COMPARATIVE DIGITAL EXAMINATION OF THE TALOCRURAL (ANKLE) JOINT PROVIDES INSIGHT INTO HUMAN BIPEDAL LOCOMOTION

by

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Comparative Digital Examination of the Talocrural (ankle) Joint Provides Insight into Human bipedal locomotion

Abstract
by
ALLISON ZIMMERMAN

Abstract
Locomotion strategies across human evolution are a prominent topic of discussion. The talocrural joint, a major weight-bearing ankle joint, is a feature of this discussion since all animals, including humans and our ancestors, have different functional requirements depending on locomotor modality. These requirements, featuring flexion and extension of the foot, are reflected in morphology of the bones that comprise the talocrural joint (tibia, fibula, and talus). Using a high resolution 3-dimensional laser scanner (FARO Arm EDGE), digital models of these bones from a sample of humans (N=19), fossil hominins (4.4 million year old *Ardipithecus ramidus*, 3.2 Ma *Australopithecus afarensis*, 1.8 Ma *Homo habilis*), non-human primates (N=29), ursids (n=3), and felids (n=2) were created and shapes of the talocrural joint surfaces were analyzed to identify locomotor patterns. Locomotor modality was identifiable through orientation of the joint surfaces and various morphological traits. Body size was also considered as another factor in morphology.
I. Background Information

**Talocrural Joint**

The talocrural joint is a major weight-bearing joint of the ankle and is comprised of the distal articular surfaces of the tibia (tibial plafond) and fibula as well as the proximal surface, or trochlea, of the talus (Figure 1.1a). The proximal articular surface of the talus (talar trochlea) can be represented by a cone with the apex, which faces medially in this model, removed. The distal articular surface of the tibia (tibial plafond) can be represented by a surface of similar conical dimensions with a smaller medial radius, corresponding to the general shape of the talus. Both surfaces are covered with a thin layer of elastically deformable material, articular cartilage (Figure 1.1b) (Hlaváček, 2000). This joint, otherwise known as the ankle mortise, is a hinge joint with an axis of rotation located just distal to the lateral and medial malleoli of the fibula and tibia respectively.

![Figure 1.1](image.png)

**Figure 1.1.** Basic construction of the talocrural joint: (a) a coronal section through the complete talocrural joint, showing the hyaline cartilage in orange and the axis of rotation in green; (b) a representation of the tibial plafond slightly separated from the talus, represented by the frustum of a cone, weighted lines represent the articular faces of the joint.
In examining the load distribution on the talocrural joint during weight-bearing, it has been determined that the tibia is responsible for the majority of loading (Lambert, 1971). Although the weight-bearing function of the fibula has been studied, the percentage estimated from strain gauge studies on cadaver specimens is reported to be minimal (Goh et al., 1992; Lambert, 1971). The loading placed upon the fibula could also be the product of muscular activity, where the muscles that attach at the fibula could be responsible for producing a load through contraction (Inman, 1976). This nominal role in supporting the body has been utilized in the common use of the fibula during surgery to supply bone grafts with few issues in ankle instability (Goh et al., 1992, Nakagawa et al., 1984).

The fibula has also been proposed to add some degree of talocrural joint stability through ligaments that attach to the distal surface of the bone (Goh et al., 1992; Johnson & Markolf, 1983; Konradsen, Ravn, & Sørensen, 1992; Lambert, 1971). The anterior talofibular ligament in particular has been highlighted due to its uniform presence in humans as a primary stabilizer (Johnson & Markolf, 1983; Konradsen et al., 1992). However, the uniform presence of this ligament in the human ankle among the great apes does not correspond with additional strength. Sprains of the human ankle have been found to be predominantly caused during instances of extreme inversion, in which the anterior talofibular ligament is among the first structures to be damaged (DeSilva, 2009). This particular ligament in the ankle highlights the mechanism of ligaments of proprioception.

Proprioception, or awareness of a part of the body in space, is dependent
upon a rapid reflex arc that triggers muscular contraction as a response (Frank, 2004). Following an injury, proprioceptive deficits have been documented that result in ankle instability in the absence of re-training (Freeman, Dean, & Hanham, 1965; Johnson & Markolf, 1983; Konradsen et al., 1992). The fibula’s primary purpose is one of muscular attachment, providing attachment for the biceps femoris, peroneus longus, brevis, and tertius, extensor hallucis longus and extensor digitorum longus. While there have been attempts to explain the fibula’s function in the talocural joint, discussion of the analyses frequently results in a commentary on fibular morphology, rather than on how the fibula impacts joint mechanics due to the lack of function the fibula has during weight-bearing in the talocural joint (Stern & Susman, 1983; Takebe, Nakagawa, Minami, Kanazawa, & Hirohata, 1984). The focus of joint mechanics will therefore remain on the tibia and talus to better understand how these two bones function as a unit under loads. The relationship between the tibia and talus will be described in multiple species to identify various osteological signatures of locomotor patterns.

Movements possible at the talocural joint are mainly dorsiflexion and plantarflexion (Figures 1.3 and 1.4, pg. 10). The cone-shaped morphology of the talus, being wider anteriorly than it is posteriorly, causes some external rotation during dorsiflexion and internal rotation during plantarflexion (Barnett & Napier, 1985; Close, 1956; DeSilva, 2009, 2010; Inman, 1969, 1976; Isman & Inman, 1969) Throughout the range of motion, both the lateral and medial malleoli are constantly articulated with the lateral and medial aspects of the talus respectively, despite the misconception that the wedging of the talus would lead to
forced separation of the malleoli in dorsiflexion or joint laxity in plantarflexion (Inman, 1976). The ligaments that attach to the three bones facilitate the stable mortise structure of this joint (DeSilva, 2009; Freeman et al., 1965; Konradsen et al., 1992). The anterior and posterior tibiofibular ligaments connect the distal tibia and fibula, while the strong deltoid ligament stabilizes the medial side and anterior and posterior talofibular and calcaneofibular ligaments support the lateral aspect of the ankle (Figure 1.2) (Close, 1956; DeSilva, 2009).

Deltoid ligament: -Posterior tibiotalar -Tibiocalcaneal -Tibionaviculare

Anterior tibiofibular
Posterior tibiofibular
Posterior talofibular
Anterior talofibular
Calcaneofibular

Figure 1.2. Illustrations of the medial (left) and lateral (right) ligaments of the talocrural joint.

Dorsiflexion is the motion at the ankle that brings the toes closer to the anterior aspect of the leg and has a normal range of 10-30° in the human joint (Figure 1.3). Soft tissue limitations to a higher range of dorsiflexion include the Achilles tendon. More influential is the bony morphology, which limits dorsiflexion to the point at which the anterior distal tibia contacts the neck of the talus.
Plantarflexion is defined as the motion at the ankle that increases the distance between the leg and toes and has a normal range of motion in humans of 20-50° (Figure 1.4). Plantarflexion is limited by the posterior margin of the distal tibia contacting either one or both of the posterior bony tubercles on the talus (Latimer, Ohman, & Lovejoy, 1987). The soft tissue also imposes substantial limitations through the anterior ligaments of the ankle.
The talus is a unique bone, having no muscular attachments whatsoever. Movement at the talocrural joint is therefore a product of the activity of the muscles that make up the compartments of the lower leg and insert onto the surrounding tarsal bones. Muscular activity takes one of three forms of contraction. Concentric contraction occurs when the muscle contracts and shortens as tension builds to lift a load that is less than the force generated by the muscle. Eccentric contraction involves contraction of the muscle as it lengthens due to the load being greater than the force generated by the muscle. In isometric contraction the muscle neither shortens nor lengthens. The force generated by the muscle in this type of contraction matches the load, and the muscle neither shortens nor elongates (Figure 1.5).

![Figure 1.5](image)

Figure 1.5. Three types of muscular contraction demonstrated in the biceps brachii muscle: (a) isometric contraction, with no movement of the limb, (b) shortening of the muscle during concentric contraction, and (c) lengthening of the muscle during eccentric contraction.

Concentric contraction of the *m. tibialis anterior*, *m. extensor digitorum longus*, *extensor hallucis longus*, and *peroneus tertius* results in dorsiflexion, along with eccentric contraction of the posterior leg compartment. These muscular factors are augmented by passive elements, most notably resistance provided by the substrate. Plantarflexion occurs through concentric contraction of the posterior compartment - the *triceps surae, plantaris, flexor hallucis longus,*
flexor digitorum longus, tibialis posterior and peroneus longus.

