**3D ANALYSIS OF HIP JOINT MOBILITY AND THE EVOLUTION OF
LOCOMOTOR ABILITIES IN MIOCENE HOMINIDS**

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By
ASHLEY S. HAMMOND
Dr. Carol V. Ward, Dissertation Supervisor

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The undersigned, appointed by the dean of the Graduate School,
have examined the Dissertation entitled
3D ANALYSIS OF HIP JOINT MOBILITY AND THE EVOLUTION OF
LOCOMOTOR ABILITIES IN MIOCENE HOMINIDS

Presented by Ashley S. Hammond

A candidate for the degree of

Doctor of Philosophy

And hereby certify that, in their opinion, it is worthy of acceptance.

Carol V. Ward

J. Michael Plavcan

Gregory Blomquist

Scott Maddux

Casey Holliday

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Ashley Hammond

Dr. Carol V. Ward, Dissertation Supervisor

ABSTRACT

The emergence of extant ape-like locomotor behaviors has become a defining issue in reconstructing ape evolution. Suspensory positional behaviors, such as antipronograde bridging, climbing, clambering and transfer, distinguish extant hominoids from Old World monkeys and most New World monkeys. It has been widely theorized that suspensory behaviors involve highly abducted hip joint postures, potentially permitting suspensory behaviors to be inferred from joint function rather than relying on isolated morphologies. This thesis tests whether adaptations for suspensory behaviors can be inferred in fossil nonhuman hominoids from the hip joint.

The first study tests the association between suspensory behaviors and hip mobility in anesthetized living anthropoids (n=104). Suspensory taxa were found to have significantly higher passive ranges of abduction and external rotation compared to non-suspensory taxa.

The second study developed a digital modeling technique to estimate range of hip abduction and then tested the accuracy of the modeling approach against the live animal data. Hip joint abduction and the abducted knee position were reconstructed in a large sample of extant anthropoids (n=252) and then quantitatively compared these simulations to the *in vivo* data for passive range of abduction. Suspensory taxa were significantly larger in both simulated abduction (degrees) and abducted knee position

(mm), although there was overlap between locomotor groups. The results provided a hypothetical framework for how to interpret abduction modeled in fossil taxa.

The final study modeled hip abduction in early Miocene hominoid *Proconsul nyanzae*, late Miocene crown hominoid *Rudapithecus hungaricus*, and several large-bodied Plio-Pleistocene fossil cercopithecoids (*Paracolobus mutiwa*, *Paracolobus chemeroni*, *Theropithecus oswaldi*) using the validated modeling approach from the second study. Abduction simulations in *Proconsul nyanzae* and fossil cercopithecoids yielded abduction consistent with a non-suspensory locomotor reconstruction. Abduction in *Rudapithecus hungaricus* was exclusively in the range of extant suspensory anthropoids and was most similar to the values observed in spider monkeys and hylobatids. This study provides the first evidence for suspensory behavior in a Miocene ape based on joint function.

CHAPTER 1: INTRODUCTION

This thesis addresses whether adaptations for suspensory behaviors can be inferred in fossil nonhuman hominoids (ape taxonomy in Figure 1.1) from the hip joint based on range of abduction. Suspensory positional behaviors are forelimb-dominated behaviors, and include brachiation, antipronograde bridging, vertical climbing, and orthograde clambering and transfer. These behaviors distinguish extant apes from Old World monkeys and most New World monkeys, and presumably primitive early hominoids. The emergence of these extant ape-like locomotor behaviors has become a defining issue in reconstructing ape evolution (recent review in Crompton et al. 2008).

However, we have a poor understanding of how and when the evolution of below-branch locomotor behaviors occurred. Fossil stem hominid *Pierolapithecus* (or, hominine per Begun and Ward 2005) seems to lack suspensory adaptations in the hands (Moyà-Solà et al. 2004; Almécija et al. 2009; Alba et al. 2010a), suggesting that suspension evolved independently in hylobatids and great apes. The fossil ape *Sivapithecus* is probably closely related to the orangutan based on craniofacial similarities yet retains a primitive hominoid body plan, suggesting that great ape-like locomotor behaviors evolved at least twice within great apes (Pilbeam et al. 1990; Ward 1997; Larson 1998; Pilbeam and Young 2001). More recently, it has been argued that the lack of derived features in *Ardipithecus ramidus* requires that great ape-like locomotor behaviors and morphologies evolved in African apes after the *Pan*-human split (Lovejoy 2009; Lovejoy et al. 2009a; Lovejoy et al. 2009b). If so, human ancestors

never passed through an extant great ape-like locomotor stage and somewhat more generalized hominoids may, in fact, be a better model of the more immediate ancestral condition. All of our scenarios about how hominoids evolved depend on an accurate reconstruction of locomotor behavior in apes that lived during the Miocene epoch (~23-5 Ma).

The hip joint is hypothesized to be a key site of postural and morphological change during the evolution of hominoid and hominin locomotion. Specifically, below branch behaviors are thought to require a mobile hip joint with a higher range of abduction compared to quadrupedal locomotion, due to the need to reach distantly-spaced discontinuous arboreal supports with the knee and ultimately the foot. This is particularly important for larger-bodied animals using bridging and other suspensory behaviors, rather than leaping behaviors, because large-bodied animals must more cautiously transfer weight from one support to the next (Cartmill 1985). Because these supports are often erratically positioned and oriented, lateral hip abduction abilities are emphasized over the more adducted parasagittal limb movements used when walking on the top of tree branches (Grand 1968; Rodman 1979). In theory, mobility of the hip joint should be the most important hindlimb joint for determining foot position because all movements at the hip joint direct the distal limb segments. Although limb abduction is a frequently cited behavioral component of forelimb-dominated suspensory behaviors (Grand 1972; 1984; Cartmill 1985; Isler 2005; Crompton et al. 2008), it has not been demonstrated that hip abduction abilities differ between suspensory and non-suspensory primates.

Miocene apes have a surprising mix of morphological features of the femur and the pelvis, especially when considered alongside other regions of the postcranium. The

proximal femur is one of the most frequently preserved hominoid postcranial elements, known from *Proconsul* (Kenya, 17-20 Ma), *Morotopithecus* (Uganda, 20.6 Ma), *Afropithecus* (Kenya, ~17 Ma), *Equatorius-Kenyapithecus* (Kenya, 15 Ma), *Nacholapithecus* (Kenya, ~15 Ma), *Sivapithecus* (Pakistan, 9-12 Ma), *Hispanopithecus* (Spain, 9.5 Ma), *c.f. Dryopithecus* (Spain, 11.8 Ma), *Rudapithecus* (Hungary, 10 Ma), and *Oreopithecus* (Italy, 7-9 Ma). Despite the high number of Miocene ape femora preserved, we still do not know how to interpret the mosaic morphology in the hip region. For instance, *Hispanopithecus* has limb proportions and forelimb morphologies that suggest suspensory adaptations (Moyà-Solà and Köhler 1993; 1996; Almécija et al. 2007; Alba et al. 2012; Pina et al. 2012) and yet has a femur that is more similar in shape to other Miocene apes than extant great apes (Moyà-Solà and Köhler 1993; Pina et al. 2012; Almécija et al. 2013). This suggests that suspensory adaptations in large-bodied crown hominoids do not always look exactly like the great apes, making locomotor reconstructions based on comparisons to extant bony morphology extremely challenging.

If joint mobility can be reconstructed in fossil hominoids, this would allow us to side-step the issue of how to reconstruct locomotor behavior in fossils with no extant morphological analog. As the articular morphology of the opposing pelvic and femoral joint surfaces should *reflect* normal limits of motion imposed by soft tissues, it should be possible to reconstruct hip abduction in fossils using just the bones (Jenkins and Camazine 1977; MacLatchy 1996; MacLatchy and Bossert 1996), providing a method for evaluating locomotor abilities in fossil hominoids.

In order to assess whether adaptations for suspensory behaviors can be inferred in fossil nonhuman hominoids, I first test whether suspensory and non-suspensory

anthropoids actually differ in hip mobility. Chapter 3 presents baseline *in vivo* measures of hip joint mobility in a large sample of suspensory and non-suspensory nonhuman anthropoids and provides statistical comparisons. Since past workers have emphasized the role of abduction in suspensory behaviors, attention is given to range of abduction and the functional outcome of abduction—the position of the knee relative to the midline. The results presented in Chapter 3 provide compelling evidence that abduction is significantly greater in suspensory anthropoids.

Next, I develop a digital (*in silico*) model for estimating hip joint abduction using the bony morphology of the pelvis and femur. Hip abduction was reconstructed in Chapter 4 using surface scans of the pelvis aligned to the midline plane and articulating the femur in maximal hip abduction, building on digital modeling parameters outlined by MacLachy (1995, 1996, 1998) and MacLachy and Bossert (1996). As in the live animals reported in Chapter 3, abduction ability is significantly increased in suspensory anthropoids when modeled digitally. The *in silico* models are then validated (following definition from Hutchinson 2011) against live animal measures to provide an estimation of how the models deviate from empirical measures of abduction. This approach provides a model of hip abduction that reliably classifies locomotor group in extant taxa and has a known predictable relationship with empirical measures of joint mobility.

Abduction was then estimated for early Miocene hominoid *Proconsul nyanzae* (KNM-MW13142) from Kenya and late Miocene *Rudapithecus hungaricus* (unpublished) from Hungary. These are the only two fossil hominoids preserving undistorted femora and pelves from the same individuals and, more importantly, both species have distinctly different locomotor reconstructions. *Proconsul* is widely hypothesized to have been an above-branch quadruped (Le Gros Clark and Leakey 1951; McHenry and Corruccini

1983; Walker and Pickford 1983; Beard et al. 1986; Ward 1993; Ward et al. 1993; Kelley 1997; Ward 2007), whereas phalangeal and wrist morphology of *Rudapithecus* has been related to suspensory behaviors (Begun 1992; 1993; Kivell and Begun 2009; Begun and Kordos 2011; Begun et al. 2012). The results presented in Chapter 5 are consistent with the hypothesized locomotor behaviors used by both *Proconsul* and *Rudapithecus*, and suggest that *Proconsul* would probably not have been capable of the range of abducted hip postures that *Rudapithecus* could use. This study provides the first evidence for suspensory behaviors based on hindlimb joint mobility in a Miocene ape, and provides important data about hindlimb abilities which are critical for locomotor reconstructions in Miocene apes.

Figure 1.1. Superfamily Hominoidea with hypothesized positions of fossil apes
 Figure adapted from Crompton et al. (2008), with terminology following Wood and Harrison (2011). Most work supports a distinct group of stem hominoids (Begun et al. 1997a; Finarelli and Clyde 2004; Young and MacLatchy 2004), although the relationships of the fossil hominids is still highly debated among most authors.

CHAPTER 2: BACKGROUND

This chapter summarizes previous works that detail anthropoid locomotor behaviors, hip joint soft tissues, and bony morphologies. Locomotor reconstructions for Miocene apes are reviewed within the context of existing hypotheses for locomotor behaviors in Miocene apes. The difficulties in inferring locomotor behaviors in Miocene apes are discussed and followed-up with a discussion of the analytic approach advocated here-- assessing locomotor capabilities in Miocene apes using an *in vivo*-validated hip joint modeling approach.

RANGE OF MOTION AND ADAPTATION

Forelimb-dominated arboreality, such as that used during anti-pronograde bridging, brachiation, and vertical climbing, distinguishes hominoids from nearly all cercopithecids, as well as from most anthropoids in general (Keith 1923; Avis 1962; Erikson 1963; Napier 1963). Suspension is a key component to forelimb-dominant locomotor behaviors and is a particularly important adaptation for larger-bodied species, conferring more positional stability by allowing the animals to distribute their weight among multiple arboreal supports rather than balancing over a single support (Grand 1972; Fleagle and Mittermeier 1980) (Figure 2.2). Even though suspensory behaviors only account for a relatively small percentage of locomotor behaviors in the great apes (see Table 2.1), the importance of suspensory behaviors is thought to explain the derived morphologies shared among suspensory anthropoids, such as large intermembral indices and relatively large shoulder breadth (review in Larson 1998). The hypothesis that arboreal versatility is associated with an increased range of hip joint mobility has influenced

functional inferences made about hip morphology when reconstructing the behavior of fossil primates (Walker 1974; e.g., Fleagle 1983; Rose 1983; Ruff 1988; Ward 1993; Ward et al. 1993; MacLatchy 1996; MacLatchy and Bossert 1996; Köhler et al. 2002; Hogervorst et al. 2009).

Suspensory behaviors have different biomechanical requirements of both the fore- and hindlimbs than does generalized quadrupedalism (Grand 1972; Nakatsukasa and Kunimatsu 2009). In particular, suspensory behaviors require reaching for discontinuous, variably-oriented arboreal supports with both the hands and feet (Nakatsukasa and Kunimatsu 2009) (Figure 2.2). Large body size is often cited as being integral to below-branch locomotion because large-bodied animals are more stable when moving below-branch rather than on top of a similarly-sized branch (Fleagle and Mittermeier 1980; Cartmill 1985; Sarmiento 1995; Almécija et al. 2007; Ward 2007), but it is also worth noting that large body size itself facilitates below-branch locomotion. Large body size, particularly when distributed in the forelimbs, increases momentum during below-branch swinging (Demes and Gunther 1989). Additionally, with increasing limb length the physical reach of the animal increases relative to the center of mass, which opens up a greater range of arboreal supports within the animal's reach (Figure 2.1). The concept of the spatial “envelope” (e.g., Stevens and Parrish 1999), whereby the range of distal segment positions show the potential for overall abilities, has been considered in a limited capacity within primates (Grand 1972) but is of extreme importance for understanding locomotor adaptation and overall abilities.

Range of hand and foot positions are influenced by angular excursions at the proximal shoulder and hip joints, making mobility at these joints important determinants of the range of supports within reach of the hand and foot. In particular, increased

abduction ability at the shoulder and hip joint are attributed to the non-stereotyped reaching movements used during climbing, suspensory, and/or less cursorial behaviors (Jenkins 1974; Walker 1974; Fleagle 1976b; Jenkins and Camazine 1977; Grand 1984; Cartmill 1985; Larson 1993; Ward 1993; 2007; Crompton et al. 2008; Nakatsukasa and Kunitatsu 2009; Schmidt and Krause 2011). Attributions of higher abduction ability in certain locomotor groups are not informed by quantitative data, however, and instead result from qualitative observations regarding joint morphology or limb usage and/or position.

EXTANT ANTHROPOID LOCOMOTOR BEHAVIORS

Reconstructing the evolution of suspensory behaviors in fossil apes requires identifying morphological functional signals for suspension in extant taxa. Finding clear functional signals is challenging because anthropoids vary in their reliance on suspensory behaviors, and even suspensory apes and atelines, which are highly derived for forelimb-dominated behaviors, vary in their frequency and agility of suspensory behaviors. A large obstacle to all workers interested in anthropoid locomotor behaviors is that it is extraordinarily difficult to classify primates into precise locomotor categories because of their versatility (Rose 1983). All locomotor classifications and descriptive terminology are considerable simplifications of diverse behaviors exhibited by anthropoids but are necessary to test hypotheses regarding functional differences among taxa.

A summary of locomotor behaviors is provided below for the extant taxa considered in this study, and quantitative behavioral observations are provided in Table 2.1 for available taxa. All descriptive terminology for locomotor behaviors follow

definitions provided by Thorpe and Crompton (2006), Gebo (1992), Cant (1987), and Rose (1973b).

Gibbons (*Hylobates*) and Siamangs (*Symphalangus*)

The hylobatids inhabit dense tropical and subtropical forests in Southeast Asia and travel primarily via below-branch brachiation (reviews in Napier 1967; Napier and Napier 1967; Hunt 1991). White-handed gibbons (*Hylobates lar*) are very versatile in their locomotor abilities and can move through the canopy via "...diving, leaping, bridging, bipedal walking, running, quadrumanous climbing, and scrambling (Vereecke et al. 2006)." Siamang (*Symphalangus syndactylus*) locomotion is primarily brachiation along large boughs, supplemented by climbing, leaping, and bipedalism (Fleagle 1976a) (see Table 2.1). Siamangs, larger than most gibbons, are capable of gibbon-like ricochetal brachiation and acrobatic behaviors but exhibit these behaviors with less frequency, for shorter periods of time, and across shorter distances than gibbons (Avis 1962; Chivers 1972; Stern and Oxnard 1973; Fleagle 1976a). There are no known sex differences in locomotor behaviors in gibbons or siamangs.

Orangutans (*Pongo pygmaeus*, *Pongo abelii*)

Orangutans are native to dense rainforests of Indonesia and Malaysia, but are currently restricted to areas of Sumatra and Borneo. There are no major differences known to exist between Sumatran (*Pongo abelii*) and Bornean (*Pongo pygmaeus*) orangutan locomotor repertoires, although there may be differences in frequencies of behaviors used between these two species (Cant 1987; Thorpe and Crompton 2006; Manduelli et al. 2011). Orangutans use virtually all forms of arboreal travel, including quadrupedal or tripedal walking, vertical climbing, bipedal walking, orthograde (torso

upright) suspensory clambering, and brachiation (Cant 1987; Thorpe and Crompton 2006) (Table 2.1, Figure 2.3). With the exception of brachiation, all forms of locomotion used by orangutans are slow and cautious—with three of the four extremities typically grasping a substrate at any given time (Davenport 1967). Females tend to be even more cautious in their selection of support types, preferring supports lower in the canopy and larger in diameter (Thorpe and Crompton 2006; Thorpe et al. 2007a; Thorpe et al. 2009).

Western lowland gorillas (*Gorilla gorilla gorilla*) and Mountain gorillas (*G. beringei beringei*)

Gorillas inhabit tropical and subtropical forests, swamps, and marshes of Africa. Large interspecific locomotor differences exist between lowland gorillas and the high-altitude mountain gorillas. These locomotor differences are a function of habitat differences, particularly in canopy continuity and availability of foods, which necessitate divergent foraging strategies (Yamagiwa et al. 1998; Goldsmith 1999; Tocheri et al. 2011). Within gorillas, the western lowland gorilla (*G. g. gorilla*) is the most arboreal throughout its ontogeny and the mountain gorilla (*G. b. beringei*) is the least arboreal (Doran and Hunt 1994; Remis 1995; Doran 1997; Remis 1998). The western lowland gorilla uses vertical climbing for up to 48% of arboreal locomotion (Remis 1995) (Table 2.1). There is evidence that gorilla social structure and body size influence locomotor behaviors, with males less likely to use smaller supports and/or suspensory positions than females (Remis 1995). The adult mountain gorilla is almost exclusively terrestrial, although it will use cautious climbing (Schaller 1963; Reynolds 1965; Doran 1996; Doran and McNeillage 1998). Brachiation, swinging, leaping, and prolonged hanging are not observed in the adult mountain gorilla (Reynolds 1965; Doran 1997).

Chimpanzees (*Pan troglodytes*) and Bonobos (*Pan paniscus*)

Chimpanzees (*Pan troglodytes*) inhabit forests and savannahs of West and Central Africa whereas the bonobo (*Pan paniscus*) is found exclusively in Central African forests. Chimpanzee locomotion is dominated by arboreal vertical climbing and terrestrial knuckle-walking (Susman et al. 1980; Doran 1993a; Thorpe and Crompton 2006) (Table 2.1). Male chimpanzees use more arboreal climbing and scrambling and less arboreal quadrupedalism, but are slightly less arboreal overall compared to females (Doran 1993b). The locomotor behavior of bonobos is similar to the chimpanzee, although bonobos are more arboreal than chimpanzees (Doran 1993a). Some studies suggest that bonobos engage in more arm-swinging (brachiation), leaping, diving, and bipedalism when compared to the chimpanzee (Susman et al. 1980; Doran 1993a), with hand and foot postures of captive climbing bonobos described as more variable than other African apes (D'Aout et al. 2004; Isler 2005). The two taxa may also differ subtly in substrate preference during vertical climbing, with chimpanzees preferring large-diameter tree trunks and bonobos more frequently using smaller boughs and branches (Doran 1993a).

