a digitizing tablet, and the endosteal and periosteal contours digitized. Cross-sectional properties were computed from the sections in a PC-DOS version of SLICE (Nagurka & Hayes, 1980, Escheman, 1992).

Analysis

It is necessary to standardize cross-sectional properties by a mechanically relevant measure of body size (Ruff, 2018). For this analysis, body mass was predicted based on formulae developed specifically for immature individuals, which predict body mass from femoral distal metaphyseal mediolateral breadth and femoral head size (Ruff, 2007). Within the comparative sample, the femoral metaphyseal breadth measurement was not available for 17% of younger individuals possessing one lower limb element; in these cases, femoral metaphyseal breadth was predicted from proximal tibial metaphyseal mediolateral breadth (Cowgill, 2010). Body masses predicted using Ruff's (2007) formulae correlated well with crural and brachial indices suggesting that they do reflect likely body mass differences among the samples due to ecogeographic differences in body width (Cowgill, 2010). To remove the effect of body mass on tibial cross-sectional properties, logged cross-sectional properties were regressed on logged body mass (cortical area) or logged body mass × beam length^2 (polar second moment of area) using Ordinary Least Squares regression. Unstandardized residuals were then used in comparisons between groups.

To evaluate if there is a relationship between age and tibial retroversion during growth in different populations, least squares regressions were fit to tibial retroversion on age both across the sample as a whole and within each group. Similarly, to evaluate if there is a relationship between age and tibial retroversion during growth in different subsistence strategies and samples, least squares regressions were fit to tibial retroversion on age within each group. 95% confidence intervals were used to determine if the population and subsistence-based slopes differed from one another. To determine if mean retroversion angle varies across populations and subsistence strategies, a one-way ANOVA was performed and a Tukey Post-Hoc test used to evaluate differences in tibial retroversion. Age-corrected residuals from the regressions above were used when testing for differences when there was a significant relationship between retroversion and age. Finally, to assess the relationship between long bone robusticity and retroversion angle, size-standardized cross-sectional properties were regressed on measures of tibial retroversion for the entire pooled sample.

RESULTS

The pattern of tibial retroversion during growth was visually evaluated using a LOESS line, with the “tension value” set to fit to 20% of the data points. This is a fairly narrow range that preserves the visual representation of minor fluctuations in the growth curve (Figure 1). Tibial retroversion is high at birth, drops during the first year of life, and then remains relatively stable throughout the rest of growth (Figure 1, Figure 1a).