**Synovial Joints**

Synovial joints are the most mobile joint type in the body, due to the combination of hyaline cartilage-covered articular surfaces and the synovial capsule that encompasses the joint space. This results in a virtually frictionless joint (Hlaváček, 2000; Siegler & Moskowitz, 1984). Hyaline cartilage, found in the talocrural joint coating the tibial plafond and the trochlea of the talus, is comprised of three zones. Each zone, superficial, middle and deep, has a different organization of the cells and patterning of the cartilage fibers (Hlaváček, 2000; Walker et al., 1968). This cartilage, which varies only slightly in density between the different joints of the body, is avascular. This means that nutrients in the synovial fluid can supply the articular cartilage only through diffusion (Walker et al., 1968). Articular cartilage presents viscoelastic properties as a hydrated gel-like substance, combining solid and liquid phases. The cartilage fibrils tense under strain and respond to loading in a non-linear manner (Li, et al., 1999). Once the cartilage deteriorates through aging or excessive loading, its capacity for self-repair and regeneration is poor, frequently observed in the human hip and knee joints and necessitating the need for joint replacement technologies.

The synovial capsule is full of synovial fluid, comprised of hyaluronic acid and protein molecules suspended in water. Depending on the concentration of molecules, the viscosity and elastic properties vary from joint to joint. The patterns of talocrural loading are dependent on the interaction between the
accumulation of forces coupled with the properties of synovial fluid and articular cartilage. The “squeeze-film” loading pattern represents what occurs during weight-bearing at the talocrural joint (Figure 1.6). In this model, there is an upper solid (the tibia) that contacts a lower solid (the talus). In the middle of the two solids, both covered with articular cartilage, is the synovial fluid whose viscosity keeps the two cartilaginous surfaces from touching. As the duration of loading increases, the viscosity of the fluid increases along with the thickness of the synovial film (Balazs, 1974, Hlaváček, 2000; Walker et al., 1968). In normal motion, both the articular cartilage and synovial fluid function to eliminate the friction that would occur during flexion and extension under loads. The negligible friction originating from the cartilaginous surfaces and synovial fluid results in an inherently unstable joint surface. This requires the major transarticular forces be perpendicular to the joint surface in normal joints in order to avoid injury.

![Figure 1.6](image.png)

Figure 1.6. The talocrural joint is an example of a squeeze film lubrication method under loading, adapted from Walker et al., 1968.

**Bone Scaling**

As an individual’s body size increases, there is an increase of the forces to which the joints are subjected. Both Wolff’s Law and the Heuter Volkmann Law state that the load across a bone’s growth plate will modify the joint surface topography due to the principle that bone constantly renews (Mullender & Huiskes, 1995; Rubin, 1984; Villemure & Stokes, 2009). Loading patterns are
therefore assumed to modify the specific morphology of the talocrural joint, representing habitual behaviors during formative years. Body size comes into consideration since all forces must load the synovial joint perpendicularly across the articular surfaces to avoid injury, and will increase in magnitude along with body size if all other variables are constant.

For individuals of larger body size, several hypotheses have been proposed as to how the increased weight is managed by the joints (Biewener, 1983, 1989; Christiansen, 1999, 2002; Latimer et al., 1987). The increased transarticular loading placed upon the joint’s surface must remain perpendicular to the frictionless hyaline cartilage. The avascular properties of hyaline cartilage limit this variable in joint mechanics, as the tissue thickness cannot increase with body size (Walker et al., 1969). An increased surface area of the articular faces would appropriately dissipate the force, although this would have to coincide with a decrease of curvature and a subsequent loss of excursion in order to achieve normal loading (Biewener, 1983; Latimer et al., 1987). Another modification is found in the relative angle between the limb and the ground. Smaller animals that do not achieve the velocity of larger individuals can maintain a sprawling posture and have effective momentum and direction changes. Larger animals such as horses have a more perpendicular limb posture to the ground. As the size of the animal increases, these adaptations may work together to maintain a manageable load in synovial joints (Biewener, 1983, 1989; Christiansen, 1999; Jungers, 1988).

**Quadrupedal Locomotion**

Quadrupedalism is part of the locomotor repertoire of a wide range of
mammals. With the diversity of species utilizing this locomotor style comes a number of ways in which the feet make contact with the ground (Figure 1.7). A plantigrade foot posture, in which the entire foot comes in contact with the substrate, is seen in the quadrupedal locomotion of apes and ursids. Primate locomotion is specialized with the flexible hindfeet that can conform to the substrates with which these animals interact, especially valuable with branches of different size encountered during arboreal locomotion (DeSilva, 2009, 2010; Elftman, 1944; Keith, 1923; Thorpe & Crompton, 2005; Thorpe, Holder, & Crompton, 2007; Tuttle, 1981). Primate locomotion includes knuckle-walking, seen in chimpanzees and gorillas, terrestrial quadrupedalism, seen in baboons, suspensory brachiation seen in gibbons and spider monkeys, and vertical climbing which is also mostly observed in the non-human great apes. Primates and ursids also practice facultative bipedalism with a range of success that will be discussed in Chapter III.

Animals such as felids and canids do not contact the ground with their heels during their normal gait cycle, which is a defining trait of digitigrade posture. Here, the heel, tarsus, and the proximal aspects of the metatarsals are kept off the ground during footfall. Two other mammalian foot postures exist that will not be discussed in detail here: ungulates practice unguligrady, in which only the distal phalanx is contacting the ground in the form of the hoof; heavier animals such as elephants use graviportal stance, a form of digitigrady, in which a substantial fat pad supports the foot, resulting in a broad foot shape (Langman et al.).
The earliest indicators of hominin bipedalism emerged with the fossil material from the genera *Orrorin, Sahelanthropus* and *Ardipithecus* that indicated movements and loading patterns specific to bipedal locomotion (Senut et al., 2001). The fossils have been dated to the Late Miocene at around 7-4 million years ago (Ma) and represent the earliest known members of the hominin lineage (Galik et al., 2004; White et al., 1994). Despite the limited evidence for bipedalism associated with these specimens, future discoveries of these genera have the potential to offer evidence of an early adoption of this locomotor style (Senut et al., 2001). Prior to this evidence at 7 Ma, there is evidence of a wide radiation of ape-like arboreal quadrupeds that dispersed across Africa and into what is now Europe and Asia. These animals display locomotor signatures indicating similar behaviors to extant great apes and several have been proposed to be ancestors of several extant species, including modern humans (Galik et al.,
Important examples of sustained habitual bipedalism had been found long before the discovery of the previously mentioned specimens. Fossil specimens from the Pliocene and Pleistocene epochs were discovered in Hadar, Ethiopia (Johanson & Taieb, 1976) and Laetoli, Tanzania (Leakey & Hay, 1979) in the 1970s that proved the existence of a human ancestor that was capable of sustained bipedal walking in representatives of *Australopithecus afarensis* such as the A.L. 288-1 (“Lucy”) specimen (Johanson & Taieb, 1976). From this partial female skeleton, multiple signatures of bipedalism were pinpointed, including her knee, which has a valgus (or “knock-kneed”) alignment, an adducted great toe (hallux) and the presence of a lateral arch. These skeletal features were subsequently confirmed by the uncovering of the Laetoli footprints (Leakey & Hay, 1979; Tuttle, 1991). Although no pedal fossils accompany the 3.6 Ma fossilized prints at this site, this path of footprints provides behavioral evidence for the use of habitual bipedalism by three individuals. Several other species of australopithecines have been discovered across Africa with a range of available fossil material, some offering enough postcranial information to identify locomotor patterns as in *Australopithecus africanus* (Lovejoy & Heiple, 1970; Robinson, 1959). It was not until recent fossils were described that the transitional forms of bipedal locomotion were illuminated in greater detail.