Colobines (Subfamily Colobinae)

Colobine monkeys are best described as arboreal quadrupeds (Napier 1967; Napier and Napier 1967). Six colobine taxa are considered within this study, and five of these taxa have few known differences in locomotor behavior. The black and white colobus (*Colobus guereza*) and western red colobus (*Piliocolobus badius*¹) are moderately-sized arboreal quadrupeds that will often cover large linear distances by

¹ *Procolobus badius* is a junior synonym of *Piliocolobus badius*, and both names are frequently used in colobine literature.

leaping (Rose 1973b; Morbeck 1977; Rose 1979; Gebo and Chapman 1995; Struhsaker 2010). Both these species of colobus monkey live in African forests and savannah woodlands. The golden snub-nosed monkey (*Rhinopithecus roxellana*) lives in montane, temperate forests of southern China and is a highly arboreal species, spending >97% of their time in the trees (Li 2007). The golden snub-nosed monkey will use leaping, jumping, and only very rarely semibrachiation (Wu 1993). Proboscis monkeys (*Nasalis larvatus*) monkeys are large-bodied arboreal quadrupeds, found in mangrove swamps of Malaysia and Borneo, that are reported to leap and dive as frequently as smaller colobines (Kern 1964; 1965; Rose 1973b). Lutungs (e.g., *Trachypithecus cristatus*) are small agile arboreal quadrupeds that also frequently leap and climb (Furuya 1961; Fleagle 1998; Harding 2010). Lutungs inhabit a range of habitats in Southeast Asia but prefer rainforests.

Within the Old World Monkeys, doucs (*Pygathrix*) are the only group reported to use below-branch suspensory behaviors (Workman and Covert 2005; Wright et al. 2008), although the majority of reports are based on captive primates. Doucs are entirely arboreal (Lippold 1998) and live in rainforests on mainland Southeast Asia. Captive doucs travel via brachiation or suspension as often as they travel quadrupedally, with pulling-up, climbing and/or leaping comprising only a small percentage of behaviors (Wright et al. 2008). Until doucs are more extensively studied, it is difficult to identify how important below-branch behaviors are in this group.

Cercopithecines (Subfamily Cercopithecinae)

Three cercopithecine taxa, patas monkeys (*Erythrocebus patas*), baboons (*Papio sp.*), and geladas (*Theropithecus gelada*), are highly terrestrial (Rose 1973b; a; 1977; Hunt 1991; Fleagle 1998) and typically only use arboreal behaviors for safety from

predators (Enstam and Isbell 2004). These species inhabit open habitats and grasslands with limited opportunities to use arboreal substrates, and are particularly limited in opportunities to leap between trees, which are distantly spaced (Hall 1966; Rose 1973b; Isbell et al. 1998). Terrestrial quadrupedalism accounts for 97% of all locomotion in baboons (*Papio*) (Rose 1977; Hunt 1991). The time geladas spend moving each day in search of food is the highest of any primate, although the distance traveled per day may be less than some baboon species (Iwamoto 1993). No documentation of suspensory locomotion or posturing could be found for wild baboons, geladas, or patas monkeys.

Although some cercopithecines are somewhat terrestrial, many cercopithecines use arboreal behaviors in high frequencies. The blue monkey (*Cercopithecus mitis*) is primarily an arboreal quadruped, whose dominant forms of locomotion are quadrupedalism and climbing, with suspensory behaviors (e.g., bridging, bimanualism) rarely observed (Gebo and Chapman 1995).

Macaques are quadrupedal monkeys, although there are interspecific differences in arboreal proclivities. Crab-eating macaques (*Macaca fascicularis*) are primarily arboreal quadrupeds (Rodman 1979; Cannon and Leighton 1994). Other modes of travel include scrambling (15%), climbing (12%), and leaping (6.4%) (Cannon and Leighton 1994). The pigtail macaque (*Macaca nemestrina*) is substantially more terrestrial than the crab-eating macaque, preferring to return to the ground to travel between tree crowns rather than leaping (Rodman 1979).

Spider monkeys (*Ateles*)

Spider monkeys (*Ateles* sp.) live in tropical forests and rainforests of Central and South America. Spider monkeys are the most agile and suspensory of the New World

monkeys (Erikson 1963; Eisenberg and Kuehn 1966; Napier and Napier 1967; Campbell 2008). Locomotor behaviors frequently include most forms of arboreal locomotion, including forelimb, hindlimb and/or tail-assisted suspensory behaviors, quadrupedalism on large-diameter supports, leaping to cross discontinuous gaps, and climbing (Mittermeier and Fleagle 1976; Mittermeier 1978; Cant 1986; Cant et al. 2001; Youlatos 2002). Quantitative data from Mittermeier (1978) shows that suspensory behaviors and climbing behaviors are preferentially used over quadrupedal behaviors in both *Ateles paniscus* (suspension 39%, climbing 31%, quadrupedalism 25%) and *Ateles geoffroyi* (suspension 26%, climbing 40%, quadrupedalism 22%).

Howler monkeys (*Alouatta*)

The howler monkey (*Alouatta caraya*) lives in similar New World environments as the spider monkey, but, whereas the spider monkey is highly suspensory, the howler monkey moves by slow quadrupedal progression along relatively large horizontal arboreal supports (Grand 1968; Mendel 1976; Fleagle and Mittermeier 1980). The deliberate, non-acrobatic quadrupedalism of the howler is potentially derived within atelids (Rosenberger and Strier 1989; Jones 2008). Howlers are reported to climb frequently when on smaller-diameter supports (Fleagle and Mittermeier 1980; Gebo 1992; Bicca-Marques and Calegario-Marques 1995). Arm-swinging and leaping behaviors are only rarely observed (Grand 1968; Fleagle and Mittermeier 1980; Ybarra 1984; Gebo 1992), although quadrumanous bridging behaviors are frequent (Prates and Bicca-Marques 2008). The howler monkey stabilizes itself with its prehensile tail (Lawler and Stamps 2002).

Capuchin monkeys (*Cebus sp.*)

Capuchin monkeys (*Cebus sp.*) are New World monkeys that can inhabit tropical, subtropical, and dry forests, as well as sometimes more open, disturbed habitats. Capuchins are arboreal quadrupeds and occasional leapers (Fleagle and Mittermeier 1980; Fleagle et al. 1981a; Gebo 1992; Wright 2007). The small body size of capuchins allows these animals to leap more frequently than the larger atelids (Fleagle and Mittermeier 1980).

Locomotor adaptation

Adaptive traits have a current functional role in an organism and are maintained in the population by means of natural selection. A species adapted for suspensory behaviors will have their survival and reproductive success increased by suspensory behaviors. Testing the importance of suspensory behaviors for an organism's survival and reproduction is virtually impossible, however. It is possible to measure an organism's frequency of suspension and qualitatively assess the agility and willingness to perform suspensory behaviors, and, although not ideal, functional morphologists interested in suspensory behaviors often base inferences about suspensory locomotor adaptation from frequency data.

It is difficult to classify extant primates into distinct locomotor groups (Erikson 1963; Napier 1967; Napier and Napier 1967) and, in fact, none of the extant primates can be considered exclusively "suspensory" or "non-suspensory". Most primates are probably capable of using suspensory behaviors. Locomotor classifications are further complicated by the fact that even within the more strictly suspensory taxa there is a spectrum of reliance on suspensory behaviors, with hylobatids using suspension for at least 50% of locomotion (Napier 1963; Napier and Napier 1967; Fleagle 1976a; Hunt

2004) and species such as chimpanzees using pure suspension for only 7% of locomotor bouts (Doran 1996).

The published behavioral literature has been used to classify the extant taxa considered in this study into very broad categories based on reliance on suspension (Table 2.2, Figure 2.4). Non-suspensory taxa are those that never use suspension when moving by pronograde movement is an alternative, and includes generalized arboreal and terrestrial quadrupeds such as capuchins (*Cebus*) and most cercopithecoids (Napier and Napier 1967; Rose 1973b; a; Morbeck 1977; Rose 1977; 1979; Fleagle and Mittermeier 1980; Fleagle et al. 1981a; Gebo and Chapman 1995; Struhsaker 2010). Species classified as suspensory include the hylobatids (*Hylobates*, *Symphalangus*), orangutans (*Pongo* sp.), lowland gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), and spider monkeys (*Ateles* sp.). Hylobatids and orangutans prefer to move via below-branch locomotion, and are able to negotiate almost all arboreal substrate sizes, orientations, and continuities with ease (Davenport 1967; Chivers 1972; Fleagle 1974; Fleagle 1976a; Cant 1987; Thorpe and Crompton 2006; Manduelli et al. 2011). Chimpanzees, bonobos, western lowland gorillas, and spider monkeys use less suspension but it is still an important part of their locomotor repertoire (see Table 2.2) (Susman et al. 1980; Cant 1986; Doran 1993a; Doran and Hunt 1994; Remis 1995; Doran 1997; Remis 1998; Cant et al. 2001; Youlatos 2002).

Additionally, there are taxa that are difficult to classify into suspensory or non-suspensory categories and have been excluded from categorization in this study. As previously discussed, howler monkeys (*Alouatta*) and mountain gorillas (*G. beringei*) are generally quadrupedal but probably still retain some suspensory adaptations (Schaller 1963; Reynolds 1965; Fleagle and Mittermeier 1980; Bicca-Marques and Calegari-

Marques 1995; Doran 1996; Doran and McNeillage 1998). Doucs (*Pygathrix*) seem to use brachiation quite frequently in captivity but it is unclear how substantial an adaptation this might be in wild-populations (Workman and Covert 2005; Wright et al. 2008). Data for *Pygathrix*, *Alouatta*, and *G. beringei* are presented in this dissertation, in the hope that future behavioral work will more clearly determine whether these taxa can be assigned to a locomotor category.

EXTANT ANTHROPOID HIP JOINT RANGE OF MOTION

Behavioral data suggests that that below-branch behaviors require high joint mobility, particularly abduction, in the shoulder (Le Gros Clark 1959; Grand 1972; Rose 1973b; Jenkins 1974; Grand 1984; Larson 1993; Hunt 2004; Crompton et al. 2008) and hip joints (Cartmill 1985; MacLatchy 1996) to enable reaching for distantly spaced arboreal supports, although very little quantitative data exist. Some inferences of joint motion can be gathered from 3D kinematic studies (e.g., Isler 2005) but the majority of kinematic studies are 2D and incapable of measuring anything other than flexion-extension angles. Isler (2005) measured hip abduction during vertical climbing in a small sample of captive hominoids, finding abduction to be similar across the great apes during vertical climbing tasks and slightly reduced in hylobatids. The thigh achieved maximal abduction in great apes during more flexed postures. Unfortunately, these are the only known data on hip abduction in nonhuman anthropoids and, problematically, laboratory and zoo kinematic data probably do not represent the extreme, or possibly even the typical, ranges of motion that are elicited in wild environments (Vereecke et al. 2011).

Some data exist for passive joint mobility, which is the best metric of overall range of motion but has limited inferential utility regarding specific ranges of joint motion

used during different locomotor behaviors. DeRousseau et al. (1983) report data for passive hip joint abduction in free-ranging *Macaca mulatta* (n=126), representing the only known passive hip joint abduction data in nonhuman anthropoids. The authors report no significant differences between right and left hip joints or age, and but some differences between sexes (see Table 2.3). Two other studies have examined range of passive hip joint motion in non-human anthropoids, although these studies focused on range of flexion-extension and did not quantify abduction. A large cross-sectional study by Turnquist and Kessler (1989) examined joint mobility in free-ranging *Macaca mulatta* (n=661), finding that range of hip flexion-extension decreased with age. A related study examined caged (n=85) and free-ranging (n=64) *Erythrocebus patas*, finding that joint mobility in caged animals can be highly variable (Turnquist 1983), with the largest differences in mobility attributed to animals raised in cage confinement from a young age (Turnquist 1983). Hip extension was the only hip variable measured but was found to be particularly susceptible to reductions in mobility due to caging compared to joints such as the wrist, ankle, and shoulder (Turnquist, 1983).

There is a large amount of data available for human hip joint mobility (see Table 2.3). Professional ballet dancers, who elicit extreme hindlimb postures, have similar ranges of passive hip joint motion as the general population, but have significantly increased ranges of flexion, abduction, and external rotation (Charbonnier et al. 2011). The large amount of human data shows that there is minimal difference between goniometric and more technologically advanced (e.g., Vicom) range of motion measurement techniques (American Academy of Orthopedic Surgeons 1965; Cole 1971; Kendall et al. 1971; Esch and Lepley 1974; Hoppenfeld 1976; Cailliet 1978; Boone and Azen 1979; Roaas and Andersson 1982; Mohr 1989; Pedretti 1996; Steinberg et al.

2006; Kubiak-Langer et al. 2007; Charbonnier et al. 2011; Kumar et al. 2011; Moreside and McGill 2011), indicating either approach will converge on similar values.

Unfortunately, most work examining hip mobility and limb postures has been restricted to a single taxon or clade, limiting the ability to extend conclusions about joint function to locomotor adaptation. Because it is untested whether hip mobility actually differs between species with different locomotor adaptations, it is unknown whether hip function actually reflects behavioral adaptation. This has been highlighted by recent work on the shoulder joint (Chan 2007b; a; 2008), which tested the assumption that suspensory primates have an increased range of motion at the shoulder joint to facilitate below-branch behaviors and whether thoracic shape actually promotes different levels of shoulder mobility. Chan's work found that the hominoid shoulder joint does not actually produce a greater range of circumduction than other primates (Chan 2007a), which would imply that non-suspensory monkeys have high shoulder mobility but do not routinely use locomotor behaviors which elicit the arm postures used by suspensory species. This scenario is difficult to reconcile with the different glenohumeral morphologies observed between apes and non-suspensory monkeys, and underscores the importance of comparing models of joint motion with empirical data.

INFLUENCE OF SOFT TISSUE MORPHOLOGY ON HIP MOBILITY

This study aims to reconstruct range of motion in fossil taxa using just bony morphology, making it necessary to consider the role of soft tissues in limiting hip mobility. Since range of hip motion is primarily determined by ligament, tendon and passive muscle tension (Kapandji 1970; Wright and Radin 1993; Levangie and Norkin 2005; Safran et al. 2012), there could be a considerable loss of information in models that do not include soft tissues (see Hutson and Hutson 2012). It is possible to build

models from living animals with intact soft tissues (Brainerd et al. 2010; Gatesy et al. 2010) or to incorporate information about muscle dimensions and attachments into simulations of joint motion (Ogihara et al. 2009; Seth et al. 2011; O'Neill et al. 2013). However, Incorporating soft tissue constraints into models of extinct species includes substantial guesswork regarding ligament and muscle fiber orientation, size, tension, etc. (Wang et al. 2004; Hutchinson et al. 2005; Nagano et al. 2005), with each additional parameter adding another level of uncertainty (and potentially error) to the model (Hutchinson and Garcia 2002; Hutchinson 2004; 2011). In order to facilitate discussions of why the models deviate from empirical range of motion data when soft tissues are not present, the soft tissue structures of the anthropoid hip joint must be considered.

Hip joint capsule and capsular ligaments

The joint capsule, particularly in reference to the three capsular ligaments, is one of the strongest soft tissue limits on femoral head movement within the acetabulum (Myers et al. 2011; Smith et al. 2011; Smith et al. 2012). The capsule surrounds most of the neck of the femur, attaching along the intertrochanteric line anteriorly and at the base of the neck posteriorly, and along the border of the acetabular labrum on the pelvis. The hip joint capsule physically limits femoral head movements via the capsular ligaments, keeps the femoral head tight in the acetabulum by creating negative intra-articular pressure, provides information about joint posture due to its high number of proprioceptive nerve endings, and even provides acute sensory (e.g., pain) information about joint position (Ralphs and Benjamin 1994; Levangie and Norkin 2005).

The three capsular ligaments are the iliofemoral (Y-ligament of Bigelow), ischiofemoral, and pubofemoral. The human ischiofemoral, pubofemoral, and the two limbs of the iliofemoral ligament, each have discrete functions to resist femoral head

translation as the hip moves through its range of motion (Martin et al. 2008; Smith et al. 2012). Within humans, the iliofemoral ligament attaches along the anterior inferior iliac spine and iliac acetabular margin, with the superior band attaching at the proximal intertrochanteric line and base of the greater trochanter and the inferior band attaching along the distal intertrochanteric line (Martin et al. 2008; Wagner et al. 2012). The iliofemoral is the strongest of the ligaments, and functions to resist extension and external rotation in humans (Myers et al. 2011), with the superior band primarily responsible for limiting external rotation and the inferior band limiting extension (Wagner et al. 2012). The ischiofemoral ligament attaches along the caudal acetabular border and the superior aspect of the femoral neck and intertrochanteric line, limiting internal rotation (Wagner et al. 2012). The pubofemoral ligament originates along the obturator crest and superior pubic ramus and blends with the iliofemoral ligament distally to insert near the lesser trochanter, acting to limit abduction (Wagner et al. 2012).

Little information is available on the hip joint capsule in primates. The capsule in the rhesus macaque is strong, with a broad, thick iliofemoral ligament (Howell and Straus 1933). The orangutan joint capsule is lax with capsular ligaments that are not distinct (Sonntag 1924). The chimpanzee joint capsule lacks all ligaments except one band of the iliofemoral (Sonntag 1923). These limited data suggest that the great ape capsule is looser and allows more mobility than that of cercopithecids.

Ligamentum teres femoris

The human ligamentum teres femoris primarily arises from the acetabular transverse ligament, but also arises from the cranial and caudal margins of the acetabular notch (Cerezal et al. 2010). The ligament is fully intracapsular, with an external synovial layer bounding the dense, well-organized collagen fibers that compose

the ligament proper (Chen et al. 1996). It is normally 30-35 mm long in humans (Chen et al. 1996; Bardakos and Villar 2009). In most mammals, the ligamentum teres transmits the artery of ligamentum teres, a branch of the obturator artery, to the capital femoral epiphysis during growth.

After the artery of ligamentum teres closes in adulthood, it is unclear what functional role of the ligamentum teres retains. Several studies have found a link between adult joint stability and ligamentum teres integrity, although whether the intra-articular ligament confers joint stability via proprioceptive feedback (Leunig et al. 2000; Sarban et al. 2007) or biomechanically limiting joint motion (Chen et al. 1996; Demange et al. 2007; Wenger et al. 2007; Dodds et al. 2008; Bardakos and Villar 2009; Martin et al. 2011) is uncertain. If the ligamentum teres is mechanically limiting joint movements, it appears to do so when the femur is in a position of combined adduction, flexion, and external rotation (Dodds et al. 2008).

The ligamentum teres configuration has become a central point in discussions of hip joint mobility and locomotor behavior (Walker 1974; Crelin 1988; MacLatchy 1995; 1996; MacLatchy and Bossert 1996; Harmon 2007), largely because the habitual use of joint positions that impinge the ligamentum teres between the femoral and lunate articular surfaces could potentially lead to cartilage degradation, osteoarthritis, and traumatic joint injury (Kapandji 1970; Jenkins and Camazine 1977; Mow et al. 1989; Ward et al. 1993; Notzli et al. 2001). The orangutan, a large-bodied and long-lived species that employs extreme hip joint postures, has a ligamentum teres configuration which theoretically minimizes the potential for degenerative hip joint diseases by positioning the ligamentum teres away from the joint loading surface. Secondary support for this being an adaptation related to minimizing joint degradation comes from

the “sloth-like” subfossil paleopropithecids, which also lack a ligamentum teres insertion on the femoral head and are hypothesized to have been completely suspensory (Godfrey et al. 2010). The orangutan ligamentum teres insertion has been called unique among anthropoids because it occurs at the base of the posterior medial articular surface of the proximal femur, on the femoral neck rather than in the center of subchondral bone (Crelin 1988), essentially removing it from the joint loading surface. Indian elephants also lack a subchondral ligamentum teres insertion (Crelin 1988), so this morphology does not exclusively relate to joint mobility and arboreal versatility, and it is emphasized here that a repositioned ligamentum teres insertion probably relates to maximizing joint loading surface to minimize potential for joint degradation. Although the unusual ligamentum teres insertion in orangutans has received considerable attention, little information on ligamentum teres structure has been published in other nonhuman primates.

