Université de Montréal

Age and species related variation in the development of growth plates of the knee and implications for the locomotion of *Australopithecus afarensis*

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Résumé

Comprendre l'évolution de la bipédie est un élément essentiel à la recherche en paléoanthropologie, car ce comportement est le trait le plus important utilisé pour identifier les fossiles comme appartenant à la lignée des hominines. La topographie de la surface infradiaphysaire du fémur et du tibia pourrait donner un aperçu du comportement locomoteur des espèces fossiles, mais n'a pas été étudiée de façon approfondie. Ce trait reflète directement les différences dans la locomotion, puisque la surface change de topographie pour mieux résister aux charges encourues par les mouvements réguliers. Le plan infradiaphysaire du fémur chez les humain est relativement plat, tandis que la surface est plus irrégulière chez les grands singes.

Dans ce projet, les métaphyses du genou ont été étudiées d'une manière quantifiée afin de percevoir les différences entre espèces et mieux comprendre le développement ontogénique de ces traits. Les angles formés par les protrusions et les creux de ces surfaces ont été mesurés à partir de points de repère enregistrés en trois-dimensions sur les métaphyses du genou chez les humains, chimpanzés, gorilles, et orangs-outans, et chez trois fossiles *Australopithecus afarensis*, afin d'observer de l'effet de facteurs tel le stade de croissance et l'appartenance à une espèce sur la topographie des plaques de croissance du genou. Les angles d'obliquité du fémur et du tibia ont aussi été mesurés et analysés. Les résultats ont révélé que le stade développemental et l'appartenance à une espèce et, par association, le mode de locomotion, ont un effet significatif sur les métaphyses du genou. Il a également été constaté que les mesures *d'Australopithecus afarensis* chevauchent les valeurs trouvées chez les humains et chez les grands singes, ce qui suggère que cette espèce avait possiblement conservé une composante arboricole dans son comportement locomoteur habituel.

Mots-clés

Bipédie, genou, angle d'obliquité, plaque de croissance, métaphyses, biomécanique, *Australopithecus afarensis*

Abstract

Understanding the evolution of bipedality is a critical part of research in paleoanthropology, as it is the single-most important trait used to identify fossils as belonging to the hominin lineage. The topography of the infradiaphyseal plane could provide insight into the locomotor behaviour of fossil species, but has not been studied extensively. This trait directly reflects differences in locomotion, as the surface changes to resist loads incurred by regular movement. Humans have an infradiaphyseal plane that is relatively flat, while this feature is very convoluted in great apes.

This project studied this feature in the femur and tibia quantifiably to allow for statistical comparisons between species and to provide a better understanding of its ontogenic development. Three-dimensional landmarks were recorded from the metaphyses of the knee in humans, chimpanzees, gorillas, orang-utans, and three *Australopithecus afarensis* fossils. Using these landmarks, angles formed by the salient points of these planes were analyzed to confirm observations that development and species have a significant effect on the topography of growth plates of the knee. Carrying angles of the femur and tibia were also measured and analyzed. Results revealed that development and species, and by extension, mode of locomotion, have a significant effect on the overall metaphyses of the knee, especially on the sagittal plane. It was also found that *A. afarensis* have values that overlap human and great ape ranges, suggesting this species had probably retained an arboreal component in its regular locomotion.

Key words

Bipedality, knee, obliquity angle, growth plates, metaphysis, biomechanics, *Australopithecus afarensis*

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Chapter 1: Introduction

In paleoanthropology, fossils are key indicators of a particular species environment, physical activity, and even social behaviour. The shape of a skeletal element is genetically determined and best adapted to its habitual functions. Bone morphology can, in addition, also be plastic, especially during development. In particular, it is heavily influenced by its mechanical environment. Thus, many features of the skeleton directly reflect the regular activity for which it is used. One of the most significant features that is specific to the human lineage is bipedality. The anatomical traits that are associated with this behaviour are therefore helpful in determining if a new fossil belongs to this family or not. Since bone is shaped in part by its mechanical environment, bipedality leaves numerous indicators, particularly on the pelvis and lower limb bones. The purpose of this thesis is to examine the direct effects of locomotion on the knee joint and explore metrically the differences in morphology between humans, great apes, and hominids during ontogeny, or individual development.

1.1. Skeletal biology

Knowledge of bone composition and development is essential to understanding the relationship between mechanical factors and skeletal morphology. While inorganic calcium phosphate salts form the majority of bone, approximately forty percent of bone matrix is made of organic material – mostly collagen fibres (Standring 2005). This organic component of bone is what makes it a living tissue, one that can actively react and adapt to external factors during development as well as after maturation.

1.1.1. Ossification processes

1.1.1.1. Endochondral Ossification

The majority of the postcranial skeleton is formed through *endochondral ossification,* where cartilage models will define the initial shape and position of a skeletal element. Cartilaginous tissue is composed of young chondrocytes which divide and secrete an extra cellular matrix of collagen fibers as they do so. This tissue will be replaced by bone through an ordered sequence of events (Standring 2005). Variation in bone development depends on the type of skeletal element; long bones, such as the femur and tibia, have multiple centres of ossification. The centre of primary ossification is located in the centre of the shaft, where the ossification process is marked by the expansion in diameter of the diaphysis and its elongation at both ends of the shaft. The centres of secondary ossification are located at both ends of the shaft, where the process of fusion of the epiphyses to the diaphysis will begin when the bone approaches maturity (Standring 2005). All long bones have growth plates between the epiphysis and the diaphysis. These cartilaginous plates are of particular interest for this thesis. They are responsible for the longitudinal growth of long bones, and importantly, react to external loads in specific ways and can therefore alter the very formation and growth of bone. At a microscopic level, these epiphyseal plates can be divided into four zones. The activity at each zone will play a precise role in the axial growth of long bones until they reach maturity, when the epiphyses fuse to the diaphysis. The following is a brief summary of the different levels of the epiphyseal plate following Cormack (1987).

The **zone of resting cartilage** is closest to the bony tissue of the epiphysis. The chondrocytes at this level are not contributing actively to bone growth, as their principal function is to connect the other levels of the growth plate to the bony epiphysis. Capillaries pass through this zone and allow oxygen and nutrients to travel to the epiphysis, and at the same time they also nourish all other zones of the epiphyseal plate. The **zone of proliferating cartilage**, as the name suggests, is marked by very active chondrocytes that are constantly dividing to provide new chondrocytes to replace the ones that disappear on the diaphyseal side of the growth plate. As they multiply, they arrange themselves into columns in the **zone of maturing cartilage**, (also known as the zone of hypertrophying cartilage) where they increase in size and produce alkaline phosphatase, which is presumed to assist in the calcification of the extracellular matrix. The cartilage matrix becomes saturated with bone mineral in the **zone of calcifying cartilage or** the zone of provisional calcification. Capillaries enter this zone from the diaphysis and provide a vascularised environment thereby favouring the deposition of bone matrix on the calcified cartilage (Fig. 1.1.)

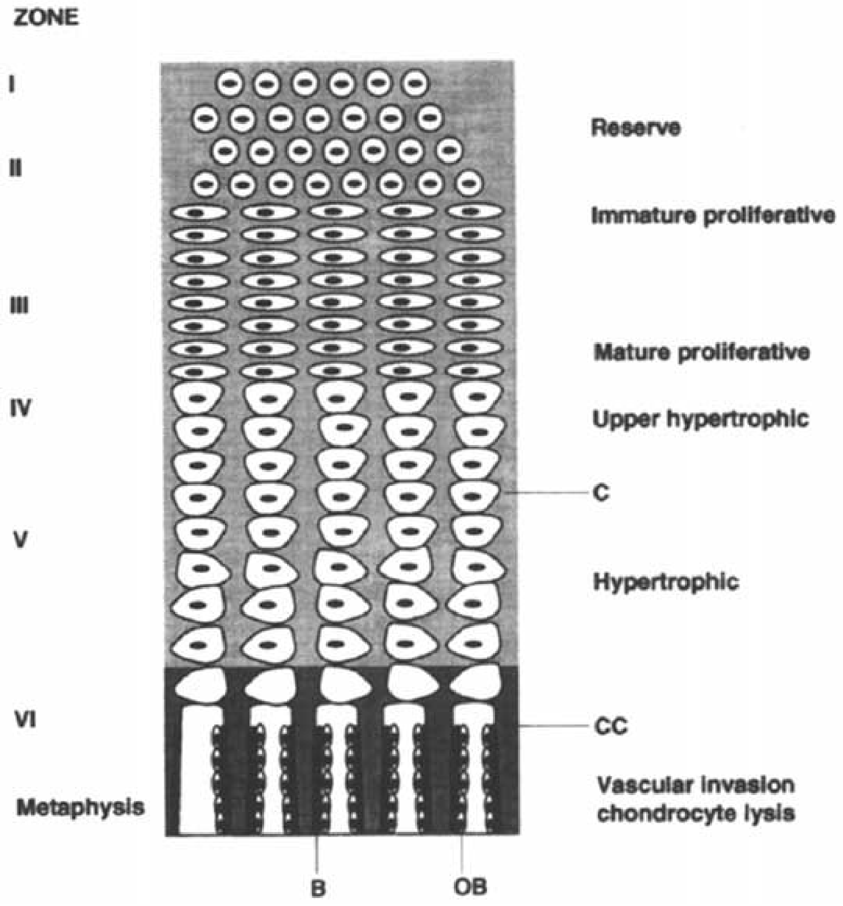

Figure 1.1.: Diagram of a longitudinal section through the epiphyseal growth plate. B = bone, OB = osteoblast, CC = calcified cartilage, C = cartilage matrix. From Waterlow (1994).

1.1.1.2. Intramembraneous Ossification

The other ossification process is known as intramembraneous ossification, and is not preceded by cartilage, but rather by membrane tissue, as the name suggests. Intramembraneous ossification starts (Gray (2000 [1918])) with a membrane composed of a matrix of fibers and granular cells which stands in place of the future bone, and will ultimately form the periosteum. The process begins with the formation of little bone spicules which radiate from a center of ossification. These “rays” consist of osteogenic fibers (precollagenous fibers formed by osteoblasts, cells responsible for bone formation), and granular corpuscles with an intervening ground substance. Calcareous granules are being deposited between the fibers and in the intervening matrix (Fig. 1.2.). The fibers calcify as they grow out on the periphery, and in turn give rise to new bone spicules, creating a network of bone containing blood vessels, connective tissue and osteoblasts. This bony trabecula thickens as more layers of bone are added upon it.

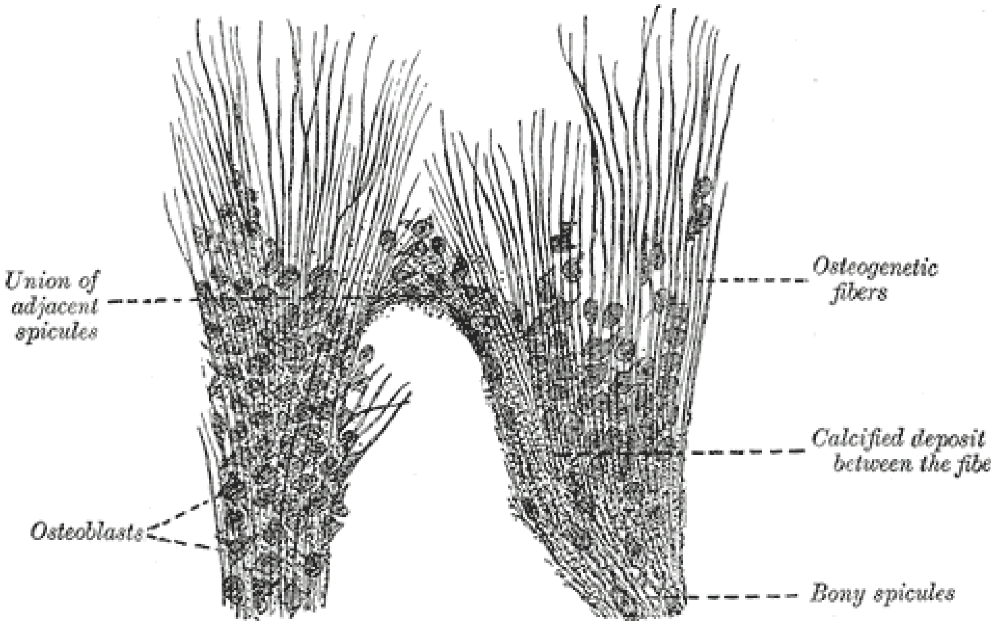

Figure 1.2.: Sketch showing the intramembraneous ossification process of the parietal bone in a fetal cat. From Gray (2000 [1918]).

After it has reached maturity, bone is maintained throughout an adult's life by a process of internal remodelling. Indeed, a cycle of bone resorption and bone formation prevents the bony tissue from weakening as some of the osteocytes die and microcracks form (Cormack 1987, p.305). A number of external factors, such as trauma and disease and mechanical loading, influence the formation of skeletal tissue during the modelling and remodelling cycles. The impact of mechanical stress on bone formation and properties will be explored next. The adaptability and resistance of bone to external factors, such as the regular exposure to mechanical loading, is dictated by its composition and by the process by which it develops (Carter 1987). The relationship between mechanical environment and skeletal morphology is bilateral, as the mechanical environment – movement and pressure – will influence the morphology of an element mostly as it develops and the shape of skeletal elements in turn dictates the range of movements that is possible and how much load they can resist.

1.2. The influence of the mechanical environment on bone modelling and remodelling

1.2.1. Initial research

The link between bone morphology and mechanical factors has been known since the 19th century, when German anatomist Julius Wolff suggested that bones will remodel to adapt to their mechanical function. Wolff's Law of Bone Remodelling states that that a bone's internal structure will alter according to mathematical rules to adapt to the external stresses to which it is exposed; similarly, secondary morphological alterations throughout an adult's life will follow these same rules. Therefore, according to this law, the precise shape of a skeletal element could be predicted depending on the mechanical loads that are applied to it (Wolff 1986).

Nineteenth century research on the relationship between bone remodelling and mechanical stress was also advanced by the development of Heuter and Volkmann's Law. These two German researchers have suggested that pressure influenced the cellular proliferation of the epiphyseal plate. This law states that compressive forces decreased plate growth while tensile forces would increase it. In other words, an increase in pressure will hinder the growth at the epiphyseal plates and a decrease in pressure will lead to an acceleration of their growth (Hert 1969). This initial work on the relationship between skeletal morphology and mechanical stress has prompted more recent authors to theorize on the mechanism by which growth plates react to outside forces.

1.2.2. Current understandings

Wolff's Law concerning the relationship between skeletal morphology and mechanical environment, while an insightful idea at the time, cannot account for all instances of bone modelling, such as, for example, the modelling observed when bone fractures heal (Lovejoy et al. 2003). The mechanism by which stress affects a growth plate's cellular activity still remains poorly understood. Nevertheless, the factors contributing to, or inhibiting cartilage growth and chondro-osseous activity, are now better known. These include the activity of adjacent tissue, nutrients, hormones, vascularity, and of course stress caused by mechanical loading (Carter 1987). Loading comes from many sources: muscle forces, body weight, and acceleration and deceleration of the body mass (Frost 1997). The many influences acting on bone modelling further confirm how complex this relationship is and ultimately, how difficult it is to describe in precise mathematical terms how bone will react to mechanical influences.

As mentioned previously, the growth plate, or the metaphysis, is the area of the long bone that is of central interest to this research project. Shear or deviatory and compressive hydrostatic stresses may not only slow or stop, but conversely, can also stimulate the cartilaginous activity at the growth plate level that was described above – proliferation, maturation, degeneration and ossification (Carter 1987). Experiments have allowed researchers to further understand the cause-effect relationship of bone growth and mechanical stress. Frost (1997) has determined that increased compression loads corresponds to increased growth up to a certain limit. Past this limit, any increase in compression will correspond to a deceleration in bone growth, and large enough compression loads will eventually stop growth activity. Carter et al. (1998) found that high shear stresses also act similarly, accelerating growth and ossification up to a limit, but suggest that compressive hydrostatic stresses reduce growth rate and maintain the cartilage shape when applied intermittently. Furthermore, it has been posited that if the pressure is unequal across the growth plate, then its growth will be uneven in length (Pauwels 1980), which is consistent with the relationship between compression and growth described above. The orientation of the growth plates is another response of the bone, during growth, to the potentially damaging effects of mechanical stresses. Growth plates will lie perpendicularly to the direction of the joint force caused by the principal compressive and tensile stresses acting on this plate, which minimizes shear forces across the plates and reduces risk of injury to the sutures (Carter et al. 1987; Preuschoft and Tardieu 1996; Smith 1962a; Smith 1962b). Cusps and facets on this plate may also develop in order to resist the large shearing forces acting on the same joint (Preuschoft and Tardieu 1996).

In short, the main biomechanical concept on which this thesis is based is that endochondral ossification directly responds to mechanical stresses or forces. Differential forces on the joint, such as those resulting from different locomotion, will induce differential apposition on a histological level, and this will ultimately result in the variable morphology seen on an individual's limb bones.

1.3. Bipedality and its influence on bone morphology

1.3.1 Ontogenic development of features associated with bipedality

Bipedal locomotion produces different types of mechanical loads, the influence of which is visible in the morphology of lower limb bones. Because bipedality is rather specialized, movement of the knee is limited, and in turn the directions of mechanical loading on the femur are rather standardized. Because of that, the relationship between pressure and femoral development in humans, albeit complex, is better understood than in great apes, whose knee allows for movement in more directions, and therefore have knee joints that are subjected to many loads from less standardized directions (Tardieu and Preuschoft 1996). The development of bipedality, with the trunk upright, results in a centre of gravity shifted backwards, creating the need for more even distribution of anterior and posterior mass (Jaanusson 1991). Along with movement, the positional requirements of bipedality also induce morphology-altering forces. Bipedality requires the knee to be placed under the center of gravity. In addition, the knee joint needs its axis of flexion to be horizontal for stability as well as for habitual full knee extension (Tardieu 1999; Tardieu and Damsin 1997). The ability to fully extend the knee favours a longer stride, thereby increasing the efficiency of this type of locomotion (Tardieu et al. 2006). The loads due to body weight, gravity and acceleration and deceleration and incurred during locomotion and during stationary placement of the knee are associated with a series of developmental and genetic traits of the distal femur that are related to bipedality; these include, but are not limited to: a bicondylar angle of 8 to 11 degrees, a protuberant lateral troclear lip, and an elliptical lateral profile of the external condyle (Tardieu 1981; Tardieu 1983; Tardieu 1998). This section is devoted to describing each feature brought about by the ontogenic development of locomotion and explaining their functional adaptation. The homologous anatomy found in the tibio-femoral joint of great apes will also be discussed, as anatomical comparisons will provide some insight into the locomotor behaviour of extinct hominid species such as *Australopithecus afarensis*. The focus will be on the infradiaphyseal plane of the distal femur – the area where the diaphysis comes into contact with the epiphysis before fusion – a trait on which little work has been done.

1.3.1.1. Femoral obliquity angle

The femoral obliquity angle, also referred to as the diaphyseal angle or bicondylar angle, is the most significant marker of bipedality. It is the angle between the axis perpendicular to the plane on which lie the two condyles in adults or the metaphysis in juveniles, and the axis of the femoral diaphysis (Fig. 1.3.). Its formation has consequences on the morphology of the distal femoral epiphysis, which displays traits that are functionally associated with the obliquity of the femur. The development of the femoral obliquity angle arises from the need to keep the knee below the centre of gravity during the single stance phase, in spite of the large interacetabular distance – the distance between the two femoral joints of the pelvis – of humans (Tardieu 2010). Indeed, it allows the knee to be placed below the center of gravity while facilitating flexion and extension of the knee in the parasagittal plane (Tardieu 1999; Tardieu and Damsin 1997). A horizontal

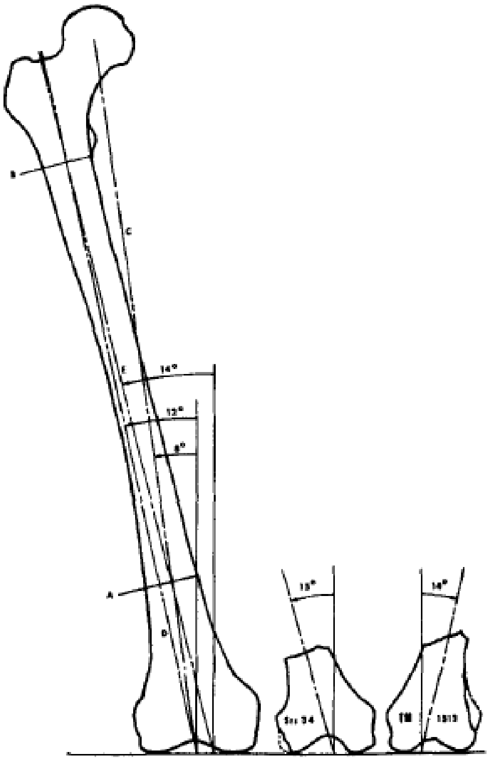

Figure 1.3.: Various axes that can be used to measure the femoral obliquity angle. From Heiple and Lovejoy (1971).

mediolateral metaphyseal and infracondylar plane will also minimize the shear stress that will be applied on the joint (Tardieu and Trinkaus 1994).

Posture and locomotion affect the development of the femoral obliquity angle occurs through differential apposition of bony tissue at the mediolateral metaphyseal level: there is additional medial metaphyseal apposition compared to the lateral side (Tardieu 2010). In essence, the placement of the knee joint in a valgus position, underneath the centre of gravity and close to the ground reaction force, applies just enough pressure on the medial portion of the cartilage growth plate to stimulate metaphyseal apposition on the medial side of the plate, which in turn creates the obliquity angle (Preuschoft and Tardieu 1996; Tardieu and Damsin 1997; Tardieu and Trinkaus 1994). However, the medial portion of the growth plate is not the area subjected to the most pressure. In fact, a greater amount of pressure is applied to the lateral side (Tardieu et al. 2006), but as mentioned earlier, excessive pressure can slow or even interrupt growth. This is why we observe differential apposition at the medial and lateral level of the growth plate. The increased pressure on the lateral side is in all probability decreasing the activity level of the growth plate.