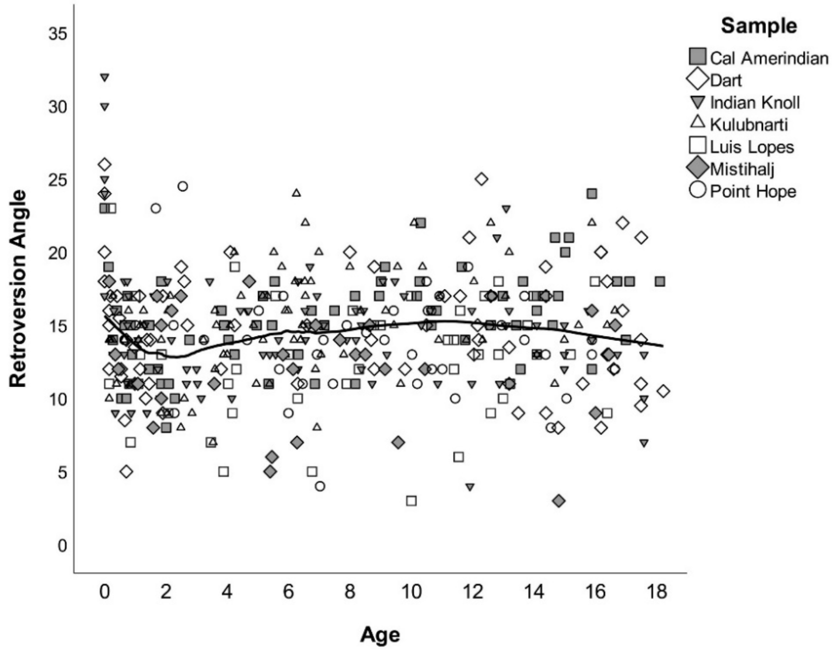

Figure 1: Angle of tibial retroversion on age fit with a LOESS regression line

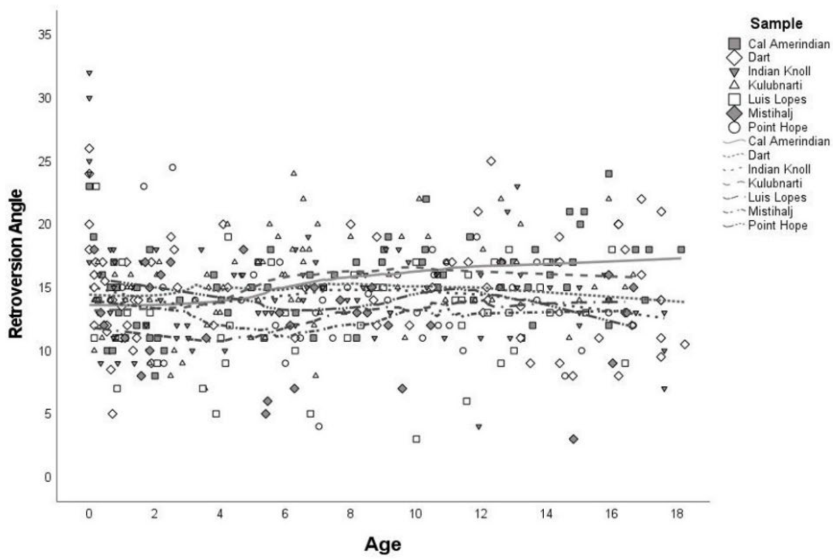

Figure 1a: Angle of tibial retroversion on age fit with Loess regression lines for subgroups.

As the early drop in tibial retroversion likely reflects fetal growth more than post-natal functional factors, specimens less than six months old were removed, which also allows the use of linear models to fit the data. While a linear model can be fit to the data (p = 0.006), age explains only 2% of the variation in tibial retroversion under the age of 18. When retroversion within samples and subsistence groups is regressed on age, similar patterns emerge.

For specific samples, only the regressions for Kulubnarti and the California Amerindians achieved significance (p <0.05), with 9% and 25% of the variation in retroversion explained respectively. Furthermore, 95% confidence intervals around the sample slopes display significant overlap, indicating that patterns of change do not differ among the sample populations (Figure 2). None of the regressions for subsistence strategy attained significance.

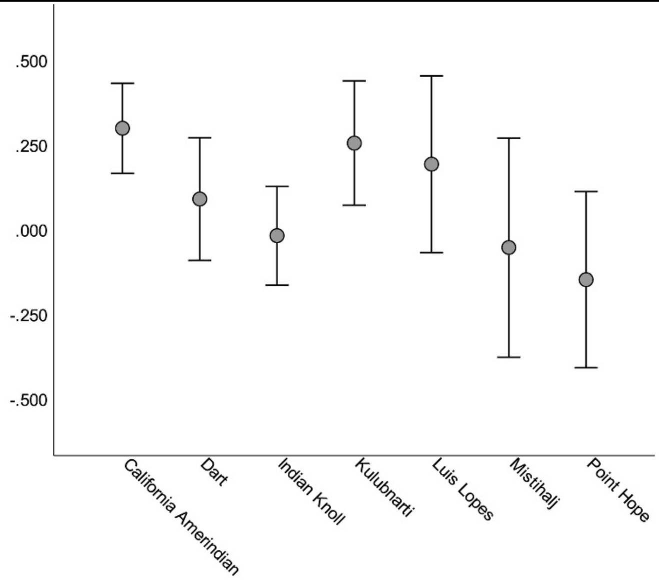

Figure 2: 95% Confidence intervals around least squares slope of retroversion on age. Note that only Kulubnarti and the California Amerindian regressions were statistically significant.

While the amount of variation explained is small, we used age-corrected residuals from the regression of retroversion on age to explore differences in samples and subsistence groups. The mean angle of retroversion is significantly different across populations (p = <0.001). Post hoc testing reveals the mean angle of retroversion in Mistihalj ($\bar{x}$ =12.14) and Luis Lopes is lower and therefore less retroverted ($\bar{x}$ =12.32) than all other populations, while Kulubnarti ($\bar{x}$ =15.16) and Cal Amerindian ($\bar{x}$ =15.34) have higher angles and more retroverted tibia (Figure 3). The mean angle of retroversion is significantly different across subsistence groups (p=0.042). Tukey Post hoc testing reveals that agriculturalists ($\bar{x}$=13.5) have the lowest mean angle of all subsistence groups followed by the urban group ($\bar{x}$=14.3), with foragers having the highest mean angle ($\bar{x}$ = 14.5) (Figure 3).

