The Development of the Anterior Inferior Iliac Spine:
A Comparative Analysis Among Hominids and African Apes

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A Descriptive Look at the Anterior Inferior Iliac Spine

The anterior inferior iliac spine (AIIS) has been suggested to be an adaptation to bipedality because of a putative functional relationship with the straight head of rectus femoris and/or the iliofemoral ligament, and hominids are argued to be unique among primates in having an apophysis associated with the emergence of their AIIS. Adult gorillas can possess a sizeable prominence in the AIIS area (Lovejoy, 2010), and some adult Pan exhibit this morphology as well. Its presence has also been claimed to suggest bipedality in some fossil taxa (e.g., Oreopithecus bambolii) (Rook et al., 1999). The origin of the straight head of rectus femoris in humans is on the superior portion of the AIIS (White and Folkens, 2005). The rectus femoris is part of the quadriceps muscle group and contracts during the "toe off" portion of swing phase in bipedal locomotion. As a direct antagonist to the hamstrings, a powerful hip flexor and an extensor of the leg at the knee, rectus femoris appears to be a muscle that may be intimately involved in the bipedal condition. Pan troglodytes (Pan) and Gorilla sp. (Gorilla) are often described as having one origin of the rectus femoris muscle and humans are understood to have two origins (Barnard, 1875; Sigmon, 1974; Swindler & Wood, 1973). Because the AIIS in hominids displays such uniqueness, the difference in rectus femoris origin could be very telling of the pelvic reorganization that took place to accommodate bipedality in hominids.

Hominids are known for having a very robust AIIS that has an anteromedial orientation. In modern humans, when viewing the acetabulum laterally, the reflected head of rectus femoris is found at the 12-o’clock position above the acetabular margin and the straight head is found
between the 1-o’clock and 1:30 position, with a small void of tendon coverage between the two (Hapa et al., 2013). In *Pan* and *Gorilla*, the relative position of the origin of rectus femoris appears intermediate between the reflected origin and the direct origin in humans. At a glance, the rectus femoris positioning in hominids would seem to offer a biomechanical advantage to the bipedal gait but attempting to isolate the impact of this orientation is a challenge. In addition to this, it could be said that much of anthropology has been reluctant to acknowledge the distinction between true adaptations and traits that are mere byproducts of an adaptation. Gould and Lewontin (1979) cite this failure as being part of the “adaptationist programme” which tends to treat every trait as one that was formed by natural selection to employ a specific, adaptive function. It is in the interest of contemporary biological anthropology to attempt to parse out “targets” (adaptations) and what Gould and Lewontin would have called a “spandrel” (a trait that was not the target of selection but a byproduct of an adaptation). To take this further, we have incorporated into this comparative study, the “proposed analytical trait types” proposed by Lovejoy et al. (1999). Our hope is to more appropriately describe the AIIS by acknowledging not only the developmental biology involved in its growth but also its place among the suite of evolutionary pelvic modifications that make the hominid lineage unique.

The AIIS is a consequential trait of interest in the study of hominid evolution by virtue of its role in being one of many traits often used to predict the locomotor condition of fossil taxa as well as the developmental differences that exist between humans and our closest living relatives. Descriptions of the AIIS in fossil taxa have recently been discussed in specimens such as *Australopithecus sediba* (1.95-1.78 mya), *Ardipithecus ramidus* (4.4 mya), and *Oreopithecus bambolii* (7-9mya), to name a few (Berger et al., 2010; Lovejoy et al., 2009; Rook et al., 1999). *Australopithecus sediba* is described as having a “sigmoid-shaped anterior inferior iliac spine” (Berger et al., 2010, p. 202); *Ardipithecus ramidus* is said to have a “prominent” AIIS (Lovejoy
et al., 2009, p. 71e1); and Oreopithecus bambolii is claimed to have a “well-developed anteroinferior iliac spine” (Rook et al., 1999, p. 8796). In order to fully appreciate the AIIS as an informative anatomical character and its relevance to possible locomotor condition in other taxa, it is essential to understand it in Homo sapiens.

Perhaps no anatomical structure between humans and apes shows a more striking difference than that of the pelvis. Differences in pelvic structure denote differences in function. Gorilla and Pan locomote using a peculiar bent-hip, bent-knee lower limb orientation described as knuckle-walking. Because Pan locomotion appears to be a slight variant on the knuckle-walking seen in Gorilla, differences in locomotion, behavior, and morphology have led some to suggest that knuckle walking between the two groups arose in parallel (Dainton & Macho, 1998). For example, gorillas are known to distribute their weight over their fifth metacarpal more than Pan of comparable size (Inouye, 1994). Even when Pan grows larger with age, reliance on the fifth metacarpal as a weight-bearing unit does not increase (Inouye, 1994). This information, in addition to heterochronic differences in carpal morphology, has led some to view the emergence of knuckle-walking in these two genera as the result of independent evolutionary pathways that are not simply explainable by allometric dissonance (Dainton & Macho, 1998).

The same independent evolutionary pathway that resulted in slight differences in knuckle-walking between the two African ape genera appears to have also resulted in a similar vertebral and pelvic configuration as a way to deal with varying degrees of arboreality and vertical climbing with terrestrial quadrupedalism. Pan and Gorilla are known for having a short, stiff back with a reduced number of lumbar, some of which are entrapped by the exceptionally long ilia. Thus, the orientation of Pan and Gorilla pelves being perpendicular to the lower limb during knuckle-walking displays a unique modification that accommodates their respective locomotor condition. In contrast, humans have the only primate ilium that is wider than it is tall.
(Straus, 1929) thus giving an overall appearance much different than that of any other hominoid. The human pelvis is short, wide, and basin-shaped (Aiello & Dean, 2002). The orientation of the human pelvis in anatomical position is in line with the lower limb axis, rather than perpendicular to it as in Pan and Gorilla. This peculiar hominid pelvic morphology and positioning are likely due to a myriad of anatomical modifications that took place on the path to bipedality. In humans, the wide, curved sacrum lies posterior to the hip joint whereas African apes display an extremely narrow, straight sacrum that is more anteriorly oriented in relation to the hip joint (Aiello & Dean, 2002). The anterior portion of the human ilium exhibits the robust, anteromedially-aligned AIIS just inferior to the acetabular margin and superior to the acetabulum (Figure 1). From a lateral view, the stark contrast between human and African ape pelves is appreciable as the human iliac isthmus is generously expansive (Figure 2). A lateral view of an African ape pelvis is nearly two-dimensional in appearance (Aiello & Dean, 2002) with only a slight iliac isthmus expanse. Just superior to the iliac isthmus, humans and apes show marked differences in not only morphology but also musculature. In Pan and Gorilla, the gluteus maximus origin is much longer than in humans, attaching from the distal sacrum, superior portion of the coccyx, as well as from the proximal portion of the ischial tuberosity (Aiello & Dean, 2002). The femoral insertion of gluteus maximus in Pan and Gorilla is extremely elongated compared to humans and encompasses the length of the femur from the gluteal tuberosity to the lateral epicondyle rather than the short gluteal ridge femoral insertion seen in Homo (Aiello & Dean, 2002). The origin of gluteus medius in Pan and Gorilla makes up by far the largest muscle attachment area of the posteromedial surface of the ilium whereas in humans, the origin takes up a much reduced area
Figure 1. The Human Anterior Inferior Iliac Spine (AIIS).
Figure 2. Illustrations depicting lateral innominates of *Pan troglodytes* (A), *Gorilla sp.* (B), and *Homo sapiens* (C) for morphological comparison (not in anatomical position). Overall size is not to scale. Horizontal bars (in red) have been placed over the iliac isthmus area to convey a measure of breadth. Vertical scale bars (in black) have been placed to the right of each individual, representing approximately 2cm.
(Aiello & Dean, 2002). In fact, when comparing weight of the gluteal muscles as a percentage of the total weight of hip musculature among humans and African apes, Haughton (1873) found that both *Pan* and *Gorilla* display a gluteus medius weight percentage higher than gluteus maximus (11.7% gluteus maximus, 14.6% gluteus medius for *Pan* and 13.3% gluteus maximus, 14% gluteus medius for *Gorilla*). Human gluteus maximus percentage is higher than gluteus medius (18.3% gluteus maximus and 12.3% gluteus medius) (Haughton, 1873). Although the cross-sectional area of each muscle should also be considered, the varying composition of hip musculature between these groups clearly denotes a shift in reliance and function.