The emergence of the femoral obliquity angle in humans, and the manner in which it develops, depend on the pattern of biomechanical loading that is representative of normal development of posture and locomotion in that species (Tardieu and Damsin 1997). Because it is a physiological phenomenon, the development of the femoral obliquity angle should parallel the development of normal bipedal walking in children. This is what is observed in human juveniles. The femoral angle is of 0° in foetuses and newborns, and for the first year of life. It starts to steadily increase during the second and third year of life which corresponds to the age at which children acquire bipedal walking, and reaches low adult values between four to eight years of age (Tardieu and Damsin 1997; Tardieu and Trinkaus 1994). Moreover, radiographic records of individuals that could not walk due to handicaps do not display an obliquity angle: an individual who learned to walk at the age of 12 had a 0° obliquity angle, while one who learned to walk using a walker at the age of six showed a bicondylar angle of 1.5° a year later (Tardieu and Trinkaus 1994). This further confirms that the femoral obliquity angle is a physiological trait. The angle of obliquity of the femur also modifies the relative provision of the proximal portion of the femur: the greater trochanteric apophysis remains stationary relative to the proximal femur during growth because of associated muscle groups, but its orientation changes relative to the femoral diaphysis as the latter becomes oblique (Duren and Ward 1995). Tardieu (1994) has found that the development of femoral obliquity is not strictly correlated with children's ages, which suggests that the angle depends on other growth parameters that are associated with the development of the femur, such as interacetabular distance or lengthening of the femoral neck. Still, there is a visible trend of gradual increase in angle values in children who are at the age where they normally learn to walk bipedally.

This pattern is quite different from that observed in juvenile great apes. When testing for a correlation between diaphyseal length and bicondylar or diaphyseal angle in great apes, Tardieu and Preuschoft (1996) found that the development of such angles was highly irregular and that there was no apparent relation between the two variables. When a bicondylar angle was present in older juveniles, these authors have found it was caused by differential height in the medial and lateral femoral condyles. We know that the femoral obliquity angle in humans is a diaphyseal trait because the two condyles are of approximately equal height (Tardieu 2010). Thus, the angle occasionally found in apes is not a true femoral obliquity angle. This lack of correlation is expected as great apes' modes of locomotion are strikingly different and much more varied than the upright bipedality of humans. Indeed, knuckle-walking and arboreality require the knee joint to be more flexible and to be placed in various positions rather than just under the center of gravity as in humans. Also, during the few instances when great apes engage in bipedal locomotion, it is done with bent knees and bent hips, and the knee finds itself constantly flexed in an abducted position as opposed to adducted, which results in an unstable stance (Lovejoy 2007; Tardieu 1997; Tardieu 1998; Tardieu and Damsin 1997). In some species, this trait also has genetic limitations. It was shown that, in an experiment where Japanese macaques were trained to walk bipedally, they never developed a femoral obliquity angle: the diaphysis remained straight (Hayama et al. 1992). It has been suggested that the bicondylar angle measurement method, which involves placing the femur vertically on a flat surface as a plane of reference, corresponds to the natural position of the femur in humans (Lovejoy 2007). This may further explain why patterns of femoral obliquity angles are not observed in great apes. Indeed, the natural, or most usual position, of the femur in great apes is not vertical, but rather should be angled posteriorly as in a bend-knee posture, and therefore using the bicondylar or metaphyseal plane as a base axis might be yielding incorrect results. It is necessary to re-evaluate the definition of femoral obliquity angle for chimpanzees, gorillas and orang-utans, as this would allow for the development of a measurement method that is more appropriate for the usual stance of each species.

1.3.1.2. Flattening of the distal femoral epiphysis

The distal epiphysis of the femur undergoes several morphological changes that are a functional response to the development of the femoral obliquity angle in humans. Distally, the epiphysis is elongated antero-posteriorly, to the point where it has a more squarish shape while in pongids the inferior aspect of the epiphysis is more rectangular (Fig. 1.5.;Tardieu 1981; Tardieu 1997). In side view, the profile of the femoral condyles will become elliptical because of this elongation (Fig. 1.4. and1.5.). The lateral condyle will be flatter and longer since bipedal locomotion applies more pressure to this side of the distal femur. The flattening of the epiphysis creates a larger area of contact between the femur and the tibia; this increases the area on which the load passing through the knee joint during full extention is distributed and therefore reduces high strains that could damage the articular cartilage (Aiello and Dean 1990; Heiple and Lovejoy 1971; Lovejoy 2007; Tardieu 1981).

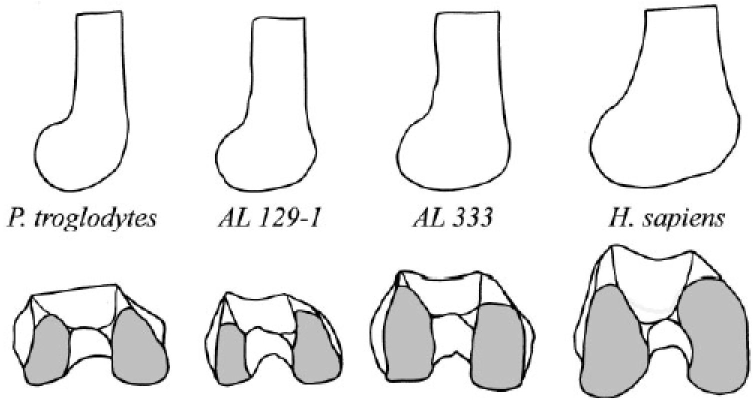

Figure 1.4.: Lateral view and inferior view of the right distal femoral epiphysis of *Pan troglodytes*, two *A. afarensis* fossils, and *Homo sapiens*. From Ward (2002) .

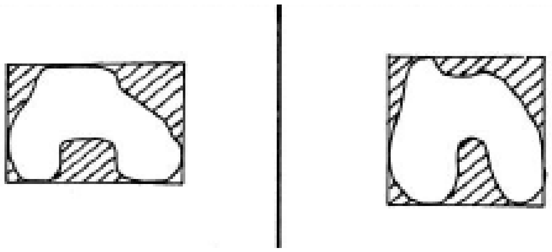

Figure 1.5.: Inferior view of the distal femoral epiphysis of a pongid (left) and human (right). After (Tardieu 1983).

Specifically, it means that humans experience a greater area of cartilage contact during the last 20 degrees of extension, which reduces strain from ground reaction forces and body weight, and in turn prevents early breakdown of the cartilage of the knee (Heiple and Lovejoy 1971; Lovejoy 2007). The large area of contact thus develops as a response to habitual full knee extension during walking or standing. This feature develops in association with the development of the obliquity angle; the lateral pillar will extend more anteroposteriorly than the medial one, because it is the lateral condyle that bears the most weight during the stance and gait portion of walking due to the femoral obliquity angle (Heiple and Lovejoy 1971; Tardieu et al. 2006).

The distal femoral epiphyses of great apes are not anteroposteriorly elongated as those of humans. They display a lateral condyle that is more circular and not elliptical when viewed laterally (Tardieu 1997; Tardieu 1998). This morphology is not adapted to the increased weight bearing that occurs during full extension of the knee, as it is in humans, which explains, in part, the unstable bent-knee bent-hip stance great apes assume during bipedal episodes (Heiple and Lovejoy 1971). In fact, mediolateral lengthening and circular condyles are traits that are best suited for a mobile knee joint (Tardieu 1998).

1.3.1.3. Area of contact between diaphysis and distal epiphysis

The infradiaphyseal plane is a feature that is subject to much influence from mechanical loading as it is the region directly adjacent to the growth plate. It is a trait on which little research has been done, and therefore it is still relatively absent from the current literature, yet it is probably the one trait of the knee joint that provides a direct demonstration of the effects of pressure on the growth plate and on the development of the femur. As previously mentioned, the growth plate adjusts its orientation such that it lies perpendicularly to the combined forces acting on it. In humans, the infradiaphyseal plane is relatively flat throughout childhood and youth. Because the ground reaction force and the force generated by body weight do not deviate much

Figure 1.6.: The distal metaphyseal surface of the femur in chimpanzees (far left), humans (middle), and *A. afarensis* (far right). From (Tardieu 2010).

from the tibial and femoral long axes, this flatness allows the growth plate to lie perpendicularly to these forces (Preuschoft and Tardieu 1996). The simple fitting of the diaphysis into the epiphysis is likely to be related to the limited repertoire of movements in relation to gravity that humans exhibit; bipedal running, walking and jumping mean that the knee joint, when loaded, is extended most of the time, and that it is exposed to high compressive force and very little shear stress, leaving the infradiaphyseal plane relatively flat, with only a few low cusps to resist the minimal shearing loads (Preuschoft and Tardieu 1996; Tardieu and Preuschoft 1996).

The infradiaphyseal plane of great ape femora is very different (Fig. 1.6.). It is highly convoluted, with deep mediolateral and anteroposterior grooves creating a very irregular surface (Tardieu and Preuschoft 1996). This creates a very tight fit between the epiphysis and the diaphysis. In the same way that the flat infradiaphyseal plane reflects bipedal locomotion in humans, the irregular plane and the tight fit with the epiphysis are direct femoral responses to great ape locomotor behaviour. Great apes use their hind limbs in various positions during arboreal activity. The tight fit of the diaphysis into the epiphysis could serve to prevent separation by resisting loads and shearing forces that come from all directions (Tardieu and Preuschoft 1996). The many different movements result in forces that have more variable directions, which largely deviate from the long axis of the femur; the many different facets allow the growth plate to resist forces coming from various directions, minimizing shearing forces across the entire surface (Preuschoft and Tardieu 1996). The irregularity of this surface is perhaps what makes it difficult to obtain consistent values when measuring diaphyseal angles, because its development is probably dissimilar to the development of the infradiaphyseal plane in humans, which remains mostly flat until fusion (Tardieu and Preuschoft 1996). Knowing how the surface develops in apes should allow researchers to identify a plane of reference that remains consistent throughout growth and therefore, which would permit more precise measurement and thus more meaningful values of femoral obliquity angles in those species.

1.3.1.4. Proximal Tibia

While the femur undergoes the most changes as a result of bipedality, the tibia also displays morphological characteristics that are indicative of bipedal locomotion. As the proximal femoral joint is horizontal, we can reasonably expect the tibial plateau to be horizontal as well. Because the ankle also needs to be directly below the center of gravity, an obliquity angle of the tibia is not observed in humans. Because knuckle-walkers take a bent-knee bent-hip stance when walking bipedally, the ankle is located medially relative to the knee joint, meaning the tibia in chimpanzees and gorillas should show an obliquity angle.

The topography of the tibial plateau, however, is indicative of the mode of locomotion. In humans, the medial portion of the plateau is slightly concave, which increases the area of contact between it and the medial femoral condyle (Javois et al. 2009). This increases knee stability during full extension and minimizes stress. In contrast, the lateral portion of the tibial plateau in great apes is more convex, reducing the area of contact with the lateral femoral condyles and increasing mobility of the knee joint. However, it was found that there is some significant overlap in the degree of curvature of the lateral tibial condyle between humans and great apes (Javois et al. 2009). Fossil data is similar to great apes but also falls within the human range. This lack of distinction in the morphology of the lateral tibial condyle between species with different locomotor behaviour suggests that this trait is not suitable for reconstruction of mode of locomotion in fossil hominid species (Organ and Ward 2006).

1.3.2. Genetic features of the knee associated with bipedality

1.3.2.1. Genetic traits of the femur

The distal end of the femur in humans is also marked by an anterior trochlear groove, with an elevated lip on the lateral side. While the elevation of the lateral trochlear lip and the deepening of the trochlear groove are associated with a bipedal gait, they are traits, unlike the previously mentioned features, that are already present in foetuses, and therefore appear to be genetically determined. There is no correlation between the degree of femoral obliquity and the degree of projection of the lateral lip, supporting the hypothesis that a high lateral trochlear lip and trochlear groove do not develop through the same process as the bicondylar angle and the flattening of the epiphysis; instead of resulting from developmental plasticity, the two trochlear traits appear to be determined genetically (Tardieu et al. 2006).

Despite the lack of correlation between a bicondylar or metaphyseal angle and the elevation of the lateral trochlear lip, the latter must have been genetically selected because of femoral obliquity. The angle resulting from the position of the knee - under the centre of gravity - inflicts a high lateral force vector on the patella. The *quadriceps femoris* muscle, which attach to the patella, pull it laterally and tends to dislocate it when contracting (Preuschoft and Tardieu 1996). The lateral lip prevents this lateral pull from dislocating the patella during extension of the knee and the deep trochlear groove also provides more mediolateral stability (Heiple and Lovejoy 1971; Preuschoft and Tardieu 1996; Tardieu 1981; Tardieu et al. 2006). Similarly, horses, for instance, possess very deep trochlear grooves which permit very rapid flexion and extension motion, but only in the parasagital plane, while bears display a flat trochlea and therefore a knee joint that has little movement restrictions (Tardieu 1981). As such, a flat trochlea is also a feature of pongids' femora which allows for a repertoire of varied motion for tree-dwellers or knuckle-walkers, as the patella is less constrained in its movements (Heiple and Lovejoy 1971; Tardieu 1997; Tardieu 1998).

1.3.2.2. Genetic traits of the tibia

Non-skeletal traits designed to protect the knee joint from damage caused by muscle forces are also present at the proximal tibial epiphysis, namely, the lateral meniscal shape and insertions. Menisci are pieces of cartilaginous tissue in the knee that serve to prevent friction and disperse the weight load from the point at which the femoral condyles and the tibial plateau come into contact (Standring 2005). This "soft-tissue" trait leaves insertion marks on the tibial plateau, which allowed researchers to evaluate the presence of this trait in fossil species. The results suggest that the shape and number of insertions is likely a genetically determined trait (Tardieu 2010). In humans, the lateral meniscus is in the form of a crescent and inserts in two places, leaving two visible insertion points on the tibial plateau. This double insertion, unique among mammals, restricts mobility of the lateral meniscus which prevents it to move forward excessively during full extension; it provides more stability which is necessary for regular full extensions of the knee joint as we see in bipedality (Javois et al. 2009; Tardieu 1988; Tardieu 1999). Non-human primates exhibit varied lateral menisci shapes, but the lateral menisci is always marked by a single insertion point, which is, again, a marker of a more mobile knee joint. Another interesting effect of bipedality on the tibia is the width of the tibial spine, linked to the width of the intercondylar notch. These two values are similar in humans, creating a tight fit which provides more stability to the knee, again at the expense of mobility (Tardieu 1981).

1.3.3. Summary of biological context

The effects of mechanical pressure brought about by bipedality on skeletal development have been described, and it can be concluded that a growth plate's activity is influenced by both the magnitude of the forces acting on it as well as by their orientation. In the lower limbs of humans, positioning of the knee under the center of gravity sets in motion the development of traits such as the remodelling of the carrying angle, the anteroposterior elongation of the distal femoral epiphysis in inferior view, and development of the elliptical profile of the lateral femoral condyles. Additionally, this posture in our ancestors also triggered selection for genetic traits of the knee joint, such as a double meniscal insertions and a deep trochlea with a prominent lateral lip. Mechanical loading also creates forces that modify the appearance of the infradiaphyseal plane of the femur, maintaining it much flatter than in non-human primates. The emergence of all these characteristics in the palaeoanthropological record should reflect an increasing use of full extension of the knee joint in our ancestors.

1.4. Palaeoanthropological context

Anatomical comparisons of the knee joints in humans and great apes allow researchers to infer locomotor behaviour from the remains of fossil hominids. Some contextual information on *A. afarensis* is necessary because this thesis is devoted to comparing the anatomy of certain traits of the knee in humans, gorillas, chimpanzees, orang-utans with that of this species, one of the earliest known hominids. Additionally, since ontological development of knee traits related to bipedality is the main focus of this project, an assessment of growth patterns in humans, great apes and *A. afarensis* is also essential.

1.4.1. Australopithecus afarensis: dates, environment, morphology

If *Australopithecus afarensis* is a famous species in the popular scientific literature, it is for good reasons. The large quantity of fossils – more than 300 hominin specimens and countless animal fossils– discovered in Eastern Africa since the 1970's have yielded a great deal of information about the environment in which that species evolved, as well as provided clues to their diet, social behaviour, and cognitive ability. The following is a brief description of *A. afarensis* anatomy and environment after (Boyd and Silk 2003). Their crania showed ape-like traits: a prognathic lower face, and an endocranial capacity of less than 500 cc, which is not too different from that of modern chimpanzees. Also, their bodies were shorter, and their arms were long with curved fingers. They were strongly sexually dimorphic. Their jaws and teeth, however, presented features that place them between great apes and humans; namely, we see little sexual dimorphism in the canines, which were smaller, and their jaw is marked by a V-shaped dental arcade. The fossils date from 3.9 to 2.9 million years, and their location suggests that *A. afarensis* lived in different types of environment, ranging from woodland, scrubs and grasslands such as at Hadar, to dry grasslands such as in Laetoli. The fact that this species has survived for close to one million years suggests that the mix of ape-like and human-like physical attributes allowed them to successfully adapt to a range of different environmental conditions.

1.4.2. Locomotion information and debate

Because so many *Australopithecus afarensis* fossils have been discovered compared to other hominid species, a great deal of skeletal and biomechanical information has been extracted by researchers. While fossils are often incomplete, there is enough material to make realistic inferences, but because it is an extinct species with its unique morphology, uncertainties about its locomotion remain. Thus, researchers still debate whether this species was completely bipedal, bipedal with some degree of arboreality, or arboreal with some degree of bipedality. Many skeletal traits are involved in those discussions but the following is an overview of the debate with focus on the lower limb traits in *A. afarensis* that provide clues on their behaviour.

At one extreme lies the argument that *A. afarensis* was a palmigrade-plantigrade quadruped, putting the whole hand and foot upon the ground when walking (Sarmiento 1998). However, there are very few supporters of this hypothesis (Ward 2002). The two following hypotheses have many proponents and both sides agree that the bipedality of *A. afarensis* is undeniable. One position proposes that *A. afarensis* was bipedal in conjunction with arboreal activity, while the other suggests that *A. afarensis* was exclusively bipedal. Some features of the lower limb bones in *A. afarensis* are not consistent with a human-like bipedality and therefore have lead some researchers to doubt the idea that the members of this species were exclusively bipedal. For instance, the tibia only presents one lateral meniscal insertion, not two as in humans (Javois et al. 2009; Tardieu 1999). Other traits, like curvature of the toe bones, or the retention of brachiation traits in the upper limbs are also use as evidence for the assertion that *A. afarensis* regularly climbed trees (Prost 1980; Stern and Susman 1983; Susman et al. 1984). Supporters of this theory operate under the assertion that the retention of primitive, ape-like features in *A. afarensis* was a functional adaptation (Ward 2002).

For others, *A. afarensis* was fully bipedal, and rarely engaged in arboreality. The total morphological pattern seen in *A. afarensis* is so indicative of bipedality that some authors speak of a directional vector of natural selection moving away from traits associated with arboreality to those adapted to bipedality, most of which are found on the pelvis, femur and tibia (Latimer 1991; Ward 2002). The pelvis of *A. afarensis* is quite similar to that of humans: the ilia have rotated in a more sagittal plane to accommodate a fully upright posture, and they show attachment points for the abductor muscles, muscles which stabilize the pelvis during walking (Lovejoy 1988). The femoral obliquity angle found in a number of fossils of this species gave values ranging in the upper limits of those of modern human, even in younger individuals (Lovejoy and Heiple 1970; Tardieu and Trinkaus 1994). For instance, two well known juvenile specimens, AL 333-110 and AL 333-111, already present a diaphyseal angle of 6 and 11 degrees respectively, while adult values for australopithecines exceed that of humans (Lovejoy 2007; Tardieu and Preuschoft 1996). The high values, which are dependent on the large interacetabular distance on the pelvis, allow the knee to be placed under the center of gravity during the single support phase of gait in spite of the wider pelvis in *A. afarensis* (Heiple and Lovejoy 1971; Lovejoy and Heiple 1970; Tardieu 2010). This has been interpreted by many as proof that *A. afarensis* individuals practiced bipedal walking, a new behavioural trait, from an early age, doing so frequently enough that the trait appears early in their development, since we know that the femoral obliquity angle is a developmental, epigenetic trait (Preuschoft and Tardieu 1996; Tardieu 2010). The presence of a human-like obliquity angle on the femur is also evidence against *A. afarensis* having retained a certain degree of arboreality, for a high knee valgus would have induced shear forces high enough to cause injury during arboreal activities (Lovejoy 2007). In fact, the high femoral obliquity angle of *Australopithecus afarensis* is such a solid proof of bipedality that it is the predominant feature that has allowed them to be included in the human lineage (Tardieu and Damsin 1997).

As in humans, it is hypothesized that the presence of a femoral obliquity angle in *A. afarensis* triggers the appearance of its associated traits. In fact, the distal femoral epiphysis of *A. afarensis* is similar in morphology to that of humans. The lateral condyles are flattened and display an elliptical profile and, in distal view, also present a slight anteroposterior elongation, a shape that appears to be intermediate between humans and chimpanzees (Fig. 1.4.); this would have allowed for efficient force transfer during full extension of the knee during bipedal gait (Heiple and Lovejoy 1971). Furthermore, the deep trochlear groove seen in humans is also found in *A. afarensis* femora along with a slightly elevated lateral lip. The presence of these genetic traits suggests that they are the result of selection for patellar stability on the mediolateral plane during full knee extension, a safety feature associated with the carrying angle and bipedality in humans (Heiple and Lovejoy 1971). The distal femoral infradiaphyseal planes of juvenile specimens AL 333-110 and AL 333-111 are also similar to what is observed in human juveniles. The surface in both great apes and humans is marked by four cusps, where their elevation creates grooves in between them, one running mediolaterally and the other anteroposteriorly (Fig. 1.6). Great apes, as we have seen, have a more convoluted growth plate surface, with highly elevated cusps and deep grooves, while humans exhibit only very low cusps. In the fossil specimens, the mediolateral and anteroposterior grooves appear to be shallow, and the cusps only slightly elevated, giving the surface an overall flat and horizontal appearance (Preuschoft and Tardieu 1996). This suggests that the growth plates were subjected to more or less vertical loads which are associated with a fully extended posture. This further suggests that they are not adapted to resist large loads coming from any other direction, as it is inferred for arboreal locomotion in apes. However, the morphology of the femur of *A. afarensis* is mostly described qualitatively. Quantified measurements of the infradiaphyseal surface of the femur will be useful for comparison between species, and may provide more insight as to whether *A. afarensis* is really closer to humans in terms of femoral morphology.