Characteristics of both the Early Pliocene species *Ardipithecus ramidus* as well as *Australopithecus afarensis* have been described in recent publications.
The 2009 series on the partial ARA-VP 6/500 skeleton from the Middle Awash project site (“Ardi”), described the mosaic of morphology and the resulting transitional locomotor style (Lovejoy et al., 2009). Findings consisted of an abducent hallux combined with evidence of a knee positioned closer to the midline. These two observations coupled with increased stability through the longitudinal and transverse arches, demonstrates that *Ar. ramidus* was capable of a toe-off motion through the lateral four toes. However, the abducted hallux represents the preservation of arboreal behaviors at 4.4 Ma (Lovejoy et al., 2009).

*Australopithecus afarensis* has some other remarkably informative specimens linked to the species. In 2006, a juvenile female skeleton from the Dikika project area (DIK-1/1) was described that demonstrated a developing bipedal lower limb through the knee and partial foot (Alemseged et al., 2006). A partial fossil skeleton (KSD-VP-1/1) described in 2010 from Woranso-Mille project area in Ethiopia is one of the larger individuals representing *Au. afarensis*. Although the skeletal remains are less complete than “Lucy”, this presumed male confirms bipedality in this species (Haile-Selassie et al., 2010).

While the partial skeletons discussed above offer substantial behavioral evidence for the species they are assigned to, there is also valuable information that can be discussed for fossil specimens whose species have yet to be determined. A recent example of this, and one relevant to the subject of bipedal locomotion, is available in the pedal fossils found and described by Haile-Selassie and colleagues in 2012, dated to a range from 3.2-3.8 Ma provide another
interesting mosaic. The specimen, contemporaneous with *Au. afarensis*, exhibits an abducted hallux and metatarsophalangeal joints with similar ranges of motion. However, this individual possessed neither a longitudinal arch nor the ability to toe-off through the transverse metatarsophalangeal axis (Haile-Selassie et al., 2012). This specimen indicates that the grasping hindfoot persisted past *Ar. ramidus* and led to at least two coexisting hominin locomotor strategies during the Pliocene.

These individuals offer evidence of the mosaics of locomotion that led to the habitual bipedalism observed in *Au. afarensis* (Haile-Selassie et al., 2010; Latimer et al., 1987; Tuttle, 1991; Ward et al., 1999). The understanding of the development of bipedal locomotion is only as complete as the applicable fossil specimens available for research. Determining where certain species belong respective to extant and better-defined species as well as what sorts of locomotion were present within each species is an ongoing puzzle that will continue to be elaborated upon.

**Bipedal Locomotion**

Habitual striding bipedalism, practiced among extant mammals exclusively by humans, is defined as walking on extended hindlimbs in which the feet cycle between roles as deformable shock absorbers during weight bearing and rigid levers during propulsion (Lovejoy et al., 2009). Human bipedalism is associated with a fully upright (orthograde) posture that allows weight to be distributed directly over the hips throughout the gait cycle (Figure 1.8) (Lovejoy,
This cycle illustrates three of the key attributes of bipedal locomotion: balancing on one leg at a time, stepping forward and contacting the ground with the heel first, and pushing off through all five toes (Elftman & Manter, 1935; Isman & Inman, 1969; Keith, 1923; Lovejoy, 2005a, 2005b, 2007).

These specializations of habitual bipedalism are what set humans apart from other mammals who practice different locomotor styles. The ability to balance on one leg at a time has been obtained largely through the reorganization of the pelvis and the hip and knee joints (Latimer et al., 1987; Lovejoy, 1981, 2005b, 2007). The bipedal heel strike has developed an enlarged calcaneus, one byproduct of full extension of the knee. The construction of the bipedal forefoot is identifiable through an adducted first ray that is the longest in the length progression of the toes. The morphologies of decreased curvature in the metatarsal shafts and dorsal canting of the bases of the proximal phalanges have also been documented to define human pedal structure. These traits have all been established as indicators of a particular toe-off characteristic of habitual terrestrial bipedality (DeSilva, 2009, 2010; Haile-Selassie et al., 2012; Harcourt-Smith & Aiello, 2004; Latimer et al., 1987).
The transition within the human lineage from quadrupedal to bipedal locomotion required certain anatomical changes that made orthograde posture a possibility. Although these changes are present throughout the body, the factors affecting the talocrural joint can be observed at the knee and have been proposed to maladapt humans to primate locomotion, such as vertical climbing (Crompton, Vereecke, & Thorpe, 2008; D'Aout et al., 2004; DeSilva, 2009; Latimer et al., 1987; Lovejoy, 2005a, 2005b, 2007). The knee of a habitual biped contributes to maintaining the vertical loading of the ankle through a valgus knee that positions the tibial shaft perpendicular to the substrate, in keeping with the required loading on the synovial talocrural joint. The knees of non-human great apes posses a varus, or “bow-legged” orientation to their knees, resulting in an oblique superolateral angle of the tibial shaft to the ground during facultative bipedalism (DeSilva, 2009). The talus of a biped also is hypothesized to bear markers of this unusual method of locomotion. Latimer (1987) and DeSilva (2009) discussed the reflection of the varus knee present in the measurement of the angle between the talar trochlea and the axis of talocrural rotation. The measure of dorsiflexion in the bipedal talocrural joint has also been observed to be lower in humans, as the magnitude of dorsiflexion in bipedal locomotion only needs to be great enough to allow the foot to clear the substrate during swing phase (DeSilva, 2009; Latimer et al., 1987).

The skeletal morphology that changed to allow bipedal locomotion has been well documented. Humans gave up the plasticity of locomotion observed in our fossil ancestors, other primates and representatives of other mammal orders.
in favor of the singular modality of bipedalism. Multiple theories have been developed to explain the behavioral advantages that established a selective pressure to adopt habitual bipedal locomotion. One poorly supported hypothesis deals with the concept of energetics, claiming that bipedal locomotion is a more efficient style of traveling over long distances (Jablonski & Chaplin, 1993). This theory has been disproven through observations of the muscular functions of gibbons and other primates who demonstrate efficient bipedal running, despite not being the same habitual bipedalism of humans (Berillon et al., 2011; Harcourt-Smith, 2007; Lovejoy, 1981). A second theory postulates that the orthograde posture assumed during bipedal gait protected early hominins from exposure to a greater percentage of their bodies to the sun. This would have been an advantage during the shift from a predominantly forested environment to surroundings that were much more open (Harcourt-Smith & Aiello, 2004; Jablonski & Chaplin, 1993). Another theory, which has gathered more support than the energetic efficiency proposition, centers on a selective pressure to use the forelimbs to carry food. This provisioning theory is based upon the sexual dimorphism seen in early hominins, drawing parallels between increased parental investment and the division of labor to provide for the young (Lovejoy, 1981). These theories attempt to provide a rational backdrop that attempts to bring together the ‘why’ and ‘how’ of habitual bipedalism, yet most have been dismissed (Jablonski & Chaplin, 1993; Lovejoy, 1981).

**Introduction**

This study was undertaken with the goal of applying previously used
successful methods, reported in Latimer (1987) and DeSilva (2009) to a cross-species comparison of talocrural joint mechanics. These methods provided accurate mechanical analysis of the talocrural joint when applied to photographs, casts, and actual specimens. This sample of species (members of the orders Primates and Carnivora) was analyzed with the help of three-dimensional (3D) surface scans, which presented an opportunity to confirm the accuracy of these methods using this new technology.

Chapter I presented the background information crucial to understanding the mechanics of different types of locomotion of extant and extinct species. Chapter II will elaborate on the usage of 3D surface scanning and how these methods can benefit the field of paleoanthropology. Chapter III discusses the rationale behind which species were included in this analysis, the morphometric analysis of their talocrural joints, and what the results mean in terms of locomotor signatures.

The specific aims of this study are:

**Aim 1:** Use the FARO-Arm Scanner to collect high-resolution three-dimensional surface scans of the tibia, fibula, and talus (talocrural joint components).

- It is expected that using 3D surface scans will streamline the analytical process through use of an easily accessible, portable collection of specimens that can be manipulated in numerous ways.

**Aim 2:** Implement three-dimensional (3D) surface scans of the tibia and talus in a cross-species comparison of talocrural joint mechanics.

- It is hypothesized that body size will play a factor in the curvature
of the distal tibia and talar trochlea, with heavier individuals having larger and flatter joint surfaces, defined by the best-fit circle of the distal tibia.