Labrum

The acetabular labrum, a fibrocartilaginous ring around the border of the acetabulum, constrains movements of the femoral head within the acetabulum by deepening the acetabular socket and by increasing the negative pressure of the joint (Crawford et al. 2007; Myers et al. 2011; Smith et al. 2011; Safran et al. 2012). A larger acetabular labrum is implicated in certain types of femoroacetabular impingement in humans, with patients having a decrease in joint mobility associated with labral overcoverage of the femoral head (Tannast et al. 2007). No data are currently available on labrum size in nonhuman anthropoids.

Muscles

Muscle-tendon units can contribute to differences in mobility observed between species, with movements probably limited by differences in muscle extensibility and length (Gajdosik 2001; Gerling and Brown 2013). Thick muscles spanning the joint could also hypothetically limit motion at joints by physically obstructing movements at the joint, although this has not been reported in clinical literature. Most anthropoids have muscle insertion and origin patterns that broadly correspond to humans but the muscles attach on bones that may differ markedly in shape between taxa, which could result in different muscular orientations across joints. Moreover, it is known that some apes have muscle-chains (e.g., muscles that insert on other muscles) which span joints (Jungers and Stern 1980), although this is entirely unexplored in terms of how this might affect joint mobility.

The gluteus maximus muscle in apes (excluding orangutans) has 2 functional portions (Sigmon 1974). The proximal portion of the gluteus maximus inserts on the iliotibial tract and functions to abducts, laterally rotates, and tenses the iliotibial tract (Sonntag 1924; Sigmon 1974). The distal portion inserts from the gluteal tuberosity distally along the femur, and functions to extend, adduct, and laterally rotate the thigh (Sonntag 1924; Sigmon 1974). The gluteus maximus in cercopithecines is considered a single functional unit, although associated slips of muscle traveling from the base of the tail to the femur are sometimes attributed to caudofemoralis or femorococcygeus as in other quadrupeds (Howell and Straus 1933). It should be noted that the reorientation of the iliac blades in humans results in a drastically different gluteus maximus action (primarily hip extension) than is observed in quadrupeds such as cercopithecoids.

Only the cranial portion of the gluteus maximus is present in orangutans, which has a functionally similar yet distinct muscle called the ischiofemoralis muscle in place of the distal (caudal) portion. The orangutan ischiofemoralis originates in common with the long head of the biceps femoris muscle and inserts along the proximolateral border of the femoral shaft, almost to the lateral epicondyle. The actions of the ischiofemoralis muscle include extension, lateral rotation, and adduction of the femur. Additionally, the orangutan gluteal region can be further differentiated from other primates in that the tensor fascia lata muscle is absent (Sigmon 1974).

The iliopsoas muscle is a small variably present slip muscle that assists in hip flexion (Raven 1950; Satoh 1965; Sigmon 1974). It arises deep to the origin of the rectus femoris and inserts on the lesser trochanter, inferior to the iliopsoas insertion (Sigmon 1974). However, it should be noted that iliopsoas will often arise from the hip joint capsule itself (Raven 1950; Satoh 1965).

The adductor magnus, a single muscle with adductor and hamstring portions in humans, generally presents as two distinct portions in nonhuman anthropoids. The hamstring portion, or ischial portion, is called the long head, with the short head being the portion that attaches on the pubis (Preuschoft 1961; Sigmon 1974). Although adductor magnus is described in terms of two functional portions in platyrrhines, it is not clear if the two functional portions have two distinct heads as in catarrhines (Stern 1971).

Biceps femoris structure is highly variable in primates. In cercopithecids, the biceps femoris consists of just the long head, running from the ischial tuberosity to the tibia and fascia lata (Howell and Straus 1933). Apes and most New World monkeys have the bicipital form (Sonntag 1923; 1924; Raven 1950; Schön 1968; Stern 1971), although occasionally this muscle presents as a single head in hylobatids and

chimpanzees (Sigmon 1974). In the extant apes, the long head inserts on the lateral prominence of the tibia, as well as potentially on the iliotibial tract. The long head of the biceps femoris in orangutans may also insert on the femoral shaft (Howell and Straus 1933). The biceps femoris short head arises on the distal femoral shaft and joins the long head to insert on the lateral tibia, or on the head of the fibula and crural fascia (Raven 1950; von Klaus Uhlmann 1968; Sigmon 1974).

The scansorius muscle is consistently found in orangutans (Sonntag 1924; Sigmon 1969) but is variably present in other great apes (Raven 1950; Payne 2001), hylobatids (Diogo 2012), and cercopithecids (Sato 1965). The scansorius muscle assists in thigh abduction, flexion, and medial rotation (Sigmon 1969; 1974). In particular, the scansorius is thought to aid in drawing the thigh up towards the body in a scanning movement, from a position of abduction to flexion, as might be used in climbing (Sigmon 1969). Scansorius arises from the dorsolateral surface of the iliac blade and inserts anterior to the greater trochanter, just distal to the gluteus minimus insertion (Waterman 1929; von Klaus Uhlmann 1968; Sigmon 1969).

Additional muscles (i.e., iliotochantericus, scansorius) and additional functional portions of muscles (i.e., gluteus maximus, adductor magnus, biceps femoris) in nonhuman primates likely provide finer control of thigh movements or potentially increase force in certain movements. In terms of maximum (passive) range of motion at the hip, there is no reason to expect that these muscles are positioned in a way that would obstruct joint movement. Detailed dissection and histological work would be required to assess variation in muscle elasticity, architecture, and fiber lengths and how they relate to mobility. However, should there be differences in range of motion between

locomotor groups *in vivo*, differences in muscular structure should be explored as a contributing factor.

OSTEOLOGICAL CORRELATES OF SUSPENSION

Although suspensory behaviors range from high-speed ricochet brachiation in hylobatids, a more cautious climbing and clambering in great apes, and tail-assisted quadrupedal clambering in atelines, there are certain osteological features attributed to suspension across species. Osteological correlates of suspension include a high intermembral index, long curved phalanges, relatively small pollex, broad shoulders and often a broad ribcage, reduced or lost ulnocarpal articulation, laterally-facing glenoid, and a ventral displacement of the vertebral column (Erikson 1963; Tuttle 1975; Cartmill and Milton 1977; Sarmiento 1995; Larson 1998). In great apes, the reduction in the number of lumbar vertebrae, and dorsally displaced transverse processes on the vertebrae are also attributed to orthograde behaviors (Schultz 1950; 1961; Sarmiento 1995).

Features of the femur and pelvis attributed to high hip mobility

In all anthropoids, the spherical femoral head fits within the cup-shaped acetabular socket and articulates against a raised C-shaped portion of the acetabulum called the lunate surface. The lunate surface and the femoral head (not including the fovea capitis) are covered by articular hyaline cartilage. All movements of the femoral head within the acetabulum are centered at the hip joint center (Kapandji 1970; Pauwel 1980; Levangie and Norkin 2005). Movements are primarily limited by soft tissue constraints, however, as previously outlined. Of particular interest here, the ligamentum teres (and therefore, its insertion on the femur -- the fovea capitis) is necessarily

confined to the acetabular fossa to avoid risk of potentially damaging peak pressures on articular cartilage during normal joint loading (Kapandji 1970), which can lead to cartilage degeneration (Mow et al. 1989; Notzli et al. 2001). Based on this model of joint movement outlined by (Kapandji 1970) and (Jenkins and Camazine 1977), many bony morphologies of the pelvis and femur are specifically hypothesized to relate to hip mobility and/or suspension (Waterman 1929; Napier and Walker 1967; Schultz 1969; Jenkins 1972; Walker 1974; Jenkins and Camazine 1977; Stern and Susman 1983; Fleagle and Anapol 1992; Ward 1993; Ward et al. 1993; MacLatchy 1995; 1996; MacLatchy and Bossert 1996; MacLatchy 1998). It has thus been interpreted that a correspondingly shallow acetabulum, large acetabular fossa, large femoral head, a centrally-positioned fovea capitis (when present), long and steeply-inclined femoral neck, and a short greater trochanter reflect high abduction abilities (Schultz 1969; Jenkins 1972; Walker 1974; Lovejoy 1975; Jenkins and Camazine 1977; Ruff 1988; Ward et al. 1993; MacLatchy and Bossert 1996) (see Figures 2.5-2.6).

Most workers agree that a fovea capitis that is absent or centrally-positioned on the subchondral surface indicates a mobile hip joint (Walker 1974; Jenkins and Camazine 1977; Crelin 1988; MacLatchy 1995; 1996; MacLatchy and Bossert 1996; MacLatchy et al. 2000; Harmon 2007), although there is not a consensus among authors as to how to interpret articular surface distribution in anthropoids. The articular morphology of the opposing femoral and lunate surfaces should *reflect* the limits of normal motion at the hip, and therefore also reflect the positions of the joint during routine loading. The extent of the acetabular fossa within the lunate surface reflects maximum normal movements of the femoral head within the acetabulum (Kapandji 1970), but the femoral head articular surface generally receives the most discussion.

Asfaw (1985) suggests that the articular margin is variable within a single species, with the range of variation observed in humans encompassing what is described as the normal chimpanzee morphology by Jenkins (1972). Other authors argue for broad patterns in femoral head articular configuration that correspond to different locomotor modes or habitual hip postures. For instance, a relatively larger amount of subchondral bone on the anterior aspect of the femoral head has been related to a greater emphasis on adducted hip postures during locomotion (Fleagle 1976b; MacLatchy and Bossert 1996), although a distally-positioned fovea with the articular surface expansive posterosuperiorly has also been attributed to typically adducted, parasagittal limb movements (Walker 1974; Jenkins and Camazine 1977; Fleagle and Meldrum 1988) (Figure 2.6). Fleagle (1976b) relates an expansive anterior articular surface with an articular surface extending onto the femoral neck posteriorly as being related to adducted posture, although it has been observed that chimpanzees typically have a posteriorly expansive articular surface as well (Jenkins 1972; Stern and Susman 1983). Strepsirrhines have a slightly different femoral head articular structure probably related to different, highly-specialized leaping behaviors in this group (Walker 1974; Godfrey 1988; Anemone 1990; Dagosto and Schmid 1996).

A large and spherical femoral head is typically taken as an indicator of high mobility at the hip joint (Fleagle 2013). Ruff (1988) argues that high sphericity of the femoral head allows continued contact between femoral head and the acetabulum. Specifically, a large femoral head relative to the anteroposterior dimension of the femoral neck allows increased joint excursion compared to a relatively smaller femoral head (see Figure 7 in Ruff 1988). Given that *Pongo* has the most spherical femoral heads (77% of a sphere), they should have increased potential for joint excursion compared to *Pan* and

Gorilla (~71%) (Ruff 1988). Of course, joint size is a function of competing demands for mobility and weight-bearing, and a *relatively* large femoral head is alternatively attributed to either high levels of hip mobility or increased joint loading (Ruff 1988; Harmon 2007). When humans are excluded, hindlimb joint surface area typically scales isometrically across non-human primates (Alexander 1980; Ruff 1988; Godfrey et al. 1991; Jungers 1991). Because of the overlap between highly suspensory species and bipedal species in terms of femoral head proportions and shape (Harmon 2007), it can be challenging to identify locomotor behavior in fossil taxa for which both scenarios are plausible (e.g., *Oreopithecus*, *Orrorin*).

Moreover, how the femoral head is hafted onto the femoral neck affects the freedom of the femoral head from the neck, affecting movement within the acetabulum (Hogervorst et al. 2009). The declination of femoral head (e.g., superoinferior orientation of the femoral head articular surface on the neck) and the anteversion of the femoral head (e.g., anteroposterior orientation of the femoral head articular surface on the neck) are related to how the femoral head actually sits within the acetabulum. Orientation of the femoral head is often used interchangeably with articular surface distribution and approached as a non-metric trait (Jenkins 1972; Stern and Susman 1983; Asfaw 1985), and so there are no formalized hypotheses as to how variation in this feature might relate to hip mobility.

Depth of the acetabulum should also affect the maneuverability of the femoral head within the hip socket, and some work on humans suggests that acetabular orientation influences femoral head configuration and movement as well (D'Lima et al. 2000; Levangie and Norkin 2005; Steppacher et al. 2008). The acetabulum in suspensory species is usually described as being somewhat shallow, although there is a

range of variation, with *Pongo* being extremely shallow and *Gorilla* being quite deep by comparison (Schultz 1969; Ward 1991; Ward et al. 1993; Hogervorst et al. 2009). The C-shaped lunate surface, which articulates with the femoral head, displays differences in width of the anterior (cranial) horn and the width of the acetabular notch (Schultz 1969; Ward 1991; Ward et al. 1993). There is limited evidence that *Gorilla* may also have a reduced amount of articular cartilage present on the anterior horn (i.e., the anterior horn is not fully covered by cartilage in some individuals), which would correspond to an apparently reduced articular surface area distal (inferior) to the fovea capitis (Tillmann 1978).

Although most work has focused on the hip joint articulation, bony geometry of the proximal femur is also cited as an indicator of abduction ability. A long femoral neck will theoretically increase the distance between the bony pelvis and the greater trochanter, allowing for more abduction potential (Fleagle and Meldrum 1988). Likewise, it is hypothesized that a lower greater trochanter should enable more abduction before impingement of bony or soft tissues occurs (MacLatchy 1995; 1996). A tall greater trochanter will also reduce the range of powered abduction because the gluteus medius and minimus will more quickly approach the end of their effective length-tension range (Rodman 1979; Ting 2001). A higher neck-shaft angle could mitigate some of the effects of a tall greater trochanter by positioning the femoral head above the greater trochanter (Ward 1992), especially when coupled with a long femoral neck length (Marivaux et al. 2008).

The function of the crista trochanterica, a tubercle on the posterior aspect of the femoral neck, is unknown but there are hypotheses that the crista trochanterica relates to either an increase or a decrease in hip joint mobility. It has been hypothesized to

increase the leverage of the obturator internus muscle running over the tubercle, specifically during hip flexion in primates with a short femoral neck (see Alan Walker communication in Napier 1964). In this scenario, the crista trochanterica would confer enhanced external rotational abilities. However, the tubercle is present in many lemurs, platyrrhines, cercopithecoids, and hylobatids (Napier 1964; Rose et al. 1992; MacLatchy et al. 2000; Bacon 2001; Köhler et al. 2002), as well as in early Miocene hominoids (e.g., *Equatorius* BMNH 16331, *Morotopithecus* MUZ-M80, *Nacholapithecus* KNM-BG 35250, *Proconsul* KNM-RU 1753 and KNM-MW 13142) (Le Gros Clark and Leakey 1951; Napier 1964; Rose et al. 1992; MacLatchy et al. 2000; Nakatsukasa et al. 2012). It is unclear why cercopithecoids would require powerful external rotation and hylobatids do not fit with the short neck model. An alternate hypothesis, favored here, is that the tubercle relates to a stronger or thickened ischiofemoral ligament (Le Gros Clark and Leakey 1951), which would suggest that a large tubercle might reflect reduced joint mobility. Interestingly, the position of the crista trochanterica differs between extant taxa, with *Ateles* displaying a superior position and *Papio* being positioned more inferiorly on the posterior femoral neck (Bacon 2001). When found in Miocene femora, the crista trochanterica is described as being superiorly positioned (Bacon 2001; Nakatsukasa et al. 2012), perhaps reflecting hip joint mobility more similar to *Ateles*.

Features of the femur and pelvis that increase span at the foot

Ultimately, hip mobility is important for increasing the spatial envelope, or the range of positions that the distal limb segments can occupy (Figure 2.1). However, positions of the knee, and ultimately the foot, are also determined by factors other than mobility. Most notably, this includes body size. Absolutely and relatively larger femoral diaphysis lengths, femoral neck lengths, and bi-acetabular breadths can all facilitate

positions of the distal limb segment that are further from the midline of the body simply because they are larger. A large neck-shaft angle increases the abduction and lateral position of the knee for a given position of the hip (Walker 1974; Fleagle 1977; Jenkins and Camazine 1977; Rose 1983; Harrison 1986; Fleagle and Meldrum 1988), accomplishing the opposite of a large bicondylar angle (see Figure 2 in Jenkins 1972).

HOMINOID EVOLUTION

Fossil evidence of locomotor evolution in Miocene apes

Hominoids diverged from other catarrhines more than 20 Ma (review in Stewart and Disotell 1998), and probably closer to 25 Ma based on a few recently discovered fossils (Stevens et al. 2013). Most stem catarrhines, except perhaps *Apidium* (Fleagle and Simons 1995), share a large number of postcranial similarities with the later Miocene hominoids (review in Simons 1995; femur specific morphology in Ankel-Simons et al. 1998). A few authors suggest that early hominoid *Proconsul* may be a stem catarrhine (Harrison 1987; 1993; Rossie et al. 2002), but this thesis follows the more conventional phylogenetic placement of *Proconsul* within Hominoidea.

Early Miocene hominoids assumed to reflect the basal condition all display some type of postcranial apomorphies, but none appear to have the forelimb or thoracic specializations that characterize extant hominoids and Late Miocene hominoids (review in Ward 2007). The best-known early hominoid is *Proconsul* (*P. africanus*, *P. nyanzae*, *P. heseloni*, *P. major*; 17-20 Ma) from multiple sites in Kenya and Napak in Uganda. *Proconsul* species have dental morphology distinct from one another but the postcrania are quite similar and are most easily distinguished on a basis of size, as well as location of discovery. *Proconsul major* (19-20 Ma; Koru, Songhor, Napak) was as large as a

gorilla, estimated to be 63-87 kg (Rafferty et al. 1995)². *Proconsul africanus* (18 Ma; Koru) had a body size between a gibbon and chimpanzee, between 12-27 kg (Gingerich 1977; Gingerich et al. 1982; Conroy 1987). *Proconsul nyanzae* (17-18.5 Ma; Rusinga Island, Mfangano Island) was approximately the size of a chimpanzee, 18-31 kg. (Conroy 1987) or maybe even as large as 40 kg (Walker et al. 1983; Walker and Pickford 1983). *Proconsul heseloni* (17-18.5 Ma; Mfangano Island, Rusinga Island, Kaswanga Primate Site) was similar in size to *P. africanus*, weighing 9-20 kg (Harrison 2002).

Most regions of the skeleton are preserved for *Proconsul*, with multiple partial skeletons known from *P. nyanzae* and *P. heseloni* (e.g., Figure 2.7). *Proconsul nyanzae* hip morphology is primarily known from multiple specimens from Kenya (KNM-RU 1753, KNM-RU 5527, KNM-RU 1633, KNM-MW 13142). All specimens are characterized by a moderate to high neck-shaft angle (mean 130° per MacLatchy 2000), a robust femoral shaft, a prominent crista trochanterica on the posterior aspect of the femoral neck, and the trochanteric fossa is closed off posteriorly by a ridge of bone (Rose et al. 1992). The *Proconsul nyanzae* (KNM-MW 13142) male femur from Mfangano Island, Kenya (~17.8 Ma) is the most discussed femur because of its completeness. The KNM-MW 13142 femur has a spherical femoral head that is large relative to the femoral neck and a high neck-shaft angle (134°) (Ruff et al. 1989; Ward 1991; Ward et al. 1993). The KNM-MW 13142 fovea capitis is described as intermediate between the proximally-positioned fovea in apes and the distally-positioned fovea in monkeys (Ward et al. 1993). There is some indication that the KNM-MW 13142 articular surface does not extend as equally in the posteroinferior direction as in *Pan* (MacLatchy and Bossert 1996).

² Some authors consider the fossils from Napak as a separate genus, *Ugandapithecus* (Senut et al. 2000; Gommery et al. 2002; Senut et al. 2004).

