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Bipedalism is a Balancing Act: Talus Landmarking in Facultative Bipedal Primates

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BIPEDALISM IS A BALANCING ACT:
Talus Landmarking in Facultative Bipedal Primates

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Abstract

Obligate bipedal locomotion, mandatorily walking on two legs, is vastly important as it is the fundamental precursor to the human lineage; it precedes tool usage and language. Chimpanzees, our closest living ancestors for the human ancestral condition, are often the proxy and are the dominant subject of human bipedalism studies. However, there are additional species, such as arboreal Black Spider Monkeys (*Ateles paniscus*) who habitually travel through the trees bipedally. Including these facultative bipedal primates (FBP) introduces a new lens to how modern human talus and calcaneus' mobility has adapted to environmental shifts such as the transition from arboreal to terrestrial habitation. Studying ankle and heel morphology across multiple species with varying levels of bipedalism allows us the opportunity to better understand how lower limb mobility and stability differ as primates become more terrestrial. I provide quantitative and comparative analyses of tarsal morphology in *Homo habilis*, an early human ancestor, along with various FBPs: chimpanzee *(Pan troglodyte),* Black spider monkey *(Ateles paniscus)* and Western Gorilla (*gorilla gorilla)*, as well as obligate bipedal primates (*Homo sapiens sapiens*) by using a visual quantitative method known as geometric morphometrics (GM). GM is a standard in the field of comparative functional anatomy and paleoanthropology which allows researchers to identify patterns in variation of morphology by essentially stacking images taken in a standardized way "on top of one another." We found that the morphology of the ankle joint will be more similar between early hominins and modern humans than that of FBP. This research continues to improve our current understanding of how paleoenvironmental changes in the past 3 million years might have influenced the evolution of bipedalism in primates, particularly in hominins

and more recently, humans. We also hope this work will facilitate broader inclusion of FBPs in studies of hominin functional morphology.

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I'd also like to acknowledge my friends and family, particularly my boyfriend Jose, and my grandfather, Grandpa "Greg" Bunner (he/him), with whom I have spent nearly every Sunday evening with having homecooked meals, movies, and tangents of conversations with for multiple years now. One can get lost trying to balance being a student, worker, and everything that entails becoming an adult. Thank you for reminding me that growing up is a learning act, and for allowing me that space to grow. Your wisdom and humor are unmatched, and I am grateful to have you by my side. I know that Grandma Linda looks down from Heaven, smiling, that we have each other. I will forever love and miss you, Grandma, and will continue to keep my promise to seek out what makes me happy, even if I have to keep that cast-iron at my side (a joke, we had). I also need to acknowledge my best friends, Paperclip and Mouse, who have been at my side since high school, and (hopefully) throughout graduate school. Your beautiful meows and assortment of calico fur are forever in my heart and inked on my arms. Lastly, I’d like to thank an old friend for recommending Anthropology to me; I finally found my niche.

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Introduction

Walking on two legs, bipedalism, is a form of physical movement that exists in more than just modern humans. Animals of all sizes exhibit different forms of bipedalism; from kangaroos who exhibit a hopping gait to quadrupedal animals like chimpanzees and gorillas, and even cockroaches who have been known to run bipedally at high speeds (Alexander, 2004).

While there are stark phenotypical (visible) differences between modern humans and quadrupedal primates like chimpanzees, gorillas and monkeys, there are incredible similarities when it comes to movement; all primates exhibit a form of bipedal locomotion, although it is not as efficient or fluid as modern humans. This does not suggest that their anatomy is “less developed”, but rather that it suffices the environmental pressures they inhabit, such as climbing trees and quadrupedal knuckle-walking.

Paleoanthropologists like Jeremy DeSilva (he/him) continue to decipher the intricacies of bipedalism by studying extant (contemporary) and extinct primates, using footprints and facultative bipedal primates (FBP) such as chimpanzees and gorillas to draw conclusions about our shared lineage. Linking mobility and stability in the talus and calcaneus between hominins like *Homo habilis (H. habilis)* and other facultative bipedal primates (chimpanzees and black spider monkeys) has been a missing link to these studies, of which I intend to delve into. The importance behind this study is to quantitatively decipher and visualize the temporal space that existed between the two of these groups.

