

FUNCTIONAL MORPHOLOGY OF  
THE ANTHROPOID TALOCRURAL JOINT

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## ABSTRACT

The form and function of the talocrural joint of anthropoids is frequently used to infer positional behaviors of fossil catarrhines without clear and quantitative data to support these inferences. Specifically, greater medial and posterior trochlear wedging, shallower trochleae and more obliquely oriented groove for the tendon of the flexor hallucis longus muscle on the talus, and a more anteriorly oriented posterior talar facet on the calcaneus, have been hypothesized to reflect a greater emphasis on vertical climbing in anthropoids. This research evaluated these features in extant anthropoids, and compared them between pairs of taxa representing different emphases on climbing in their locomotor repertoires. Although taxa vary in these features, they do not do so in predicted ways. Results suggest that these aspects of talocrural joint functional morphology are not associated with climbing in extant anthropoids, and cannot be used in isolation to predict behavior of fossil taxa. Although this research has evaluated only broad, pairwise contrasts between diverse groups of extant taxa, variation identified here provides justification for a more in depth, detailed analysis of talocrural functional morphology in anthropoids.

## Chapter 1: Introduction

Reconstructing locomotor adaptations in extinct anthropoids provides important information for understanding their biology and evolutionary history. Because the foot directly contracts the substrate during locomotion, the pedal skeleton should vary among anthropoids with different positional behaviors, and be potentially useful for locomotor reconstruction. Tali and calcanei are commonly preserved in the fossil record, and often are the only postcranial bones known for some taxa, so the ability to reconstruct locomotor adaptation using these bones stands to be particularly useful. Despite its functional relevance and frequent preservation in the fossil record, however, no systematic analysis of the bony aspects of the talocrural joint that affect its function has been conducted across anthropoids.

The talocrural joint is involved with determining overall movements of the foot, and motion of this joint is presumed to be affected by, or determined by, morphology of the talar trochlea. In addition, orientation of the talocrural and subtalar joints should reflect habitual foot postures during load bearing behaviors, because joints must be oriented normal to habitual load (Latimer et al., 1987).

There are common inferences found in the literature about several specific features of the anthropoid talocrural joint morphology. Those inferences have been used as basis for analysis of fossil anthropoids and to define clades within anthropoids based on presumed functional differences, even though they lack evidentiary support from systematic testing of extant anthropoids. Langdon (1986) inferred behavioral reasons for apparent differences in talocrural joint morphology between hominoids and non-hominoid anthropoids. He concluded that hominoids have “increased accessory

mobility” in the foot for a greater emphasis on climbing behaviors versus non-hominoid anthropoids. During vertical climbing, the feet are dorsiflexed and slightly supinated to grasp a vertical substrate. Supination requires non-parasagittal movement at the talocrural joint, and because hominoids have highly asymmetrical talar trochleae, the shape of the trochlea indicates the degree of dorsiflexion and supination—also referred to as conjunct rotation-- at the talocrural joint (Lewis, 1982). Therefore, the shape of the trochlea is inferred to be related to presumed climbing behaviors, and because hominoids vertically climb more frequently than most non-hominoids, this is suggested to be related to observed differences in talar trochlear shape (Langdon, 1986).

Qualitative differences in talar and calcaneal features between cercopithecines and colobines have led to similar interpretations for the morphology based primarily on locomotor differences (Strasser, 1988). For example, colobines emphasize climbing behaviors as compared to cercopithecines (Strasser, 1988). Just as with hominoids, Strasser states that colobines have asymmetrical talar trochleae, which are presumed to allow for increased conjunct rotation at the talocrural joint. If climbing behaviors of colobines and hominoids are reflected in particular features of the talus and calcaneus, then one would predict that similar talocrural joint morphology should be observed in all anthropoids that move their feet in a similar fashion during climbing.

Because previous assessments of the talocrural joints have made broad statements about functional variation among taxa with different locomotor emphases, this study tests aspects of the anthropoid talocrural joint quantitatively on a similarly broad level. It is important to establish accurate functional correlates of the talocrural joint of extant

anthropoids before features from the joint are used to reconstruct the positional behaviors of fossil catarrhines.

Of course the talocrural joint is only one region of the foot, and all variation among taxa in pedal functional morphology cannot be explained solely by this research, but analyses presented here represent an important first step. Further examination of the transverse tarsal joint, subtalar joint, and more distal elements will be necessary to more fully understand functional variations in foot anatomy in anthropoids. Still, results from this research provide important new information about variation in talocrural joint morphology and foot postures in extant and fossil anthropoids, and so provides context for the interpretation of other anthropoid fossil tali and calcanei, which are often found in isolation in the fossil record.

## Chapter 2. Background

Tali and calcanei are some of the most commonly preserved postcranial bones for fossil hominoids, and are the only postcranial fossils preserved for some species. Because the foot contacts the substrate during locomotion, these bones have the potential to reveal important information about the positional behavior of these fossil taxa. The talocrural joint consists of three bony structures, the tibia, the fibula, and the talus, and the anatomic subtalar joint consists of the posterior talocalcaneal joint and the anterior talocalcaneal joint, which is anatomically part of the transverse tarsal joint. The particular position and morphology of the talus and calcaneus influences the movements of the ankle and the foot at these joints. Joint orientations also reflect habitual foot postures during load bearing behaviors, as joints must be oriented normal to habitual load (Latimer, Ohman, & Lovejoy, 1987). Therefore, anatomy of the talus and calcaneus can shed light on habitual foot positions and movements during weight-bearing activities. This section briefly reviews the anatomy and function of the talus and calcaneus and provides the context for this study.

### Anatomy of the Talus

The talus has five articular surfaces and articulates with four bones (tibia, fibula, calcaneus, and navicular). The trochlea is a convex articular surface located on the dorsal surface of the talus that articulates with the tibia (Figure 2.1). All weight from the body is transmitted through this surface from the tibia, and the talus transmits these stresses in various directions (Kapandji, 1987). Directly medial to the trochlea is the facet for the

medial malleolus of the tibia and directly lateral to the trochlea is the facet for the lateral malleolus of the fibula. The head of the talus extends distally and medially from the trochlea and articulates with the navicular distally and the superior surface of the calcaneus inferiorly. The plantar surface of the talus consists of three articular surfaces for articulation with the calcaneus, the anterior calcaneal surface, the middle calcaneal surface, and posterior calcaneal surface, that together form the functional subtalar joint (Drake et al, 2005). Located on the posterior talus is the flexor hallucis longus groove, which contains the tendon of the *m. flexor hallucis longus* (Warwick & Williams, 1973). The groove is flanked by the medial and the lateral talar tubercles.

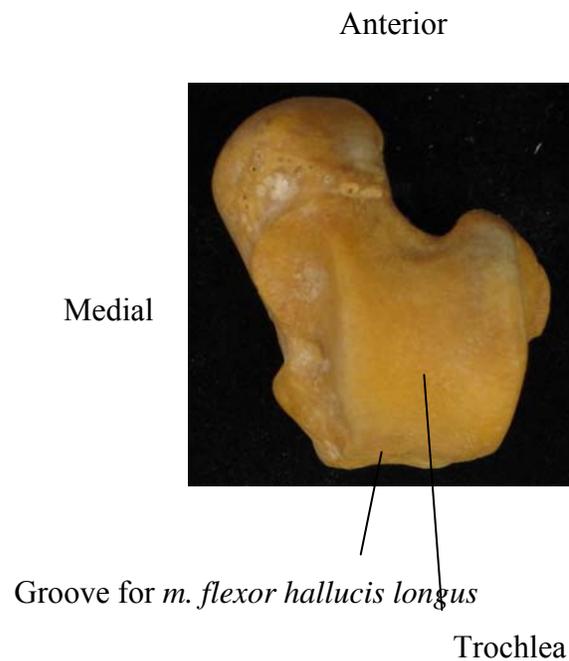


Figure 2.1. Superior view of the right *Nasalis larvatus* talus.

## Anatomy of the Calcaneus

The calcaneus is the largest tarsal bone. The calcaneus articulates with two bones: the talus superiorly at the functional subtalar joint and cuboid distally at the calcaneocuboid joint. The superior surface of the calcaneus has three facets that articulate with the talus: the posterior, middle, and anterior talocalcaneal facets (Warwick & Williams, 1973) (Figure 2.2). The middle talocalcaneal facet lies on the sustentaculum tali, a process that projects medially from the body of calcaneus. The plantar surface consists of three significant features: the anterior tubercle, the calcaneal tuberosity, and the groove for the tendon of *m. flexor hallucis longus*.

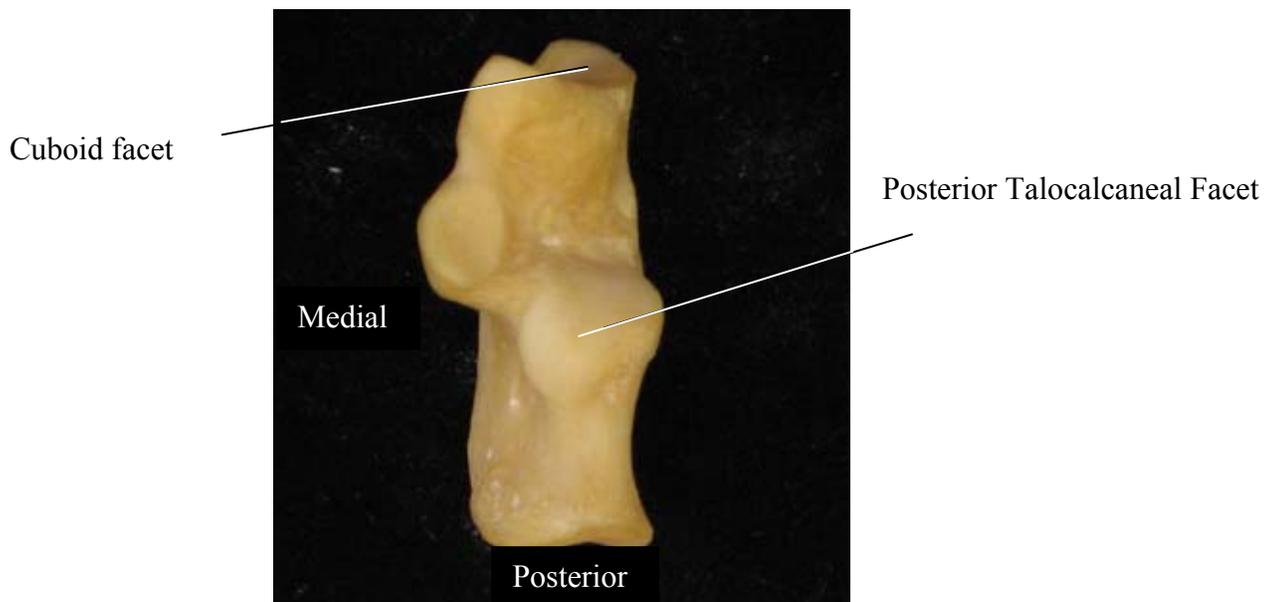


Figure 2.2. Superior view of the right *Trachypithecus cristata* calcaneus.

The number of joints present in the subtalar joint is dependent on the genus and/or family of anthropoid (Strasser, 1988). The anterior talocalcaneal facet may be split into two separate facets as in the case of cercopithecids or fused into one as in hominoids (Sullivan, 1933; Strasser, 1988). Another distinction among anthropoids is the presence

of a pressure facet for increased surface area on the lateral border of the posterior talocalcaneal facet. This pressure facet is rare in platyrrhines (Strasser, 1988).

### Ligaments Surrounding the Talus and Calcaneus

There are several ligaments that connect the talus to the fibula and tibia. The deltoid ligament is the most substantial ligament on the medial aspect of the talocrural joint. It consists of the posterior and anterior tibiotalar, tibiocalcaneal, and tibionavicular ligaments. The posterior and the anterior talofibular ligament connect the talus to the fibula on the lateral aspect of the talocrural joint.

Four ligaments attach the talus to the calcaneus: the lateral talocalcaneal, the posterior talocalcaneal, and the interosseous talocalcaneal ligament that is composed of anterior and posterior bands (Kapandji, 1987). Since the talus is the keystone bone between the leg and the foot, without these powerful ligaments, the integrity of the lower limb would be substantially compromised. However, muscular tension caused by contraction of muscles whose tendons pass the talocrural joint medially and laterally are also critical for joint support (Palastanga et al, 1998). Still, the strength of the talocalcaneal ligaments can be considered key to the entire stability of the body.

### The Ligaments Surrounding the Calcaneus

The ligaments previously mentioned for the subtalar joints attach onto the calcaneus as well as the superior band of the deltoid ligament of the ankle and the calcaneofibular ligament of the talocrural. The long and short plantar ligaments on the plantar surface of the calcaneus stabilized the longitudinal arch of the foot. The plantar

calcaneonavicular ligament connects the calcaneus and the navicular on the inferior surface of the talus. The plantar aponeurosis is a thick fascia that lies superficial to all musculature and also originates from the calcaneus (Warwick & Williams, 1973).

### Musculature Surrounding the Talus

The talus has been referred to as the “caged bone” (Kapandji, 1987) because it lacks muscular insertions. Rather, it is held into place by the ligaments and tendons of muscles surrounding it.

The tendons of the *m. extensor digitorum communis*, *m. tibialis anterior*, and *m. extensor hallucis longus* pass dorsally over the neck and head of the talus before inserting on the dorsal surfaces of the proximal phalanges of digits two through five, on the base of the first metatarsal, and the base of the dorsal surface of the distal phalanx of digit one respectively (Warwick & Williams, 1973). Conversely, the tendons of *m. tibialis posterior* and *m. flexor digitorum communis* muscles run on the medial aspect of the talus.

The *m. flexor hallucis longus* originates from the posterior aspect of the fibula and interosseus membrane and passes through a groove on the posterior surface of the talus and inferior to the sustentaculum tali of the calcaneus. The tendon eventually inserts onto the plantar surface of the distal phalanx of the hallux (Warwick & Williams, 1973).

### Musculature Associated with the Calcaneus

Many extrinsic and intrinsic muscles of the foot originate or insert onto the calcaneal tuberosity and the plantar surface of the calcaneus. The *m. triceps surae* include the *m. gastrocnemius*, *m. plantaris*, and *m. soleus*, which insert via the common calcaneal tendon, which, in turn, inserts onto the superior surface of the calcaneal tuberosity (Warwick & Williams, 1973). The *m. triceps surae* provide the muscular contraction for plantarflexion.

Five intrinsic muscles of the foot originate from the calcaneus in humans: *m. extensor digitorum brevis*, *m. abductor hallucis*, *m. flexor digitorum brevis*, *m. abductor digiti minimi* and *m. quadratus plantae*.

The tendons of the *m. flexor hallucis longus*, *m. flexor digitorum communis*, and the *m. tibialis posterior* as well as the tibial nerve and posterior tibial artery pass on the posteriolateral side of the talus and calcaneus through the tarsal tunnel. The calcaneus and talus compose the lateral wall and the flexor retinaculum the medial wall of the tarsal tunnel. The flexor retinaculum is a band of connective tissue that stretches from the medial malleolus of the tibia to the medial surface of the calcaneus (Warwick & Williams, 1973). Similarly on the lateral calcaneus, the tendons of the *m. peroneus longus* and *m. peroneus brevis* pass through two retinaculae (fibrous bands) attached to the calcaneus before insertion onto the base of the first metatarsal and the fifth metatarsal respectively.

## The Talocrural Joint

Most understanding of the soft tissue and movements associated with the posterior tarsus comes from studies on human and non-human cadavers and disarticulated museum collections of humans and anthropoids. The tibia and fibula, bound together distally by the anterior and posterior tibiofibular ligaments, and the talus compose the talocrural joint. The result of this is an upside-down U-shaped structure, which articulates with the superior, lateral and medial sides of the talar trochlea (Figure 2.3).



Figure 2.3. Anterior view of the human U-shaped superior surface of the right talocrural joint (modified from Aiello & Dean, 1990).

The talocrural joint is a synovial joint, between the superior and inferior ankle, and primarily unidirectional movements of flexion and extension occur at this joint. In anatomical terminology, flexion of the ankle is termed plantarflexion and extension termed dorsiflexion.

The axis of rotation for the talocrural joint is inferolaterally sloped instead of horizontal to the substrate or to the trochlear surface (Figure 2.4).



Figure 2.4. Anterior view of human right talocrural joint (modified from Latimer et al., 1987). The line indicates the axis of rotation of the talocrural joint.

Conjunct medial rotation of the talocrural joint is any non-parasagittal, accessory movement that occurs during dorsiflexion and plantarflexion, or supination that accompanies dorsiflexion and pronation with plantarflexion. During dorsiflexion of the joint, the obliquity of the transverse axis of rotation causes conjunct medial rotation of the tibia relative to the foot, or lateral rotation of the foot relative to the tibia. Because the talocrural joint is not a simple hinge with uniaxial movements, secondary movements such as medial or lateral rotation of the tibia and fibula can occur. In the fully dorsiflexed position of the ankle, the foot is slightly supinated (Latimer, Ohman, & Lovejoy, 1987; Palastanga et al 1998). An increased obliquity of the axis of rotation of the talocrural joint would allow increased conjunct medial rotation of the tibia and an increased supination of the foot during dorsiflexion because the habitual position of the talocrural joint is already slightly supinated.

Conjunct but medial conjunct rotation of the tibia will increase with obliquity of the talocrural rotational axis. In African hominoids, the axis of rotation for the talocrural

joint is more oblique than that of obligate bipeds and is sloped inferolaterally (Figure 2.5) (Latimer et al., 1987).

In addition, because the trochlea can be relatively broader anteriorly than posteriorly, full dorsiflexion is the position of most stability for the ankle that would permit the least medial or lateral rotation at the joint because the tibia and fibula are tightly locked with the talus (Palastanga et al, 1998). When the trochlea is narrower posteriorly than anteriorly, the talocrural joint should be capable of more medial and lateral translation during plantarflexion than dorsiflexion.

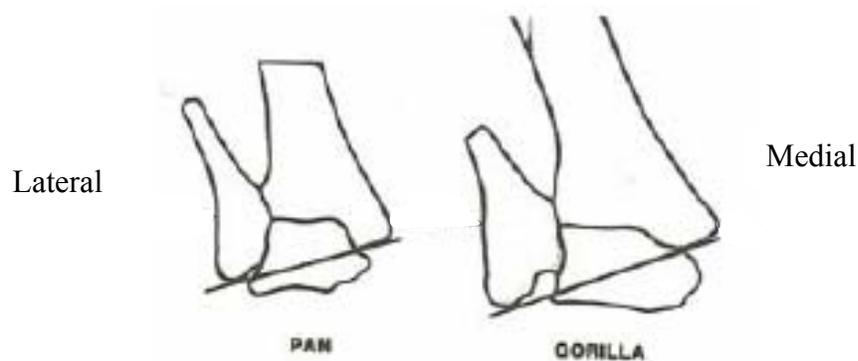


Figure 2.5. Anterior view of the right talocrural joint of African hominoids showing the axis of rotation (modified from Latimer et al., 1987).

Load is transferred from talus to calcaneus during gait, and ground reaction force from calcaneus to talus. Contraction of muscles surrounding these bones also loads the joints. Thus, joints experience the greatest degree of loading during dynamic locomotor, rather than static, activities. Because joints are covered with slick articular cartilage, they must be oriented normal to the direction of habitual and/or maximum loading. Therefore, joint orientation will reflect habitual bone orientation during locomotor activities (Latimer, et al., 1987; Latimer & Lovejoy, 1989).

Joints are not static bridges between bones, but dynamic systems where ossification and orientation are affected by pressure and loading (Frost, 1990). Loads incurred during growth may affect joint structure as adults (Hamrick, 1999). The extent of bone growth to shape joint morphology has not been fully explored, but certainly occurs at some level. For the purposes of this study, joint shape and form is a reflection of behavior, but genetics and plasticity probably do affect joint morphology to a limited extent.

#### The Anatomic Subtalar Joint and the Talocalcaneonavicular Joint

A shared synovial capsule, forming the anatomic subtalar joint, encloses the three bony articulations between talus and calcaneus on the posterior talocalcaneal surface. The anterior and middle talocalcaneal surfaces are enclosed within the synovial capsule of the talocalcaneonavicular joint (Palastanga et al, 1998). The functional subtalar joint is the combination of two joints between the calcaneus and the talus, that together produce one plane of motion (Sullivan, 1933; Grand, 1968).

The primary movements of the functional subtalar joint coupled with the transverse tarsal joints (talocalcaneonavicular and calcaneocuboid joints) are inversion and eversion of the foot. Inversion results from the movements of adduction and supination (pointing the talar head medially) of the anterior calcaneus relative to distal foot. Simultaneously, the transverse tarsal joints rotate laterally and supinate the distal foot (Kapandji, 1987; Gebo, 1993; Palastanga et al, 1998). Eversion is the opposite set of movements.

### Movements of the Talocrural Joint

Different locomotor patterns in anthropoids are related to morphological variation of the talus and the calcaneus. Most anthropoids have a greater degree of plantarflexion than dorsiflexion (Grand, 1968). The anterior tibia is prevented from further anterior movement by the talar neck during dorsiflexion at 30 degrees from normal posture, but the posterior tibia is not prevented from further posterior movement until 50 degrees during plantarflexion. There are proportionally more degrees of movement posteriorly on the talar trochlea articular arc than anteriorly. In humans, the tibia and fibula can rotate an estimated 20-30 degrees anteriorly (dorsiflexion) and 30-50 degrees posteriorly (plantarflexion) past normal stance position (Palastanga et al, 1998). The analysis of lower limb anatomy of howler monkeys, in particular, yielded a specific two-to-one ratio of plantarflexion muscle mass to dorsiflexion muscle mass because of the need for relatively strong plantarflexion to propel the animal during locomotion (Grand, 1968).

Bony features such as the medial and lateral malleoli of the tibia and fibula and the deltoid ligament, the posterior talofibular ligament, and the anterior talofibular ligament affect motions of the talocrural joint. The lateral malleolus of the fibula contacts the lateral tubercle of the talus, and that contact inhibits further lateral rotation. The medial malleolus of the tibia contacts the medial tubercle of the talus and inhibits further medial rotation. The talofibular ligaments accomplish resistance of medial rotation of the talocrural joint in anthropoids through the strong bond of the fibula to the talus (Fleagle, 1976b). The deltoid ligament resists lateral rotation of the joint on the medial aspect of the talocrural joint.

The relative length and width of the talocalcaneal facets reflect the limits of inversion and eversion (Kapandji, 1987; Strasser, 1988). For example, cercopithecine talocalcaneal facets are relatively wider mediolaterally than colobines. Strasser hypothesized that the increase in width increases the subchondral contact area, but restricts the degree of inversion by providing a larger and more stable base for the talus (Strasser, 1988). The widening of the surface is a greater area to minimize cartilage pressure on the talus, and is important for the more terrestrial cercopithecines than colobines that require little transverse movements of the foot.

The medial obliquity of the posterior talocalcaneal facet to the long axis of the calcaneus reflects hindfoot orientation relative to the posterior tarsus. While it has important implications, it is not directly related to talocrural function and is not considered further here (Dagosto, 1986; Ford, 1986; Langdon, 1986).

### Talar and Calcaneal Morphological Variation in Anthropoids

#### *Trochlear Shape & Depth*

The shape of the trochlea in anthropoids is often described as wedged versus rectangular or parallel-sided (Figure 2.6) (Langdon, 1986; Strasser, 1988). The trochlea can be wedged posteriorly, with the anterior breadth exceeding the posterior, and can also be wedged medially, with the lateral margin longer than the medial one.

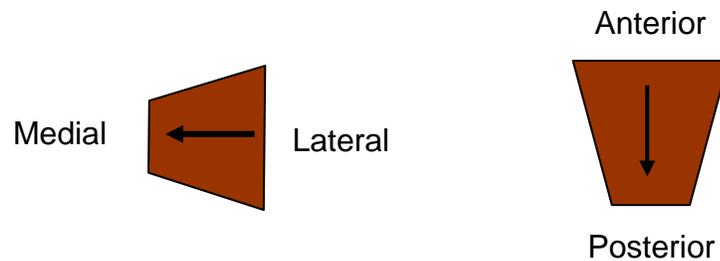


Figure 2.6. Schematic diagram of the right talar trochlea in superior view showing on the left medial wedging of the trochlea and on the right posterior wedging. Arrow is pointing to the narrower medial and posterior portions.

Variation in medial wedging of the trochlea has been observed among anthropoid taxa (Lewis, 1980; Langdon, 1986; Latimer et al., 1987). For instance, great apes have more medial wedging than humans. Great apes invert their feet during dorsiflexion to climb more often than humans (Latimer et al., 1987). One would predict that animals that habitually invert their feet such as is likely to occur during climbing like great apes would have more wedged trochleae mediolaterally than animals that do not climb such as humans. Fleagle (1976b) noted that the asymmetry or wedging of the medial and lateral trochlear margins is seen in *Presbytis obscura* and symmetry of the trochlear margins in *Presbytis melalophos*, and that *P. obscura* inverts its feet but *P. melalophos* does not during the same quadrupedal arboreal behaviors (ibid). Thus, the asymmetry of the trochlea has been hypothesized to indicate conjunct rotation of the tibia in the talocrural joint (ibid). Because an inverted, dorsiflexed foot is thought to be a typical foot position during climbing for anthropoids, increased medial trochlear wedging should be related to arboreal climbing specialization (Figure 2.7).

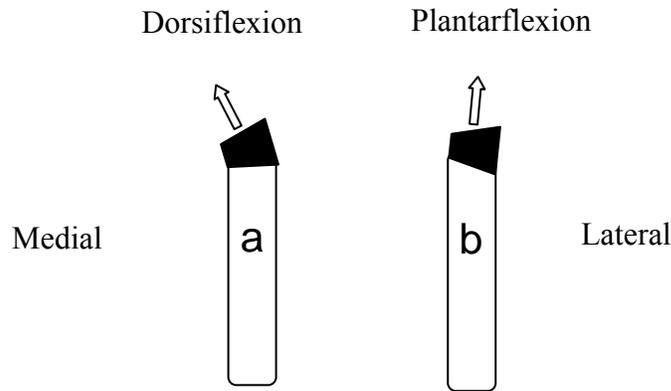


Figure 2.7. Schematic diagram of the right talocrural joint in anterior view. Black represents the talar trochlea, white represents the leg, and the arrow shows the direction of the foot during each movement. a) medial rotation of the superior talocrural joint during dorsiflexion b) lateral rotation of the superior talocrural joint during plantarflexion.

Langdon (1986) observed that cercopithecines (baboons and patas monkeys) have more asymmetric trochleae than do colobines. He hypothesized that the use of smaller branches by cercopithecines places the foot closer to the midline of the animal, simultaneously inverting the foot (ibid). Atelines and hominoids do not show asymmetric trochleae morphology according to Langdon because they have strong hallucal grasping. Also, the feet are more widely spaced when baboons and patas monkeys walk on the ground rather than a branch and to adapt to a wide, horizontal substrate, the talocrural joint is tilted oblique to the substrate to resist the loading forces (ibid). Quantitative documentation of the position of the feet relative to the midline of the body does not exist for cercopithecines or colobines. The lack of data to support Langdon's conclusions renders his argument conjectural.

The asymmetry of the anterior and posterior trochlea is also functionally relevant. For instance, ape talar trochleae are more posteriorly wedged than those of humans (Latimer et al., 1987)(Figure 2.6). This means that in dorsiflexion, the greater the posterior wedging, the tighter the talar trochlea fits between the malleoli, restricting lateral motions at the talocrural joint. In plantarflexion, in contrast, relatively more lateral motion would be permitted.

A less posteriorly wedged talar trochlea should be associated with similar restriction on lateral movement in all talocrural joint postures (Aiello & Dean, 1990). Strasser (1988) examined posterior wedging across cercopithecoids, and hypothesized that posterior wedging increases the amount of abduction possibly during dorsiflexion, but she did not compare cercopithecines to colobines for this feature, although behaviors should be reflected in the morphology of each species.

If so, increased posterior wedging of the trochlea should be seen in taxa that have increased transverse movement at the talocrural joints such as Asian apes, atelines, and colobines than African apes, non-ateline platyrrhines, and cercopithecines because more lateral motion of the talocrural joint is hypothesized to be necessary for climbing behaviors.

The depth of the trochlea, as with the corresponding keel on the talar articular surface on the distal tibia, is also an important feature of the talocrural joint. Depth should increase stability of the joint by restricting medial or lateral rotation, and restricting motions to a parasagittal plane (Fleagle 1976b; Langdon, 1986; Strasser, 1988). The selection for deep trochleae will be greater in non-climbing quadrupedal anthropoids versus anthropoids that emphasize climbing behaviors. Quadrupedal anthropoids should

require less medial and lateral movements at the talocrural joint to grasp branches or vertical substrates. Rather, terrestrial quadrupeds are expected to emphasize uniaxial movements of plantarflexion and dorsiflexion and restrict transverse joint movements of the talocrural joint. Therefore, terrestrial quadrupeds are expected to have more deeply grooved trochleae than anthropoids that emphasize climbing .

### *Posterior Talocalcaneal Facet*

The posterior talocalcaneal facet on the calcaneus is a convex surface that articulates with the concave posterior calcaneal facet of the talus within the anatomic subtalar joint. The anteroposterior angle of the posterior talocalcaneal facet relative to the cuboid facet has been used as a measurement for the degree of habitual dorsiflexion of the talocrural joint (Gebo, 1993). The orientation of the posterior talocalcaneal facet on the calcaneus, therefore, is hypothesized to reflect the position of the talocrural joint during normal gait. The angle of the posterior talocalcaneal facet should be higher (more parallel to the cuboid facet) in taxa that emphasize climbing, as these taxa should experience more habitual dorsiflexion during vertical ascent than during quadrupedal gait.

Another factor that may affect posterior talocalcaneal facet joint orientation is the presence or absence of heel strike. The calcaneus is the first bone of the foot to directly contact the substrate in normal striding gait of humans. During terrestrial gait of African apes, the lateral calcaneus contacts the substrate first, then the rest of the lateral foot follows, and lastly, the weight of the body is transferred medially (Weidenreich, 1923; Morton, 1924; Keith, 1929; Tuttle, 1970; Susman, 1983; Gebo, 1986, 1987, 1992; Meldrum, 1991). Most anthropoids do not have a heel strike during habitual gait, and

locomote with a heel-elevated, semiplantigrade foot position (Gebo, 1993). This is an important variable to consider in order to compare the posterior talocalcaneal facet between Asian apes and African apes. The semiplantigrade foot position of Asian apes orients the calcaneus oblique to the substrate, but the cuboid is positioned parallel to the substrate (ibid). Conversely, the plantigrade, heel-strike foot position of African apes orients the calcaneus parallel to the substrate, and the cuboid is positioned parallel to the substrate. The slope of the posterior talocalcaneal facet must be measured against the calcaneocuboid joint as an angle (as seen in Figure 2.8) because the position of the cuboid is different in African apes versus Asian apes. Asian apes are expected to have the posterior talocalcaneal facet more oblique (more vertically oriented to the rest of the distal foot) to the calcaneocuboid joint.

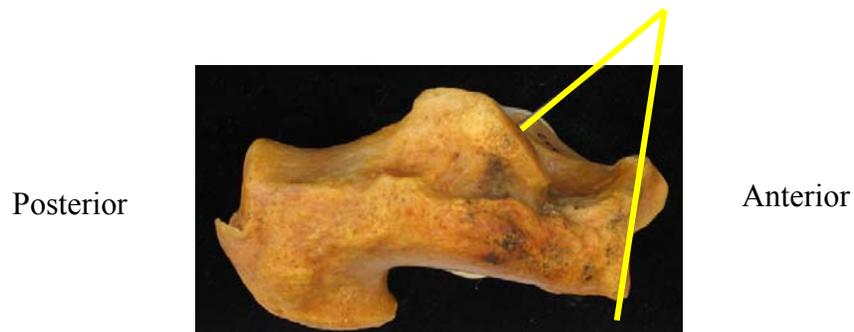


Figure 2.8. Lateral view of the right calcaneus of *Gorilla gorilla* showing a normal to the posterior talocalcaneal facet relative to a tangent to the lateral plane of the cuboid facet.

### *The M. flexor hallucis longus groove*

The relative angle and shape of the *m. flexor hallucis longus* groove on the talus is thought to coincide with the relative orientation of the foot and leg (Latimer et al., 1987). A tendon is aligned along the path of primary action of a muscle (ibid). This groove is oriented parallel to the leg and since the leg is oriented normal to the talocrural joint in humans, the *m. flexor hallucis longus* groove is vertical (Latimer et al., 1987). *Pan* and *Gorilla* have more medially inclined *m. flexor hallucis longus* grooves than do humans, reflecting the varus angle of their leg. Because of the obliquity of the leg, the foot would be slightly everted on the ground. Terrestrial anthropoids might be expected to have more vertically oriented *m. flexor hallucis longus* grooves than species that emphasize climbing behaviors because there is no need to invert/evert the feet on the ground. So, animals that emphasize climbing should have more oblique *m. flexor hallucis longus* grooves and animals that are terrestrial should have more vertically oriented grooves.