Proconsul torso and forelimb morphology suggest a pronograde above-branch quadrupedal locomotor profile (Le Gros Clark and Leakey 1951; McHenry and Corruccini 1983; Walker and Pickford 1983; Beard et al. 1986; Ward 1993; Ward et al. 1993; Kelley 1997; Ward 2007). The back of *Proconsul* was long, with elongate vertebral bodies, more similar to cercopithecoid monkeys than extant apes (Ward 1991; 1993; Ward et al. 1993). Likewise, the ribcage was narrow and dorsoventrally deep and the pelvis was narrow with laterally-facing ilia (Ward 1991; 1993; Ward et al. 1993). However, *Proconsul* had long manual and pedal phalanges with strong flexor insertions, indicating a powerful grip (Begun 1993; Begun et al. 1994), high ranges of possible forearm pronation and supination (Kelley 1997; Rose 1997), and also lacked a tail (Ward et al. 1991; Nakatsukasa et al. 2004). It has been hypothesized that tail loss in hominoids is associated with powerful manual and pedal grasping associated with deliberate, cautious arboreal behaviors, reducing the importance of the tail for balancing during rapid and/or frequent leaping (Cartmill and Milton 1977; Begun et al. 1994; Kelley 1997; Rose 1997; Ward 2007).

Other fossil Miocene apes provide an opportunity to test the hypothesis that early apes have features consistent with below-branch species. *Afropithecus* (*A. turkanensis*; 17-17.5 Ma) is a hominoid with dental features distinct from *Proconsul* (Ward 1998; Deane 2012), although known postcranially from only a few elements from the sites of Kalodirr and Buluk (Leakey and Walker 1985; Leakey et al. 1988). The femora of *Afropithecus turkanensis* (17-17.5 Ma) are known from two femoral heads from Buluk (Leakey and Walker 1985; Leakey and Leakey 1986; Leakey et al. 1988). KNM-WS 12604 is an eroded femoral head and a small portion of femoral neck, whereas KNM-WS 12605 is an eroded femoral head. These femoral heads have been largely ignored

because of the weathering of the subchondral bone, which has made functional inferences nearly impossible. Overall, the *Afropithecus* postcrania suggest a chimpanzee-sized body (~35 kg) (Harrison 2002), and are described as similar to *P. nyanzae* and *P. africanus* (Leakey and Walker 1985; Leakey and Leakey 1986; Leakey et al. 1988).

Morotopithecus (*M. bishopi*; 20.6 Ma) possesses primitive cranial features similar to the younger *Afropithecus* but displays derived features associated with orthograde locomotion, including a dorsally-positioned lumbar transverse process, oval scapular glenoid and mobile knee joint (Ward 1993; MacLatchy et al. 2000; MacLatchy 2004). Other features such as a tall greater trochanter, short femoral neck, and small femoral head suggest more limited range of motion at the hip joint (MacLatchy et al. 2000; MacLatchy 2004), which would be inconsistent with arboreal orthograde. The femur of *Morotopithecus bishopi* is known from two femora from the same individual (Gebo et al. 1997; MacLatchy et al. 2000), with the right femur being relatively complete and preserving the greater and lesser trochanters, femoral neck, a separate but adjoining femoral head, three distal diaphyseal sections, and a condylar portion (MacLatchy et al. 2000). Since the original description in 2000, the adjoining pieces of the right proximal femoral shaft have been discovered (MacLatchy and Kingston 2013). The proximal femoral morphology has been interpreted as favoring fore and aft movements and little abduction (MacLatchy et al. 2000). The MUZ-M80 right femoral neck shaft angle is high (traditional NSA 135°) (MacLatchy et al. 2000) but this is seemingly countered by a small femoral head relative to neck dimensions, a short femoral neck, and a greater trochanter that approximates the superior aspect of the femoral head. In addition, the fovea capitis is not centrally located and is instead more

posteroinferiorly positioned on the subchondral bone as in monkeys (MacLatchy and Bossert 1996; MacLatchy et al. 2000). The *Morotopithecus* right femur is unusual among African Miocene hominoids in that the femoral head is not anteriorly displaced or anteverted (MacLatchy et al. 2000; Nakatsukasa et al. 2012).

If the *Morotopithecus* postcranials are indeed 20.6 Ma and derived for orthograde behaviors, this presents several intriguing scenarios. The first scenario is that *Morotopithecus* is a crown hominid (i.e., great apes, see Figure 1.1), which would mean that the divergence date of hylobatids has been underestimated and that hominids evolved earlier than originally thought (Young and MacLatchy 2004). The second possibility is that similarities between extant nonhuman hominids and *Morotopithecus* are the result of homoplasy. Neither scenario can currently be falsified with the fossil data available (MacLatchy et al. 2000; MacLatchy 2004; Young and MacLatchy 2004).

Nacholapithecus kerioi (~15 Ma) is a particularly enigmatic ape, differing from all other hominoids in having a narrow trunk coupled with relatively small hindlimbs and strikingly large forelimbs (Ishida et al. 2004; Nakatsukasa et al. 2007; Nakatsukasa and Kuniatsu 2009) (Figure 2.8). Prior to the discovery of *Nacholapithecus*, all known hominoids with enlarged forelimbs also had the characteristic torso rearrangement associated with orthograde. However, the small monkey-like vertebral bodies, humeral trochlea, and unspecialized phalanges of *Nacholapithecus* seem to indicate pronograde (Ishida et al. 2004; Nakatsukasa et al. 2007; Nakatsukasa and Kuniatsu 2009).

Nacholapithecus kerioi hip morphology is known from a few isolated femoral head fragments and a partial skeleton (KNM-BG 35250), which preserves portions of the femora and a partial ischium (Ishida et al. 1999; Ishida et al. 2004). The KNM-BG 35250 right femur is the most complete of the *Nacholapithecus* femora, although suffering from

some plastic deformation distally. This femur has a short femoral neck and high neck-shaft angle (140°), with a femoral head that extends just proximally to the greater trochanter (Ishida et al. 2004; Nakatsukasa et al. 2012). The femoral head is strongly anteverted, to such an extent that it is attributed to deformation (Nakatsukasa et al. 2012). The articular surface contours are well preserved, missing only a small portion posteriorly, and the articular surface appears to “mushroom” over the neck (Nakatsukasa et al. 2012). The fovea capitis is positioned posteroinferiorly to the equator of the femoral head (Nakatsukasa et al. 2012), in a similar position as *Proconsul nyanzae* (KNM-MW 13142). The hip joint thus has a combination of morphologies which are hypothesized to both enhance (i.e., high neck-shaft angle, femoral head projects above trochanter, expansive articular surface) and limit (i.e., short femoral neck, non-centrally positioned fovea) hip joint mobility.

*Equatorius africanus*³ is a large hominoid species with postcrania known from the Maboko Formation, the Nachola Formation, and the Tugen Hills of Kenya (14-15.5 Ma) (Ward et al. 1999; Ward and Duren 2002). This species appears to have been similar to early arboreal hominoids, having a long flexible back, ulnar styloid contact with the wrist, and a retroflexed humerus (Ward et al. 1999). *Equatorius* was probably semi-terrestrial based on limited shoulder mobility, a retroflexed olecranon, terrestrial hand proportions, and relatively straight phalanges that are robust (Ruff et al. 1989; Benefit and McCrossin 1995; McCrossin and Benefit 1997; Sherwood et al. 2002; Patel et al. 2009). A femur attributed to *Equatorius africanus* (BMNH 16331, previously attributed to *Proconsul* and *Kenyapithecus*) is known from Maboko Island, Kenya (14-15.5 Ma) (Le Gros Clark and Leakey 1951; Rose et al. 1996). The femur preserves the femoral head and neck,

³ Junior synonyms include *Kenyapithecus africanus* Leakey 1967 and *Griphopithecus africanus* Begun 1987.

lesser trochanter and much of the anterior aspect of the greater trochanter, and the most proximal portion of the diaphysis. The neck-shaft angle is moderate (125°) (MacLatchy et al. 2000) to high (130°) (Bacon 2001). The *Equatorius* femur is described as having a long femoral neck, high greater trochanter, and a femoral head to neck ratio that is smaller than *Proconsul* (Benefit and McCrossin 1995). The articular surface is highly spherical and extends anteriorly and posteriorly to smoothly transition into the femoral neck (Rose 1983), although there is some damage to the anterosuperior aspect of the articular surface. The articular profile is similar to *Sivapithecus* and *Proconsul* (MacLatchy and Bossert 1996), and the fovea capitis is relatively centrally-positioned. The Maboko Island femur has been likened to ambling, palmigrade arboreal quadrupeds (McCrossin and Benefit 1994), which would suggest a locomotor repertoire with no extant homolog if paired with terrestrial knuckle-walking.

Kenyapithecus wickeri is also a large hominoid species, known from specimens recovered at Fort Ternan, Kenya (14 Ma) (Simons 1969; Andrews and Walker 1976). Extensive dental and some mandibular materials are known for *Kenyapithecus*, but the morphology is more derived than specimens attributed to *Equatorius* (Pickford 1985; Harrison 1992; Ward et al. 1999; Sherwood et al. 2002). The only postcranial element referred to *Kenyapithecus* is a distal unassociated humerus, characterized by a wide trochlea relative to capitulum breadth, pronounced lateral trochlear keel, prominent supracondylar crest, deep olecranon fossa, small and posteriorly oriented medial epicondyle, and a shaft that is oval in cross-section (Simons 1969; Andrews and Walker 1976; Morbeck 1983; Ward and Duren 2002). Little can be inferred from this humerus other than that it was probably capable of powerful flexion-extension movements.

Several middle Miocene taxa are found outside Africa, the earliest being *Griphopithecus*. *Griphopithecus*, known primarily from chimpanzee-sized thickly-enameled molars discovered in Slovakia, Austria, Germany, and Turkey (Abel 1902; Heizmann and Begun 2001; Holec and Emry 2003), is hypothesized to have been closely related to *Equatorius* based on the dental morphology (Begun 2000; 2002)⁴. The *Griphopithecus* material is potentially as old 16.5 Ma (Heizmann and Begun 2001; Begun et al. 2003a; Begun et al. 2003b), although there is an argument for a later appearance for European hominoids at 14 Ma (Böhme et al. 2011; Casanovas-Vilar et al. 2011), which seems in better accord with timing of *Equatorius-Kenyapithecus* in Africa (Feibel and Brown 1991; Pickford et al. 2006). Although little is known of *Griphopithecus*, the association with *Kenyapithecus* could indicate that this taxon was either not a great ape at all (Begun 2002) or might be a plausible hominid ancestor (Begun 2007). Postcrania have been recovered at Paşalar in Turkey, although the only material published are phalanges consistent with mixed semi-terrestrial and semi-arboreal locomotor behaviors (Ersoy et al. 2008). A partial ulna and robust humerus from Klein Hadersdorf, Austria (Ehrensberg 1938) have been attributed to *Griphopithecus* based on similarities with *Kenyapithecus-Equatorius* (Begun 2002), and these forelimb elements are compatible with generalized quadrupedalism (Begun 2002; Alba et al. 2010b). However, it will remain unclear what locomotor behaviors characterized the earliest expansion of apes into Eurasia until associated dental and postcranial materials are recovered.

⁴ Begun (2000) hypothesizes that there is also a Eurasian connection to *Kenyapithecus* in addition to *Equatorius*. *Griphopithecus alpani* (Devínska Nová Ves in Slovakia, Paşalar and Çandır in Turkey) is linked to *Equatorius africanus* (Kipsaramon, Maboko, Nachola, and Tugen Hills, Kenya), with *Kenyapithecus wickeri* (Fort Ternan, Kenya) linked to a putative second hominoid species (*c.f. Kenyapithecus kizili*) at Paşalar, Turkey.

Sivapithecus (*S. parvada*, *S. indicus*, *S. sivalensis*; 9-12 Ma) from the Siwaliks formation in India and Pakistan is a putative fossil pongine based on facial morphology (Ward and Kimbel 1983; Ward and Pilbeam 1983). *Sivapithecus parvada* is thought to have a monkey-like torso and humerus and has been interpreted on this basis to not have had forelimb-dominant locomotion like *Pongo*, possibly implying independent evolution of great ape-like below branch arboreality in pongines and hominines (the "Sivapithecus dilemma"-- Pilbeam et al. 1990; Ward 1997; Larson 1998; Pilbeam and Young 2001; Madar et al. 2002; Young 2003).

Sivapithecus sivalensis proximal femur and pelvic morphology is known from isolated remains found in the Siwalik exposures. Little can be said about the *Sivapithecus* pelvis until the specimen is fully described, but early reports suggest it is "least unlike *Proconsul nyanzae*" (Morgan et al. 2011). Specimen YPM-GSP 12654 is a femoral neck and intertrochanteric region of a left femur. It has a steeply inclined femoral neck that is extremely anteroposteriorly narrow, a characteristic of all *Sivapithecus* specimens preserving a femoral neck (Pilbeam et al. 1980). Three femoral heads (YPM-GSP 13929, YPM-GSP 11867, YPM-GSP 15782) are attributed to *S. sivalensis*, although little can be said about these. Specimen YPM-GSP 11867 is a left proximal femoral head with a portion of the femoral neck, preserving a minimally abraded articular surface with distinct articular borders. The YPM-GSP 11867 fovea capitis is extremely shallow but expansive, and somewhat posteroinferiorly displaced on the subchondral surface, and the femoral neck is very anteroposteriorly narrow. Specimen YPM-GSP 13929 and YPM-GSP 15782 preserve foveal morphology but it is difficult to estimate whether the fovea was centrally-positioned. The YPM-GSP 15782 fovea capitis is deeper than YPM-GSP 11867 and similar to that observed in all non-

pongine anthropoid primates. Overall, the *Sivapithecus* femoral morphology has been taken to indicate a high amount of hip abduction and lateral rotation abilities (Pilbeam et al. 1980; MacLatchy and Bossert 1996), which is somewhat inconsistent with pronogrady. The disjunct between pongine forelimb and hindlimb morphology might indicate that the hindlimb was the initial target of selection in pongine orthograde behaviors, contrary to *Morotopithecus* and *Nacholapithecus*.

Pierolapithecus catalaunicus (11.9 Ma; Spain) is a stem great ape with adaptations in the vertebrae and ribcage that suggest more frequent use of orthograde behaviors (Moyà-Solà et al. 2004; Susanna et al. 2010) (Figure 2.9). It has been inferred that *Pierolapithecus* was not suspensory based on phalanges that are relatively short and not strongly curved (Almécija et al. 2009; Alba et al. 2010a; but see Deane and Begun 2008, 2010). A recent study of the *Pierolapithecus* pelvis fragments suggests that this species maintained a pelvis structure generally similar to the early hominoid *Proconsul nyanzae* (Hammond et al. 2013a), and not unlike the morphology described for *Sivapithecus* (Morgan et al. 2011).

*Dryopithecus fontani*⁵ (11-12 Ma) is primarily known from three partial mandibles and two isolated teeth from France (Lartet 1856) and a maxilla from Spain (Moyà-Solà et al. 2009), although other isolated skeletal and dental elements are attributed to this taxon. The *Dryopithecus* hypodigm once included most hominoid material in Europe but has recently undergone substantial revision, with most postcranial remains re-assigned

⁵ The type-specimen of a second species, *Dryopithecus brancoi*, was named after a single molar from Salmendigen, Germany (Schlosser 1901; Abel 1931; Szalay and Delson 1979). Molars from Rudabánya, Hungary share characters with the Salmendigen molar and thus the Rudabánya hominoid species was referred to as *Dryopithecus brancoi* (Begun and Kordos 1993). However, the discovery of several new European middle and late Miocene crania led to generic revisions (Begun et al. 2008). The genus *Rudapithecus* (Kretzoi 1969) has been resurrected for the hominoid material from Rudabánya, Hungary (Begun 2006; Begun et al. 2008), with *Hispanopithecus* (Villalta Comella and Crusafont Pairó 1944) formally resurrected for Spanish materials (Moyà-Solà et al. 2009). In addition, the taxonomic status of the *Dryopithecus brancoi* type specimen is unresolved (Begun et al. 2006), with some concern that the Salmendigen molar may not belong to a hominoid (Andrews et al. 1996).

to *Hispanopithecus-Rudapithecus* (Begun 2006; Almécija et al. 2007; Begun et al. 2008; Ward et al. 2008; Moyà-Solà et al. 2009; Casanovas-Vilar et al. 2011; Begun et al. 2012). Pollical phalanges probably belonging to *D. fontani* discovered in Castell de Barberà (Spain) are broadly similar to all other Miocene apes and suggest powerful grasping abilities (Almécija et al. 2011). A partial femur (IPS-41724) from Abocador de Can Mata (Spain) tentatively attributed to *Dryopithecus fontani* has features typically associated with pronograde quadrupedalism, including a posteriorly directed femoral head, tall greater trochanter, and a low femoral neck shaft angle (Moyà-Solà et al. 2009; Alba et al. 2010b; Pina 2011). The IPS-41724 femur is attributed to *Dryopithecus* because it is unlike the femora of *Hispanopithecus* (see below) and generated body size estimates (44kg) that are larger than the body mass estimated for the other Miocene ape from this region, *Pierolapithecus catalaunicus*. The IPS-41724 femur has a neck-shaft angle estimated to be somewhat low (123°) (Moyà-Solà et al. 2009), with a spherical femoral head is large relative to the femoral neck (Pina 2011) and positioned low relative to the greater trochanter (Moyà-Solà et al. 2009). Taken together, these features suggest more limited hip mobility than some of the other Miocene taxa from Europe. Likewise, a humerus from the Saint Gaudens type-site in France (Lartet 1856; Le Gros Clark and Leakey 1951; Pilbeam and Simons 1971) and a humerus from Castell de Barberà in Spain (Alba et al. 2010b; Alba 2012) have both been tentatively attributed to *D. fontani*. These humeri are consistent with quadrupedal behaviors, and seem to differ from the *Griphopithecus* humerus in having a less triangular cross section, a more developed lateral supracondylar ridge, and a medial and anterior concavity to the shaft (Alba et al. 2010b). Although the postcranial evidence is limited, *Dryopithecus* may have been less orthograde than the late European fossil apes.

Hispanopithecus (*H. laietanus*, *H. crusafonti*) (9.5 Ma; Spain) is a late Miocene European ape but is argued to have highly derived forelimbs and hands, suggesting a strong suspensory component to its locomotor repertoire (Moyà-Solà and Köhler 1996; Almécija et al. 2007; Almécija et al. 2009; Alba et al. 2012). The hands are long (Figure 2.9), with long curved phalanges with strong flexor insertions and robust metacarpals built for powerful grasping (Moyà-Solà and Köhler 1996; Almécija et al. 2007; Almécija et al. 2009). The lumbar vertebrae have transverse processes originating on the pedicle and the spinous process is caudally oriented, indicating reduced mobility (Moyà-Solà and Köhler 1996). The forelimb bones are elongate and provide extensive areas for forelimb muscular attachment, with the ulna having reduced contact with the wrist and allowing for more mobility at this joint (Moyà-Solà and Köhler 1996; Alba et al. 2012). Although pelvic material is unknown for *Hispanopithecus*, two femora, both nearly 2/3 complete, are preserved (Moyà-Solà and Köhler 1996). The femoral head extends above the greater trochanter, the neck-shaft angle is high (132°), and the breadth of the femoral head is large relative to the neck (Moyà-Solà and Köhler 1996; Köhler et al. 2002; Moyà-Solà et al. 2009). The femora are argued to have a homogeneous cortical distribution in the neck that is most similar to suspensory apes (Pina et al. 2012), with a high neck-shaft angle (132°) and a proportionately large femoral head that should promote hip mobility (Moyà-Solà and Köhler 1996).