Literature Review

Bipedalism, as mentioned, is a defining feature of hominins. It is central to interpretations for what phenotypical traits and morphologies the elusive common ancestor to modern *Homo sapiens sapiens* may have looked like. The elusive traits of the early forms of bipedalism are inferred from the scarce fossilized remains of various genera of early hominins such as *Sahelanthropus*, *Australopithecus* and early *Homo*. In order to attempt to understand bipedalism in the past, we must first understand its processes in the present. Therefore, in this review, I aim to support the discussion surrounding the quantification of lower limb bone morphology, particularly in two of the seven tarsals: the talus, and calcaneus, specifically. The importance behind this review adds to discussions supporting bipedalism and impacts upon the mysteries of human evolution.

Definition and significance of bipedalism

There are several forms of bipedal locomotion that modern *Homo sapiens* complete including walking, skipping, hopping, and running. These forms of locomotion, among others, exhibit a gait, or style of movement. One such important gait used by all FBPs and obligate bipedal primates is heel-strike. Secondly, bipedalism is one of the defining features that scientists use to define the human lineage, spanning approximately 7 million years ago (mya). There are several skeletal and muscular factors that must be present for bipedal locomotion to occur. These factors will be discussed further below. In the interest of understanding our own origins, the evolution of bipedalism has been a prominent discussion in the field of paleoanthropology, creating debate on mankind's place in the natural world and placing scrutiny upon the interpretations of the origins of modern *Homo sapiens*. Having anthropological discussions around the morphology of the tarsals directly impacting interpretations of bipedalism supports scientific inferences of the phenotypical traits and morphologies our/the elusive last common ancestor of humans may have looked and locomoted.

Evolutionary timeline (*Sahelanthropus* to modern *H. sapiens*)

Because of the scarcity of hominins in the archaeological record and strict requirements for fossil preservation, understanding our shared ancestry and divergence from the Great Apes is not well known, and thus highly interpretative. Human evolution spans back at least 7mya; a blink in the eye of the 4 billion years of Earth's existence beginning with the excavation of *Sahelanthropus tchadensis (S. tchadensis)* and several of their bones, including a femur with a bicondylar angle in 2001 to 2002 by Michel Brunet and his team in Chad, Africa.

The Australopithecines were highly adaptable and fully bipedal hominins ranging from 4.4 to 1.4mya who retained arboreal (habitation in the trees) adaptations likely due to the highly variable climate they existed within. The Australopithecines, like all ancient hominins, originated from various parts of Africa; from the eastern side with the infamous Lucy (*A. afarensis),* and others like *A. boisei and A. robustus*. The southern side boasts the incredible *A. sediba* and *A. africanus* (Mascia-Lees & Black). They were chimpanzee-like in nature, with much longer arms than legs and had curved, rather than straight phalanges (finger/toe bones), indicative of environmental pressures that favored adaptations for climbing. The Australopithecines are one of the best studied early hominins due to their availability in the archaeological record, with a whopping I300 individuals. *S. tchadensis* and the Australopithecines span a temporal time of 3 to 4 million years. While scientists attempt to paint a picture of how *S. tchadensis* looked and moved, the comparisons made between their femur and the Australopithecines are striking. Since the discovery of *A. africanus*, paleoanthropologists have posited that the origin of bipedality has been a result of or linked to the changing environment in Africa. What exactly brought about the change in the environment continues to intrigue scientists and paleo-enthusiasts in prior and future decades to come. The expansion of the savannah and open-grassland habitats have been connected to the decrease in arboreal adaptations present in many primates today, such as the shoulder (clavicle) and immense dorsiflexion of the foot. *S. tchadensis* likely lived in a mosaic of environments, ranging from forests at the edge of lakes to savanna woodlands along water margins (Su, 2013). Around 2.7mya, major climate shifts occurred from ice age to interglacial periods, suggesting locomotor and morphological adaptations for hominins like the Australopithecines and the origin of the genus *Homo*. (McNutt, E. J. et al, 2021). This means that selection for bipedalism did not evolve on the open savannahs, as scientists originally hypothesized, but in more mosaic, closed environments.