### Anthopoid Climbing

There are particular aspects of climbing that are presumed to drive variation in talocrural joint morphology. For the purpose of this study, climbing is defined as ascension of a vertical substrate greater than 45° using both forelimbs and hindlimbs (Hunt et al., 1996). The issue is the emphasis that the organism places on the behavior in relation to other behavioral movements such as quadrupedal running, leaping, or suspension. As presumed by observations in the literature, increased medial conjunct rotation of the talocrural joint during dorsiflexion is necessary to grasp a vertical substrate (Latimer et al., 1987; Langdon, 1986). Therefore, the form and orientation of

talus trochleae, posterior talocalcaneal facets, and *m. flexor hallucis longus* grooves mentioned in the previous sections of the extant anthropoid groups that emphasize climbing should reflect increased transverse movements of the talocrural and anatomic subtalar joints.

### Anthropoid Positional Behavior

Anthropoids vary in their foot postures during locomotor activities. Although precise foot postures are not always known, basic locomotor habits are known and patterns of foot use can be inferred. Anthropoid species may be specialized for particular behaviors, most anthropoids engage in a variety of positional behaviors and so cannot be classified into distinct locomotor groups (Erikson, 1963; Napier & Napier & Napier, 1967; Ripley, 1967; Mittermeier & Fleagle, 1976; Rodman, 1979; Langdon, 1986). The following is a summary of the basic locomotor habits of each extant species considered in this study. Quantitative behavioral observations are included. Note that the classification of observed behaviors is not standardized across anthropoids.

Some genera are sufficiently rare in museum collections so that sufficient monospecific samples were not possible to obtain (*Ateles*, *Alouatta*, *Pithecia*, and *Papio*), so specimens of multiple species are grouped for this study. No species considered here have dramatically different locomotor adaptations than congeners with which they are combined. Thus, locomotor adaptations for these taxa are described for the genus as a whole. For a complete list of each species see Appendix 1.

*Ateles sp.*

Spider monkeys inhabit coastal forests of Central and South America. Spiders are almost exclusively arboreal. They frequently use both forelimb, hindlimb and/or tail suspensory and bridging behaviors when foraging for food, in addition to quadrupedal behaviors on relative large substrates (Napier & Napier, 1967; Cant et al., 2001). Instances of upside-down quadrupedal running, arm-swinging, leaping, and bipedal locomotion on the ground have also been observed in *Ateles* (Mittermeier & Fleagle, 1976; Mittermeier, 1978; Cant et al., 2001; Ramos-Fernandez et al., 2004). Behavior observations of *Ateles geoffroyi* show 22% quadrupedalism, 26% suspension, 39.8% climbing, 11.4% leaping, and .8% bipedalism (Mittermeier, 1978).

*Alouatta sp.*

Howler monkeys inhabit the tropical rainforests of Central and South America, and are also almost exclusively arboreal. Howlers' movements are primarily slow and cautious quadrupedal climbing and prefer the upper canopies of the forest (Gebo, 1992b). Howlers tend to use arm-hang and tail-hang for feeding more than for locomotion (ibid). The tail is predominantly used for balance rather than its prehensile ability (Grand, 1968). Howlers avoid leaping except when descending deliberately from one branch to the next (Gebo, 1992b). Behavior observations of *Alouatta palliata* show 47% quadrupedalism, 37% climbing, and 10% bridging (ibid).

### *Lagothrix lagothricha*

Humboldt's woolly monkey is a large, robust primate that occupies the Amazon River basin of South America. These monkeys travel freely through the trees utilizing mainly arboreal quadrupedal movements and clambering (Cant et al., 2001). Descent of trees is normally head first, while *Ateles* tend to descend tail first. They often hang solely from their tails. (ibid). Behavioral observations of *Lagothrix lagothricha* show 28.7% quadrupedalism, 44.5% vertical climbing and clambering, 11.1% suspension, and 15.7% other modes (ibid).

### *Cebus capucinus*

Capuchin monkeys are small-bodied primates that occupy forests of Central and South America (*C. capucinus*) and some higher altitude regions of Brazil (*C. apella*). The relative size of capuchins compared to atelines allows the monkeys to perform more leaps and jumps from branch to branch rather than brachiate or climb like the larger platyrrhines (Fleagle et al, 1981). Exclusively arboreal monkeys, capuchins inhabit the top canopy of forests (ibid). Tail use is primarily for balance. Behavioral observations of *Cebus capucinus* show 54% quadrupedalism, 26% climbing, and 15% leaping (Gebo, 1992b).

### *Cebus apella*

Black-capped capuchin monkeys are medium-bodied platyrrhines that occupy higher altitude regions of Brazil (Fleagle & Mittermeier, 1980). Black-capped capuchins engage in long bouts of leaping during travel (ibid). Behavioral observations show 84%

quadrupedalism (the definition of quadrupedal movements encompasses all four limb pronograde locomotion), 5% climbing, and 10% leaping (ibid).

*Chiropotes satanas*

Black saki monkeys are small (3 kg) arboreal monkeys of Amazonian rain forests of South America. Very little is known of the black sakis in the wild, but captive monkeys predominantly move quadrupedally (Napier & Napier, 1967; Fleagle & Meldrum, 1988). Behavioral observations show 80% quadrupedalism, rare occasions of climbing, and 18% leaping (Fleagle & Mittermeier, 1980).

*Pithecia sp.*

Sakis monkeys are small-bodied primates (1.8 kg) that occupy tropical rain forest regions of South America. Primarily arboreal quadrupeds and climbers, sakis have been observed to move rapidly through trees and leap across gaps (Napier & Napier, 1967). *Pithecia* generally leaps more frequently than *Chiropotes* in the wild (Fleagle & Meldrum, 1988). Behavioral observations of *Pithecia pithecia* show 75% leaping and the remaining 25% quadrupedalism and climbing (Fleagle & Mittermeier, 1980).

*Papio sp.*

Baboons are largely terrestrial quadrupeds that occupy plains and savannah environments of Central and South Africa (Hill, 1970; Prost, 1974; Rose, 1976, 1977; Wrangham, 1980). Hands and feet are primarily plantigrade on the ground and pronograde in the trees during movement (Napier & Napier, 1967). Baboons spend the

majority of the time on the ground, but may also venture into the trees for food or protection from predators (Prost, 1974; Rose, 1977). Behavioral observations of *Papio anubis* show the majority of locomotion is quadrupedalism with less than 1% climbing (Rose, 1977).

#### *Macaca fascicularis*

Crab-eating macaques are the smallest of extant macaques. They inhabit mainly arboreal regions along the coasts or swampy areas of Indonesia (Napier & Napier, 1967). They are exclusively arboreal, mostly using above-branch quadrupedalism, with occasional leaping or climbing (Rodman, 1979; 1991). Hands and feet are positioned plantigrade in arboreal travel (Napier & Napier, 1967). Behavioral observations of crab-eating macaques show 70% quadrupedalism and 15-25% climbing/clambering (Cant, 1988).

#### *Macaca nemestrina*

Pig-tailed macaques inhabit predominantly tropical rain forest regions in Indonesia, Malaysia and Southeast Asia. Although these monkeys occupy forests, some time is spent on the ground foraging (Napier & Napier, 1967). As their name suggests, pig-tail macaques have shorter tails than crab eating macaques. The reduced length may be a functional adaptation for an increased amount of time on the ground as seen in similar studies between terrestrial versus arboreal squirrel tail lengths (Rodman, 1979; 1991). The home range of pig-tail macaques in the trees and on the ground is quite large,

and the majority of arboreal travel is along sturdy branches and substrates (Rodman, 1979; Caldecott, 1986). No quantitative behavioral data was found for *M. nemestrina*.

#### *Macaca mulatta*

Rhesus monkeys inhabit a wide range of habitats including villages and towns of India (Napier & Napier, 1967). Predominantly terrestrial quadrupeds, rhesus monkeys, due to their surroundings, occasionally occupy trees. Hand and foot postures are primarily digitigrade on the ground and pronograde in the trees during movement (Dunbar, 1989). Behavioral observations show 71% quadrupedalism, 12% climbing, 10% leaping (Wells & Turnquist, 2001).

#### *Trachypithecus cristata*

Silver-leaf monkeys are predominantly arboreal quadrupeds that occupy forests and canopies of Malaysia. Running and walking along the branches along with vertical climbing is common with rare spouts of leaping (Fleagle, 1976b). Suspensory movements are infrequent compared to atelines, but more frequent than in *Papio* or *Macaca* (Ashton & Oxnard, 1964a; Napier & Napier, 1967; Rose, 1973). No quantitative behavioral observations were found.

#### *Nasalis larvatus*

Proboscis monkeys are known only from Borneo. Proboscis monkeys are mainly arboreal quadrupeds, but often leap across gaps in branches using the propulsion of branches as a springboard (Napier & Napier, 1967). *Macaca fascicularis* and *Nasalis*

*larvatus* are often sympatric in the coastal swamps of Borneo as well as several other species of primates (Kawabe & Mano, 1972). Their range is large and overlaps several different habitats suggesting that their adaptations are not limited to one specialized area or habitat, but proboscis monkeys have the capacity to exploit different resources (Kawabe & Mano, 1972; Bennett & Sebastian, 1988). These monkeys are also known to frequently vertically climb and drop into the mangrove swamp below and swim freely (Bennett & Sebastian, 1988). No quantitative behavioral data was found for *Nasalis larvatus*.

### *Gorilla gorilla*

Lowland gorillas are the largest extant primates, and occur in lowland regions of Central Africa. Lowland gorillas spend a considerable amount of their time in the trees for foraging, nesting, and playful purposes (Remis, 1995). On the ground, gorillas predominantly knuckle-walk with their feet in a plantigrade position (Jenkins & Fleagle, 1975; Susman & Stern, 1979; Tuttle, 1967; 1969a, b, 1970; 1975). Arboreal locomotion is cautious climbing and brachiation with little to no bouts of leaping (Ashton & Oxnard, 1964a,b; Avis, 1962; Erikson, 1963; Lewis, 1971a,b; Napier, 1963; 1967; 1976). Large silverback males locomote in the trees less frequently than females and juvenile males, and rarely venture out from the core of trees (Remis, 1995). Bipedality is rare and occurs during aggressive displays or charges (Tuttle, 1986). No quantitative locomotor behavioral datum was found for lowland gorillas, although there is significant work on highland gorillas, but with no quantitative data.

*Pongo pygmaeus*

Orangutans are large-bodied apes that occupy forested regions of Borneo and Sumatra. Orangutans are almost exclusively arboreal, engaging in suspension quadrumanous climbing and bridging (Thorpe & Crompton, 2006; Thorpe et al., 2007; Andrews & Groves, 1976; Napier, 1976; Tuttle, 1986). Orangutans proceed cautiously between branches, and they are rarely seen on the ground except for the Borean subspecies, and then only males (ibid). Although their feet have a powerful grasp, the hallux is significantly reduced and often the distal phalanx and the flexor hallucis longus muscle are absent (Schultz, 1963). Behavioral observations show 15% quadrupedalism, 43% suspension, 22% climbing, and 7% arboreal bipedalism (Thorpe & Crompton, 2006).

*Pan troglodytes*

Chimpanzees are primarily terrestrial quadrupeds that occur in tropical rain forests, forest savannahs, and woodland regions of Central and West Africa. Chimpanzees spend more time (50-80%) in the trees than lowland gorillas. On the ground, chimpanzees knuckle-walk and commonly stand bipedal to assist their vision and/or carry materials short distances (Hunt, 1992; Jenkins & Fleagle, 1975; Susman & Stern, 1979; Tuttle, 1967; 1969, 1970; 1975). Resting posture in chimpanzees can be sitting, squatting, or supine in arboreal nests or branches (Hunt, 1992). Behavioral observations show 26% quadrupedalism and 74% climbing (Doran, 1993).

### *Hylobates lar*

White-handed gibbons inhabit the forest regions of Indo-China and Thailand and the island of Sumatra. Gibbons are true brachiators that swing freely and efficiently from branch to branch in the dense upper canopy of tropical forests (Carpenter, 1940; Napier & Napier, 1967; Tuttle, 1986). The majority of locomotion in gibbons is suspensory (Carpenter, 1940; Fleagle, 1976a). White-handed gibbons frequently move bipedally on a solid and stable substrate with their arms flexed, held at shoulder height (Carpenter, 1940; Tuttle, 1972). Behavioral observations show 56% suspension, 21% climbing, 15% leaping and 8% bipedalism (Fleagle, 1976a).

### Summary of the Extant Anthropoids

The taxa are grouped into pairs based on overall similarities within and differences between groups. Colobines, atelines, Asian apes, and hominoids are considered to emphasize climbing behaviors more than cercopithecines, non-ateline platyrrhines, African apes, and non-hominoids, respectively. These groups are tested on a pairwise basis to provide some control for shared phylogeny on morphology. This study primarily focuses on the function of each morphological feature, but it is difficult to separate function from phylogeny for the samples. Therefore, the grouping of the taxa is based on both function and phylogeny. That being said, the datum of this study may yield undetermined results. The quantitative behavioral data is unknown for the colobines, but known for cercopithecines. Without the behavioral data, definitive responses to the results will be lacking for the pairwise cercopithecoid tests. On the contrary, quantitative behavioral data is known for both atelines and non-ateline

platyrrhines. With this data, more definitive responses can be made for the pairwise platyrrhine tests. The locomotor behaviors of the colobines are said to be (*Nasalis larvatus* and *Trachypithecus cristata*) primarily arboreal with an emphasis on climbing (Strasser, 1988), but no quantitative behavioral data is known. This study uses the two species of colobines, the former *Presbytis melalophus* and *Presbytis obscura* as analogs for the behavior of *Nasalis larvatus* and *Trachypithecus cristata* (Fleagle, 1976b). Fleagle quantified the muscular mass of the hips, knees, and shoulders of both *Presbytis* species and compared the results to other colobines. He found many similarities between *Presbytis obscura* and *Trachypithecus cristata*. Behavioral quantitative data from *Presbytis obscura* shows more quadrupedal movements versus *Presbytis melalophus*'s emphasis on leaping and suspensory activities (Fleagle, 1976b). Although little quantitative behavioral data for *Nasalis larvatus* and *Trachypithecus cristata* (except for the comparison with *Presbytis obscura* through Fleagle's work) is available, in the literature, climbing behaviors of colobines are said to distinguish them from cercopithecines (*Papio sp.*, *M. fascicularis*, *M. nemestrina*, and *M. mulatta*). Foot morphology should be, as a result, different between cercopithecines and colobines based on said behavioral differences. Similarly, atelines (*Aloutta*, *Ateles*, and *Lagothrix*) emphasize climbing more than non-atelines platyrrhines (*Cebus*, *Chiropotes*, and *Pithecia*), and talocrural joint morphology should reflect these differences if features such as medial wedging of the trochlea and trochlear depth are linked to behavior. Asian apes versus African apes should reflect similar patterns and, according to Langdon (1986), hominoids versus non-hominoid anthropoids should reflect behavioral differences.

The comparison of hominoids versus non-hominoids is problematic because there is little overlap in body size between these two groups. Langdon (1986) inferred behavioral reasons for apparent differences in talocrural joint morphology between hominoids and non-hominoid anthropoids, but he did not specify what those behavioral differences are. Aside from significant body size differences and phylogenetic factors between hominoids and non-hominoid anthropoids, Langdon concluded that hominoids have “increased accessory mobility” than non-hominoids (ibid). This mobility of the feet might allow hominoids to move in different ways than non-hominoids, but again there is little to no positional behaviors produced by the vague description provided by Langdon. Therefore, the use of the pairwise comparison is solely for the purpose of comparison between the results from this study and Langdon’s previous work (1986).

Anthropoids are divided into two parvorders, playrrhini and catarrhini (Napier & Napier, 1967). Catarrhines are divided into cercopithecoids and hominoids. Cercopithecoids are represented in this study by two subfamilies: cercopithecini (*Papio* and *Macaca*) and colobinae (*Nasalis* and *Trachypithecus*). Cercopithecines are more terrestrial than colobines, and therefore, differences in talocrural morphology between groups should represent differences in positional behaviors. Note that *Macaca fascicularis* is the smallest cercopithecine and often climbs and leaps more than *Macaca nemestrina* (Rodman, 1979; Table 2.1). *Macaca fascicularis* may emphasis climbing more than the other cercopithecines because of its size, but it is included with cercopithecines primarily based on phylogeny. Because the behavior of *M. fascicularis* is similar to colobines, data for this study should show *M. fascicularis* as similar in morphology to *Nasalis* and *Trachypithecus*. If that is not the case, the related

morphology of the talocrural joint among cercopithecids is controlled by something other than functional behavior. Ultimately, if phylogeny is a strong factor in morphologic form, then *M. fascicularis* talocrural joint morphology should be more similar to cercopithecines rather colobines, but if the features under investigation in this study are related to locomotor behaviors, then *M. fascicularis* morphology should be more similar to colobines based on behavioral similarities. This study is not about phylogeny, rather it is a study that attempts to identify locomotor functions from particular features of the talocrural joint morphology of anthropoids. *Macaca fascicularis* is an important species in this study because it should help isolate the factors for the form of the talocrural joint.

Similarly, the platyrrhine species in this study are divided into atelines (*Alouatta*, *Ateles*, and *Lagothrix*) and non-ateline platyrrhines (*Cebus*, *Chiropotes*, and *Pithecia*). Because both atelines and non-ateline platyrrhines are predominantly arboreal animals, atelines emphasize climbing more than do non-ateline platyrrhines. *Cebus*, *Chiropotes*, and *Pithecia* are smaller animals and emphasize leaping and quadrupedal walking and running, rather than climbing behaviors (Walker, 2005). As observed by Fleagle and Mittermeier (1980), as the size of the animal increases, the frequency of climbing increases and the frequency of leaping decreases. Therefore, partly because of size and prehensile tails, *Alouatta*, *Ateles*, and *Lagothrix* tend to climb more than *Cebus*, *Pithecia*, and *Chiropotes*.

Hominoids are divided into two groups, Asian apes and African apes, based on presumed locomotor behaviors. *Pongo* and *Hylobates* are predominantly arboreal Asian apes, and *Gorilla* and *Pan* represent the more terrestrial African apes. Like colobines and atelines, Asian apes should exhibit talocrural morphology adapted to arboreal climbing

behaviors. The results from the posterior talocalcaneal facet angle should also show differences between African apes and Asian apes based on the presence of a heel-strike in *Gorilla* and *Pan* and absence of a heel-strike in *Pongo* and *Hylobates*.

Body size, along with phylogeny and form, is an important aspect of locomotor behavior. Hominoids, in general, are relatively larger than catarrhines and platyrrhines. Body size would seem to have an effect on the movement of an animal. For instance, an elephant would have a much harder time climbing and swinging in a tree versus a raccoon or opossum. The locomotor behaviors of large hominoids would consequently be different than small non-hominoid anthropoids. This aspect of body size compared to behavior may have a tremendous effect on the results of this study. Large animals need wide and sturdy branches to support the mass of the animal. Those same wide branches are easy for a small anthropoid to run across with no lateral movement of the foot. The large anthropoid would need to invert its feet in order to grasp the branch. Therefore, the body size does have an effect on the movements of the foot whether the animal is on a wide or narrow substrate.

Table 2.1. Summary of quantitative behavioral data for extant taxa. Note that *Trachypithecus cristata*, *Nasalis larvatus*, *Macaca nemestrina* and *Gorilla gorilla gorilla* have no data.

<b>Taxa</b>	<b>Quadrupedal</b>	<b>Suspension</b>	<b>Climbing</b>	<b>Leaping</b>
<b>Atelines</b>				
<i>Ateles sp.</i>	22%	26%	39.8%	11.4%
<i>Alouatta sp.</i>	47%	--	37%	--
<i>Lagothrix lagothricha</i>	28.7%	11.1%	44.5%	--
<b>Non-ateline platyrrhines</b>				
<i>Cebus capucinus</i>	54%	--	26%	15%
<i>Cebus apella</i>	84%	--	5%	10%
<i>Chiropotes satanas</i>	80%	--	--	18%
<i>Pithecia sp.</i>	<25%	--	<25%	75%
<b>Cercopithecines</b>				
<i>Papio sp.</i>	99%	--	<1%	--
<i>Macaca fascicularis</i>	70%	--	15-25%	--
<i>Macaca nemestrina</i>	--	--	--	--
<i>Macaca mulatta</i>	71%	--	12%	10%
<b>Colobines</b>				
<i>Trachypithecus cristata</i>	--	--	--	--
<i>Nasalis larvatus</i>	--	--	--	--
<b>Hominoids</b>				
<i>Gorilla gorilla gorilla</i>	--	--	--	--
<i>Pongo pygmaeus</i>	15%	43%	22%	--
<i>Pan troglodytes</i>	26%	--	74%	--
<i>Hylobates lar</i>	--	56%	21%	15%

The quantitative behavioral information summarized in Table 2.1 shows justification for the ateline versus non-ateline platyrrhine pairwise functional comparisons. Atelines, as a whole, emphasize climbing behaviors (greater than 37% of the time) than non-ateline platyrrhines (less than 26% of the time). Non-ateline platyrrhines emphasize quadrupedal movements (greater than 50% of the time, with the exception of *Pithecia*) more frequently than atelines (less than 47% of the time). The lack of data for colobines limits the use of the cercopithecoid pairwise comparison for functional purposes, although both Langdon (1986) and Strasser (1988) used these groups to demonstrate the function of form in the talocrural joint. The frequency of quadrupedal movements among cercopithecines is high (greater than 70% of the time) and the climbing is relatively low (less than 15% of the time), but there is no quantitative data for colobines to compare those cercopithecine frequencies to. *Macaca fascicularis* has a much higher frequency of climbing (greater than 15%) than the other cercopithecines. This species may present potential problems with the overall statistics for cercopithecines, but if *M. fascicularis* overlaps statistically with colobines, then the talocrural joint morphology could potentially be useful for concluding locomotor behaviors of a species. Lastly, there is no quantitative information for gorillas, but the information for chimpanzees is available. Orangutans and gibbons emphasize suspension and climbing, whereas chimpanzees emphasize quadrupedal movements and climbing. This might indicate that the differences between Asian apes and African apes have little to do with climbing and more with quadrupedal movements.

There are also many problems that are presented by this information for the hominoid versus non-hominoid comparison. The within group variation appears to be as vast as the between group variation. Clearly, the many holes in Table 2.1 demonstrates a lack of basic behavioral knowledge of extant anthropoids, but the justification for the grouping in this study are pulled directly from the literature. Langdon (1986) presumes behavioral differences between hominoids and non-hominoid anthropoids because the talocrural joint morphologies are different. This assumes that the form is a direct product of function. This study uses Langdon's same groups in order to investigate his original conclusions. Likewise, Strasser (1988) uses similar justification for the colobine versus cercopithecine groups. Because the form of the talar trochlea is different between the two cercopithecoid groups, Strasser hypothesized that the locomotor behavior is a primary factor for the morphologic differences. Therefore, although these groups of anthropoids each have a high degree of variation within, the justification for the grouping of anthropoid species is to test the previous conclusions and assumptions that lace the functional morphologic literature for anthropoid talocrural form.

#### Fossil Catarrhines Considered in This Study

##### *Proconsul major*

*Proconsul major* was a basal hominoid that inhabited regions of modern Kenya and Uganda (Harrison, 2002). The site of Songhor, Kenya yielded an associated talus (KNM-SO 390) and calcaneus (KNM-SO 389) attributed to *P. major* (Le Gros Clark & Leakey, 1951). The Songhor deposits date from 19 to 20 Ma and have yielded great quantities of small arboreal frugivores and semi-arboreal organisms and relatively low

quantities of grazing and terrestrial mammals suggesting relatively wet and humid forests similar to modern day equatorial tropical rain forests (Andrews et al, 1997). Body mass of this individual has been estimated from the articular dimensions of the talocrural joint surfaces of these specimens to be 63.4 to 86.7 kilograms (Rafferty et al, 1995). Relative length and shape of the calcaneus and the posterior wedging of the talar trochleae is similar to colobines (Strasser, 1993; Walker, 1997). The groove for *m. flexor hallucis longus* tendon on the calcaneus is deep. A more robust tendon and *m. flexor hallucis longus* suggests strong hallucal grasping (Langdon, 1986; Rose, 1983). These similarities with colobines in the feet are suggested to indicate that *P. major* must have primarily occupied arboreal environments and engaged in climbing behaviors similar to extant colobines (Walker, 1997). However, if these functional inferences are inaccurate, so may be locomotor reconstructions of *P. major*. If *P. major* was more similar in locomotion to extant colobines, then talocrural morphology should reflect this.

#### *Proconsul nyanzae*

*Proconsul nyanzae* (17-18.5 MYA) has been excavated at Mfangano and Rusinga Islands, Kenya. An associated talus and calcaneus from the partial skeleton KNM-MW 13142 was excavated from the site at Mfangano Island. Another isolated talus (KNM-RU 1745) is also known from Rusinga (Le Gros Clark & Leakey, 1951). The sites are associated with the Kisingiri volcano, where the environment was relatively wet and forested (Andrews & Van Couvering, 1975; C. Ward, 1993). *Proconsul nyanzae* was a moderately sexually dimorphic species where males ranged from 35 to 38 kilograms and females ranged from 26 to 28 kilograms (Ruff et al, 1989; C. Ward, 1997; Harrison,

2002). The body mass for KNM-MW 13142 was estimated using femoral head dimensions at 34 kilograms and KNM-RU 1745 was slightly smaller than this fossil (C. Ward, 1993). Postcranial morphology from the vertebrae, pelvis, and feet suggests generalized quadrupedal behaviors without below-branch specializations (Ruff et al, 1989; Rose, 1993; C. Ward, 1993; Harrison, 2002; Kelley, 1997). The *Proconsul nyanzae* specimens have deeply grooved talar trochleae and deeply grooved *m. flexor hallucis longus* grooves on the talus and calcaneus. These features suggest powerful pedal grasping abilities. As hypothesized, deeply grooved asymmetric talar trochleae should indicate more talocrural joint stability than colobines and little mediolateral movement at the joint as seen in cercopithecines.

#### *Afropithecus turkanensis*

*Afropithecus turkanensis* (17-18 MYA) was another basal hominoid excavated from Kalodirr, Kenya. The environment at Kalodirr probably also was forested and wet (R. Leakey et al., 1988). Kalodirr has yielded a nearly complete talus, KNM-WK 18120 (ibid) from an individual that weighed about 25 kg (Leakey & Walker, 1997). Although not necessarily phylogenetically related to *Proconsul nyanzae* (Begun et al, 1997), it is strikingly similar in preserved postcrania to it, although there are some profound differences in the cranium and dentition (Leakey & Walker, 1997; C. Ward, 1997, 1998; Harrison, 2002). Therefore, positional behavior of *Afropithecus* is reconstructed as primarily arboreal above-branch pronograde locomotion similar to that of *P. nyanzae* from the postcrania and limited pedal segments (R. Leakey et al., 1988; C. Ward 1998).

### *Sivapithecus parvada*

*Sivapithecus parvada* (8 to 8.8 Ma) is a hominoid known from Pakistan and South Asia. It is likely a member of the *Pongo* clade (S. Ward, 1997; Begun et al., 1997).

*Sivapithecus parvada* is known from two calcanei (GSP 17152, GSP 17606) from Potwar Plateau, Pakistan (Rose, 1986). Potwar Plateau consists of fluvial deposits that yielded a rich diversity of flora and fauna on the southern edge of the Himalayan Mountains. The climate was wet, humid, and the environment consisted of tropical forests (Khan, 1997). Body mass estimate for *Sivapithecus parvada* is approximately 50 to 69 kilograms, but GSP 17152 and GSP 17606 were nearer to the smaller end of the range (Rose, 1993). GSP 17606 is 84% as long as GSP 17152. The average difference in calcaneal length between sexes in great apes is approximately 86 % (Rose, 1986). So, Rose (1986) concluded that GSP 17152 was a male and GSP 17606 was a female. The postcranial morphology including a robust hallux, distal femur, curved humeral shafts, navicular, and curved phalanges of *S. parvada* suggests above –branch arboreality, although with stronger hallucal grasping ability than earlier hominoids, based on the calcaneal fragment GSP 14046, which has a deep groove for the *m. flexor hallucis longus* (Pilbeam, et al., 1980; Rose, 1986, 1993; S. Ward, 1997; Madar et al., 2002).

### *Paracolobus mutiwa*

*Paracolobus mutiwa* was a cercopithecoid dated to between 3.36 and 1.88 MA from northern Kenya (Harris et al. 1988). The locale's paleoenvironment was a volcanic plain that contained numerous amounts of riverine and arboreal organisms (ibid). It is known from a partial skeleton (KNM-WT 16827) that has not been formally described,

but includes an associated complete talus and calcaneus. Craniodental fossils indicate that *P. mutiwa* was a highly sexually dimorphic species with the males around 52 kilograms and the females around 27 kilograms (Delson et al., 2000). The KNM-WT 16827 specimen was that of a male, and slightly smaller than *Proconsul nyanzae* KNM-MW 13142. Some work has been done on other regions of the *P. mutiwa* anatomy (Leakey & C. Ward, 1995; Ting, 2003), there is little formal description and functional interpretations from the talocrural joint for *P. mutiwa*. This study will not attempt to predict the behavior of *P. mutiwa*, but simply record and analyze its talar morphology.

#### *Paracolobus chemeroni*

*Paracolobus chemeroni* (2.0 Ma) from the Chemeron Formation of the Baringo District, Kenya is known from a largely complete skeleton, including associated talus and calcaneus (KNM-BC 3) (Birchette, 1982). The paleoecology of Lake Baringo was a fluvial environment that contained tropical rainforests and a high diversity of flora and fauna (Birchette, 1982). Body mass of male *P. chemeroni* is estimated at 30 to 37.5 kilograms, slightly smaller than the ranges *P. mutiwa* (Delson, Terranova et al., 2000), but this specimen appears nearly identical in joint size to KNM-WT 16827. Overall, *Paracolobus chemeroni* and *P. mutiwa*, although within the same genus, have slight morphological differences in their postcrania. Unlike extant colobines, it appears that *P. chemeroni* was a terrestrial quadruped and a climber (Leakey & C. Ward, 1995; Ting, 2003).

## Summary of the Fossils

Postcranial remains for each of these fossil specimens have yielded basic interpretations for the positional behaviors of the species, but questions still remain. The *Proconsul* specimens' and *Afropithecus*' locomotor behaviors are reconstructed as above-branch quadrupeds. *Sivapithecus* is reconstructed as an above-branch quadruped with strong grasping ability. Ting (2001) concluded that hip and thigh morphology of *Paracolobus mutiwa* was similar to extant cercopithecines. The results from this study coupled with Ting's study show that *P. chemeroni* and *P. mutiwa* had mosaic colobine/cercopithecine morphology. Therefore, *Paracolobus mutiwa* and *Paracolobus chemeroni* are reconstructed as large-bodied terrestrial climbers. If locomotor behaviors can be reconstructed based on the form of the talocrural joint in extant catarrhines, then the locomotor behaviors of extinct catarrhines can be reconstructed based on the fossilized tali and calcanei. Therefore, the fossils will be compared to the extant groups of catarrhines. Researchers have inferred foot postures and locomotor behaviors of these fossil specimens based on features such as talar trochlear shape and depth, but whether those features are correlated with the inferred locomotor behaviors remains untested. Therefore, this study tests those broad conclusions from the talocrural joint for both extant and extinct species of anthropoids.

## Chapter 3: Materials and Methods

### Hypotheses

Previous work on talar and calcaneal form in restricted samples of extant and fossil anthropoids provide testable hypotheses about the functional anatomy of the talocrural joint among anthropoids. Comparisons between pairs of anthropoid taxa with generally different foot use during locomotion can provide tests of these hypotheses.

A: Medial wedging of the talar trochlea increases conjunct inversion during dorsiflexion and eversion during plantarflexion of the talocrural joint (Latimer et al., 1987; Lewis, 1980), and so should be greater in anthropoids that emphasize climbing behaviors during locomotion than those that do not.

Hypotheses:

1. Colobines will have greater medial trochlear wedging than cercopithecines.
2. Atelines will have greater medial trochlear wedging than non-ateline platyrrhines.
3. Asian apes will have greater medial trochlear wedging than African apes.
4. Hominoids will have greater medial trochlear wedging than non-hominoids.