- It is hypothesized that habitual quadrupeds will exhibit a much greater angle of the tibial plafond compared to the vertical shaft of the tibia than habitual bipeds, due to the orientation of the quadruped knee.

- It is hypothesized that quadrupeds will have a larger measure of dorsiflexion to accommodate climbing.

- It is hypothesized that strategies for relative joint stability will differ among the mammal species represented here, and that signatures for joint stability will be recognized in analyses of the talar trochlea.

II. Application of 3-Dimensional Morphometrics

**Introduction**

Traditional morphometrics methods have been successfully used to demonstrate morphology and functional anatomy in the field of physical anthropology for many years. Sliding or digital calipers are still used in comparative studies as a means of collecting these measurements. Casting, also implemented frequently in the case of valuable fossil material, has a history of good accuracy and repeatability once the mold is made. Casts are also used for cross sections, since the skeletal collections are far too valuable to section, as previously discussed.

Accessibility to the collection has also proved to be a problem for many museums. As traffic increases through a collection of specimens, damage and
misplacement of specimens or individual bones becomes inevitable. Especially in the cases of the fragile specimens or individuals of smaller size whose bones are liable to be lost or broken, a mechanism needs to be in place for museums to protect their material but still maintain an attractive research option. There is also a factor of accessibility, since the collections and casting labs housed at museums are not portable, are limited by hours of business, and must be protected by climate control.

Digital data collection, in the forms of photography, tomographic imaging (MRI, CT, microCT, OCT), and 3D laser surface imaging offers methods of analysis of specimens that are portable and highly detailed and protect the specimens. Radiograph and tomographic imaging, also used in medical practices, has the benefit of providing feedback on the internal structure of the bone with good resolution. This provides information about trabecular structure, a very valuable aspect of bone loading. Surface scans provide a high level of detail while capturing the observable qualities of the bone such as texture (Arias-Martorell et al., 2012; Friess 2012). In recent years the advances in laser imaging, 3D scanners, and the software needed to process the models have made this technology more affordable and reasonable for research purposes. Another clear benefit of 3D scanning is that the specimens, once processed in a digital manner, do not need to be physically handled but can still be analyzed. Analysis of cross sections, topography analysis, surface area, curvatures, linear distances, and comparison to other specimens can be completed in a single program, cutting down on hours spent performing these processes as well as the time spent
handling the physical specimen. 3D scanning has been included in the methodology used for studies of physical anthropology for at least the last 50 years (Friess, 2012, Langdon et al., 1991). The notable series published in 2009 discussing a partial *Ar. ramidus* fossil skeleton, for example, utilized high-grade 3D scans to reconstruct the cranium and scapulae, as the fossils themselves were too fragile to handle (Lovejoy et al., 2009).

3D analysis of the ankle joint has been performed with the use of CT, MRI, and 3D laser technology. These reviews have been largely medically oriented, with interest focused on cartilage deformation and injury, especially in the case of surgical methodology (Li et al., 2008; Richter et al., 2005; Valderrabano et al., 2007). Total joint replacements at the ankle are similar to those of the shoulder, hip, and knee for reasons of either extreme wear to the joint surfaces or traumatic injury. Currently, the options for ankle replacement are limited, and this surgery is performed much less frequently than total shoulder, hip, or knee operations. The FARO Arm Scanner, used in this study, has been used to document morphology, again in a medical setting that has so far been focused on knee replacements (Martelli & Pinskerova, 2003; Pitto et al., 2006; Zaffagnini et al., 2004). This study was undertaken to apply 3D geometric morphometric analysis to the talocrural joint in the effort of identifying differences in the joint across representatives of the Primates, Ursidae, and Felidae groups as they apply to locomotor signatures.
Methods

Each bone used in this study was scanned using a FARO Arm EDGE Scanner, available to the CMNH through funding from the Cleveland Clinic. The FARO Arm Scanner is a 3D laser scanner that is still predominantly used in engineering, due to its high degree of precision (accurate to 0.005 mm). The FARO differs from traditional stationary scanners by having functional joints (Figure 2.1). This feature allows a complete scan of a bone to be completed in a minimum of two changes of position.

![Figure 2.1. The FARO Arm Edge Scanner, a 3D laser surface scanner with three joints of movement. Photo from the FARO Edge Tech Sheet ("EDGE: features, benefits & technical specifications,").](image)

Stabilizing the long bones required the use of putty, which held the distal end of the bone during scanning of the proximal articular surface and diaphysis. This began a scanning “session” that was comprised of a number of “passes” over the bone. A session serves to merge the whole collection of points captured for that one position, and is broken down into as many passes as are necessary to capture all aspects of the bone. Each session was completed with the goal of having as few passes as possible with the greatest amount of detail, so that there are not a superfluous number of layers to the scan. Once the proximal aspect of
the bone was scanned, a new session was started with the proximal end suspended in putty so that the distal end could be captured. The whole diaphysis was scanned in this second session, providing overlap with the first session that is valuable during the process of merging the two layers. These two layers were merged together using landmarks present in both scans to create a complete 3D model of the bone.

The FARO scanner was equipped with software from the Polyworks suite, which has the ability to calculate linear distances, curvatures, generate cross sections, surface comparisons to other specimens, and reverse engineer models of bones (“Innovmetric”). Unfortunately, due to restrictions on the use of this equipment, continuing the analysis of the scans with this suite of programs was not possible. Scans were therefore analyzed with a combination of two programs from the Adobe CreativeSuite 5.1 software package, obtained through the Case Western Reserve University Software Center. While the Polyworks suite provided the positional data that could be used to generate measurements directly from the 3D image, Photoshop did not retain these qualities. Therefore, the digital images were augmented by manual measurements taken on all the physical specimens to assign a scale for each of the scanned images. Maximum lengths of the tibia, fibula, and talus were taken for each specimen along with width of the femoral head as an estimator of body size.
**Digital Analysis of the Tibia**

The first cross sections of the tibia were taken at a medial point, just lateral to the medial malleolus, at the lateral edge of the articular surface, and at a point midway between the two first sections. The three cross sections for each tibia were then taken into Adobe Illustrator to identify the best-fit circle and central angle and Adobe Photoshop to find the radius of curvature (Figure 2.2).

![Figure 2.2. Distal *H. sapiens* right tibia, shown in inferior view. Three cross sections were taken- one just after the lateral aspect of the medial malleolus, one on the lateral-most joint surface, and another midway between the first two. Best-fit circles were applied to the curvatures of the three cross sections to measure included angle, radius of the circle, and arc and chord of the included angle.](image)

The second round of tibial cross sections were taken on the approximate axis of talocrural rotation, through the medial malleolus and the fibular notch. These cross sections were oriented in posterior view and analyzed with Adobe Illustrator. The angle measured here documented the orientation of the tibial plafond compared to the vertical axis of the diaphysis (Figure 2.3).
Digital Analysis of the Talus

The first round of cross sections on the talus were taken at the same intervals as the tibia; the first section placed at the medial-most aspect of the trochlea, the second at the lateral-most aspect of the trochlea, and the third in between the first two sections. These images were then taken into Adobe Illustrator to identify the best-fit circle and central angle and Adobe Photoshop to find the radius of curvature (Figure 2.4).

Figure 2.3. H. sapiens right tibia next to G. gorilla right tibia shown in posterior view. One cross section was taken in a semi-coronal plane. Yellow lines show the angle between the tibial plafond and the axis of the diaphysis. Green lines show the bisecting of the medial malleolus.

Figure 2.4. H. sapiens right talus, shown in superior view at the left. Three cross sections were taken: at the lateral aspect of the trochlea, the medial aspect of the trochlea, and midway between the first two. Best-fit circles were applied to the curvatures of the three cross sections in lateral view to measure included angle, radius of this circle, and arc and chord of the included angle. Also measured were the angles of plantarflexion (P) and dorsiflexion (D).
The second cross section of the talus mirrored the second set of tibial cross sections, taken through the estimated axis of rotation. These sections were used to measure the angle from the axis of rotation to the superior margin of the trochlea with the use of Adobe Illustrator. Analysis also included linear measurements, taken in Adobe Photoshop, on the trochlea to determine the depth of the groove in the middle of the trochlea (Figure 2.5).