Anatomy and Function: A connection between fossils and the past

While bipedalism is a behavioral trait, we can diagnose it in extinct species thanks to clues left behind in fossilized anatomy. The discussion around the femur is important when analyzing bipedalism because it directly impacts gait and impact absorption in the talus. The femur is the heaviest and strongest bone in the body. It supports the body’s weight entirely during all different types of bipedal locomotion. The femur is central to identifying bipedalism by analyzing the slope, or bicondylar angle between the proximal femoral head and the distal end. Because of its robusticity, it is often frequently recovered in archaeological sites and medical contexts. The femoral head and distal end of the femur have two circular ends, epicondyles, that connect to the hip and knee joint respectively. In humans, the only obligatory bipedal primates, the bicondylar angle is extremely evident if the femur is viewed anteriorly on its distal end. The evolution of the bicondylar angle is of utmost importance; it is definitive proof of bipedal locomotion, and as such, is a key characteristic when identifying hominins and early humans. This angle is unique to humans and spans between 8 and 14 degrees; it supports the body by placing the knee and foot directly under the body's center of gravity which runs directly vertical to the body's stature. In quadrupedal primates, the bicondylar angle is non-existent due to their center of gravity being perpendicular to their ventral (chest/stomach) region, and several anatomical discrepancies.

Further down, the talus and calcaneus work together as two of the seven articulated foot tarsals in human and non-human primates. The talus is a tarsal bone that sits between the tibia and fibula (distal leg bones) and on top of the calcaneus. The talus allows for movement of the foot in several directions, which assists in the efficiency of bipedal locomotion and vertical climbing in non-human primates. The talus has undergone significant changes in its degree of movement and is inversely related to the stability of the foot, discussed further below. The calcaneus, however, is the largest tarsal bone and forms the base of the distal part of the foot. It plays a significant role in providing stability and support for the foot during all weight-bearing activities, including bipedalism. The calcaneus additionally distributes the weight evenly across the body, absorbing and dissipating the forces generated during locomotion. Together, these tarsals along with the femur bone provide a stable foundation for the foot while allowing enough mobility for efficient bipedal locomotion.

Functional anatomy is the study of how various organisms, and their associated musculoskeletal systems respond to their environments through anatomical description. Standard Anatomical Position (SAP) is a highly valued standard in the field of anatomy, encompassing several different scientific fields, including paleoanthropology. The SAP terminology is provided from the perspective of the individual being studied, rather than the researcher. AP and descriptions of movements are crucial to the usage of functional anatomy as it provides strict locations for various points on the body. The use of functional anatomy in understanding the evolution of bipedalism strengthens arguments when describing the various morphology of the calcaneus and talus throughout our shared evolution.

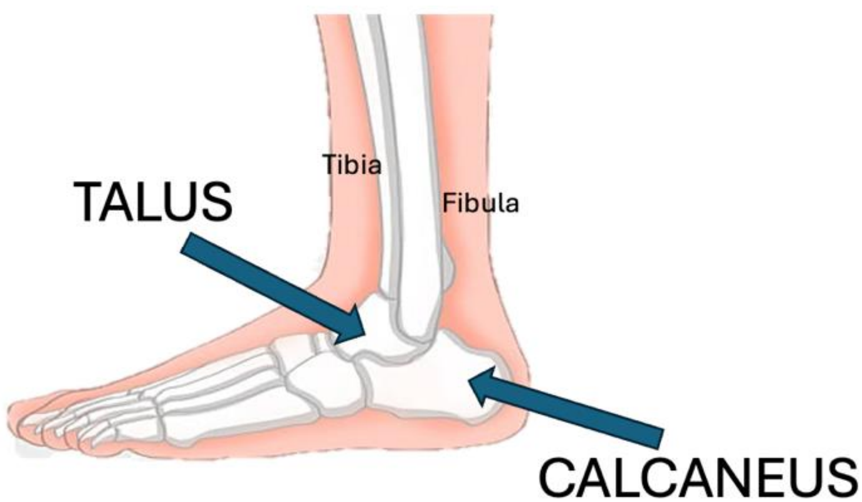

Figure 1 An image of a left lateral modern human foot with arrows depicting the location of the talus and calcaneus.