B: Posterior wedging of the trochlea increases stability and decreases potential for transverse movement at the talocrural joint during dorsiflexion (Strasser, 1988; Aiello & Dean, 1990) and more in plantarflexion, allowing stability during the beginning of propulsion but allowing adjustment near the end of it, and so should be greater in primates who emphasize climbing behaviors during locomotion.

Hypotheses:

1. Colobines will have greater posterior trochlear wedging than cercopithecines
2. Atelines will have greater posterior trochlear wedging than non-ateline platyrrhines.
3. Asian apes will have greater posterior trochlear wedging than African apes.
4. Hominoids will have greater posterior trochlear wedging than non-hominoids.

C: The anteroposterior angle of the posterior talocalcaneal facet relative to the cuboid facet is a measurement for the degree of habitual dorsiflexion of the talocrural joint (Gebo, 1993). The angle of the posterior talocalcaneal facet should be higher (more parallel to the cuboid facet) in taxa that emphasize climbing, as these taxa load their foot more heavily in dorsiflexion for propulsion in vertical ascent than during quadrupedal gait.

Hypotheses:

1. Colobines will have more oblique posterior talocalcaneal facets than cercopithecines.
2. Atelines will have more oblique posterior talocalcaneal facets than non-ateline platyrrhines.
3. Asian apes will have more oblique posterior talocalcaneal facets than African apes.
4. Hominoids will have more oblique posterior talocalcaneal facets than non-hominoids.

D: The *m. flexor hallucis longus* groove on the talus coincides with the relative orientation of the leg relative to the talocrural joint. Climbing species should have a more oblique orientation of this groove, and thus of the leg, reflecting habitual inversion of the foot that occurs during climbing (Latimer et al, 1987).

Hypotheses:

1. Colobines will have more oblique *m. flexor hallucis longus* grooves than cercopithecines
2. Atelines will have more oblique *m. flexor hallucis longus* grooves than non-ateline platyrrhines.
3. Asian apes will have more oblique *m. flexor hallucis longus* grooves than African apes.
4. Hominoids will have more oblique *m. flexor hallucis longus* grooves than non-hominoids.

E: The depth of the trochlea is associated with greater keeling of the talocrural joint, restricting lateral movements of the foot during locomotion (Fleagle, 1976b; Strasser, 1988; Langdon, 1986). Thus, taxa that emphasize climbing should have shallower trochlear grooves than more quadrupedal ones.

Hypotheses:

1. Colobines will have more shallow talar trochleae than cercopithecines
2. Atelines will have more shallow talar trochleae than non-ateline platyrrhines.
3. Asian apes will have more shallow talar trochleae than African apes.
4. Hominoids will have more shallow talar trochleae than non-hominoids.

## Materials

**Sample:** Extant comparative osteologic specimens were obtained from the Museum of Comparative Zoology (MCZ) and the Field Museum of Natural History (FMNH). Casts of fossil specimens are from the University of Missouri, Columbia.

Extant samples consisted of 132 individuals from 29 extinct and extant species of anthropoids chosen to represent a variety of locomotor adaptations (see Chapter 2).

Table 3.1. Extant sample.

<b>Species</b>	<b>N</b>	<b>Collection</b>
<b>Cercopithecines</b>		
<i>Papio papio</i>	10	MCZ, FMNH
<i>Macaca sp.</i>	7	MCZ
<i>Macaca fascicularis</i>	12	MCZ
<b>Colobines</b>		
<i>Trachypithecus cristata</i>	7	MCZ
<i>Nasalis larvatus</i>	7	MCZ
<b>Atelines</b>		
<i>Ateles sp.</i>	11	FMNH
<i>Lagothrix lagothricha</i>	9	FMNH
<i>Alouatta sp.</i>	8	FMNH
<b>Non-ateline platyrrhines</b>		
<i>Cebus apella</i>	7	FMNH
<i>Cebus capucinus</i>	4	FMNH
<i>Chiropotes satanas</i>	5	FMNH
<i>Pithecia sp.</i>	6	FMNH

<b>Great apes</b>		
<i>Gorilla gorilla</i>	10	MCZ
<i>Pan troglodytes</i>	10	MCZ, FMNH
<i>Pongo pygmaeus</i>	11	MCZ, FMNH
<b>Hylobatids</b>		
<i>Hylobates lar</i>	8	MCZ

Table 3.2. Fossil specimens used in analysis.

<b>Species</b>	<b>Sites</b>	<b>Specimen</b>	<b>Bone</b>
<i>Proconsul major</i>	Songhor, Kenya	KNM-SO 390 (Le Gros Clark & Leakey, 1951) KNM-SO 389 (Le Gros Clark & Leakey, 1951)	talus  calcaneus
<i>Proconsul nyanzae</i>	Mfangano Island, Kenya  Rusinga Island, Kenya	KNM-MW 13142 (Ward, 1993)  KNM-RU 1745 (Le Gros Clark & Leakey, 1951)	talus, calcaneus  talus
<i>Afropithecus turkanensis.</i>	Kalodirr, Kenya	KNM-WK 18120 (Leakey & Leakey 1986)	talus
<i>Sivapithecus parvada</i>	Potwar Plateau, Pakistan	GSP 17152 GSP 17606 (Rose, 1986)	calcaneus (partial) calcaneus (partial)
<i>Paracolobus chemeroni</i>	Lake Baringo, Kenya	KNM-BC 3 (Leakey 1969) KNM-BC 3	talus  calcaneus
<i>Paracolobus mutiwa</i>	Nachakui Formation, Kenya	KNM-WT 16827 unpublished KNM-WT 16827 unpublished	talus  calcaneus

## Methods

**Measurements:** Five aspects of talar morphology that reflect hypothesized components of talocrural joint function were quantified.

*Medial wedging of the talar trochlea* (Figure 3.1): Photos were taken of each talus in superior view with scale bars placed at the same level as the plane of measurements for calibration. Using *ImageJ* software (Rasband, 2006; <http://rsb.info.nih.gov/ij/>), three linear dimensions were measured, the medial and lateral lengths of the trochlear margins, and the width of the trochlea at its anteroposterior midpoint. Using these distances, medial wedging was calculated following Digiovanni and colleagues (1989):

$$\text{Wedging} = 2 \arctan (Y/X)$$

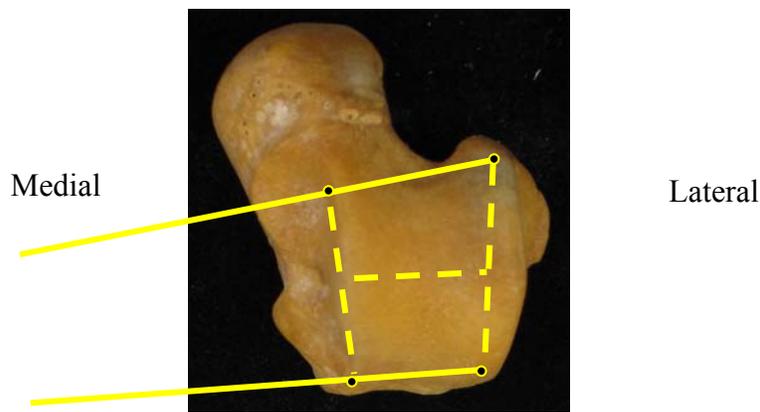
$$\text{Where } Y = \frac{\text{Lateral length} - \text{Medial length}}{2}$$

$$2$$

$$\text{And } X = \text{Trochlear width}$$

The lengths and width were manually measured using printouts of the calibrated digital photographs.

Figure 3.1. Right talar trochlea in superior view showing medial wedging (*Nasalis larvatus*).



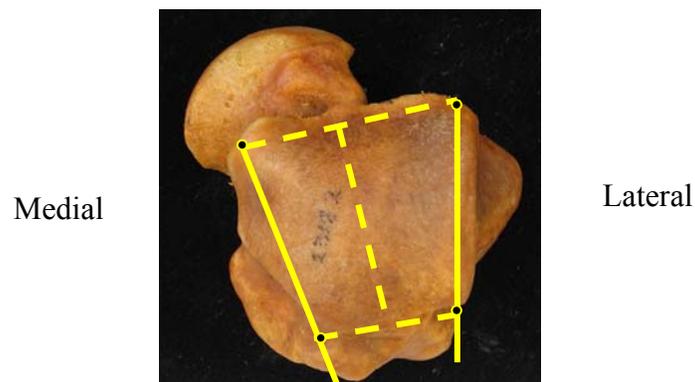
*Posterior wedging of the talar trochlea* (Figure 3.2): Posterior wedging was also calculated using the same formula (Digiovanni et al, 1989) from the same set of digital photographs used for medial wedging. Linear dimensions were mediolateral breadths of the anterior and posterior margins of the trochlea, and anteroposterior length along the trochlear midline:

$$\text{Wedging} = 2 \text{ arc tan } (Y/X)$$

$$\text{Where } Y = \frac{\text{Anterior width} - \text{Posterior width}}{2}$$

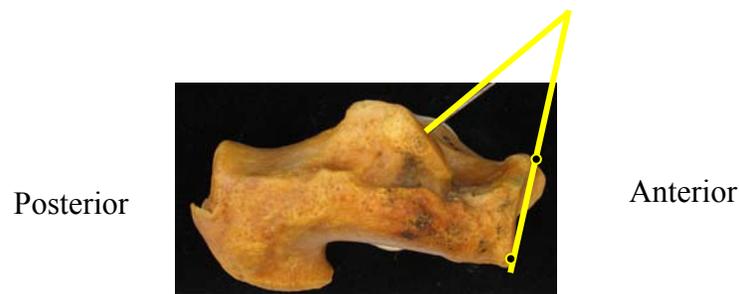
$$\text{And } X = \text{Trochlear length}$$

Figure 3.2. Right talar trochlea in superior view showing posterior wedging (*Gorilla gorilla*).



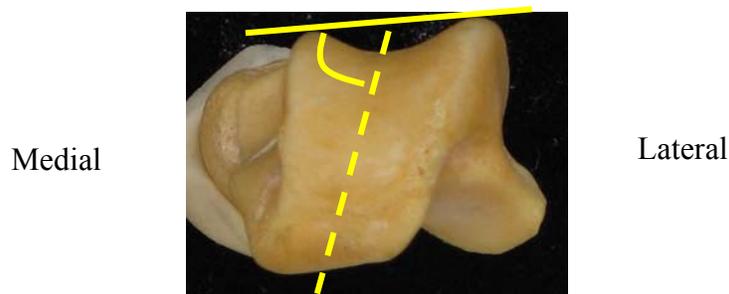
*Posterior talocalcaneal facet* (Figure 3.3): This angle was calculated from photographs of each calcaneus taken in lateral view. Using *ImageJ*, the angle was measured between a line perpendicular to the anterior portion of the posterior talar facet and a second line parallel to the cuboid facet of the calcaneus.

Figure 3.3. Right calcaneus in lateral view showing the posterior talocalcaneal facet angle (*Gorilla gorilla*).



*M. flexor hallucis longus* groove angle (Figure 3.4): *M. flexor hallucis longus* groove orientation was measured from photographs taken of tali in posterior view using *Image J* on the posterior tali relative to a horizontal trochlea. The angle was measured between a line drawn across the medial and lateral trochlear margins and another along the midline axis of the groove.

Figure 3.4. Right talus in posterior view showing the *m. flexor hallucis longus* groove of the talus (*Macaca fascicularis*).



*Trochlear depth:* Trochlear depth (Figure 3.5) was also quantified with *ImageJ* using photographs taken of tali in anterior view. The depth was measured from a line perpendicular to a line across the medial and lateral trochlear margins.

Figure 3.5. Right talus in anterior view showing trochlear depth of the talus taken from *Macaca fascicularis*.



*Body size surrogate:*

Body mass is one of the most important aspects of a species adaptation (Rose, 1973; Cartmill & Milton, 1977; Fleagle & Mittermeier, 1980; Kay, 1984; Temerin et al, 1984; Jungers, 1985), and can significantly affect locomotor anatomy. Therefore, it is important to establish any potential allometric relations between morphologies hypothesized to affect talocrural joint function and body mass.

Mass is not known for most extant specimens available for this study, and of course is not known for fossil individuals. Therefore, body mass is commonly estimated using skeletal dimensions, particularly articular dimensions. The femur is commonly chosen, but most fossils do not have associated femora (Ruff et al, 1991; Jungers et al, 1995). Therefore, for this study a

size surrogate was constructed using the geometric mean (Smith, 1993; Jungers et al, 1995) of talar trochlear dimensions: medial, lateral, anterior, and posterior trochlear breadths. During analysis of the samples of anthropoids, the use of trochlear dimensions as a body size surrogate does not work for all groups namely atelines and Asian apes. Although this body size surrogate is problematic and does not correctly identify the relative body sizes for some groups, this study had no other choice to use, based on the limited fossil remains. Geometric mean is chosen over arithmetic mean, because arithmetic mean often overestimates the average of several factors, especially if the variance is large. Geometric mean can underestimate the average, but it more accurately estimates the actual value than the arithmetic mean (Smith, 1993).

#### Interobserver Error Studies

*Intraobserver Errors:* All five measurements were recorded from individuals of *Macaca fascicularis* thrice by the same observer (Marquardt). The re-measurements were performed no less than one month from the original measurement to increase objectivity. In some cases, there was more than 5% measurement error for the individual measures, and all but trochlear depth have a species average less than 5% measurement error. In the majority of cases, the error is minor enough to ignore. The higher interobserver error in trochlear depth may have a slight effect on the statistical results, which is acknowledged by this study.

*Medial Wedging:* The results are as follows: the mean error between trials is 1.950% (Table 3.3).

Table 3.3. Interobserver Errors for medial wedging.

Specimen	Trial 1 (degrees)	Trial 2 (degrees)	Trial 3 (degrees)	% Error
1	12.018	12.018	12.018	0
2	12.680	12.680	12.680	0
3	6.026	6.026	6.026	0
4	6.360	6.026	6.026	5.252
5	12.018	12.018	12.018	0
6	10.085	10.085	10.712	3.109
7	9.028	8.578	8.578	4.984
8	13.420	12.680	13.420	2.757
9	16.732	15.814	16.732	2.743
10	15.814	14.992	15.814	2.600
11	10.712	10.712	10.712	0
				X=1.950

*Posterior Wedging:* The results are as follows: the mean error between actual results and re-measurements is 1.547% (Table 3.4).

Table 3.4. Interobserver Errors for posterior wedging.

Specimen	Trial 1 (degrees)	Trial 2 (degrees)	Trial 3 (degrees)	% Error
1	13.578	13.578	13.578	0
2	16.260	16.260	17.061	2.463
3	10.881	10.881	10.881	0
4	13.578	12.966	13.578	2.254
5	8.171	7.801	8.171	2.264
6	15.814	15.814	14.992	2.600
7	10.389	10.389	10.389	0
8	17.062	16.260	17.062	2.350
9	14.250	14.992	14.250	2.604
10	13.578	13.578	13.578	0
11	10.881	10.881	11.421	2.481
				X=1.547

*Posterior talocalcaneal facets:* The results are as follows: the mean error between *ImageJ* actual results and *ImageJ* re-measurements is 5.687% (Table 3.5).

Table 3.5. Interobserver Errors for posterior talocalcaneal facets.

Specimen	Trial 1 (degrees)	Trial 2 (degrees)	Trial 3 (degrees)	% Error
1	61.713	57.216	58.073	6.593
2	58.621	56.439	57.423	2.883
3	66.046	63.493	63.685	3.720
4	67.908	65.970	69.871	1.841
5	56.736	57.110	57.359	0.879
6	56.803	56.546	59.842	2.449
7	58.899	64.589	65.908	10.780
8	49.386	50.672	54.777	6.760
9	54.229	60.985	62.650	13.993
10	52.031	49.648	51.624	2.681
11	51.661	55.944	57.685	9.976
				X=5.687

*The m. flexor hallucis longus groove:* The results are as follows: the mean error between *ImageJ* actual results and *ImageJ* re-measurements is 2.181% (Table 3.6).

Table 3.6. Interobserver Errors for *m. flexor hallucis longus* groove.

Specimen	Trial 1 (degrees)	Trial 2 (degrees)	Trial 3 (degrees)	% Error
1	68.378	66.345	68.004	1.760
2	66.897	67.841	77.471	8.609
3	63.370	61.921	65.621	0.633
4	62.587	61.889	59.972	2.647
5	66.601	64.386	65.782	2.278
6	68.629	71.045	66.988	0.565
7	67.820	65.794	69.063	0.577
8	69.634	72.624	69.74	2.227
9	72.290	69.520	72.546	1.739
10	72.096	70.427	70.75	2.091
11	71.840	72.403	72.52	0.865
				X=2.181

*Trochlear depth:* The results are as follows: the mean error between *ImageJ* actual results and *ImageJ* re-measurements is 10.795% (Table 3.7). This is a high value and may have some effect on the statistical analyses.

Table 3.7. Interobserver Errors for trochlear depth.

Specimen	Trial 1 (cm)	Trial 2 (cm)	Trial 3 (cm)	% Error
1	1.351	1.184	1.316	7.476
2	1.184	1.316	1.447	16.596
3	0.946	1.061	1.081	13.214
4	0.946	1.089	0.946	7.558
5	1.216	1.111	1.053	11.020
6	0.789	0.946	0.946	19.900
7	1.061	0.956	1.061	4.948
8	1.316	1.224	1.316	3.495
9	1.316	1.089	1.184	13.640
10	1.486	1.216	1.447	10.397
11	1.453	1.351	1.250	10.500
				X=10.795

### Statistical Methods

Anthropoid species exhibit a large range of body mass. To evaluate the effects of body mass on the talocrural joint measurements, least squares regression analysis was used to assess the effect of body mass on the functional variables considered here. The limitation of least squares regression is that it assumes no error in variance in the body mass variable, but the correlation between body mass and the morphological features is relatively high and therefore, least squares regression was used instead of reduced major axis regression, which carries no assumptions about variance error. The geometric mean of trochlear dimensions was used as the size surrogate (Smith, 1993). Pearson's product-moment correlation and coefficients of relatedness were used to explore the effects of body mass on the variables considered here.

Bivariate regression line approximates a “best fit” trend line through normally distributed data and correlation estimates the strength and directionality of the relationship. Correlation was tested for significance using the significance test for Pearson's  $r$  (Cohon, 1988). The null hypothesis for correlation was rejected if the significance is  $p > .05$ . If the within group correlation between the geometric mean for the size surrogate and each feature was significant at  $p < .05$  for at least one group, ANCOVA was performed for the pairwise comparison. If the within-group correlation between the geometric mean for the size surrogate and each feature was not significant for both groups, non-parametric Mann-Whitney U tests were conducted. Although parametric statistics were justified for the overall data set, each individual pairwise comparison has a low sample size and non-parametric statistics were a better measure of differences between groups (Zar, 1999).

ANCOVA (analysis of co-variance) for each feature significantly correlated with the geometric mean of trochlear measurements was conducted to test the hypotheses for each pairwise groups (cercopithecines versus colobines, atelines versus non-ateline platyrrhines, Asian apes versus African apes, and hominoids versus non-hominoids). ANCOVA tests differences among variances for two variables for each pairwise comparison. The null hypothesis was that the means of each taxon are equivalent and  $p > 0.05$ . Taxa that were significantly different from another have  $p < 0.05$ , and for this study,  $p$ -values less than 0.1 were considered a statistical trend or signal. Two  $p$ -values were given from the results of the ANCOVA,  $y$ -intercept differences and slope differences. The  $y$ -intercept  $p$ -value indicates if there was a  $y$ -intercept difference between the pairs in the analysis and the slope  $p$ -value indicates if there was a slope difference between the pairs.

In special cases where there was little overlap between groups in the ANCOVA, narrow allometric analysis was conducted. Narrow allometry tested differences between groups within a particular range of the body size surrogate using a Mann-Whitney U non-parametric test.

To qualitatively explore variation among extant taxa, and better understand the results of the statistical comparison, variation among pairs was illustrated using bivariate scatter plots. Scatter plots show the range of variation for each taxon, and allow comparison of sample distributions. Discriminant function analysis was performed to summarize the datum for the quantitative measurements of each pairwise comparison.

To explore morphological affinities of fossil specimens with extant groups, discriminant function analysis was performed for catarrhines. Discriminant function analysis is a multivariate statistical analysis that incorporates a number of variables simultaneously to predict group memberships of individuals and displays them on a two-dimensional plot (Lachenbruch & Goldstein, 1979). If differences among dependent variables are significant, pure separation among taxa is quantitatively accurate and significant for extant anthropoids.

Discriminant function analysis was run on the 6 continuous measurements (geometric mean of trochlear measurements, medial wedging of the trochlea, posterior wedging of the trochlea, posterior talocalcaneal facet angles, and *m. flexor hallucis longus* groove angles, and trochlear depth).

Lastly, there is a high probability that not all four pairwise comparisons will yield the same significant findings. In those cases, the findings will be assessed using the quantitative behavioral data and the known information about each group. All findings will be summarized at the end of Chapter 4. Without universal acceptance of all four pairwise comparisons, the hypotheses must be false.

## Chapter 4: Results

### Medial Wedging

Colobines, atelines, Asian apes, and hominoids are predicted to have a higher degree of medial wedging than cercopithecines, non-ateline platyrrhines, African apes, and non-hominoids respectively.

#### *Cercopithecoids*

Pearson's product moment correlation between medial wedging and trochlear size was tested for each group. Within both cercopithecines and colobines, the degree of medial wedging is not significantly correlated with trochlear size (Table 4.1). Because trochlear size is not significantly correlated with medial wedging, a Mann-Whitney U non-parametric test was performed (Table 4.2) and the results show a significant difference between cercopithecines and colobines for medial wedging. Cercopithecines have relatively higher medial wedging than colobines (Figure 4.1).

Table 4.1. Within group least-squares line values for cercopithecines and colobines.

Source	R	Significance	Slope	y-Intercept
Cercopithecines	-.214	.264	-.252±.452	13.393±5.449
Colobines	-.410	.130	-.486±.649	10.221±8.383

Table 4.2. Mann-Whitney U non-parametric results for pairwise comparison of cercopithecines and colobines.

	Mean	Feature	Mann-Whitney U	Z	Significance (2-tailed)
Cercopithecines	10.475	Medial Wedging	47.500	-4.213	<b>.000</b>
Colobines	4.085				

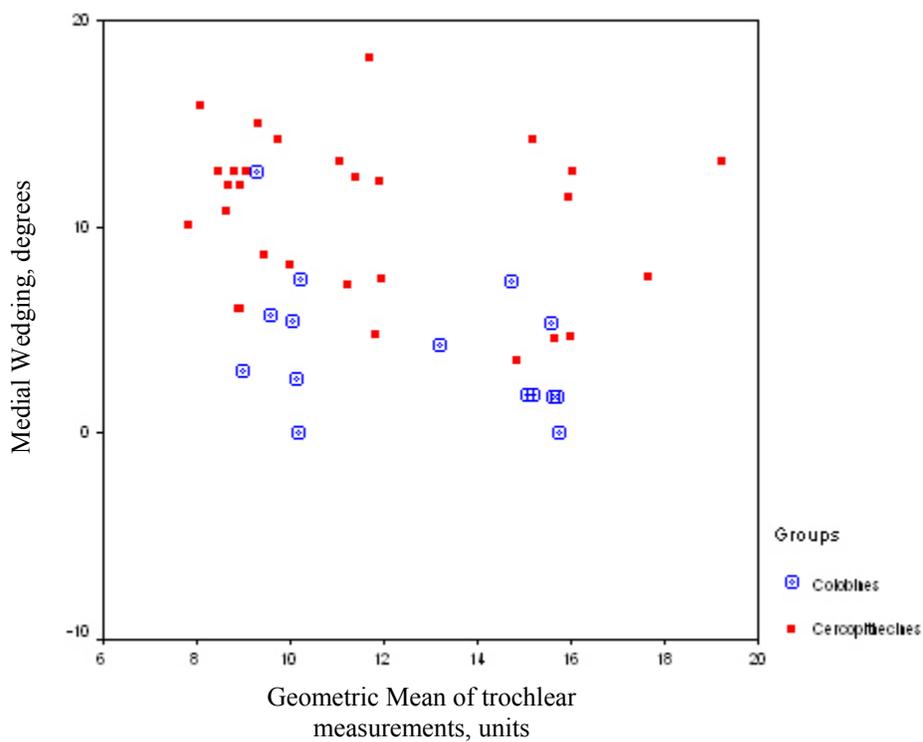


Figure 4.1. Bivariate plot of medial wedging for cercopithecoids against the geometric mean of trochlear measurements.

*Platyrrhines*

Pearson’s product moment correlation between medial wedging and trochlear size was tested for each group. Within atelines, but not non-ateline platyrrhines, trochlear size has a negatively statistically significant effect on the degree of medial wedging (Table 4.3). Because medial wedging is significantly correlated with trochlear size, an ANCOVA test was performed and results show a significant difference in the y-intercept between atelines and non-ateline platyrrhines and a significant difference ( $<.1$ ) in slopes (Table 4.4; Figure 4.2). Non-ateline platyrrhines have relatively more medial wedging than atelines.

Table 4.3. Within group least-squares line values for atelines and non-ateline platyrrhines.

Source	Significance	R	Slope	y-Intercept
Atelines	<b>.038</b>	-.394	-.865±.812	13.608±9.577
Non-atelines	.497	.153	.704±2.122	4.446±18.324

Table 4.4. ANCOVA results for pairwise comparison of atelines and non-ateline platyrrhines.

Source	Significance	Partial Eta Squared
y-intercept	<b>.002</b>	.181
Slope	.080	.064

Due to the little group overlap, narrow allometry for individuals less than 9.65 for the geometric mean of trochlear measurements was performed. Narrow allometry is the non-parametric statistical analysis of the differences between two groups within a limited range of the geometric mean of trochlear measurements. The narrow allometry results show no difference between atelines and non-ateline platyrrhines for medial wedging (Table 4.5).

Table 4.5. Narrow allometry for pairwise comparison of atelines and non-ateline platyrrhines.

	Mean		Z	df	Significance
Atelines	8.609	Medial wedging	-.607	1	.544
Non-atelines	10.502				

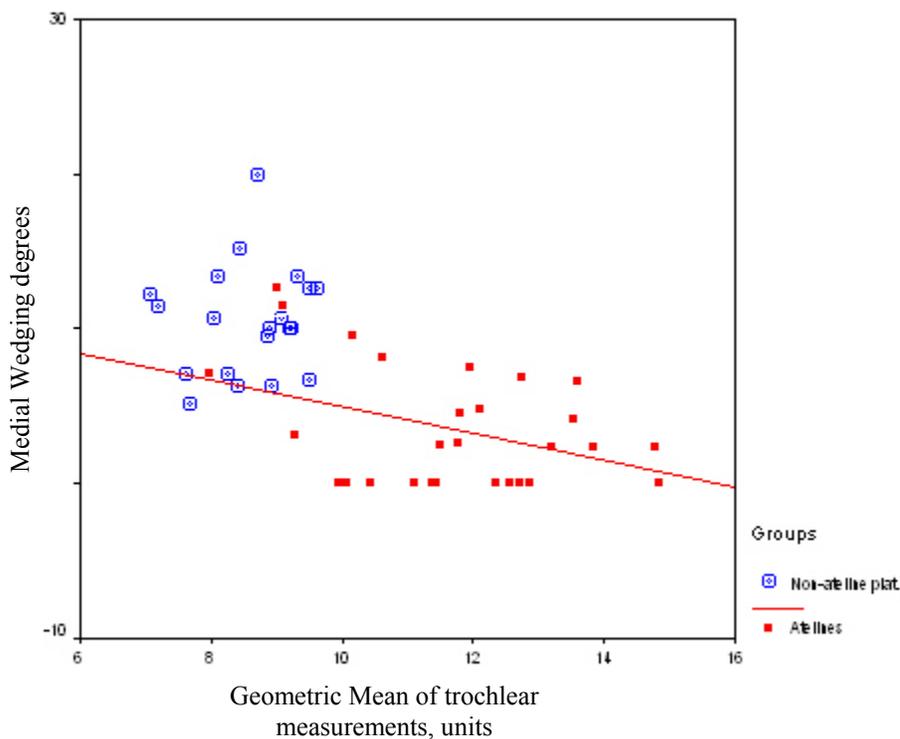


Figure 4.2. Bivariate plot of medial wedging for platyrrhines against the geometric mean of trochlear measurements. The line signifies that the slope for atelines is statistically significant and the slope for non-atelines is not significant.

## *Hominoids*

Pearson's product moment correlation between medial wedging and trochlear size was tested for each group. Within Asian apes and not African apes, medial wedging is significantly negatively correlated with trochlear size (Table 4.6). Because medial wedging is significantly correlated with trochlear size for one group, an ANCOVA was performed and results show no y-intercept difference between Asian and African apes, but there is a significant difference between the slopes (Table 4.7; Figure 4.3). Because of the slope difference, the test for the y-intercept is meaningless since where the lines cross the x-axis is different and unrelated to the relative relationship between x and y variables between groups.

Table 4.6. Within group least-squares line values for African apes and Asian apes.

Source	R	Significance	Slope	y-Intercept
Asian apes	-.642	<b>.003</b>	-.446±.273	15.069±5.297
African apes	-.430	.059	-.299±.311	11.437±8.878

Table 4.7. ANCOVA results for pairwise comparison of hominoids.

Source	Significance	Partial Eta Squared
y-intercept	.994	.000
Slope	<b>.000</b>	.326

Due to the little group overlap, narrow allometry for individuals between 20 and 30 for the geometric mean of trochlear measurements was performed. The narrow allometry results show no significant difference between Asian apes and African apes for medial wedging (Table 4.8)

Table 4.8. Narrow allometry for pairwise comparison of Asian apes and African apes.

	Mean		Z	df	Significance
Asian apes	4.105	Medial wedging	-.270	1	.787
African apes	4.326				

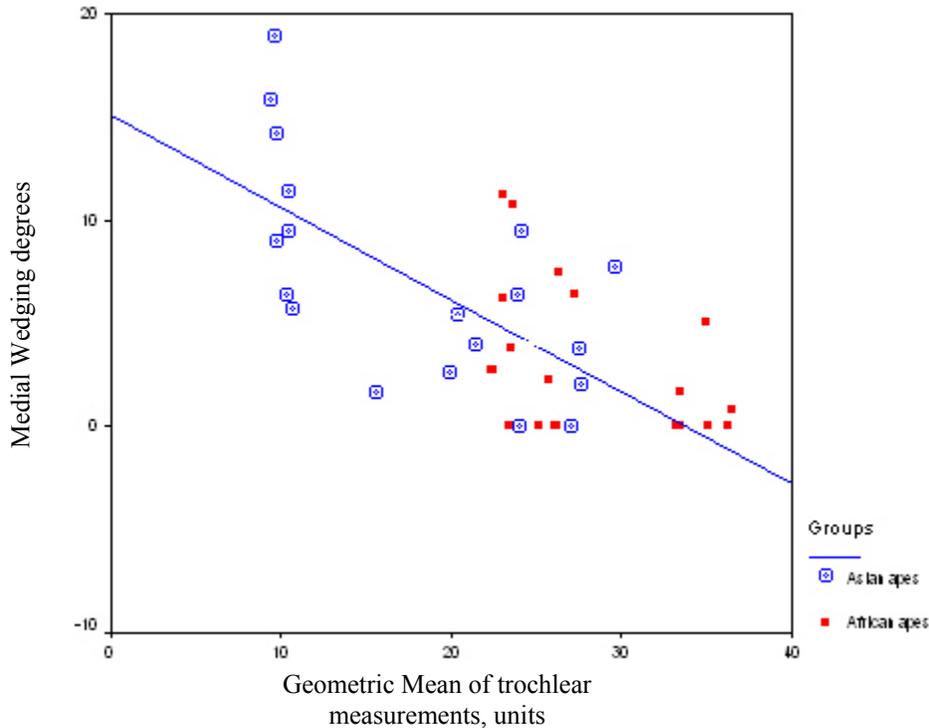


Figure 4.3. Bivariate plot of medial wedging for hominoids against the geometric mean of trochlear measurements. The line signifies that the slope for Asian apes is statistically significant and the slope for African apes is not significant.

### *Anthropoids*

Pearson's product moment correlation between medial wedging and trochlear size was tested for each group. Within both hominoids and non-hominoids, medial wedging is significantly negatively correlated with trochlear size (Table 4.9). Because medial wedging is significantly correlated with trochlear size, an ANCOVA was performed and results show a significant difference in both the y-intercepts and the slope between hominoids and non-

hominoids for medial wedging (Table 4.10). Hominoids have relatively more medial wedging than non-hominoids (Figure 4.4).

Table 4.9. Within group least-squares line values for hominoids and non-hominoids.