**Human AIIS Morphology & Development**

The AIIS is a bony eminence of the ilium that lies superior to the acetabulum and inferior to the anterior superior iliac spine (White & Folkens, 2005) (See Figure 1). The superior portion of the AIIS serves as the origin of the straight head of the rectus femoris muscle and the inferior portion is the insertion site of the iliofemoral ligament (Drake et al., 2005). The rectus femoris muscle is one of four muscles that comprise the quadriceps femoris muscle group and it is considered a powerful hip flexor as well as an extensor of the leg at the knee joint (Drake et al., 2005). Although the origin of the straight head of rectus femoris is located on the AIIS, the origin of the reflected head of rectus femoris lies just superior to the acetabular rim (Drake et al., 2005). The two origins of rectus femoris converge to form the bipenniform muscle belly which terminates as one tendon, the quadriceps femoris, inserting into the superior portion of the patella (Drake et al., 2005; Rasch et al., 1989). The iliofemoral ligament is one of three ligaments that surround the synovial membrane of the acetabulofemoral joint and functions to stabilize the hip (Drake et al., 2005). The inferior portion of the AIIS is also the partial origin for the iliocapsularis muscle (with the main attachment coming from the anteromedial hip capsule) and inserts just distal of
the lesser trochanter (Babst et al., 2011; Ward et al., 2000). Although the function of the iliocapsularis remains unknown, it has been suggested that it is a hip stabilizer (Babst et al., 2011). Babst et al. (2011) showed that in cases of acetabular deficiency (dysplasia), the iliocapsularis is hypertrophied, possibly stabilizing the femoral head in the abnormal acetabulum. The os coxae in humans is formed by three primary (ilium, ischium, pubis) and five secondary ossification centers (iliac crest, anterior inferior iliac spine, ischial tuberosity, pubic symphysis, and the triradiate acetabulum; the location of the os cotylo
don deep within the acetabulum) (White et al., 2011; Scheuer and Black, 2004). The AIIS in humans begins as a vertical advancement of the superior acetabular epiphysis (Scheuer and Black, 2004). The superior acetabular epiphysis is said to travel upward as a "tongue of bone" to form the lower portion of the AIIS and this area corresponds with the attachment of the upper band of the iliofemoral ligament (Scheuer and Black, 2004). The superior aspect of the AIIS develops as a separate "flake-like" epiphysis that matches with the site of attachment for the straight head of rectus femoris (Scheuer and Black, 2004).

The AIIS in humans arises as a secondary ossification center (SOC), meaning that it forms as an epiphysis that emerges after the primary centers of ossification of the pelvis (Scheuer and Black, 2004). This ossification of the AIIS begins between the ages of 10-13 and will often reach full fusion by age 20 (Scheuer and Black, 2004) (Figure 3). SOCs generally take three forms; articular cancellous, articular flake/smear, and non-articular ligament/muscle (NALM) (Scheuer and Black, 2004). The SOC that forms the AIIS is categorized as the non-articular ligament/muscle type (Scheuer and Black, 2004). The NALM SOC’s form at the site of ligament or tendon attachment and growth may be influenced by the
Figure 3. Primary & Secondary Ossification Centers of the Human Pelvis.

A= Appearance (solid black line and denoted in blue); F= Fusion. Blue (dotted black line and denoted in yellow). Modeled after (Scheuer and Black, 2004).
mechanical stresses placed upon them (Scheuer and Black, 2004). This type of secondary center is more commonly known as a “traction epiphysis” (Parsons, 1904) or an "apophysis". Hereinafter, the term "apophysis" will be used in this analysis. Although apophysis formation is endochondral in nature (e.g. hyaline cartilage anlage as a bone precursor), this particular type of ossification may display attributes of perichondral development (Scheuer and Black, 2004).

Perichondral intramembranous growth may be induced by the pull of attached muscles and even the stretching of surrounding soft tissue (Carter and Beaupré, 2001). The stresses of muscle contraction at the attachment site are relayed to the perichondrium by Sharpey’s fibers (Scheuer and Black, 2004). Developing apophyses may also be impacted by stresses in this way (Scheuer and Black, 2004). The AIIS epiphyseal “cap” during development is unfused from the main body of the ilium yet connected by a cartilaginous matrix known as the growth plate (Scheuer and Black, 2004). The metaphyseal region of the ilium that corresponds to the AIIS epiphysis, like all SOC’s, is characterized by a billowed surface (Scheuer and Black, 2004). These grooves are canals through which the vascular system has invaded the area of bone formation to supply blood and osteoprogenitor cells (Scheuer and Black, 2004). Cartilage canals develop from the perichondrium and deliver mesenchymal cells to the SOC (Blumer et al., 2006). In addition to being multipotent, mesenchymal cells contain positional information that determines the expression of bone-specific proteins in the SOC (Blumer et al., 2006). During growth, it is likely that the AIIS SOC develops much like the ends of long bones in that they are composed of cell zones, each with a respective action attributed to them. Although the terms for these zones are not universal, the actions are generally agreed upon (Scheuer and Black, 2004). The germinial (or resting) zone is composed of diminutive chondrocytes that receive a vascular supply and in the proliferative zone chondrocytes undergo mitotic division as well as transition from the random arrangement of germinal zone cells to a more organized columnar alignment
(Mackie et al., 2008; Scheuer and Black, 2004). The transformation (or hypertrophic/maturation) zone is where chondrocytes begin to hypertrophy and excrete extracellular matrix which will become mineralized (Mackie et al., 2008). Hypertrophic cells will eventually apoptose and the surrounding material deteriorates to leave vertical columns which are then invaded by the ossification front which includes osteogenic cells, bone marrow cells, and blood vessels (Mackie et al., 2008; Scheuer and Black, 2004). This ossification front will replace the cartilage with a bony matrix that will eventually fuse the epiphysis to the metaphysis, often leaving "sclerotic lines" (dense bony plates) which may be seen well into adult life by radiograph (Scheuer and Black, 2004).

Further investigation of bone eminence formation by Blitz et al. (2013) has revealed that rather than bony eminence regions developing from progenitor cells derived from the primary cartilage, they are actually derived from a previously unknown set of progenitor cells that express Sox9 and Scx. The development of long bones and bony eminences appear to rely on separate progenitor fields to form in a modular fashion (Blitz et al., 2013). TGFβ signaling specifies bone eminence progenitors and BMP appears to contribute to the differentiation of Sox9- and Scx-positive eminence progenitor cells to chondrocytes (Blitz et al., 2013). Further investigation into the nature of modular bone growth appears to be a fruitful area of inquiry and could also reveal more about the mechanisms of development concerning the tendon/ligament-bone interface.
Natural History of Ossification

The process of ossification has evolved for over 500 million years. The first evidence of intramembranous ossification in the fossil record is found in the heterostracans of the early Ordovician (Carter and Beaupré, 2001). Heterostracans were jawless fishes that developed external bony plates known as craniopharyngeal armor, composed of a dentin-like mineralization and an acellular bone-like tissue called aspidin which formed by intramembranous ossification (Carter and Beaupré, 2001). Perichondral bone also appears in the Ordovician (~500 mya) heterostracans and is thought to have emerged after intramembranous ossification (Carter and Beaupré, 2001). A major transition takes place between the Ordovician and the Devonian in that some taxa, like osteichthyes (bony fishes), developed an ossified endoskeleton rather than the external craniopharyngeal armor of the heterostracans. The first fossil evidence of endochondral ossification does not appear until the Devonian (~410 mya) in osteichthyes and bony epiphyses initially surface in the Mesozoic (~208mya) in sphenodontids, lizard-like reptiles whose only extant member is the tuatara (Carter and Beaupré, 2001). Finally, bony sesamoids emerge from the fossil record in the early Cenozoic (~65mya) and these are seen in several groups such as amphibians, squamates, mammals, and birds (Carter and Beaupré, 2001). Admittedly, this perceived late appearance of sesamoids could also be the result of sampling bias in bones that are difficult to recover. Early tetrapods utilized endochondral ossification and this process became more organized in lizards and mammals and was secondarily lost in many amphibians (Carter and Beaupré, 2001). In mammals, the trend appears to be toward a more efficient endochondral ossification which also includes a greater occurrence of sesamoid bones and secondary ossification centers which early crocodiles, dinosaurs, and turtles lack (Haines, 1969). Bony epiphyses and sesamoids exist in many taxa but are especially common in larger animals and, interestingly, primates (Carter and Beaupré, 2001). Haines (1969) claims that the arrival of SOCs
and sesamoids in many taxa may be indicative of evolutionarily enhanced genetic capacity for endochondral ossification. Carter and Beaupré (2001) take it one step further, stating that vertebrate skeletal tissue became especially sensitive to mechanical stimuli over evolutionary time. Early tetrapod bone formation was very basic, heavy, and well-ossified while the ability to remodel the endoskeleton came much later (Carter and Beaupré, 2001).

**Molecular Regulation of Endochondral Ossification**

**Chondrocyte Cell Proliferation**

The molecular processes driving endochondral ossification are complex and questions remain as to the specifics of these dynamic interactions (Mackie et al., 2008). What is known is that there is an elaborate interplay between various hormones, growth factors, genes, and proteins that take place in the process of replacing cartilage with bone during endochondral ossification. Much of the molecular process is outside the scope of this review but a summary of growth regulation will be discussed in brief. Mackie et al. (2008) provided an outline for endochondral growth regulation by dividing the components into three main categories: systemic factors, secreted factors, and transcription factors.