Buttressing and Ligaments

The longitudinal and transverse arches of the foot play a crucial role in balancing stability and mobility during walking and running. These arches, supported by ligaments (muscle attachments) act as natural shock absorbers and are responsible for maintaining the structural integrity of the foot. However, there is a trade-off between mobility and stability. In order to adapt to uneven terrain or absorb shocks during dynamic activities, the foot may need to exhibit mobility, which can involve changes in arch height (pronation and supination). During normal gait, the foot should be mobile enough to adapt to the ground's contours but stable enough to stabilize and support the individual’s body weight. Therefore, too much stability limits the foots natural adaptation to terrain and shock absorption, resulting in further energy consumption and thus less efficient bipedal locomotion.

The ankle joint, specifically the tali-calcanei joint, exhibits a complex system of ligaments and bony structures that contribute to the balancing act that bipedal locomotion treads. This balancing act between mobility and stability results in buttressing in and anteriorly around the ankle joint. Buttressing is the reinforcement of the joint’s structural integrity through the development and (re)arrangement of ligaments and bony structures. While buttressing in the ankle joint can be challenging to identify, morphological traits such as the size and shape of specific bony landmarks and the presence of ligament attachments provide valuable information.

Key Differences in anatomy between quadrupedal and facultative bipedal primates (FBP)

The primary key differences between quadrupedal and FBP in the discussion of the evolution of bipedalism surround two major pieces of anatomy: (1) the pelvis, including the hip joints, and (2) the feet. The pelvis and hip joints of quadrupeds differ in orientation (direction), shape, and by the amount of weight disbursement across the body. The orientation of a quadruped's pelvis, such as the case with *Ateles paniscus* and chimpanzees, disburses the body weight across all four limbs in contrast to humans' disbursement between their legs. modern humans' pelves are much more 'bowl shaped' and oriented circular to support the weight of the body during locomotion as a result of the center gravity being directly vertical to the knees.

The feet, on the other hand, features a crucial difference between quadrupedal primates and FBP. The human foot features three primary arches: the medial longitudinal, lateral longitudinal, and transverse arch (White et al., 2012). These arches are formed by the arrangement of bones, ligaments, and tendons (connective tissues) in the foot. They allow the foot to adapt to a variety of terrain by flexing and stiffening the arches as necessary; this is crucial for maintaining balance and stability.

Implications of bipedalism

The anatomy of chimpanzees does not allow them the ability to stand upright; the connection between the proximal (closer to the center, or median of the body) femoral point and the pelvis is comparatively shorter in chimpanzees than it is in modern humans;

the hip muscles cannot contract effectively. This removes the possibility for the body to support them during upright walking. Additionally, the shape and orientation of a chimpanzee's pelvis is much more rectangular than rounded as seen in early hominins. (Alexander, 2004) states that the slope of the chimpanzee trunk places the center of mass of the body forward of the hips, causing them to wobble and have more imbalance during bipedal locomotion. For bipedal walking at a constant rate, the downward forward on the foot must be perpendicular and vertical to the center of mass (Alexander, 2004).

Next Steps

In order to further study how bipedal locomotion works, the study and statistical analyses of biomechanics has been crucial. Changing the locations of stress upon the body (i.e., the location of the weight, the fulcrum (origin), the load itself) changes the speed, strength, and durability of multiple levers within the body and thus changes how the human body interacts with its surroundings. Various gaits are exhibited by these changes in musculoskeletal levers in several taxa; the kangaroo, for example, exhibits a much more powerful force arm than modern humans do as a result of a lengthened force arm resulting in incredibly powerful hops compared to the average hop possible in a human.

The purpose of this study will be to quantify one aspect of bipedal locomotion – ankle stability vs mobility, and how it varied from obligate to facultative bipeds and from terrestrial to arboreal primates. To do this, I employed a frequently used practice of statistical method known as geometric morphometrics (GM). GM is a technique where a set of similar images can be grouped together using chosen positions, referred to as landmarks, to draw comparisons and visually depict variation in shape. GM is a standard in the field of paleoanthropology as it uses a digital landmarking technique to discern levels of variation between similarly shaped objects.