Source	R	Significance	Slope	y-intercept
Hominoids	<b>-.665</b>	<b>.000</b>	-.398±.149	14.199±3.643
Non-hominoids	<b>-.360</b>	<b>.000</b>	-.655±.351	14.652±4.010

Table 4.10. ANCOVA results for pairwise comparison of anthropoids.

Source	Significance	Partial Eta Squared
y-intercept	<b>.016</b>	.044
Slope	<b>.000</b>	.207

Due to the little group overlap, narrow allometry for individuals between 8 and 16 for the geometric mean of trochlear measurements was assessed. The narrow allometry results show no significant difference between hominoids and non-hominoids for medial wedging (Table 4.11)

Table 4.11. Narrow allometry for pairwise comparison of hominoids and non-hominoids.

	Mean		Z	Df	Significance
Hominoids	10.304	Medial wedging	-1.510	1	.131
Non-hominoids	7.184				

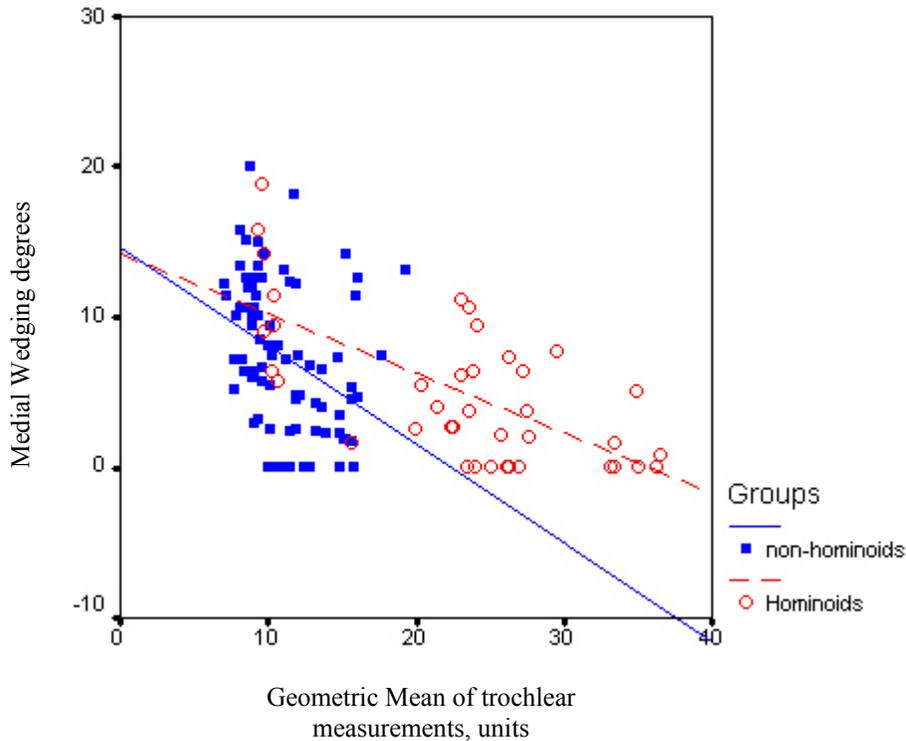


Figure 4.4. Bivariate plot of medial wedging for anthropoids against the geometric mean of trochlear measurements. The lines signify that the slopes for hominoids and non-hominoids are statistically significant.

### Posterior Wedging

It was hypothesized that emphasis on climbing should be associated with greater posterior trochlear wedging. Therefore, colobines, atelines, Asian apes, and hominoids should have greater posterior trochlear wedging than cercopithecines, non-ateline platyrrhines, African apes, and non-hominoids respectively.

#### *Cercopithecoids*

Pearson's product moment correlation between posterior wedging and trochlear size was tested for each group. Within both cercopithecines and colobines, posterior wedging is significantly positively correlated with trochlear size (Table 4.12). Because posterior wedging is

correlated with trochlear size, an ANCOVA was performed and results show a significant difference in both the y-intercepts and the slopes between cercopithecines and colobines. Cercopithecines have relatively more posterior wedging than colobines (Table 4.13; Figure 4.5).

Table 4.12. Within group least-squares line values for cercopithecines and colobines.

Source	R	Significance	Slope	y-Intercept
Cercopithecines	.446	<b>.015</b>	.422±.335	9.025±4.025
Colobines	.529	<b>.043</b>	.698±.672	.404±8.670

Table 4.13. ANCOVA results for pairwise comparison of cercopithecines and colobines.

Source	Sig.	Partial Eta Squared
y-intercept	<b>.000</b>	.420
Slope	<b>.002</b>	.220

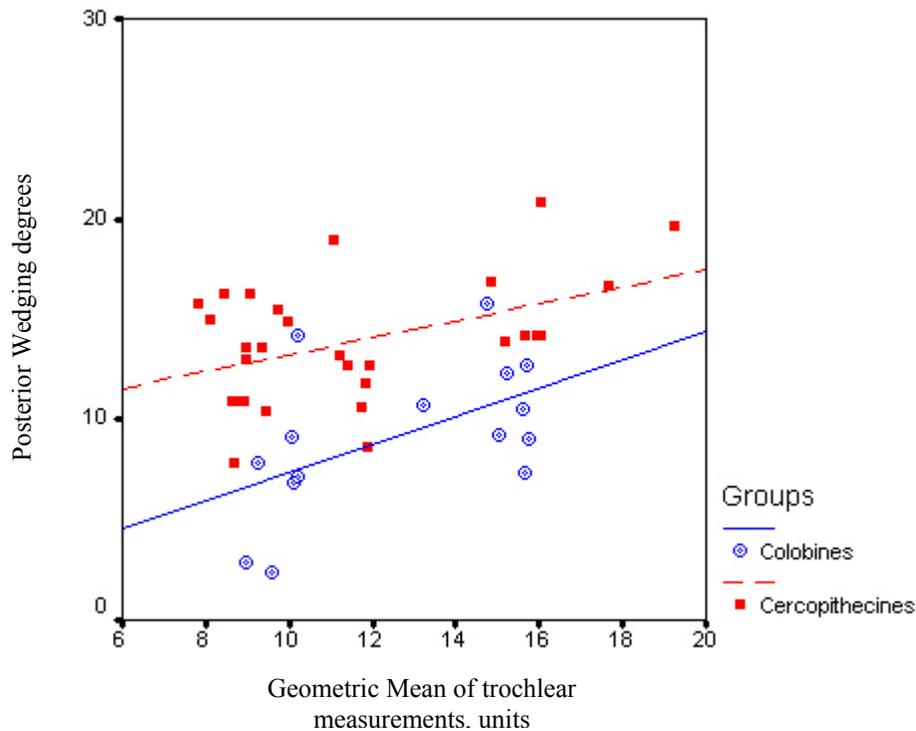


Figure 4.5. Bivariate plot of posterior wedging for cercopithecoids against the geometric mean of trochlear measurements.

*Platyrrhines*

Pearson’s product moment correlation between posterior wedging and trochlear size was tested for each group. Within both atelines and non-atelines, the degree of posterior wedging is not significantly correlated with trochlear size (Table 4.14). Because trochlear size is not significantly correlated with posterior wedging, a Mann-Whitney U non-parametric test was performed (Table 4.15) and the results show a significant difference between atelines and non-atelines for posterior wedging. Atelines have relatively more posterior wedging than non-atelines (Figure 4.6).

Table 4.14. Within group least-squares line values for atelines and non-ateline platyrrhines.

Source	R	Significance	Slope	y-Intercept
Atelines	.263	.065	-.734±1.011	27.131±11.926
Non-atelines	-.303	.170	-1.197±1.756	23.485±15.164

Table 4.15. Mann-Whitney U non-parametric results for pairwise comparison of atelines and non-ateline platyrrhines.

	Mean	Feature	Mann-Whitney U	Z	Significance
Atelines	18.568	Posterior Wedging	95.500	-4.155	<b>.000</b>
Non-atelines	13.188				

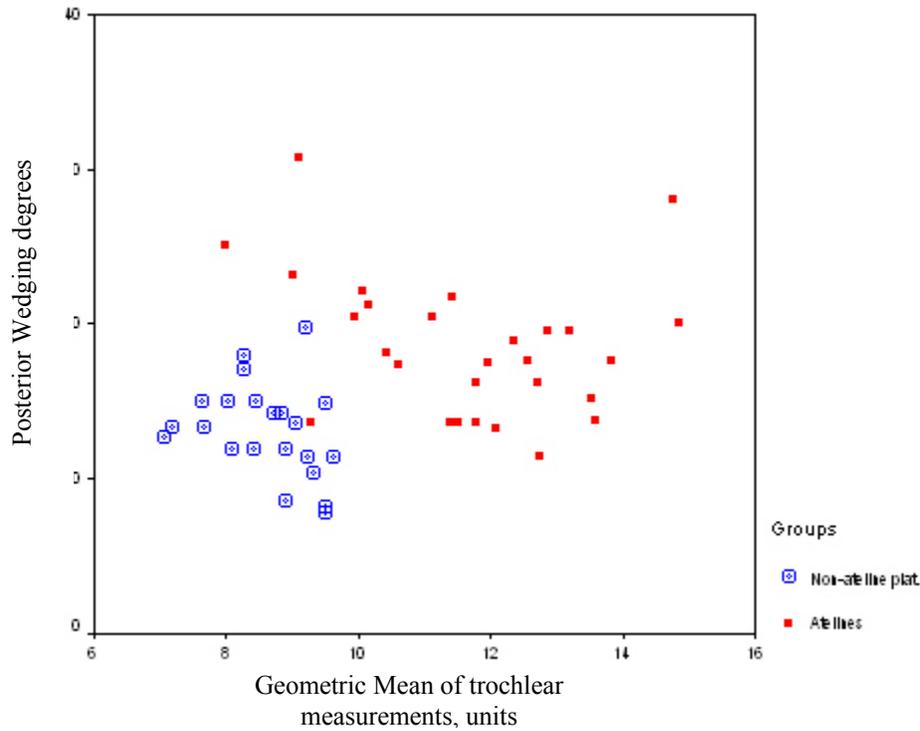


Figure 4.6. Bivariate plot of posterior wedging for platyrrhines against the geometric mean of trochlear measurements.

### *Hominoids*

Pearson's product moment correlation between posterior wedging and trochlear size was tested for each group. Within Asian apes, posterior wedging is negatively significantly correlated with trochlear size and within African apes, posterior wedging is significantly positively correlated with trochlear size (Table 4.16). Because posterior wedging is significantly correlated with trochlear size, an ANCOVA was performed and results show a significant difference in the y-intercepts between Asian apes and African apes for posterior wedging, but not a difference in slopes (Table 4.17). African apes have relatively more posterior wedging of the trochlea than Asian apes (Figure 4.7).

Table 4.16. Within group least-squares line values for African apes and Asian apes.

Source	R	Significance	Slope	y-Intercept
Asian apes	-.616	<b>.005</b>	-.392±.257	16.514±4.983
African apes	.637	<b>.003</b>	1.051±.630	-12.438±17.946

Table 4.17. ANCOVA results for pairwise comparison of hominoids.

Source	Significance	Partial Eta Squared
y-intercept	<b>.028</b>	.127
Slope	.630	.007

Due to the little group overlap, narrow allometry for individuals between 20 and 30 for the geometric mean of trochlear measurements was performed. The narrow allometry results show no significant difference at  $p < .05$  between Asian apes and African apes, but there is a statistical signal at  $p < .1$  (Table 4.18). The statistical trend shows Asian apes as having relatively more posterior wedging than African apes.

Table 4.18. Narrow allometry for pairwise comparison of Asian apes and African apes.

	Mean		Z	Df	Significance
Asian apes	13.076	Posterior Wedging	-1.836	1	.066
African apes	7.055				

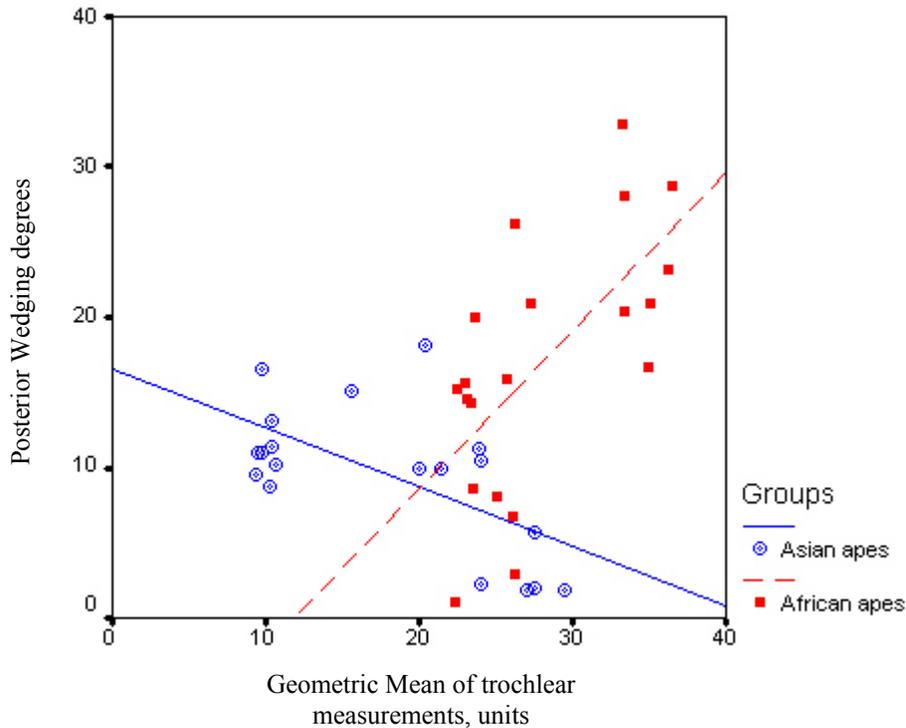


Figure 4.7. Bivariate plot of posterior wedging for hominoids against the geometric mean of trochlear measurements.

### *Anthropoids*

Pearson's product moment correlation between posterior wedging and trochlear size was tested for each group. Within hominoids and not non-hominoids, posterior wedging is significantly positively correlated with trochlear size (Table 4.19). Because posterior wedging is significantly correlated with trochlear size, an ANCOVA was performed and results show a significant difference in y-intercepts and slopes between hominoids and non-hominoids for the degree of posterior wedging (Table 4.20). Non-hominoids have relatively more posterior wedging than hominoids (Figure 4.8).

Table 4.19. Within group least-squares line values for hominoids and non-hominoids.

Source	R	Significance	Slope	y-Intercept
Hominoids	.356	<b>.026</b>	.345±.301	5.391±7.377
Non-hominoids	.112	.281	.198±.362	12.193±4.13

Table 4.20. ANCOVA results for pairwise comparison of hominoids.

Source	Significance	Partial Eta Squared
y-intercept	<b>.004</b>	.063
Slope	<b>.002</b>	.070

Due to the little group overlap, narrow allometry for individuals between 8 and 16 for the geometric mean of trochlear measurements was performed. The narrow allometry results show no significant difference at  $p < .05$  between hominoids and non-hominoids. (Table 4.21).

Table 4.21. Narrow allometry for pairwise comparison of hominoids and non-hominoids.

	Mean		Z	Df	Significance
Hominoids	11.862	Posterior Wedging	-1.560	1	.119
Non-hominoids	14.111				

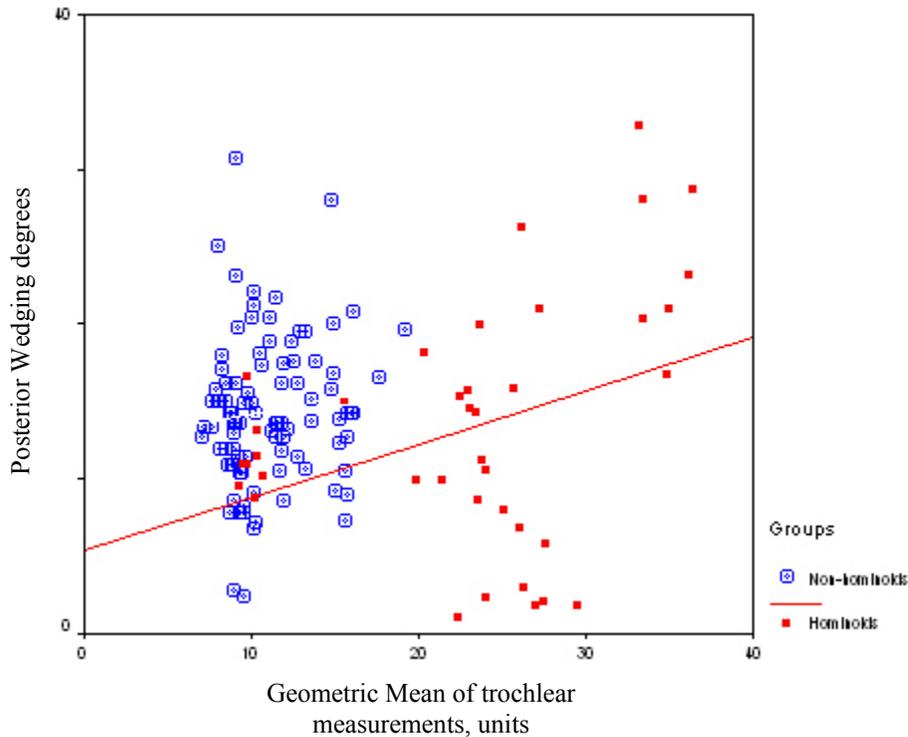


Figure 4.8. Bivariate plot of posterior wedging for anthropoids against the geometric mean of trochlear measurements.

### Posterior Talocalcaneal Facet Angle

Anthropoids that emphasize climbing in their locomotor repertoires are predicted to have more anteriorly inclined posterior talocalcaneal facets than are more quadrupedal taxa. Colobines should have more anteriorly inclined facets than cercopithecines; atelines should have more anteriorly inclined facets than non-ateline platyrrhines; Asian apes should have more anteriorly inclined facets than African apes; and hominoids should have more anteriorly inclined facets than non-hominoids.

*Cercopithecoids*

Pearson’s product moment correlation between the angle of the posterior talocalcaneal facet and trochlear size was tested for each group. Within both cercopithecines and colobines, the angle is not significantly correlated with trochlear size (Table 4.22). Because trochlear size is not significantly correlated with the angle of the posterior talocalcaneal facet, a Mann-Whitney U non-parametric test was performed (Table 4.23) and the results show no significant difference between cercopithecines and colobines for the angle of the posterior talocalcaneal facet (Figure 4.9).

Table 4.22. Within group least-squares line values for cercopithecines and colobines.

Source	R	Significance	Slope	y-Intercept
Cercopithecines	-.057	.769	-.088±.606	57.611±7.292
Colobines	-.243	.383	-.434±1.038	62.318±13.399

Table 4.23. Mann-Whitney U results for pairwise comparison of cercopithecines and colobines.

	Mean	Feature	Mann-Whitney U	Z	Significance (2-tailed)
Cercopithecines	56.595	PTF angle	202.000	-.384	.701
Colobines	56.844				

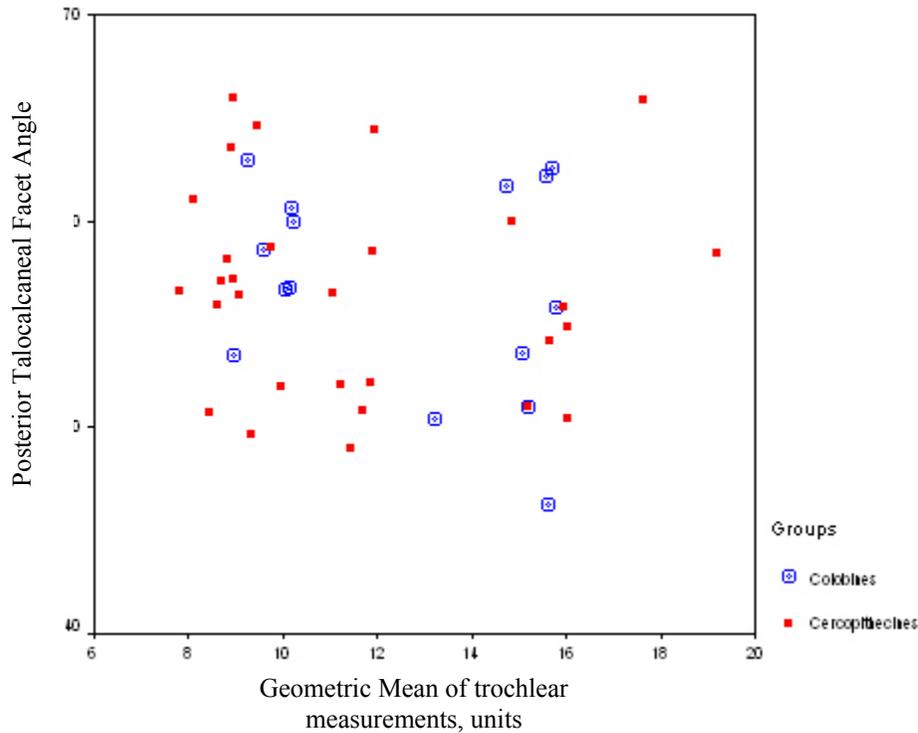


Figure 4.9. Bivariate plot of posterior talocalcaneal facet angle for cercopithecioids against the geometric mean of trochlear measurements.

### *Platyrrhines*

Pearson's product moment correlation between the angle of the posterior talocalcaneal facet and trochlear size was tested for each group. Within both atelines and non-atelines, the angle of the posterior talocalcaneal facet is not correlated with trochlear size (Table 4.24). Because the angle is not correlated with trochlear size, a Mann-Whitney U non-parametric test was performed and results show a difference in y-intercepts and slopes between atelines and non-ateline platyrrhines for the angle of the posterior talocalcaneal facet (Table 4.25; Figure 4.10). Atelines have relatively more oblique angles of the posterior talocalcaneal facets than non-ateline platyrrhines.

Table 4.24. Within group least-squares line values for atelines and non-ateline platyrrhines.

Source	R	Significance	Slope	y-Intercept
Atelines	.046	.749	1.870±1.688	46.239±19.885
Non-atelines	.288	.194	2.328±3.614	51.970±31.195

Table 4.25. Mann-Whitney U results for pairwise comparison of atelines and non-ateline platyrrhines.

	Mean	Feature	Mann-Whitney U	Z	Significance (2-tailed)
Atelines	68.057	PTF angle	202.000	-2.072	.038
Non-atelines	71.990				

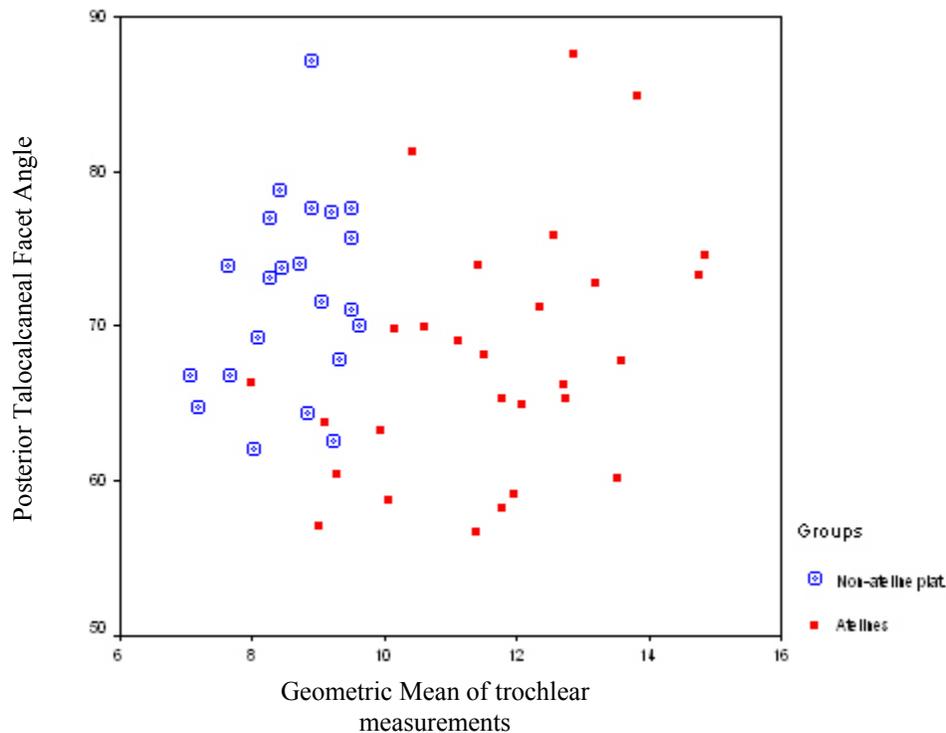


Figure 4.10. Bivariate plot of posterior talocalcaneal facet angle for platyrrhines against the geometric mean of trochlear measurements.

## *Hominoids*

Pearson's product moment correlation between the angle of the posterior talocalcaneal facet and trochlear size was tested for each group. Within both Asian apes and African apes, the angle of the posterior talocalcaneal facet is significantly negatively correlated with trochlear size (Table 4.26). Because the angle of the posterior talocalcaneal facet is significantly correlated with trochlear size, an ANCOVA was performed and results show a significant difference in y-intercepts and slopes between Asian apes and African apes for the angle (Table 4.27). Asian apes have relatively more oblique angles of the posterior talocalcaneal facets than African apes (Figure 4.11).

Table 4.26. Within group least-squares line values for African apes and Asian apes.

Source	R	Significance	Slope	y-Intercept
Asian apes	-.525	<b>.021</b>	-.536±.445	64.526±8.639
African apes	-.780	<b>.000</b>	-.917±.364	80.316±10.372

Table 4.27. ANCOVA results for pairwise comparison of hominoids.

Source	Significance	Partial Eta Squared
y-intercept	<b>.008</b>	.179
Slope	<b>.000</b>	.380

Due to the little group overlap, narrow allometry for individuals between 20 and 30 for the geometric mean of trochlear measurements was performed. The narrow allometry results show a significant difference at  $p < .05$  between Asian apes and African apes (Table 4.28). Asian apes have relatively more oblique angles of the posterior talocalcaneal facets than African apes.

Table 4.28. Narrow allometry for pairwise comparison of Asian apes and African apes.

	Mean		Z	Df	Significance
Asian apes	51.847	PTF angle	-2.504	1	.012
African apes	57.506				

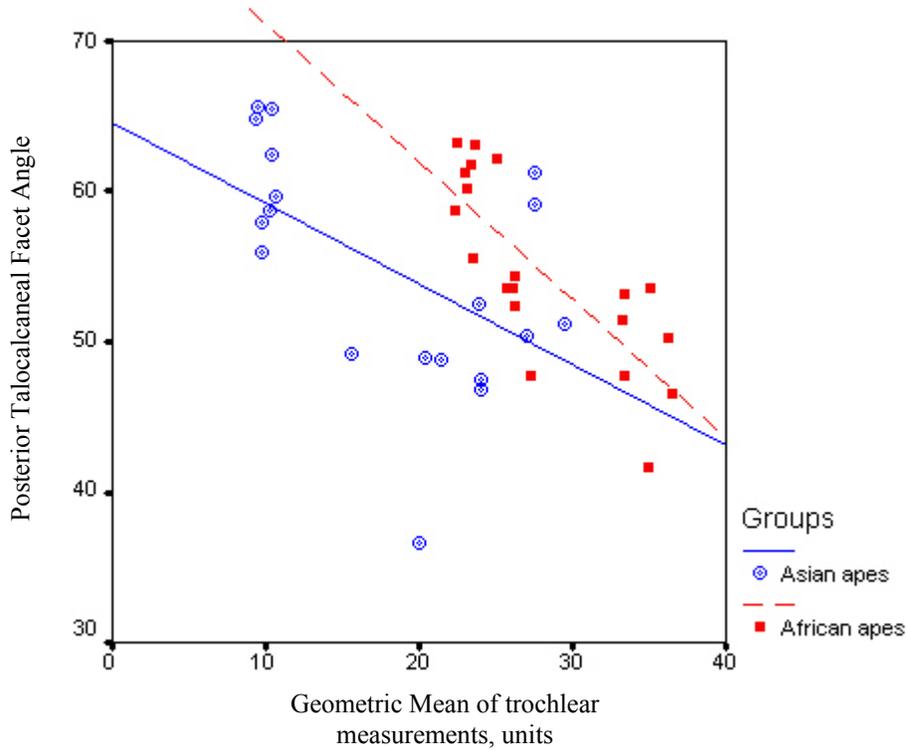


Figure 4.11. Bivariate plot of posterior talocalcaneal facet angle for hominoids against the geometric mean of trochlear measurements.

### *Anthropoids*

Pearson's product moment correlation between the angle of the posterior talocalcaneal facet and trochlear size was tested for each group. Within both hominoids and non-hominoids, the angle of the posterior talocalcaneal facet is significantly negatively correlated with trochlear size (Table 4.29). Because the angle of the posterior talocalcaneal facet is significantly correlated with trochlear size, an ANCOVA was performed and results show no difference in y-

intercepts between hominoids and non-hominoids for the angle of the posterior talocalcaneal facet, but a significant difference in slopes (Table 4.30; Figure 4.12).

Table 4.29. Within group least-squares line values for hominoids and non-hominoids.

Source	R	Significance	Slope	y-Intercept
Hominoids	-.495	<b>.001</b>	-.416±.243	64.378±5.959
Non-hominoids	-.231	<b>.025</b>	-.773±.676	72.221±7.712

Table 4.30. ANCOVA results for pairwise comparison of anthropoids.

Source	Significance	Partial Eta Squared
y-intercept	.208	.012
Slope	<b>.001</b>	.082

Due to the little group overlap, narrow allometry for individuals between 8 and 16 for the geometric mean of trochlear measurements was performed. The narrow allometry results show no difference between hominoids and non-hominoids (Table 4.31).

Table 4.31. Narrow allometry for pairwise comparison of hominoids and non-hominoids.

	Mean		Z	Df	Significance
Hominoids	59.984	PTF angle	-.962	1	.336
Non-hominoids	63.791				

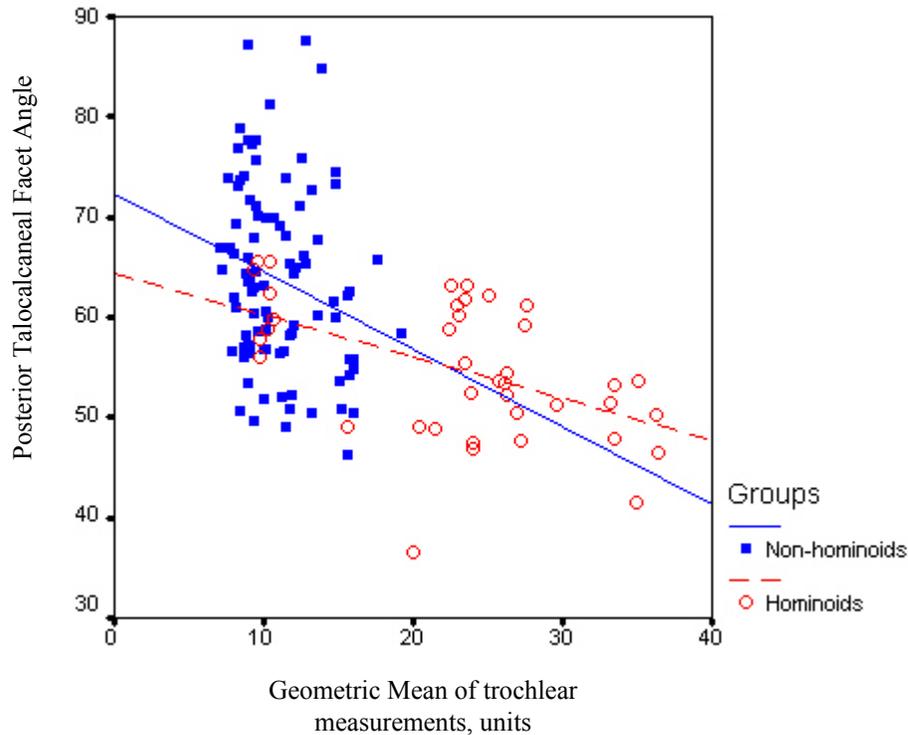


Figure 4.12. Bivariate plot of posterior talocalcaneal facet angle for anthropoids against the geometric mean of trochlear measurements.

### *M. Flexor Hallucis Longus (FHL) Groove Angle*

Anthropoids that emphasize climbing behaviors are expected to have a more oblique angle than non-climbing counterparts. Therefore, colobines, atelines, and hominoids should have a more oblique angle than cercopithecines, non-ateline platyrrhines, and non-hominoids.

#### *Cercopithecoids*

Pearson's product moment correlation between the angle of the *m. flexor hallucis longus* groove and trochlear size was tested for each group. Within both cercopithecines and colobines, the angle of the *m. flexor hallucis longus* groove is not significantly correlated with trochlear size (Table 4.32). Because trochlear size is not significantly correlated with the angle, a Mann-

Whitney U non-parametric test was performed (Table 4.33) and the results show no significant difference between cercopithecines and colobines for the angle of the *m. flexor hallucis longus* groove (Figure 4.13).