Systemic factors include growth hormone (GH), triiodothyronine ($T_3$), and oxygen tension (Mackie et al., 2008). Longitudinal bone growth is stimulated by GH and regulated by a host of factors such as leptin, vitamin D, estrogens, and androgens (Nilsson et al., 2005). For example, estrogens inhibit chondrocyte proliferation and androgens stimulate it (Nilsson et al., 2005). The ratio of these hormones during development contributes to differences in timing and amount of growth between the sexes. In addition to its direct impact on chondrocyte proliferation, GH acts indirectly as a stimulator of secreted factors such as liver-derived insulin-
like growth factor-1 (IGF1), wingless-type MMTV integration sites (Wnt’s), bone morphogenetic proteins (BMP’s), and Indian hedgehog (ihh). Each one of these secreted factors plays a role in the chondrocyte proliferation process. The ihh transcription factor inhibits glioblastoma family 3 (Gli3) (Mackie et al., 2008). Transcription factor Gli3 acts to inhibit chondrocyte proliferation so ihh partakes in the growth process by impacting the ability of Gli3 to suppress this growth (Mackie et al., 2008). Fibroblast growth factors (FGF’s) are also involved, like Gli3, with chondrocyte proliferation inhibition but are not known to be impacted by GH (Mackie et al., 2008) (Figure 4).
Figure 4. Molecular Regulation of Endochondral Ossification (reproduced from Mackie et al., 2008). Endochondral ossification requires a number of transcription factors, secreted factors, and systemic factors. In addition to the major role of growth hormone (GH), this figure also highlights the importance of the Ihh/PTHrP complex.
Chondrocyte Cell Hypertrophy and PTHrP Negative-Feedback Loop

Chondrocyte cell hypertrophy is also stimulated by IGF’s and FGF’s and both of these secreted factors are, in turn, activated by T₃ (Mackie et al., 2008). A large number of FGF genes and receptors are represented during the entire process of endochondral ossification and they play a role in both stimulating cell hypertrophy and act as inhibitors to Ihh (Kronenberg, 2003; Mackie et al., 2008). The presence of T₃ inhibits parathyroid hormone-related peptide (PTHrP) but Ihh stimulates PTHrP and together they form a negative-feedback loop (Kronenberg, 2006). PTHrP is secreted during fetal life and acts on the same receptor as parathyroid hormone (PTH) (Kronenberg, 2003). PTHrP keeps chondrocytes in a proliferative state and delays differentiation (Kronenberg, 2006). PTH inhibits the runt-related transcription factor 2 (Runx2), which normally stimulates chondrocyte hypertrophy (Mackie et al., 2008). PTHrP also stimulates Sry-related HMG box 9 (Sox9), a transcription factor which may delay chondrocyte hypertrophy (Mackie et al., 2008). The Ihh/PTHrP negative-feedback loop is a mechanism that regulates long bone growth (Kronenberg, 2003). PTHrP induces chondrocyte proliferation and inhibits Ihh (Kronenberg, 2003). When the end of the bone (source of PTHrP) reaches a sufficient distance from the source of Ihh, proliferation ends and Ihh converts perichondral cells to osteoblasts (Kronenberg, 2003) (Figure 5).
Figure 5. Ihh/PTHrP Negative-Feedback Loop (modeled after Kronenberg, 2003) in the growth of a typical long bone. Although bone growth requires a complex assortment of factors, it is clear that the Ihh/PTHrP complex plays a central role.
Development of an Enthesis

An enthesis is an area of bone that serves as the attachment site for tendons or ligaments (Benjamin, 2002). An apophysis, such as the AIIS, develops from a secondary ossification center but entheses do not. The origin of the reflected head of the rectus femoris muscle is an enthesis that develops just superior to the acetabular rim (Drake et al., 2005). As a general rule, entheses can be divided into two main types: fibrous and fibrocartilaginous (Benjamin, 2002). Fibrous attachment sites tend to occur in metaphyses and diaphyses, whereas fibrocartilaginous sites attach to epiphyses or apophyses (Gao et al., 1996). Differences in tissue composition of these two attachment types appear to be related to the need for fibrous type entheses to migrate as the bone grows (Gao et al., 1996). In rats, the medial collateral ligament (MCL), for example, displays a fibrous attachment at its tibial metaphysis and a fibrocartilaginous enthesis on the femoral epiphysis (Gao et al., 1996; Wei and Messner, 1996). Although both attachments arise embryonically from fibrocartilage, in postnatal life the two entheses are differentiated (Gao et al., 1996). At birth, there are three zones that can be distinguished as being associated with the fibrocartilaginous enthesis: ligament (or tendon), perichondrium, and epiphyseal cartilage (Wei and Messner, 1996). No collagen was detected at the enthesis before day 2 and the site remained more cellular in appearance than the ligament (Wei and Messner, 1996). Before the SOC has formed, the enthesis (rat, femoral MCL) begins by displaying Type II collagen at the attachment site and Type I collagen in the ligament (Gao et al., 1996). As growth continues, Type I collagen advances into the enthesis and can be seen as bony spicules (Gao et al., 1996). Five distinct zones can be distinguished after day 15- ligament, fibrocartilage, proliferative epiphyseal cartilage, calcified cartilage, and trabecular bone (Wei and Messner, 1996). After 30 days, Type II collagen advances into the ligament and at 45 days, Type I collagen can be seen in both the
enthesis and ligament (Gao et al., 1996). Interestingly, with advanced age, the Type II collagen from the enthesis advances more and more into the ligament itself (Gao et al., 1996).

The formation of fibrous entheses begins the same as the fibrocartilaginous types, with the ligament (rat, tibial MCL) labeling for Type I collagen whereas the enthesis is composed of Type II collagen (Gao et al., 1996). Eventually, the cartilage at the attachment site is replaced by bone and from that point forward, only Type I collagen is found in the ligament itself (Gao et al., 1996). The ligament attached to perichondrium or periosteum and either metaphyseal cortical bone or growth plate cartilage (Wei and Messner, 1996). Type I collagen is the most abundant collagen in the body and found in bone, ligaments, tendons, dermis, and the cornea (Gelse et al., 2003). Type II collagen is found in cartilage (primarily hyaline), notochord, nucleus pulposus, and the vitreous body (Gelse et al., 2003). The enthesis composition covered here is abridged but it should be stated that there are a multitude of other molecules found in any given enthesis that may include other collagens (such as III, V, and IV), chondroitin 4 sulphate, dermatan sulphate, chondroitin 6 sulphate, keratan sulphate, and aggrecan, to name a few (Benjamin, 2001).

**AIIS Morphology, Deformity, and Trauma**

When comparing the size, shape, location and position of the AIIS between sexes in modern humans, there are no significant differences between males and females for the following metrics: length, height, as well as vertical, horizontal, and straight distances between the apex of the AIIS and the acetabular rim (Amar et al., 2013). There are also no significant differences between the AIIS on the left and right sides of the human pelvis (Amar et al., 2013). The only metric found to be significant after being normalized for size between males and females was the difference in AIIS width (Amar et al., 2013). Defining the range of normal size
and shape can be important due to the occurrence of femoroacetabular impingement (Amar et al., 2013). Figure 6 gives a stylized depiction of the AIIS complex.
Figure 6. Schematic depiction of the human AIIS. This model depicts the AIIS as an anatomical landmark made up of several parts. The SAE is highly stylized to show the general orientation of subchondral bone that advances from the unfused acetabulum during development. This advancement eventually leads to the formation of the AIIS.
Femoroacetabular Impingement

Femoroacetabular impingement (FAI) occurs when the acetabular rim and femoral neck come into contact, usually due to abnormalities of the proximal femur (Beck et al., 2005). This contact can restrict movement, induce severe groin pain, breakdown labrum fibrocartilage, and lead to early osteoarthritis (Larson, 2012). The two main types of femoroacetabular impingement are cam and pincer (Beck et al., 2005). Cam impingement involves asphericity of the femoral head which impedes its ability to properly fit into the acetabulum and pincer impingement is the result of an over coverage of bone from the acetabular rim (Beck et al., 2005). Although much of FAI literature describes impingement caused by these two patterns, it has been observed that abutment in the hip can also occur due to a hypertrophic anterior inferior iliac spine (Pan et al., 2008). Pan et al. (2008) describe a case study of a 30 year old active male who suffered pain and limited movement due to a hypertrophic AIIS that made contact with the anterior portion of the femoral head and neck when the hip was flexed near 90°. This patient required resection of the hypertrophic portion of the AIIS and was able to return to normal function five weeks post-operation and eventually regained hip flexion of 120° (Pan et al., 2008). Growths such as this can occur as a “traction spur” or enthesophyte (Pan et al., 2008) which are said to form at the bony attachment site of a tendon or ligament due to either stress or injury (Tol & van Dijk, 2004) but can also form due to inflammation of the enthesis from seronegative spondarthropathies or from indiscernible causes (Rogers et al., 1997).