Rudapithecus hungaricus (formerly *D. brancoi*) from Rudabánya, Hungary (10 Ma) preserves postcranial elements from the elbow, hip, hand, knee, ankle, and foot (Kretzoi 1975; Morbeck 1983; Begun 1993; Begun et al. 2012). Like other middle and late Miocene taxa, this species was highly dimorphic postcranially, with males approximately twice as large as females (Begun and Kordos 2011). *Rudapithecus*

hungaricus displays similar features as the contemporaneous *Hispanopithecus* but differs in having a less concave frontal bone (Begun 1994), less developed temporal lines, and less robust manual proximal phalanges (Begun et al. 2012). Because *Hispanopithecus* and *Rudapithecus* only differ by a few characters, they have been suggested to be sister taxa with similar locomotor adaptations (Begun et al. 2012) or the same genus (Casanovas-Vilar et al. 2011; Alba 2012), but the debate will not be resolved until additional material common to both taxa are recovered.

Rudapithecus hungaricus appears to have been suspensory. *Rudapithecus hungaricus* has long and curved phalanges (Figure 2.10), features attributed to high elbow mobility, proximal femoral morphology described as similar to *Hispanopithecus*, and scaphoid and capitate morphology most similar to *Pongo* and *Hispanopithecus* (Begun 1992; 1993; Kivell and Begun 2009; Begun and Kordos 2011; Begun et al. 2012). The forelimb bones are large relative to femoral head diameter (Morbeck 1983). The pelvis and femur of *Rudapithecus* have not been formally described (but see Begun and Kordos 2011; Begun et al. 2012) but initial work suggests that the pelvis displays transverse flaring as in extant suspensory apes (Ward et al. 2008). Several hominoid femora are known from Rudabánya, and these femora are characterized by “a large head, low neck-shaft angle, and a robust, curved and platymeric shaft” (Begun and Kordos 2011). A right (RUD 184) and a left femur (RUD183) (Kordos and Begun 2001) of similar size are likely from the same individual, and are associated with an undescribed pelvis (see Chapter 5). The right femur (RUD 184) is mostly complete proximally but missing the distal end and the greater trochanter, and suffering from some crushing in the diaphysis (Begun et al. 2012). The left femur (RUD 183) is a partial femoral head and proximal portion of the femoral neck. A large femur, probably from a

male, is roughly twice as large as the other femora (Begun and Kordos 2011).

Additional morphological assessments cannot be made until these femora are formally described, but the morphologies attributed to these specimens are consistent with morphologies attributed to high joint mobility.

Oreopithecus bambolii (6.7-8.3 Ma) was the latest known ape in Europe, surviving past the Vallesian extinction event (~9.6 Ma) responsible for eliminating the other hominoids in Europe (Rook et al. 2011). The majority of specimens come from Baccinello and Monte Bamboli in Tuscany (Gervais 1872; Hürzeler 1949; 1958), Sardinia (Cordy and Ginesu 1994), and potentially from Moldova as well (see discussion in Delson 1986 and references therein). It is one of the most well-represented fossil apes, with materials from multiple individuals and most regions of the body. A remarkably complete, although distorted, skeleton (IGF 11778) has allowed estimations of body mass (32 kg.) and intermembral index (Jungers 1987; 1990).

Historically, locomotor behaviors used by *Oreopithecus* have been highly disputed although there is a growing consensus that *Oreopithecus* was an orthograde suspensory ape (Schultz 1960; Straus 1963; Jungers 1987; Sarmiento 1987; Harrison 1991; Harrison and Rook 1997; Rose 1997; Begun 2002; Susman 2004; Ward 2007; Russo and Shapiro 2013) or perhaps had evolved from a suspensory species (Köhler and Moyà-Solà 1997; Rook et al. 1999). Support for *Oreopithecus* using forelimb dominant locomotion comes from its high intermembral indices matched only by orangutans (Jungers 1987) with large articular dimensions of the limb joints (Schultz 1960; Harrison 1986). However, *Oreopithecus* has shorter hands (Jungers, 1987; Moyà-Solà et al., 1999; Rook et al., 1999; but see Susman, 2004) and less specialized wrist bones (Harrison 1986) than living suspensory apes and *Hispanopithecus* (Almécija et al.

2007). The *Oreopithecus* femur has been suggested to have a human-like bicondylar angle (Kummer 1965; Köhler and Moyà-Solà 1997), although the specific femur in question (IGF 11778) suffers from severe diagenetic compression throughout except for the well-preserved femoral head. Because both bipedal and suspensory species use hindlimb extension and display a large femoral head on a steeply inclined femoral neck (e.g., Harmon 2009), and because *Oreopithecus* lacks adaptations for suspension in the phalanges, there are still some lingering questions about bipedalism in *Oreopithecus* (Harrison 1991; Köhler and Moyà-Solà 1997; Rook et al. 1999).

Several specimens from the hip are preserved for *Oreopithecus bambolii*, with multiple partial femora and a deformed pelvis known (Harrison 1986; 1991). Unfortunately, these specimens are typically too fragmentary or distorted to be highly informative regarding hip function. The most well-known *Oreopithecus* specimen is IGF 11778, which displays features thought to facilitate a wide range of rotation and full extension at the hip joint, indicated by a large, globular femoral head positioned on a long and steeply-inclined neck, a centrally-positioned fovea capitis, and a well-developed iliofemoral ligament insertion site on the pelvis (Harrison 1991). Another *Oreopithecus* femur, IGF 2011V, is a left proximal femur preserving a greater trochanter, femoral neck, and femoral head. The IGF 2011V articular surface is beautifully preserved and complete, with a deep fovea capitis centrally located on the subchondral bone. Additionally, there are *Oreopithecus* specimens (BA74, BA75, BA86, BA128) from the Baccinello lignite mines of Tuscany housed in Basel that are in the process of being described. These specimens are just femoral heads, all of which are characterized by an extremely deep fovea capitis that is centrally located on the subchondral surface. All

of the features described for *Oreopithecus* femora are compatible with high levels of mobility at the hip joint.

Problems in understanding evolution of fossil apes

One of the biggest obstacles to reconstructing locomotor abilities in Miocene apes is that there is no extant analog for them, and it is difficult to characterize their anatomy as either primitive or derived. All later Miocene forms (e.g., *Hispanopithecus*, *Rudapithecus*, *Oreopithecus*) appear to have suspensory adaptations, although not as highly derived as the extant apes. This has led some to speculate that the morphological and behavioral adaptations of the extant hominoids, particularly the hominids, are specialized patterns that have evolved somewhat recently (Harrison 1991; Larson 1998; Moyà-Solà et al. 2004; Lovejoy 2009; Lovejoy et al. 2009a; Lovejoy et al. 2009b). As Miocene hominoids are a surprising mixture of monkey-like and extant ape-like features (e.g., Harrison 1991; MacLatchy and Bossert 1996; Moyà-Solà and Köhler 1996; McCrossin and Benefit 1997; Ward et al. 1999; MacLatchy et al. 2000; Ishida et al. 2004; Moyà-Solà et al. 2009), functional analyses that have attempted to elucidate locomotor abilities based on comparisons to highly derived extant ape and cercopithecoid morphologies are almost certainly lacking the resolution necessary to identify what kinds of behaviors these animals were actually capable of using. *Proconsul nyanzae*, for instance, has features assumed to both limit (e.g., small femoral head, tall greater trochanter, non-centrally positioned fovea capitis) and reflect high hip abduction abilities (e.g., a large acetabular fossa, large neck shaft angle) (Ward et al. 1993), and has been interpreted as an ambling, clambering above-branch quadruped (Kelley 1995). It is unclear how different morphological combinations work together to produce, or reflect, functional abilities.

Moreover, the work by Chan (Chan 2007b; a; 2008) has posed difficult questions for the trait-function association in extant species (for broader scope, see also Hickman 1988; Van Valkenburgh 1994; Lauder 1995; Koehl 1996). When testing the assumption that suspensory primates have an increased range of motion at the shoulder joint to facilitate below-branch behaviors, Chan found that the hominoid glenohumeral joint does not actually produce a greater range of circumduction than other primates (Chan 2007a), nor does the shape of the shoulder joint and thorax necessarily promote increased mobility (Chan 2007b). Additionally, Chan found that the same level of mobility was achieved via different combinations of morphologies in different species (e.g., hominoids vs. lorines) and that different morphologies can even “cancel each other out” (Chan 2008). Chan’s findings reaffirm that joint function, and the relationship between mobility and anatomical form, must be approached as a system.

MODELING JOINT FUNCTION

The only method for evaluating hip joint function as a system in fossil hominoids is by modeling hip joint movement using both the acetabulum and femur. The theory for modeling hip joint abduction was outlined by MacLatchy (MacLatchy 1995; 1996; MacLatchy and Bossert 1996; MacLatchy 1998). Although MacLatchy’s digital sample was small by today’s standards, her 3D techniques were extremely sophisticated and show much foresight. The methodologies for hip joint modeling described later in this thesis derive primarily from MacLatchy’s (1995) thesis work, from which her subsequent publications are based (1996, 1998; and Bossert, 1996).

MacLatchy summarized the limits of how the hip joint should be positioned during loading based on joint functional biology (Kapandji 1970; Jenkins 1972; Jenkins and Camazine 1977; Latimer et al. 1987; Ward 1991; 1993; Ward et al. 1993) and used this

framework to conduct a study of hip joint abduction in primates. MacLatchy's digital modeling technique aligned the femoral head within the acetabulum using centroids of best-fit spheres fit to the femoral head and lunate surface within a sample of anthropoids (*Pan*, *Pongo*, *Homo*, *Mandrillus*, *Macaca*) and prosimians (*Galago*, *Perodicticus*, *Lepilemur*, *Cheirogaleus*, *Microcebus*). She maximally abducted the femur in positions of flexion and extension following 3 boundary constraints (1995, p. 116). First, during simulations, the fovea capitis was limited to the confines of the acetabular fossa. Second, the greater trochanter was not allowed to intersect the pelvis. Third, MacLatchy allowed the subchondral borders of the femoral head and lunate surface to only "slightly" overlap, using Jenkins and Camazine (1977) as a guide for normal joint boundary positions.

MacLatchy's study found a spectrum of abduction capabilities in anthropoids corresponding to what is known about their locomotor behaviors. As would be predicted, abduction was consistently highest in *Pongo*, followed by *Pan*. In the flexed position, humans have the most limited range of abduction, followed by the monkeys and chimpanzees. During extension, range of abduction separates humans and monkeys from the chimpanzees and orangutans. These differences were related to different hindlimb postures required during suspensory behaviors versus more generalized arboreality. When abduction was measured in Miocene hominoid *Proconsul nyanzae*, *Proconsul* appears similar to the monkeys during flexion but closer to chimpanzees during the extended posture, which suggests that *Proconsul* was probably capable of climbing postures that would be difficult for most cercopithecids. These results provided more specificity about hip use and locomotor abilities in *Proconsul* than was previously possible.

Model validation

Models, such as those derived from imaging techniques (e.g., MRI, CT, optical and laser scanning), are anatomically realistic and complex 3D representations of a real structure. However, even biologically complex, high-fidelity models are simplifications of real-world systems. The utility of modeling as a tool thus depends on how well the model replicates reality. The only way to know how closely a model matches reality is by comparing it to empirical data, a procedure often called model validation (see reviews in Richmond et al. 2005; Hutchinson 2011). When modeling joint positions using just the bones, abstraction of the system is introduced by not including the overlying soft tissues (e.g., articular cartilage, ligaments, labrum, muscles). It is therefore imperative to assess the limiting influence that the absent soft tissues might have on the results (Hutchinson and Garcia 2002; Gatesy et al. 2009; Hutchinson 2011; Hutson and Hutson 2012; Pierce et al. 2012). This is particularly true for the hip joint, where mobility is determined primarily by soft tissues (Kapandji 1970; Wright and Radin 1993; Levangie and Norkin 2005; Safran et al. 2012).

The regulations associated with living nonhuman primates makes *in vivo* validation of primate models difficult. Not surprisingly, MacLatchy was limited in her ability to collect live animal measures to test the accuracy of her models. MacLatchy (1995; 1998) gathered *in vivo* abduction data for 4 prosimian species (n=8; 2 individuals per species) that she modeled abduction in, and was unable to collect *in vivo* data on anthropoids. MacLatchy's *in vivo* data points are within a single standard deviation of the mean abduction during flexion, but abduction during extension does not as closely correspond to the mean values. Although a relationship can be tentatively inferred from these

limited data points, the small *in vivo* sample size and taxonomic composition prevent confirmation that MacLatchy's models are representative of her *in vivo* data.

Table 2.1 Comparison of percentages of adult locomotion in extant anthropoids

Species	Arboreal quadrupedal	Terrestrial quadrupedal	Climbing	Suspension (includes brachiation)	Leap	Other
<i>Hylobates</i> ¹			21%	56%	15%	8% bipedalism
<i>Symphalangus syndactylus</i> ²			37%	51%	6%	6% bipedalism
<i>Pongo abelii</i> ³	18%		26%	16%		22% clambering, 7% tree sway
<i>Pongo pygmaeus</i> ⁴	12%		18%	12%		51% clambering, 7% tree sway
<i>Gorilla beringei</i> ⁵		97%	<2%	<1%		
<i>Gorilla gorilla</i> ⁶	64%		20%	5%		3% transfer, 6% bipedalism
<i>Pan troglodytes</i> ⁷	22%		68%	7%		3% bipedalism
<i>Pan paniscus</i> ⁸	35%		50%	9%	3%	
<i>Pygathrix nemaeus</i> ⁹	54%			46%		
<i>Nasalis larvatus</i>	*		*		*	
<i>Rhinopithecus roxellana</i>	*		*		*	
<i>Trachypithecus sp.</i> ¹⁰	~50%		~10%		~40%	
<i>Colobus guereza</i> ¹¹	39%		11%		44%	
<i>Ptilocolobus badius</i>	*				*	
<i>Macaca fascicularis</i> ¹²	59%	<2%	12%		6%	15% scrambling
<i>Macaca nemestrina</i>	*	*				
<i>Theropithecus gelada</i>		*				
<i>Papio sp.</i> ¹³		97%	<1%			
<i>Cercopithecus mitis</i> ¹¹	54%		37%		11%	
<i>Erythrocebus patas</i>		*				
<i>Ateles paniscus</i> ¹⁴	25%		39%	31%	4%	
<i>Alouatta caraya</i> ¹⁵	69%		19%		3%	10% bridging
<i>Cebus capucinus</i> ¹⁶	54%		26%		15%	

* indicates a known significant component of locomotor repertoire but unknown percentage values.

¹ Hunt (2004) calculated from Gittins (1982), Fleagle (1980), and Srikosamatara (1984), ² Hunt (2004) calculated from Fleagle (1980), ³ Thorpe and Crompton (2006), ⁴ Cant (1987) using data only for females, ⁵ Doran (1996), ⁶ Hunt (2004) calculated from Remis (1995), ⁷ Doran (1996), ⁸ Hunt (2004) calculated from arboreal locomotor bouts from Susman et al. (1980), Doran (1996), and Susman (1984), ⁹ Byron and Covert (2004), ¹⁰ Fleagle (1998) for *Trachypithecus obscura*, ¹¹ Gebo and Chapman (1995), ¹² Cannon and Leighton (1994), ¹³ Hunt (1991), ¹⁴ Mittermeier (1978) and Fleagle and Mittermeier (1980), ¹⁵ Prates and Bicca-Marques (2008), ¹⁶ Gebo (1992) .

Table 2.2 Broad locomotor categorization of extant anthropoids considered in this study

Category	Reliance on suspensory behaviors	Taxa
Suspensory	suspensory behaviors dominant	<i>Hylobates, Symphalangus, Pongo</i>
	suspensory behaviors very important	<i>Pan, G. gorilla, Ateles</i>
Unclassified	indeterminate	<i>G. beringei, Alouatta, Pygathrix</i>
Non-suspensory	suspensory behaviors rarely observed	<i>Rhinopithecus, Colobus, Piliocolobus, Nasalis, Trachypithecus, Cercopithecus, Macaca, Cebus</i>
	suspensory behavior extremely rare	<i>Papio, Erythrocebus, Theropithecus</i>

Table 2.3 Comparison of published values for anthropoid hip joint mobility

Population	n	Age (years)	Abduction	Adduction	Internal rotation	External rotation	Flexion	Extension
<i>H. sapiens</i> ¹	--	--	40°	35°	45°	45°	120°	30°
<i>H. sapiens</i> ²	56	19-54	41°	26°	44°	44°	121°	12°
<i>H. sapiens</i> (dancers) ³	11	18-38	73°	--	38°	28°	117°	43°
<i>H. sapiens</i> ⁴	33	25-74	63°	33°	35°	103°	122°	57°
<i>H. sapiens</i> ⁵	57	15-25	44°	--	--	--	139°	--
<i>H. sapiens</i> ⁵	104	25-100	43°	--	--	--	137°	--
<i>H. sapiens</i> ⁶	105	30-40	39°	31°	33°	34°	120°	9°
<i>H. sapiens</i> ⁷	1,683	25-74	42°	--	32°	32°	121°	19°
<i>H. sapiens</i> (dancers) ⁸	1,320	8-16	54-64°	--	56-66°	56-59°	143-151°	--
<i>H. sapiens</i> ⁸	226	8-16	44-49°	--	53-64°	48-61°	143-147°	--
<i>M. mulatta</i> ⁹	126	<1-21	~30°(all)	36°(adults)	--	--	--	--
<i>M. mulatta</i> ¹⁰	232	6-25	--	--	--	--	11-49°	116-158°
<i>E. patas</i> ¹¹	38	>2	--	--	--	--	--	145-155°
<i>E. patas</i> (caged) ¹¹	53	>2	--	--	--	--	--	140-150°

All published data was collected with a goniometer on healthy adults unless otherwise indicated. Human and quadruped measures of extension-flexion are measured inversely to each other.¹ American Academy of Orthopedic Surgeons (1965) and Esch and Lepley (1974). These values are reported as healthy adult "normal" values and adapted by numerous secondary sources, such as Kendall et al. (1971), Daniels and Worthingham (1972), Hoppfeld (1976), Mohr (1989), Cailliet (1978), Cole (1971), and Pedretti (1996).² Boone and Azen (1979),³ Charbonnier et al. (2011).⁴ Range of motion was measured on advanced/professional dancers by using digital models created from MRI guided by kinematic (i.e., Vicom) data. Kubiak-Langer et al. (2007). Range of motion estimated from digital simulations.⁵ Kumar et al. (2011).⁶ Roaas and Andersson (1982).⁷ Roach and Miles (1991) using First National Health and Nutrition Examination Survey.⁸ Steinberg et al. (2006). The dancer population sampled students of classical ballet and modern dance classes, not elite dancers.⁹ DeRousseau et al. (1983).¹⁰ Turnquist and Kessler (1989). Ranges in the table represent the max/min values, back-calculated from means and standard deviations provided by Turnquist and Kessler (1989), across the adult ages ranges for macaques.¹¹ Turnquist (1983).

Figure 2.1 Large hindlimb spatial envelope increases the range of foot positions
 (a) The range of positions of the knee is a proxy for the hindlimb spatial envelope, or the overall range of foot positions. An increase in joint mobility and/or body size will increase the hindlimb spatial envelope. Image modified from Kapandji (1970). (b) An increase in the spatial envelope of the limbs will increase the range of supports, as well as the feeding space, available to an animal. Image modified from Grand (1972).

Figure 2.2 Hindlimb postures used by anthropoids during different locomotor behaviors

(a) Quadrupedal arboreal behaviors in *Alouatta* emphasize adducted and flexed thigh postures. Image modified from Grand (1968). (b) Vertical climbing in *Pan* elicits abducted and laterally rotated positions of the thigh. Image modified from Stern and Susman (1981). (c) Suspensory bridging and transfer behaviors in *Symphalangus* elicit thigh postures throughout the ranges of flexion-extension, adduction-abduction, and rotation. Image modified from Fleagle (1976a).