Table 4.32. Within group least-squares line values for cercopithecines and colobines.

Source	R	Significance	Slope	y-Intercept
Cercopithecines	.212	.270	.274±.499	64.406±6.009
Colobines	.192	.493	.106±.326	67.437±4.203

Table 4.33. Mann-Whitney U results for pairwise comparison of cercopithecines and colobines.

	Mean	Feature	Mann-Whitney U	Z	Significance (2-tailed)
Cercopithecines	67.586	FHL angle	197.000	-.508	.612
Colobines	68.778				

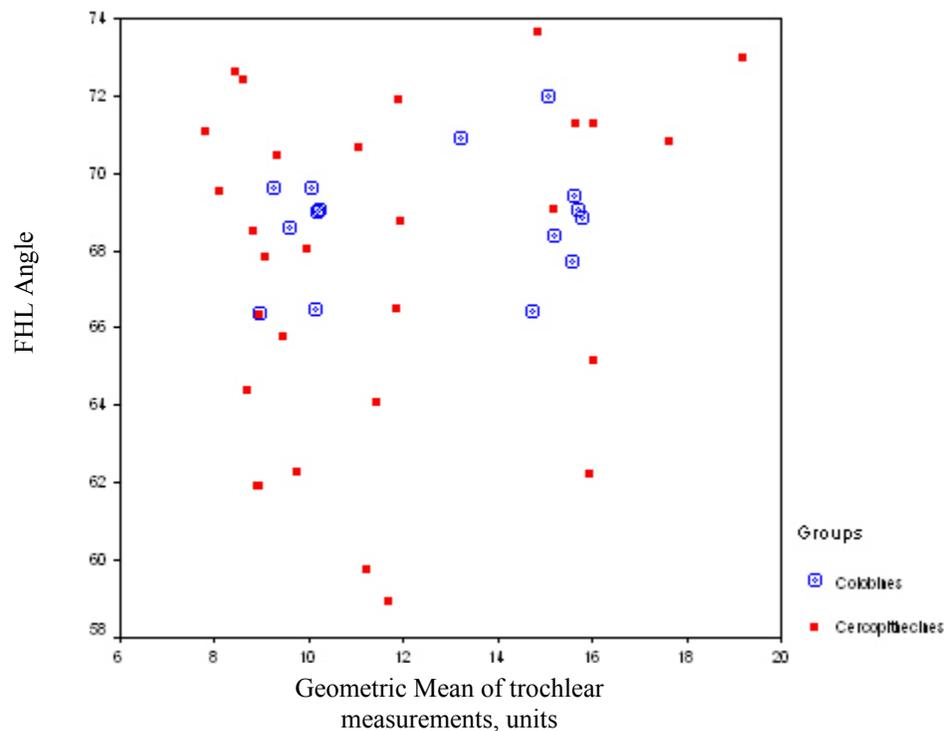


Figure 4.13. Bivariate plot of *m. flexor hallucis longus* groove angle for cercopithecoids against the geometric mean of trochlear measurements.

*Platyrrhines*

Pearson’s product moment correlation between the angle of the *m. flexor hallucis longus* groove and trochlear size was tested for each group. Within non-atelines, but not in atelines, the angle of the *m. flexor hallucis longus* groove is significantly positively correlated with trochlear size (Table 4.34). Because the angle of the *m. flexor hallucis longus* groove is significantly correlated with trochlear size, an ANCOVA was performed and results show no difference in y-intercepts or slopes between atelines and non-ateline platyrrhines for this angle (Table 4.35; Figure 4.14).

Table 4.34. Within group least-squares line values for atelines and non-ateline platyrrhines.

Source	R	Significance	Slope	y-Intercept
Atelines	.085	.556	.076±.971	74.793±11.455
Non-atelines	.438	<b>.041</b>	2.230±2.134	56.456±18.421

Table 4.35. ANCOVA results for pairwise comparison of atelines and non-ateline platyrrhines.

Source	Significance	Partial Eta Squared
y-intercept	.551	.008
Slope	.405	.015

Due to the little group overlap, narrow allometry for individuals less than 9.65 for the geometric mean of trochlear measurements was performed. Narrow allometry results also show no difference between groups for the angle of the *m. flexor hallucis longus* groove (Table 4.36).

Table 4.36. Narrow allometry for pairwise comparison of atelines and non-ateline platyrrhines.

	Mean		Z	df	Significance
Atelines	73.000	FHL angle	-1.208	1	.227
Non-atelines	75.638				

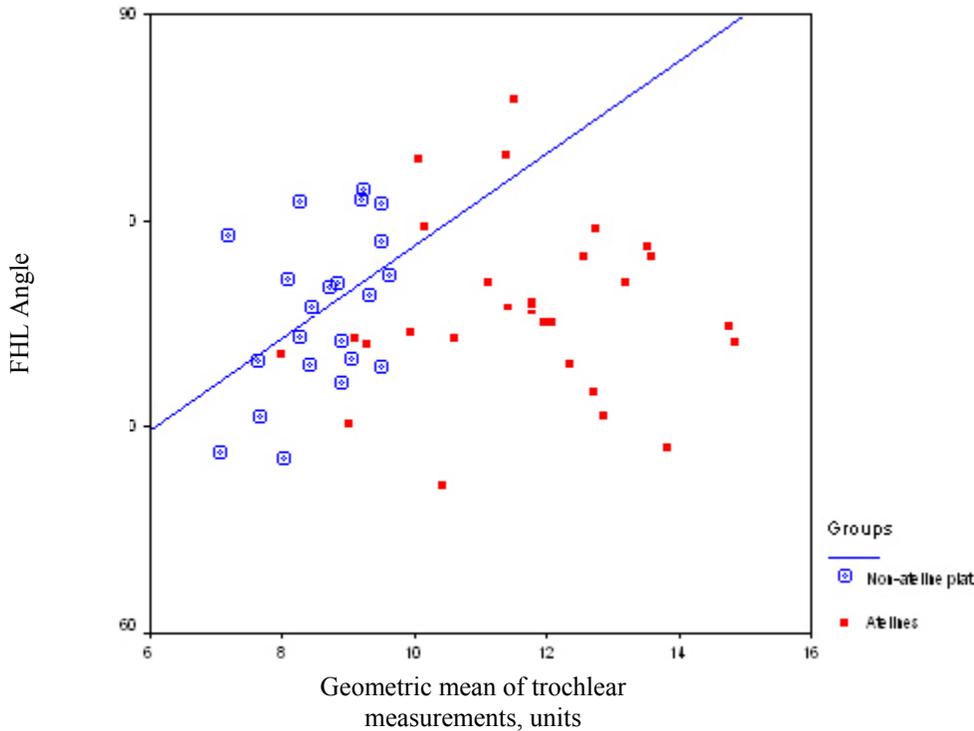


Figure 4.14. Bivariate plot of *m. flexor hallucis longus* groove angle for platyrrhines against the geometric mean of trochlear measurements.

### *Hominoids*

Pearson's product moment correlation between the angle of the *m. flexor hallucis longus* groove and trochlear size was tested for each group. Within Asian apes and not African apes, the angle of the *m. flexor hallucis longus* groove is significantly positively correlated with trochlear size (Table 4.37). Because the angle of the *m. flexor hallucis longus* groove is significantly correlated with trochlear size for one group, an ANCOVA was performed and results show no

difference in y-intercepts between Asian apes and African apes based on the angle of the groove, but there is a significant difference in slopes between the two groups (Table 4.38; Figure 4.15).

Table 4.37. Within group least-squares line values for African apes and Asian apes.

Source	R	Significance	Slope	y-Intercept
Asian apes	-.599	<b>.007</b>	-.434±.297	73.449±5.770
African apes	-.334	.150	-.348±.486	74.666±13.829

Table 4.38. ANCOVA results for pairwise comparison of hominoids.

Source	Significance	Partial Eta Squared
y-intercept	.101	.073
Slope	<b>.002</b>	.231

Due to the little group overlap, narrow allometry for individuals between 20 and 30 for the geometric mean of trochlear measurements was performed. The narrow allometry results show no significant difference at  $p < .05$  between Asian apes and African apes (Table 4.39).

Table 4.39. Narrow allometry for pairwise comparison of Asian apes and African apes.

	Mean		Z	Df	Significance
Asian apes	61.967	FHL angle	-1.703	1	.089
African apes	65.975				

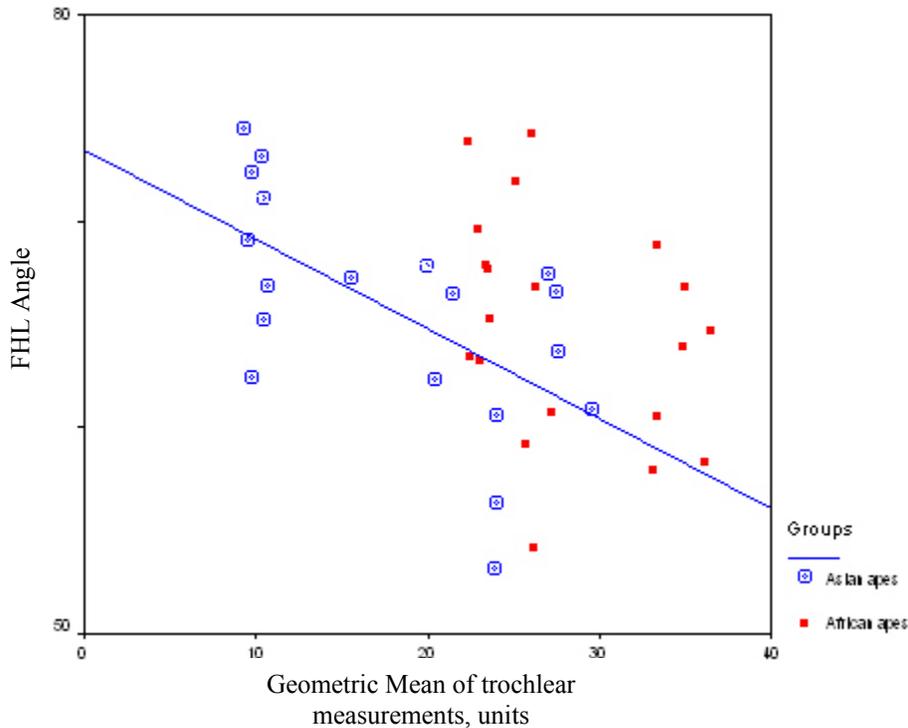


Figure 4.15. Bivariate plot of the angle of the *m. flexor hallucis longus* groove for hominoids against the geometric mean of trochlear measurements.

### *Anthropoids*

Pearson's product moment correlation between the angle of the *m. flexor hallucis longus* groove and trochlear size was tested for each group. Within hominoids and not non-hominoids, the angle of the *m. flexor hallucis longus* groove is significantly negatively correlated with trochlear size (Table 4.40). Because the angle of the *m. flexor hallucis longus* groove is significantly correlated with trochlear size for one group, an ANCOVA was performed and results show a significant difference in y-intercepts and slopes between hominoids and non-hominoids for this angle (Table 4.41; Figure 4.16). Hominoids have relatively more oblique angles than non-hominoids.

Table 4.40. Within group least-squares line values for hominoids and non-hominoids.

Source	R	Significance	Slope	y-Intercept
Hominoids	-.418	<b>.008</b>	-.276±.200	71.666±4.896
Non-hominoids	-.110	.290	-.218±.407	74.490±4.648

Table 4.41. ANCOVA results for pairwise comparison of anthropoids.

Source	Significance	Partial Eta Squared
y-intercept	<b>.017</b>	.043
Slope	<b>.005</b>	.059

Due to the little group overlap, narrow allometry for individuals between 8 and 16 for the geometric mean of trochlear measurements was performed. The narrow allometry results show no significant difference at  $p < .05$  between hominoids and non-hominoids (Table 4.42).

Table 4.42. Narrow allometry for pairwise comparison of Asian apes and African apes.

	Mean		Z	Df	Significance
Hominoids	69.114	FHL angle	-1.611	1	.107
Non-hominoids	72.119				

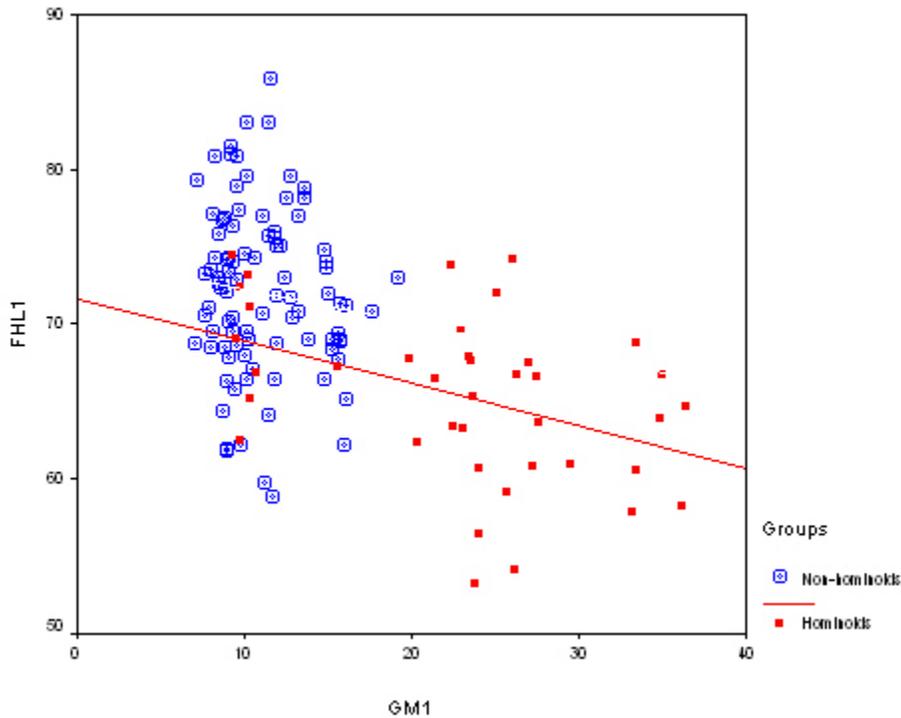


Figure 4.16. Bivariate plot of FHL angle for anthropoids against the geometric mean of trochlear measurements.

### Depth of the Talar Trochlea

Anthropoids that emphasize more quadrupedality than climbing should have more deeply grooved trochleae.

#### *Cercopithecoids*

Pearson’s product moment correlation between trochlear depth and trochlear size was tested for each group. Within both cercopithecines and colobines, the depth of the trochlea is significantly positively correlated with trochlear size (Table 4.43). Because trochlear depth is significantly correlated with trochlear size, an ANCOVA was performed and results show no

significant y-intercept difference between cercopithecines and colobines, but there is a slope difference (Table 4.44).

Table 4.43. Within group least-squares line values for cercopithecines and colobines.

Source	R	Significance	Slope	y-Intercept
Cercopithecines	.562	<b>.001</b>	.048±.028	.827±.333
Colobines	.926	<b>.000</b>	.128±.031	-.087±.403

Table 4.44. ANCOVA results for pairwise comparison of cercopithecines and colobines.

Source	Significance	Partial Eta Squared
y-intercept	.322	.024
Slope	<b>.000</b>	.465

Because the slopes for colobines and cercopithecines are greatly different, narrow allometry was performed for individuals with geometric mean trochlear measurements less than 12 and greater than 12. Narrow allometry was done twice because there is overlap between cercopithecines and colobines below and above 12 unlike platyrrhines that only overlap under 10.

A Mann-Whitney U non-parametric test was performed for individuals greater than 12 and results show a significant difference between *Nasalis* and *Papio* for trochlear depth. *Nasalis* has relatively more deeply grooved trochleae than *Papio* (Table 4.45a).

Table 4.45a. Greater than 12 (*Nasalis* & *Papio*)

	Mean		Z	df	Significance
<i>Papio</i>	1.574	Trochlear depth	-2.319	1	<b>.020</b>
<i>Nasalis</i>	1.855				

A Mann-Whitney U non-parametric test was performed for individuals less than 12 and results shows no significant difference between *Macaca* and *Trachypithecus* for trochlear depth (Table 4.45b).

Table 4.45b. Less than 12 (*Macaca* & *Trachypithecus*)

	Mean		Z	df	Significance
<i>Macaca</i>	1.305	Trochlear depth	-1.490	1	.136
<i>Trachypithecus</i>	1.150				

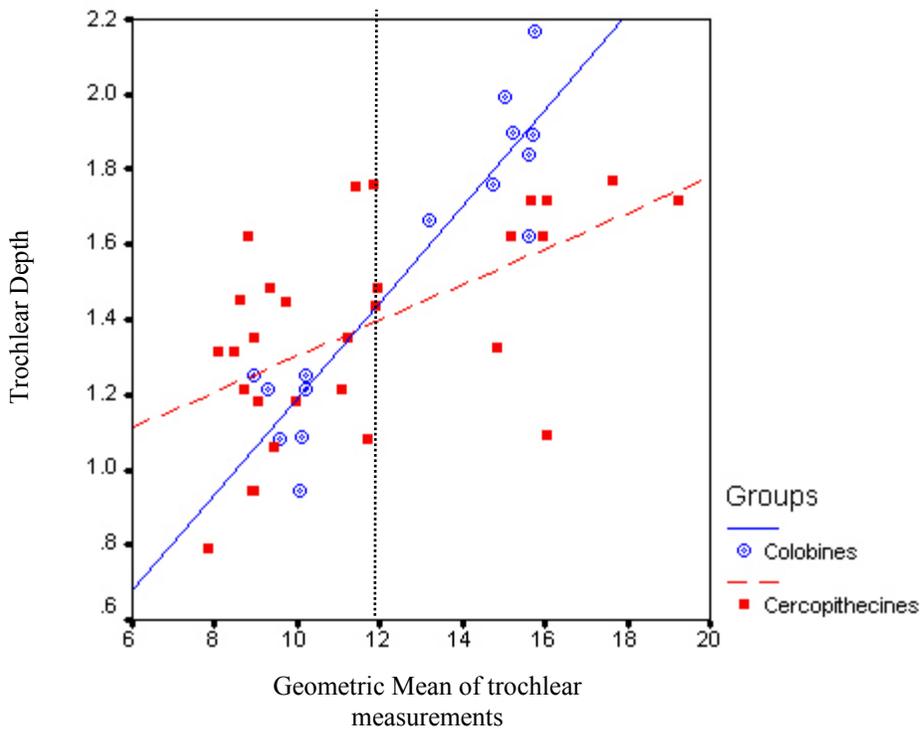


Figure 4.17. Bivariate plot of trochlear depth for cercopithecoids against the geometric mean of trochlear measurements.

*Platyrrhines*

Pearson’s product moment correlation between trochlear depth and trochlear size was tested for each group. Within atelines and not non-ateline platyrrhines, the depth of the trochlea is significantly positively correlated with trochlear size (Table 4.46). Because trochlear depth is significantly correlated with trochlear size, an ANCOVA was performed and results show no significant difference in y-intercepts between atelines and non-ateline platyrrhines, but there is a significant difference in the slopes (Table 4.47; Figure 4.18).

Table 4.46. Within group least-squares line values for atelines and non-ateline platyrrhines.

Source	R	Significance	Slope	y-Intercept
Atelines	.603	<b>.000</b>	.135±.085	-.911±.987
Non-atelines	-.198	.376	-.039±.091	.679±.785

Table 4.47. ANCOVA results for pairwise comparison of atelines and non-ateline platyrrhines.

Source	Significance	Partial Eta Squared
y-intercept	.895	.000
Slope	<b>.001</b>	.214

Due to the little group overlap, narrow allometry for individuals less than 9.65 for the geometric mean of trochlear measurements was performed. Narrow allometry shows a significant difference between groups for trochlear depth (Table 4.48). Atelines have relatively more deeply grooved trochleae than non-ateline platyrrhines.

Table 4.48. Mann-Whitney U test for pairwise comparison of atelines and non-ateline platyrrhines.

	Mean		F	df	Significance
Atelines	.582	Trochlear Depth	-2.102	1	.036
Non-atelines	.340				

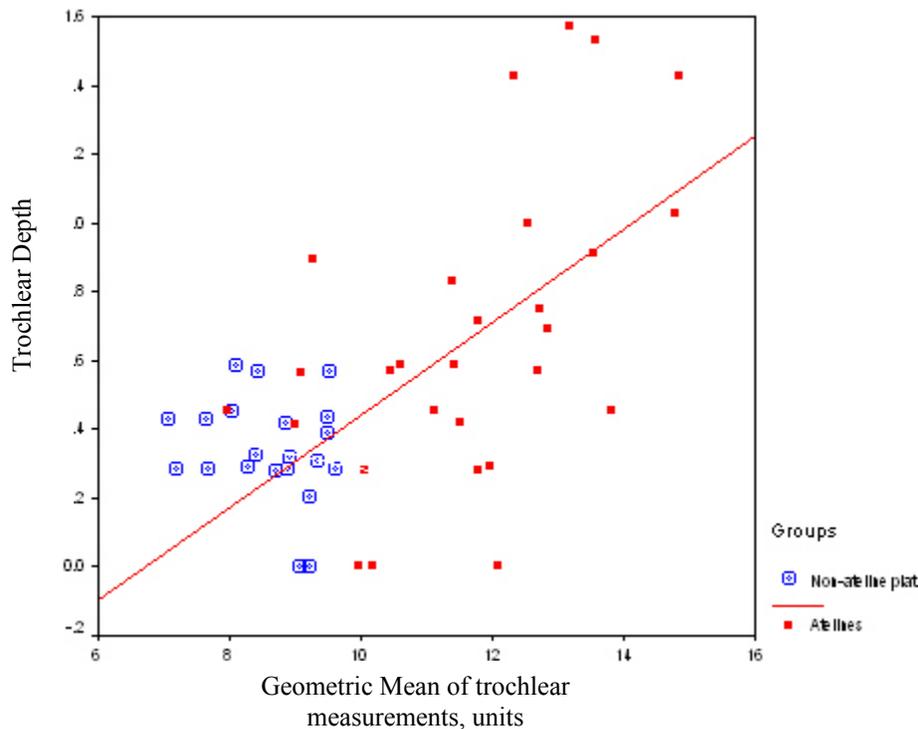


Figure 4.18. Bivariate plot of trochlear depth for platyrrhines against the geometric mean of trochlear measurements.

### *Hominoids*

Pearson’s product moment correlation between trochlear depth and trochlear size was tested for each group. Within both Asian apes and African apes, the depth of the trochlea is significantly positively correlated with trochlear size (Table 4.49). Because trochlear depth is significantly correlated with trochlear size, an ANCOVA was performed and results show a

significant difference in y-intercepts and slopes between Asian apes and African apes (Table 4.50). Asian apes have relatively more deeply grooved trochleae than African apes (Figure 4.19).

Table 4.49. Within group least-squares line values for African apes and Asian apes.

Source	R	Significance	Slope	y-Intercept
Asian apes	.920	<b>.000</b>	.108±.023	-.384±.457
African apes	.708	<b>.000</b>	.036±.072	-.253±2.055

Table 4.50. ANCOVA results for pairwise comparison of hominoids.

Source	Significance	Partial Eta Squared
y-intercept	<b>.000</b>	.337
Slope	<b>.000</b>	.424

Due to the little group overlap, narrow allometry for individuals between 20 and 30 for the geometric mean of trochlear measurements was performed. The narrow allometry results show a significant difference between Asian apes and African apes (Table 4.51). Asian apes have relatively deeper talar trochleae than African apes.

Table 4.51. Narrow allometry for pairwise comparison of Asian apes and African apes.

	Mean		Z	Df	Significance
Asian apes	2.311	Trochlear depth	-3.408	1	<b>.001</b>
African apes	1.165				

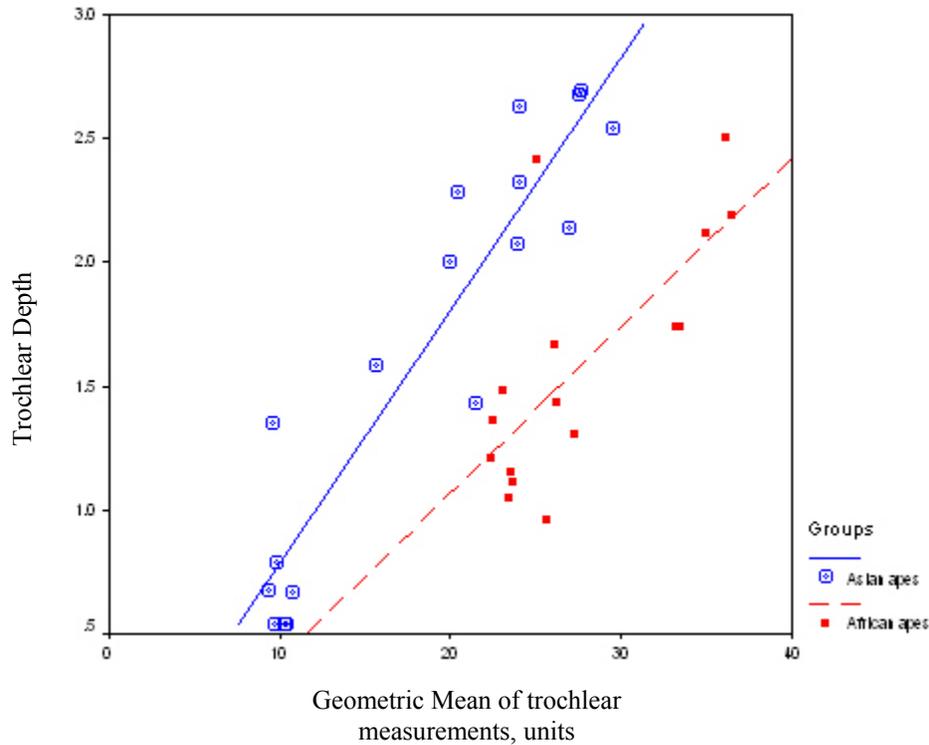


Figure 4.19. Bivariate plot of trochlear depth for hominoids against the geometric mean of trochlear measurements.

### *Anthropoids*

Pearson's product moment correlation between trochlear depth and trochlear size was tested for each group. Within both hominoids and non-hominoids, the depth of the trochlea is significantly positively correlated with trochlear size (Table 4.52). Because trochlear depth is significantly correlated with trochlear size, an ANCOVA was performed and results show no difference in y-intercepts between hominoids and non-hominoids for the relative depth of the trochlea, but there is a significant difference in slopes between groups (Table 4.53).

Table 4.52. Within group least-squares line values for hominoids and non-hominoids.

Source	R	Significance	Slope	y-Intercept
Hominoids	.396	<b>.013</b>	.041±.031	.470±.767
Non-hominoids	.601	<b>.000</b>	.126±.035	-.453±.397

Table 4.53. ANCOVA results for pairwise comparison of hominoids.

Source	Significance	Partial Eta Squared
y-intercept	.144	.016
Slope	<b>.000</b>	.196

Due to the little group overlap, narrow allometry for individuals between 8 and 16 for the geometric mean of trochlear measurements was performed. The narrow allometry results show no significant difference between hominoids and non-hominoids (Table 4.54).

Table 4.54. Narrow allometry for pairwise comparison of hominoids and non-hominoids.

	Mean		Z	Df	Significance
Hominoids	.744	Trochlear depth	-.890	1	.373
Non-hominoids	.953				

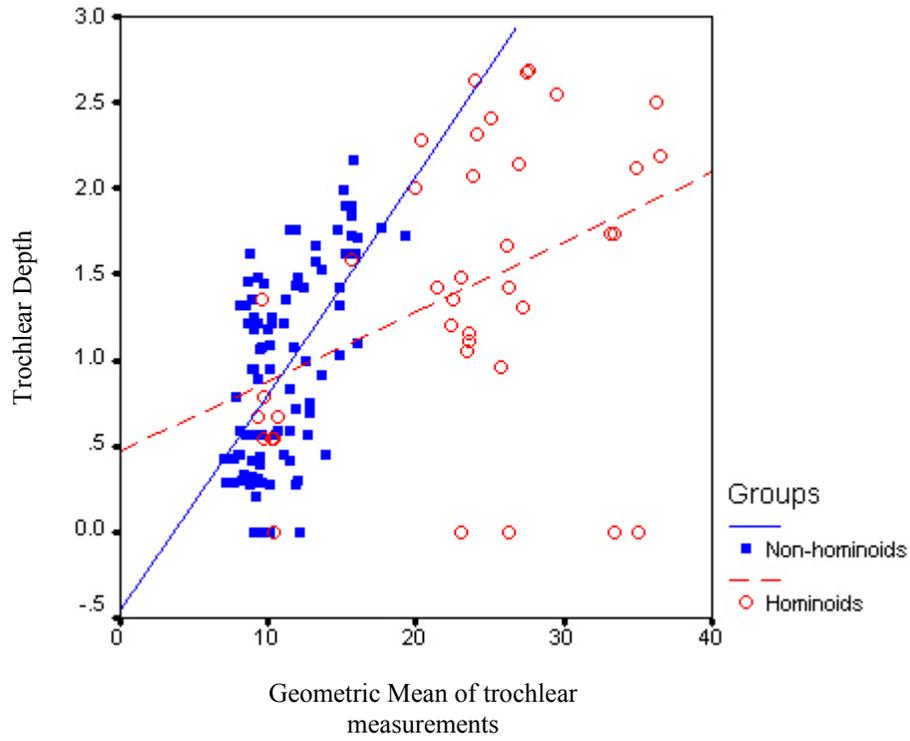


Figure 4.20. Bivariate plot of trochlear depth for anthropoids against the geometric mean of trochlear measurements.

## Discriminant Function Summary of Pairwise Tests

### *Cercopithecoids*

The discriminant function analysis for cercopithecoids correctly classified 93.1% of cercopithecines as cercopithecines and 92.9% of colobines as colobines. Function 1 is positively loaded primarily by trochlear size and negatively loaded by posterior wedging and the angle of the posterior talocalcaneal facet. Function 2 is positively loaded primarily by posterior wedging and to a lesser extent medial wedging and negatively loaded by the angle of the *m. flexor hallucis longus* groove (Table 4.55; 4.56). As expected from the bivariate and/or univariate results, trochlear size, posterior wedging and medial wedging are loading heavily in the multivariate analysis (Figure 2.21). These features showed significant differences between cercopithecines and colobines.

Table 4.55. Eigenvalues for the discriminant function analysis of cercopithecoids.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	7.257	75.7	75.7	.937
2	1.399	14.6	90.3	.764
3	.867	9.0	99.3	.682
4	.065	.7	100.0	.248

Table 4.56. Standardized Canonical Discriminant Function Coefficients for cercopithecoids.

	Function			
	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>
Geometric Mean	1.208	-.084	.489	-.123
Medial Wedging	.213	.485	.149	.533
Posterior Wedging	-.306	.874	.566	.702
PTF angle	-.262	-.140	.583	.376
FHL angle	.012	-.440	-.418	-.115
Trochlear depth	-.175	.197	-1.045	.462

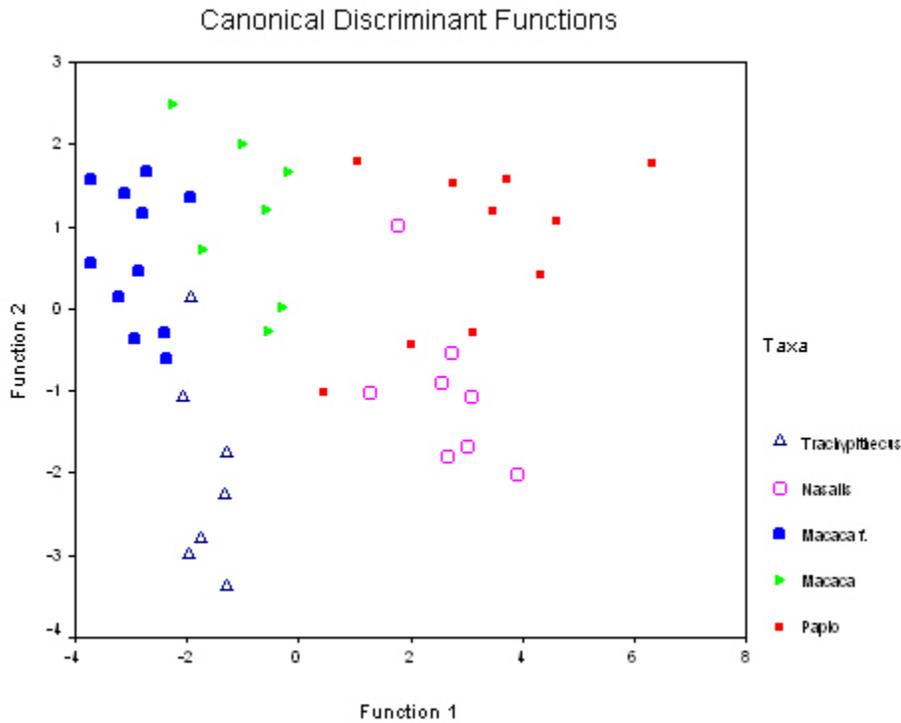


Figure 4.21. Canonical Discriminant Function plot for cercopithecoids.