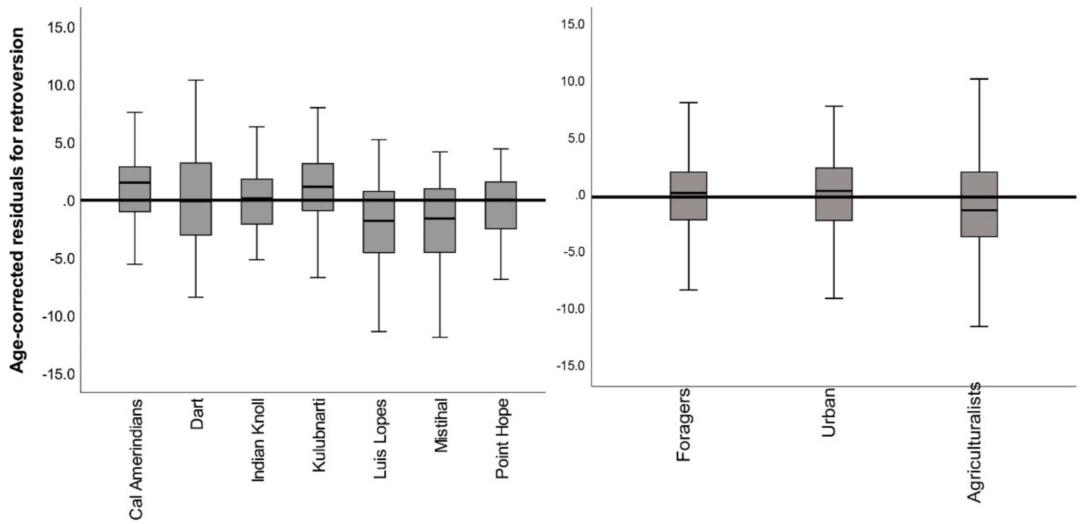

Figure 3: Age corrected residuals for tibial retroversion by sample and by subsistence group.

Size-standardized cross-sectional properties are not significant predictors of tibial retroversion across populations or subsistence groups. Age-standardized tibial retroversion was regressed on standardized polar second moment of area, cortical area, and I_{max}/I_{min}. No model yielded significant results: polar second moment of area (J): (p =0.718, r^2=0.00); cortical area: (p =0.313, r^2=0.003); I_{max}/I_{min} (p= 0.091, r^2=0.008). Patterns are similar within samples and subsistence strategies. When age-standardized retroversion angle was regressed on size-standardized cross-sectional properties within populations, only two models out of 21 attained significance (California Amerindian I_{max}/I_{min}, p=0.013, Kulubnarti Cortical Area, p=0.023). However, these models explain only 10% and 7% of variance, respectively. Finally, there are no statistically significant relationships between age standardized retroversion and size-standardized cross-sectional properties within subsistence groups.

DISCUSSION

There is a noticeable decrease in the angle of tibial retroversion between birth and six months of age. Previous researchers (Charles, 1893, 1894; Huard & Montagne, 1950, 1953; Lustig, 1915; Retzius, 1900; Boulle & Coussement, 1997) have suggested that, following the Heuter-Volkman Law, hyper flexed knees in the fetal environment compress the proximal end of the tibia, affecting the angle of retroversion. After an infant is born, the compression is released. Our results support this interpretation.

However, when the first six months of life are removed from the data, age explains very little variation. Several researchers (Boulle, 2001, Retzius, 1900, and Titze, 1951) have suggested that populations of habitual squatters would maintain flexion of the knee joint over the lifespan, and therefore higher retroversion angles than those who did not assume squatting posture. However, there is little evidence that the relationship between age and retroversion varies across samples given that few relationships are significant, and all slopes are equivalent. Given that there is no decrease in tibial retroversion in any sample, this likely suggests that cultural differences in activities (i.e., habitual squatting) might not be affecting the growth trajectory of retroversion angle.