Figure 2.3 Examples of arboreal behaviors used by orangutans

Orangutans are the most acrobatic of the hominids and used virtually all forms of arboreal locomotion, including (a) assisted bipedalism, (b) palmigrade quadrupedalism, and (c) suspension with weight-transfer through both forelimbs and hindlimbs. Image modified from Thorpe et al. (2007b).

Figure 2.4 Phylogenetic relationships between extant taxa with locomotor classification mapped onto tree

Consensus tree for extant primates based on the 10k Trees Website (Arnold et al. 2010). Locomotor categories from Table 2.2 are mapped onto the taxa (black=suspensory, light grey=non-suspensory, dark gray=indeterminate/unclassified). Extant suspensory primates have evolved from at least two evolutionary events (i.e., hominoids, atelids) and potentially a third (i.e., *Pygathrix*), providing multiple independent instances in which to evaluate the relationship between suspensory behaviors and morphology.

Figure 2.5 Posterior and anterior views of anthropoid femora

Posterior views of femora (above) and anterior views (below) show variation in femoral morphology. All femora are oriented based on a horizontal orientation of the femoral condyles. Suspensory taxa are described as having a relatively large, spherical femoral head (indicated by dashed line) on a long (arrows) and steeply inclined femoral neck (angle indicated by white lines), freeing the femoral head from the femoral neck in suspensory anthropoids. Additionally, the femoral head is positioned proximal to the greater trochanter in suspensory species whereas the greater trochanter is positioned above the femoral head in non-suspensory taxa. *Pongo pygmaeus* (USNM 49768 ♀), *Pan troglodytes* (CMNH B1755 ♀), *Symphalangus syndactylus* (ZSM 1905.108 ♀), *Nasalis larvatus* (MCZ 37328 ♂, mirrored), *Papio anubis* (USNM 384228 ♀) are shown. Femora are not to scale.

Figure 2.6 Medial views of anthropoid femora, with an emphasis on femoral head articular configuration

The most obvious interspecific differences from medial view are differences in how the femoral head is hafted onto the femoral neck. The femoral head is oriented superiorly in *Pongo*, anterosuperiorly oriented in *Pan*, somewhat posteriorly in *Symphalangus*, and both cercopithecids have a more medially directed femoral head. The positions of the foveae are also distinct. *Pongo* lacks a fovea, but *Pan* and *Symphalangus* have foveae that are centrally positioned on the subchondral bone, whereas the two cercopithecids have fovea that are more posteroinferiorly displaced. Because the femoral heads of hominoids are a more complete sphere, the centrally-positioned fovea contributes to a more expansive posteroinferior articular surface. The inset photos of *Pan* and *Papio* highlight these differences, with the posteroinferior aspect of the femoral head indicated by a white arrow. *Pongo pygmaeus* (USNM 49768 ♀), *Pan troglodytes* (CMNH B1755 ♀), *Symphalangus syndactylus* (ZSM 1905.108 ♀), *Nasalis larvatus* (MCZ 37328 ♂, mirrored), *Papio anubis* (USNM 384228 ♀) are shown. Femora are not to scale.

Figure 2.7 An early Miocene hominoid, *Proconsul heseloni* (KNM-RU 7290 skull and KNM-RU 2036 skeleton), from Rusinga Island, Kenya

Photo from Wikimedia Commons, allowed for reproduction with citation of online location (http://commons.wikimedia.org/wiki/File:Proconsul_nyanzae_skeleton_7.JPG).

Figure 2.8 A middle Miocene hominoid, *Nacholapithecus kerioi* (KNM-BG 35250), from Nachola, Kenya
Image modified from Nakatsukasa and Kunitatsu (2009).

Figure 2.9 Middle to late Miocene hominoids, *Pierolapithecus catalaunicus* (IPS-21350) and *Hispanopithecus laietanus* (IPS-18800), from the Vallès-Penedès basin in Spain

Pierolapithecus (left) and *Hispanopithecus* (right) are notably different in their phalangeal morphology and manual proportions, with *Hispanopithecus* having long and curved proximal phalanges only matched by *Pongo* and potentially fossil hominoid *Rudapithecus*. Images modified from Moyà-Solà et al. (2004) and Moyà-Solà and Köhler (1996).

Figure 2.10 Late Miocene hominoid, *Rudapithecus hungaricus*, from Rudabánya, Hungary
Rudapithecus hungaricus images are from Begun et al. (2012).

CHAPTER 3: *IN VIVO* RANGE OF MOTION

The hypothesis that arboreal versatility is associated with an increased range of hip joint mobility has influenced functional inferences made about hip morphology when reconstructing the behavior of fossil primates (Walker 1974; e.g., Fleagle 1983; Rose 1983; Ruff 1988; Ward 1993; Ward et al. 1993; MacLatchy 1996; MacLatchy and Bossert 1996; Köhler et al. 2002; Hogervorst et al. 2009). To date, it has never been shown empirically that suspensory anthropoids have higher levels of hip joint mobility than in non-suspensory taxa. Limited data on passive hip joint mobility are available for cercopithecids (DeRousseau et al. 1983; Turnquist 1983; 1985; Turnquist and Kessler 1989) but there are no data from suspensory taxa for comparison. Quantifying range of possible hip joint motion in suspensory and non-suspensory anthropoids would provide empirical data with which to test the hypothesis that suspensory primates have higher levels of hip joint mobility. The goal of this chapter is to evaluate whether suspensory primates actually do have a greater range of motion in the hip joint than non-suspensory primates.

OBJECTIVE

The hypothesis being tested that there are significant differences in hip joint mobility between suspensory and non-suspensory taxa is tested. Accordingly, the null hypothesis is that there are not significant differences in hip joint mobility between suspensory and non-suspensory taxa.

SAMPLE

The handling and use of animals described herein was approved by the University of Missouri Animal Care and Use Committee (protocol #6862) and by the animal care committees of the participating zoos and research centers (listed in Table 3.1). *In vivo* measurements were collected during primate immobilizations for routine veterinary procedures. The use of captive caged animals is not ideal but, because captive animals can be measured in a controlled setting with experienced veterinary professionals in attendance, the use of captive animals was the only realistic and safe method of collecting ROM data. Measurements were collected on live animals rather than cadaveric specimens to avoid changes in soft tissue compliance from decay (e.g., rigor mortis) or chemical embalming (Viidik and Lewin 1966; Tolhurst and Hart 1990; Wilke et al. 1996).

All institutions visited during this study are fully-accredited with the Aquarium and Zoological Association (AZA), the Zoological Association of America (ZAA), and/or the Council on Accreditation of the Assessment and Accreditation of Laboratory Animal Care International (AAALAC). Animal housing was determined by each research location and follow the animal husbandry guidelines for each species. All animals had access to climbing structures within their enclosures, except *Macaca* individuals. *Macaca* were housed in cages at the Wisconsin National Primate Research Center.

The subjects used in this study are listed in Table 3.1. Primates categorized as “suspensory” are those species reported to use suspensory behaviors in the wild (*Hylobates*, *Symphalangus*, *Pongo*, *Gorilla*, *Pan*, *Ateles*), whereas “non-suspensory” taxa are those with no reported use of suspension (*Colobus*, *Trachypithecus*, *Macaca*, *Papio*, *Cebus*) (see references in Table 1). All animals were weaned and considered

adults by veterinary staff. However, based on the age of some of the animals (sex-specific means presented in Table 3.2), it is unlikely that they were all skeletally mature at the time of study. Any age effects are considered to be unlikely, as range of motion in cercopithecoids has been shown to be relatively stable and only changing significantly during young (first 18 months) and advanced ages (Turnquist 1983; Turnquist and Kessler 1989). Veterinary records indicate that four of the *Ateles* included in this study are hybrids of *Ateles fusciceps-geoffroyi-robustus* and that all *Papio* are hybrids of *Papio hamadryas-anubis-cynocephalus*. All animals were selected in consultation with veterinary staff, and animals with a known history of arthritis, lameness, or hindlimb injury were excluded from the study.

METHODS

Measurements

The handling and sedation of all subjects was done by licensed veterinarians or veterinary technicians in compliance with the Institutional Animal Care and Use Committee protocols for each research location. Most institutions use an anesthetic-sedative combination during animal immobilizations. Excluding *Cebus apella*, all animals were in a deep anesthetic plane at time of study and muscle tone was fully passive. *Cebus apella* individuals were immobilized using only an oral sedative and ketamine, resulting in some muscle tension during manipulation. Muscle resistance only noticeably occurred in *Cebus* during measures of hip extension.

Direct measures of (1) flexion, (2) extension, (3) adduction, (4) abduction, (5) internal rotation, and (6) external rotation were measured with each subject laying supine on an examination table. All measurements were collected by the author. In the

case of male great apes, it became necessary to recruit the assistance of the veterinary staff during some manipulations of the hindlimb. Data were collected using disposable double-armed goniometers and measuring tapes. Measures are based on standard goniometric techniques used in humans (Cole 1971; Norkin and White 1995).

Hip extension and flexion were measured in a parasagittal plane from a lateral view, measuring the angle formed between the femoral diaphysis and the iliac blade (Figure 3.1). Total range of movement from flexion to extension was calculated for each individual by subtracting the value for flexion from the extension value.

A “horizontal” femur posture was then identified for each individual, defined as when the femur approximated a 90° orientation (perpendicular) to the horizontal surface of the examination table. Although defined based on perpendicular thigh orientation relative to the examination table, this position is termed “horizontal” here because abduction from the horizontal posture matches the “horizontal abduction” described in Stern and Larson (1993)⁶. Measures of adduction, abduction, internal rotation, and external rotation were all measured starting at the “horizontal” posture, which acted as a neutral position to begin measurements across taxa.

The femoral diaphysis was positioned in the horizontal posture and subsequently moved into the maximum positions of adduction and abduction. Abduction and adduction were calculated by measuring the angle formed between the femoral diaphysis and a horizontal plane parallel to the examination table (Figure 3.1) and then adjusting the measures to reflect angles from the midline. In a few overweight apes, it was necessary to measure and convert the inverse angle due to the large amount of

⁶ “Horizontal abduction” of the femur requires additional explanation here. The origins for the term used by Stern and Larson (1993) come from horizontal abduction of the humerus, which brings the arms and forearms horizontal relative to the ground.

abdominal fat that obstructed the placement of the goniometer over the abdomen. Total range of movement from adduction to abduction was calculated for each individual by adding the adduction and abduction values.

Internal and external rotation were measured following the technique used in humans (Cole 1971; Norkin and White 1995), where femoral rotation is calculated based on tibial movement relative to the observer (Figure 3.1). Accordingly, hip rotation measures could be partially influenced by interspecific differences in mediolateral rotation of the tibia on the femoral condyles. Published data on primate range of motion at the knee are lacking, and so this must remain an untested possibility. Internal and external rotation of the femur were measured with the femur oriented in the “horizontal” posture. Total range of movement from internal to external rotation was calculated for each individual by adding the two values together.

Mass (kg) and four linear measures of body size were collected using a digital scale and soft tape measure. All linear measures were rounded to the nearest centimeter (cm) and include overlying soft tissues, making these measures less precise. Linear measures were (1) pelvic breadth measured across the pelvis at the fold between thigh and abdomen, which was identified by flexing the legs, (2) thigh circumference at the level of mid-thigh, (3) thigh length approximated from the anterior hip joint to the anterior center of the patella, and (4) femoral bi-epicondylar breadth measured across the posterior aspect of the knee.

Several additional measures were collected, including (1) maximum hip abduction during flexion, (2) maximum hip abduction during extension, and the (3) distance spanned between the knees during abduction (“abducted knee position”, cm). Abduction during flexion was measured by positioning the leg into the maximally flexed

position and then maximally abducting the thigh. Likewise, abduction during extension was measured by positioning the leg into the maximally extended position and then maximally abducting the thigh. The abducted knee position was measured by positioning both the thighs into the abducted posture and then measuring the distances between the centers of the palpable patellae. Because the animals sampled in this study were not anesthetized specifically for this project and there were strict time limits for data collection, these three additional measurements could not be collected for all animals and were only measured on a subset of the animals (*Pan*, *Gorilla*, *Pongo*, *Symphalangus*, *Macaca*).

Quantitative Analyses

Quantitative analyses were performed in R (version 3.0.1, R Core Team 2012). Cleveland dot plots were used to visually inspect for differences between groups (Figure 3.2-3.4). Descriptive statistics (mean, standard deviation, and maximum and minimum values) were calculated for both ROM variables and body size variables. Significant differences in ROM between suspensory and non-suspensory anthropoids were tested by means of one-way analysis of variance (ANOVA), with significance assessed at $p \leq 0.05$.

In certain measures (e.g., maximum flexion), ANOVA detected significant differences between locomotor groups when visual inspection of the descriptive plots suggested substantial overlap between the broad locomotor groups. In order to provide a finer resolution of the significant ANOVA results, post-hoc Tukey's honestly significant difference test (Tukey's HSD) was used as conservative method of multiple comparisons between species. Tukey's HSD is appropriate for testing groups of unequal sample

sizes. Male and female data were grouped for ANOVA and Tukey's HSD comparisons due to the small sample sizes for some species.

Phylogenetic regression and ordinary least squares regression

Range of motion variables were tested for a significant relationship with log-transformed body mass (kg) using non-parametric Spearman's rank correlations. A significant correlation ($p \leq 0.05$) indicates a relationship with body mass.

The ROM variables were then examined versus log-transformed body mass between locomotor groups, with slopes and intercepts of the locomotor-specific regressions tested for significant differences. Allometric slopes were estimated using a phylogenetic generalized least squares (PGLS) and an ordinary least squares (OLS)⁷ approach. PGLS models are included in this study because comparative data violate the assumption of non-independence of data points in OLS (Felsenstein 1985; Grafen 1989). PGLS and independent contrasts are statistically equivalent techniques to detect correlated evolution (Garland Jr and Ives 2000; Rohlf 2001) but PGLS has more flexibility in modeling the process of evolution (i.e., independent contrasts assumes a genetic drift model) and uses raw data rather than contrasts, allowing a more intuitive assessment of the results (e.g., intercepts and standard errors can be directly extracted) (review in Nunn 2011). Some workers also argue that PGLS is more reliable than independent contrasts (Martins et al. 2002; Rohlf 2006).

Within the *caper* package of R (Orme et al. 2012), regressions are weighted by incorporating phylogenetic distances between taxa, calculated from branch lengths of a phylogeny. Phylogenetic distances are introduced as the error term via the variance-

⁷ OLS was appropriate over standardized major axis regression (SMA) because ROM values were regressed on body size, which was measured precisely using a digital scale and should therefore introduce virtually no error on the x-axis.

covariance matrix. The variance-covariance matrix represents tree structure with the matrix diagonal representing the distance (i.e., length in time) from root to tip for each species, with the off-diagonals containing the distances between pairs of species, as measured from the root of the last common ancestor to the tip (Freckleton et al. 2002). The variance-covariance matrix is then scaled by Pagel's lambda (λ) parameter (Pagel 1999; Freckleton et al. 2002), a measure of the dependence of a trait on a specified tree. Pagel's λ was estimated from the data via a maximum likelihood approach. Pagel's λ typically ranges from 0-1, with data showing increasing phylogenetic dependence as λ approaches 1. When λ is estimated to be equal to 0, the PGLS regression should converge on the OLS model.

The phylogenetic tree used for PGLS analyses (Appendix A) was a consensus tree downloaded from the 10k Tree Project (Arnold et al. 2010). *Papio cynocephalus* and *Ateles geoffroyi* were used for *Papio hamadryas-anubis-cynocephalus* and *Ateles fusciceps-geoffroyi-robustus* hybrids. PGLS requires a single value for each tip in the phylogeny and, because averaging male and female data can result in unrealistic values for sexually dimorphic species, only female data points were used. It should therefore be emphasized that the PGLS linear modeling used here differs from traditional OLS in two key ways. First, OLS regression by default assumes no phylogenetic relationship between the data points (e.g., independent data points) whereas PGLS incorporates information about phylogenetic distances. Second, because PGLS regression requires that a single value is assigned to each terminal tip in the tree, the PGLS (female means only) regressions have half the number of data points of OLS (male and female means).

RESULTS

ANOVA results

Sex-specific descriptive statistics for range of motion are provided in Tables 3.3-3.5, with additional size measures from the sample reported in Table 3.6. Data are also shown in descriptive plots in Figures 3.2-3.5. This study found significantly larger ranges of motion in suspensory taxa for maximum measures extension ($p < 0.001$), abduction ($p < 0.001$), external rotation ($p < 0.001$), range of abduction-adduction ($p < 0.001$), and range of internal-external rotation ($p < 0.001$). Non-suspensory taxa had significantly higher mobility in flexion ($p < 0.001$) and internal rotation ($p = 0.03$). Adduction ($p = 0.73$) and range of flexion-extension ($p = 0.63$) were not significantly different between suspensory and non-suspensory taxa. Suspensory anthropoids also have significantly larger abduction during flexion ($p < 0.001$), abduction during extension ($p < 0.001$), and abducted knee positions ($p < 0.001$) (descriptive statistics presented in Table 3.10).

Tukey's HSD pairwise comparisons

Although there are statistically significant differences by locomotor group, there is substantial overlap between the two groups in degree of flexion, extension, and internal rotation (Figure 3.2 and 3.4). Tukey's HSD pairwise comparisons provide a finer resolution of the significant differences detected with ANOVA by identifying which pairs of species are significantly different from one another (Tables 3.7-3.9, 3.11). Tukey's HSD comparisons found more comparisons between suspensory and non-suspensory taxa to be significant at ($p \leq 0.05$) than within a single locomotor group (e.g., suspensory vs. suspensory, non-suspensory vs. non-suspensory). However, many comparisons within the same locomotor group were also significant.

Spearman correlations and regressions

Flexion, range of flexion-extension, and external rotation were found to have significant Spearman rank correlations with body mass (Table 3.12). External rotation increases with increasing body size, although flexion and range of flexion-extension decrease with increasing body size. It is important to note that, although flexion has a significant positive Spearman rank correlation value ($\rho=0.68$, $p=0.02$) indicates a positive scaling relationship between numerical values for flexion and body size, higher numerical values for flexion indicate a reduced range of motion (refer to Figure 3.1). The result therefore indicates that range of motion in flexion is decreasing with body size, which is clarified by the significant negative relationship between range of flexion-extension and body mass.

Female suspensory and non-suspensory ROM data were regressed against body size using phylogenetic regression (Table 3.13). The slopes and intercepts were not significantly different between locomotor groups for any variable except internal rotation (p_{slope} and $p_{\text{intercept}}$, Table 3.13). Flexion and range of flexion-extension, had non-significant differences in slopes and intercepts between the two locomotor groups. This result suggests that, although flexion and range of flexion-extension have a significant correlation with body size, the scaling properties are not different between locomotor groups. Interestingly, the slopes for suspensory and non-suspensory primates denotes opposite scaling relationships for internal and external rotation. With increasing mass in suspensory primates, internal rotation *decreases* and external rotation *increases*, whereas internal rotation *increases* and external rotation *decreases* with increasing mass in non-suspensory primates. However, the differences in external rotation are not statistically different between locomotor groups. The lambda values

used in the phylogenetic regressions were estimated to be zero using a maximum-likelihood approach, suggesting little phylogenetic signal in the data. The allometric patterns found using female-specific data in phylogenetic regression are similar to those produced using male and female data in OLS (see Table 3.12), which is not surprising given that there is not phylogenetic signal present in the data.

DISCUSSION

This study finds significantly larger abduction and external rotation in suspensory taxa. It has previously been hypothesized that limb abduction is a critical movement during climbing and suspensory behaviors (Grand 1972; Jenkins 1974; Grand 1984; Cartmill 1985; Larson 1993; Crompton et al. 2008; Schmidt and Krause 2011), and these results support an association between hip abduction and suspensory behaviors. However, not all measures of joint mobility are necessarily increased in suspensory species relative to the non-suspensory species. Levels of adduction are not significantly different, and non-suspensory primates are actually capable of larger amounts of flexion and internal rotation.