### *Platyrrhines*

The discriminant function analysis for platyrrhines correctly classified 100% of atelines as atelines and 100% of non-ateline platyrrhines as non-ateline platyrrhines. Function 1 is positively loaded by trochlear size and trochlear depth and negatively loaded by medial and posterior wedging. Function 2 is positively loaded primarily by the angle of the posterior talocalcaneal facet and to a lesser extent medial wedging and is negatively loaded by posterior wedging (Table 4.57; 4.58; Figure 4.22). As expected from the results of the bivariate and/or univariate tests, posterior wedging, the angle of the posterior talocalcaneal facet, and trochlear depth are loading heavily on the discriminant function analysis. These features showed significant differences between atelines and non-ateline platyrrhines.

Table 4.57. Eigenvalues for the discriminant function analysis of platyrrhines.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	12.053	84.6	84.6	.961
2	1.679	11.8	96.4	.792
3	.343	2.4	98.8	.505
4	.113	.8	99.6	.319
5	.062	.4	100.0	.242

Table 4.58. Standardized Canonical Discriminant Function Coefficients of platyrrhines.

	Function				
	1	2	3	4	5
Geometric Mean	.922	.167	.104	.061	.579
Medial Wedging	-.248	.482	.597	-.198	.662
Posterior Wedging	.203	-.674	.131	.808	-.220
PTF angle	-.008	.879	.119	.561	.475
FHL angle	-.194	.303	-.747	.006	.282
Trochlear depth	.441	.250	.296	.191	-.265

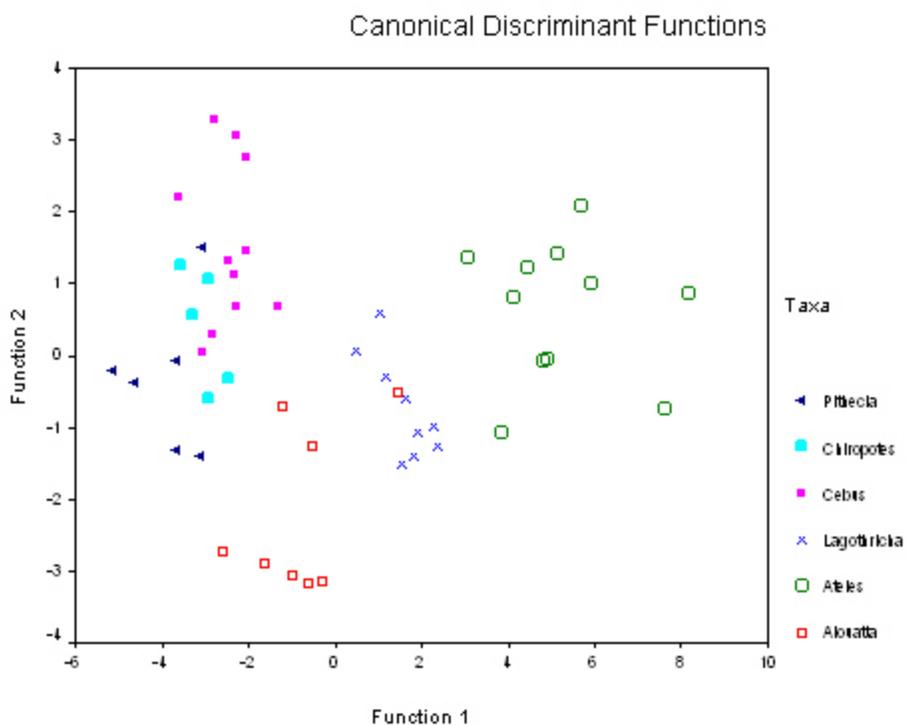


Figure 4.22. Canonical Discriminant Function plot for platyrrhines.

## Hominoids

The discriminant function analysis for hominoids correctly classified 100% of the Asian apes as Asian apes and 100% of the African apes as African apes. Function 1 is positively loaded by trochlear size and posterior wedging and negatively loaded by the angle of the posterior talocalcaneal facet, the angle of *m. flexor hallucis longus* groove, and trochlear depth. Function 2 is positively loaded by primarily posterior wedging and the angle of the *m. flexor hallucis longus* groove and negatively loaded by trochlear depth (Table 4.59; 4.60; Figure 4.23). As expected from the bivariate and/or univariate tests, posterior wedging, the angle of the *m. flexor hallucis longus* groove, and trochlear depth are loading heavily on the multivariate analysis. These features showed significant differences or significant signals between Asian apes and African apes.

Table 4.59. Eigenvalues of the Discriminant Function Analysis for hominoids.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	13.443	84.3	84.3	.965
2	1.965	12.3	96.7	.814
3	.532	3.3	100.0	.589

Table 4.60. Standardized Canonical Discriminant Function Coefficients for hominoids.

	Function		
	<b>1</b>	<b>2</b>	<b>3</b>
Geometric Mean	1.066	.213	.324
Medial Wedging	-.191	.210	.586
Posterior Wedging	.439	.644	.320
PTF angle	-.470	.398	-.311
FHL angle	-.252	.527	-.418
Trochlear depth	-.398	-.615	.018

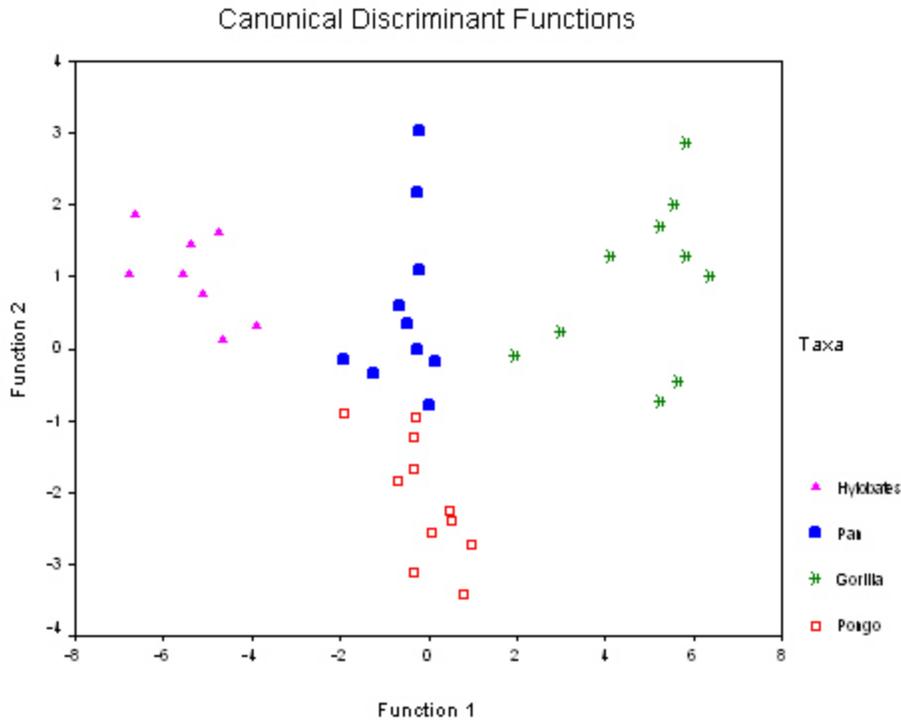


Figure 4.23. Canonical Discriminant Function plot for hominoids.

### *Anthropoids*

The discriminant function analysis for anthropoids correctly classified 71.8% of the hominoids as hominoids and 98.9% non-hominoid anthropoids as non-hominoids. One-hundred percent of the gibbons are classified as non-hominoids. Function 1 is positively loaded by trochlear size and negatively loaded by primarily trochlear depth. Function 2 is positively loaded by trochlear size, the angles of the posterior talocalcaneal facet and the *m. flexor hallucis longus* groove and negatively loaded by trochlear depth (Table 4.61; 4.62). Because none of the bivariate and/or univariate tests between hominoids and non-hominoids showed differences between these morphological features, hominoids are not quantitatively different from non-hominoids.

Table 4.61. Eigenvalues for the discriminant function analysis for anthropoids.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	3.433	49.8	49.8	.880
2	2.668	38.7	88.5	.853
3	.547	7.9	96.4	.594
4	.247	3.6	100.0	.445
5	.002	.0	100.0	.040

Table 4.62. Standardized Canonical Discriminant Function Coefficients for anthropoids.

	Function				
	1	2	3	4	5
Geometric Mean	1.174	.616	.413	-.115	.224
Medial Wedging	.136	-.224	.961	.344	.236
Posterior Wedging	-.196	.329	-.246	.929	.072
PTF angle	-.165	.540	.302	-.187	.536
FHL angle	-.237	.576	-.065	-.022	.318
Trochlear depth	-.561	-.706	-.308	.272	.860

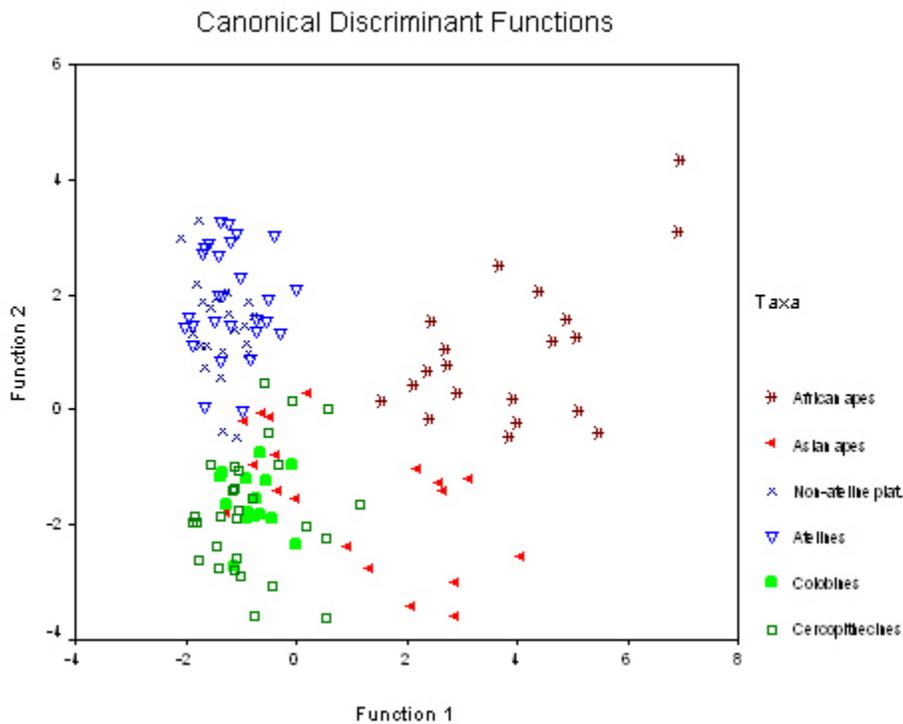


Figure 4.24. Canonical Discriminant Function plot for anthropoids.

### Discriminant Function Analysis

As predicted *Proconsul major* and the *Paracolobus* species should have talocalcaneal morphology most similar to extant colobines; *Proconsul nyanzae* and *Afropithecus turkanensis* should be most similar to extant cercopithecines; and *Sivapithecus parvada* should be most similar to extant hominoids.

The overall pattern of variation among catarrhines in all features including the geometric mean of trochlear measurements was tested using discriminant function analysis. The discriminant function classified 78.3% of the cases correctly and is highly significant ( $P < 0.001$ , Wilkes-Lambda). Those individuals incorrectly classified are primarily gibbons (Table 4.63). Gibbons are classified as colobines and not as other hominoids.

Function 1 is positively loaded by trochlear size and negatively loaded by posterior wedging and trochlear depth. Function 2 is positively loaded by medial wedging and posterior wedging and negatively loaded by the angle of the *m. flexor hallucis longus* groove. (Table 4.63; Table 4.64). Colobines are lower on the Function 2 axis and cercopithecines are higher. Medial wedging and posterior wedging showed significant differences between cercopithecines and colobines.

Table 4.63 Eigenvalues for catarrhines.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	1.391	75.9	75.9	.763
2	.441	24.1	100.0	.553

Table 4.64. Standardized Canonical Discriminant Function Coefficients

	Function	
	1	2
Geometric mean	1.305	.435
Medial wedging	.066	1.062
Posterior wedging	-.538	.433
PTF angle	.080	-.048
FHL angle	-.099	-.115
Trochlear depth	-.627	.005

Figure 4.25. Canonical Discriminant Functions scatter plot for catarrhines.

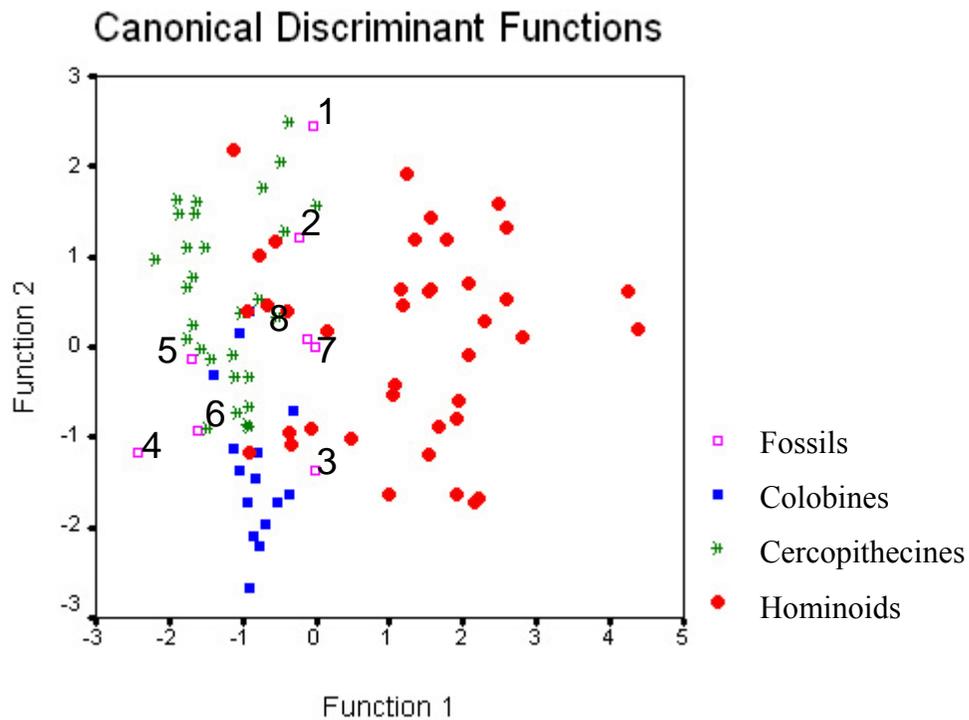


Table 4.65. Predicted group membership of fossil specimens.

	<b>Fossil Specimen</b>	<b>Group</b>
<b>1</b>	<i>Proconsul major</i> KNM-SO 390	Cercopithecines
<b>2</b>	<i>P. nyanzae</i> KNM-RU 1745	Cercopithecines
<b>3</b>	<i>P. nyanzae</i> KNM-MW 13142	Colobines
<b>4</b>	<i>Afropithecus turkanensis</i> KNM-WK 18120	Colobines
<b>5</b>	<i>Paracolobus chemeroni</i> KNM-BC 3 AQ	Cercopithecines
<b>6</b>	<i>Paracolobus mutiwa</i> KNM-WT 16822	Colobines
<b>7</b>	<i>Sivapithecus parvada</i> GSP 17152	Hominoids
<b>8</b>	<i>Sivapithecus parvada</i> GSP 17606	Cercopithecines

The extinct catarrhines show a large amount of variability within the discriminant function analysis. All species, with the exception of *Sivapithecus parvada* GSP 17152, are grouped with extant cercopithecoids, although some overlap with extant gibbons. As expected from the cercopithecoid and hominoid univariate, bivariate, and multivariate tests, posterior wedging and medial wedging are loading heavily on the catarrhine discriminant function analysis. These features showed significant differences between cercopithecines and colobines and to a minor extent between Asian apes and African apes. Therefore, the classification of the fossils is consistent with the univariate, bivariate, and multivariate tests between the paired groups of catarrhines.

Table 4.66. Summary of the bivariate/univariate analyses compared to the hypotheses of this study.

	<b>Medial wedging</b>	<b>Posterior wedging</b>	<b>PTF angle</b>	<b>FHL angle</b>	<b>Trochlear depth</b>
<b>Cercopithecoids</b>	No support (opposite of hypothesis)	No support (opposite of hypothesis)	No support (no difference)	No support (no difference)	No support (opposite of hypothesis)
<b>Platyrrhines</b>	No support (no difference)	<b>Support</b>	<b>Support</b>	No support (no difference)	No support (opposite of hypothesis)
<b>Hominoids</b>	No support (no difference)	No support (signal opposite of hypothesis)	<b>Support</b>	No support (signal support of hypothesis)	No support (opposite of hypothesis)
<b>Anthropoids</b>	No support (no difference)	No support (no difference)	No support (no difference)	No support (no difference)	No support (no difference)

Table 4.67. Summary of the differences between the pairwise analyses of extant anthropoids.

<b>Paired Taxa</b>	<b>Differences</b>
Colobines/Cercopithecines	<ul style="list-style-type: none"> <li>• Cercopithecines have greater medial and posterior wedging than colobines</li> <li>• <i>Nasalis</i> has deeper trochleae than <i>Papio</i></li> </ul>
Atelines/non-ateline platyrrhines	<ul style="list-style-type: none"> <li>• Atelines have greater posterior wedging than non-atelines</li> <li>• Atelines have more oblique PTF angles</li> <li>• Atelines have deeper trochleae</li> </ul>
Asian apes/African apes	<ul style="list-style-type: none"> <li>• Asian apes have more oblique PTF angles</li> </ul>
Hominoids/non-hominoids	<ul style="list-style-type: none"> <li>• No statistical differences</li> </ul>

Table 4.68. Summary of the fossil specimen morphology compared to the extant catarrhines.

<b>Fossil Specimen</b>	<b>Comparative Morphology with extant catarrhines</b>
<i>Proconsul major</i> KNM-SO 390	<ul style="list-style-type: none"> <li>• High medial wedging like <b>cercopithecines</b></li> <li>• Greatly oblique <i>m. flexor hallucis longus</i> groove angle</li> <li>• Deeply grooved trochlea like <b>hominoids</b></li> </ul>
<i>P. nyanzae</i> KNM-RU 1745	<ul style="list-style-type: none"> <li>• Low medial wedging like <b>colobines</b></li> <li>• Deeply grooved trochlea like <b>hominoids</b></li> </ul>
<i>P. nyanzae</i> KNM-MW 13142	<ul style="list-style-type: none"> <li>• High medial wedging like <b>cercopithecines</b></li> <li>• Deeply grooved trochlea like <b>hominoids</b></li> </ul>
<i>Afropithecus turkanensis</i> KNM-WK 18120	<ul style="list-style-type: none"> <li>• Low medial wedging like <b>colobines</b></li> <li>• High posterior wedging like <b>cercopithecines</b></li> <li>• Deeply grooved trochlea like <b>hominoids</b></li> </ul>
<i>Paracolobus chemeroni</i> KNM-BC 3 AQ	<ul style="list-style-type: none"> <li>• High posterior wedging like <b>cercopithecines</b></li> <li>• Greatly oblique <i>m. flexor hallucis longus</i> groove angle</li> <li>• Deeply grooved trochlea like <b>hominoids</b></li> </ul>
<i>Paracolobus mutiwa</i> KNM-WT 16822	<ul style="list-style-type: none"> <li>• Low medial wedging like <b>colobines</b></li> <li>• High posterior wedging like <b>cercopithecines</b></li> <li>• Deeply grooved trochlea like <b>hominoids</b></li> </ul>
<i>Sivapithecus parvada</i> GSP 17152	<ul style="list-style-type: none"> <li>• Greatly oblique posterior talocalcaneal facet angle like <b>hominoids</b></li> </ul>
<i>Sivapithecus parvada</i> GSP 17606	<ul style="list-style-type: none"> <li>• Moderately oblique posterior talocalcaneal facet angle like <b>cercopithecoids</b></li> </ul>

#### Behavioral Inferences

Based on the univariate, bivariate, and multivariate analyses between pairs of anthropoid taxa, behavioral inferences are limited. The datum is mixed and sometimes unclear.

## Chapter 5: Discussion

Variation in the functional morphology of the anthropoid talocrural joint has been hypothesized to be associated with differences in positional behaviors of extant anthropoids. This study did not find universal support for the hypotheses put forward by Langdon (1986) and Strasser (1988) about relationships between form and locomotor behavior of extant anthropoids. Langdon (1986) concluded that hominoid talocrural joint morphology is different from non-hominoid anthropoid morphology because hominoids emphasize climbing behaviors. Strasser (1988) observed differences in talocrural joint morphology between extant colobines and cercopithecines, which she linked to locomotor behavioral differences. The results from this study are mixed. They do not support the use of broad functional interpretations for the anthropoid talocrural joint as previously proposed.

### Medial Trochlear Wedging

Contrary to predictions (Fleagle, 1976b; Langdon, 1986), results from this research demonstrate that animals that emphasize climbing behaviors during locomotion do not have greater medial wedging of the talar trochlea than those that do not. Apes do not have more medially wedged trochleas than do monkeys, and atelines are not more wedged than non-atelines. Cercopithecines do differ from colobines, however, but the difference is in the opposite direction from the hypothesis; cercopithecines have greater medial wedging than colobines. Due to the lack of support from the other paired taxa, medial wedging does not distinguish differences between anthropoids that emphasize climbing versus anthropoids that emphasize quadrupedal behaviors.

These results differ from others in the literature. Fleagle (1976b) observed more medial trochlear wedging (trochlear asymmetry) in the more arboreal *Presbytis obscura* versus *Presbytis melalophos*, which he attributed to the degree of inversion of the foot to grasp arboreal supports, and symmetry of the trochlea suggests limited inversion of the foot and primarily uniaxial movements of dorsiflexion and plantarflexion (ibid). However, given the lack of association between climbing and medial wedging in this study, it may be that the differences he saw were unrelated to climbing or attributable to some other differences between these species. Alternatively, it may be that medial wedging does differ in the predicted way between closely related pairs of taxa who share most other aspects of pedal morphology. Only a more extensive and detailed study that can explore variation among closely and more distantly related taxa could discriminate between these possibilities.

Results of this study also are not fully consistent with the reasons that Latimer and colleagues (1987) used to explain the observed more medial trochlear wedging in great apes compared to humans. They explained this because high medial wedging increases conjunct rotation at the talocrural joint and so should be found in animals that climb regularly (see also Lewis, 1980). Although the present study did not include human samples, climbing does not appear to be an explanation for high medial wedging. Humans, of course, are the only exclusively terrestrial bipedal primates. All other primates are at least partly arboreal and/or quadrupedal, and must maintain the ability to invert their feet to grasp arboreal supports, and this may serve as a constraint on trochlear form.

Langdon (1986) offered a different, yet unclear, interpretation of medial wedging of the cercopithecoid trochlea. He hypothesized that the adaptation of more medial wedging of the trochlea of baboons and patas monkeys is due to the use of small branches. In order to balance

on small branches, the feet are oriented closer to the midline of the body and inverted to grasp the support. Langdon's interpretation is both unclear and lacks support from behavioral studies of baboons and patas monkeys, who are both primarily terrestrial animals.

*Macaca fascicularis* is an important species to consider for functional interpretations of cercopithecines versus colobines because it has similar arboreal behaviors and substrate use to *Trachypithecus cristata* (Cant, 1988). The results from this study show that *Macaca fascicularis* (4.96 kg; Ruff, 2003) have high medial wedging compared to *Trachypithecus cristata* (7.09 kg; Ruff, 2003; Cant, 1988). If medial wedging is an indication of behavior, *Macaca fascicularis* should have morphology similar to that of *Trachypithecus cristata*. The functional signal for medial wedging is weak from both the bivariate/univariate and multivariate analyses across anthropoids. According to the results from this study, using the degree of medial wedging for functional interpretations of fossils is problematic because medial wedging, in isolation, does not separate paired groups of extant taxa. This means that medial wedging of the trochlea is not a useful measure of positional behaviors in anthropoids.

As Latimer and colleagues (1987) observed and the datum from this study suggest, differences in medial wedging between pairwise groups may not be a climbing versus non-climbing signal but a terrestrial versus arboreal signal. Platyrrhines are predominantly arboreal animals and because there are no terrestrial species within platyrrhines like there is within cercopithecoids, no significant difference in medial wedging within platyrrhines is observed. Latimer and colleagues (1987) found differences between humans and apes because humans are more terrestrial than apes and similarly, this study found differences between colobines and cercopithecines because cercopithecines are more terrestrial than colobines.

### Posterior Trochlear Wedging

High posterior wedging was hypothesized to be associated with an increase in lateral movements of the talocrural joint and an increase in mobility is associated with animals that emphasize climbing behaviors (Langdon, 1986; Strasser, 1988). However, this does not seem to be the case across anthropoids. Data presented here show atelines do have more posteriorly wedged trochleae than non-ateline platyrrhines, which supports this hypothesis. However, African apes do not differ from Asian apes (although there is a signal at  $p < .1$ ), and apes do not have more posteriorly wedged trochleas than do monkeys. Furthermore, cercopithecines are more wedged than colobines. Differences in the degree of posterior wedging do exist between colobines versus cercopithecines and atelines versus non-ateline platyrrhines, but the differences between cercopithecoids are in the opposite direction. Colobines have less posterior wedging than cercopithecines, while atelines have greater posterior wedging than non-atelines. Therefore within catarrhines, animals that emphasize climbing have lower wedging than the animals that emphasize quadrupedalism. The functional interpretation for these differences are unclear, but this feature can certainly be used to separate colobines from cercopithecines.

Langdon (1986) and Strasser (1987) hypothesized that increased posterior wedging increases the amount of lateral movements and looseness of the talocrural joint during plantarflexion. During vertical climbing, transverse movements of the talocrural joint during both dorsiflexion and plantarflexion are necessary to grasp vertical substrates, and according to Langdon (1986) because hominoids have highly asymmetrical talar trochleae, the shape of the trochlea indicates the degree of conjunct supination accompanying dorsiflexion at the talocrural joint. Because the results from this research show that colobines and Asian apes have less posterior wedging than cercopithecines and African apes, respectively, it appears that increased

posterior wedging is associated with terrestrial movements rather than arboreal climbing. These results are opposite from previous analyses reported in the literature.

### Posterior Talocalcaneal Facet Angle

Assuming that posterior talocalcaneal facet angle reflects the position of the distal foot relative to talocrural joint, anthropoids that emphasize vertical climbing were expected to have more oblique angles of the posterior talocalcaneal facet because vertical climbing requires dorsiflexion of the talocrural joint while the distal foot remains parallel to the substrate (Latimer & Lovejoy, 1989; Gebo, 1993).

Results presented here demonstrate that atelines have more oblique facets than non-ateline platyrrhines, and Asian apes more oblique facets than African apes, which support this hypothesis, which support the hypothesized association with climbing.

However, cercopithecines and colobines do not differ. There are several possible explanations. It could be that all cercopithecoids have similar foot orientations during locomotion, perhaps due to their shared evolutionary history. Blue and colleagues (2006) among others hypothesized that cercopithecoids underwent a terrestrial behavioral phase, and extant colobines retain some morphologic features associated with this behavioral phase. It is possible the posterior talocalcaneal facet is one terrestrial morphologic feature that extant colobines have retained from the earlier evolutionary terrestrial phase. It also may be that the species included in the colobine and cercopithecine samples do not represent a sufficiently broad range of variation in foot use.

There is a significant difference for posterior talar facet angles between Asian and African apes. This difference may be related to climbing, but could also be the result of a heel-

strike in African apes and the absence of a heel-strike during gait in Asian apes (Gebo, 1993). Effectively, a heel-strike would decrease the obliquity of the angle between the posterior talocalcaneal facet and the calcaneocuboid joint during gait for African apes because the posterior talocalcaneal facet is practically parallel to the distal foot. Conversely, a semi-plantigrade position of the foot is more oblique to the distal foot as seen in Asian apes. This may partly contribute to the fact that orangutans and gibbons have more oblique angles of the posterior talocalcaneal facet relative to the calcaneocuboid joint.

Although a heel-strike functional conclusion is possible for apes, it fails to take into account the differences seen between atelines and non-ateline platyrrhines. Because quantitative behavioral data for platyrrhines show that atelines climb more than non-ateline platyrrhines, morphologic differences observed between atelines and non-ateline platyrrhines should be a more controlled representation of climbing versus non-climbing behaviors than hominoids and cercopithecoids. The more oblique angle in atelines compared with non-ateline platyrrhines supports the hypothesis, and provides a clearer signal than cercopithecoids and hominoids. Therefore, the posterior talocalcaneal facet is not universally associated with locomotor behavioral differences in pairwise comparisons between colobines versus cercopithecines and Asian apes versus African apes, but the results from differences between atelines and non-ateline platyrrhines suggest that this feature warrants further investigation. Observations of foot postures and movements within all anthropoids are needed to accurately assess form versus function of the subtalar joint.

### M. Flexor Hallucis Longus Groove Angle

This study tested the hypothesis that the angle of the *m. flexor hallucis longus* groove would reflect reliance on vertical climbing because it should reflect the position of the foot relative to the knee. However, data presented here show no strong functional signal for the angle of the *m. flexor hallucis longus* groove of the talus. The angle of the groove is equivalent in cercopithecines and colobines, in atelines and non-ateline platyrrhines, and in Asian and African apes. Latimer et al. (1987) observed that African apes have more oblique grooves than humans, which he attributed to an emphasis on climbing in apes. However, this may simply mean that morphology of the talocrural joint for bipeds and quadrupeds is distinct and different. Because most taxa in this study are predominantly quadrupedal on a horizontal substrate with the exceptions of gibbons and orangutans, the differences in orientation of the knee relative to the ankle are minimal between different types of quadrupedal movements versus the differences in knee positions between bipedalism and quadrupedalism. Therefore, the lack of significant differences in knee positions relative to the foot among quadrupedal movements may account for the lack of significant differences in the angle of the *m. flexor hallucis longus* groove among quadrupedal anthropoids.

### Depth of the Talar Trochlea

Contrary to expectations in the literature (Langdon, 1986) that animals emphasizing vertical climbing should have shallower talar trochleae than those emphasizing quadrupedal locomotion, data from this study show that large colobines (*Nasalis*), atelines, and Asian apes have more deeply grooved trochleae than large cercopithecines (*Papio*), non-ateline platyrrhines, and African apes respectively. There was no significant difference between small colobines

(*Trachypithecus*) and small cercopithecines (*Macaca*). If depth limits lateral movements and permits non-parasagittal motion of the talocrural joint, then cercopithecines should have deeper trochleae than colobines, non-ateline platyrrhines deeper than atelines, and African apes deeper than Asian apes, but they do not. Thus, results from this study suggest that animals that emphasize climbing having more deeply grooved trochleae than animals that emphasize quadrupedalism. The broad assumption that deeply grooved trochleae are associated with climbing is not supported from this study.

The datum from this study shows that trochlear depth decreases with increasing body size. This supports Latimer's and colleagues' (1987) hypothesis that joint surface area increases with an increase in body size to decrease cartilage pressure. This is problematic for functional interpretations for trochlear depth because variation observed between pairs in trochlear depth is affected by body size, and because hominoids versus non-hominoid anthropoids and atelines versus non-ateline platyrrhines vary in both behavior and body size, functional interpretations from trochlear depth is difficult to divorce from body size effects on the joint morphology. Therefore, Langdon's (1986) use of trochlear depth to compare hominoids and non-hominoid anthropoids is problematic.

#### Summary of Trochlear Size and Trochlear Shape

Although the geometric mean of trochlear measurements was used as the body size surrogate as suggested from the literature (Rafferty et al., 1995), the measurement appears to be a problematic proxy for body mass. The trochlear sizes of atelines and orangutans do not appear to correspond with body mass. Crosschecking of known body masses with trochlear size from all anthropoids is needed to accurately assess the validity of the body size surrogate. From this

study, although howler monkeys (7.275 kg; Fleagle & Mittermeier, 1980) are known to be similar in body mass to spider monkeys (7.775 kg; Fleagle & Mittermeier, 1980), the geometric mean of trochlear measurements estimates howlers as being the same size as capuchins (3.450; Fleagle & Mittermeier, 1980 kg) and the smallest within atelines. Spider monkeys have the highest geometric mean of trochlear measurements, although they have generally the same body mass as howlers (Gebo, 1992b). Similarly, male orangutans, (80.25 kg; Smith & Jungers, 1997) are generally larger than male chimpanzees (56 kg; Smith & Jungers, 1997), but the geometric mean of trochlear measurements estimated the same body size for orangutans and chimpanzees. This could suggest that trochlear size is unrelated to body mass consistently across anthropoids. Certainly, it appears that orangutans and howlers have small tali relative to mass, or that the individual orangutans and howlers used in this study are smaller than those reported by Fleagle and Mittermeier (1980) and Smith and Jungers (1997). The body size surrogate appears to be representative of the body mass within cercopithecoids, but problematic across anthropoids.