Figure 2.5. Comparison of the semi-coronal cross sections of three right tali from *H. sapiens*, *P. troglodytes*, and *P. tigris*. Green lines indicate the measurements taken on each section to determine the depth of the trochlear groove. One line (a) was drawn between the medial and lateral-most aspects of the trochlea and was used to draw a perpendicular line (b) to the deepest part of the groove.

**Results and Discussion**

The scanning sessions produced high-resolution 3D models of each bone of the talocrural joint for each specimen. Cross sections were taken with good repeatability and will be analyzed and discussed in Chapter III. These scans may now be used in future studies, if the appropriate analysis software becomes available, to repeat this study using the intended software. Future directions could include reverse engineering, topographical analysis of joint surfaces and comparison of articular surfaces, and overall bone surface morphology between species and to the fossil record.
III. Cross-species comparison and evolution of talocrural joint mechanics

Introduction
Observation of the locomotion of other animals can be used to assess human bipedal locomotion. Force plate experiments, motion analysis, cadaver dissections, and observation of the skeleton or fossil remains are all methods of collecting data on locomotor patterns (DeSilva, 2009; Freeman et al., 1965; Goh et al., 1992; Latimer et al., 1987). In this study, extant great apes, select New World Monkeys, and fossil human ancestors were used to compare the morphology of the talocrural joint. To further augment the comparative nature of this study, the families of Ursidae and Felidae were also represented (Ursus maritimus, Ursus americanus, Panthera tigris, and Panthera onca), although the postcranial remains for non-primate mammals were limited. Members of the great ape family included in this study were humans (Homo sapiens), fossil hominins (H. habilis, Au. afarensis and Ar. ramidus), gorillas (Gorilla gorilla), chimpanzees (Pan troglodytes), and orangutans (Pongo pygmaeus). Other non-hominoid primates examined include baboons (Papio hamadryas) and gibbons (Hylobates agilis, Hylobates concolor).

Setting aside the clear anatomical differences between humans and other anthropoids in other parts of the foot, this analysis will focus on the tibia and talus and the morphological signatures of locomotion that they present. It is hypothesized that signatures of locomotion at the species level will be observed in the analysis of the orientation of the long axis of the tibia to the ground, the amount of wedging present in the articular surface of the talus, and the
depth of the trochlear groove on the talus. It is also hypothesized at the individual level that body size will affect the joint surfaces, with larger individuals having a longer sagittal joint surface of the tibia and talus.

**Primates**

The order Primates is separated into two suborders, Haplorrhini and Strepsirrhini. Strepsirrhini contains all the wet-nosed primates - the lemurs, lorises, and galagos. Haplorrhini, the dry-nosed primates, includes the two infraorders of Tarsiiformes (the tarsiers) and Anthropoidea (New World and Old World Monkeys). Anthropoidea is further subdivided into two parvorders, Catarrhini including the Old World Monkeys: the Cercopithecoids and Hominoids (great apes); and Platyrrhini, which groups the New World Monkeys: prehensile-tailed, flat-nosed primates such as spider monkeys. All extant primates used in this study (humans, chimpanzees, bonobos, gorillas, orangutans, gibbons, and baboons) are members of Primates parvorder Catarrhini, representing the families of Hominidae, Hylobatidae, and Cercopithecidae.

The great apes were included foremost due to their common grouping within the same family, Hominidae. Chimpanzees, the great ape species most commonly used in comparative studies of human origins, is widely recognized as our closest living relative, with a high degree of genomic similarity to humans. Fixation on comparison between chimpanzees and humans is understandable, given the similarities observed through several behaviors, including the use of bipedal locomotion (Sayers & Lovejoy, 2008). However, all primates referenced in this study exhibit bipedal locomotion in some form, usually short durations of
walking, sprinting, or hopping on two legs (Berillon et al., 2011; D.L Gebo, 1996; 
Wang & Crompton, 2004; Yamazaki, 1984)

Chimpanzee and gorilla locomotion styles involve quadrupedal knuckle 
walking, vertical climbing, and bouts of bipedalism (Figure 3.1, pg. 35). 
Observation of their locomotion and other behaviors have been used to develop a 
“troglyodytian” hypothesis which stated that knuckle-walking would have been a 
major component of the locomotor repertoire of the last common ancestor of 
chimpanzees and humans rather than arboreal locomotion (Crompton et al., 2008; 
Richmond et al., 2001) However, analysis of the bipedalism practiced by 
chimpanzees and gorillas proved that the mechanics of the trunk, hip, knee, ankle, 
and foot function substantially differently when compared to humans (Sayers & 
Lovejoy, 2008). The unique features of heel strike, full-foot force dispersal, toe- 
off, and the ability to keep the center of mass directly over the hips in a fully 
orthograde posture is not present during bipedal gait used in chimpanzees or 
gorillas (Crompton et al., 2008; D’Aout et al., 2004; DeSilva, 2009; Lovejoy, 

Orangutans, fellow members of the great ape group, were also used for 
analysis due to their favoring of orthograde suspensory arboreal locomotion and 
vertical climbing in the expansion upon the idea of arboreal locomotion as the 
precursor to bipedalism (Thorpe & Crompton, 2005). Orangutan adaptation to 
varying arboreal substrates has been reported to mirror human locomotor changes 
when faced with variable ground surfaces (Thorpe et al., 2007). In the arboreal 
paleoenvironments associated with early hominins, the ability to adapt
body position to a wide range of arboreal substrates would have been a great advantage in food and safety seeking (Thorpe & Crompton, 2005; Thorpe et al., 2007).

Members of the Hylobatidae family (gibbons) exhibit vertical climbing and arboreal bipedalism, and can also sustain bipedal locomotion that has a more vertical, bouncing style (Crompton et al., 2008; Yamazaki, 1984). Studies of these behaviors as well as the anatomy of the prehensile foot helped develop the hylobatian model of the development of human bipedalism (Keith, 1923). This model considers the possibility that a gibbon-like primate animal with this type of locomotor style acted as a precursor to the larger-bodied apes resembling the hominoids.

The final primate group used for this study is the family Cercopithecoidae. This group predominantly employs terrestrial quadrupedalism (Figure 3.2), rarely using vertical climbing or any other arboreal locomotor style. Cercopithecoids use their flexible mid-foot break to achieve a higher degree of dorsiflexion, not
achieved through the talocrural joint. Despite the variation in morphology, cercopithecoid monkeys can still achieve the close body position relative to the substrate being climbed, as observed in the vertical climbing strategy of chimpanzees (DeSilva, 2009; D.L Gebo, 1996).

While the facultative bipedalism practiced by these primates is quite different than human habitual bipedal locomotion, chimpanzees and gorillas along with orangutans, gibbons, and baboons are at the center of another prominent hypothesis, the vertical climbing hypothesis (Berillon et al., 2011; Crompton et al., 2008; D'Aout et al., 2004; DeSilva, 2009; Elftman, 1944; D.L Gebo, 1996; Thorpe & Crompton, 2005; Thorpe et al., 2007; Tuttle, 1981; Vereecke, D’Août, Payne, & Aerts, 2005; Yamazaki, 1984). Thoroughly documented through the use of kinematic observation, dissection, osteological analysis, and comparison to the fossil record, vertical climbing has been established as an important hominoid behavior that has been hypothesized to shed light on the development of bipedal locomotion. Through collected data on the muscle groups of the lower limb, it has been demonstrated that the active muscles during vertical climbing promote an extended hip and knee as well as a vertically oriented trunk. The muscular
involvement in vertical climbing is an essential aspect in establishing an arboreal last common ancestor (Crompton et al., 2008; D'Aout et al., 2004; DeSilva, 2009; Elftman, 1944; Stern, 2000; Thorpe et al., 2007; Tuttle, 1981; Yamazaki, 1984).