Methods

Data collection was carried out by taking several (n=5) 2D images that were then processed by open source, free to use software known as TPSDig2, TPSUtil, and a graphing software known as MorphoJ, which all work collaboratively to digitize specific landmarks (points of interest) on the lateral side of the right foots' talus to visually depict buttressing in the bone. Using a smartphone's (iPhone 13 Pro) front-facing camera fixed to hand-made apparatus using corrugated cardboard and duct-tape, images were then taken in landscape mode at a fixed distance of 30.5cm (12inches) from the bone casts. The bones were positioned directly in front of a yardstick in lateral position to procure easily identifiable landmarks, chosen through the identification of specific ligaments: the calcaneofibular, anterior talofibular, and posterior talofibular ligament. This methodology not only enhances the efficiency of the resulting dataset generated by GM and Principal Component Analysis (PCA) but also ensures a standardized approach for all bone casts involved. Using this methodology, all specimens with the exception of the bone casts remain in a fixed, unmoved position to ensure accuracy. The captured images were uploaded to the aforementioned programs and used to discern varying levels of buttressing on the lateral aspect of each specimen's tali-calcanei joint. The calcaneofibular, anterior talofibular, and posterior talofibular ligaments served as landmarks for reference.

This study uses extant FBP for a few reasons, including: the utilization of living primate species to build a comparative framework to understand fossil data is standard best practice within paleoanthropology, allowing us to mitigate much of the unknowns and subjectivity when using extinct species; concretely linking anatomical form to known functional significance. Additionally, using extant species was a data limitation due to the lack of availability of bone fossils. The majority of specimens (*Homo habilis, Homo sapiens sapiens, Gorilla gorilla, Pan troglodyte)* used in this study came from the Anthropology Lab at the University of Northern Colorado, Greeley, Colorado, and the remainder of the specimens (*Ateles paniscus*) were graciously provided by Colorado State University's primate research lab in Fort Collins, Colorado. Pictures were taken both at Colorado State University and the University of Northern Colorado.

Figure 2 From top left: In yellow, vertical shaft and associated base. Laptop, tape measure, counterweight, pen, AirPods Pro, Field Notebook.

Results

Depicted in the first and second components, it is found that *Homo habilis* (pictured top left, Figure 1) is the most distant from all the other specimens used, particularly the *Homo sapiens sapiens*, (pictured bottom, center). This came as a surprise because *H. habilis* and *H. sapiens sapiens* were, and currently are fully bipedal primates.

Focusing upon the secondary figure, we find that the largest variation in landmarks (n=11) exists predominantly in the first and eleventh landmark; moreso in the former. This was a surprise to find as I expected there to be a large amount of variation in the 5th through 8th landmark, indicative of the anterior talofibular ligament (ATFL) and Posterior Talofibular Ligament (PTFL), which both connect the fibula to the anterior side of the talus in differing depths. However, because the first and eleventh landmark exhibit the highest variation, future studies should consider how the anterior and posterior ends of the anterior talus joint may contribute more buttressing when compared to the superior and inferior ends of it, such as seeing how landmarks one and eleven contribute more than potentially five and eight, or any similarly placed landmarks.