The allometric problems with an analysis of talar morphology of anthropoids are apparent from this study. The body size range for anthropoids is great and consequently, the analysis and interpretation of talar morphology of the various anthropoids is complicated by body size and phylogenetic signals. To isolate the functional signals from the morphology therefore requires better techniques and allometric analyses.

#### Summary of univariate/bivariate tests

The results from the univariate/bivariate tests are mixed and in some cases, the datum from the pairwise contrasts support the hypotheses that climbers and non-climbers have different morphology dependent on behavior, while other pairs from for the same feature do not support

the climbing hypothesis. For example, there are significant differences between atelines versus non-ateline platyrrhines and Asian apes versus African apes and no significant differences between colobines and cercopithecines for the angle of the posterior talocalcaneal facet. Although the hypotheses are not universally supported by these results, the differences within platyrrhines and hominoids are important to consider for functional interpretations of this feature. It is possible that heel-strike is related to this feature for hominoids, but heel-strike fails to explain the differences within platyrrhines. The functional explanation for observed differences in trochlear shape and depth is unclear, but the results from this study show that medial wedging and posterior wedging separate colobines and cercopithecines and body size separates hominoids from non-hominoid anthropoids. These observed differences should appear in the multivariate analyses of catarrhines.

There is little by the way of behavioral conclusions that can be said about these pairwise contrasts, except there are observed differences between colobines versus cercopithecines, atelines versus non-ateline platyrrhines, and Asian apes versus African apes for particular features of the talocrural joint, but there is no universal support for these pairwise contrasts for any one feature. Therefore, the differences in talocrural joint morphology observed between these pairs can only be accurately assessed with further studies that focus on groups, such as atelines versus non-ateline platyrrhines, that have documented and quantified behavioral differences. Without quantitative behavioral information to support the morphological differences, too many assumptions can be made about form and function.

### Summary of Discriminant Function Analysis of Talocrural Morphology

There is slight overlap of taxa in the discriminant function analysis, but there is a general separation of cercopithecines from colobines, colobines from hominoids, and cercopithecines from hominoids. As discussed above, the observed differences such as the shape of the talar trochleae in talocrural joint morphology of colobines and cercopithecines are reflected in the results from the discriminant function analysis. Because cercopithecines and colobines have observed morphologic differences in posterior and medial wedging of the trochlea, those two features primarily contribute to the separation of taxa in the discriminant function analysis. Two points arise from the discriminant function analysis for catarrhines. First, the discriminant function analysis separates groups among catarrhines. The differences between groups reflect the univariate/bivariate differences, primarily trochlear shape and body size, and as discussed above, the functional signal for medial wedging is weak because differences in medial wedging are only seen between cercopithecines and colobines. The functional signal for posterior wedging is stronger for catarrhines and not platyrrhines because it separates cercopithecines from colobines and Asian apes from African apes. Second, the discriminant function analysis shows where the fossils fall within extant catarrhine groups according to the morphology. Although the functional signals from the morphology of the talocrural joint are unclear, the predicted classification of the fossils within an extant catarrhine group (colobines, cercopithecines, or hominoids) is still an important result the discriminant function sorts extant individuals based on the quantified features. The quantified features of the talocrural joint for each fossil are similar to the group at which the fossil is placed.

As with the univariate/bivariate comparison results, the posterior talocalcaneal facet angle, the angle of the *m. flexor hallucis longus* groove, and the depth of the talar trochlea do not

separate taxa based on climbing emphasis. Therefore, this study suggests posterior talocalcaneal facet angle the angle of the *m. flexor hallucis longus* groove, and trochlear depth are not useful for reconstructing the amount of climbing in fossil catarrhine species. The posterior talocalcaneal facet has minimal effect on the discriminant function analysis because it does not include platyrrhines and it lumps Asian apes and African apes into one hominoid category. Latimer and colleagues (1987) used the angle of the *m. flexor hallucis longus* groove to separate bipeds from quadrupeds, but the differences within quadrupeds are minimal and therefore, quadruped within group comparisons show no differences in this angle. If there is no functional signal between extant catarrhine taxa for the angles of the posterior talocalcaneal facet and the *m. flexor hallucis longus* groove, these features should not be used to hypothesize behavior of fossil catarrhine quadrupeds.

The discriminant function analysis classified gibbons as cercopithecoids. This may be related to body size and/or behavior. Gibbons (5.09 kg; Ruff, 2003) are similar in body size to crab-eating macaques (4.96 kg; Ruff, 2003) and small atelines (*Alouatta*) and body size contributes heavily to the discriminant function analysis of catarrhines. Also, gibbons use their forelimbs for locomotion during suspensory activities, but there is a lack of behavioral observations of gibbon foot postures (Fleagle, 1976a; Rodman, 1979). More future behavioral research is needed to understand gibbon foot movements and postures in order to include them in form and function discussions for catarrhines.

## Fossils

### *Proconsul*

Both *Proconsul nyanzae* specimens are most similar to cercopithecoids, not extant hominoids. Although the *Proconsul* specimens are grouped with extant cercopithecoids based on talocrural joint morphology, the functional signals from that morphology are unclear and this study cannot accurately link form to function. Because there are observed differences in talocrural joint morphology between extant colobines and extant cercopithecines, the results from this study can only conclude that *Proconsul major* and KNM-RU 1745 have similar morphology to extant cercopithecines and KNM-MW 13142 has similar morphology to extant colobines. Previous interpretations of the functional morphology of the *Proconsul* pelvis, vertebrae, ankle, and elbow suggest that *Proconsul* species did not appear to have specialized adaptations for climbing and suspension like extant hominoids, but this study cannot conclusively support or refute those interpretations. Previous observations of *Proconsul tali* show deeply grooved trochleae, which was interpreted as a restriction in transverse movements of the talocrural joint (Rose, 1993), but the univariate/bivariate results from this study indicate that trochlear depth is influenced by body size and the influence of body size makes it difficult to tease out function.

The discriminant function analysis classified KNM- RU 1745 as a cercopithecine, but KNM-MW 13142 as a colobine. This variation between the two *P. nyanzae* specimens exceeds that for even the broad categories used in this study and the variation of any extant species in the multivariate analysis. Either *P. nyanzae* talocrural joint morphology was incredibly variable, or KNM-MW 13142 and KNM-RU 1745 talocrural joint morphologies exceed species or even genus variation and should be classified as different species.

### *Afropithecus turkanensis*

This study showed that *Afropithecus turkanensis* has talocrural joint morphology similar to extant colobines based mainly because its trochleae is more symmetrical than that of cercopithecines and hominoids. *Afropithecus* is morphologically similar to *Proconsul* overall (Rose, 1993; Leakey & Walker, 1997; Ward 1998), but its talocrural joint differs. *Afropithecus* has higher posterior and lower medial wedging than the *Proconsul* specimens, and those differences in trochlear shape and size resulted in different classifications within the multivariate analysis. However, KNM-MK 13142 is more similar in trochlear shape to *Afropithecus* than *Proconsul major* and KNM-RU 1745. What can be said about *Afropithecus* locomotor behavior based on this study is minimal because the functional signals from these talocrural joint features are still unclear. Its morphology is more similar to extant colobines than extant cercopithecines, but how the talocrural joint morphology reflects locomotor behavior is unknown.

### *Sivapithecus parvada*

The posterior talocalcaneal facet angle was the only measurement taken for *Sivapithecus* in this study, but univariate analysis of this measurement shows *Sivapithecus* as most similar to extant hominoids and not extant cercopithecoids. For the multivariate analysis, the two *Sivapithecus* specimens are found at zero for Function 1 and zero for Function 2. This means that the posterior talocalcaneal facet angle is contributing very little to the multivariate analysis because the angle is the only datum for *Sivapithecus* from this study

### *The Paracolobus species*

*Paracolobus mutiwa* classifies as an extant colobine, but *P. chemeroni* as cercopithecine, although it overlaps with the outer range of extant colobines. As seen in the univariate/bivariate and multivariate analyses from this study, medial wedging and posterior wedging primarily separate extant colobine and cercopithecine talocrural joint morphology. Extant cercopithecines have more medial and posterior wedging than extant colobines. *Paracolobus mutiwa* has a more symmetrical talar trochlea than *Paracolobus chemeroni*, which is an observed morphological difference, but as discussed above, the functional significance for the differences between extant colobines and extant cercopithecines are unclear. The discriminant function analysis used trochlear shape as basis for Function 2 and consequentially classified the fossils according to those features. *Paracolobus chemeroni* and *P. mutiwa* were large-bodied monkeys and their body size may have limited how much climbing they did. Previous assessments for the locomotor repertoire of the *Paracolobus* species have grouped them with extant colobines being that *Paracolobus* is a colobine (Birchette, 1982; Harris et al., 1988), but qualitative observations of the tali of *P. mutiwa* and *P. chemeroni* reveal two different morphologies similar to the differences noted by Strasser (1988) between colobines and cercopithecines. *Paracolobus chemeroni* has features characteristic of cercopithecines such as an asymmetric talar trochlea.

Morphologic variation within genera is not uncommon for anthropoids as seen with *Presbytis obscura* and *Presbytis melalophos* (Fleagle, 1976b) and *Macaca fascicularis* and *Macaca nemestrina* (Rodman, 1979). Like *Presbytis* and *Macaca*, the *Paracolobus* species have both cercopithecine and colobine traits and therefore, the talocrural joint morphology of *Paracolobus* was variable. The classification of *Paracolobus chemeroni* and *Paracolobus mutiwa* from this study is the opposite of the conclusions from Ting's (2001) observations from

the hip and thigh. Ting (2001) concluded that hip and thigh morphology of *Paracolobus mutiwa* was similar to extant cercopithecines. The results from this study coupled with Ting's study show that *P. chemeroni* and *P. mutiwa* had mosaic colobine/cercopithecine morphology. Whether *P. chemeroni* and *P. mutiwa* were behaving differently based on talocrural joint morphology is unclear, but further research from other joints of the foot and ankle are needed to accurately assess the importance of the talocrural joint morphology of extinct fossils.

## Chapter 6: Conclusions

This study has demonstrated that several common generalizations made about the functional anatomy of the talocrural joint are not universally supported by data for anthropoids. Results presented here are significant and important, because these generalizations have been used to infer behavior of fossil catarrhines, which are sometimes known only from tali or calcanei. Although this research has evaluated only broad, pairwise contrasts between diverse groups of taxa, it has tested hypotheses present in the literature, identified potential pitfalls in making broad inferences from talar and calcaneal form, and provides justification for a more in depth, detailed analysis of talocrural functional morphology.

In particular, shape of the talar trochlear surface is hypothesized to affect talocrural joint motion in important ways. Langdon (1986) and Strasser (1988) predicted that high medial and posterior wedging is associated with climbing behaviors, but the results from this study do not support these predictions, rather, the differences between animals that emphasize climbing and animals that emphasize quadrupedalism are in the opposite direction than previous functional interpretations (Langdon, 1986; Fleagle, 1976b; Latimer et al., 1987; Lewis, 1980). There are no differences between pairs for the *m. flexor hallucis longus* groove and little functional significance for trochlear depth. The posterior talocalcaneal facet angle had mixed results and may have multiple reasons for the degree of obliquity, but a more narrow analysis of each pairwise contrast for platyrrhines and hominoids are needed to clarify the differences in morphology. More careful analyses of anthropoid behavior and foot postures are needed before these interpretations of talocrural joint form related to function can be concluded. Further, the classification of extant species into behavioral groups is a tenuous task because as seen with *Macaca fascicularis* and *Macaca nemestrina* (Rodman, 1979) and *Presbytis obscura* and

*Presbytis melalophos* (Fleagle, 1976b), there is behavioral variation within genera. The classification of extant species has the most value when the species have quantitative behavioral data to support the groups as in atelines and non-ateline platyrrhines. Unfortunately for cercopithecoids, no quantitative data was available for the extant colobines.

This study is a narrow analysis of the functional morphology of the anthropoid talocrural joint. Future comprehensive studies of the mid-tarsal joints, subtalar joint, and talocrural joint of anthropoids are needed to supplement this study before anything can be said about fossil tali and calcanei. Rather than focusing on one joint or one aspect of the foot, the morphology and movements of each joint within the foot need to be closely observed and quantified and considered together. The movements of the foot are complex and involve several joints, and three-dimensional analysis of the foot would give a clearer picture of the interaction of those joints.

The classification of the fossil specimens was based on the multivariate differences between the pairwise contrasts of cercopithecoids and hominoids. There is high within species variation for *Proconsul nyanzae* and high within genus variation for *Paracolobus*, which has implications for current interpretations of taxonomy and behavior. Because of their body size and morphology, the *Paracolobus* species may have been engaged in locomotor behaviors unlike any behaviors of extant anthropoids. The functional interpretations of the fossil talocrural morphology are unclear from this study, it is difficult to conclude behavior for any fossil specimen. This study has important implications for the functional interpretations of fossil tali and calcanei.

The results from this study concludes that the functional morphology of the talocrural joint is more complicated than previously considered in the literature (Langdon, 1986; Strasser,

1988) and more work both in behavioral studies of extant anthropoids and functional morphological studies of anthropoid feet is needed (Fleagle, 1976b; Lewis, 1980; Langdon, 1986; Latimer et al., 1987; Strasser, 1988). More extant anthropoid samples with known body masses are needed to examine the correlation of talar size with body mass, and more species are needed to understand the full range of variation in each taxonomic group with larger samples for proper phylogenetic considerations. A narrow focus on one of the four pairwise contrasts is needed to more closely evaluate structure-function relationships without the confounds of phylogenetic distance. A detailed comparison involving taxa with behavioral data would be an appropriate and beneficial place to start for talar morphology. In addition, comparing all joints of the anthropoid foot to one another within a functional context would potentially reveal covariation among foot regions that may be related to function. Lastly, vast amounts of functional morphologic analyses of strepsirrhine feet have yielded useful information on function and form of primates (Gebo, 1986; Dagosto, 1986; Ford, 1988). The techniques and insights from these strepsirrhine analyses may be an important spring-board for future analyses of talar form to infer behavior in other primates. All of these approaches will be important to obtain a comprehensive understanding of pedal functional morphology in anthropoids that would permit accurate interpretation of locomotor behavior in fossil anthropoids represented by tali and calcanei.

## Appendix 1

<b>Species</b>	<b>MCZ #</b>	<b>ML wedging</b>	<b>PA wedging</b>	<b>PTF Angle</b>	<b>FHL Angle</b>
<i>Papio hamadryas</i>	5008	14.2500327	13.8686978	50.949	69.081
<i>Papio doguera</i>	10748	18.18055384	10.58016241	50.842	58.926
<i>Papio doguera furax</i>	21161	11.42118627	14.2500327	55.799	62.222
<i>Papio doguera furax</i>	21160	4.64306118	20.8749507	54.9	71.268
<i>Papio doguera neumanni</i>	15378	12.68038349	14.2500327	50.372	65.167
<i>Macaca nemestrina</i>	35670	4.771888061	11.81228223	52.193	66.511
<i>Macaca n. nemestrina</i>	35631	8.17123356	14.86281594	51.953	68.013
<i>Macaca maurus</i>	34462	13.16388931	18.92464442	56.475	70.645
<i>Macaca mullata</i>	61554	14.2500327	15.53033204	58.692	62.278
<i>Macaca mullata</i>	61553	7.15266875	13.16388931	52.057	59.767
<i>Macaca mullata</i>	61414	12.4068958	12.68038349	49.016	64.084
<i>Macaca mullata</i>	19991	7.462793998	12.68038349	64.38	68.772
<i>Macaca fascicularis f.</i>	37406	12.01801191	13.57794915	57.216	66.345
<i>Macaca fascicularis f.</i>	37414	12.68038349	16.26020471	56.439	67.841
<i>Macaca fascicularis f.</i>	35729	6.025575008	10.88066406	63.493	61.921
<i>Macaca fascicularis f.</i>	35731	6.025575008	12.96614739	65.97	61.889
<i>Macaca fascicularis f.</i>	35681	12.01801191	7.800987485	57.11	64.386
<i>Macaca fascicularis f.</i>	35677	10.08490214	15.81432541	56.546	71.045
<i>Macaca fascicularis f.</i>	35673	8.578306658	10.38885782	64.589	65.794
<i>Macaca fascicularis f.</i>	35656	12.68038349	16.26020471	50.672	72.624
<i>Macaca fascicularis f.</i>	35629	15.81432541	14.99171528	60.985	69.52
<i>Macaca fascicularis f.</i>	35611	14.99171528	13.57794915	49.648	70.427
<i>Macaca fascicularis f.</i>	35608	10.71165009	10.88066406	55.944	72.403
<i>Trachypithecus cristata u.</i>	37396	7.462793998	14.2500327	59.999	69.054
<i>Trachypithecus cristata u.</i>	37399	3.014871518	2.864192368	53.503	66.388
<i>Trachypithecus cristata u.</i>	37665	2.603905345	6.867260725	56.773	66.485
<i>Trachypithecus cristata u.</i>	37671	12.68038349	7.800987485	62.999	69.611
<i>Trachypithecus cristata u.</i>	37675	5.452621988	9.14784252	56.724	69.611
<i>Trachypithecus cristata u.</i>	35685	0	7.15266875	60.633	69.031
<i>Trachypithecus cristata u.</i>	35672	5.724810452	2.386978848	58.661	68.623
<i>Nasalis larvatus</i>	37328	5.367550319	10.5247908	62.147	67.718
<i>Nasalis larvatus</i>	37327	1.909682508	9.270926854	53.572	72.013
<i>Nasalis larvatus</i>	37330	0	9.027976916	55.774	68.862
<i>Nasalis larvatus</i>	37325	7.382771973	15.81432541	61.667	66.455
<i>Nasalis larvatus</i>	107099	1.736102899	12.68038349	62.562	69.085
<i>Nasalis larvatus</i>	37326	4.242192793	10.71165009	50.407	70.888
<i>Nasalis larvatus</i>	41563	1.909682508	12.34035019	50.951	68.411
<i>Nasalis larvatus</i>	41557	1.79034742	7.335576111	46.29	69.434
<i>Gorilla gorilla beringia</i>	23182	0	20.95484719	53.609	66.763
<i>Gorilla gorilla gorilla</i>	29048	0	28.07248694	47.788	68.791
<i>Gorilla gorilla gorilla</i>	23160	5.052233823	16.73177225	41.597	63.892
<i>Gorilla gorilla gorilla</i>	20039	0.818497216	28.69866409	46.531	64.634
<i>Gorilla gorilla gorilla</i>	20043	0	26.20557988	52.335	54.144
<i>Gorilla gorilla gorilla</i>	29049	0	23.15037763	50.325	58.26
<i>Gorilla gorilla gorilla</i>	57482	1.685048521	20.35102169	53.173	60.543
<i>Gorilla gorilla gorilla</i>	20038	0	32.82156919	51.499	57.871
<i>Gorilla gorilla gorilla</i>	37264	6.35966024	20.91981819	47.732	60.742

<b>Species</b>	<b>MCZ #</b>	<b>ML wedging</b>	<b>PA wedging</b>	<b>PTF Angle</b>	<b>FHL Angle</b>
<i>Gorilla gorilla gorilla</i>	17684	2.20341223	15.86551663	53.609	59.122
<i>Pongo pygmaeus</i>	37362	2.083253352	5.724810452	61.221	63.672
<i>Pongo pygmaeus</i>	50960	6.35966024	11.19867867	52.495	53.211
<i>Pan trolodyte</i>	15312	3.818304866	8.63205504	55.511	67.678
<i>Pan trolodyte</i>	23183	6.221681307	14.50638923	60.149	63.207
<i>Pan trolodyte</i>	26849	2.727855063	1.041712749	58.719	73.811
<i>Pan trolodyte</i>	20041	0	14.2500327	61.785	67.823
<i>Pan trolodyte</i>	26847	2.727855063	15.25629934	63.245	63.435
<i>Pan trolodyte</i>	19187	11.17448793	15.63058709	61.266	69.555
<i>Pan trolodyte</i>	48686	10.71165009	19.95542524	63.169	65.273
<i>Hylobates lar lar</i>	41545	5.724810452	10.2043305	59.723	66.857
<i>Hylobates lar lar</i>	41492	9.027976916	16.59428994	55.967	62.458
<i>Hylobates lar lar</i>	41501	15.81432541	9.527283381	64.796	74.469
<i>Hylobates lar lar</i>	41505	9.527283381	13.16388931	65.514	65.229
<i>Hylobates lar lar</i>	41534	6.35966024	8.79741071	58.793	73.142
<i>Hylobates lar lar</i>	41512	18.92464442	10.98464911	65.615	69.053
<i>Hylobates lar lar</i>	41495	11.42118627	11.42118627	62.394	71.157
<i>Hylobates lar lar</i>	41529	14.2500327	10.98464911	57.897	72.387
<b>Species</b>	<b>FMNH #</b>	<b>ML wedging</b>	<b>PA wedging</b>	<b>PTF Angle</b>	<b>FHL Angle</b>
<i>Cebus apella</i>	60751	12.68038349	11.42118627	70.12	77.336
<i>Cebus apella</i>	95471	10.08490214	19.85249101	77.332	81.052
<i>Cebus apella</i>	95474	13.41967362	10.38885782	67.902	76.367
<i>Cebus apella</i>	95470	6.35966024	12.01801191	77.7	74.219
<i>Cebus apella</i>	95336	20.0159596	14.2500327	74.041	76.813
<i>Cebus apella</i>	93261	10.08490214	8.578306658	87.229	72.121
<i>Cebus apella</i>	95473	6.732921327	14.86281594	71.147	80.839
<i>Cebus capucinus capucinus</i>	69650	12.68038349	7.800987485	75.671	78.969
<i>Cebus capucinus capucinus</i>	68843	10.08490214	11.42118627	62.549	81.494
<i>Cebus capucinus capucinus</i>	68841	12.68038349	8.17123356	77.641	72.897
<i>Cebus capucinus capucinus</i>	68837	10.71165009	13.57794915	71.652	73.355
<i>Ateles belzebuth belzebuth</i>	121215	6.603731349	13.76344726	67.813	78.187
<i>Ateles fusciceps robustus</i>	68820	2.386978848	19.50484988	72.778	76.987
<i>Ateles fusciceps robustus</i>	68811	0	17.6407591	75.847	78.223
<i>Ateles fusciceps robustus</i>	68823	0	20.0159596	74.558	74.068
<i>Ateles fusciceps robustus</i>	68810	0	16.26020471	66.169	71.692
<i>Ateles geoffroyi</i>	49336	0	18.92464442	71.176	72.998
<i>Ateles geoffroyi</i>	54037	2.291525676	28.07248694	73.251	74.868
<i>Ateles geoffroyi</i>	60660	0	19.50484988	87.538	70.492
<i>Ateles paniscus paniscus</i>	95498	2.291525676	17.6407591	84.895	69.019
<i>Ateles paniscus paniscus</i>	93244	4.090816978	15.18928674	60.158	78.756
<i>Ateles sp.</i>	127276	6.867260725	11.42118627	65.318	79.601
<i>Lagothrix lagothricha</i>	98050	0	18.07896561	81.235	67.145
<i>Lagothrix lagothricha</i>	98054	8.17123356	17.30508358	69.961	74.32
<i>Lagothrix lagothricha cana</i>	98056	0	21.77105411	73.983	75.75
<b>Species</b>	<b>FMNH #</b>	<b>ML wedging</b>	<b>PA wedging</b>	<b>PTF Angle</b>	<b>FHL Angle</b>
<i>Lagothrix lagothricha cana</i>	98055	7.462793998	17.49232453	59.167	75.029
<i>Lagothrix l. lagothricha</i>	70593	0	20.40794744	69.077	77.005
<i>Lagothrix l. lagothricha</i>	70597	2.490728534	13.68554683	68.103	85.825
<i>Lagothrix l. lugens</i>	70576	4.581220085	16.26020471	58.249	75.968
<i>Lagothrix l. poeppigii</i>	127404	2.603905345	13.68554683	65.28	75.616
<i>Lagothrix l. poeppigii</i>	60662	0	13.68554683	56.691	83.117

<i>Alouatta seniculus seniculus</i>	69591	11.42118627	30.7525025	63.701	74.32
<i>Alouatta seniculus seniculus</i>	18869	9.527283381	21.23931055	69.848	79.644
<i>Alouatta palliata palliata</i>	22395	12.68038349	23.12026159	57.124	70.159
<i>Alouatta palliata palliata</i>	57119	0	20.40794744	63.269	74.592
<i>Alouatta seniculus insulans</i>	61857	0	22.14040516	58.769	82.994
<i>Alouatta seniculus insulans</i>	61855	7.15266875	25.05761542	66.306	73.53
<i>Alouatta seniculus</i>	93248	4.771888061	13.30885009	64.932	75.041
<i>Alouatta sp.</i>	127401	3.182280542	13.57794915	60.4	73.992
<i>Chiropotes satanas c.</i>	93522	7.15266875	17.94525323	73.153	74.362
<i>Chiropotes satanas c.</i>	95512	7.15266875	17.06153122	76.947	80.887
<i>Chiropotes satanas c.</i>	95519	13.41967362	12.01801191	69.271	77.172
<i>Chiropotes satanas c.</i>	93255	9.527283381	14.2500327	64.354	76.943
<i>Chiropotes satanas c.</i>	95518	6.35966024	12.01801191	78.795	73.027
<i>Pithecia monachus milleri</i>	70635	5.205124405	13.41967362	66.903	70.536
<i>Pithecia monachus milleri</i>	70638	10.71165009	14.99171528	62.077	68.484
<i>Pithecia monachus milleri</i>	70641	7.15266875	14.99171528	73.896	73.235
<i>Pithecia monachus monachus</i>	127796	15.18928674	14.99171528	73.758	75.834
<i>Pithecia pithecia pithecia</i>	95510	11.42118627	13.41967362	64.77	79.293
<i>Pithecia pithecia pithecia</i>	46176	12.23100713	12.68038349	66.863	68.798
<i>Papio anubis</i>	18868	3.471409178	16.91005535	59.933	73.648
<i>Papio anubis</i>	127998	7.52806973	16.65130066	65.843	70.785
<i>Papio anubis</i>	134614	12.23100713	8.664627966	58.505	71.869
<i>Papio cynocephalus</i>	13263	13.16388931	19.63860128	58.398	72.996
<i>Papio leucophaeus</i>	99426	4.521003822	14.2500327	54.209	71.293
<i>Pongo pygmaeus</i>	57231	9.527283381	2.291525676	46.834	60.633
<i>Pongo pygmaeus</i>	53203	1.685048521	15.07889028	49.159	67.27
<i>Pongo pygmaeus</i>	153745	0	1.848090706	50.373	67.475
<i>Pongo pygmaeus</i>	153744	3.995759713	9.939481456	48.825	66.493
<i>Pongo pygmaeus</i>	153732	7.757049006	1.818760898	51.211	60.901
<i>Pongo pygmaeus</i>	35533	5.452621988	18.13300548	48.979	62.382
<i>Pongo pygmaeus</i>	44724	2.603905345	9.939481456	36.611	67.8
<i>Pongo pygmaeus</i>	153717	0	10.4942778	47.482	56.386
<i>Pongo pygmaeus</i>	91723	3.755754895	2.046060377	59.202	66.551
<i>Pan troglodytes</i>	137079	0	8.028351391	62.154	71.944
<i>Pan troglodytes</i>	127419	7.416856314	2.912717269	54.372	66.741
<i>Pan troglodytes</i>	51319	0	6.789847084	53.532	74.194

Species	MCZ #	T. depth	Geometric Mean
<i>Papio hamadryas</i>	5008	1.622	15.1925121
<i>Papio doguera</i>	10748	1.081	11.71108677
<i>Papio doguera furax</i>	21161	1.622	15.94749603
<i>Papio doguera furax</i>	21160	1.719	16.01821837
<i>Papio doguera neumanni</i>	15378	1.094	16.04158564
<i>Macaca nemestrina</i>	35670	1.762	11.84060207
<i>Macaca n. nemestrina</i>	35631	1.184	9.980568435
<i>Macaca maurus</i>	34462	1.216	11.07804185
<i>Macaca mullata</i>	61554	1.447	9.733944225
<i>Macaca mullata</i>	61553	1.351	11.21780652
<i>Macaca mullata</i>	61414	1.757	11.42001051

<i>Macaca mullata</i>	1991	1.486	11.94493463
<i>Macaca fascicularis f.</i>	37406	1.351	8.941169499
<i>Macaca fascicularis f.</i>	37414	1.184	9.062846033
<i>Macaca fascicularis f.</i>	35729	0.946	8.903553311
<i>Macaca fascicularis f.</i>	35731	0.946	8.956475408
<i>Macaca fascicularis f.</i>	35681	1.216	8.681728442
<i>Macaca fascicularis f.</i>	35677	0.789	7.820200727
<i>Macaca fascicularis f.</i>	35673	1.06	9.439038851
<i>Macaca fascicularis f.</i>	35656	1.316	8.453776566
<i>Macaca fascicularis f.</i>	35629	1.316	8.090257888
<i>Macaca fascicularis f.</i>	35611	1.486	9.331073797
<i>Macaca fascicularis f.</i>	35608	1.453	8.619553497
<i>Trachypithecus cristata u.</i>	37396	1.216	10.20089589
<i>Trachypithecus cristata u.</i>	37399	1.25	8.965161749
<i>Trachypithecus cristata u.</i>	37665	1.089	10.1198289
<i>Trachypithecus cristata u.</i>	37671	1.216	9.266832318
<i>Trachypithecus cristata u.</i>	37675	0.946	10.06000463
<i>Trachypithecus cristata u.</i>	35685	1.25	10.18303796
<i>Trachypithecus cristata u.</i>	35672	1.081	9.577750733
<i>Nasalis larvatus</i>	37328	1.622	15.58621285
<i>Nasalis larvatus</i>	37327	1.991	15.0484316
<i>Nasalis larvatus</i>	37330	2.166	15.76570927
<i>Nasalis larvatus</i>	37325	1.761	14.72451731
<i>Nasalis larvatus</i>	107099	1.895	15.68205402
<i>Nasalis larvatus</i>	37326	1.667	13.2011667
<i>Nasalis larvatus</i>	41563	1.897	15.20970034
<i>Nasalis larvatus</i>	41557	1.84	15.6280043
<i>Gorilla gorilla beringia</i>	23182	0.001	35.05743863
<i>Gorilla gorilla gorilla</i>	29048	1.739	33.41703545
<i>Gorilla gorilla gorilla</i>	23160	2.115	34.92835172
<i>Gorilla gorilla gorilla</i>	20039	2.185	36.46490693
<i>Gorilla gorilla gorilla</i>	20043	0.001	26.22625541
<i>Gorilla gorilla gorilla</i>	29049	2.5	36.20846866
<i>Gorilla gorilla gorilla</i>	57482	0.001	33.42976333
<i>Gorilla gorilla gorilla</i>	20038	1.739	33.19560626
<i>Gorilla gorilla gorilla</i>	37264	1.304	27.25427298
<b>Species</b>	<b>MCZ #</b>	<b>T. depth</b>	<b>Geometric Mean</b>
<i>Gorilla gorilla gorilla</i>	17684	0.962	25.71315972
<i>Pongo pygmaeus</i>	37362	2.692	27.5866631
<i>Pongo pygmaeus</i>	50960	2.075	23.85812186
<i>Pan trolodyte</i>	15312	1.154	23.51500998
<i>Pan trolodyte</i>	23183	1.481	23.06072318
<i>Pan trolodyte</i>	26849	1.207	22.36884533
<i>Pan trolodyte</i>	20041	1.048	23.42469637
<i>Pan trolodyte</i>	26847	1.36	22.47495822
<i>Pan trolodyte</i>	19187	0.001	22.98418275
<i>Pan trolodyte</i>	48686	1.111	23.63634931
<i>Hylobates lar lar</i>	41545	0.667	10.68146579
<i>Hylobates lar lar</i>	41492	0.541	9.723083462
<i>Hylobates lar lar</i>	41501	0.676	9.318933947