1.4.3. Growth patterns

To provide accurate comparisons of the development of knee traits linked to locomotion between humans, great apes and australopithecines, it is essential to understand the differences in growth rate between these species. Humans and great apes do not mature at the same rate: both sexual and osteological maturation take about five to seven years longer to occur in humans (Tardieu 1997). This is seen in the fusion of femoral epiphyses: they fuse at the age of 16-18 years in humans and at 11-12 years in chimpanzees (Tardieu 1997). Therefore, the appearance of a particular feature at the age of three, for example, has different ontological implications in each species. Humans also differ from the great apes in that they go through a short period of very rapid growth, referred to as the “adolescent growth spurt”. During this period, which occurs relatively late in chronological age, the femur grows rapidly and develops further the epiphyseal traits that are associated with the bicondylar angle (Tardieu 1998). In australopithecine juveniles, the patterns and rates of dental growth, patterns of facial growth, short hind-limbs, and ape-like growth of the pelvis are all indicative of a short growth period in childhood and in adolescence more similar to that of chimpanzees (Tardieu 1997; Tardieu 1998). So, even though *Australopithecus afarensis* fossils present some very human-like characteristics, especially in the post-cranial skeleton, they still retain many features which suggest they had a short, ape-like growth.

1.5. Objectives

The biomechanical, palaeoanthropological and ontological information provided in this chapter raises many interesting issues, one of which relates to the development of bipedality in *Australopithecus afarensis*. While the development of the knee joint is well known in humans, there is a lack of quantifiable data from great ape species, and even less from fossil species. As mentioned earlier, one problem when it comes to the measurement of the femoral obliquity angle, for example, is the absence of a proper method to measure it on great ape femora, since the shape and most likely the development of the metaphyseal plane differs greatly from what is observed on human elements. If hard data was available on the development of the infradiaphyseal plane, accurate comparisons could be made between human and great ape femora at different growth stages, and those comparative methods could be applied to the fossils of *A. afarensis* juveniles. The purpose of this thesis is therefore to test a 3D measurement method on the metaphyseal plane of the distal femora and proximal tibiae of humans, great apes, and *A. afarensis* fossils of different ages, with the objective of obtaining quantifiable data regarding the development of tibial and femoral knee growth plates, and use these data to evaluate the morphology and development of bipedality in *Australopithecus afarensis*.

In light of the current data on the development and locomotor behaviour of *A. afarensis*, the hypotheses to be tested through this project are as follows:

1. The distal femoral metaphyseal topography should change in parallel with the acquisition of locomotion. This means in humans, we should see a development of slight cusps and grooves in response to the minor shearing forces associated with bipedality. The topography should remain nearly flat, however, since there are never

much transverse loads. In chimpanzees, gorillas and orang-utans, we should expect the development of more pronounced facets and a more convoluted surface in response to the development of the individual, as these three species have modes of locomotion which, albeit different, apply loads coming from many different directions. This hypothesis opposes the null one, which is that there is no significant effect of age or development on the topography of the metaphyses of the knee.

2. The pattern and rates at which the topography develops differs depending on the species, or primary mode of locomotion. The null hypothesis would see no significant effect of species on the development of the topography of the metaphyses.
3. If *A. afarensis* was exclusively bipedal and had abandoned arboreal locomotion, the distal femoral metaphysis of *A. afarensis* juveniles will remain similar to that of humans, that is relatively even, with low cusps to resist minor shearing forces.

Chapter 2: Materials and Methods

2.1. Materials

The comparative data consists of human and great ape juveniles at different stages of development. A total of 138 individuals were examined. The human sample consisted of individuals aged 0 to 18 years from the Mistihalj archaeological collection curated by the Peabody Museum of Archaeology and Ethnology of Harvard University. The Mistihalj skeletons were excavated by the joint Stanford University-Yugoslavian Expedition to the Trebisnjica River Valley during the summer of 1967. The Mistihalj cemetery is located in Bosnia-Herzegovina and dates to late medieval period; analysis of tombstones, grave goods and coins date the site to 1400-1475 A.D. The remains are culturally associated with the Vlakhs, a group of nomadic pastoralists.

Table II.I: Sample size of the taxa included in the infradiaphyseal analyses and the photographic femoral obliquity analysis

Species	**Femur Infradiaphyseal**	**Tibia Infradiaphyseal**	**Femur Photographic**
Homo sapiens	34	17	46
Pan troglodytes	13	26	24
Gorilla gorilla	17	26	29
Pongo pygmaeus	6	16	20

The non-human sample included chimpanzees (*Pan troglodytes*), aged 1 to 12 years old; gorillas (*Gorilla gorilla*), aged 2 to 12 years old; and orang-utans (*Pongo pygmaeus*), aged 0 to 12. The apes are curated in the Mammals Collection of the Smithsonian Museum of Natural History and the Haman-Todd Osteological Collection at the Cleveland Museum of Natural History. The breakdown of individuals on which data was analyzed is presented in Table II.I. While more specimens were included in the initial data collection, many could not be included in the analysis, as the infradiaphyseal area was not accessible or too damaged. Some of the elements were fragmented or missing, some long bones were still connected by dried tissue, and in some cases the unfused epiphyses had been re-glued to the shafts prior to this study. One method for measuring the femoral obliquity angle was based on photographs. This method was therefore not as dependent on the state of the specimens with regards to fragmentation and similar issues. Thus, the sample for femoral obliquity photographical analysis is larger, as presented in Table II.I. Right elements were chosen when available. Seven juvenile *A. afarensis* fossils, which are curated at the National Museum of Ethiopia, were also measured. However, due to the aforementioned issues, only 4 could be included in the analyses: A.L. 333-110, A.L. 333-111, A.L. 333-140, and A.L. 333-39.

2.2. Methods

The nature of this project necessitated two distinct data-collecting and processing methods. The first was photography and applied only to the measurement of femoral obliquity angles. The second is the collection of three-dimensional data and applied to the analysis of femoral and tibial obliquity angles, as well as to the analysis of the topography of the knee joint's metaphyses.

2.2.1. Data Collection

2.2.1.1. Photography

The femurs were photographed using a Canon Rebel XT (8 MP, EF-S 18-55mm lens) for humans, a Panasonic DMC-FZ18 (8.3MP, 28-504mm lens) for great apes, and a Canon PowerShot A100-IS (10 MP) for the fossils. They were placed proximal side up, posterior side against a metric board. The femurs were rested on the two condyles or on the metaphyseal surface depending on whether the epiphyses were attached to the diaphysis or not. To eliminate the possibility of parallax distortion, the camera was placed at a distance of at least 12 times the length of the element being photographed (Griffin and Richmond 2010). This resulted in the camera being placed at a distance of about 5 meters from the elements, except in the case of a few very small specimens, where the camera had to be placed at a distance of 2 meters for picture clarity. The picture was taken using a remote trigger, or if not available, using the multiple shot function, in order to keep the camera as stable as possible during exposure.

2.2.1.2. Three Dimensional Data Collection

Three-dimensional analysis of the infradiaphyseal plane was done from points recorded in 3D space using a Microscribe digitizer. In total, more than 100 landmarks were chosen on the femur and tibia. For each landmarks, x, y, and z coordinates were recorded. These landmarks were chosen to give the best quantifiable morphology of the knee epiphyses, as well as the position of the diaphysis (Fig. 2.1.). As mentioned in Chapter 1, the femoral metaphysis is marked by peaks and grooves, and these are more developed in great ape specimens, resulting in a much more convoluted topography. Landmarks were selected to allow calculation of angles between these protuberances, and to get the general the topography of the metaphysis.

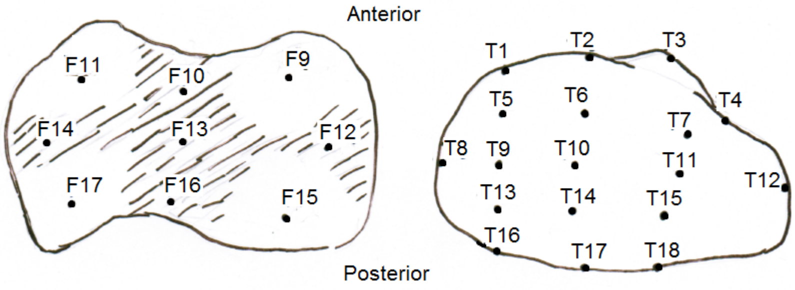

Figure 2.1.: Diagram of landmarks used in this study. Distal view of the right distal femoral metaphysis (left) and proximal view of the right proximal tibial metaphysis (right). Shaded area represents grooves or creases in the surface of the femoral metaphysis.

The infradiaphyseal plane of the proximal tibia, unlike that of the femur, is much less convoluted with no clear grooves of peaks, so points were taken at regular intervals, again with the intention of measuring angles, but more specifically, to see if there was a difference in general trends of curvature of this plane between humans and great apes. In both the tibia and femur, three points were taken along the diaphyseal axis, at 25%, 50% and 75% of the total diaphyseal length. Data collection started first with the femur or tibia being stabilized with museum putty or modelling clay. The points were then recorded in the exact same order and sent directly to a Microsoft Excel (2007) file, with a separate sheet for every individual. In the sheet, each row corresponded to a different landmark and the x, y and z coordinates were in three separate, consecutive cells, thus resulting in an x column, a y column and a z column. When a landmark was not recordable because of fragmentation or because of attached epiphyses, for example, the points were skipped and the corresponding cells in the sheet were left blank.

2.2.2. Preparation

2.2.2.1. Measurement of femoral obliquity angle from photographs

The femoral obliquity angles were measured from the photos using the program ImageJ (Abramoff et al. 2004). The angles were measured between the long axis of the diaphysis and the axis perpendicular to the plane on which the condyles rested or, in the case of unfused epiphyses, the plane on which rested the distal end of the femur (Fig. 2.2.). Adducted knee joints result in a positive femoral obliquity value as the diaphyseal axis pivots counter clockwise from the plane of reference, while abducted knee joints, where the axis of the diaphysis pivots clockwise from the axis of reference, result in negative angle values. The program allows the user to define two axes and calculates the angle between them. To minimize intra-observer variation, the angles were measured 10 times for each specimen, and the average of those 10 results was plotted as the final value for each individual. When the right femur was not available, the photo of the left femur was taken and the photographs were flipped prior to taking the measurement.

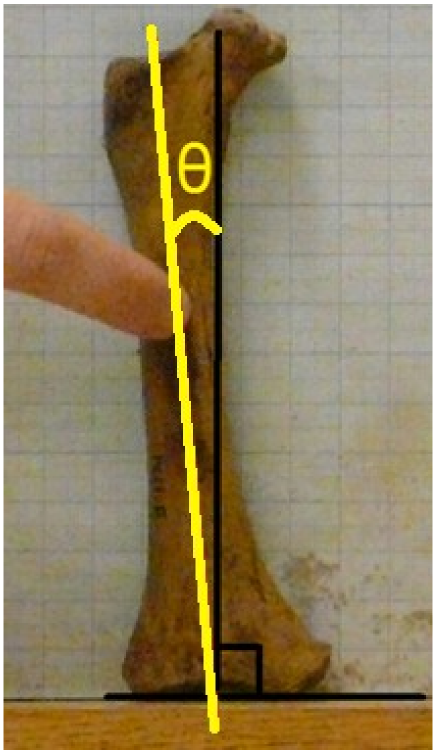

Figure 2.2.: An example of the method used for measuring the femoral obliquity angle, using the right femur of a juvenile *Gorilla* individual.

2.2.2.2. Preparation of 3D Data

Conversion to text files and realignment

The coordinates that were collected on the femoral and tibial metaphyses were converted to text files using SAS software (v. 9.1.3., SAS Institute, Carey, NC). This process resulted in two text files: one for the femur data and one for the tibia data. The coordinates had to be realigned so that all elements would be oriented along the same anatomical axes. The realignment was performed using GRF-ND (Slice 1992, 1994), using the two original text files. The femur landmarks were realigned three-dimensionally using the points 12 and 14 as the mediolateral axis, and the landmark in the middle of the diaphysis. For the tibia, the points 8 and 12, defining the mediolateral axis, and the landmark in the middle of the diaphysis were used as references for the realignment of the tibia. This realignment resulted in two new text files for the femur and the tibia in which the x coordinates varied along the mediolateral axis, the y coordinates varied along the proximo-distal axis and the z coordinates varied along the anteroposterior axis.

PCA and Procruste analysis of raw data

The two files produced by the GRF-ND program were imported, one at a time, into the program Morphologika (O'Higgins and Jones 1998), where a principal component analysis (PCA) was performed. The first step was to perform a full Procrustes Superimposition (PS), where the 3D data was scaled, rotated and reflected and then superimposed to minimize the variation among individuals. All specimens were examined to determine if the values were realistic and eliminate any far outlying points that would have been due to either human or technical error while collecting data.

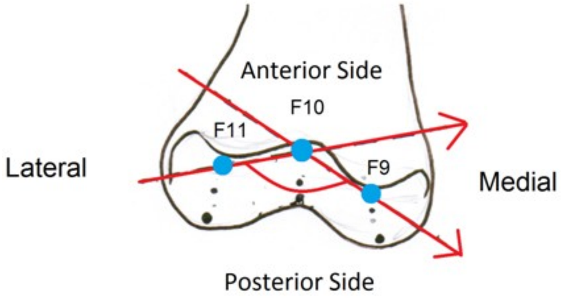

Figure 2.3.: Diagram of the right distal femoral metaphysis representing how the anterior mediolateral angle was measured.

Once error points were removed, a PCA was conducted in order to see if there was any kind of structure to the data. Specifically, the purpose of the analysis was to confirm that the human values were separate from the great apes values, which would support the hypothesis that the mode of locomotion does affect the overall shape and topography of the metaphysis during development.

Calculation of angles

Next, the angles between two axes formed by three points or landmarks were selected. The femoral and tibial obliquity angles (FOA and TOA) were defined by the mediolateral axis of the metaphysis in the central groove and the long axis of the diaphysis. Metaphyseal angles, for the femur, were defined by the peaks and grooves. Medial and lateral cusps on the anterior and posterior sides formed, with the floor of the mediolateral groove, the angles FMLA and FMLP respectively, and anterior and posterior cusps on the medial and lateral sides, with the floor of the anteroposterior groove, formed the angles FAPM and FAPL. The angles of the mediolateral and anteroposterior grooves were measured using the points between the two pairs of mediolateral peaks (FAPG), and of anteroposterior peaks (FMLG) and a central point at the intersection of the two grooves. The tibial metaphysis, as mentioned, is not defined by any particular landmark. TMLA, TMLC, and TMLP, therefore, are defined as mediolateral angles on the anterior, central and posterior regions of the metaphysis. TAPM, TAPC, and TAPL are the anteroposterior angles of the medial, central and lateral portions of the metaphysis. The exact landmarks for each angle are given in Tables II.II. and II.III, and Fig. 2.3. provides an example of how the angle FMLA was calculated.

Table II.II.: Definition of the two axes between which angles were measured to quantify the morphology of the distal femoral infradiaphyseal plane

Angle	**Axis 1**		**Axis 2**	
	Landmark 1	**Landmark 2**	**Landmark 1**	**Landmark 2**
FOA	F12	F14	F19	F20
FMLA	F11	F10	F10	F9
FMLP	F17	F16	F16	F15
FAPL	F11	F14	F14	F17
FAPM	F9	F12	F12	F15
FMLG	F12	F13	F13	F14
FAPG	F10	F13	F13	F16

Table II.III.: Definition of the two axes between which the angles were measured to quantify the morphology of the proximal tibial infradiaphyseal plane.

Angle	**Axis 1**		**Axis 2**	
	Landmark 1	**Landmark 2**	**Landmark 1**	**Landmark 2**
TOA	T8	T12	T20	T21
TMLA	T1	T2	T2	T4
TMLC	T9	T10	T10	T11
TMLP	T16	T17	T17	T18
TAPM	T5	T9	T9	T13
TAPC	T6	T10	T10	T14
TAPL	T7	T11	T11	T15

Depending on the angle measured, one of the three dimensions had to be eliminated. To measure an angle on the sagittal plane, for example, the coordinates on the y and z plane were used, whereas an angle on the coronal plane required calculations using coordinates on the x and y plane. Using the software SAS, the slopes between the first and the second point, and between the second and third point were calculated. The angle between the two axes formed by these slopes was then computed. The group of angles is a simplified shape and provides quantifiable data that can be measured and compared. The differences between these values in humans and great apes will reflect the differences in overall infradiaphyseal topography and the development of this trait between the species.

2.2.3. Analysis

Statistical analyses were done using the program SPSS (Version 19, 2010). The independent variables used in this study were the relative ontogenetic stage, expressed as a percentage of development and femoral length. The latter variable, which on its own is not a precise indicator of age, but femoral length was known for a greater number of specimens resulting in greater sample sizes than when using percentage of development. The percentage of development was calculated as the chronological age divided by the adult age for the species multiplied by 100. Chronological age was estimated from the dental eruption patterns for apes and was provided by the Peabody museum for humans. The development was considered to be complete (100%) when the third molars had emerged. On average, this happens at ages 20.22 for humans, 11.25 for chimpanzees, 11.23 for gorillas, and 10 for orang-utans (Dean and Wood 1981; Smith 1989; Smith et al. 1994). *Australopithecus* *afarensis* fossils present unfused knee epiphyses, but because of their size comparable to adult specimens of the same species, they are considered to be late juvenile individuals, which corresponds roughly to dental stage 5. This stage occurs between the partial or full eruption of M^2 and the full eruption of M^3 in chimpanzees (Shea 1981), and it occurs between 6.79 and 11.25 years old, on average (Dean and Wood 1981; Smith 1989; Smith et al. 1994). Since we have used the full eruption of the third molar as an indicator of full development, this would mean that dental stage five would occur at between approximately 60 and 100% of development. It was therefore estimated that the *A. afarensis* fossils used in this study were at 80% of their development.

2.2.3.1. Statistical analyses

All variables were tested for normality before the following analyses were done. Statistical analyses did not include the fossil specimens as the sample consisted of either 1 or 2 individuals, but they were included in the graphs.

Regressions

Linear regressions were performed on all angles plotted against the percentage of development and against the natural log of the femoral length (as more data was available with this variable). The regressions were done separately for each species.

Principal Component Analysis

As was done with the raw data, a principal component analysis was conducted on all angle values for the femur and for the tibia, once again in order to establish if there was a general tendency for human values to separate themselves from angle values calculated in great apes.

ANCOVA

An analysis of covariance was done to evaluate the effect of species in the development of the topography of the metaphyseal plane. The ANCOVA is similar to the analysis of variance but compares means between multiple groups while controlling for the effect of a variable called covariate – in this case, developmental stage was controlled for. First, the data was evaluated to see if the conditions were met: 1) the variables are normally distributed, 2) the variances are equal, and 3) the samples are random and independent. Specifically, the variance needed to be the same across all species, so an analysis of variance was first performed to evaluate the hypothesis that all variances were equal. If this hypothesis could not be rejected, then the sample was suitable for an ANCOVA. Second, we needed to verify that there was no significant interaction between the covariant (the percentage of development or the femoral length) and the fixed factor (species). Samples that did not meet either of these requirements were excluded from the ANCOVA: FAPL, FAPG, and TAPC because all variances were not equal for these samples; and FOA (photos) plotted against the percentage of development, and, FMLA and FMLG plotted against femoral length because there was a significant interaction between the covariates and the species. The ANCOVA was performed on the rest of the samples.

Posthoc analyses

Bonferroni posthoc analyses were performed on the samples that met the conditions for the ANCOVA.

Chapter 3: Results

3.1. Femur

Mean values obtained on femoral angle are presented in Table III.I.I. Fossils A.L. 333-110 and A.L. 333-111 were estimated to be at 80% of maturity and their respective values are therefore included in age group 4.

Table III.I.I: Mean values (º) for each species in four age groups for each femoral angle

Age Group	Species	FMLA		FMLP		FMLG		FAPL		FAPM		FAPG		FOA (photos)		FOA (lm)	
		n	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean
1	*Homo*	11	169.3	10	154.4	13	190.4	11	172.9	10	180.7	12	174.4	16	1.6	13	1.9
	Pan	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA
	Gorilla	1	149.2	1	144.9	1	212.2	1	164.7	1	140.8	1	190.2	1	-1.6	1	-1.2
	Pongo	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	2	2.1	1	-3.1
2	*Homo*	6	166.5	7	149.1	7	196.3	7	161.5	5	163.1	7	179.2	13	7.3	7	6.7
	Pan	1	167.0	1	146.8	1	170.0	1	107.3	1	122.8	1	166.4	4	3.3	1	1.1
	Gorilla	2	153.9	2	156.4	2	201.0	2	154.8	2	133.8	2	183.8	4	0.6	2	-1.3
	Pongo	1	180.0	1	156.3	1	197.7	1	174.8	1	187.7	1	191.2	2	3.8	1	6.1
3	*Homo*	11	161.2	12	148.1	12	189.5	11	143.9	11	146.3	12	170.5	14	7.0	12	4.6
	Pan	6	158.9	6	145.1	6	179.5	6	110.4	6	118.4	6	185.1	16	3.7	6	3.1
	Gorilla	3	141.0	3	164.3	3	180.7	3	118.2	3	120.5	3	197.1	10	2.7	3	-2.8
	Pongo	0	NA	0	NA	0	NA	1	118.3	1	135.3	0	NA	9	5.3	0	NA
4	*Homo*	2	150.8	2	141.7	1	188.0	2	119.8	3	148.7	1	168.9	4	7.4	2	5.5
	Pan	6	149.7	5	151.2	6	167.3	6	101.3	5	101.0	6	178.7	12	3.0	6	0.8
	Gorilla	10	133.7	11	159.5	11	163.6	10	104.5	9	92.5	11	183.8	15	2.8	11	-3.7
	Pongo	4	144.6	4	155.9	4	169.7	4	113.7	4	116.9	4	173.1	11	5.8	4	3.2
	AL 333-110	1	156.8	1	155.7	1	164.4	1	169.6	1	179.4		NA	1	4.0	1	7.4
	AL 333-111	1	148.9	1	164.5	1	153.9	1	163.6	1	196.5		NA	1	9.8	1	15.0

Age group 1: 1-10% of maturity reached; age group 2: 11-30% of maturity reached; age group 3: 31-65% of maturity reached; age group 4: 66-100% of maturity reached.