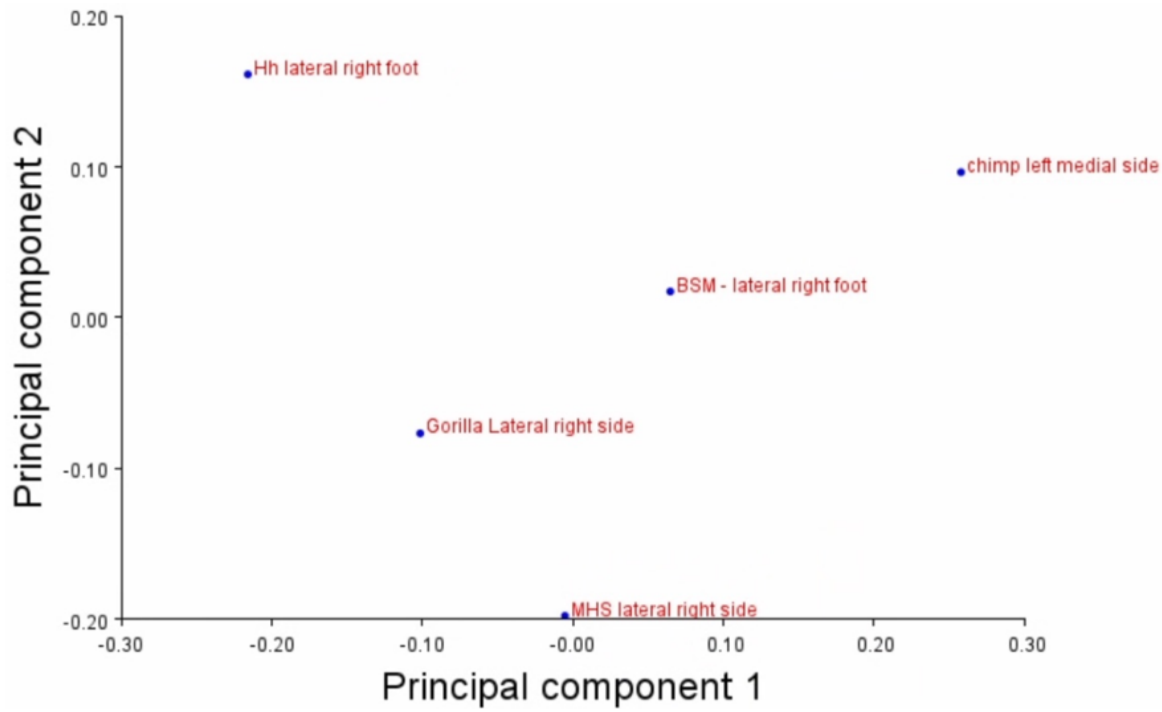

Figure 3

A Principal Component Analysis graph depicting levels of variation found between the five (5) specimens analyzed using geometric morphometrics in MorphoJ

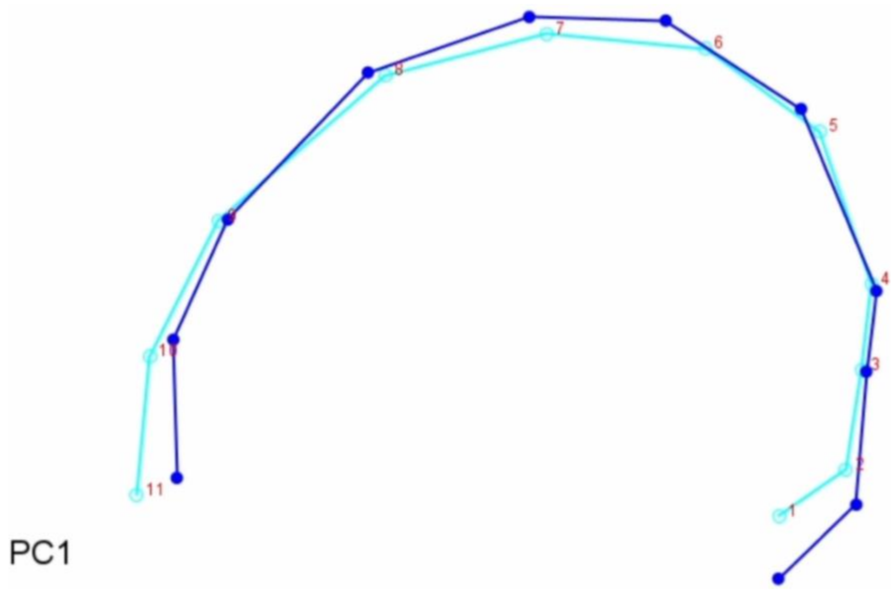

Figure 4:
A wireframe graph depicting the varying levels of variation depicted from each of the 11 landmarks and semilandmarks depicted by MorphoJ.