<i>Hylobates lar lar</i>	41505	0.001	10.41652688
<i>Hylobates lar lar</i>	41534	0.541	10.2677992
<i>Hylobates lar lar</i>	41512	1.351	9.542666218
<i>Hylobates lar lar</i>	41495	0.541	10.38779136
<i>Hylobates lar lar</i>	41529	0.789	9.760871023
<b>Species</b>	<b>FMNH #</b>	<b>T. depth</b>	<b>Geometric Mean</b>
<i>Cebus apella</i>	60751	0.286	9.615935214
<i>Cebus apella</i>	95471	0.208	9.205796074
<i>Cebus apella</i>	95474	0.311	9.324605111
<i>Cebus apella</i>	95470	0.319	8.903553311
<i>Cebus apella</i>	95336	0.278	8.695972507
<i>Cebus apella</i>	93261	0.286	8.879904887
<i>Cebus apella</i>	95473	0.571	9.501730829
<i>Cebus capucinus capucinus</i>	69650	0.439	9.486832981
<i>Cebus capucinus capucinus</i>	68843	0.001	9.225918152
<i>Cebus capucinus capucinus</i>	68841	0.393	9.486832981
<i>Cebus capucinus capucinus</i>	68837	0.001	9.056563293
<i>Ateles belzebuth belzebuth</i>	121215	1.528	13.58943278
<i>Ateles fusciceps robustus</i>	68820	1.571	13.19286612
<i>Ateles fusciceps robustus</i>	68811	1	12.55700881
<i>Ateles fusciceps robustus</i>	68823	1.428	14.85799619
<i>Ateles fusciceps robustus</i>	68810	0.571	12.70247512
<i>Ateles geoffroyi</i>	49336	1.429	12.34595162
<i>Ateles geoffroyi</i>	54037	1.029	14.77731213
<i>Ateles geoffroyi</i>	60660	0.694	12.85490864
<i>Ateles paniscus paniscus</i>	95498	0.454	13.83330265
<i>Ateles paniscus paniscus</i>	93244	0.909	13.53894486
<i>Ateles sp.</i>	127276	0.75	12.73773164
<i>Lagothrix lagothricha</i>	98050	0.571	10.44008682
<i>Lagothrix lagothricha</i>	98054	0.588	10.60529202
<i>Lagothrix lagothricha cana</i>	98056	0.588	11.43298683
<b>Species</b>	<b>FMNH #</b>	<b>T. depth</b>	<b>Geometric Mean</b>
<i>Lagothrix lagothricha cana</i>	98055	0.294	11.96206003
<i>Lagothrix l. lagothricha</i>	70593	0.452	11.10617267
<i>Lagothrix l. lagothricha</i>	70597	0.417	11.50983983
<i>Lagothrix l. lugens</i>	70576	0.714	11.79234242
<i>Lagothrix l. poeppigii</i>	127404	0.278	11.78614408
<i>Lagothrix l. poeppigii</i>	60662	0.833	11.39297353
<i>Alouatta seniculus seniculus</i>	69591	0.566	9.091197054
<i>Alouatta seniculus seniculus</i>	18869	0.001	10.16802976
<i>Alouatta palliata palliata</i>	22395	0.416	9.013344776
<i>Alouatta palliata palliata</i>	57119	0.001	9.960706509
<i>Alouatta seniculus insulans</i>	61857	0.278	10.0731925
<i>Alouatta seniculus insulans</i>	61855	0.452	7.977443845
<i>Alouatta seniculus</i>	93248	0.001	12.09775727
<i>Alouatta sp.</i>	127401	0.895	9.274950445
<i>Chiropotes satanas c.</i>	93522	0.294	8.263682636
<i>Chiropotes satanas c.</i>	95512	0.294	8.263682636
<i>Chiropotes satanas c.</i>	95519	0.589	8.090257888

<i>Chiropotes satanas c.</i>	93255	0.417	8.842356879
<i>Chiropotes satanas c.</i>	95518	0.329	8.397377903
<i>Pithecia monachus milleri</i>	70635	0.286	7.667317251
<i>Pithecia monachus milleri</i>	70638	0.452	8.030103099
<i>Pithecia monachus milleri</i>	70641	0.429	7.621991222
<i>Pithecia monachus monachus</i>	127796	0.571	8.429490832
<i>Pithecia pithecia pithecia</i>	95510	0.286	7.181586721
<i>Pithecia pithecia pithecia</i>	46176	0.429	7.061324976
<i>Papio anubis</i>	18868	1.324	14.85799619
<i>Papio anubis</i>	127998	1.771	17.65698574
<i>Papio anubis</i>	134614	1.436	11.89996037
<i>Papio cynocephalus</i>	13263	1.72	19.21879158
<i>Papio leucophaeus</i>	99426	1.72	15.67508087
<i>Pongo pygmaeus</i>	57231	2.321	24.04793158
<i>Pongo pygmaeus</i>	53203	1.589	15.57894486
<i>Pongo pygmaeus</i>	153745	2.143	26.98066053
<i>Pongo pygmaeus</i>	153744	1.429	21.45816633
<i>Pongo pygmaeus</i>	153732	2.545	29.54212372
<i>Pongo pygmaeus</i>	35533	2.281	20.39663786
<i>Pongo pygmaeus</i>	44724	2	19.93799348
<i>Pongo pygmaeus</i>	153717	2.632	24.01742576
<i>Pongo pygmaeus</i>	91723	2.679	27.48863232
<i>Pan troglodytes</i>	137079	2.414	25.11340206
<i>Pan troglodytes</i>	127419	1.429	26.2703335
<i>Pan troglodytes</i>	51319	1.667	26.08415718

<b>Extinct species</b>		<b>ML wedging</b>	<b>PA wedging</b>	<b>PTF Angle</b>	<b>FHL Angle</b>
<i>Proconsul major</i>	KNM-SO 390, 389	15.88694362	13.72738383	52.887	74.084
<i>Proconsul nyanzae</i>	KNM-RU 1745	12.01801191	10.28552912	n/a	71.618
<i>Proconsul nyanzae</i>	KNM-MW 13142	0	13.68554683	55.632	69.445
<i>Afropithecus turkanensis</i>	KNM-WK 18120	1.469042069	17.94525323	n/a	71.804
<i>Sivapithecus parvada</i>	GSP 17606	n/a	n/a	54.88	n/a
<i>Sivapithecus parvada</i>	GSP 17152	n/a	n/a	46.111	n/a
<i>Paracolobus chemeroni</i>	KNM-BC 3	6.025575008	16.80674218	58.419	65.893
<i>Paracolobus mutira</i>	KNM-WK 16827	0	22.61986495	57.07	69.236

<b>Extinct species</b>		<b>T. depth</b>	<b>Geometric Mean</b>
<i>Proconsul major</i>	KNM-SO 390, 389	2.179	21.24257569
<i>Proconsul nyanzae</i>	KNM-RU 1745	2.462	20.10221375
<i>Proconsul nyanzae</i>	KNM-MW 13142	2.069	21.35323218
<i>Afropithecus turkanensis</i>	KNM-WK 18120	2.838	15.60368049
<i>Sivapithecus parvada</i>	GSP 17606	n/a	n/a
<i>Sivapithecus parvada</i>	GSP 17152	n/a	n/a
<i>Paracolobus chemeroni</i>	KNM-BC 3	2.037	13.65588676
<i>Paracolobus mutira</i>	KNM-WK 16827	2.308	18.61403564

## List of References

- Aiello, L.; C. Dean. 1990. Human Evolutionary Anatomy. London: Academic Press.
- Andrews, P.; D.R. Begun; M. Zylstra. 1997. Interrelationships between Functional Morphology and Paleoenvironments in Miocene Hominoids. In: Begun, D.; Ward, C.V.; Rose, M.D. (eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press, 29-58.
- Andrews, P.; C.P. Groves. 1976. Gibbons and brachiation. *Gibbon and Siamang* **4**: 167-218.
- Andrews, P.; J.A.H. Van Couvering. 1975. Paleoenvironments in the east African Miocene. *Contributions to Primatology* **5**: 62-103.
- Ashton, E.H.; C.E. Oxnard. 1964a. Locomotor patterns in primates. *Proc. Zool. Soc. London* **142**: 1-28.
- Ashton, E.H.; C.E. Oxnard. 1964b. Functional adaptations in the primate shoulder girdle. *Proc. Zool. Soc. London* **142**: 49-66.
- Avis, V. 1962. Brachiation: the crucial issue for man's ancestry. *Southwestern Journal of Anthropology* **18**: 119-148.
- Bennett, E. L.; A. C. Sebastian. 1988. Social Organization and Ecology of Proboscis Monkeys (*Nasalis larvatus*) in Mixed Coastal Forest in Sarawak. *International Journal of Primatology* **9**: 233-255.
- Bernor, R.L. 1983. Geochronology and Zoogeographic Relationships of Miocene Hominoidea. In: R.L. Ciochon and R.S. Corruccini (eds.), New Interpretations of Ape and Human Ancestry, 21-66. New York: Plenum Press.
- Birchette, M. 1982. The Postcranial Skeleton of *Paracolobus chemeroni*. Ph.D. dissertation, Harvard University.
- Blue, K.T.; M.L. McCrossin; B.R. Benefit. 2006. Terrestriality in a Middle Miocene Context: *Victoriapithecus* from Maboko, Kenya. In: H. Ishida; R. Tuttle; M. Pickford; N. Ogihara; M. Nakatsukasa (eds.), Human Origins and Environmental Backgrounds, 45-58. New York: Springer.
- Caldecott, J.O. 1986. An Ecological and Behavioral Study of the Pig-Tailed Macaque. *Contributions to Primatology* **21**: 1-259.
- Cant, J.G.H. 1988. Positional behavior of long-tailed macaques (*Macaca fascicularis*) in northern Sumatra. *American Journal of Physical Anthropology* **76**: 29-37.

- Cant, J.G.H.; D. Youlatos; M.D. Rose. 2001. Locomotor behavior of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador: general patterns and nonsuspensory modes. *Journal of Human Evolution* **41**: 141-166.
- Carpenter, C.R. 1940. A Field Study in Siam of the Behavior and Social Relations of the Gibbon (*Hylobates lar*). *Comparative Psychology Monographs* **16**: 1-212.
- Cartmill, M.; K. Milton. 1977. The lorisiform wrist joint and the evolution of “brachiating” adaptations in the Hominoidea. *American Journal of Physical Anthropology* **47**: 249-272.
- Clark, W. E. Le Gros; L.S.B. Leakey. 1951. The Miocene Hominoidea of Africa. Fossil mammals of Africa, **1**: 1-117. London: British Museum (Natural History).
- Cohen, J. 1988. Statistical power analysis for the behavioral sciences (2nd ed.) Hillsdale, NJ: Lawrence Erlbaum Associates.
- Dagosto, M. 1986. The joints of the tarsus in the strepsirhine primates: functional, adaptive, and evolutionary implications. Ph.D. Dissertation, City University of New York.
- Delson, E. 1973. Fossil colobine monkeys of the circum-Mediterranean region and the evolutionary history of the Cercopithecidae (Primates Mammalia). Ph.D. Dissertation, Columbia University.
- Delson, E. 1975. Evolutionary history of the Cercopithecidae. *Contributions to Primatology*, **5**: 167-217.
- Delson, E.C. Terranova, et al. 2000. Body mass in Cercopithecidae (Primates, Mammalia): estimation and scaling in extinct and extant taxa. *Anthropologica Papers of the American Museum of Natural History* **83**: 1-159.
- Digiovanni, B.F.; P.V. Scoles; B.M. Latimer. 1989. Anterior Extension of the Thoracic Vertebral Bodies in Scheuermann’s Kyphosis, An Anatomic Study. *Spine* **14**: 712-716.
- Doran, D.M. 1993. Comparative Locomotor Behavior of Chimpanzees and Bonobos: The Influence of Morphology on Locomotion. *American Journal of Physical Anthropology* **91**: 83-98.
- Drake, R.; W. Vogl; A.W.M. Mitchell. 2005. Gray’s Anatomy for Students. Philadelphia: Elsevier, Inc.
- Dunbar, D.C. 1989. Locomotor behavior in rhesus macaques (*Macaca mullata*) on Cayo Santiago. *P R Health Sci J*, **8**: 79-85.

- Erikson, G.E. 1963. Brachiation in New World Monkeys and in Anthropoid Apes. *Symp. Zool. Soc. London*.
- Fleagle, J.G. 1976a. Locomotion and posture of the Malayan siamang and implications for hominid evolution. *Folia Primatologica* **26**: 245-269.
- Fleagle, J.G. 1976b. Locomotor Behavior and Skeletal Anatomy of Sympatric Malaysian Leaf-Monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Yearbook of Physical Anthropology* **20**: 440-453.
- Fleagle, J.G.; R.A. Mittermeier. 1980. Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *American Journal of Physical Anthropology* **52**: 301-314.
- Fleagle, J.G.; R.A. Mittermeier; A.L. Skopec. 1981. Differential habitat use by *Cebus apella* and *Saimiri sciureus* in Central Surinam. *Primates* **22**: 361-367.
- Fleagle, J.G.; D.J. Meldrum. 1988. Locomotor behavior and skeletal morphology of two sympatric pitheciine monkeys, *Pithecia pithecia* and *Chiropotes satanas*. *American Journal of Primatology*, **16**: 227-249.
- Ford, S.M. 1980. A systematic revision of the Platyrrhini based on selected features of the postcranium. Ph.D. Dissertation, University of Pittsburgh.
- Ford, S.M. 1988. Postcranial adaptations of the earliest platyrrhine. *Journal of Human Evolution* **17**: 155-192.
- Frost, H.M. 1979. A Chondral Modeling Theory. *Calc. Tissue International* **28**: 181-200.
- Frost, H.M. 1990. Skeletal Structural Adaptations to Mechanical Usage (SATMU): 3. The Hyaline Cartilage Modeling Problem. *The Anatomic Record* **226**: 423-432.
- Gebo, D. L. 1986. The Anatomy of the Prosimian Foot and Its Application to the Primate Fossil Record. Ph.D. dissertation, Duke University.
- Gebo, D. L. 1987. The functional anatomy of the tarsier foot. *American Journal of Physical Anthropology* **57**: 9-31.
- Gebo, D. L. 1992. Plantigrady and foot adaptation in African apes: implications for hominid evolution. *American Journal of Physical Anthropology* **89**: 29-58.
- Gebo, D. L. 1992b. Locomotor and postural behavior in *Alouatta palliata* and *Cebus capucinus*. *American Journal of Primatology*, **26**: 277-290.

- Gebo, D. L. 1993. Functional Morphology of the Foot in Primates. In: Gebo, D.L. (ed.) Postcranial Adaptation in Nonhuman Primates. DeKalb, IL: Northern Illinois University Press, 175-198.
- Gebo, D. L.; E. L. Simons. 1987. Morphology and Locomotor Adaptations of the Foot in Early Oligocene Anthropoids. *American Journal of Physical Anthropology* **74**: 83-101.
- Grand, T. I. 1968. The Functional Anatomy of the Lower Limb of the Howler Monkey (*Alouatta caraya*). *American Journal of Physical Anthropology* **28**: 163-182.
- Gray, H. 1901. Gray's Anatomy, 15<sup>th</sup> Edition. New York: Barnes & Noble Books.
- Hamrick, M.W. 1996. Articular Size and Curvature as Determinants of Carpal Joint Mobility and Stability in Strepsirrhine Primates. *Journal of Morphology* **230**: 113-127.
- Hamrick, M.W. 1999. A Chondral Modeling Theory Revisited. *Journal of Theoretical Biology* **201**: 201-208.
- Harris, J., F. Brown, et al. 1988. Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. Contributions in Science 399.
- Harrison, T. 2002. Late Oligocene to middle Miocene catarrhines from Afro-Arabia. The Primate Fossil Record. Cambridge, United Kingdom: Cambridge University Press, pg. 311-338.
- Hill, W.C.O. 1970. Primates: comparative anatomy and taxonomy. Vol. VIII Cynopithecinae: Papio, Mandrillus, Theropithecus. New York: Interscience Pub., Inc.
- Hunt, K.D. 1992. Positional Behavior of *Pan troglodytes* in the Mahale Mountains and Gombe Stream National Parks, Tanzania. *American Journal of Physical Anthropology* **87**: 83-106.
- Hunt, K.D.; J.G.H. Cant; D.L. Gebo; M.D. Rose; S.E. Walker; D. Youlatos. 1996. Standardized descriptions of primate locomotor and postural modes. *Primates* **37**: 363-387.
- Jablonski, N.G. 2002. Late Neogene Cercopithecoids. The Primate Fossil Record. Cambridge, United Kingdom: Cambridge University Press, pg. 255-300.

- Jenkins, F.A.; J.G. Fleagle. 1975. Knuckle-walking and the functional anatomy of the wrists in living apes. Primate functional morphology and evolution. The Hague: Mouton.
- Jungers, W.L. 1985. Body size and scaling of limb proportions in primates. In (W.L. Jungers, ed.) Size and Scaling in Primate Biology. New York: Plenum Press, 345-381.
- Jungers, W. L.; A. B. Falsetti; C. E. Wall. 1995. Shape, Relative Size, and Size-Adjustments in Morphometrics. *Yearbook of Physical Anthropology* **38**: 137-161.
- Kapandji, I.A. 1987. The Physiology of the Joints, Volume Two. New York: Churchill Livingstone.
- Kawabe, M.; T. Mano. 1972. Ecology and Behavior of the Wild Proboscis Monkey, *Nasalis larvatus* (Wurmb), in Sabah, Malaysia. *Primates* **13**: 213-228.
- Kay, R.F. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In (P.S Rodman & J.G.H. Cant, eds) Adaptations for Foraging in Nonhuman Primates. New York: Columbia University Press, 21-53.
- Keith, A. 1923. Man's posture: Its evolution and disorders. *British Medical Journal* **1**: 669-672.
- Kelley, J. 1997. Paleobiological and Phylogenetic Significance of Life History in Miocene Hominoids. In: Begun, D.; Ward, C.V.; Rose, M.D. (eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press, pg. 173-208.
- Khan, I.A.; J.S. Bridge; J. Kappelman; R. Wilson. 1997. Evolution of Miocene fluvial environments, eastern Potwar plateau, northern Pakistan. *Sedimentology* **44**: 221-251.
- Kortlandt, A. 1974. Ecology and paleoecology of ape locomotion. *Symp. 5<sup>th</sup> Cong. International Primat. Soc.* 361-364.
- Lachenbruch, P.A.; M. Goldstein. 1979. Discriminant Analysis. *Biometrics* **35**: 69-85.
- Langdon, J. 1986. Functional Morphology of the Miocene Hominoid Foot. *Contributions to Primatology* **22**: 1-225.
- Latimer, B.; J. Ohman; C. O. Lovejoy. 1987. Talocrural Joint in African Hominoids: Implications for *Australopithecus afarensis*. *American Journal of Physical Anthropology* **74**: 155-175.

- Latimer, B.; C. O. Lovejoy. 1989. The Calcaneus of *Australopithecus afarensis* and Its Implications for the Evolution of Bipedality. *American Journal of Physical Anthropology* **78**: 369-386.
- Leakey, M.; A. Walker. 1997. *Afropithecus*: Function and Phylogeny. In: Begun, D.; Ward, C.V.; Rose, M.D. (eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press, pg. 225-240.
- Leakey, M.; C.V. Ward. 1995. New skeletons of large-bodied Plio-Pleistocene colobines from northern Kenya. *American Journal of Physical Anthropology Supplement* **20**.
- Leakey, R. 1969. New Cercopithecidae from the Chemeron Beds of Lake Baringo, Kenya. Fossil Vertebrates of Africa. L.S.B. Leakey. New York, Academic Press **1**: 53-69.
- Leakey, R.; M. Leakey. 1986. A new Miocene hominoid from Kenya. *Nature* **324**: 143-146.
- Leakey, R.; M. Leakey; A.C. Walker. 1988. Morphology of *Afropithecus turkanensis* from Kenya. *American Journal of Physical Anthropology* **76**: 289-308.
- Lewis, O.J. 1971a. Brachiation and the early evolution of the hominoidea. *Nature* **230**: 577-578.
- Lewis, O.J. 1971b. The contrasting morphology found in the wrist joints of semibrachiating monkeys and brachiating apes. *Folia primatologica* **16**: 248-256.
- Lewis, O.J. 1972. The evolution of the hallucial tarsometatarsal joint in the Anthropoidea. *American Journal of Physical Anthropology* **37**: 13-34.
- Lewis, O.J. 1980. The joints of the evolving foot. Part I. The ankle joint. *Journal of Anatomy* **130**: 527-543.
- Madar, S.; M. Rose; J. Kelley; L. MacLatchy; D. Pilbeam. 2002. New *Sivapithecus* postcranial specimens from the Siwaliks of Pakistan. *Journal of Human Evolution* **42**: 705-752.
- Meldrum, D.J. 1991. Kinematics of the cercopithecine foot on arboreal and terrestrial substrates with implications for the interpretation of hominid terrestrial adaptations. *American Journal of Physical Anthropology* **83**: 403-418.
- Mendel, Frank. 1976. Postural and Locomotor Behavior of *Alouatta palliata* on Various Substrates. *Folia Primatologica* **26**: 36-53.

- Mittermeier, R. A.; J. G. Fleagle. 1976. The Locomotor and Postural Repertoires of *Ateles geoffroyi* and *Colobus guereza*, and a Reevaluation of the Locomotor Category Semibrachiation. *American Journal of Physical Anthropology* **45**: 235-256.
- Mittermeier, R. A. 1978. Locomotion and Posture in *Ateles geoffroyi* and *Ateles paniscus*. *Folia Primatologica* **30**: 161-193.
- Morton, D. 1922. Evolution of the human foot I. *American Journal of Physical Anthropology* **4**: 305-336.
- Morton, D. 1924. Evolution of the Human Foot II. *American Journal of Physical Anthropology* **7**: 2-46.
- Napier, J.R. 1963. Brachiation and brachiators. *Symp. Zool. Soc. London* **10**: 183-195.
- Napier, J.R. 1967. Evolutionary aspects of primate locomotion. *American Journal of Physical Anthropology* **27**: 333-341.
- Napier, J.R. 1976. Primate locomotion. *Oxford Biology Readers* **41**.
- Napier, J.R.; P.H. Napier 1967. A Handbook of Living Primates: Morphology, Ecology, and Behavior of Nonhuman Primates. London: Academic Press.
- Oxnard, C.E. 1963. Locomotor adaptations in the primate forelimb. *Symp. Zool. Soc. London* **10**: 165-182.
- Palastanga, N.; D. Field; R. Soames. 1998. Anatomy & Human Movement: Structure & Function. Third Edition. Oxford: Butterworth Heinemann.
- Pilbeam, D.; M.D. Rose; C. Badgley; B. Lipschutz. 1980. Miocene hominoids from Pakistan. *Postilla* **181**: 1-94.
- Pilbeam, D. 1997. Research on Miocene Hominoids and Hominid Origins: The Last Three Decades. In: Begun, D.; Ward, C.V.; Rose, M.D. (eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press, pg. 13-28.
- Prost, J.H. 1974. Postural variety in baboons and humans. *Symp. 5<sup>th</sup> Cong. Int'l Primat. Soc.* 315-330.
- Ramos-Fernandez, G.; JL Mateos; O Miramontes; G Cocho; H Larralde; B Ayala-Orozco. 2004. Levy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behavioral Ecology and Sociobiology*, **55**: 223-230.

- Rafferty, K.L.; A. Walker; C.B. Ruff; M.D. Rose; P.J. Andrews. 1995. Postcranial estimates of body weights in *Proconsul*, with a note on a distal tibia of *Proconsul major* from Napak, Uganda. *American Journal of Physical Anthropology* **97**: 391-402.
- Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, □Maryland, USA, <http://rsb.info.nih.gov/ij/>, 1997-2006.
- Remis, M. 1995. Affects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. *American Journal of Physical Anthropology* **97**: 413-433.
- Ripley, S. 1967. The leaping of langurs: a problem in the study of locomotor adaptation. *American Journal of Physical Anthropology* **26**: 149-170.
- Rodman, P. 1979. Skeletal Differentiation of *Macaca fascicularis* and *Macaca nemestrina* in Relation to Arboreal and Terrestrial Quadrupedalism. *American Journal of Physical Anthropology* **51**: 51-62.
- Rodman, P. 1991. Structural Differentiation of Microhabitats of Sympatric *Macaca fascicularis* and *M. nemestrina* in East Kalimantan, Indonesia. *International Journal of Primatology* **12**: 357-375.
- Rose, M. 1973. Quadrupedalism in primates. *Primates* **14**: 337-357.
- Rose, M. 1976. Bipedal behavior of olive baboons (*Papio anubis*) and its relevance to an understanding of the evolution of human bipedalism. *American Journal of Physical Anthropology* **44**: 247-262.
- Rose, M. 1977. Positional behavior of olive baboons (*Papio anubis*) and its relationship to maintenance and social activities. *Primates* **18**: 59-116.
- Rose, M. 1983. Miocene hominoid postcranial morphology: Monkey-like, ape-like, neither, or both? In: R.L. Ciochon and R.S. Corruccini (eds.), New Interpretations of Ape and Human Ancestry, 405-417. New York: Plenum Press.
- Rose, M. 1986a. Further hominoid postcranial specimens from the late Miocene Nagri Formation of Pakistan. *Journal of Human Evolution* **15**: 333-367.
- Rose, M. 1986b. Functional anatomy of the orang-utan cheiridia. In: J.H. Schwarz (ed.). Biology of the Orang-Utan. New York: Oxford University Press.
- Rose, M. 1993. Locomotor Anatomy of Miocene Hominoids. Postcranial Adaptation in Nonhuman Primates. DeKalb, IL: Northern Illinois University Press, pg. 252-272.

- Rose, M. 1994. Quadrupedalism in some Miocene catarrhines. *Journal of Human Evolution* **26**: 387-411.
- Ruff, C. B.; A. Walker; M. F. Teaford. 1989. Body mass, sexual dimorphism and femoral proportions of *Proconsul* from Rusinga and Mfangano Islands, Kenya. *Journal of Human Evolution* **18**: 515-536.
- Ruff, C.B.; W.W. Scott; A.Y.-C. Liu. 1991. Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *American Journal of Physical Anthropology* **86**: 397 – 413.
- Ruff, C.B. 2003. Long Bone Articular and Diaphyseal Structure in Old World Monkeys and Apes. II: Estimation of Body Mass. *American Journal of Physical Anthropology* **120**: 16-37.
- Sarmiento, E.E. 1983. The significance of the heel process in anthropoids. *International Journal of Primatology* **4**: 127-152.
- Schultz, A.H. 1963. Relations Between the Lengths of the Main Parts of the Foot Skeleon in Primates. *Folia primatologica* **1**: 150-171.
- Sigmon, B.A.; D. L. Farslow. 1986. The Primate Hindlimb. Systematics, Evolution, and Anatomy. New York: Alan R. Liss, Inc.
- Smith, R.J. 1993. Logarithmic transformation bias in allometry. *American Journal of Physical Anthropology* **90**: 215-228.
- Smith, R.J.; W.L. Jungers. 1997. Body mass in comparative primatology. *Journal of Human Evolution* **32**: 523-559.
- Sonntag, C.F. 1923. On the Anatomy, Physiology, and Pathology of the Chimpanzee. *Proc. Zool Soc (London)* **22**: 323-429.
- Strasser, E. 1988. Pedal evidence for the origin and diversification of cercopithecoid clades. *Journal of Human Evolution* **17**: 225-245.
- Strasser, E. 1993. Kasawanga *Proconsul* foot proportions. *American Journal of Physical Anthropology Supplement* **16**: 191.
- Sullivan, W.E. 1933. Chapter 5: Skeleton and Joints. The Anatomy of the Rhesus Monkey (*Macaca mulatta*). New York; Hafner Publishing Co.
- Susman, R.L. 1983. Evolution of the human foot: Evidence from Plio-Pleistocene hominids. *Foot and Ankle* **3**: 365-376.

- Susman, R.; J.T. Stern. 1979. Telemetered electromyography of flexor digitorum profundus and flexor digitorum superficialis in *Pan troglodytes* and implications for interpretation of the O.H. 7 hand. *American Journal of Physical Anthropology* **50**: 565-574.
- Szalay, F.S.; Dagosto M. 1988. Evolution of hallucial grasping in the Primates. *Journal of Human Evolution* **17**: 1-33.
- Temerin, L.A.; B.P. Wheatley; P.S. Rodman. 1984. Body size and foraging in primates. In (P.S. Rodman & J.G.H. Cant, eds) Adaptations for Foraging in Nonhuman Primates. New York: Columbia University Press, 217-248.
- Thorpe, K.S.; R.H. Crompton. 2006. Orangutan Positional Behavior and the Nature Arboreal Locomotion in Hominoidea. *American Journal of Physical Anthropology* **131**: 384-401.
- Thorpe, K.S.; R.L. Holder; R.H. Crompton. 2007. Origin of Human Bipedalism as an Adaptation for Locomotion on Flexible Branches. *Science* **316**: 1328-1331.
- Ting, N. 2001. The hip and thigh of *Paracolobus mutiwa* and *Paracolobus chemeroni*. MA thesis. University of Missouri, Columbia.
- Tuttle, R.H. 1967. Knuckle-walking and the Evolution of Hominoid Hands. *American Journal of Physical Anthropology* **26**: 171-206.
- Tuttle, R.H. 1969a. Knuckle-walking and the problem of human origins. *Science* **166**: 953-961.
- Tuttle, R.H. 1969b. Quantitative and functional studies of the hands of the anthropoidea I The Hominoidea. *Journal of Morphology* **129**: 309-364.
- Tuttle, R.H. 1970. Postural, propulsive, and prehensile capabilities in the cheiridia of chimpanzees and other great apes. *Chimpanzee* **2**: 167-253.
- Tuttle, R.H. 1972. Functional and Evolutionary Biology of Hylobatid Hands and Feet. In: Rumbaugh, Duane M. (ed.). Gibbon and Siamang, vol. 1. Karger: Basel, 136-206.
- Tuttle, R.H. 1975. Knuckle-walking and knuckle-walkers: a commentary on some recent perspectives on hominoid evolution. Primate functional morphology and evolution. The Hague: Mouton, 203-209.
- Tuttle, R.H. 1986. Apes of the World. Park Ridge, NJ: Noyes.

- Walker, A. 1997. *Proconsul*: Function and Phylogeny. In: Begun, D.; Ward, C.V.; Rose, M.D. (eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press, pg. 209-224.
- Walker, A.C.; M. Pickford. 1983. New Postcranial Fossils of *Proconsul*. In: R.L. Ciochon and R.S. Corruccini (eds.), New Interpretations of Ape and Human Ancestry, 325-352. New York: Plenum Press.
- Walker, S.E. 2005. Leaping behavior of *Pithecia Pithecia* and *Chiropotes satanas* in eastern Venezuela. *American Journal of Primatology* **66**: 369-387.
- Ward, C.V. 1991. Functional Anatomy of the Lower Back and Pelvis of the Miocene Hominoid *Proconsul nyanzae* from Mfangano Island, Kenya. Ph.D. Dissertation, Johns Hopkins University.
- Ward, C.V. 1993. Torso Morphology and Locomotion in *Proconsul nyanzae*. *American Journal of Physical Anthropology* **92**: 291-328.
- Ward, C.V. 1997. The Hominoid Trunk and Hindlimb. In: Begun, D.; Ward, C.V.; Rose, M.D. (eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press, pg. 101-130.
- Ward C.V. 1998. *Afropithecus*, *Proconsul* and the early hominoid postcranium. In: E. Strasser, J. Fleagle, A. Rosenberger, & H. M. McHenry, (eds.). Primate Locomotion: Recent Advances, Plenum Press, New York. pp. 337-352.
- Ward, C.V.; A. Walker; M.F. Teaford; I. Odhiambo. 1993. Partial Skeleton of *Proconsul nyanzae* from Mfangano Island, Kenya. *American Journal of Physical Anthropology* **90**: 77-111.
- Ward, S. 1997. The Taxonomy and Phylogenetic Relationships of *Sivapithecus* Revisited. In: Begun, D.; Ward, C.V.; Rose, M.D. (eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press, pg. 269-290.
- Weidenreich, F. 1923. Evolution of the human foot. *American Journal of Physical Anthropology* **26**: 473-487.
- Wells, J.P.; J.E. Turnquist. 2001. Ontogeny of Locomotion in Rhesus Macaques (*Macaca mulatta*): Postural and Locomotor Behavior and Habitat Use in a Free-Ranging Colony. *American Journal of Physical Anthropology* **115**: 80-94.

Wrangham, R.W. 1980. Bipedal locomotion as a feeding adaptation in gelada baboons, and its implications for hominoid evolution. *Journal of Human Evolution* **9**: 329-331.

Zar, J.H. 1999. Biostatistical Analysis. New Jersey: Prentice Hall.