3.1.1. Effect of development on the topography of the infradiaphyseal plane

3.1.1.1. Effect of development on the Femoral Anterior Medio-Lateral Angle (FMLA)

Linear regression analyses revealed that the percentage of development significantly predicted the values of FMLA for humans, where the angle becomes more acute with the degree of development, but not for chimpanzees, gorillas and orang-utans (Table III.I.II.,

Fig. 3.1.1.). Linear regression analyses revealed that the femoral length significantly predicted the values of FMLA for humans, chimpanzees, and gorillas. In these taxa, the angles become more acute as the femur gets longer. There were no significant relationships between the femoral length and the values for angle FMLA for orang-utans.

Table III.I.II: Regression results for the angle FMLA

	% Maturity				ln (femoral length, cm)			
Species	n	R^2	b	p	n	R^2	b	p
Homo	30	**0.272**	**-0.252**	**0.003**	30	**0.370**	**-11.855**	**0.000**
Pan	9	0.166	-0.218	0.277	13	**0.496**	**-49.940**	**0.007**
Gorilla	8	0.428	-0.242	0.078	16	**0.356**	**-20.494**	**0.015**
Pongo	5	0.748	-0.408	0.058	4	0.762	-31.130	0.127

Bold face indicates significant at $\alpha < 0.05$.

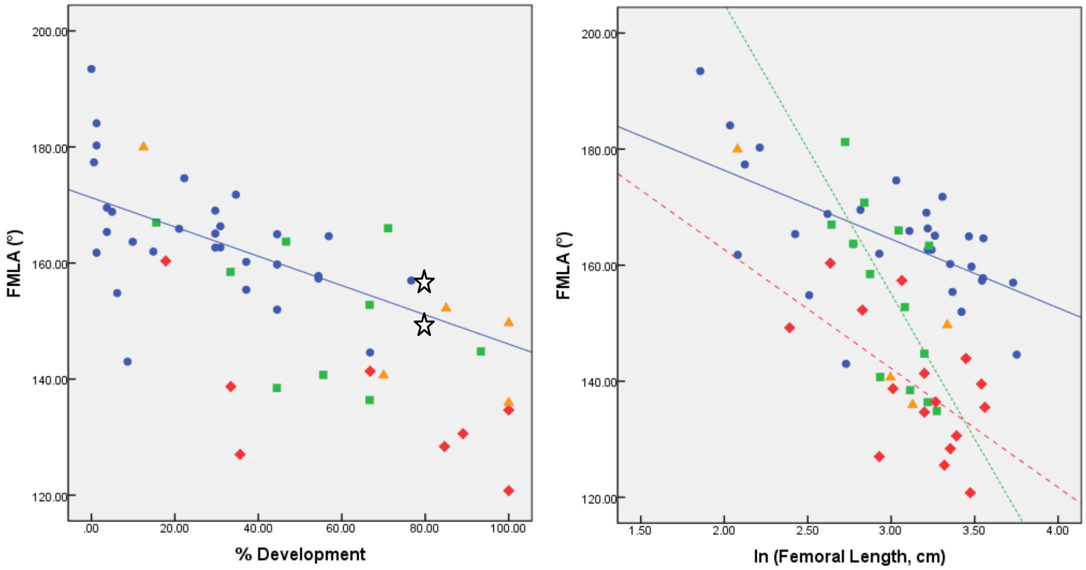

Figure 3.1.1: Linear regressions between the values for angle FMLA and the percentage of development (left), and the natural logarithm of femoral length (right). *Blue circles and solid blue line: Homo sapiens; green squares and dotted green line: Pan troglodytes; red diamonds and dashed red line: Gorilla gorilla; orange triangles and long dashed orange line: Pongo pygmaeus; stars: Australopithecus afarensis.*

3.1.1.2. Effect of development on the Femoral Posterior Medio-Lateral Angle (FMLP)

Linear regression analyses revealed that the percentage of development significantly predicted the values of FMLP for humans, and that the femoral length also significantly predicted the values of FMLP for this taxa. In both comparisons, the angle became more acute with the development or femoral growth. There were no significant relationships between either the percentage of development or the femoral length and the values for angle FMLP in great ape samples (Table III.I.III., Fig. 3.1.2.).

Table III.I.III. Regression results for angle FMLP

	% Maturity				ln (femoral length, cm)			
Species	n	R^2	b	p	n	R^2	b	p
Homo	30	**0.181**	**-0.179**	**0.019**	30	**0.248**	**-9.315**	**0.005**
Pan	9	0.290	0.200	0.135	12	0.167	17.466	0.188
Gorilla	8	0.018	-0.032	0.751	17	0.044	5.567	0.421
Pongo	5	0.124	-0.063	0.560	4	0.114	-4.360	0.662

Bold face indicates significant at $\alpha < 0.05$.

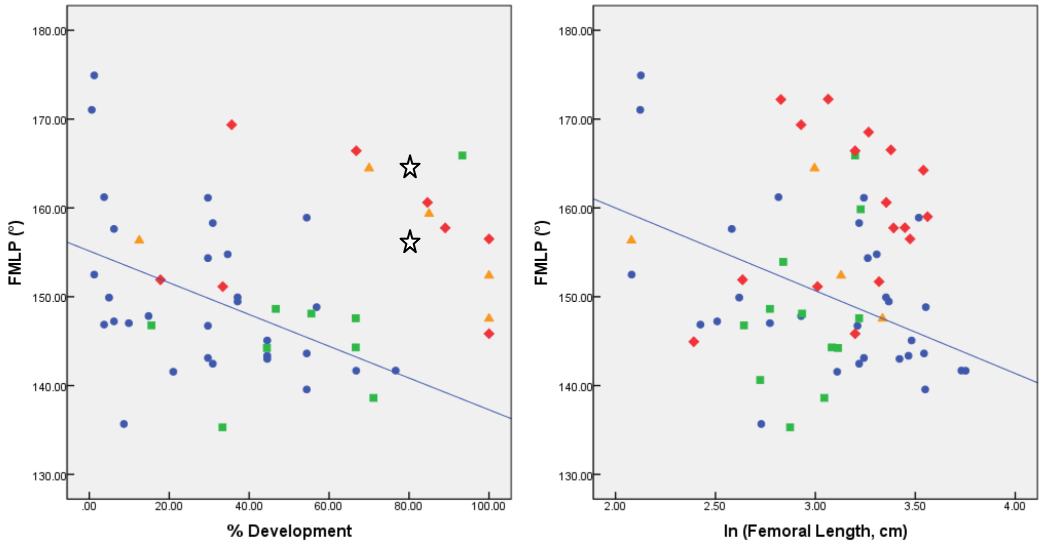

Figure 3.1.2.: Linear regressions between angle FMLP values and the percentage of development (left) and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*

3.1.1.3. Effect of development on the angle of the Femoral Medio-Lateral Groove (FMLG)

Linear regression analyses revealed that the percentage of development significantly predicted the values of FMLG for gorillas. The angle became more acute with the degree of development. However, no significant relationships between the two variables were found in the other species. Tests also showed that the femoral length significantly predicted the values of FMLG for chimpanzees and gorillas. In these species, the angle became more acute with femoral growth. Femoral length did not significantly predict FMLG values in humans or orang-utans (Table III.I.IV., Fig. 3.1.3.).

Table III.I.IV. Regression results for angle FMLG

Species	% Maturity				ln (femoral length, cm)			
	n	R	b	p	n	R	b	p
Homo	33	0.001	-0.018	0.838	33	0.045	3.956	0.237
Pan	9	0.150	-0.157	0.303	13	**0.468**	**-31.499**	**0.010**
Gorilla	8	**0.621**	**-0.402**	**0.020**	17	**0.821**	**-45.936**	**0.000**
Pongo	5	0.598	-0.290	0.125	4	0.764	-24.133	0.126

Bold face indicates significant at α < 0.05.

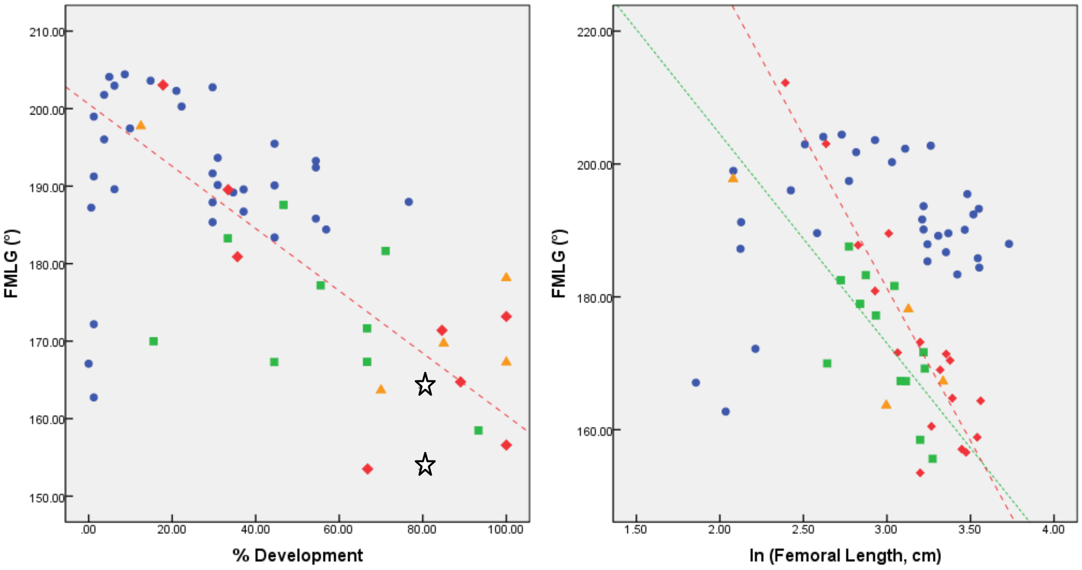

Figure 3.1.3.: Linear regressions between angle FMLG values and the percentage of development (left), and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*.

3.1.1.4. Effect of development on the Femoral Lateral Antero-Posterior Angle (FAPL)

Linear regression analyses revealed that the percentage of development significantly predicted the values of FAPL for humans and gorillas, but not for chimpanzees and orang-utans. For the former, an increase in the degree of development was accompanied by an increase of the acuteness of FAPL. Results also showed that the femoral length significantly predicted the values of FAPL for humans, chimpanzees, and gorillas, but not for orang-utans. In the three former taxa, the angle became more acute with an increase in femoral length (Table III.I.V., Fig. 3.1.4.).

Table III.I.V.: Regression results for angle FAPL

	% Maturity				ln (femoral length, cm)			
Species	n	R^2	b	p	n	R^2	b	p
Homo	31	**0.656**	**-0.756**	**0.000**	31	**0.549**	**-28.530**	**0.000**
Pan	9	0.175	-0.121	0.262	13	**0.344**	**-24.486**	**0.035**
Gorilla	7	**0.698**	**-0.754**	**0.019**	16	**0.562**	**-53.321**	**0.001**
Pongo	6	0.375	-0.499	0.196	5	0.541	-43.538	0.157

Bold face indicates significant at $\alpha < 0.05$.

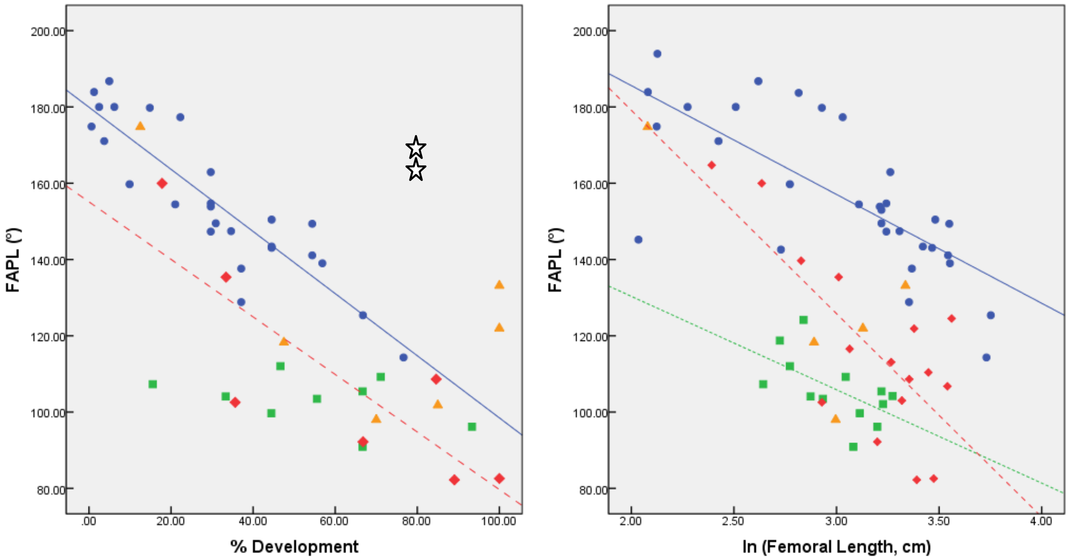

Figure 3.1.4.: Linear regressions between angle FAPL values and the percentage of development (left), and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*

3.1.1.5. Effect of development on the Femoral Medial Antero-Posterior angle (FAPM)

Linear regression analyses revealed that the percentage of development significantly predicted the values of FAPM for humans, chimpanzees, and gorillas. These analyses have also revealed that the femoral length significantly predicted the values of FAPM for humans, chimpanzees, and gorillas. In both comparisons, the angle became more acute with the degree of development or femoral growth. While the relationships between growth indicators and FAPM values for orang-utans are not statistically significant, we can note that the R^2 values in these cases are still considerable (Table III.I.VI., Fig. 3.1.5.).

Table III.I.VI. Regression results for angle FAPM

Species	% Maturity				ln (femoral length, cm)			
	n	R^2	b	p	n	R^2	b	p
Homo	28	**0.571**	**-0.755**	**0.000**	29	**0.425**	**-29.421**	**0.000**
Pan	9	**0.547**	**-0.463**	**0.023**	12	**0.482**	**-55.396**	**0.012**
Gorilla	7	**0.806**	**-0.605**	**0.006**	15	**0.786**	**-53.538**	**0.000**
Pongo	6	0.524	-0.650	0.104	5	0.697	-54.961	0.079

Bold face indicates significant at α < 0.05.

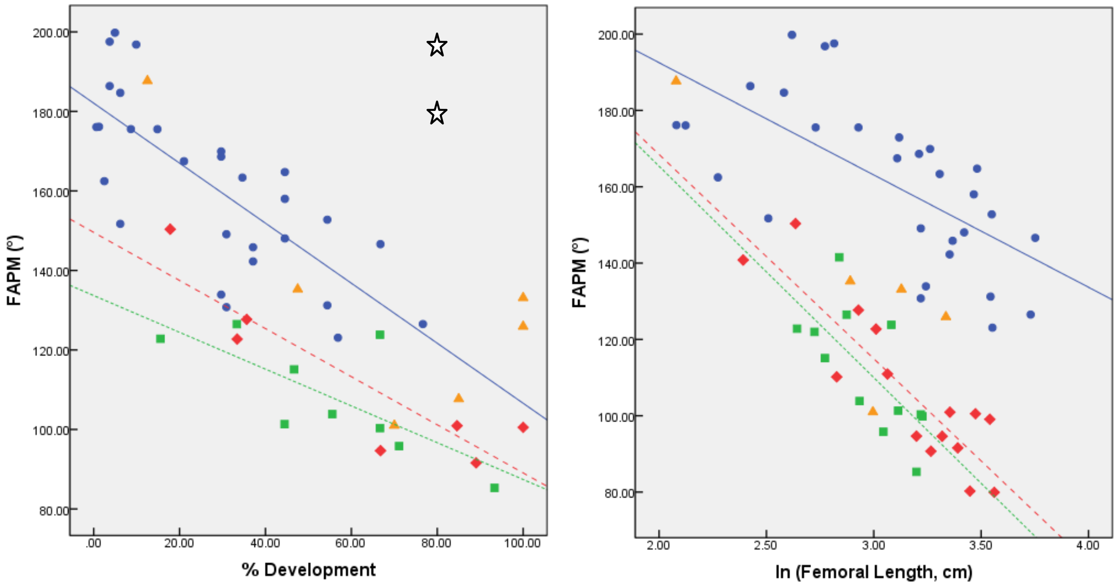

Figure 3.1.5.: Linear regressions between angle FAPM values and the percentage of development (left), and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*

3.1.1.6. Effect of development on angle of the Femoral Antero-Posterior Groove (FAPG)

Linear regression analyses did not reveal significant relationships between either one of the growth indicators and the values of angle FAPG in any of the species. Values could not be obtained for fossil specimens (Table III.I.VII., Fig. 3.1.6.).

Table III.I.VII. Regression results for angle FAPG

Species	% Maturity				ln (femoral length, cm)			
	n	R^2	b	p	n	R^2	b	p
Homo	32	0.021	0.084	0.429	32	0.018	-3.037	0.458
Pan	9	0.000	0.003	0.991	13	0.005	6.594	0.823
Gorilla	8	0.030	0.137	0.680	17	0.002	-3.289	0.855
Pongo	6	0.087	-0.108	0.569	5	0.044	-3.799	0.736

Bold face indicates significant at α < 0.05.

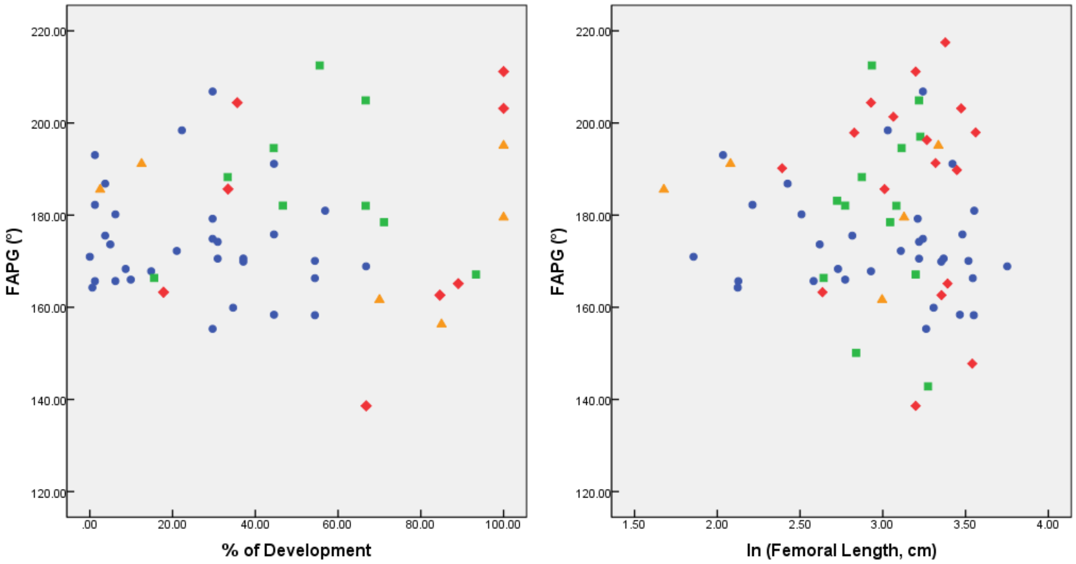

Figure 3.1.6.: Linear regressions between angle FAPG values and the percentage of development (left), and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*

3.1.1.7. Effect of development on femoral obliquity

Linear regression analyses revealed that the percentage of development significantly predicted the values of femoral obliquity angles for humans (when measured from photographs) (Table III.I.VIII., Fig. 3.1.7.). Femoral length also significantly predicted the values of femoral obliquity angles for humans with this method. The femoral obliquity increased with development and femoral growth, in the sense that the knee's valgus position increases further. Linear regressions showed that there were no significant relationships between the femoral obliquity values obtained from 3D data and either growth indicator (Table III.I.IX, Fig. 3.1.8.). Humans are the only exception to this, the regression tests revealed that the femoral length significantly predicted the femoral obliquity. The femoral obliquity increased with femoral growth.

Table III.I.VIII. Regression results for Femoral Obliquity Angles measured from photographs

	% Maturity				ln (femoral length, cm)			
Species	n	R²	b	p	n	R^2	b	p
Homo	46	**0.328**	**0.090**	**0.000**	47	**0.523**	**4.879**	**0.000**
Pan	26	0.003	0.006	0.774	31	0.004	-0.631	0.729
Gorilla	15	0.137	-0.039	0.174	29	0.049	2.002	0.251
Pongo	20	0.078	0.260	0.232	21	0.177	2.613	0.057

Bold face indicates significant at α < 0.05.

Table III.I.IX. Regression results for Femoral Obliquity Angle measured from landmarks

Species	% Maturity				ln (femoral length, cm)			
	n	R^2	b	p	n	R	b	p
Homo	34	0.107	0.054	0.059	34	**0.180**	**2.795**	**0.012**
Pan	9	0.012	-0.010	0.780	13	0.149	-5.025	0.192
Gorilla	8	0.225	-0.068	0.235	17	0.068	-3.125	0.311
Pongo	6	0.064	0.019	0.628	5	0.108	1.675	0.589

Bold face indicates significant at α < 0.05.