Research done on AIIS-specific FAI found that AIIS morphology could be divided into three subcategories: Type I, Type II, and Type III (Hetsroni et al., 2013). Type I variants are noted for having a smooth length of ilium between the AIIS and the acetabular rim which gives non-obstructive spacing between the two features (Hetsroni et al., 2013). Type II variants display an AIIS that is inferiorly protuberant enough to meet the plane of the acetabular rim as well as
exhibiting bony prominences exterior to the main body of the AIIS that obstruct the smooth “path” of ilium seen in Type I (Hetsroni et al., 2013). Type III variants display an AIIS that is so inferiorly protuberant that it extends beyond the plane of the acetabular rim and is noted for having a “spur appearance” (Hetsroni et al., 2013). These AIIS Types had mean hip flexion values of 120°, 107°, and 93° as well as mean medial hip rotation values of 21°, 11°, and 8°, respectively (Hetsroni et al., 2013). A generally acceptable normal range of motion for hip flexion in males ≤ 19 years of age is ~123.4° and ~50.3° for internal rotation of the hip (Boone et al., 1979). These values show the impact AIIS size and morphology can have on individuals suffering from AIIS-specific FAI.

**AIIS Avulsion Fracture**

In addition to morphological deformities that can lead to hip impingement, there is also a particular debilitating injury that can occur at the AIIS known as an avulsion fracture. Avulsion fractures are a failure of bone in the area of tendon or ligament attachment due to trauma or the application of a tremendous amount of tensile force pulling on the region (Metzmaker & Pappas, 1985). Avulsion fractures of the pelvic apophyses are, in general, considered infrequent injuries but they do occur almost exclusively and are not uncommon in adolescent athletes that engage in rigorous sports that demand explosive contraction of muscles during actions such as kicking a ball, running, and jumping (Rossi & Dragoni, 2001; Rasch et al., 1989). In particular, it is likely that these injuries occur when the rectus femoris muscle is in full extension and undergoes a sudden and forceful contraction (Yildiz et al., 2005).

Due to the timing of the appearance and fusion of the AIIS, the injured individual is often an adolescent (Rossi & Dragoni, 2001). Between the ages of 10-13 (but also occurring up to age 20) the AIIS is forming as a bony epiphysis that has a cartilaginous layer separating it from the
main body of the ilium (Scheuer & Black, 2004). Peripheral growth of pelvic secondary centers of ossification during adolescence display a mechanical weakness at their cartilaginous center and in the case of the AIIS, due to the pull of the rectus femoris muscle; these factors contribute to making it vulnerable during this time (Metzmaker & Pappas, 1985). Diagnosis of the avulsion fracture usually involves localized sharp groin pain, restricted movement of the hip and radiological inspection to confirm that a fracture has taken place (Metzmaker & Pappas, 1985).

In general, if the avulsion fracture separates the AIIS epiphysis from the ilium no more than 1.5 cm, the injury can usually be managed in a conservative, non-surgical manner (Yildiz et al., 2005). Most AIIS fractures are unilateral, however, there are isolated instances of bilateral fractures and in these cases the sports responsible for the injuries were long jumping and 100 m dash runs (Yildiz et al., 2005).

In two separate studies, the mean age of those injured was 13.8 years (Rossi & Dragoni, 2001; Sundar, 1994) and the sports most associated with AIIS avulsion injuries were soccer, athletics, and gymnastics (Rossi & Dragoni, 2001). When looking at 193 adolescent athletes with a total of 203 injuries, 45 of the traumas were avulsion fractures of the AIIS, while avulsion fractures of the ischial tuberosity made up a striking 109 cases (Rossi & Dragoni, 2001). Out of 45 AIIS avulsion fractures, the injuries per sport were 18 soccer, 10 athletics, 10 tennis, 3 gymnastics, 2 wrestling, and 2 fencing (Rossi & Dragoni, 2001). It is likely that the injuries to the AIIS in soccer, specifically, were caused by explosive upward kicking at maximum flexion at the hip along with extension of the knee (Rossi & Dragoni, 2001). Although most studies do show that these injuries occur mostly in males, Rossi and Dragoni expanded the study and found that not only are avulsion fractures in adolescent athletes more common than previously thought but also show injuries in a group that has been previously overlooked, female gymnasts (Rossi & Dragoni, 2001).
Some avulsion fractures of the AIIS require surgical intervention but the majority of cases are treated with a conservative multi-phase approach (Yildiz et al., 2005; Resnick et al., 1996). Phase one (week one) is a period of rest, phase two (weeks 2-4) entails non-weight bearing “passive” motion with the aid of crutches, phase three (weeks 4-6) involves active motion, and phases four and five (weeks 7-9) call for utilizing resistance training and isokinetic exercises (Yildiz et al., 2005).

When considering trauma that involves the locomotor system, it is important to consider such injuries in the light of our evolutionary history. At 4.4 mya we know that species such as *Ardipithecus ramidus* spent some time arboreally as well as terrestrially (Lovejoy et al., 2009) in a woodland-to-forest habitat (White et al., 2009a). Australopithecines may have inhabited more open woodland savannahs (Brain, 1969) or sub-tropical, thick bush (Rayner et al., 1993). Added to the complexity of negotiating dynamic environments is the acknowledgement that early hominids lived in a faunal mosaic (White et al., 2009b). South African carnivore bone assemblages that include australopithecine fossils reveal an environment of competition and predation from Pleistocene big cats such as leopards that utilize deep recesses in caves to process prey (de Ruiter & Berger, 2000). With this in mind, it is easy to see that injuries such as an avulsion fracture of the AIIS could have posed some danger to our ancestors as they coped with rigors of everyday life.
Hypothesis

We posit that the exuberant growth required to achieve the unique mediolateral expansion of the hominid iliac isthmus is ultimately responsible for emergence of its novel apophysis. If correct, then relative isthmus breadth can be reasonably used to determine the presence/absence of a true AIIS in extinct taxa for which there are no appropriate subadult specimens.
CHAPTER II
MATERIALS & METHODS

The study sample included *Gorilla* sp. (n = 32), *Pan troglodytes* (n = 31), and *Homo sapiens* (n = 34) innominates and femora. *Gorilla* and *Pan* specimens are housed in the Cleveland Museum of Natural History (CMNH). Human specimens are from the Libben collection (Lovejoy et al., 1977) at Kent State University. Adults and subadults were surveyed for the presence of a secondary ossification center for the AIIS. Additional metrics were taken and are listed below.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Subadult (n)</th>
<th>*Adult (n)</th>
<th>Total (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Gorilla</em> sp.</td>
<td>22</td>
<td>10</td>
<td>32</td>
</tr>
<tr>
<td><em>Pan troglodytes</em></td>
<td>21</td>
<td>10</td>
<td>31</td>
</tr>
<tr>
<td><em>Homo sapiens</em></td>
<td>26</td>
<td>16</td>
<td>42</td>
</tr>
</tbody>
</table>

*NOTE: “Adult” for *Gorilla* and *Pan*: ≥ Dental Age 10. “Adult” for *Homo sapiens* in this study: (≥ 21), the upper limit of AIIS fusion

Table 1a. Taxa and sample size.
Additional Specimens

*Ardipithecus ramidus, Australopithecus afarensis, Australopithecus africanus, Australopithecus robustus, Homo erectus, and Homo neanderthalensis* were casts and/or reproductions in the Dr. Owen Lovejoy collection at Kent State University. *Hylobates sp., Indri sp.,* and *Pongo sp.* were actual skeletal material from the CMNH. Due to the fragmentary nature of some of the specimens, not all measures could be performed on all individuals.

<table>
<thead>
<tr>
<th>Additional specimens</th>
<th>Subadult</th>
<th>Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ardipithecus ramidus</em> &quot;Ardi&quot; (ARA-VP-6/500)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>(Pelvic reconstruction, 3D print cast)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Australopithecus afarensis</em> &quot;Lucy&quot; (A.L.-288-1, cast)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Australopithecus africanus</em> (MLD 7 &amp; MLD 25, casts)</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><em>Australopithecus africanus</em> (STS-14, cast)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Australopithecus robustus</em> (SK-50 &amp; SK-3155, casts)</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><em>Homo erectus</em> (OH-28, cast)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Homo neanderthalensis</em> (Feldhofer 1, cast)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Hylobates sp.</em></td>
<td>4</td>
<td></td>
</tr>
<tr>
<td><em>Indri sp.</em></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Pongo sp.</em></td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>

Table 1b. Additional taxa and sample size.