Because hip mobility shows differences in mobility that track locomotor behavior, hip joint mobility seems to be a better indicator of habitual limb postures used during locomotion than glenohumeral joint mobility. Recent work has shown that the hominoid glenohumeral joint does not actually produce a greater range of circumduction than other primates (Chan 2007a; b), with few differences in passive range of motion observed between suspensory hominoids and non-suspensory cercopithecids (Chan 2008). One potential reason that Chan's work may not have detected significant differences between locomotor groups relates to the structure of the anthropoid shoulder itself. The humeral head is surrounded by soft tissues with only a small receiving

articular glenoid on the scapula, whereas the femoral head is more deeply received by the cup-like acetabulum and surrounding soft tissues. Moreover, the humerus is indirectly attached to the trunk by the scapula via the clavicle, with movements possible at the acromioclavicular and sternoclavicular articulations. These secondary articulations might provide some additional shoulder mobility that cannot be strictly differentiated from glenohumeral joint movements in a goniometric study. In contrast, the femoral head directly articulates with the trunk (i.e., in the acetabulum of the bony pelvis) and femoral movements are therefore easier to isolate.

Some differences detected between suspensory and non-suspensory taxa using ANOVA are potentially influenced by the values for *Pan* and *Macaca*, necessitating pairwise comparisons between all species. Overall, pairwise comparisons between suspensory and non-suspensory taxa yielded a higher number of significant differences than within a single locomotor group. Not surprisingly, highly suspensory *Pongo* was found to have significantly larger abduction and external rotation than all non-suspensory taxa. Because males and females were grouped together for the (species-specific) pairwise comparisons due to small sample sizes, some male and female differences within a species might be obscured by these comparisons. In particular, the *Gorilla* intraspecific means for maximum flexion and ranges of flexion-extension differ by more than 30° (Tables 3.3-3.5). Therefore some caution should be used when interpreting the results for *Gorilla*, as there may actually be significant sex-specific differences in degree of flexion or range of flexion-extension that are not detected when using the species mean value. A larger sample of gorillas might clarify whether significant inter- and intraspecific differences exist, but this cannot currently be determined with the sample size in this study.

Body size does not influence range of hip mobility overall (Table 3.13, supplemented by OLS in Table 3.12). There is a significant correlation (p_{rho}) between mass and flexion but the PGLS slopes and intercepts for flexion do not differ significantly by locomotor group. Descriptive plots of the data (Figure 3.2) show that all taxa except *Pongo* and some *Gorilla* have similar ranges of flexion. Thus, for flexion, it seems that grouping taxa into “suspensory” and “non-suspensory” categories for regression might mask some of the allometric differences. Moreover, although there is a non-significant correlation (p_{rho}) between body mass and internal rotation, the suspensory and non-suspensory locomotor groups have significantly different scaling relationships. However, when the raw values for internal rotation are examined in the descriptive plots (Figure 3.4), it is apparent that there is substantial overlap between locomotor groups. Because there is little evidence for a relationship between range of motion variables and body mass, this supports the hypothesis that differences in mobility are related to locomotor behavior and are not strictly a consequence of allometry.

Distance between the knees during abduction (Table 3.10), a proxy for the hindlimb spatial envelope (see Chapter 2), was evaluated as a potential metric of locomotor adaptation within anthropoids. Although the abducted knee position is largely a consequence of body size, it is also a factor of hip mobility. For instance, *Symphalangus syndactylus* has a span at the knee that is approximately double similarly-sized male *Macaca mulatta*. Interestingly, *Gorilla* has a significantly smaller range of angular abduction than *Pan* and *Pongo* yet has an equivalent distance between the knees during abduction (Tables 3.10-3.11), suggesting that the functional outcome of hip mobility (abducted knee position) is influenced by both body size and hip

morphology. The relationship between range of motion, morphological variation in the hip, and the spatial envelope warrants further consideration.

Additionally, the influence of external rotation in locomotor abilities should be considered. According to Stern and Larson (1993), when the hip is flexed, external rotation of the hip simultaneously occurs in order to achieve an abducted thigh posture. Specifically, Stern and Larson (1993) state that when the femur is flexed to 90° and then abducted (as in this study), 90° of lateral femoral rotation simultaneously occurs. The abducted position measured here, which begins at the “horizontal” posture (defined in Materials and Methods), is near the middle of the flexion-extension range for most species and some conjunct external rotation would therefore be expected to accompany abduction. Because external rotation occurred in unison with abduction, it was not possible here to quantify how much external rotation contributed to abduction ability. However, this study confirmed that non-suspensory taxa achieved abducted femur positions primarily by lateral excursions relative to the midline, whereas abducted femoral postures in suspensory taxa were accompanied by a high level of conjunct external rotation (Figure 3.6). Thus, lateral rotational ability at the hip appears to be a key determinant of abduction ability which has been largely neglected. Because this study suggests that an ability to highly abduct the thigh in suspensory primates is conferred with a concomitant ability to externally rotate the femur, hypotheses regarding the evolution of hominoid locomotor behaviors should consider the use of laterally rotated hip postures in addition to abduction.

The joint modeling work by MacLachy (1995; 1996) predicted that range of abduction would discriminate locomotor adaptation, specifically that “differences in abduction during extension may be an indicator of differential ability to assume versatile

climbing postures, while abduction during flexion may be a more general indicator of arboreality” (MacLatchy 1996, p. 471-472). Mean abduction in flexed and extended postures was found to be within 10° of the mean for abduction from the horizontal posture in all hominoids except male gorillas (Tables 3.4 and 3.10). With the exception of male gorillas, which displayed a substantially reduced degree of abduction in an extended posture (mean 48° from horizontal vs. 9° in extension), range of abduction in hominoids is similar throughout the flexion-extension range. As hypothesized by MacLatchy (1996), the ability to abduct the thigh in extended positions is associated with high levels of arboreal versatility (e.g., suspension), although large abduction ability in *any* position appears to be associated with arboreal versatility. However, these data show that hip abduction during flexion is probably not a strong indicator of arboreality in general, as *Macaca fascicularis* is a skilled arboreal quadruped (Rodman 1979) with a low range of abduction possible during flexed hip postures.

There are certain considerations for the baseline values reported in this study. First, this study relies on an opportunistic sample of captive primates. The animals sampled almost certainly did not use their hindlimbs exactly as they would in the wild, and may potentially have ranges of motion, morphologies, and body masses that are different from wild counterparts. Past studies have typically found captive animals to have a greater range of motion rather than free-ranging individuals (Turnquist 1983; 1985). Relying on captive animals may increase the variation of the sample, potentially reducing the likelihood of detecting significant differences between groups. However, significant differences were detected between locomotor groups, and the range of motion data collected for cercopithecids is consistent with all other published ROM data (DeRousseau et al. 1983; Turnquist 1983; 1985; Turnquist and Kessler 1989). The degree of hip abduction in this study is consistent with DeRousseau et al. (1983)’s

findings for *Macaca mulatta* (mean ~30° to midline, versus 25° here), and the mean values for adduction are identical in both studies (mean 36°). The range of hip flexion documented here in cercopithecids is also consistent with previous measures of hip flexion provided by Turnquist and Kessler (1989), who reported low maximum hip flexion values in *M. mulatta* (approximately 11-49° versus 28-41° here).

Second, passive range of motion is the maximum range of motion allowed at the joint, and it is worth noting that a passive range might differ substantially from the range normally employed by a living animal. Unfortunately, there are few data available to compare the key measures of passive abduction and external rotation due to difficulties measuring these with traditional kinematic techniques. The passive data presented here are consistent with Isler's (2005) data on hominoid active hip abduction and range of adduction-abduction during vertical climbing. Isler's (2005) values for *Hylobates* indicate that they use a substantially lower range of abducted hip postures during vertical climbing than they are capable of passively. Isler (2005) also finds a single male gorilla showing an increased ROM relative to a single female gorilla, which is a pattern opposite of what was observed in this study. It remains unknown whether the *Hylobates* and *Gorilla* values differ due to sampling or perhaps real differences in active ROM.

Third, questions remain as to what determines hip joint range of motion. Multiple morphologies of the pelvis and femur have been related to hip mobility (e.g., Napier and Walker 1967; Schultz 1969; Walker 1974; Stern and Susman 1983; Fleagle and Anapol 1992; Ward 1993; Ward et al. 1993; MacLatchy 1995; 1996; MacLatchy and Bossert 1996; MacLatchy 1998). For instance, a longer femoral neck length has been related to mobility at the primate hip joint by increasing the distance between the bony pelvis and the greater trochanter, allowing for more abduction potential (Fleagle and Meldrum

1988). A lower greater trochanter should enable more abduction before impingement of bony or soft tissues occurs (MacLatchy 1995; 1996), and this effect could even be amplified by having a high neck-shaft angle, which would further position the femoral head above the greater trochanter. The distribution of the subchondral bone on the femoral head (Jenkins 1972; Fleagle 1976b; Jenkins and Camazine 1977; Ward et al. 1993; MacLatchy 1996; MacLatchy and Bossert 1996) and potentially femoral head size (Ruff 1988) are hypothesized to relate to hip mobility. The geometry of the femur itself might be especially influential in measuring abduction-adduction, as higher neck-shaft angles will increase the angle of the thigh relative to the midline for any given hip position. In order to test the relationship between morphologies and ROM, future studies should attempt to directly quantify morphologies using x-ray or CT data from the same individuals that ROM data is collected from.

Joint pathologies such as osteoarthritis reduce joint mobility (e.g., Steultjens et al. 2000), limiting normal joint gliding movements by atypical bone growth, fusions, or joint erosions. Naturally-occurring osteoarthritis and other inflammatory diseases of the joints are observed in catarrhines (DeRousseau 1988; Rothschild and Woods 1989; 1992b; 1996; Rothschild 2005; Rothschild and Ruhli 2005), although incidences of arthritis specifically at the anthropoid hip joint are either rare or under-reported (Schultz 1944; Bramblett 1967; Rothschild and Woods 1992a; 1996; DeGusta and Milton 1998; Nakai 2003). In healthy joints, such as those sampled in this study, species-specific differences in observed ranges of motion are likely to originate from bony or soft tissue features.

However, in normally functioning joints, range of motion is determined primarily by soft tissue structures surrounding the joint itself, such as ligament, tendon and

passive muscle tension (Kapandji 1970; Wright and Radin 1993; Levangie and Norkin 2005; McGinnis 2005; Standing and Gray 2008; Safran et al. 2012). A number of soft tissues probably influence the movements at the hip joint, including the ligamentum teres femoris, the acetabular labrum, the hip joint capsule and associated ligaments, and surrounding (passive) hip musculature. Interspecific variation in soft tissue attachments and/or size can contribute to differences in mobility observed between species, limiting movement by differences in length, orientation, and even by physical obstruction.

Little is known about the composition, material properties, variation, size/strength of the deep hip joint soft tissue structures in nonhuman anthropoids (Sonntag 1923; 1924; Howell and Straus 1933; Raven 1950; von Klaus Uhlmann 1968; Sigmon 1969; 1974; Payne 2001; Payne et al. 2006a; b) and how these factors might relate to hip mobility. The joint capsule, particularly in reference to the three capsular ligaments, is thought to be one of the strongest soft tissue limits on femoral head movement within the acetabulum (Myers et al. 2011; Smith et al. 2011; Smith et al. 2012). The limited data on the non-human primate hip capsule suggest that the chimpanzee and orangutan capsule is loose with indistinct capsular ligaments (Sonntag 1923; 1924), allowing more mobility than that of cercopithecids, which have a broad, thick iliofemoral ligament (Keith 1894; Howell and Straus 1933; Walji 1988). Several studies have found a link between hip stability and ligamentum teres integrity (Chen et al. 1996; Demange et al. 2007; Wenger et al. 2007; Dodds et al. 2008; Bardakos and Villar 2009; Martin et al. 2011). *If* the ligamentum teres actually is mechanically limiting joint movements, it appears to do so when the femur is in a position of combined adduction, flexion, and external rotation (Dodds et al. 2008), and so it is not necessarily an explanation for the limited abduction in cercopithecoids here. Likewise, the acetabular labrum limits movements of the

femoral head within the acetabulum by deepening the acetabular socket and by increasing the negative intra-articular joint pressure (Crawford et al. 2007; Myers et al. 2011; Smith et al. 2011; Safran et al. 2012), but no data are published on labrum size or structure in nonhuman anthropoids.

Muscular structure can also limit active (voluntary) range of motion through mechanoreceptor feedback, as well as limit motion passively by physically obstructing movement at the joint or through tension in the antagonistic muscles and associated tendons (Brinckmann et al. 2002b; Levangie and Norkin 2005). Although anthropoid hip muscle attachments are generally similar (Anapol and Barry 1996; Thorpe et al. 1999; Payne et al. 2006a; b; Myatt et al. 2011), the mechanical arrangement of the muscles around the joint differs due to skeletal structure. For instance, great ape and hylobatid gluteal, hip adductor, quadricep, and hamstring muscles have smaller physiological cross section areas and longer fascicles compared to *Homo sapiens* (Payne 2001; Payne et al. 2006b; a; Channon et al. 2009), which would allow a higher range of motion at the hip joint (Payne 2001). Interspecific differences in muscle attachments, orientations, size, extensibility/stretch and tone could therefore affect range of passive movement at the hip joint.

It is difficult to speculate as to what soft tissue structures specifically restricted or enabled the different ranges of motion observed in this study. As was previously noted, hip rotation as measured here could potentially be increased by a more mobile knee joint, and so this may have factored into the results. However, manual manipulations of the hip joint through its range of circumduction implicated strong, deep ligamentous hip structures in limiting both abduction and external rotation in the non-suspensory taxa. This inference is made by the author because the limits were not bony and there was no

observable muscle tension during maximum positions of the limb, except perhaps in hip extension. As previously mentioned (Chapter 2), there is some evidence that cercopithecids have stronger, more distinct ligaments in the hip joint capsule compared to orangutans and chimpanzees (Sonntag 1923; 1924; Howell and Straus 1933). Given that the superior band of the iliofemoral on the anterior aspect of the capsule limits external rotation in humans, it is possible that the iliofemoral ligament plays an important role in limiting external rotation (and in turn, abduction) in cercopithecids. This is supported by the histological findings on the vervet hip joint capsule by Walji (1988) described the anterior and superior portions of the capsule as having a strong collagenous structure which would limit excessive range of motion. Detailed comparative dissection and histological work is necessary to evaluate how interspecific differences in size, strength, and/or configuration of soft tissue structures relate to hip joint mobility.

CONCLUSIONS

For the first time, *in vivo* data on hip joint range of motion in hominoids and *Ateles* are presented and quantitatively compared to cercopithecids and *Cebus*. The data for cercopithecids is comparable to other studies. The null hypothesis that there are no significant differences in hip joint mobility between suspensory and non-suspensory taxa can be rejected, with significant increases in suspensory anthropoids in range of external hip rotation and hip abduction. It is hypothesized here that the ability to differentially abduct the thigh is facilitated by an increased range of external rotation at the hip joint. Moreover, the analyses show that range of motion is not strictly a consequence of body size but does indicate that higher mobility increases the “spatial envelope” for a given body size. Limits on external rotation and abduction in non-

suspensory taxa are soft-tissue constraints and it is proposed here that range of motion was probably primarily constrained by strong capsular ligaments of the hip joint. Formal characterization of bony and soft tissue structures in anthropoids is needed to clarify why non-suspensory species have a reduced range of abduction and external rotation.

Table 3.1 *In vivo* sample

Species	N	Location	Frequency of suspensory	Frequency data reference
<i>Pan troglodytes</i>	31	YNPRC, SNPRC	7%	Doran (1996)
<i>Gorilla gorilla</i>	6	OHD	5%	Hunt (2004) from Remis (1995)
<i>Pongo pygmaeus</i>	6	OHD	12%	Cant (1987) for ♀, excludes quadrumanous
<i>Symphalangus syndactylus</i>	4	LCS, OHD	51%	Hunt (2004) calculated from Fleagle (1980)
<i>Hylobates lar</i>	2	LCS	56%	Hunt (2004) calculated from Gittins (1982),
<i>Trachypithecus francoisi</i>	1	TZ	rarely observed/not observed	Zhou et al. (2012)
<i>Colobus guereza</i>	2	TZ	rarely observed/not observed	Gebo and Chapman (1995)
<i>Macaca fascicularis</i>	16	WNPRC	rarely observed/not observed	Cannon and Leighton (1994)
<i>Macaca mulatta</i>	16	WNPRC	rarely observed/not observed	Wells and Turnquist (2001)
<i>Papio</i> sp.*	8	SNPRC	rarely observed/not observed	Hunt (1991)
<i>Ateles</i> sp.*	6	OHD, LCS	31%	Mittermeier (1978) and Fleagle and Mittermeier
<i>Cebus apella</i>	6	SNPRC	rarely observed/not observed	Gebo (1992)

Abbreviations for institutions: LCS, Lion Country Safari; OHD, Omaha's Henry Doorly Zoo; YNPRC, Yerkes National Primate Research Center; TZ, Toledo Zoo; WNPRC, Wisconsin National Primate Research Center; SNPRC, Southwest National Primate Research Center. Asterisk (*) indicates species-level hybridization in these subjects.

Table 3.2 Sex-specific descriptive statistics for age and body size

Species	Sex	n	Age (years)		Mass (kg)	
			Mean $\pm$ SD	Max, Min	Mean $\pm$ SD	Max, Min
<i>Pan troglodytes</i>	F	13	20.2 $\pm$ 8.4	31.0, 5.6	54.1 $\pm$ 14.3	79.5, 30.6
	M	18	21.1 $\pm$ 5.3	31.9, 14.0	67.4 $\pm$ 7.3	79.3, 56.8
<i>Gorilla gorilla</i>	F	2	13.3 $\pm$ 5.6	17.2, 9.4	70.8 $\pm$ 5.3	74.5, 67.0
	M	4	18.3 $\pm$ 6.6	28.0, 13.2	198.8 $\pm$ 19.2	225.0, 179.0
<i>Pongo pygmaeus</i>	F	3	10.5 $\pm$ 2.2	12.0, 7.9	47.6 $\pm$ 14.5	62.1, 33.1
	M	3	12.8 $\pm$ 7.5	20.2, 5.1	74.4 $\pm$ 64.9	148.3, 27.2
<i>Symphalangus syndactylus</i>	F	2	17.4 $\pm$ 12.1	25.9, 8.8	13.6 $\pm$ 6.2	17.9, 9.2
	M	2	17.6 $\pm$ 8.1	23.3, 11.9	14.3 $\pm$ 4.8	17.7, 10.9
<i>Hylobates lar</i>	F	1	23.5	N/A	6.5	N/A
	M	1	23.9	N/A	10.7	N/A
<i>Colobus guereza</i>	F	1	2.9	N/A	7.0	N/A
	M	1	4.5	N/A	13.2	N/A
<i>Trachypithecus francoisi</i>	M	1	3.0	N/A	7.0	N/A
<i>Macaca fascicularis</i>	F	8	9.4 $\pm$ 1.4	12.1, 7.7	4.8 $\pm$ 0.9	6.0, 3.5
	M	8	7.7 $\pm$ 0.5	8.6, 7.0	6.9 $\pm$ 1.1	9.2, 6.1
<i>Macaca mulatta</i>	F	8	9.1 $\pm$ 0.3	9.5, 8.6	8.3 $\pm$ 1.3	9.8, 7.0
	M	8	9.0 $\pm$ 0.2	9.3, 8.8	12.1 $\pm$ 1.9	14.1, 9.1
<i>Papio sp.</i>	F	3	9.6 $\pm$ 0.8	10.4, 8.9	17.7 $\pm$ 1.1	18.8, 16.6
	M	5	10.5 $\pm$ 0.5	11.4, 10.1	28.4 $\pm$ 1.7	31.0, 26.5
<i>Ateles sp.</i>	F	3	18.0 $\pm$ 10.5	27.9, 7.0	9.3 $\pm$ 1.8	11.2, 7.7
	M	3	18.7 $\pm$ 15.8	37.0, 9.2	8.2 $\pm$ 0.2	8.3, 7.9
<i>Cebus apella</i>	F	4	14.7 $\pm$ 12.5	28.3, 3.0	2.6 $\pm$ 0.1	2.7, 2.5
	M	2	4.4 $\pm$ 1.3	5.3, 3.5	3.2 $\pm$ 0.9	3.8, 2.6

Sex-specific samples consisting of n=1 individual are not mean values. *mean, standard deviation, maximum, and minimum values were calculated with one less animal than the total n listed. SD= standard deviation, N/A= not applicable.