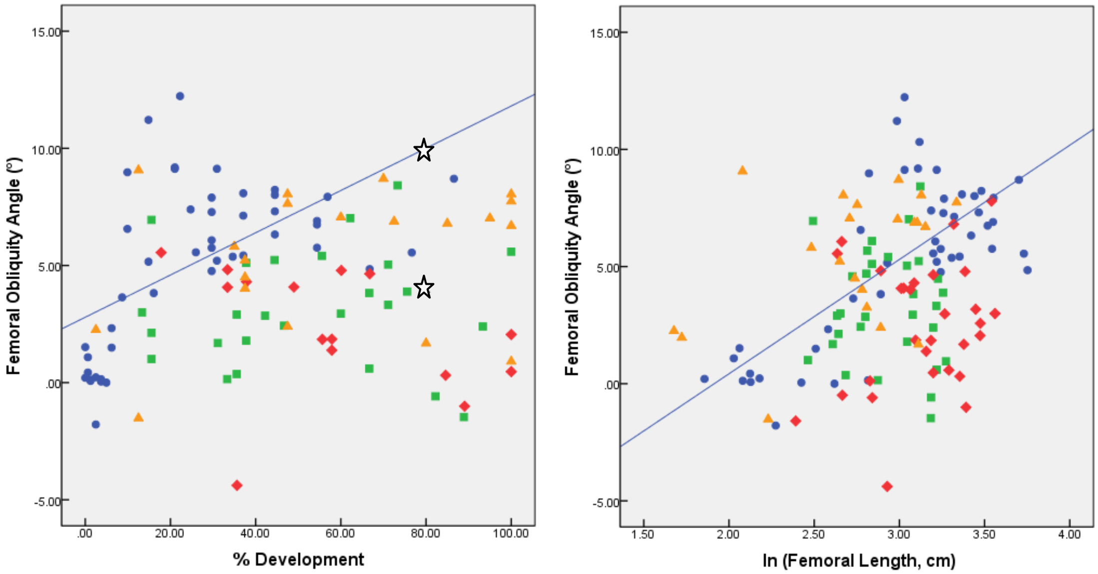

Figure 3.1.7.: Linear regressions between the femoral obliquity angle measured from photographs and the percentage of development (left), and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*

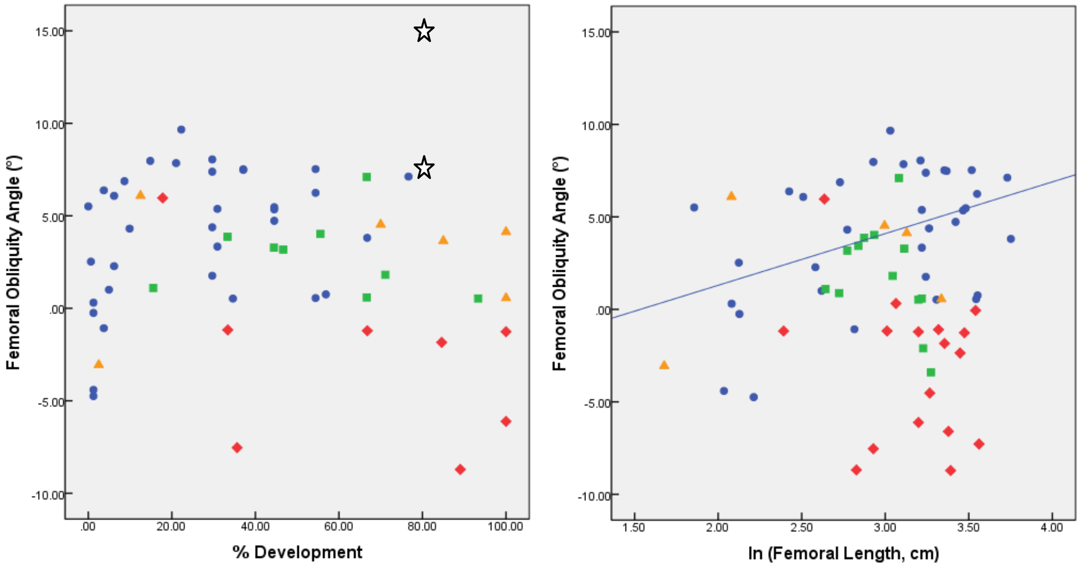

Figure 3.1.8.: Linear regressions between the femoral obliquity angle and the percentage of development (left), and the natural logarithm of femoral length (right). Angles measured digitally. *Legend as in Fig. 3.1.1.*

3.1.2. Interspecies differences in the development of the infradiaphyseal plane

A principal component analysis on the landmarks of the distal femoral diaphysis, followed by an analysis of covariance, shows that there is a significant variation between species with regards to the first component (Table III.I.X. and III.I.XI.). The first component explains 26% of the variance, and clearly separates humans from the great apes, as seen on the scatter plot of the first two principal component values, with humans showing a flatter infradiaphyseal plane and great apes showing more convolution of this trait (Fig 3.1.9.). The second component explains 13% of the variance, and it seems, from the scatter plot, that this component corresponds to age groups, with younger individuals being higher on this axis and having a flatter infradiaphyseal plane and older group being lower and associated with a more convoluted plane. The posthoc analysis confirms that humans are separated from great apes in the first component (Table III.I.XII.). From the wireframe diagrams, it appears that the femoral metaphysis is flatter in anteroposterior view in humans, while the surface appears much more convoluted in great ape species. Great apes are not significantly different from each other.

Table III.I.X.: Variance explained for the first two principal components of the analysis done on landmarks of the distal femoral metaphysis

Component	Initial Eigenvalues		
	Total	% of Variance	Cumulative %
1	0.78262	26.73562	26.73562
2	0.38323	13.09180	39.82742

Table III.I.XI.: ANOVA results for metaphyseal landmarks of the distal femur

	n	F	Sig.
PC 1	47	**39.803**	**0.000**
PC 2	47	2.063	0.119

Bold face indicates significant at α < 0.05.

Table III.I.XII.: Bonferroni posthoc analysis results for metaphyseal landmarks of the distal femur

	Species		Mean Difference	Std. Error	Sig.
PC 1	*Homo* (n=15)	*Pan* (n=12)	**0.154**	0.018	**0.000**
		Gorilla (n=15)	**0.169**	0.017	**0.000**
		Pongo (n=5)	**0.150**	0.024	**0.000**
	Pan	*Gorilla*	0.015	0.018	1.000
		Pongo	-0.004	0.025	1.000
	Gorilla	*Pongo*	-0.019	0.024	1.000

Bold face indicates significant at α < 0.05.
PC2 was not included as it had no significant effect.

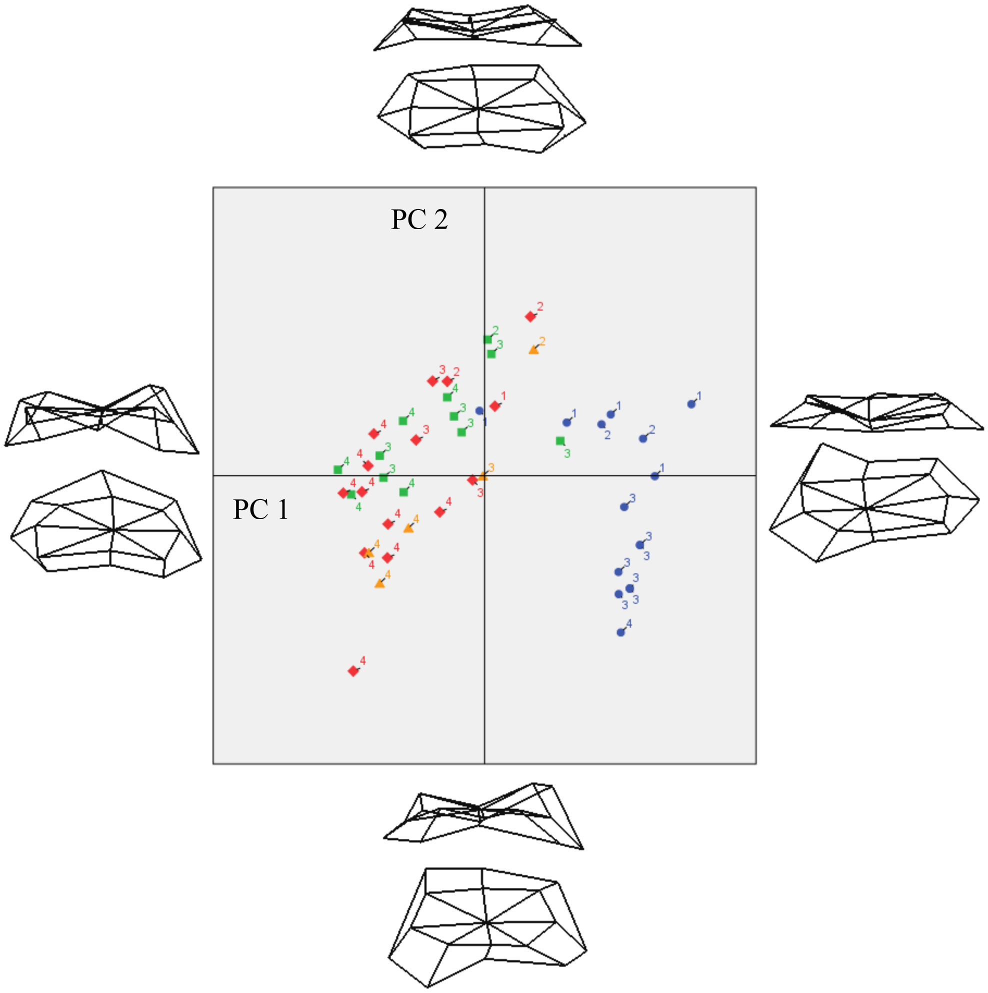

Figure 3.1.9.: Principal Component Analyses scatter plot for metaphyseal landmarks of the femur. *Legend as in Fig. 3.1.1. Medial side is on the right, and anterior side is on top in proximal view.*

A principal component analysis on all the angles of the distal femoral diaphysis was performed. From the graph (Fig. 3.1.10.), it appears that the first component separates species, with gorillas to the left, humans to the right, and chimpanzees and orang-utans overlapping in the middle. However, we also see that age groups also tend to align themselves on this axis with younger individuals in each species being to the right. Most angles are positively correlated with the first component, specifically, FAPM, FMLG, FAPL, and FMLA. These angles are the variables that principally separate humans from other great ape species on the first component (Table III.I.XIV.). The second component does not appear to separate species or age groups and the correlation values were therefore not included. Indeed, the eigenvalues show that the first component accounts for 57% of the variance, and the second for only 17% (Table III.I.XIII.). The analysis of variance shows that there is a significant variation among species with regards to the first component (Table III.I.XV.). Results from the posthoc analysis (Table III.I.XVI.) confirm that humans are significantly different from the great ape species, but that ape species do not separate from each other.

Table III.I.XIII: Variance explained for the first two principal components of the analysis done angles values of the distal femoral metaphysis

Component	Initial Eigenvalues		
	Total	% of Variance	Cumulative %
1	3.439	57.312	57.312
2	1.033	17.216	74.528

Table III.I.XIV: Correlation between femur angles and components

Variable	PC1
FMLA	0.778
FMLP	-0.449
FMLG	0.922
FAPL	0.911
FAPM	0.929
FAPG	-0.299

Table III.I.XV. ANOVA femur angles

	n	F	Sig.
PC 1	52	**22.456**	**.000**
PC 2	52	.999	.402

Bold face indicates significant at α<0.05

Table III.I.XVI: Boneferroni post hoc analysis results for femur angles

	Species		Mean Difference	Std. Error	p
PC 1	*Homo* (n=20)	***Pan*** **(n=12)**	**1.334**	**0.241**	**.000**
		Gorilla **(n=15)**	**1.742**	**0.225**	**.000**
		Pongo **(n=5)**	**1.133**	**0.330**	**.007**
	Pan	*Gorilla*	0.407	0.256	.706
		Pongo	-0.201	0.351	1.000
	Gorilla	*Pongo*	-0.608	0.341	.484

Bold face indicates significant at α<0.05
PC2 was not included as it had no significant effect.

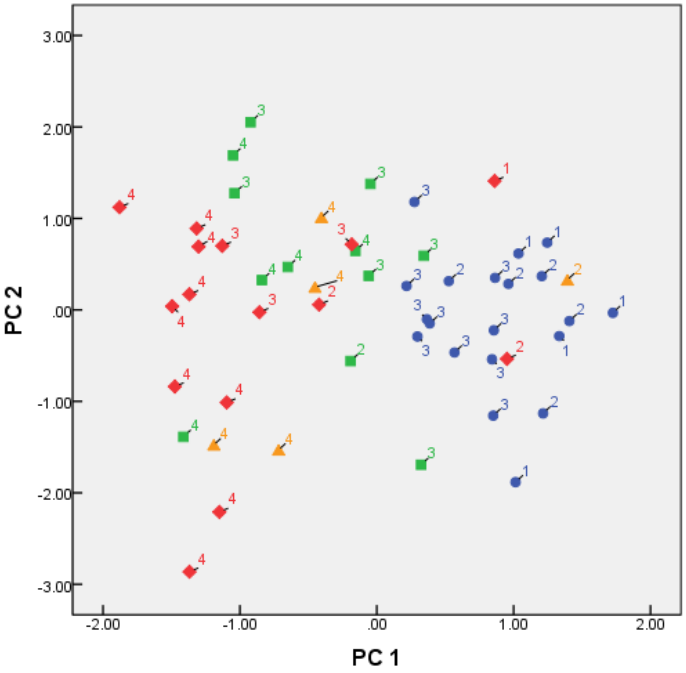

Figure 3.1.10.: Principal Component Analyses scatter plot for metaphyseal angles of the femur. *Legend as in Fig. 3.1.1.*

3.1.2.1. Interspecies variation in the Femoral Anterior Medio-Lateral angle (FMLA)

An analysis of covariance has shown that the relationships between the percentage of development and FMLA values are different among species for the percentage of maturity only (Table III.I.XVII). Post hoc tests on values for FMLA revealed that gorilla values were significantly more acute than that of other species, but that other species did not differ significantly from each other (Table III.I.XVIII).

Table III.I.XVII. ANCOVA results for angle FMLA

Variable	N	F	p
% Maturity	52	**6.866**	**0.001**

Bold face indicates significant at $\alpha < 0.05$

Table III.I.XVIII: Bonferroni posthoc analysis results for angle FMLA vs % Maturity

Species		Mean Difference	p
Homo (n=30)	*Pan* (n=9)	4.861	1.000
	Gorilla (n=8)	**18.641**	**0.001**
	Pongo (n=5)	0.120	1.000
Pan	*Gorilla*	**13.780**	**0.033**
	Pongo	-4.741	1.000
Gorilla	*Pongo*	**-18.522**	**0.010**

Bold face indicates significant at $\alpha < 0.05$.

3.1.2.2. Interspecies variation in the Femoral Posterior Medio-Lateral angle (FMLP)

The main effect of species on angle FMLP relative to the percentage of maturity and femoral length was significant, showing that the FMLP angle relative to either independent variables is different among species (Table III.I.XIX.). Post hoc tests on values for FMLP when plotted against the percentage of development revealed that the means for chimpanzees were significantly lower – or more acute – than those of gorillas, but that other species did not differ significantly from each other. When the values were plotted against femoral length, post hoc analyses revealed that the angle values for gorillas were significantly more obtuse than that of humans and chimpanzees, but that other species were not significantly different from each other (Table III.I.XX.). This is the only case where humans have significantly lower values than gorillas, showing the metaphysis in this area is more convoluted.

Table III.I.XIX.: ANCOVA Results for FMLP

Variable	N	F	p
% Maturity	52	**3.715**	**0.018**
ln (femoral length, cm)	63	**6.813**	**0.001**

Bold face indicates significant at α < 0.05.

Table III.I.XX.: Bonferroni posthoc analysis for angle FMLP

% Maturity				ln (femoral length, cm)			
Species		Mean Dif	p	Species		Mean Dif	p
Homo (n=30)	*Pan* (n=9)	1.543	1.000	*Homo* (n=30)	*Pan* (n=12)	2.677	1.000
	Gorilla (n=8)	-10.081	0.071		*Gorilla* (n=17)	**-10.339**	**0.001**
	Pongo (n=5)	-9.189	0.329		*Pongo* (n=4)	-4.241	1.000
Pan	*Gorilla*	**-11.625**	**0.047**	*Pan*	*Gorilla*	**-13.017**	**0.001**
	Pongo	-10.732	0.192		*Pongo*	-6.919	1.000
Gorilla	*Pongo*	0.893	1.000	*Gorilla*	*Pongo*	6.098	1.000

Bold face indicates significant at α < 0.05.

3.1.2.3. Interspecies variation in the Femoral Medio-Lateral Groove angle (FMLG)

The main effect of species on angle FMLG was significant when the values were plotted against the percentage of development (Table III.I.XXI.). Post hoc tests on values for FMLG revealed that the mean values for chimpanzees were significantly lower, or more acute, than that of humans, but that other species did not differ significantly from each other (Table III.I.XXII.).

Table III.I.XXI.: ANCOVA results for angle FMLG

Variable	N	F	p
% Maturity	55	**2.992**	**0.040**

Bold face indicates significant at α < 0.05.

Table III.I.XXII.: Bonferroni posthoc analysis results for angle FMLG vs % Maturity

Species		Mean Difference	p
Homo (n=33)	*Pan* (n=9)	**12.209**	**0.045**
	Gorilla (n=8)	9.977	0.273
	Pongo (n=5)	7.445	1.000
Pan	*Gorilla*	-2.232	1.000
	Pongo	-4.764	1.000
Gorilla	*Pongo*	-2.532	1.000

Bold face indicates significant at α < 0.05.

3.1.2.4. Interspecies variation in the Femoral Medial Antero-Posterior angle (FAPM)

The analysis of covariance revealed that there is a significant difference between species in the relationships between the two growth indicators and the values for angle FAPM (Table III.I.XXIII.). Post hoc tests on values for FAPM, when plotted against percentage of development, revealed that the means for humans and orang-utans were significantly higher than the means for other species, but did not differ significantly from each other. No other comparisons were significant (Table III.I.XXIV.). When the test was done on values plotted against femoral length, results revealed that the mean values for humans were significantly higher, or more obtuse, than that of other species while the means for other species did not differ significantly from each other.

Table III.I.XXIII. ANCOVA results for FAPM

Variable	N	F	p
% Maturity	50	**14.96**	**0.000**
ln (femoral length, cm)	61	**55.762**	**0.000**

Bold face indicates significant at α < 0.05.

Table III.I.XXIV.: Bonferroni posthoc analysis results for angle FAPM

% Maturity				ln (femoral length, cm)			
Species		Mean Dif.	p	Species		Mean Dif.	p
Homo (n=28)	*Pan* (n=9)	**34.923**	**0.000**	*Homo* (n=29)	*Pan* (n=12)	**53.093**	**0.000**
	Gorilla (n=7)	**26.500**	**0.002**		*Gorilla* (n=15)	**51.229**	**0.000**
	Pongo (n=6)	2.003	1.000		*Pongo* (n=5)	**31.260**	**0.000**
Pan	*Gorilla*	-8.422	1.000	*Pan*	*Gorilla*	-1.864	1.000
	Pongo	**-32.920**	**0.001**		*Pongo*	-21.833	0.053
Gorilla	*Pongo*	**-24.498**	**0.023**	*Gorilla*	*Pongo*	-19.969	0.087

Bold face indicates significant at α < 0.05.

3.1.2.5. Interspecies variation in femoral obliquity

The predicted main effect of species was significant on the development of the femoral obliquity angle measured from photographs and regressed against the femoral length. Similarly, the main effect of species was also significant when obliquity angle values measured from landmarks were regressed against the percentage of development, and against the of the femoral length (Table III.I.XXV.). For the femoral obliquity angles measured from photographs, post hoc tests revealed that humans and orang-utans had mean values that were significantly higher than values for chimpanzees and gorillas, while not being significantly different from each other, suggesting the femoral obliquity is more pronounced in these species than in chimpanzees and gorillas. Similarly, chimpanzees and gorillas were not significantly different from each other. Post hoc tests on digitally measured obliquity values revealed that gorilla means were significantly lower than that of other species, but that other species did not differ significantly from each other (Table III.I.XXVI.).

Table III.I.XXV.: Analysis of covariance results for the effect of species on the development of femoral obliquity

Independent variable	FOA (photograph values)			FOA (digital values)		
	N	F	p	N	F	p
% of Development	-	-		57	**7.143**	**0.000**
ln (Femoral Length)	128	**14.533**	**0.000**	69	**16.99**	**0.000**

Bold face indicates significant at $\alpha \leq 0.05$

Table III.I.XXVI.: Bonferroni posthoc analysis result for femoral obliquity angle

FOA Photos vs ln (femoral length,cm)				FOA Landmarks vs % maturity				FOA Landmarks vs ln (femoral length, cm)			
Species		Mean Dif.	p	Species		Mean Dif.	p	Species		Mean Dif.	p
Homo (n=47)	*Pan* (n=31)	**1.728**	**0.029**	*Homo* (=34)	*Pan* (n=9)	1.589	1.000	*Homo* (n=34)	*Pan* (n=13)	2.202	0.347
	Gorilla (n=29)	**3.313**	**0.000**		*Gorilla* (n=8)	**7.299**	**0.000**		*Gorilla* (n=17)	**7.497**	**0.000**
	Pongo (n=21)	-1.116	0.682		*Pongo* (n=6)	1.860	1.000		*Pongo* (n=5)	1.050	1.000
Pan	*Gorilla*	1.585	0.130	*Pan*	*Gorilla*	**5.710**	**0.012**	*Pan*	*Gorilla*	**5.295**	**0.001**
	Pongo	**-2.844**	**0.001**		*Pongo*	0.271	1.000		*Pongo*	-1.152	1.000
Gorilla	*Pongo*	**-4.429**	**0.000**	*Gorilla*	*Pongo*	**-5.438**	**0.042**	*Gorilla*	*Pongo*	**-6.447**	**0.005**

Bold face indicates significant at $\alpha < 0.05$.

3.2. Tibia

Mean values for angles measured on the tibia are presented in table III.II.I. Fossil A.L. 333-39 was estimated to be at 80% of maturity, and the values obtained on this specimen are included with means for age group 4.