*Note: One *Indri* pelvis was examined at the CMNH. Due to the accumulation of hardened, desiccating tissues surrounding areas of interest, it was difficult to make a proper evaluation and measurement on the specimen without risking damage. Because of this condition, a decision was made to not include it in the quantitative measures but to only remark qualitatively on morphology. Future studies would benefit from not only the inclusion of more taxa but also an increase in sample size, whenever possible.*
<table>
<thead>
<tr>
<th>Metric</th>
<th>Description</th>
<th>Values or Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>AIIS</td>
<td>True AIIS Present or Absent</td>
<td>1 or 0</td>
</tr>
<tr>
<td>DA</td>
<td>AIIS Distance Above</td>
<td>All measures in millimeters (mm)</td>
</tr>
<tr>
<td>DB</td>
<td>AIIS Distance Below</td>
<td></td>
</tr>
<tr>
<td>AA</td>
<td>AIIS Apex</td>
<td></td>
</tr>
<tr>
<td>AD</td>
<td>Acetabulum Diameter</td>
<td></td>
</tr>
<tr>
<td>BNL</td>
<td>Biomechanical Length of Femoral Neck</td>
<td></td>
</tr>
<tr>
<td>MFL</td>
<td>Maximum Femoral Length</td>
<td></td>
</tr>
<tr>
<td>SPREAD</td>
<td>Acetabular Spread</td>
<td></td>
</tr>
<tr>
<td>SEX</td>
<td>Sex</td>
<td>0= Indeterminate, 1= Female, 2= Male</td>
</tr>
<tr>
<td>ILHGT</td>
<td>Iliac Height</td>
<td></td>
</tr>
<tr>
<td>Degree of Fusion Metrics</td>
<td>0= Unfused, 1= Intermediate fusing, 2= Fused</td>
<td></td>
</tr>
<tr>
<td>ACE</td>
<td>Acetabulum</td>
<td>0, 1, 2</td>
</tr>
<tr>
<td>GT</td>
<td>Greater Trochanter</td>
<td>0, 1, 2</td>
</tr>
<tr>
<td>LT</td>
<td>Lesser Trochanter</td>
<td>0, 1, 2</td>
</tr>
<tr>
<td>IC</td>
<td>Iliac Crest</td>
<td>0, 1, 2</td>
</tr>
<tr>
<td>IT</td>
<td>Ischial Tuberosity</td>
<td>0, 1, 2</td>
</tr>
</tbody>
</table>
Metrics Description:

**True AIIS Present or Absent (AIIS):** Qualitative examination that looked for signs of development from a true secondary center such as flaking of the epiphysis or the billowed metaphyseal iliac surface indicative of an unfused AIIS, often found in the developing subadult.

**Iliac Isthmus Measures:**

**AIIS Distance Above:** Shortest distance between the most anterior extent of the greater sciatic notch and the most posterior extent of the acetabular margin above the AIIS (Figure 7a)

**AIIS Distance Apex:** Distance between the most anterior extent of the greater sciatic notch and the apex of the AIIS (Figure 7b).

**AIIS Distance Below:** Shortest distance between the most anterior extent of the greater sciatic notch and the most posterior extent of the acetabular margin below the AIIS (Figure 7c).

**Iliac Height:** The height of the ilium measured from the superior acetabular rim to the apex of the iliac crest (Figure 8a).

**Acetabulum Diameter:** Height of acetabulum measured from its most inferior margin to its most superior margin (Figure 8b).

**Biomechanical Length of Femoral Neck:** Length of a line from the lateral edge of the greater trochanter to its tangential intersection with the femoral head (Lovejoy, 1973)
Figure 7. AIIS above (A), apex (B), and below (C). This is a measure of iliac isthmus breadth.
Figure 8. Measure of iliac height (A) and acetabular height (B).
Maximum Femoral Length: Maximum femoral length

Acetabular Spread: The qualitative amount of vertical subchondral advancement above the superior portion of the acetabular rim (often delineated by a slight discoloration of the surface)

Sex: Male and female. In cases of some subadult specimens, no sex was determined.

*Indices:

Isthmus Apex (AIIS Apex) divided by Iliac Height: This index gives the relative dimension between maximum isthmus breadth at its apex and iliac height.

Minimum Isthmus Breadth divided by Acetabular Height: This index gives the relative dimension between the minimum isthmus breadth and the height of the acetabulum.

*See Appendix

Fusion Metrics:

0= Unfused
1= Intermediate fusing
2= Fused

Acetabulum: Fusion of acetabulum at triradiate zone.

Greater Trochanter: Fusion of greater trochanter epiphysis to the proximal femur.

Lesser Trochanter: Fusion of the lesser trochanter epiphysis to the proximal femur.

Iliac Crest: Fusion of the iliac crest epiphysis to ilium.

Ischial Tuberosity: Fusion of the ischial epiphysis for the tuberosity to the ischial ramus.
CHAPTER III

RESULTS

Human

In fetal life, the human ilium (Figure 9a) already displays the hallmark morphology of subchondral bone advancement from the superior acetabular region (Figure 9b). This uninterrupted continuation of the unfused acetabular portion of the inferior ilium can be clearly seen as a dark, subchondral discoloration that distinguishes it from the rest of the ilium (Figure 9b). Even in the first month of postnatal life, a remarkable fossa is seen in the area of the future AIIS epiphysis (Figure 9c & 9d). From formation until about age 3, the AIIS area is relatively planar when viewing the ilium laterally (Figure 10a & 10b). After around age 3, it begins to protrude and display a more sigmoid appearance. The upward advancement of subchondral bone from the acetabulum toward the AIIS remains nearly vertical until around age 5 (Figure 11a & 11b). After this point, the AIIS area begins to grow anteromedially and begins to assume the general orientation that is seen in the adult. As early as 7 years of age, the AIIS region develops a distinct morphology, with the bottom and top third forming articulation fossae and the middle third being a bulging outgrowth that can display an articulation furrow (Figure 12a & 12b). Figure 13 shows the ilium at around age 12. Although literature describes ossification beginning between 10-13 years of age, we did observe one specimen of a 9 year old that was beginning to show a faint line of separation between the superior and inferior portion of subchondral bone of the AIIS region. The ossified epiphysis "cap" did not appear until around 14-15 years of age (Figure 14). In these specimens there was a distinct "flake-like" appearance of the superior portion of the AIIS that was still partially separated from the AIIS metaphysis.
Figure 9. Human fetal ilium (A & B). Human ilium: 1 month old postnatal (C & D).
Figure 10. Human ilium 8 months old (A & B)
Figure 11. Human ilium 5 years old (A & B)
Figure 12. Human ilium 10 years old (A). Displaying characteristic wrinkled appearance and fossa of the unfused epiphysis. In zoom (B).
Figure 13. Human ilium 12 years old (A & B)
Figure 14. Human ilium 15 years old (A). Same individual (in zoom) with flake-like AIIS apophysis nearing fusion (B).
From ages 16 years of age onward, the flaking is no longer seen as these elements have now fused and the epiphyseal "cap" becomes one with the overall structure of the protuberant body of the AIIS (Figure 15).

Throughout development, the prominent subchondral region of the AIIS displays the same darkened color and furrowed surface that is seen in the developing iliac crest, acetabulum, ischial tuberosity, femoral head/neck, greater and lesser trochanter, condylar distal femur, and the sacroiliac joint. A remarkable and consistent nutrient foramen can be seen on the lateral aspect of the ilium just behind the AIIS region from the earliest point of bony development and this large foramen exists for the remainder of life, becoming quite large in adulthood. Although the growing ilium is peppered with numerous nutrient foramina that appear to display some variation, this particular foramen is large, distinct, and quite constant spatially throughout development. In fact, the only iliac foramen that compares to it in both size and consistency of placement is found on the medial aspect of the ilium near the inferior portion of the sacroiliac joint.
Figure 15. Human AIIS in zoom. 40 years old and showing complete fusion.
The development of the AIIS-region in *Pan* is highly variable in comparison to humans. Access to fetal or infant pelves of *Pan* and *Gorilla* was limited (fetal pelves n=0, infant *Pan* n=1, infant *Gorilla* n=2) but in these three cases there was no evidence of a subchondral advancement from the superior rim of the acetabulum as in humans. This is a remarkable distinction because every human from fetus to the end of adolescence showed this trait, without exception. Of the three groups (*Gorilla*, *Pan*, and human), *Pan* appeared to show the most variation in terms of AIIS-region morphology. In most cases, *Pan* displayed a fossa near the likely site of iliofemoral ligament attachment and rarely showed a protuberant area superior to this (which would likely be near the attachment of rectus femoris in life). There were instances where the superior portion of this fossa showed a discolored, calcified cartilage "island" (specimens 1767 & 1777). Any protuberance in AIIS-region in *Pan* was found to be rare and minor (specimen 1777) (Figure 16). Many *Pan* pelves simply showed no remarkable morphology and lacked any protuberance of the AIIS-region. There was no evidence of a secondary ossification center at any point throughout *Pan* development. No "flake-like" epiphyses were ever encountered. Overall, with the exception of the rare cartilaginous "island", *Pan* pelves were relatively unremarkable in the AIIS-region and in most cases even when there were slightly remarkable areas, it was due to the drop off of the iliac "shelf" of the anterior border leading into a depressed area (Figure 17), rather than an actual protuberance of bone.
Figure 16. *Pan troglodytes* innominate, specimen 1777. Arrow pointing to area of interest.
Figure 17. *Pan troglodytes* inferior portion of ilium and superior rim of acetabulum. Area circled shows drop-off of iliac "shelf" giving the appearance of a protuberance.
**Gorilla**