**Fossil Species**

Comparison to not only the modern human condition, but also the morphologies observed in extant primates and other mammals was done using fossils from a 4.4 Ma *Ar. ramidus* individual from Gona. Morphological patterns confirming habitual bipedalism have been established for *Au. afarensis* since the 1974 discovery of the first partial skeleton of this species, A.L. 288-1 (“Lucy”), a female specimen aged at 3.2 Ma (Johanson & Taieb, 1976). With the discovery and detailed 2009 discussion of *Ar. ramidus* partial skeleton, ARA-VP-6/500, a species still retaining arboreal attributes but capable of bipedal toe-off and propulsion was described (Lovejoy et al., 2009). Further recent fieldwork has uncovered an individual contemporaneous with *Au. afarensis* that demonstrates the ability to toe-off on the four lateral rays (Haile-Selassie et al., 2012). The hallux would not have been involved because it retained the abducted morphology seen in extant apes. While this study continues the investigation of the *Ar. ramidus* locomotor mosaic, comparison was also made to *H. habilis*, a species that lived around 2 Ma and demonstrated further developments of facultative bipedalism (D. L. Gebo & Schwartz, 2006; Ruff, 2009; Susman & Stern, 1982; Wood, 1974).

**Ursids and Felids**

Non-primate mammals that were part of this study were taken from the
diverse order Carnivora. This order contains the suborders of Feliformia and Caniformia and fifteen extant families between the two. Ursidae, a family under the Caniformia suborder, groups the bears. For this study, Ursidae is represented by two polar bears (*Ursus maritimus*) and a single black bear (*Ursus americanus*). Felidae, a family under the Feliformia suborder that contains domestic as well as large-bodied cats, is represented by a single jaguar (*Panthera onca*), and a single tiger (*Panthera tigris tigris*).

In general, all species used here are classified as “cursorial” mammals based on the ratio of the femur to the metatarsals, although their maximum speeds are quite different. It is interesting to note that upon examination of this ratio, only the polar bear with its long legs compared to body size was eliminated as an outlier of the predictive power of the metatarsal/femur ratio (Garland, 1993). In general, these mammals all practice quadrupedal locomotion. Bears commonly use bipedal stance in order to reach food and as a gesture of intimidation. All of these non-primate mammals are also capable of and frequently utilize their abilities to swim and climb (Vaughan et al., 2011).

Polar bears, who share the rank of largest of the extant bears with Kodiak bears, exhibit an interesting niche of locomotor behavior. Limited in distribution to the Northern Hemisphere, these bears demonstrate plantigrade forefeet and semiplantigrade hindfeet during quadrupedal locomotion (Figure 3.3, pg. 39). The bulk of the polar bear’s time is spent out on the sea-ice, hunting for seals and other mammals and birds as the opportunity arises. While their heavy claws and thick paw pads give them the ability to climb trees, this ability is only used
during the limited times of the year during which polar bears return to land (Amstrup, 2003).

![Diagram of polar bear gait cycle](image)

**Figure 3.3.** Plantigrade quadrupedal locomotion as observed in the gait cycle of the polar bear, *U. maritimus*.

Black bears (*Ursus americanus*) exhibit the same abilities for swimming, climbing, and quadrupedal locomotion with a plantigrade/semiplantigrade stance (Figure 3.3). This species’ distribution is spread across the northern part of North America and these animals, in contrast to polar bears, spend their time on land rather than on the sea-ice. Black bears learn to climb at around one to two months of age (Burghardt Gordon et al., 1970).

Bears use two observed methods to climb, representing two speeds of this behavior. In the first method, the bear “hops” up the tree, using one forelimb at a time then jumping further up the limb with both hindlimbs simultaneously. The second method, the slower of the two, resembles the terrestrial quadrupedal locomotion used by the bear, with opposite limbs moving at the same time. Descent is usually a reverse of this second method, with the bear lowering down from the tree leading with the hindlimbs (Burghardt Gordon et al., 1970). These methods of climbing, coupled with the bear’s heavier limbs, load the talocrural joint into a high degree of dorsiflexion as in primates but utilize different mechanics that can be observed in the osteology.

The jaguar (*Panthera onca*), from parts of South America, Central
America, and some territory in southwestern Mexico and the tiger (*Panthera tigris tigris*), from small areas of Asia and India, are both large-bodied felids. These animals also encounter the need for a joint strategy that can function well with their body size as well as their locomotor repertoire. Like bears, both these big cats are proficient swimmers and also climb trees, although tigers favor running up a tree instead of pulling themselves up the trunk, as observed in jaguars. On the ground, they are also both quadrupeds that use a digitigrade posture (Figure 3.4). Both these species use their digitigrade posture during climbing as well, exhibiting flexion through the metatarsophalangeal joints to bring about the dorsiflexion needed to keep their bodies close to the climbing substrate (Day & Jayne, 2007; Iwaniuk, 2000).

Figure 3.4. Digitigrade quadrupedal locomotion as observed in the gait cycle of the tiger (*P. tigris*).

Joint Mechanics

The strategies discussed in this section have been argued to prevent excessive inversion and eversion of the ankle, which result in injury, through the skeletal components of the talocrural joint. The first strategy, observed uniformly in humans, is a combination of a perpendicular orientation of the tibia coupled with a relatively flat talar trochlea. This interaction is dependent on the singularity of bipedal gait that will load the talocrural joint in a perpendicular plane. The second involves stabilization through the oblique orientation of the
tibia due to the valgus knee in species such as the non-human primates. This orientation has been proposed to limit the amount of lateral movement through the position of the fibula, which provides an obstacle to extreme inversion.

A third strategy that has been presented is the groove in the middle of the trochlea of the talus, present in some species. This groove articulates with the mating surface of the tibial plafond, and the interlocked joint surfaces have been argued to limit lateral displacement (Figure 3.5) (DeSilva, 2009; Harcourt-Smith & Aiello, 2004; Van Valkenburgh, 1987). The depth of this groove seems to be a heritable trait, more related to species lineage than to body size. This groove, while clearly variable between species, is still an element of a synovial joint, and therefore cannot be correlated with establishing a great degree of joint stability in the animals studied here.

![Figure 3.5. Three methods of orientation of the talocrural joint: (a) a human ankle joint, with perpendicular alignment of the tibia and a flat trochlea, (b) a primate joint with an oblique orientation of the tibia and slightly grooved trochlea, and (c) a felid or ursid joint, with a deep groove on the trochlear surface.](image)

**Methods**

The talocrural joints of the right limb were assessed in fifty-four total specimens, using the Hamann-Todd Osteological Collection, housed in the
Cleveland Museum of Natural History (CMNH). Males and females were scanned for each species of *Homo sapiens* (Male N=9, Female N=10), *Pan troglodytes* (Male N= 5, Female N=4), and *Gorilla gorilla* (Male N=4, Female N=5). Orangutans were also included in the sample but were more limited (one male and two females), as were baboons (four male, two female) and gibbons (one male, one female). All observed specimens were past the age of growth plate fusion and free from pathology or gross abnormality. High-resolution plaster casts of hominin fossils from *Ardipithecus ramidus* (Gona, Ethiopia, 4.3-4.6 Ma) were obtained from Dr. Scott Simpson and represented localities in Gona, Ethiopia. The Gona specimen contains one fragmented tibia that preserved the distal aspect that was able to be scanned and a partial talus that, unfortunately, was not. Several fossil cast specimens were not able to be scanned, but were included in this section with digital photographs and include *Australopithecus afarensis* (A.L. 288-1, A.L. 333-6, A.L. 333-7) and *Homo habilis* (OH-8).

Non-primate mammals from the CMNH Osteological Collection were included: one a black bear, two polar bears, one jaguar, and one tiger. Specimens were limited due to the quality of the individual bones as well as availability of postcranial remains for most non-primate specimens. The non-primate specimens were provided to the CMNH from the Cleveland Metroparks Zoo. During collection of the non-primate remains, many individuals with postcrania included exhibited growth plates that were still unfused, or pathology that led to their exclusion from the study.

As described in Chapter II, scanning of each bone was completed
using the FARO Edge Arm Scanner at the CMNH, generating the digital collection used for analysis. Photographs, also taken at the CMNH, were taken in anterior view on each available tibia and medial, lateral, anterior, and superior views for each talus. Methods described in Latimer (1987) and DeSilva (2009) were studied and combined for the measurements and cross sections taken on each scan. Adobe Illustrator and Photoshop CS5.1 were used for all angular and linear measurements, and GraphPad Prism 6 was used for all statistical analysis and formatting of all graphs.