Table III.II.I: Mean values (º) for each species in four age groups for each tibial angle

Age Group	Species	TMLA		TMLC		TMLP		TAPM		TAPC		TAPL		TOA	
		n	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean
1	*Homo*	3	177.0	4	182.1	4	186.0	4	165.7	4	178.1	4	175.3	4	-0.4
	Pan	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA
	Gorilla	1	164.2	1	175.1	1	183.0	1	172.5	1	155.9	1	155.9	1	-4.3
	Pongo	1	207.4	0	NA	1	156.4	0	NA	0	NA	0	NA	1	0.6
2	*Homo*	3	175.3	5	180.9	3	195.3	4	181.8	4	163.1	4	172.4	5	-0.3
	Pan	2	185.7	1	192.9	2	189.9	1	175.6	1	206.0	1	180.5	2	-4.6
	Gorilla	4	165.9	2	177.0	4	171.5	1	172.5	2	155.4	2	150.6	4	-5.9
	Pongo	1	171.6	1	196.0	1	195.0	1	156.5	1	200.9	1	161.7	1	2.7
3	*Homo*	5	169.9	7	180.0	6	194.1	6	185.6	6	166.5	6	166.9	7	-0.1
	Pan	13	167.4	8	188.0	13	180.4	9	174.8	8	181.1	8	168.4	13	-1.8
	Gorilla	7	168.4	2	181.6	8	186.9	1	182.6	1	197.5	1	170.2	8	-1.7
	Pongo	5	172.6	2	175.5	4	176.8	2	169.6	2	151.2	2	158.1	5	4.0
4	*Homo*	0	NA	1	180.4	1	215.0	0	NA	0	NA	1	144.1	1	2.1
	Pan	11	155.9	6	175.5	11	166.0	6	168.3	6	156.3	6	154.6	11	1.8
	Gorilla	14	161.5	4	169.7	14	171.9	5	172.9	5	164.9	5	160.1	14	-2.2
	Pongo	9	184.48	2	171.31	9	167.33	2	171.99	2	179.46	2	187.81	9	0.3387
	AL 333-39		NA	1	197.4	1	203.0	1	181.4	1	195.5	1	166.0		NA

Age group 1: 1-10% of maturity reached; age group 2: 11-30% of maturity reached; age group 3: 31-65% of maturity reached; age group 4: 66-100% of maturity reached.

3.2.1. Effect of development on the topography of the proximal metaphysis of the tibia

3.2.1.1. Effect of development on the Tibial Anterior Medio-Lateral angle (TMLA)

Linear regression analyses revealed that the percentage of development significantly predicted the values of angle TMLA for chimpanzees and gorillas. The angle became more acute with the degree of development. Results for humans and orang-utans were not significant. These analyses also showed that the femoral length did not significantly predict the values of the angle TMLA, except for chimpanzees, where the angle decreased with femoral growth (Table III.II.II**,** Fig. 3.2.1.). There was no data available for the fossil specimens.

Table III.II.II. Regression results for angle TMLA

	% Maturity				ln (femoral length, cm)			
Species	n	R^2	b	p	n	R^2	b	p
Homo	11	0.016	-0.087	0.711	11	0.024	-4.636	0.647
Pan	20	**0.223**	**-0.264**	**0.035**	26	**0.267**	**-33.113**	**0.007**
Gorilla	12	**0.338**	**-0.230**	**0.047**	25	0.068	-9.418	0.209
Pongo	15	0.031	0.093	0.533	15.000	0.001	1.086	0.921

Bold face indicates significant at $\alpha < 0.05$.

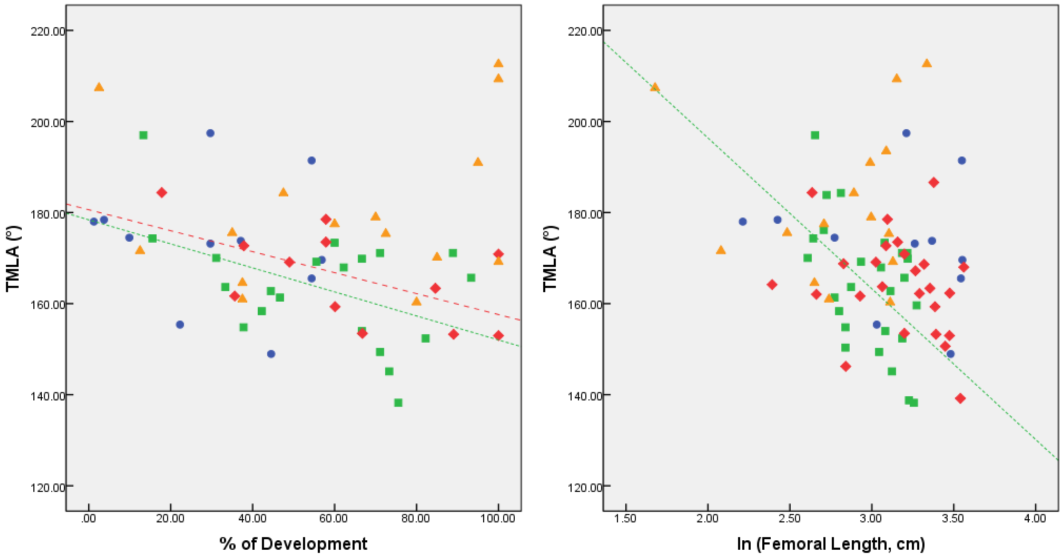

Figure 3.2.1.: Linear regressions between TMLA angle values and the percentage of development (left) and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*

3.2.1.2. Effect of development on the Tibial Central Medio-Lateral angle (TMLC)

Linear regression analyses revealed that there was no significant relationship between the growth variable and the TMLC angle for any species, except chimpanzees where TMLC has a significant relationship with the femoral length (Table III.II.III.).

Table III.II.III.: Regression results for angle TMLC

	% Maturity				ln (femoral length, cm)			
Species	n	R^2	b	p	n	R^2	b	p
Homo	17	0.114	-0.103	0.186	17	0.120	-4.531	0.174
Pan	12	0.293	-0.246	0.069	15	**0.375**	**-26.426**	**0.015**
Gorilla	5	0.217	-0.172	0.429	8	0.104	-6.763	0.436
Pongo	5	0.648	-0.337	0.100	4	0.865	-29.644	0.070

Bold face indicates significant at $\alpha < 0.05$.

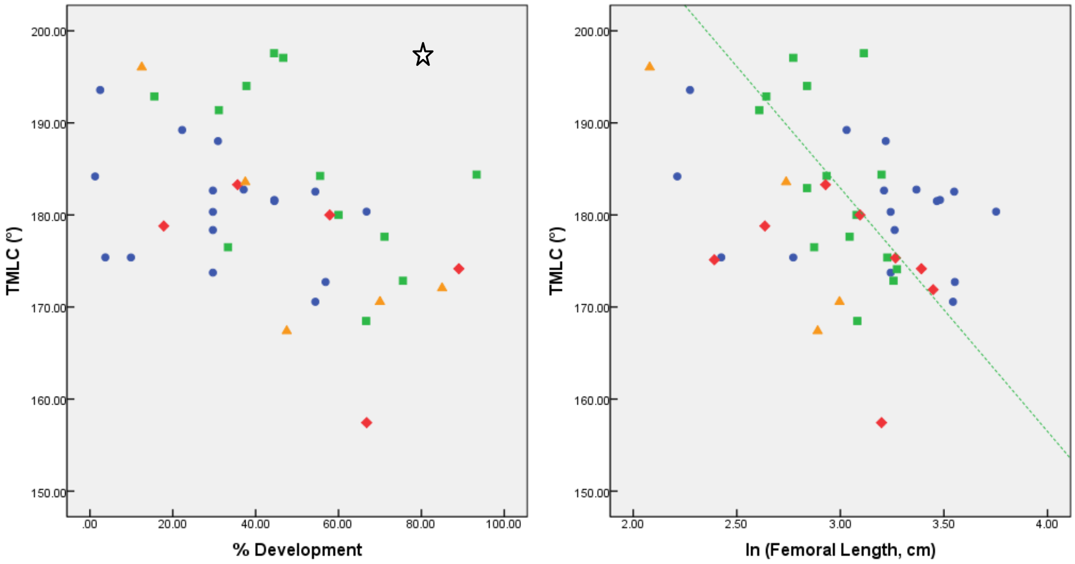

Figure 3.2.2.: Linear regressions between TMLC angle values and the percentage of development (left) and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*

3.2.1.3. Effect of development on the Tibial Posterior Medio-Lateral angle (TMLP)

Linear regression analyses revealed that, for chimpanzees, both the percentage of development and the femoral length significantly predicted the values of angle TMLP. The angle became more acute with the degree of development and with femoral growth (Table III.II.IV., Fig 3.2.3.). No significant relationships were found between either one of the growth indicators and the values for TMLP in the other three species.

Table III.II.IV.: Regression results for angle TMLP

	% Maturity				ln (femoral length, cm)			
Species	n	R^2	b	p	n	R^2	b	p
Homo	14	0.247	0.404	0.071	14	0.171	14.270	0.141
Pan	20	**0.200**	**-0.379**	**0.048**	26	**0.201**	**-42.646**	**0.022**
Gorilla	13	0.179	-0.273	0.149	26	0.002	2.831	0.843
Pongo	14	0.009	-0.052	0.749	14	0.003	-1.913	0.863

Bold face indicates significant at $\alpha < 0.05$.

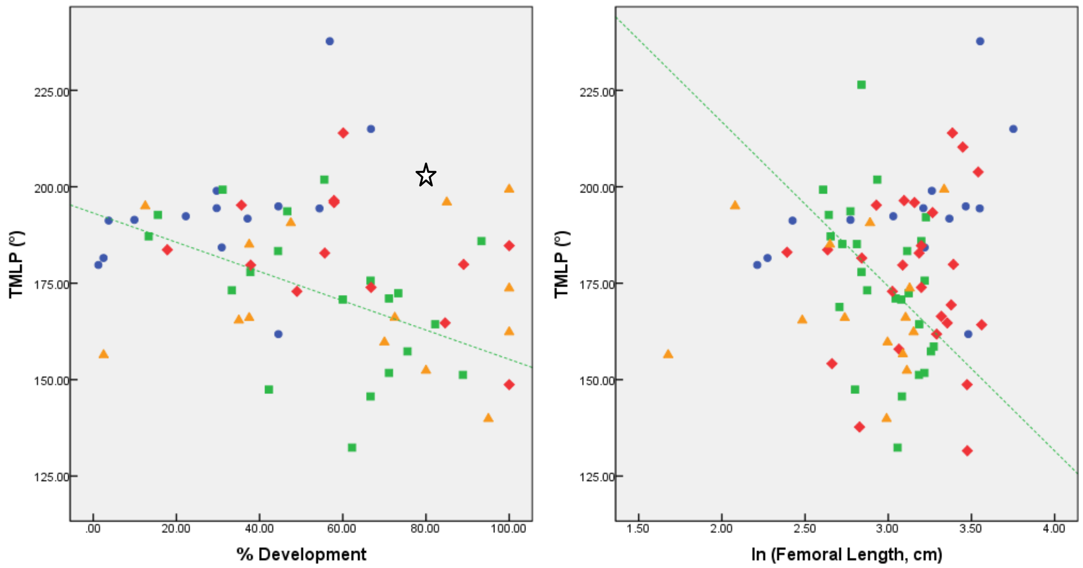

Figure 3.2.3.: Linear regressions between TMLP angle values the percentage of development (left) and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*

3.2.1.4. Effect of development on the Tibial Medial Antero-Posterior angle (TAPM)

Linear regression analyses revealed that the percentage of development significantly predicted the values of angle TAPM for humans and orang-utans. The angle becomes more obtuse with the degree of development. Regression analyses also showed that the femoral length significantly predicted the values of the angle TAPM for humans and orang-utans, where the angle becomes more obtuse with femoral length, and for chimpanzees, where the angle becomes more acute with femoral length (Table III.II.V., Fig. 3.2.4.).

Table III.II.V.: Regression results for angle TAPM

Species	% Maturity				ln (femoral length, cm)			
	n	R^2	b	p	n	R^2	b	p
Homo	14	**0.579**	**0.418**	**0.002**	14	**0.651**	**18.168**	**0.000**
Pan	12	0.092	-0.129	0.339	16	**0.251**	**-20.775**	**0.048**
Gorilla	3	0.200	-0.148	0.705	7	0.016	3.318	0.787
Pongo	5	**0.777**	**0.210**	**0.048**	4	**0.973**	**16.368**	**0.014**

Bold face indicates significant at α < 0.05.

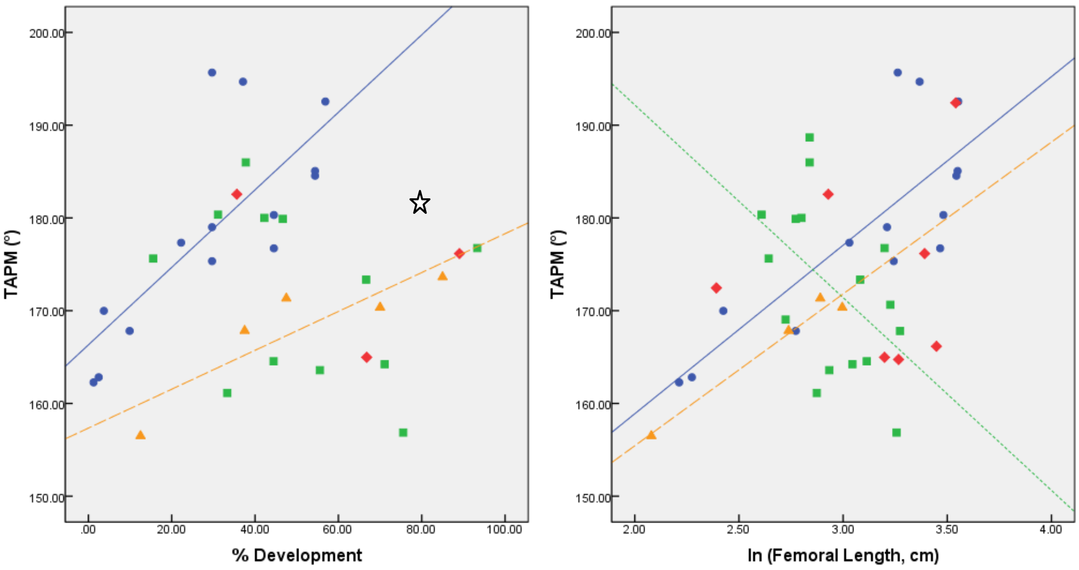

Figure 3.2.4.: Linear regressions between TAPM angle values and the percentage of development (left) and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*

3.2.1.5. Effect of development on the Tibial Central Antero-Posterior angle (TAPC)

Linear regression analyses between TAPC and the percentage of development or femoral length were significant for chimpanzees. The angle becomes more acute with the increase in development and femoral growth. Analyses found no significant relationships between the growth indicators and the values of TAPC for humans, gorillas, and orang-utans (Table III.II.VI., Fig. 3.2.5.).

Table III.II.VI.: Regression results for angle TAPC

Species	% Maturity				ln (femoral length, cm)			
	n	R^2	b	p	n	R^2	b	p
Homo	14	0.118	-0.228	0.228	15	0.651	-7.801	0.320
Pan	12	**0.345**	**-0.523**	**0.045**	11	**0.251**	**-72.722**	**0.005**
Gorilla	4	0.000	0.006	0.992	4	0.016	14.494	0.521
Pongo	5	0.001	-0.039	0.961	5	0.973	-68.257	0.135

Bold face indicates significant at $\alpha < 0.05$.

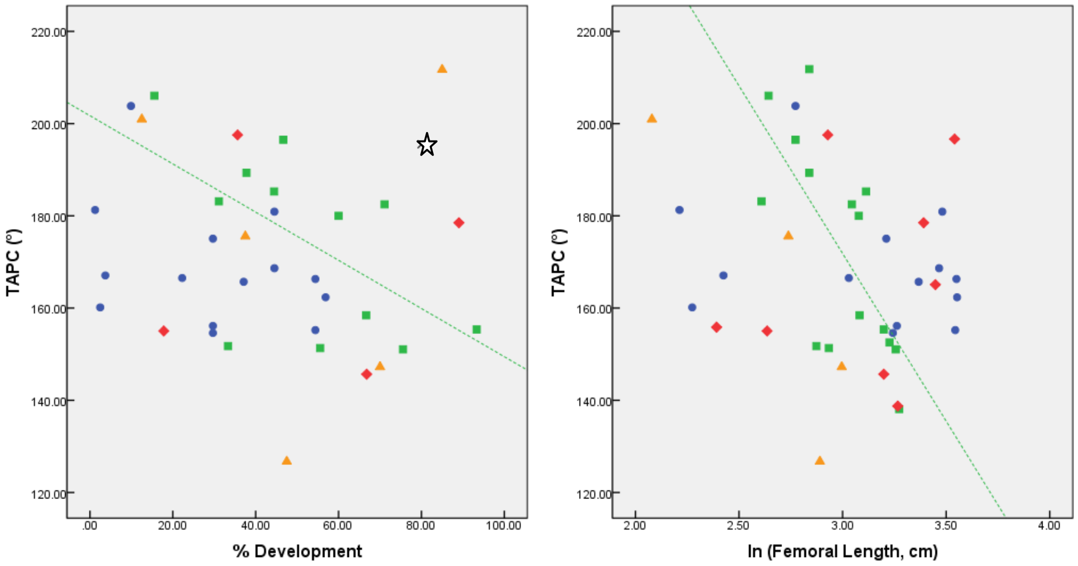

Figure 3.2.5.: Linear regressions between TAPC angle values and the percentage of development (left) and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*

3.2.1.6. Effect of development on the Tibial Lateral Antero-Posterior angle (TAPL)

Linear regression analyses revealed that both the percentage of development and the femoral length significantly predicted the values of angle TAPL for chimpanzees. The angle became more acute with the degree of development and with femoral growth. There were no significant relationships between either one of the growth indicators and the values of TAPL for humans, gorillas and orang-utans (Table III.II.VII., Fig. 3.2.6.).

Table III.II.VII.: Regression results for angle TAPL

Species	% Maturity				ln (femoral length, cm)			
	n	R^2	b	p	n	R^2	b	p
Homo	15	0.153	-0.260	0.149	15	0.141	-10.716	0.168
Pan	11	**0.423**	**-0.481**	**0.030**	15	**0.561**	**-51.606**	**0.001**
Gorilla	4	0.401	-0.342	0.367	8	0.084	14.546	0.487
Pongo	5	0.440	0.521	0.222	4	0.002	-0.951	0.959

Bold face indicates significant at $\alpha < 0.05$.

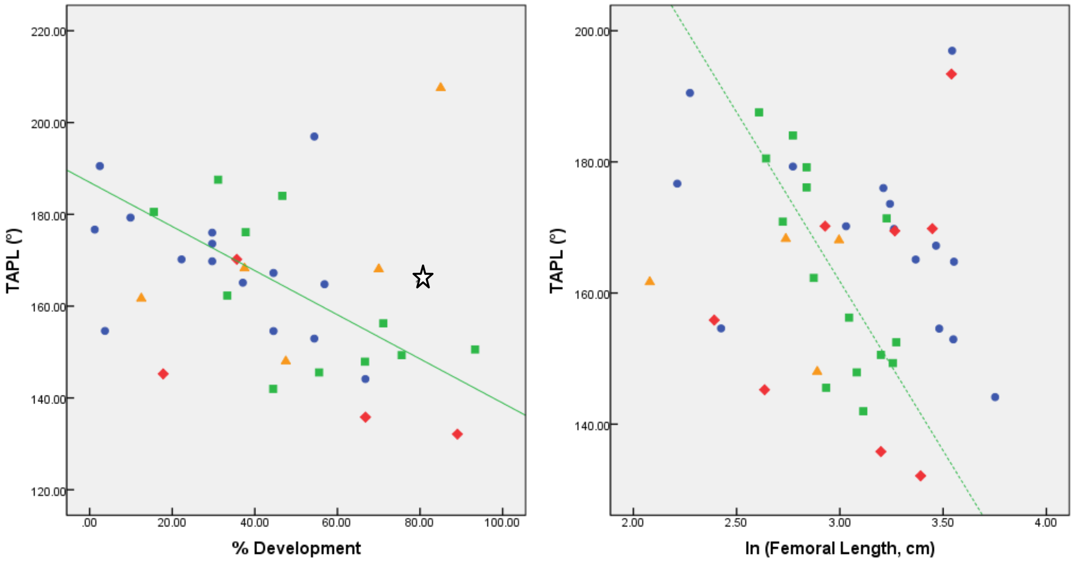

Figure 3.2.6.: Linear regressions between TAPL angle values and the percentage of development (left) and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*

3.2.1.7. Effect of development on tibia obliquity

Linear regression analyses revealed that the percentage of development significantly predicted the values of the obliquity angle of the tibia for chimpanzees, but not for humans, gorillas and orang-utans. Development is accompanied by an increase in tibial obliquity for chimpanzees. The analyses also showed that the femoral length significantly predicted the values of the obliquity angle of the tibia for chimpanzees and gorillas, where an increase in femoral length is associated with an increase in tibial obliquity. Human and orang-utan data showed no significant relationship between these two variables. No data was available for the fossil specimens (Table III.II.VIII., Fig. 3.2.7.).

Table III.II.VIII.: Regression results for tibial obliquity angle

	% Maturity				ln (femoral length, cm)			
Species	n	R^2	b	p	n	R^2	b	p
Homo	17.000	0.054	0.029	0.371	17.000	0.013	0.597	0.667
Pan	20.000	**0.418**	**0.097**	**0.002**	26.000	**0.436**	**10.804**	**0.000**
Gorilla	13.000	0.022	0.019	0.627	26.000	**0.171**	**5.162**	**0.036**
Pongo	15.000	0.063	-0.027	0.368	15.000	0.024	-1.228	0.583

Bold face indicates significant at $\alpha < 0.05$.