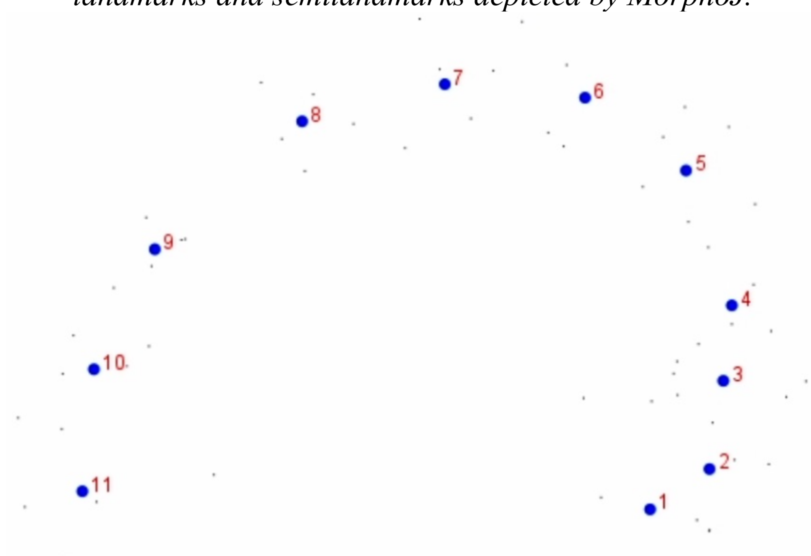

Figure 5:
A graph depicting the variation in each of the landmarks, as well as their original points. The mean of the points is notated in the larger, blue points and the original markers is the speckled-grey points surrounding them.

Discussion

The study of bipedalism cannot be divorced from the environmental contexts in which it evolved. Throughout human evolution, significant shifts in climate and habitat have influenced primate, and therefore human locomotion. For instance, during the transition from arboreal to terrestrial habitats, environmental pressures shaped primate anatomy and behavior, including the development of bipedalism. By examining fossil evidence and paleoenvironmental data, researchers can infer how these environmental changes impacted the evolution of bipedalism.: As mentioned, the transition from forested environments to open savannahs in Africa around 2.7 million years ago likely played a pivotal role in the emergence of bipedalism among early hominins. As forests receded and grasslands expanded, hominins adapted to more open terrain, leading to changes in locomotor behavior and morphology.

While obligate bipedal primates like modern humans provide valuable insights into bipedal locomotion, studying FBP offers a broader perspective. FBP exhibit a range of locomotor behaviors, from arboreal climbing to occasional bipedalism. Including FBP in comparative studies allows researchers to explore the continuum of bipedalism and better understand its adaptive advantages across diverse ecological niches, as seen in *Ateles paniscus*. By studying the talus landmarking in FBP alongside obligate bipedal primates (*Homo),* we can continue to understand how bipedalism manifests in different ecological contexts and its implications for locomotor efficiency and stability.

Limitations

The number of limitations available in this study are an understatement despite the growth of education that took place. One of the largest limitations of this study was, as expected in the field of paleoanthropology, the quantity of specimens available for study. This study could be further improved by not only having more specimens, such as multiple individuals from the same species, as well as having access to the original specimens, rather than casts. Using casts, such as BoneClones, was a limitation to this study due to the decreased quality and accuracy of the articulated surfaces.

Another limitation to this study was in the acquisition of the 2D photos. The study of geometric morphometrics requires photos to be taken with extreme caution and precision in regard to the orientation of the specimen (such as lateral versus medial orientation) and proximity from the camera for scaling purposes. Deviating from this would incur error into the study, impacting the accuracy of the results of the PCA. Therefore, future studies should standardize the usage of the rear-facing camera to avoid this issue.

Conclusion

The art of bipedalism is truly a balancing act that has several factors working together to support the forward motion of all life on Earth. Studying bipedalism through the lens of incorporating more diverse facultative bipedal primates allows us, in some ways, a broader perspective into evolutionary anatomy, functionality and the origins of humankind. By examining talus landmarking in facultatively bipedal primates, this research contributes to deepening the understanding of primate locomotion and the origins of human bipedalism.

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