Tibia

Cross sections of the tibia were taken with the 3D tools available in Adobe Photoshop. Three cross sections were taken at the distal articular surface in the sagittal plane, and the fourth was taken in a semi-coronal plane and captured the entirety of the bone (Figures 2.2 and 2.3, pgs. 29, 30). “Best-fit” circles were applied to the articular surfaces of the three sagittal sections to analyze the curvature at each of the three points as well as the average joint curvature. The central angles, radii, and chords of the best-fit circles were all calculated using the digital measurement tools in Adobe Photoshop and Illustrator. The fourth section was fitted with linear markers across the tibial plafond and along the long axis of the diaphysis of the bone. The angle between these two markers was calculated for each tibia in the sample (Figure 2.3, pg. 30).

The fossil tibia offered a challenge to complete the analysis in the semi-coronal plane, as the diaphysis is missing from this fragmented fossil. In order to obtain reliable measurements for the distal tibia of the Gona fossil, subjective
comparison was made to the extant species to first understand that factors at the
distal tibia could suggest an oblique orientation of the diaphysis (Figure 3.6). The
cross-section of the fossil has an appearance to the surface of the tibial plafond
that has a slight keel. This, coupled with the fact that the medial malleolus seems
both more robust and angled medially, compares well with *P. troglodytes.*
Multiple cross sections of the fossil samples were made to supply a range of
possible measurements.

**Figure 3.6. Embargoed material**

**Talus**

Cross sections of the talus were taken with the same methods and in the
same planes as those taken for the tibiae. For the three resulting sagittal sections,
best-fit circles were made to fit the articular surface so that measurements of the
central angles, radii, and chords could be taken (Figure 2.4, pg 30). After the best-
fit circle and central angle had been set on the cross section, a vertical radius was
drawn from the centroid at 90° so that the angular estimations of dorsiflexion and
plantarflexion could be measured. The semi-coronal section was used to
determine the depth of the trochlear groove and compare the angle between the
axis of rotation and the superior aspect of the trochlea (Figure 2.5, pg. 31).

The complete talus was analyzed in Adobe Photoshop to determine degree
of wedging and the apical angle, two related measurements. For measuring wedging, the anterior and posterior aspects of the trochlea were treated as parallel, simplifying the talus into a trapezoid-like shape. Apical angle measurements treated medial and lateral trochlear aspects as parallel, and modeled the talus as the frustum of a cone, the apex positioned medially (Figure 3.7).

Figure 3.7. Superior view of a right *G. gorilla* talus. The red superimposed cone shows the frustum of the cone that roughly fits the talus. $\beta$ is the measure of the apical angle for this talus.

Setting the scans in superior view, linear measurements were taken at the anterior aspect of the articular surface from the lateral anterior margin to the medial anterior margin, the lateral and medial borders of the trochlea, and the posterior aspect between lateral and medial posterior margins (Figure 3.8). The same linear distances were used to calculate the measure of the angle between the anterior and lateral margins, called the apical angle. The following calculations were used to determine the degree of wedging and apical angle:
Results and Discussion

Morphological Comparison

Analysis of the orientation of tibial plafond to the axis of the diaphysis demonstrated that the tibiae of habitual bipeds are oriented approximately at a 90° angle to the ground (ranging from 88-92°) (Figure 3.9). All quadrupeds were found to be statistically similar to each other (p≈0.2758), and statistically significantly different from the human mean (p<0.05). The quadrupedal tibia was found to have an average tibial orientation to the ground of 107.9° (ranging from 95-120°). The specimens representing *A. afarensis* all fall within the habitual biped range, which agrees with the known locomotor strategy of this species.

Wedge (γ) = (A-P)/M
(γ) = arctan((A-P)/M)*(180/pi)

Apical Angle

sin (β) = (P/A)
(β) = arcsin (P/A)*(180/pi)

Figure 3.8. Linear measurements and calculations taken on the superior aspect of the talus to evaluate wedging (γ) and apical angle (β). The degree of wedging was calculated by treating the anterior and posterior aspects as parallel, while the apical angle measurements treated medial and lateral aspects as parallel.
The sagittal sections of each tibia were analyzed in several ways, each of which involving the fitting of a circle to the plafond’s curvature. The most effective representation of these results is shown below as the comparison between the individual’s body mass (femoral head measurement) and the chord of the included angle of the tibial articular surface (Figure 3.10). The relationship between this chord measurement and estimated body size has a strong correlation, with $R^2 = 0.8108$.

Figure 3.9. Scatter plot of the angle between the tibial plafond and the tibial diaphysis. Non-human primates and quadrupeds all have a much higher angle than bipedal humans. *Au. afarensis* and *Au. africanus* individuals fall well within the modern human range.

The sagittal sections of each tibia were analyzed in several ways, each of which involving the fitting of a circle to the plafond’s curvature. The most effective representation of these results is shown below as the comparison between the individual’s body mass (femoral head measurement) and the chord of the included angle of the tibial articular surface (Figure 3.10). The relationship between this chord measurement and estimated body size has a strong correlation, with $R^2 = 0.8108$.

Figure 3.10. Sagittal cross section of a *G. gorilla* right tibia, showing the chord of the included angle in green (shown at the left). Regression plot (shown at the right; $R^2 = 0.8108$) of the comparison between the chord measurement and body mass estimate.
Analysis of the morphology of the talus started with analysis of the overall shape of the trochlea; the two measurements of wedging and apical angle, as related aspects of joint mechanics, displayed similar results. The gorilla was the only primate with a statistically significantly different degree of wedging (p<0.001) compared to humans (Figure 3.11). Chimpanzees were found to have a greater degree of wedging than humans, but this difference was not statistically significant. The hominin sample is shown to fall into the human range, also intersecting orangutan and gibbon values. The remaining primates did not differ from each other, falling into a range from 8-24°. The ursids and felids fell far below the primate grouping, with the average degree of wedging being 3°.

The measure of the apical angle (Figure 3.6, pg 44 & Figure 3.7, pg 45) demonstrates the same relationships as the amount of wedging, as expected (Figure 3.12, pg. 49). Again, only gorillas have a statistically significantly different mean (p<0.001) from the rest of the primates. The ursids and felids have
a very low apical angle, being significantly lower than all other groups. The hominins once again fall into the human range for apical angle, but also fall in with the orangutan and gibbon species.

The sagittal sections resulted in a similar output for the comparison of the chord of the best-fit circle, defined by the edges of the articular surface, to the estimator of body size. This comparison yielded almost identical results to the positive relationship observed between the chords measured on the distal tibia and body size with $R^2 = 0.8361$ (Figure 3.13).

![Figure 3.12. Scatter plot of the degree the apical angle for each talus. Humans have a lower degree of wedging than gorillas and chimpanzees, and ursids and felids have a lower degree of wedging than all other groups. Hominins fall, as hypothesized, into the human range for trochlear wedging.](image)

![Figure 3.13. Sagittal cross section of a G. gorilla right talus, showing the chord of the included angle in green (shown at the left). Regression plot (shown at the right; $R^2 = 0.8361$) of the comparison between the chord measurement and body mass estimate.](image)
The second analysis, performed to compare range of motion across the species, examined the available angles of dorsiflexion and plantarflexion. Plantarflexion differences were found to be statistically insignificant across all species. The measure of dorsiflexion confirmed the hypothesis that humans have a statistically significantly lower range of dorsiflexion than the quadrupedal and arboreal mammals (p=0.05) (Figure 3.14, pg. 51). Hominins sampled for dorsiflexion and plantarflexion were limited to A.L. 288-1 and OH-8. The scan of the talus from Gona was incomplete and could not render an examination of range of motion. Other hominins sampled fell within the human range for dorsiflexion, although they were positioned on the higher end of the spectrum.

![Figure 3.14. Scatter plot of the angle of dorsiflexion for each sagittal talar cross section. Humans have the lowest range among the primates, into which the hominin sample falls.](image-url)
Analysis of the grooved trochlear surface was performed on the semi-coronal sections of each talus (Figure 3.15). The shallowest groove is seen on human and gorilla tali, and the deepest observed in the ursids and felids. The complete A.L. 288-1 talus was analyzed and fell within the human range, again intersecting the ranges of the orangutans and gibbons.