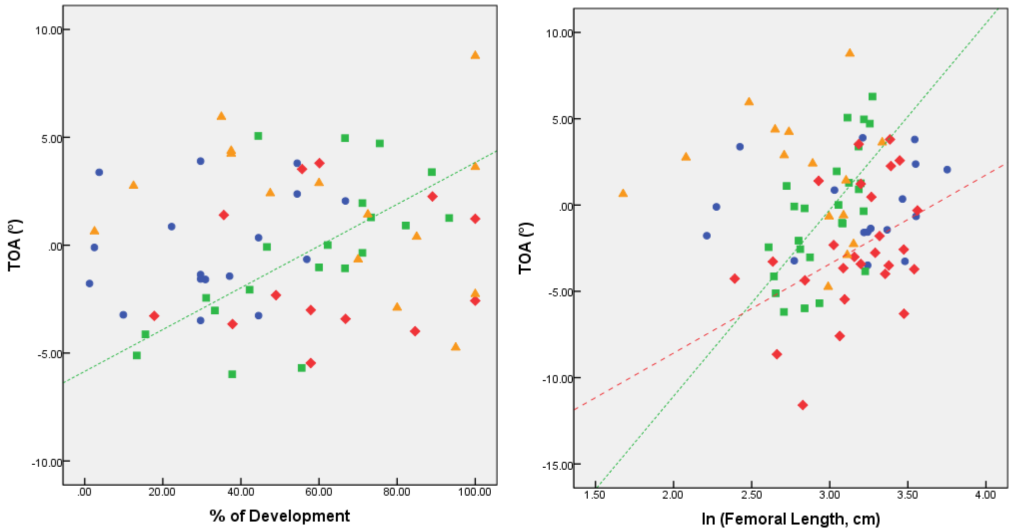

Figure 3.2.7.: Linear regressions between the obliquity angle of the tibia and the percentage of development (left) and the natural logarithm of femoral length (right). *Legend as in Fig. 3.1.1.*

3.2.2. Interspecies differences in the development of the proximal metaphysis of the tibia

A principal component analysis on the landmarks of the proximal tibial diaphysis, followed by an analysis of variance, shows that there is a significant variation among species with regards to the first and second components (Tables III.II.IX. and III.II.X.). From the scatter plot, we see that the first principal component separates humans from great apes species, and the second component seems to separate chimpanzees from gorillas and orang-utans, even though there still is come overlap (Fig. 3.2.8.). This suggests that humans and orang-utans have a "shorter" tibial tuberosity than chimpanzees and gorillas, and it also appears that humans have a metaphyseal surface that is more even. Results from the posthoc analysis confirm that humans are only significantly different from chimpanzees and gorillas and that orang-utans are significantly different from chimpanzees (Table III.II.XI.). Although the ANOVA suggests that the second principal component separates species, post hoc tests are never significant, probably because of the Bonferroni connection that tends to lower the significance level (due to multiple comparisons) relative to the ANOVA.

Table III.II.IX.: Variance explained for the first two principal components of the analysis done on landmarks of the proximal tibial metaphysis

Component	Eigenvalue	% of Variance	Cumulative %
1	0.8362	28.9321	28.9321
2	0.3553	12.2944	41.2264

Table III.II.X.: ANOVA results for metaphyseal landmarks of the proximal tibia

	n	F	Sig.
PC 1	47	**14.556**	**0.000**
PC 2	47	**3.171**	**0.037**

Bold face indicates significant at α < 0.05.

Table III.II.XI.: Bonferroni posthoc analysis of the metaphyseal landmarks of the proximal tibia

	Species		Mean Difference	Std. Error	Sig.
PC 1	*Homo* (n=15)	***Pan* (n=12)**	**0.167**	**0.026**	**0.000**
		***Gorilla* (n=15)**	**0.131**	**0.030**	**0.001**
		Pongo (n=5)	0.074	0.033	0.177
	Pan	*Gorilla*	-0.036	0.028	1.000
		Pongo	**-0.093**	**0.031**	**0.029**
	Gorilla	*Pongo*	-0.056	0.034	0.640
PC 2	*Homo* (n=15)	*Pan* (n=12)	-0.009	0.023	1.000
		Gorilla (n=15)	0.057	0.026	0.214
		Pongo (n=5)	0.041	0.028	0.956
	Pan	*Gorilla*	0.066	0.024	0.060
		Pongo	0.050	0.027	0.418
	Gorilla	*Pongo*	-0.016	0.030	1.000

Bold face indicates significant at α < 0.05.

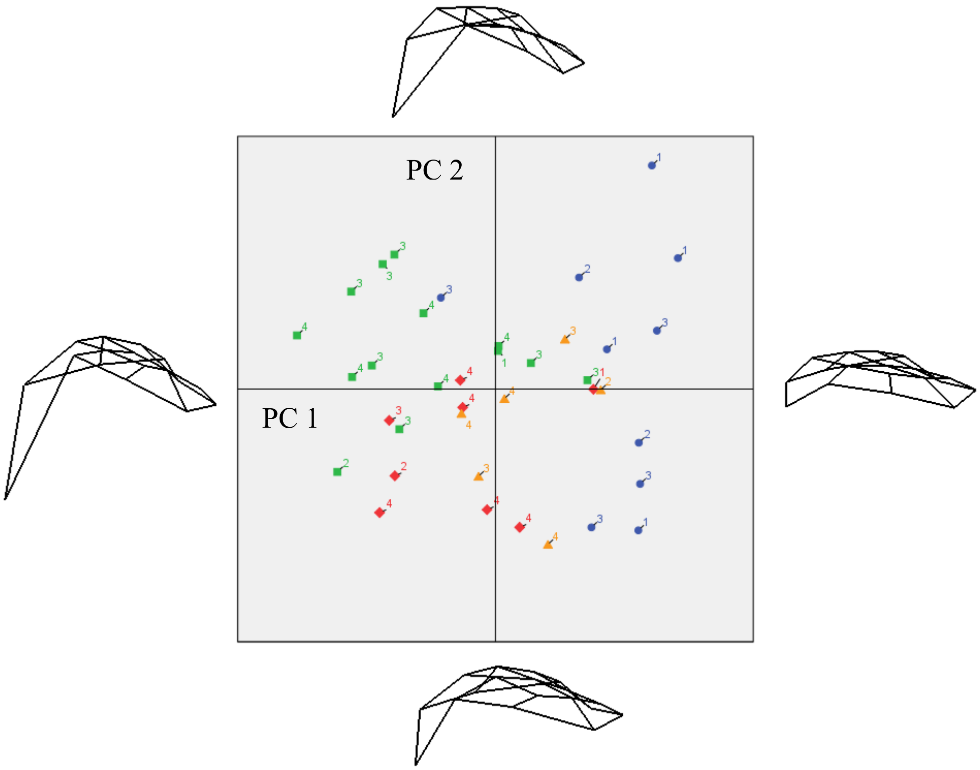

Figure 3.2.8.: Principal Component Analysis scatter plot for metaphyseal landmarks of the tibia. *Legend as in Fig. 3.1.1.*

Principal Component Analyses for the tibia angle values show that all angles are positively correlated with the first component, meaning individuals to the right of the scatter plot, i.e. humans, would show more obtuse angle values than individuals at the left, i.e. chimpanzees. The second component also creates significant difference and accounts for almost 20% of the variance (Tables III.II.XII and III.II.XIII). We see that the angles TMLA, TMLP and TAPM are positevly correlated with the second component, and the anglesTMLC, TAPC and TAPL are negatively correlated, meaning that individual higher on this axis- mostly humans – will have more obtuse and more acute values for these respective groups. The scatter plot therefore shows more overlap than in the case of the femur, but it appears that the second component separates humans from the rest of the great apes (Fig 3.2.9.). Results from the analysis of variance and posthoc analysis reveal mean angle values in humans are significantly different than that of chimpanzees, but there is no significant difference among other species (Tables III.II.XIV and III.II.XV).

Table III.II.XII.: Variance explained for the first two principal components of the analysis done on angle values of the distal femoral metaphysis

	Initial Eigenvalues		
Component	Total	% of Variance	Cumulative %
1	2.435	40.586	40.586
2	1.200	19.999	60.585

Table III.II.XIII.: Correlation between components and tibia angles

Variables	PC 1	PC 2
TMLA	.343	.598
TMLC	.646	-.435
TMLP	.670	.409
TAPM	.564	.468
TAPC	.752	-.504
TAPL	.755	-.110

Table III.II.XIV.: ANOVA for tibia angles

	n	F	Sig.
PC 1	35	1.303	.291
PC 2	35	**3.596**	**.024**

Bold face indicates significant at α<0.05

Table III.II.XV.: Boneferroni posthoc results for tibia angles

Variable	Species		Mean Difference	Std. Error	Sig.
PC 2	*Homo* (n=10)	***Pan* (n=14)**	**1.20932911***	**.37347428**	**.017**
		Gorilla (n=6)	.47933395	.46580426	1.000
		Pongo (n=5)	.65180407	.49406003	1.000
	Pan	*Gorilla*	-.72999516	.44014365	.644
		Pongo	-.55752504	.46994482	1.000
	Gorilla	*Pongo*	.17247012	.54620391	1.000

Bold face indicates significant at α<0.05

PC1 was not included as it did not show a significant effect.

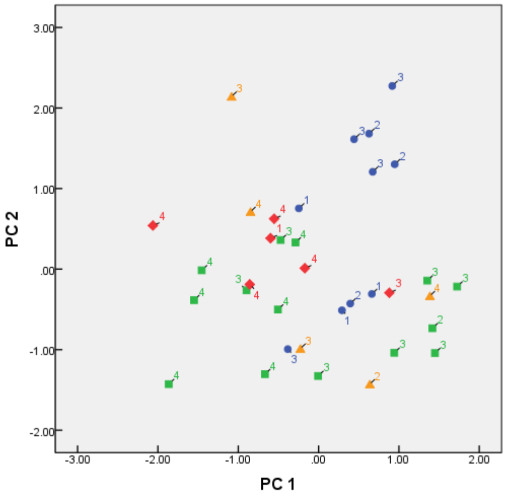

Figure 3.2.9.: Principal Component Analysis scatter plot of metaphyseal angle values tibia. *Legend as in Fig. 3.1.1.*

3.2.2.1. Interspecies variation in the Tibial Anterior Medio-Lateral angle (TMLA)

The analysis of covariance showed that the relationships between the independent variables and the values for TMLA are different among species (Table III.II.XVI.). Post hoc tests on values for TMLA revealed that the means for chimpanzees were significantly more acute than the means for orang-utans, and that the means for gorillas were also significantly more acute than the means for orang-utans when plotted against femoral length. The mean values for other species did not differ significantly from each other (Table III.II.XVII.).

Table III.II.XVI.: ANCOVA results for angle TMLA

Variable	N	F	p
% Maturity	58	**4.988**	**0.004**
ln (femoral length, cm)	77	**5.760**	**0.001**

Bold face indicates significant at α < 0.05.

Table III.II.XVII.: Bonferroni posthoc analysis results for angle TMLA

% of Maturity				ln (femoral length, cm)			
Species		Mean Dif.	p	Species		Mean Dif.	p
Homo (n=11)	*Pan* (n=20)	7.463	1.000	*Homo* (n=11)	*Pan* (n=26)	10.538	0.221
	Gorilla (n=12)	4.243	1.000		*Gorilla* (n=25)	8.918	0.450
	Pongo (n=15)	-10.165	0.547		*Pongo* (n=15)	-6.270	1.000
Pan	*Gorilla*	-3.220	1.000	*Pan*	*Gorilla*	-1.620	1.000
	Pongo	**-17.627**	**0.003**		*Pongo*	**-16.808**	**0.002**
Gorilla	*Pongo*	-14.408	0.055	*Gorilla*	*Pongo*	**-15.188**	**0.012**

Bold face indicates significant at $\alpha < 0.05$.

3.2.2.2. Interspecies variation in the Tibial Central Medio-Lateral angle (TMLC)

The main effect of species on angle TMLC was significant when the values were regressed against the percentage of development, but not significant when values were plotted against the natural logarithm of the femoral length (Table III.II.XVIII.). Post hoc tests on values for TMLC showed that, while species did have a significant effect on the angle values when plotted against the percentage of development, species did not appear to differ significantly from each other (Table III.II.XIX.), for reasons similar as described at the beginning of section 3.2.2.

Table III.II.XVIII.: ANCOVA results for angle TMLC

Variable	N	F	p
% Maturity	39	**3.220**	**0.035**
ln (femoral length, cm)	44	2.729	0.057

Bold face indicates significant at $\alpha < 0.05$.

Table III.II.XIX.: Bonferroni posthoc analysis results for TMLC

Species		Mean Differences	p
Homo (n=17)	*Pan* (n=12)	-8.008	0.079
	Gorilla (n=5)	1.838	1.000
	Pongo (n=5)	-0.773	1.000
Pan	*Gorilla*	9.846	0.116
	Pongo	7.235	0.481
Gorilla	*Pongo*	-2.611	1.000

3.2.2.3. Interspecies variation in the Tibial Posterior Medio-Lateral angle (TMLP)

The main effect of species on angle TMLP was significant when the values were plotted against the percentage of development and against the natural logarithm of the femoral length (Table III.II.XX.). Post hoc tests on values for TMLP, when plotted against the percentage of development, showed that the mean values for humans were significantly more obtuse than those of chimpanzees. When values were plotted against the natural logarithm of the femoral length, post hoc tests revealed that the means for humans were significantly higher than that of chimpanzees and orang-utans while the rest of the species did not differ significantly from each other (Table III.II.XXI.).

Table III.II.XX.: ANCOVA results for angle TMLP

Variable	N	F	p
% Maturity	61	**3.440**	**0.023**
ln (femoral length, cm)	80	**3.919**	**0.012**

Bold face indicates significant at α < 0.05.

Table III.II.XXI.: Bonferroni posthoc analysis results for angle TMLP

% Maturity				ln (femoral length, cm)			
species i	species j	Mean Dif.	p	species i	species j	Mean Dif.	p
Homo (n=14)	*Pan* (n=20)	**18.949**	**0.039**	*Homo* (n=14)	*Pan* (n=26)	**18.539**	**0.039**
	Gorilla (n=13)	7.533	1.000		*Gorilla* (n=26)	17.075	0.067
	Pongo (n=14)	18.038	0.107		*Pongo* (n=14)	**24.458**	**0.013**
Pan	Gorilla	-11.416	0.487	Pan	Gorilla	-1.464	1.000
	Pongo	-0.911	1.000		Pongo	5.919	1.000
Gorilla	Pongo	10.505	0.809	Gorilla	Pongo	7.383	1.000

Bold face indicates significant at α < 0.05.

3.2.2.4. Interspecies variation in the Tibial Medial Anterio-Posterior angle (TAPM)

The analysis of covariance has revealed that the relationships between both variables reflecting growth and TAPM values are not different among species (Table III.II.XXII.).

Table III.II.XXII.: ANCOVA results for angle TAPM

Variable	N	F	p
% Maturity	35	1.699	0.327
ln (femoral length, cm)	41	1.169	0.335

3.2.2.5. Interspecies variation in TAPL values

The main effect of species on angle TAPL was not significant when the values were plotted against the percentage of development, nor against the natural logarithm of the femoral length (Table III.II.XXIII).

Table III.II.XXIII.: ANCOVA results for angle TAPL

Variable	N	F	p
% Maturity	35	1.909	0.149
ln (femoral length, cm)	42	1.139	0.346

3.2.2.6. Interspecies variation in tibial obliquity

The main effect of species on the obliquity angle for the tibia was not significant when the values were regressed against the percentage of development, but significant when values were regressed against the natural logarithm of the femoral length (Table III.II.XXIV.). Post hoc tests on values for TOA, when plotted against the natural logarithm of the femoral length, revealed that the means for gorillas were significantly lower than those for orang-utans, suggesting that orang-utans have a higher obliquity angle than gorillas, but that the other species did not differ significantly from each other (Table III.II.XXV.).

Table III.II.XXIV.: ANCOVA results for angle TOA

Variable	N	F	p
% Maturity	65	2.332	0.083
ln (femoral length, cm)	84	**6.941**	**0.000**

Bold face indicates significant at α < 0.05.

Table III.II.XXV.: Bonferroni posthoc analysis results for the obliquity angle of the tibia

Species		Mean differences	p
Homo (n=17)	*Pan* (n=26)	-0.024	1.000
	Gorilla (n=26)	2.502	0.116
	Pongo (n=15)	-2.652	0.219
Pan	*Gorilla*	2.527	0.058
	Pongo	-2.627	0.119
Gorilla	*Pongo*	**-5.154**	**0.000**

Bold face indicates significant at α < 0.05.

Chapter 4: Discussion

The results of the analyses performed in this study raise many important questions regarding the impact of species and development on locomotion, and how these factors and behaviour are reflected in the anatomy of the metaphyses of the knee. However, the results can also indicate whether the three dimensional angle measurement method used, in particular for the obliquity angles of the lower limbs, is a suitable alternative to traditional two-dimensional measurement techniques.

4.1. Obliquity Angles

Results obtained from analyses of femoral obliquity angles suggest that the angle increases with age for humans. Growth indicators explained between 10 and 55.5% of the variation in femoral obliquity angle values, which means that growth is not the only factor affecting the development of this feature. Indeed, Tardieu (1994) has suggested that the obliquity of the femur also depends on other growth parameters associated with the development of the femur, such as interacetabular distance or lengthening of the femoral neck. No significant relationships were found in for great ape femurs, meaning that the obliquity of the femur does not change with age for chimpanzees, gorillas or orang-utans. There are differences in obliquity among species, with humans being different from knuckle-walkers (*Pan* and *Gorilla*) but not from orang-utans. As suggested in the first chapter, any obliquity angle observed in orang-utans using traditional osteometrics would be a “false” value, stemming from differential condyle height. Differential condyle height would only have an effect if the obliquity angle was measured using the bicondylar plane as one of the axes. In this project, femoral obliquity angles were measured using the metaphyseal surface as the horizontal plane, eliminating the effect of differential condyle height. Therefore, the human femoral obliquity would be expected to be significantly different from all species of great apes, including orang-utans, but results suggest that this is not the case. Rather, results indicate that humans and orang-utans, being not significantly different from each other, both show a femoral obliquity angle, which does not support the hypothesis brought forward by Tardieu (2010). It appears that orang-utans show a femoral obliquity angle that is diaphyseal. It is important to note that the Bonferroni correction is conservative and that the sample size for orang-utans is quite small, thus it is probable that these two factors mask significant differences between humans and orang-utans in femoral obliquity.

While the limited sample does not allow establishing a trend for *Australopithecus afarensis*, the location of the data points on the scatter plot indicates whether australopithecine values are more comparable to those of humans or great apes. The femoral obliquity angle of AL 333-110 and AL 333-111 were previously found to be 6º and 11° respectively (Tardieu and Trinkaus 1994). Homologous values obtained in this study are somewhat lower when measured from photographs (4.0º and 9.8º), and, conversely, higher when measured from landmarks (7.4º and 15.0º). The presence of a femoral obliquity angle in juvenile specimens of *A. afarensis* support the suggestion that this species engaged in bipedal behaviour from an early age, but the differences in values highlight the effect of inter-observer variation as well as the need for standardization of measurement methods .

Indeed, the two methods used to measure the femoral obliquity angle yielded different results overall. The regressions were stronger when angles were measured from photographs, meaning there was a significant relationship between development or femoral growth and femoral obliquity ($p = 0.000$), but the regressions were weaker when the angles were measured from landmarks ($p = 0.059$ and $p = 0.012$). As the femoral obliquity angle is strongly correlated with age, (Tardieu and Damsin 1997; Tardieu and Trinkaus 1994), it was expected that both methods would reveal significant relationships between femoral obliquity and development and femoral growth. The fact that this is not the case may indicate that the landmark method needs to be standardized, or may simply not be appropriate. Indeed, recording 3D landmarks required judgement to evaluate properly the position of the medio-lateral metaphyseal groove, which is variable among age groups, whereas measurements taken from photographs were not affected by that variation. The difference in significance may also reflect the larger size of the photographic sample.

In general, tibial obliquity was found to have a significant relationship with growth indicators for chimpanzees, but not for humans, gorillas or orang-utans. The chimpanzee knee is in a varus position, yet the ankle is positioned medially relative to the knee. Therefore, it is necessary for the tibia to be angled to bring the ankle in this position. Given the varus position of the knee in chimpanzees, it was expected that most, if not all, angle values would be associated with a medially positioned ankle. The results, however, do not conform to the expected values. Some specimens show angle values that are negative, meaning that in some cases, the ankle is positioned laterally relative to the knee. However, this may also be due to the orientation of the tibial plateau. It is likely that the tibial plateau in great apes is not horizontal as in humans, which would mean that the obliquity values of the tibia are not a direct reflection of its observed position. It is also possible that the landmark measurement method for tibial obliquity is not appropriate, as mentioned above. Measurements taken from photographs on the tibia were not possible in this project due to time constraints, but would have likely provided a clearer picture of the development of tibial obliquity in the chimpanzee. Still, the significant relationship between tibial obliquity and development or femoral growth suggests that the loads incurred by chimpanzee locomotion are applied to the proximal tibial growth plate rather than the infradiaphyseal plane of the femur and cause this pattern of tibial obliquity in this species.

4.2. Metaphyseal surface topography

4.2.1. Effect of development on the topography of the metaphyses of the knee

4.2.1.1 Distal metaphysis of the femur

The majority of results presented in this project allow us to reject the null hypothesis that there is no significant relationship between individual development and topography of the femoral infradiaphyseal plane. Regression analyses show that development, in humans, is accompanied by a change in the surface of the distal femoral metaphysis; it becomes more convoluted. However, the two angles within the mediolateral and anteroposterior grooves are not correlated with growth, since there is no significant relationship between the angle values in these areas and either one of the growth indicators. In fact it appears that the values for the grooves remain the same for much of the individual’s development. It seems that in humans, the greater convolution is the result of a development of the four peaks with little change in the shape of the groove themselves.

In knuckle-walkers, more particularly chimpanzees, there is also a development of the convolution with femoral length, but it is not generalized to all medio-lateral and antero-posterior angles as observed in humans. Unlike humans, chimpanzees do show a change of the morphology of the groove that becomes more acute during growth.

In orang-utans, none of the regression analyses could allow us to reject the hypothesis that there is no significant relationship between the angle values and the growth indicators. This might be explained by the small sample size for this species: the smaller the sample size, the higher R^2 values need to be for the relationship to be significant. Therefore, while R^2 values were still high (above 0.5 in most cases), there were not enough individuals to confirm that the relationship was significant. A larger sample size may show that there is a relationship between development and development of the convolution in that species.