Previous studies have documented differences between samples and ancestral groups in tibial retroversion. Our data corroborate the findings of most previous research which found that groups with European ancestry have less retroverted tibia than other groups (Haddad et al., 2012; Pangaud et al., 2020). In addition, contradicting historical literature (Thomson, 1889; Charles, 1893) while bolstering medical literature (de Boer et al., 2009; Weinberg et al., 2017), we found that groups of African descent had more retroverted tibia than those of European ancestry.

While there was a relationship between tibial retroversion and subsistence, it remains difficult to interpret. The foragers, as expected, had the highest retroversion, but were followed by the urban group, and lastly, agriculturalists. If this was a product of subsistence-related activity patterns, we would expect the agricultural group to show a higher level of retroversion than the urban group, either due to high levels of activity or squatting. Furthermore, while these groups did differ significantly, the difference between the mean of the highest and lowest subsistence grouping is a single degree, suggesting that this difference may not be biologically meaningful. This result, combined with our analysis of tibial retroversion and cross-sectional geometry (see below), suggests that subsistence and activity patterns may not be significant drivers of variation in tibial retroversion.

Finally, there was no real evidence of a relationship between tibial retroversion and robusticity. If retroversion were produced, as has been suggested, by higher levels of activity and overall robusticity, we would expect to see strong relationships between cross-sectional geometric properties and tibial retroversion. However, none of the models describing this relationship in the pooled samples was significant. While two samples did attain statistically significant relationships, these models explained little variation in tibial retroversion, and given the number of analyses run, are likely examples of type I error.

Taken together, these analyses paint an interesting picture and cast further doubt on the suggestions that tibial retroversion is caused by habitual squatting. If a habitual activity such as squatting were responsible for population-level differences in tibial retroversion, more substantial changes in retroversion during ontogeny would likely be expected. Furthermore, the lack of any association between long bone robusticity and tibial retroversion suggests that the angulation of the tibial plateau many not be affected by activity patterns at all. Given this, the population-level differences in mean retroversion angle detected here and in other analyses remain unexplained but may be related to underlying factors influencing postcranial morphology (e.g, genetics, etc.). Nonetheless, this analysis highlights the importance of re-evaluating long-standing "known" relationships between function and form in bioarcheology and skeletal analysis. Certain relationships, like that between squatting and tibia retroversion, are referenced and cited without critical evaluation of the original literature, with said relationship often having been published many years ago, when standards of evidence differed from our modern expectations.

LIMITATIONS

That said, we cannot conclusively test the relationship between tibial retroversion and squatting specifically here with this study design. Such an analysis would entail careful documentation of squatting frequency across the lifespan in living humans followed by *in vivo* analysis of tibial retroversion on the same individuals (admittedly, a challenging study to execute). While it is impossible with this study design to completely rule out the possibility that habitual squatting leads to tibial retroversion, we believe this analysis does effectively cast doubt on the hypothesis, as it does not appear that retroversion changes during growth, has different growth trajectories in different populations, or is correlated with overall levels of tibial robusticity.

In addition, previous clinical studies have documented higher levels of tibial retroversion in females than in males (Brandon et al., 2006; Dare et al., 2015; Haddad et al., 2012; Hashemi et al., 2008; Hudek et al., 2011; Todd et al., 2010; Weinberg et al., 2017). This suggests that sex may be a factor influencing tibial retroversion variation. While there are known differences in skeletal bone growth and maturation between the sexes, one of the primary limitations of work with bioarchaeological skeletal collections is that sex is not known and cannot be reliably determined from immature skeletal remains. Therefore, male and female remains were not analyzed separately here, and we cannot account for variation in tibial retroversion that is related to sex.

CONCLUSION

Using a diverse range of ages, ancestral populations, and subsistence strategies this research is the first to look at retroversion across ontogeny. Tibial retroversion does not appear to be developmentally plastic, unlike other articulation angles (bicondylar angle, humeral torsion) that shift with age over the course of growth. Population differences emerge at early ages and are generally maintained throughout growth, suggesting that variation in retroversion may be caused by other factors. There is no relationship between tibial retroversion and average tibial bending rigidity, implying that variation in this feature is not purely a function of loading and activity levels. The lack of evidence for a functional explanation of tibial retroversion calls into questions long standing hypotheses about a link between squatting and tibial retroversion. Further research is necessary to fully clarify the etiology of this postcranial feature.

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