The development of the AIIS-region in *Gorilla* did not display a continuous or discontinuous subchondral advancement from the superior acetabulum. There was an instance of what appeared to be a calcified cartilage "island" (Ex: specimen 1420; Figure 18) and one instance of a continuous appearing elongated calcified cartilage convexity (Ex: specimen 1760, Figure 19) which were similar to cartilaginous areas seen in *Pan*. *Gorilla* did display more instances of protuberance in the AIIS-area than *Pan* (Ex: specimens 1057, 1408, 1409, 1423, 1704, 1764) but some specimens showed little or no protuberance at all. Like *Pan*, *Gorilla* did not display the morphology associated with a secondary ossification center. Although some pelves had a slight protuberance in the general AIIS-region, when compared to the overall size of the pelvis, they were still diminutive when compared to humans. In fact, the height of the AIIS-related region in *Gorilla*, as a proportion of the height of the ilium, is roughly 9% (*Pan*= 6%; Ardi= 24%; Lucy= 26%; and humans = 34%). As an notable aside, the iliac blades of *Gorilla* did show distinction from *Pan* in that they exhibit a noticeable concavity on the ventral surface which give the blades a "wrapping around" appearance. The iliac blades of *Pan* were generally very straight and some actually had a slight concavity on the dorsal surface of the ilium.
Figure 18. *Gorilla* innominate, specimen 1420. Arrow pointing to the area of interest.
Figure 19. *Gorilla* specimen 1760 displaying calcified convexity.
Ardi, Lucy, MLD-7, MLD-25, STS-14, SK-50, SK 3155, and OH-28

The following observations were made on reconstructions/casts of fossil hominids.

*Ardipithecus ramidus* "Ardi" (ARA-VP-6/500, 4.4mya) and *Australopithecus afarensis* "Lucy" (AL-288-1, 3.2mya) both display a protuberant AIIS that appears consistent, in size, location, form, and orientation (anteromedial) with the hominid condition. Because they are both adult specimens, there is no way to observe hallmarks of the developmental trajectory that is evident only in subadults. What it does show, however, is that at least as far as 4.4mya the AIIS as we have come to know it was already established. *Australopithecus africanus* (MLD-7 & MLD-25, 3.3-2.1mya) are unique because they are subadult specimens. Not only do MLD-7 (Figure 20a-c) & MLD-25 (Figure 21a-c) show an AIIS metaphysis but their age has captured a very telling developmental feature. Both pelves show a novel fossa in the superior portion of the AIIS region. This fossa is characteristic of the AIIS development in humans on the metaphyseal surface of the ilium's anterior border. MLD-7 also has an inferior fossa and strikingly shows the classic developmental advancement of bone from the superior acetabulum to the AIIS seen in humans. Even the large lateral nutrient foramen that appears so consistent in humans is visible on MLD-7. MLD-25 not only shows a large primary, superior fossa but also a minor secondary fossa of the AIIS metaphysis. Like MLD-7, MLD-25 also shows the superior advancement of bone from the acetabulum and what appears to be the lateral nutrient foramen associated with the AIIS site in humans. This morphology was not seen in *Pan* or *Gorilla. Australopithecus africanus* (STS-14, 2.5mya) is a young adult (Bonmatí et al., 2008) that shows a large, anteromedially oriented AIIS. *Australopithecus robustus* (SK-50 & SK-3155, 1.8-1.5mya). SK-50 is an adult male that has a very large, anteromedially oriented AIIS. SK-3155 is an adult that displays a prominent AIIS, albeit smaller than SK-50, a possible lateral nutrient foramen associated with the AIIS and what appears to be the distinguishing ridge of the developing AIIS.
epiphysis interface with the metaphyseal ilium. *Homo erectus* (OH-28, 1.2-1.1 mya) is an adult specimen that has a large and fully fused, anteromedially oriented AIIS.

**Breadth of Iliac Isthmus**

We measured the breadth of the iliac isthmus (Figures 7a-c) in 9 taxa: *Ar. ramidus* "Ardi" (n= 1); *Gorilla sp.* (n= 9); *Hylobates sp.* (n=4); *A. afarensis* "Lucy" (n= 1); *H. neanderthalensis* from the Sawyer and Maley mosaic reconstruction "Feldhofer" left ilium (n= 1); *Pan troglodytes* (n= 7); *Pongo sp.* (n= 4); and *H. sapiens* (n= 14). This is a measure of width from the anteriormost advancement of the greater sciatic notch to three separate measures in the area of the AIIS (equivalent area of non-humans) on the anterior border of the ilium (above, below, and apex of the AIIS region). To account for size variation between and among taxa, we created an index using minimum isthmus breadth as the numerator and the height of the acetabulum as the denominator. Iliac height is a measure from the superiormost acetabular rim to the apex of the iliac crest (see Figure 8a). We took the minimum and maximum measures of iliac isthmus breadth of each individual as our width metric. These indices reveal the clear differences that exist between hominids and non-hominid primates (Figures 22 & 27). *Ardipithecus ramidus, Australopithecus afarensis, Homo neanderthalensis,* and *Homo sapiens* cluster together in having a short ilium and a wide isthmus while all other groups display tall ilia and a narrow iliac isthmus (Figure 22).
Figure 20. MLD 7, *Australopithecus africanus*, subadult. Displaying advancement of the superior acetabular epiphysis toward the AIIS region including remarkable fossa. Lateral view (A), anterior view (B), and anterior view in zoom (C).
Figure 21. MLD 25, *Australopithecus africanus*, subadult. Displaying advancement of the superior acetabular epiphysis toward the AIIS region including a remarkable fossa. Lateral view (A), anterior view (B), and anterior view in zoom (C).
Figure 22. Box plot index showing width of isthmus at its apex divided by iliac height. Oreo1 is a conservative measure of the *Oreopithecus bambolii* isthmus apex and Oreo2 is a generous measure (See Figure 26).
**Number of Origins of Rectus Femoris**

It is generally understood that humans have two origins of the rectus femoris muscle, the reflected head (just superior to the acetabular rim) and the straight head located on the superior portion of the AIIS. From the literature, we obtained information on the number of origins for rectus femoris in 16 separate taxa (Table 3). The majority of sources showed two origins of rectus femoris for modern humans. Occurrences of both two and three origins in humans has been documented (Journal of Anatomy and Physiology, 1897; Tubbs, 2006) with Tubbs, 2006 claiming three origins in 83% of their samples. *Pan troglodytes* display one origin in the majority of sources, with three claiming this number can vary between one and two. Wilder (1861) reported one origin for *Pan paniscus*. The consensus is that *Gorilla* sp. has one origin but three sources claim some variation (some showing one and some showing two) (Hepburn, 1892; Collard & Franchino, 2002; Gibbs, 1999). *Pongo, Hylobates, Papio*, other Cercopithecoids (Langurs & Macaques), Platyrhines (*Cebus, Alouatta, & Ateles*), Lemurs, and other Strepsirrhines (Pottos, Galagos, & Aye-Aye's) are mostly documented as having one origin but with some occurrences of two. Lemurs are said to have prominent processes superior to the acetabulum that may be homologous/analogous to the AIIS. This process is compressed laterally, exhibits a flat and "roughened summit" and serves as the attachment of a ligament that attaches to the anteroinferior process of the iliac crest (Gregory, 1920). The prominence is also the partial attachment site of the sartorius muscle and the rectus femoris (Gregory, 1920). From our own observations of skeletal Indri, we can at least vouch for the prominence of the region and peculiar morphology that seems different than all other taxa. However, the condition of the lone sample proved too difficult to perform proper quantitative measures without damaging the specimen. Moving forward, these taxa remain an unresolved area of inquiry.
In conclusion, humans most often have two origins of rectus femoris but sometimes have three. *Pan troglodytes, Pan paniscus,* and *Gorilla sp.* most often have one origin but sometimes have two. Most other primates examined had one origin but sometimes show two. It should be kept in mind that small sample size could be a limiting factor in some groups observed but likely not a constraint in humans, *Pan troglodytes,* and *Gorilla sp.* It must also be acknowledged that given the early dates of some of the sources, a bias could have existed using knowledge of the known human anatomical condition as a template (i.e. a bias to report two heads of rectus femoris when in reality these origins may have been continuous and connected by fascia rather than the triangular void of tissue seen in *Homo sapiens*). That being said, it is clear that some variation does exist in most groups.
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**Table 3. Number of Origins of Rectus Femoris** (Homo = *Homo sapiens*)

Sources:

Radiograph Analysis

We took radiograph images of human (Libben) pelves and a single gorilla pelvis (CMNH) that displayed a peculiar tissue morphology in the general area of the AIIS that we felt required additional analysis to interpret. The human radiograph AIIS regions appear to show classic growth plate morphology. The AIIS region forms as the "wake" of the ever growing breadth of the iliac isthmus. The overall pattern and organization of trabeculae in the AIIS appears continuous and congruent. In pelves where the apophysis is near fusion or completely fused, the "cap" exhibits the look of a thin layer of cortical bone (Figure 23a & 23b). This morphology is consistent with the appearance of all epiphyses that fuse. A high contrast zone can be seen at the confluence of two fusing bony elements. Figure 23b displays the "flake-like" apophysis that is characteristic of an SOC during intermediate fusion. The Gorilla specimen was chosen due to a marked discoloration in the tissue in the area of the AIIS-region. Although not consistent with the human morphology in this region per se any change in appearance or tissue type was notable. In contrast to the human specimens, the Gorilla sample exhibited a convex tissue rather than the planar surface normally seen in humans. The radiographic analysis seems to show a comparatively diffuse area in this region that is discontinuous and incongruent with the surrounding iliac body (Figure 24). Given this dissonance, in addition to its physical appearance, we posit that this is likely an area of mineralized cartilage. Hall (2005) describes cartilage at the tendon/ligament interface with bone as being enthesial fibrocartilage. In our estimation this site in Gorilla is likely either the enthesial attachment of the rectus femoris tendon or the insertion of the iliofemoral ligament and does not show the signature characteristics seen in humans as being associated with an SOC.
Figure 23. Radiograph of human innominate (A). Same individual, AIIS (in zoom) nearing complete fusion (B).
Figure 24. *Gorilla* innominate radiograph (lateral view), specimen 1420. Area of interest has been magnified for analysis. Image credit: CMNH.
Humans do, indeed, bear a unique secondary growth center for the AIIS. It also appears clear that this novel development in humans, as Raymond Dart posited in 1953, is likely a hallmark trait unique to the hominid lineage. Although AIIS-regional variation does exist both within groups and between them, it is evident that the ontogeny of the AIIS in hominids is distinct and that our closest living ancestors, *Pan* and *Gorilla*, do not share this developmental trajectory. Humans appear to develop the AIIS region as an extension of the superior acetabular epiphysis. A "tongue" of subchondral bone advancing vertically from the acetabulum toward the area that will eventually be the AIIS is seen from fetal life onward in humans. Throughout ontogeny, the AIIS-region (the anterior border of the ilium) is visually remarkable not only by the subchondral discoloration of the tissue but also because of the metaphyseal fossae that develop and later by the surface exhibiting the wrinkled appearance synonymous with a cartilaginous union between the metaphysis and the developing SOC apophysis. This morphology shares similarities with epiphyses such as the proximal and distal femur during development. Around the ages of 14-15 in humans, the partially fused epiphyseal cap can be seen and the unfused portion has a "flake-like" appearance. By ages 16-20, this apophysis becomes completely fused to the anterior border of the ilium and the discolored advancement from the acetabulum erodes, allowing for the AIIS to visually become indistinguishable with the tissue of the surrounding ilium.

The AIIS in humans can be conceptualized as being composed of two distinct parts. First, what we call the anterior border metaphysis (ABM) is formed as an extension of the superior
acetabulum and is the foundation of what we term the anterior border growth plate (ABGP). The ABM serves as the base of what will eventually be the ossified AIIS. The inferior portion of the ABM becomes the partial attachment area of the iliofemoral ligament. Secondly, the AIIS apophysis is formed and begins ossification between the ages of 10-13 atop the most superior portion of the ABM, reaching full fusion by age 20. The apophysis is the origin of the straight head of the rectus femoris muscle.

We posit that the novel AIIS SOC that develops in hominids is the result of the exuberant growth of the iliac isthmus. There are at least two developmental analogs that can be used to describe this development.

**Analog 1: Proximal Femur**

The first analog is the ontogeny of the human proximal femur which begins as a single, continuous, chondroepiphyses that, due to extensive elongation of the femoral neck, separates to form SOC's in the femoral head as well as the greater trochanter (Kriz, 2002; Ogden, 1983). In some mammals (and some primates), the ossification of the greater trochanter and the femoral head form as one osseous epiphysis (Kriz, 2002). Humans, tree shrews, rodents, and pinnipeds all share this particular separate ossification pattern (incomplete) of the proximal femur while taxa such as elephants, raccoons, opossums, and bats develop a single osseous epiphysis (complete) for this region (Kriz, 2002). In other words, due to the diverse assemblage of taxa as well as their varied life histories, it is unlikely that these ossification differences can be explained by mode of locomotion (Kriz, 2002). It is reasonable to posit that perhaps this separation of the proximal epiphysis is partially the result of either a longer growth period or by an increased rate of growth (Kriz, 2002). It seems plausible that the human iliac isthmus, due to similar rapid growth and elongation, produces an SOC similar to that seen in the proximal femur. Even
though it is understood that the human reflected head of rectus femoris is associated with an enthesis and never a SOC, it could be that the original positional information contained in this attachment area has become separated due to the breadth of the iliac isthmus, giving humans the two-head configuration generally seen. Lastly, it appears clear that the human pelvis is genetically predisposed to this exuberant growth of the iliac isthmus by placing a metaphyseal foundation (ABM) on the anterior border of the ilium to serve as a unidirectional growth plate throughout adolescence.

**Analog 2: Mammalian Metapodials & Phalanges**

The second analog to this form of growth would be the development of the mammalian metapodials and phalanges. These bones develop only a single growth plate from the distal end of metacarpals and metatarsals two through five (MT2-5) and from the proximal end of metacarpal and metatarsal of the first digit (MT1) (Reno, 2006). The proximal end of MT2-5 and the distal end of MT1 form by "direct" intramembral ossification and, thus, are not SOC's. The growth of mammalian metapodials and phalanges are unidirectional (with the exception of highly derived taxa such as Cetaceae and possible individual exceptions such as kangaroos, koalas, and elephants) (Reno, 2006). Again, given the diverse range of taxa and lifestyles present, it is unlikely that mode of locomotion or mechanical stress can account for such a ubiquitous trait in mammals. Reno (2006) suggested that genetic positional information likely plays a fundamental role in defining growth plate location and SOC formation in tetrapods. We propose that the mediolateral expansion of the hominid iliac isthmus forms a unidirectional growth plate much like that seen in mammalian metapodia and that this increase in breadth forms an SOC (the AIIS) as a result.
Given the AIIS's notable prominence in hominids and absence in apes, it is tempting to assume that this trait is an adaptation for bipedality (Type I trait) and that the anteromedial orientation of the protuberant AIIS plays a major functional role in the action of rectus femoris. Although there may be little to no disadvantage in this orientation, it is certainly plausible to simply be a result of the extension of the ABGP as it reaches its terminus. In fact, the anteromedial growth of the AIIS is likely abutted by the path of the iliacus muscle, which flexes the thigh at the hip and may contribute to medial rotation. As mentioned previously, the AIIS is a high-risk area for avulsion fracture injury in adolescents who engage in vigorous sporting activities. Surely, early hominids dealt with periods of extreme physical exertion while hunting and provisioning, as well as evading predators. One may assume that avulsion fractures of the AIIS in early hominids occurred with some frequency. To be fair, if we are to assume that very early hominids developed at a rate that was somewhat faster than modern humans yet slower than modern apes, the "window" of adolescent avulsion fractures could have been slightly smaller than we see in contemporary populations, thus, lessening the effective probability of such an injury over time. In this particular instance, we can think of no reason why having a vulnerable epiphysis throughout adolescence would offer an advantage over not having one, so the likelihood of the AIIS being an adaptation, in and of itself, seems improbable. Because there is no significant difference in the length and protuberance of the AIIS between modern human males and females (Amar et al., 2013), and the overall volume of the AIIS does not differ between modern human athletes and non-athletes (Kegelman pers comm 2014), we postulate that the vast majority of development of the AIIS is the result of genetically determined positional information due to the exuberant growth in the breadth of the iliac isthmus and not due to postnatal mechanical stimuli. The hominid path to bipedality required a wholesale reorganization of the pelvic bauplan in which the musculature and the associated bone from which it is anchored.
changed dramatically from the quadrupedal condition. A much greater devotion to the gluteus maximus is seen in hominids. Gluteus maximus can be thought of as being composed of two main parts: the superior portion functions as an abductor and the inferior portion as a hip extensor (Perry, 1992). This contribution to hip extension is vital to the bipedal condition.