Results from the analyses have allowed us to conclude that development, in most cases, does have a significant effect on the morphology of the infradiaphyseal plane, and that species has a significant effect on the relationship between these variables. This is in line with the suggestion made in the first chapter that locomotion (and its development) affects the topography of the infradiaphyseal plane of the femur. The results conform to the expectation that the metaphysis in humans and great apes develops peaks and grooves to resist shearing forces as the individual becomes mobile and this convolution intensifies as locomotion becomes habitual.

4.2.1.2 Proximal metaphysis of the tibia

The results obtained for the tibia, in most cases, do not allow us to reject the null hypothesis that there is no significant relationship between growth indicators and the topography of the proximal tibial infradiaphyseal plane in humans. Development of the individual and growth of the femur are associated with an increase in the anteroposterior angle in the medial region of the tibia (angle TAPM), suggesting that this area becomes flatter and even more rounded with individual growth. This may be associated with the tuberosity, which appears to remain short and close to the growth plate for human individuals, as seen in the wireframes resulting from the PCA shown in Fig. 3.2.8. Otherwise, there are no significant relationships observed between either percentage of development or length of the femur and the angle values on the proximal metaphysis of the tibia for humans.

Nearly all angles in chimpanzee tibiae were correlated with growth indicators. While these results were not generalized to all angles, they suggest that the surface of the proximal metaphysis of the tibia becomes more convoluted with development and femoral growth. The tibial tuberosity is located further distally in this species, as seen in Fig. 3.2.8.; this may be related to the increased convolution of the growth plate. The forces created by muscle tension are likely to be much different than in humans, resulting in a convoluted growth plate with a lower tuberosity. With a few exceptions, there were no significant relationships observed between development indicators and the topography of the tibial proximal metaphysis in gorillas and orang-utans, which again supports the null hypothesis. It appears that the surface does not change with development or femoral growth.

Analyses of the proximal metaphysis of the tibia show results that are too mixed to permit a general conclusion about the effect of development on the topography of this feature, except in the case of chimpanzees. The scatter plots for tibia angles do not show tendencies as clear as the ones observed with femur. However, it appears that, in chimpanzees, the surface of the tibia changes with age, with angles becoming more pronounced, indicating the surface may become slightly convoluted.

4.2.2. Differences in the development of the metaphyseal topography among species

Since the locomotion of humans differs considerably from that of great apes, it was expected that: 1) the shape of the metaphyseal surfaces of the knee would reflect these differences; 2) with humans values that would be significantly different from that of great apes; and 3) that within great ape taxa, knuckle-walkers would not differ significantly from each other, but would differ from the more habitually arboreal orang-utans. Since bipedality does not incur many loads outside the femoral and tibial longitudinal axes, unlike knuckle-walking and arboreal locomotion (Preuschoft and Tardieu 1996), the prediction for this study was that the morphology of the infradiaphyseal plane in the human knee would remain flatter throughout development than it would in the knee of great apes.

As predicted, humans have a distinct morphology of the knee metaphyses, with less convoluted surfaces than in the other species included in this study. In general, the pattern and degree of convolution of the infradiaphyseal plane in the femur appears to reflect the differences in locomotion, therefore allowing the rejection of the hypothesis that the species has no effect on the development of the distal infradiaphyseal plane of the femur. The scatter plots resulting from the regression analyses, found in section 3.1, also highlight the differences between species that are observed in femoral metaphyses. Most angles of the femur show that the infradiaphyseal plane in human femur remains flatter throughout development, as the values are closer to 180°. Great apes have values significantly lower than 180°, confirming that the convolution is more pronounced in chimpanzees, gorillas and orang-utans than in humans. This is consistent with the suggestion that, as opposed to human bipedality which creates few shearing loads on the growth plate, knuckle-walking and arboreal locomotion generates loads coming from many directions, forcing the growth plate to develop different facets to better resist these shearing loads to avoid separation of the plate, which results in a tight fit between the epiphysis and diaphysis that also prevents them from separating during activity (Preuschoft and Tardieu 1996; Tardieu and Preuschoft 1996). Arboreal locomotion creates loads different from those incurred by knuckle-walking, so differences between orang-utans and knuckle-walkers were expected, but they were not observed systematically. Again, the Bonferroni analysis and small sample size are factors that could possibly hide differences between groups. Then again, knuckle-walkers do occasionally engage in climbing behaviour, so the similarities may reflect an adaptation to arboreal locomotion irrelevant of the frequency of this behaviour.

While results from the principal component analyses clearly show a difference in femoral infradiaphyseal plane morphology between humans and all three species of great apes, analyses of single angles were less successful in systematically separating humans. However, they showed that the angles formed by antero-posterior peaks were the most consistent to differentiate humans from other taxa. As observed above, humans were shown to have a significantly less convoluted metaphyseal surface than knuckle-walkers, while these latter taxa were not significantly different from each other. However, humans and orang-utans did not have significantly different values, which may be due to the small size of the orang-utan sample.

The difference between humans and knuckle walkers was expected, but the similarities between humans and orang-utans were not. Along with the lack of significant difference in femoral obliquity, these results seem to support a relatively new hypothesis concerning the evolution of human bipedality. It was suggested fairly recently that, biomechanically, the bipedality of orang-utans is more comparable to human bipedality than to that of chimpanzees or gorillas (Crompton et al. 2003; Thorpe et al. 2007). The use of hindlimbs to maintain an upright position is common in orang-utan arboreal locomotion. Using branches, the hindlimbs offer support from below while the forelimbs pull the body upward (Ashton and Oxnard 1964; Thorpe et al. 2007). Additionally, their hindlimbs are extended for more than 90% of the time spent in assisted bipedal locomotion. Furthermore, the extension for the hip and knee joints exceeds that of chimpanzees and gorillas when these two species engage in bent-knee/bent-hip bipedal locomotion (Thorpe et al. 2007; Watson et al. 2009). The similarities between orang-utan and human locomotion, in addition to the advantages conferred by arboreal bipedality, have led some to hypothesize that human bipedality evolved from an arboreal type of bipedal locomotion (Thorpe et al. 2007; Watson et al. 2009). Thorpe et al. (2007) have suggested that arboreal bipedality may have been selected for because it allows arboreal bipeds such as orang-utans to negotiate branches too flexible for brachiation only. They note that the reaction of orang-utan hindlimbs to a flexible branch is not unlike that of human legs on a springy track, which lends support to the idea that human bipedality is a retention of assisted arboreal bipedality. Similarities of metaphyseal plate morphology in humans and orang-utans could reflect similarity in bipedal locomotion. However, orang-utans, unlike humans, also load their legs in numerous other positions so their metaphyses should be adapted to resist loads in many directions just like knuckle-walkers. A larger sample size will be necessary to determine if the similarities in the morphology of the knee of humans and orang-utans are real or simply the unfortunate outcome of small sample sizes in the latter.

The data for FMLP does not conform to the expectation of flatness for humans and convolutions for great apes (Tardieu and Preuschoft 1996). Our measurements suggest that, at any given age, the surface in this area is more convoluted in humans than in gorillas and orang-utans. The shape of this area may be related to the morphology of the distal epiphysis of the femur. The posterior epiphysis is characterized, in adults, by the intercondylar fossa, or notch, between the two femoral condyles. This feature presents two facets which are the femoral attachment sites for the anterior and posterior cruciate ligaments; the anterior ligament attaches to the back of the lateral wall of the fossa and the posterior attached to the front of the medial side. These ligaments link the femur and tibia, and strengthen the knee joint by keeping the bones from slipping during flexion and extension of the knee (Gray 2000 [1918]; Lovejoy 2007). It is probable that the tensile forces created by the pull of these ligaments exert enough pressure to influence the shape of attachment sites. Regular motions such as walking or climbing are therefore likely to be reflected in this feature as well: the intercondylar fossa is low and wide, and significantly asymmetrical in great apes, whereas it is high and relatively narrow, and only slightly asymmetrical in humans (Tardieu 1983). It appears that the difference in depth of that fossa between humans and apes is reflected in the convolution of the metaphyseal plane in this area, with humans being more convoluted than apes.

The principal components of the tibia, both with the landmarks and with all metaphyseal angle values, show that humans are different from apes, but the separation from the apes is not as marked as with the femur. Results from the analyses of covariance of the measurements of the tibial metaphyses similarly suggest that species are different in the development of the topography of the proximal infradiaphyseal plane of the tibia, thereby allowing rejection of the null hypothesis. Again, the posthoc pairwise analyses on single angles yielded results that were not consistent enough to support the prediction related to locomotion.

The medial region of the knee, where FAPM and TAPM are located, needs to be discussed further. For the femur, changes in topography of the medial metaphyseal surface are correlated with development, and the locomotor behaviour appears to have a very strong effect on the shape. In fact, three of the four species (*Homo*, *Pan*, and *Gorilla*) show a significant relationship between the angle FAPM and growth indicators. It has been mentioned in the first chapter that positioning the knee underneath the center of gravity in a valgus position applies enough pressure on the medial portion of the growth plate to stimulate an increase in bone apposition but not enough to decrease or even stop growth activity completely. According to Tardieu (2010), the femoral obliquity angle is the result of increased apposition on the medial side of the metaphysis. It is likely that this mechanical load is also a factor in the development of the surface of the femoral infradiaphyseal plane in humans. The angle TAPM is also the only angle in the proximal metaphysis of the tibia where the most number of species (*Homo*, *Pan*, and *Pongo*) present a significant relationship between growth indicators and angle values, suggesting the pressure exerted on the femoral growth plate might also affect that of the tibia.

Furthermore, the results presented in this study show that the two femoral infradiaphyseal angles created by pairs of anterior and posterior peaks – FAPL and FAPM – show significant relationships with development and femoral length in more groups than any of the other angles. These two angles also show some of the most significant differences between humans and apes. It is probable that the main loads acting on the knee are mostly parallel to the sagittal plane, as one of the main goals of locomotion is to move in the direction of this plane, i.e. move forward. Knuckle-walking as practiced by chimpanzees and gorillas applies many small, shearing loads which come from many different directions (Preuschoft and Tardieu 1996), thereby resulting in very acute angles at the metaphysis to resist these shearing loads in individuals that are closer to maturity. In contrast, human bipedality requires the knee to be under the center of gravity, and forces are mainly in a vertical direction. Gravity applies loads on the knee when in or close to full extension, and therefore this position does not result in many shearing loads compared to apes.

More research is needed to understand the exact loading regime of the knee in great apes. Given that their locomotor behaviour involves a number of different movements, a number of mechanical loads coming from many directions are applied to the entire growth plate. It is clear from the results that some loads are regularly applied on the medial portion of the growth plate during their development, as there is a significant relationship between the acuteness of the angle formed in this region and the developmental stage the individual has reached. Further research into the repertoire of movements of great apes may provide some insight as to which specific movement or posture applies enough pressure anteroposteriorly, especially on the medial portion of the knee, to result in such significant patterns.

4.2.3 *Australopithecus afarensis*

Results for the fossils tend to show that the distal femoral metaphyseal surface is flatter, as in humans; FMLA angles values fall on the human trend line. FAPL and FAPM angle values are closer to 180° than for any other species at the same stage of development; the femoral infradiaphyseal plane in this area is much flatter than in humans and great apes. Fossil FMLP and FMLG values fall into the range of gorillas. FMLG values in *A. afarensis* are more acute than in all other groups, suggesting this area is regularly subjected to loads in a less standardized direction than in human-like bipedal walking and suggest that there might have been other locomotor activities in that species. FMLP values for *A. afarensis* are, less acute than values for humans, perhaps reflecting a wider and lower intercondylar notch, not unlike what is observed in great apes. Values from tibial proximal metaphysis angles tend to be closer to great ape values, especially chimpanzees. The mixed results may indicate that *A. afarensis* locomotion was not as standardized as in humans and may have retained an arboreal component. These results lend support to Thorpe et al's hypothesis (2007) that arboreal locomotion, specifically arboreal bipedality, was the precursor to human-like bipedality, and not terrestrial quadrupedality or knuckle-walking as is commonly thought.

4.3. Conclusions

This study has confirmed, using quantified data, that the development of locomotion is associated with the gradual convolution of the femoral infradiaphyseal plane. In humans, this change is accompanied by an increase in femoral obliquity. Although the methods need to be re-evaluated, the data on femoral obliquity generally follows previous observations: femoral obliquity gradually increases as the human individual acquires bipedality to reach steady values between 8-11° when the behaviour becomes habitual, but that no relationship between development and femoral obliquity is present in great apes (Tardieu and Preuschoft 1996; Tardieu and Trinkaus 1994). The carrying angle of the tibia was found to be associated with development only in chimpanzees, but the results are inconclusive as measurement of obliquity from 3D landmarks may not be an appropriate method for this feature. Analyses done on the femoral infradiaphyseal plane offer further insight into the locomotion of humans, great apes and *A. afarensis*. The topography of this plane shows significant differences among the five species studied, confirming that the morphology of this trait is affected by different types of locomotion, with humans exhibiting a relatively flat metaphyseal surface and great apes showing more convolution. The proximal metaphysis of the tibia showed mixed results, but it was found that its topography is significantly correlated with development in chimpanzees. *Australopithecus afarensis* results suggest that the metaphyses of the knee in this species share features with both human and great apes, indicating that this species probably engaged, along with a human-like bipedality, in arboreal forms of locomotion as well.

The project had its limitations. A larger sample of nearly adults could have lent support to the suggestion that the topography remains more or less constant once locomotion is established. Complete femora of infant great apes were also lacking in this study. Data on this age group in great apes is required to confirm whether the femoral metaphysis also starts out rounded as in humans, or if some irregularities are already present. Increased sample sizes in general may provide further insight into the tendencies that were observed in this project.

References

Abramoff MD, Magalhaes PJ, and Ram SJ. 2004. Image processing with ImageJ. Biophotonics International 11:36-42.

Aiello L, and Dean C. 1990. An Introduction to Human Evolutionary Anatomy. London: Academic Press.

Ashton EH, and Oxnard CE. 1964. Locomotor patterns in primates. Proceedings of the Zoological Society of London 142:1-28.

Boyd R, and Silk JB. 2003. How humans evolved. New York: Norton.

Carter DR. 1987. Mechanical loading history and skeletal biology. Journal of Biomechanics 20:1095-1109.

Carter DR, Mikic B, and Padian K. 1998. Epigenetic mechanical factors in the evolution of long bone epiphyses. Zoological Journal of the Linnean Society 123:163-178.

Carter DR, Orr TE, Fyhrie DP, and Schurman DJ. 1987. Influences of mechanical-stress on prenatal and postnatal skeletal development. Clinical Orthopaedics and Related Research 219:237-250.

Cormack DH. 1987. Ham's histology. Philadelphia: Lippincott.

Crompton RH, Thorpe S, Weijie W, Yu L, Payne R, Savage R, Carey T, Aerts P, Van Elsacker L, Hofstetter A et al. . 2003. The biomechanical evolution of erect bipedality. In: Franzen JL, Kohler M, and MoyaSola S, editors. Walking Upright. Stuttgart: E Schweizerbart'sche Verlagsbuchhandlung. p 135-146.

Dean MC, and Wood BA. 1981. Developing pongid dentition and its use for ageing individual crania in comparative cross-sectional growth studies. Folia Primatologica 36:111-127.

Duren DL, and Ward CV. 1995. Femoral physeal plate angles and their relation to bipedality. American Journal of Physical Anthropology Suppl. 20:86.

Frost HM. 1997. Biomechanical control of knee alignment - Some insights from a new paradigm. Clinical Orthopaedics and Related Research 335:335-342.

Gray H. 2000 [1918]. Anatomy of the human body. Philadelphia: Lee & Frebiger. Online Edition, Bartleby.com.

Griffin NL, and Richmond BG. 2010. Joint orientation and function in great ape and human proximal pedal phalanges. American Journal of Physical Anthropology 141:116-123.

Hayama S, Nakatsukasa M, and Kunimatsu Y. 1992. Monkey performance : The development of bipedalism in trained Japanese monkeys. Acta Anatomica Nipponica 67:169-185.

Heiple KG, and Lovejoy CO. 1971. The distal femoral anatomy of *Australopithecus afarensis*. American Journal of Physical Anthropology 35:75-84.

Hert J. 1969. Acceleration of the growth after decrease of load on epiphyseal plates by means of spring distractors. Folia Morphologica 17:194-203.

Jaanusson V. 1991. Morphological changes leading to hominid bipedalism. Lethaia 24:443-457.

Javois C, Tardieu C, Lebel B, Seil R, and Hulet C. 2009. Comparative anatomy of the knee joint: Effects on the lateral meniscus. Orthopaedics & Traumatology: Surgery & Research 95:49-59.

Latimer B. 1991. Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. In: Senut B, and Coppens Y, editors. Origines de la bipédie chez les Hominidés. Paris: CNRS. p 169-176.

Lovejoy C. 1988. Evolution of human walking. Scientific American 259:118-125.

Lovejoy CO. 2007. The natural history of human gait and posture: Part 3. The knee. Gait & Posture 25:325-341.

Lovejoy CO, and Heiple KG. 1970. A reconstruction of the femur of *Australopithecus africanus*. American Journal of Physical Anthropology 32:33-40.

Lovejoy CO, McCollum MA, Reno PL, and Rosenman BA. 2003. Developmental biology and human evolution. Annual Review of Anthropology 32:85-109.

O'Higgins P, and Jones N. 1998. Facial growth in *Cercocebus torquatus*: An application of three dimensional geometric morphometric techniques to the study of morphological variation. Journal of Anatomy 193:251-272.

Organ JM, and Ward CV. 2006. Contours of the hominoid lateral tibial condyle with implications for *Australopithecus*. Journal of Human Evolution 51:113-127.

Pauwels F. 1980. Biomechanics of the locomotor apparatus. New York: Springer-Verlag.

Preuschoft H, and Tardieu C. 1996. Biomechanical reasons for the divergent morphology of the knee joint and the distal epiphyseal suture in hominoids. Folia Primatologica 66:82-92.

Prost JH. 1980. Origin of bipedalism. American Journal of Physical Anthropology 52:175-189.

Sarmiento EE. 1998. Generalized quadrupeds, committed bipeds and the shift to open habitats: an evolutionary model of hominid divergence. American Museum Novitates 3250:1-78.

Shea BT. 1981. Relative growth of the limbs and trunk in the African apes. American Journal of Physical Anthropology 56:179-201.

Slice DE. 1992, 1994. GRF-ND: Generalized rotational fitting of n-dimensional landmark data.

Smith BH. 1989. Dental development as a measure of life history in primates. Evolution 43:683-688.

Smith BH, Crummett TL, and Brandt KL. 1994. Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. Yearbook of Physical Anthropology 37:177-231.

Smith JW. 1962a. The relationship of epiphyseal plates to stress in some bones of the lower limb. Journal of Anatomy 96:58-78.

Smith JW. 1962b. The structure and stress relationship of fibrous epiphyseal plates. Journal of Anatomy 96:209-225.

Standring S. 2005. Gray's anatomy : the anatomical basis of clinical practice Edinburgh: Churchill Livingstone.

Stern JT, and Susman RL. 1983. The locomotor anatomy of *Australopithecus afarensis*. American Journal of Physical Anthropology 60:279-317.

Susman RL, Stern JT, and Jungers WL. 1984. Arboreality and bipedality in the Hadar hominids. Folia Primatologica 43:113-156.

Tardieu C. 1981. Morpho-functional analysis of the articular surfacs of the knee-joint in primates. In: Chiarelli AG, and Corrucini RS, editors. Primate Evolutionary Biology. New York: Springer-Verlag. p 68-80.

Tardieu C. 1983. L'articulation du genou des primates catarhiniens et Hominidés fossiles. Implications phylogénétiques et taxinomiques. Bulletins et Mémoires de la Société d'anthropologie de Paris 10:355-372.

Tardieu C. 1988. Evolution of the knee intra-articular menisci in primates and some fossil hominids. In: Else JG, and Lee PC, editors. Primate Evolution. Cambridge: Cambridge University Press. p 183-190.

Tardieu C. 1994. Morphogénèse de la diaphyse fémorale chez l'homme: signification fonctionnelle et évolutive. Folia Primatologica 63:53-58.

Tardieu C. 1997. Femur ontogeny in humans and great apes: heterochronic implications for hominid évolution. Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science 325:899-904.

Tardieu C. 1998. Short adolescence in early hominids: Infantile and adolescent growth of the human femur. American Journal of Physical Anthropology 107:163-178.

Tardieu C. 1999. Ontogeny and phylogeny of femoro-tibial characters in humans and hominid fossils: Functional influence and genetic determinism. American Journal of Physical Anthropology 110:365-377.

Tardieu C. 2010. Development of the human hind limb and its importance for the evolution of bipedalism. Evolutionary Anthropology 19:174-186.

Tardieu C, and Damsin JP. 1997. Evolution of the angle of obliquity of the femoral diaphysis during growth — correlations. Surgical and Radiologic Anatomy 19:91-97.

Tardieu C, Glard Y, Garron E, Boulay C, Jouve JL, Dutour O, Boetsch G, and Bollini G. 2006. Relationship between formation of the femoral bicondylar angle and trochlear shape: Independence of diaphyseal and epiphyseal growth. American Journal of Physical Anthropology 130:491-500.

Tardieu C, and Preuschoft H. 1996. Ontogeny of the knee joint in humans, great apes and fossil hominids: Pelvi-femoral relationships during postnatal growth in humans. Folia Primatologica 66:68-81.

Tardieu C, and Trinkaus E. 1994. Early ontogeny of the human femoral bicondylar angle. American Journal of Physical Anthropology 95:183-195.

Thorpe SKS, Holder RL, and Crompton RH. 2007. Origin of human bipedalism as an adaptation for locomotion on flexible branches. Science 316:1328-1331.

Ward CV. 2002. Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? American Journal of Physical Anthropology Suppl 35:185-215.

Waterlow J. 1994. Causes and Mechanisms of Linear Growth Retardation. Proceedings of an IDECG Workshop. London, January 15-18, 1993. European journal of clinical nutrition 48 Suppl 1:S1-216.

Watson J, Payne R, Chamberlain A, Jones R, and Sellers WI. 2009. The kinematics of load carrying in humans and great apes: implications for the evolution of human bipedalism. Folia Primatologica 80:309-328.

Wolff J. 1986. The law of bone remodelling. New York: Springer-Verlag.