Patterns of Locomotion

From these results, inferences can be made as to the locomotor signatures of bipedal, quadrupedal, and arboreal mammals. Analysis of the tibia served largely as an indicator of knee orientation, studied and confirmed by numerous sources prior to this analysis (Lovejoy, 2007). Bipedal locomotion, demonstrated habitually by humans, is found to require a perpendicular orientation of the tibia’s shaft to the ground and also to the talocrural joint plane. This valgus orientation of the knee coexists with many other attributes that enable the center of mass of a human to be balanced over the knees and feet during bipedal gait. The remaining
primates as well as the ursids and felids were confirmed to possess a mediolaterally oblique orientation of their tibiae, which corresponds to a varus alignment of the knee.

Another positive indication of bipedal locomotion is the range of dorsiflexion at the talocrural joint. Humans and the sample of hominin fossils fall into the same range of dorsiflexion, lower than the quadrupedal mammals. It is interesting that, among the large-bodied ursids and felids, the polar bear stands out as having the lowest range of dorsiflexion. While polar bears are capable of climbing, the percentage of their time spent in an environment where they can use this behavior is limited. This presents a probable source for the morphological differences.

The illumination of the signatures of locomotion continues at the talus. Examining the whole bone of the talus and measuring the apical angle can be used to gauge the amount of wedging present in the talus. The wedge shape of the talus has been observed in calculating the difference between the measurements of the anterior aspect and the posterior aspect of the trochlea (Barnett & Napier, 1985; Inman, 1976). For known bipeds, the range of trochlear wedging is found to fall within the range of non-human primates, echoed in the related measure of the apical angle of the talus. This wedge shape permits some inversion and eversion during the normal range of motion.

Inversion of the foot in non-human primates is useful during propulsion in climbing, coupled with the varus knee that allows for a greater total range of
extension. As bipeds, humans have no need for inversion during propulsion and rely on the ligaments and muscles surrounding the ankle to limit inversion to avoid injury. There is an interesting intersection between the observations of ankle inversion and the presence of the anterior talofibular ligament. While some sources have argued its importance as an ankle stabilizer which only humans uniformly require, it could also be argued that humans have evolved the presence of this ligament as a unique proprioceptor in the prevention of inversion sprains.

The lowest wedging and apical angle measurements were present in the ursid and felid sample. These animals whose tali have the most parallel medial and lateral margins to their trochleas also exhibited the deepest trochlear groove. This appears to suggest that ursids and felids have a much more limited talocrural joint that acts as a true single hinge joint during locomotion that inverts and everts very little through the range of motion. In comparison to arboreal primates, ursids and felids exhibit a key behavioral difference that may have some relationship with this morphology. Primates who exhibit arboreal locomotion utilize a wide range of tree branches during vertical climbing, suspensory locomotion, bridging, or quadrupedal locomotion. By comparison, ursids and felids practice vertical climbing but mainly use the trunk of the tree for propulsion. Smaller branches are used mainly for the animal to rest, sitting or bracing against the smaller branches instead of using them for climbing. These animals also have the benefit of heavy claws, presenting another obvious difference compared to the pads of the primate foot.
The joint surfaces of both the tibia and talus were found to have a definitive relationship with body size. As body size increased, the chord of the included angle of both joint surfaces increased as well. This confirms the hypothesis that one strategy for handling a larger body size is to increase the surface area upon which the increased weight can be dispersed, especially in a synovial (frictionless) joint.

IV. Conclusions and Future Directions

This thesis was undertaken with the preliminary goal of analyzing the morphology of the tibia and talus, to examine what signatures of locomotion could be determined across a range of mammal species. Species used in this comparison included extant primates, ursids, and felids as well as hominin species that could be represented by relevant fossil material. These species were included due to the range of different foot postures used during both arboreal and terrestrial locomotion for non-human species. There is also the undeniable importance of the close phylogenetic relationship between extant great apes and humans.

The study employed high-resolution 3D surface scans of the extant mammals and a fossil specimen from Gona, Ethiopia, while other fossils from Hadar (A.L. 288-1, A.L. 333-7, and A.L. 333-8) and Olduvai (OH-8) were analyzed with the use of digital photographs. Using digital scans in place of casts of the actual specimens saved time during the analysis phase, as cross-sections are easily performed using 3D tools, as demonstrated in Chapters II and III. These methods also minimized contact with the actual specimens, while providing
accurate data as reported in Chapter III. This improved the accessibility to the sample as well, since using the FARO Scanner generated a portable collection of scans.

The talus can be modeled as the frustum of a cone in humans and primates, with the apical angle positioned on the medial aspect of the talus. On top of this frustum sits the tibial plafond, which can be modeled as the interior aspect of a lengthwise-bisected cylinder. The morphology of the variations of these shapes were analyzed to identify locomotor signatures. The methods employed here were developed from work done by Latimer and colleagues (1987) in combination with those demonstrated by DeSilva and colleagues (2009). This current work was able to pinpoint several signatures of each foot posture studied in the sample.

Bipedalism, unique to humans, has been demonstrated to require a valgus knee, confirmed here, that produces a tibial diaphysis that is generally perpendicular to the plane of the talocrural joint and the horizontal substrate. In addition, bipedality is again unique in the smaller amount of dorsiflexion included in the talocrural range of motion. Analysis in superior view showed a similar degree of wedging, or the difference between the anterior and posterior transverse dimensions, of the tali of humans and most primates. From an anterior view, the bipedal trochlea was observed to be nearly flat.

Arboreal locomotion, used by non-human primates as well as the ursids and felids in this sample, is associated with almost the exact opposite suite of
morphologies. Terrestrial quadrupedal gait as well as vertical climbing benefit from a varus knee orientation, which allows for a greater range of motion at the knee (Lovejoy, 2007). Successful climbing is further enabled through an increased range of dorsiflexion possible at the talocrural joint, excepting the polar bears, who spends most of their time in a tree-less environment. In primates, the degree of talar wedging is greater than humans, displaying a possibly accentuated ability to invert the foot. However in ursids and felids the wedge shape of the talus all but disappears, resulting in a near parallel-sided talus. As discussed above, this unique shape in ursids and felids may interact with the deep trochlear groove also found in these families to produce a truer single hinge joint. This groove is also found in non-human primates, with depth in between what is described in humans and the carnivores.

Differences within the mammals sampled here were further distinguished when body size was added as a variable. Chords of the included angles belonging to best-fit circles on both talus and tibia sagittal cross sections confirmed the hypothesis that one strategy for maintaining perpendicular loading on a synovial joint, such as the talocrural joint, as body size increases is to flatten the articular surface. This change to the joint surface with increasing body weight lessens the curvature of the articular facet. The decrease in curvature is correlated with an increase in the flatness of the joint surface across which transarticular forces can be dispersed. When the frictionless element of synovial joints is considered, this change is absolutely essential to maintain normal joint loading in animals of
larger body size.

Applying these methods to the available fossil specimens demonstrated that the *Ar. ramidus* specimen used here provides some evidence of a varus knee, with similar tibial orientation as the extant arboreal species. A keeled shape of the tibial plafond, as well as a measurable groove on the trochlea of this talus further demonstrate some arboreal aspects of this talocrural joint compared to more recent human ancestors. It was confirmed using the A.L. 288-1 and OH-8 fossil casts that by the Pliocene epoch, habitual bipedal locomotion was a part of our hominin ancestors’ locomotor repertoire.

This project’s use of a new 3D scanning apparatus, which has been used predominantly in engineering and in limited applications within the medical field, has brought to light many opportunities for future directions. While the scanning technology was extremely beneficial to the accessibility of the sample size, the setbacks encountered along the way made it difficult to complete the analysis in as much detail as possible. Strategies for overcoming these setbacks are related mostly to funding and resource availability. The FARO Arm and Polyworks software together have the ability to improve the resolution of comparison of morphology in addition to the previously mentioned benefits. However, more testing of the FARO arm in non-engineering applications is absolutely essential before this technology can be established as a new standard in morphological studies.
Results from Chapter III provide proof that a perpendicular orientation of the distal tibia, flat trochlear surface, marginal amount of wedging, and a lowered range of dorsiflexion all define bipedal locomotion. In order to improve the quality of identification of signatures for bipedal gait, it would be helpful to expand the sample size. The same holds true for quadrupeds, whose sample size was further hampered by the lack of postcranial remains and the quality of specimens coming from zoos. This study would benefit from the inclusion of smaller ursids and felids at the very least, as well as the inclusion of a greater sample size of those species discussed here.
References


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