The body can be functionally divided into the "passenger unit" and the "locomotor unit" (Perry, 1992). The passenger unit (head, neck, trunk, and arms) is passively carried by the locomotor unit (pelvis and lower limbs) in the bipedal condition. Because the locomotor unit is essentially composed of several bony levers (pelvis, thigh, leg, foot, and toes), 11 main articulations, and each lower limb is controlled by 57 muscles which act with selectivity (Perry, 1992), it is difficult to treat any one of these components in complete isolation when they truly exist as an integrated, functional whole. That being said, the reorganization of the hominid ilium gives some direction of selection. The broad origins of the human gluteus medius and gluteus minimus offer a substantial range of action. Human gluteus medius and gluteus minimus muscles abduct the femur at the hip and medially rotate the thigh. During locomotion, these two muscles also prevent the pelvis from dropping in the direction of the opposite leg in swing (Stone and Stone, 2006) and provide balance. In apes, gluteus minimus has a much smaller, linear origin than in humans and sometimes can be found to separate completely (common in Pongo) to form the scansorius muscle (Aiello and Dean, 2002). The gluteus minimus and scansorius muscle in apes functions as a flexor which is said to aid in climbing (Sigmon, 1974). Given the orientation of the origins of both muscles and their place just superior to the iliac isthmus, we argue that this is likely to have been one of the major areas of selection that resulted in the broadening of the ilium in this area.

The entire complex of gluteus maximus, gluteus medius, gluteus minimus, tensor fasciae latae (hip flexion and knee stability), as well as the role rectus femoris plays in knee extension
and hip flexion, collectively contributed to an altered pelvic morphology in hominids. Sigmon (1974) describes that the change in the shape of the human iliac blades allows the pelvis to essentially carry the origins of the gluteal muscles around to a lateral orientation where they can work as abductors of the pelvis. The gluteus maximus in humans is essentially inactive while standing or walking but is utilized when climbing, running, or moving up from a sitting posture (Aiello and Dean, 2002). The other major role of gluteus maximus in humans is its action to balance the trunk during the use of the upper limbs such as carrying or throwing (Marzke et al., 1988). In apes, the gluteus maximus has a form and function altogether different than in humans. The gluteus maximus in African apes is essentially two portions, the gluteus maximus proprius (proximally) and the ischiofemoralis (caudally) which have a much longer origin than in humans (Aiello and Dean, 2002; Sigmond 1974, 1975; Tuttle et al., 1975). The human gluteus maximus is roughly equivalent to the African ape gluteus maximus proprius, which acts as an abductor and lateral rotator while the ischiofemoralis (absent in humans) acts as a hip extensor (Tuttle et al., 1975, 1978, 1979). The lateral positioning of the human gluteus medius and gluteus minimus, as abductors and medial rotators, act also to stabilize the pelvis during bipedal locomotion (Aiello and Dean, 2002). The gluteus minimus in humans has a much broader origin than in African apes, which some Pan and Gorilla exhibit as a linear, separate muscle known as scansionius (Aiello and Dean, 2002). The human tensor fascia latae, originating from the anterior edge of the iliac crest, acts as a hip flexor and a knee extensor (Aiello and Dean, 2002). Tensor fascia latae is completely absent in Pongo and due to its altered orientation in African apes, flexes rather than extends the knee but, like humans, still participates in hip flexion (Aiello and Dean, 2002).

Figure 22 gives us an example of where locomotor patterns cluster.

The expansive growth in the breadth of the iliac isthmus in humans produces a unidirectional growth plate (ABGP) similar to that seen in metapodia. This produces an
apophysis at the AIIS. We posit that the AIIS apophysis (origin of the straight head of rectus femoris) is not an adaptation but simply a byproduct of the real target of selection which is the broadening of the iliac isthmus to accommodate the bipedal, muscular locomotor complex, with a likely emphasis on gluteus medius and gluteus minimus. Using the Lovejoy et al. (1999) "analytical trait types", we propose that the hominid AIIS is likely a Type II trait, a byproduct of the real target of selection (Type I trait) which is the expansion of the iliac isthmus. Because we feel that increased iliac isthmus breadth, when accounting for iliac height, is intertwined with the bipedal condition, we also posit that it may have some predictive power when interpreting the fossil record. Moving forward, the index of the iliac height by iliac isthmus breadth could be informative in determining whether or not a true AIIS was likely to have existed in a fossil. In addition to the many other traits that must be considered, iliac isthmus breadth might also carry some predictive weight when considering locomotor pattern of fossil taxa.

On the Number of Origins of Rectus Femoris and Variation

Humans generally have two origins of rectus femoris, the reflected/indirect head and the straight/direct head. Occurrences of a third origin have been documented but appear to be in a minority of cases. In general, Pan, Gorilla, and Pongo are said to have one origin with occasional reports of two. Of the platyrrhines, catarrhines, and strepsirrhines studied, most are said to have a single origin of rectus femoris but there are reports of two heads. Sir Arthur Keith (1923) gives examples of variation that exists among hominoids. The human soleus originates from the proximo-posterior tibia and fibula (Stone and Stone, 2006). In apes, soleus generally originates from the fibula alone but occasionally can have an accessory origin on the tibia (Aiello and Dean, 2002). Keith (1923) reports that 3 out of 8 gorillas, 2 out of 12 chimpanzees, 1 out of 8 orangutans, and 2 out of 12 gibbons examined displayed a soleus that originated from the
fibula and tibia. In the human foot, the peroneus tertius muscle is said to originate from the lower third of the anterior fibula as well as from the interosseous membrane (Stone and Stone, 2006). Peroneus tertius is absent in all other primates which may lead one to believe that it may play a meaningful role in bipedality. Joshi et al. (2006) examined 110 human cadavers and found that peroneus tertius was completely absent in 10.5% of the limbs. Even when the peroneus tertius was present, it was only documented to have the "normal" origin (from the distal third of extensor surface of the fibula) approximately 50% of the time, with six other origin variations seen as well as differences between the left and right leg of the same individual (Joshi et al., 2006). These are but a couple of examples to make a point. If we follow the amount of variation that exists for some muscles and their origins to its logical end, both within and between species, we can appreciate the inherent danger in assuming an adaptationists paradigm for every feature.

At first glance, it is easy to interpret the two origins (and sometimes three origins) of rectus femoris in humans as being an adaptation for bipedality. In reality, it is plausible that a certain amount of variation simply exists and that it is not always the direct result of an adaptation (for example, seeing the straight head of rectus femoris in humans as being mechanically inordinately valuable in bipedality). In the case of the human rectus femoris, we propose that humans exhibit two origins (and sometimes three) possibly due to the expansion of the iliac isthmus which may have separated the positional information of the primitive origin of rectus femoris and like nearly all features of the musculoskeletal system, a small degree of variation will always be seen (Figure 25).
Figure 25. Schematic diagram depicting the possible origin of the AIIS positional information for the straight head of rectus femoris.
Implications for *Oreopithecus bambolii*

*Oreopithecus bambolii* (7-9 mya) has been claimed to have a human-like AIIS (Rook, 1999). The interpreted presence of the AIIS has been one of the traits used to argue that *Oreopithecus* could have had both the postural and locomotor behavior that is consistent with habitual bipedality (Rook, 1999). We would first like acknowledge that the highly compressed condition of the fossil makes it difficult to get a true sense of the proper dimensions and landmarks of the pelvis. Some features, such as the iliac crest and the anterior border do appear to be relatively well-defined. Clearly, the developmental trajectory of the AIIS region cannot be seen in this specimen and we feel the presence of a true AIIS is questionable, given the physical condition of the fossil. However, if we are to assume the dimensions of the *Oreopithecus* pelvis from Rook (1999), which include an interpreted superior rim of the acetabulum we can at least make a rough estimation because this index is simply a ratio (Figures 26 & 27). When we apply the index of minimum isthmus width/acetabular height, *Oreopithecus* falls in the general range of other apes (Figure 27). Given the above results, we posit that it is unlikely that *Oreopithecus* had a true AIIS. Due to the indices positions of *Oreopithecus*, in addition to the constraints mentioned earlier, we also find it contentious that *Oreopithecus* was capable of habitual bipedal posture or locomotion, given that its index values do not group with facultative or habitual bipeds. Of course, many traits must be considered when making determinations of locomotion but we posit that *Oreopithecus'* placement on these indices may have some predictive value in its placement among hominoids. We also propose that these indices may also have informative value in interpreting future hominoid fossil remains.
Figure 26. Radiograph of *Oreopithecus* from Rook (1999). Yellow and red line additions show areas of measure (1= conservative measure; 2= generous measure).
Figure 27. Box plot index showing the minimum isthmus width divided by acetabular height. Including *Oreopithecus bambolii*. Acetabular height for *Oreopithecus bambolii* was estimated by referencing the acetabular height equations of McHenry (1975) and converting the measures to ratios using the documented *Oreopithecus bambolii* pelvic photo to create an index value. An intermediate value was determined using McHenry’s two estimates: Human and *Pan*.

**Human Equation (McHenry, 1975):**
Femoral Diameter = Acetabular Height X 0.933 - 6.0

**Pan Equation (McHenry, 1975):**
Femoral Diameter = Acetabular Height X 0.686 + 5.2

Note: Ardi 1 & Ardi 2 represent indices using two different estimates of acetabular height of *Ardipithecus ramidus* (Lovejoy et al., 2009)
APPENDIX

Index 1: Maximum width of the iliac isthmus divided by iliac height.

Index 2: Minimum width of iliac isthmus divided by acetabular height.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Specimen</th>
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<th>Index 2 Min. Isthmus/Acetabular Height</th>
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