Table 3.3 Sex-specific descriptive statistics for flexion and extension

Species	Sex	n	Flexion		Extension		Flexion-extension range	
			Mean $\pm$ SD	Max, Min	Mean $\pm$ SD	Max, Min	Mean $\pm$ SD	Max, Min
<i>Pan troglodytes</i>	F	13	33.2 $\pm$ 10.3	52.0, 21.0	157.5 $\pm$ 6.7	168.0, 148.0	124.4 $\pm$ 11.9	139.0, 102.0
	M	18	40.4 $\pm$ 11.3	63.0, 20.0	160.5 $\pm$ 9.5	176.0, 138.0	120.1 $\pm$ 11.8	143.0, 99.0
<i>Gorilla gorilla</i>	F	2	31.5 $\pm$ 3.5	34.0, 29.0	155.5 $\pm$ 3.5	158.0, 153.0	124.0 $\pm$ 0.0	124.0, 124.0
	M	4	66.5 $\pm$ 4.4	70.0, 60.0	143.5 $\pm$ 11.4	160.0, 136.0	77.0 $\pm$ 10.9	90.0, 68.0
<i>Pongo pygmaeus</i>	F	3	42.3 $\pm$ 8.6	50.0, 33.0	156.7 $\pm$ 4.9	160.0, 151.0	114.3 $\pm$ 10.2	126.0, 107.0
	M	3	55.3 $\pm$ 7.1	63.0, 49.0	171.3 $\pm$ 1.5	173.0, 170.0	116.0 $\pm$ 8.5	124.0, 107.0
<i>Symphalangus syndactylus</i>	F	2	27.5 $\pm$ 3.5	30.0, 25.0	150.5 $\pm$ 10.6	158.0, 143.0	123.0 $\pm$ 14.1	133.0, 113.0
	M	2	28.0 $\pm$ 2.8	30.0, 26.0	161.0 $\pm$ 12.7	170.0, 152.0	133.0 $\pm$ 9.9	140.0, 126.0
<i>Hylobates lar</i>	F	1	23.0	N/A	175.0	N/A	152.0	N/A
	M	1	26.0	N/A	170.0	N/A	144.0	N/A
<i>Colobus quereza</i>	F	1	20.0	N/A	148.0	N/A	128.0	N/A
	M	1	33.0	N/A	168.0	N/A	135.0	N/A
<i>Trachypithecus francoisi</i>	M	1	22.0	N/A	116.0	N/A	94.0	N/A
<i>Macaca fascicularis</i>	F	8	29.9 $\pm$ 5.1	34.0, 19.0	155.3 $\pm$ 4.9	163.0, 150.0	125.4 $\pm$ 8.4	142.0, 116.0
	M	8	26.1 $\pm$ 3.9	30.0, 20.0	142.5 $\pm$ 4.8	149.0, 135.0	116.4 $\pm$ 7.1	129.0, 108.0
<i>Macaca mulatta</i>	F	8	33.3 $\pm$ 4.7	41.0, 28.0	157.5 $\pm$ 6.1	167.0, 150.0	124.3 $\pm$ 9.1	139.0, 109.0
	M	8	32.0 $\pm$ 2.2	35.0, 29.0	144.4 $\pm$ 7.6	153.0, 131.0	112.4 $\pm$ 8.5	121.0, 98.0
<i>Papio sp.</i>	F	3	34.0 $\pm$ 5.3	40.0, 30.0	140.7 $\pm$ 16.7	160.0, 131.0	106.6 $\pm$ 19.1	128.0, 75.0
	M	5	41.4 $\pm$ 7.3	50.0, 34.0	134.6 $\pm$ 11.4	150.0, 123.0	93.2 $\pm$ 14.7	116.0, 75.0
<i>Ateles sp.</i>	F	3	26.3* $\pm$ 4.2	31.0, 23.0	139.7 $\pm$ 18.9	161.0, 125.0	113.3 $\pm$ 21.4	138.0, 100.0
	M	3	31.3 $\pm$ 3.1	34.0, 28.0	152.0 $\pm$ 4.4	157.0, 149.0	120.7 $\pm$ 7.2	129.0, 116.0
<i>Cebus apella</i>	F	4	28.5 $\pm$ 6.0	34.0, 20.0	155.5 $\pm$ 27.2	180.0, 130.0	127.4 $\pm$ 29.4	158.0, 99.0
	M	2	26.0 $\pm$ 5.7	30.0, 22.0	159.5 $\pm$ 6.4	164.0, 155.0	133.5 $\pm$ 12.0	142.0, 125.0

Values represent degrees. Sex-specific samples consisting of n=1 individual are not mean values. SD= standard deviation, N/A= not applicable.

Table 3.4 Sex-specific descriptive statistics for adduction and abduction

Species	Sex	n	Adduction		Abduction		Add-abduction range	
			Mean $\pm$ SD	Max, Min	Mean $\pm$ SD	Max, Min	Mean $\pm$ SD	Max, Min
<i>Pan troglodytes</i>	F	13	39.5 $\pm$ 10.7	22.0, 58.0	75.4 $\pm$ 4.9	83.0, 68.0	114.9 $\pm$ 11.6	132.0, 90.0
	M	18	43.6 $\pm$ 7.1	26.0, 54.0	70.1 $\pm$ 4.4	80.0, 63.0	113.6 $\pm$ 8.2	123.0, 91.0
<i>Gorilla gorilla</i>	F	2	41.5 $\pm$ 7.8	36.0, 47.0	62.5 $\pm$ 3.5	65.0, 60.0	104.0 $\pm$ 4.2	107.0, 101.0
	M	4	45.0 $\pm$ 13.9	27.0, 61.0	48.0 $\pm$ 4.7	55.0, 45.0	93.0 $\pm$ 10.4	107.0, 82.0
<i>Pongo pygmaeus</i>	F	3	25.7 $\pm$ 11.6	18.0, 39.0	82.3 $\pm$ 3.2	86.0, 80.0	108.0 $\pm$ 14.8	125.0, 98.0
	M	3	24.3 $\pm$ 18.0	7.0, 43.0	81.0 $\pm$ 8.2	88.0, 72.0	105.3 $\pm$ 17.9	126.0, 95.0
<i>Symphalangus syndactylus</i>	F	2	34.5 $\pm$ 0.7	34.0, 35.0	52.0 $\pm$ 5.7	56.0, 48.0	86.5 $\pm$ 4.9	90.0, 83.0
	M	2	37.5 $\pm$ 12.0	29.0, 46.0	67.5 $\pm$ 3.5	70.0, 65.0	105.0 $\pm$ 15.6	116.0, 94.0
<i>Hylobates lar</i>	F	1	23.0	N/A	78.0	N/A	145.0	N/A
	M	1	31.0	N/A	69.0	N/A	128.0	N/A
<i>Colobus guereza</i>	F	1	34.0	N/A	30.0	N/A	86.0	N/A
	M	1	31.0	N/A	26.0	N/A	85.0	N/A
<i>Trachypithecus francoisi</i>	M	1	50.0	N/A	41.0	N/A	81.0	N/A
<i>Macaca fascicularis</i>	F	8	38.5 $\pm$ 9.9	19.0, 49.0	24.8 $\pm$ 3.3	31.0, 20.0	63.3 $\pm$ 10.1	80.0, 46.0
	M	8	25.4 $\pm$ 10.1	11.0, 43.0	26.0 $\pm$ 5.4	36.0, 20.0	51.4 $\pm$ 11.0	66.0, 31.0
<i>Macaca mulatta</i>	F	8	38.2 $\pm$ 8.7	29.0, 54.0	26.9 $\pm$ 9.9	37.0, 10.0	65.1 $\pm$ 14.2	86.0, 41.0
	M	8	33.2 $\pm$ 7.9	23.0, 43.0	23.9 $\pm$ 5.3	35.0, 19.0	57.1, 11.1	75.0, 44.0
<i>Papio sp.</i>	F	3	41.3 $\pm$ 10.3	30.0, 50.0	30.7 $\pm$ 5.0	36.0, 26.0	72.0 $\pm$ 7.2	80.0, 27.0
	M	5	35.4 $\pm$ 16.1	10.0, 49.0	18.4 $\pm$ 2.5	22.0, 16.0	53.8 $\pm$ 16.5	69.0, 27.0
<i>Ateles sp.</i>	F	3	29.5 $\pm$ 14.8	19.0, 40.0	62.3 $\pm$ 3.1	65.0, 59.0	90.5* $\pm$ 17.7	103.0, 78.0
	M	3	23.3 $\pm$ 15.3	10.0, 40.0	70.3 $\pm$ 0.6	71.0, 70.0	93.7 $\pm$ 15.8	111.0, 80.0
<i>Cebus apella</i>	F	4	54.7 $\pm$ 10.5	43.0, 67.0	34.8 $\pm$ 11.7	50.0, 22.0	89.5 $\pm$ 18.4	117.0, 79.0
	M	2	57.0 $\pm$ 7.1	52.0, 62.0	49.0 $\pm$ 1.4	50.0, 48.0	106.0 $\pm$ 5.7	110.0, 102.0

Values represent degrees. Sex-specific samples consisting of n=1 individual are not mean values. *mean, standard deviation, maximum, and minimum values were calculated with one less animal than the total n listed. SD= standard deviation, N/A= not applicable.

Table 3.5 Sex-specific descriptive statistics for internal and external rotation

Species	Sex	n	Internal rotation		Max, Min	External rotation		Max, Min	Range of rotation	
			Mean $\pm$ SD			Mean $\pm$ SD			Mean $\pm$ SD	Max, Min
<i>Pan troglodytes</i>	F	13	37.1 $\pm$ 9.2		49.0, 21.0	78.3 $\pm$ 8.9		92.0, 65.0	115.4 $\pm$ 14.4	132.0, 92.0
	M	18	35.4 $\pm$ 9.3		59.0, 18.0	76.1 $\pm$ 13.0		97.0, 49.0	111.4 $\pm$ 16.3	138.0, 72.0
<i>Gorilla gorilla</i>	F	2	29.5 $\pm$ 9.2		36.0, 23.0	69.5 $\pm$ 4.9		73.0, 66.0	99.0 $\pm$ 14.1	109.0, 89.0
	M	4	31.3 $\pm$ 10.7		47.0, 24.0	80.5 $\pm$ 12.1		93.0, 67.0	111.8 $\pm$ 20.1	140.0, 96.0
<i>Pongo pygmaeus</i>	F	3	32.0 $\pm$ 2.0		34.0, 30.0	97.0 $\pm$ 10.6		105.0, 85.0	129.0 $\pm$ 12.2	137.0, 115.0
	M	3	28.7 $\pm$ 7.1		35.0, 21.0	94.3 $\pm$ 14.0		108.0, 80.0	123.0 $\pm$ 11.3	130.0, 110.0
<i>Symphalangus syndactylus</i>	F	2	44.5 $\pm$ 6.4		49.0, 40.0	69.5 $\pm$ 12.0		78.0, 61.0	114.0 $\pm$ 18.4	127.0, 101.0
	M	2	56.0 $\pm$ 8.5		62.0, 50.0	67.0 $\pm$ 2.8		69.0, 65.0	123.0 $\pm$ 11.3	131.0, 115.0
<i>Hylobates lar</i>	F	1	62.0		N/A	61.0		N/A	123.0	N/A
	M	1	50.0		N/A	70.0		N/A	120.0	N/A
<i>Colobus guereza</i>	F	1	40.0		N/A	50.0		N/A	90.0	N/A
	M	1	45.0		N/A	45.0		N/A	90.0	N/A
<i>Trachypithecus francoisi</i>	M	1	50.0		N/A	32.0		N/A	82.0	N/A
<i>Macaca fascicularis</i>	F	8	45.1 $\pm$ 9.6		62.0, 30.0	61.9 $\pm$ 9.7		75.7, 47.0	107.0 $\pm$ 16.3	130.0, 81.0
	M	8	50.0 $\pm$ 5.7		59.0, 42.0	52.5 $\pm$ 7.6		67.0, 43.0	102.5 $\pm$ 10.6	115.0, 89.0
<i>Macaca mulatta</i>	F	8	39.4 $\pm$ 8.1		54.0, 29.0	63.0 $\pm$ 8.1		81.0, 55.0	102.4 $\pm$ 7.9	114.0, 91.0
	M	8	34.8 $\pm$ 4.6		40.0, 28.0	48.8 $\pm$ 6.6		59.0, 40.0	83.5 $\pm$ 5.7	90.0, 72.0
<i>Papio</i> sp.	F	3	47.7 $\pm$ 7.1		54.0, 40.0	43.0 $\pm$ 2.6		45.0, 40.0	90.7 $\pm$ 9.7	99.0, 60.0
	M	5	47.2 $\pm$ 8.2		60.0, 40.0	32.0 $\pm$ 9.1		45.0, 20.0	79.2 $\pm$ 11.6	90.0, 60.0
<i>Ateles</i> sp.	F	3	51.0 $\pm$ 10.1		60.0, 40.0	70.7 $\pm$ 3.5		74.0, 67.0	121.7 $\pm$ 12.9	131.0, 107.0
	M	3	29.0 $\pm$ 1.0		30.0, 28.0	86.3 $\pm$ 6.7		92.0, 79.0	115.3 $\pm$ 7.0	122.0, 108.0
<i>Cebus apella</i>	F	4	28.5 $\pm$ 3.8		31.0, 23.0	53.5 $\pm$ 24.2		80.0, 23.0	82.0 $\pm$ 21.6	103.0, 54.0
	M	2	24.0 $\pm$ 5.7		28.0, 20.0	54.5 $\pm$ 0.7		55.0, 54.0	78.5 $\pm$ 6.4	83.0, 74.0

Values represent degrees. Sex-specific samples consisting of n=1 individual are not mean values. SD= standard deviation, N/A= not applicable.

Table 3.6 Sex-specific descriptive statistics for linear dimensions

Species	Sex	n	Pelvic breadth (cm)			Mid-thigh circumference (cm)			Thigh length (cm)			Bi-epicondylar breadth (cm)		
			Mean $\pm$ SD	Max, Min		Mean $\pm$ SD	Max, Min		Mean $\pm$ SD	Max, Min		Mean $\pm$ SD	Max, Min	
<i>Pan troglodytes</i>	F	13	38.8 $\pm$ 8.3	53.0, 25.0		46.9 $\pm$ 7.2	62.0, 38.0		26.2 $\pm$ 2.2	30.0, 24.0		7.0 $\pm$ 2.1	11.0, 5.0	
	M	18	39.9* $\pm$ 4.9	47.0, 31.0		55.5 $\pm$ 4.4	62.0, 48.0		27.9 $\pm$ 1.5	31.0, 25.0		9.5* $\pm$ 2.2	14.0, 7.0	
<i>Gorilla gorilla</i>	F	2	43.0 $\pm$ 0.0	43.0, 43.0		50.0 $\pm$ 4.2	53.0, 47.0		25.0 $\pm$ 0.0	25.0, 25.0		7.5 $\pm$ 0.7	8.0, 7.0	
	M	4	64.8 $\pm$ 14.4	85.0, 53.0		81.5 $\pm$ 6.6	90.0, 74.0		30.8 $\pm$ 4.8	35.0, 24.0		11.5 $\pm$ 2.4	14.0, 9.0	
<i>Pongo pygmaeus</i>	F	3	35.7 $\pm$ 6.1	41.0, 29.0		40.3 $\pm$ 7.0	47.0, 33.0		22.7 $\pm$ 0.6	23.0, 22.0		6.7 $\pm$ 1.5	8.0, 5.0	
	M	3	39.0 $\pm$ 16.8	58.0, 26.0		44.7 $\pm$ 18.5	65.0, 29.0		23.0 $\pm$ 4.6	27.0, 18.0		11.3 $\pm$ 3.8	14.0, 7.0	
<i>Symphalangus</i>	F	2	19.5 $\pm$ 0.7	20.0, 19.0		19.0* $\pm$ N/A	19.0, 19.0		22.5 $\pm$ 3.5	25.0, 20.0		4.5 $\pm$ 2.1	6.0, 3.0	
	M	2	20.5 $\pm$ 0.7	21.0, 20.0		30.0* $\pm$ N/A	30.0, 30.0		20.5 $\pm$ 0.7	21.0, 20.0		5.0 $\pm$ 0.0	5.0, 5.0	
<i>Hvlobates lar</i>	F	1	18.0	N/A		15.0	N/A		21.0	N/A		4.0	N/A	
	M	1	19.0	N/A		20.0	N/A		21.0	N/A		6.0	N/A	
<i>Colobus quereza</i>	F	1	11.0	N/A		23.0	N/A		20.0	N/A		4.0	N/A	
	M	1	14.0	N/A		27.0	N/A		22.0	N/A		4.5	N/A	
<i>Trachypithecus francoisi</i>	M	1	12.0	N/A		21.0	N/A		20.0	N/A		4.0	N/A	
<i>Macaca fascicularis</i>	F	8	13.8 $\pm$ 2.2	17.0, 10.0		17.4 $\pm$ 1.0	18.5, 15.5		12.8 $\pm$ 1.6	15.0, 10.0		2.3 $\pm$ 0.4	3.0, 2.0	
	M	8	13.1 $\pm$ 1.8	17.0, 11.0		21.3 $\pm$ 1.7	24.0, 18.5		14.6 $\pm$ 1.4	17.0, 13.0		2.9 $\pm$ 0.6	4.0, 2.0	
<i>Macaca mulatta</i>	F	8	16.6 $\pm$ 1.8	19.0, 14.0		23.9 $\pm$ 1.1	26.0, 23.0		17.4 $\pm$ 1.1	18.0, 15.0		3.3 $\pm$ 0.5	4.0, 3.0	
	M	8	17.6 $\pm$ 2.1	20.0, 14.0		28.3 $\pm$ 1.7	31.0, 26.0		20.5 $\pm$ 1.4	22.0, 18.0		3.9 $\pm$ 1.0	6.0, 3.0	
<i>Papio sp.</i>	F	3	19.7 $\pm$ 0.6	20.0, 19.0		29.7 $\pm$ 3.8	34.0, 27.0		20.0 $\pm$ 1.0	21.0, 19.0		5.7 $\pm$ 0.6	6.0, 5.0	
	M	5	21.8 $\pm$ 2.3	24.0, 19.0		35.4 $\pm$ 3.2	39.0, 31.0		25.8 $\pm$ 2.8	30.0, 23.0		5.4 $\pm$ 0.9	6.0, 4.0	
<i>Ateles sp.</i>	F	3	16.3 $\pm$ 4.9	22.0, 13.0		20.8 $\pm$ 4.1	25.5, 18.0		19.3 $\pm$ 0.6	20.0, 19.0		4.7 $\pm$ 1.2	6.0, 4.0	
	M	3	15.3 $\pm$ 0.6	16.0, 15.0		21.7 $\pm$ 1.5	23.0, 20.0		19.3 $\pm$ 1.5	21.0, 18.0		3.3 $\pm$ 0.6	4.0, 3.0	
<i>Cebus apella</i>	F	4	8.3 $\pm$ 1.5	9.0, 6.0		14.8 $\pm$ 1.0	16.0, 14.0		12.3 $\pm$ 0.5	13.0, 12.0		1.9 $\pm$ 0.3	2.0, 1.5	
	M	2	7.5 $\pm$ 0.7	8.0, 7.0		17.3 $\pm$ 1.1	18.0, 16.5		14.5 $\pm$ 0.7	15.0, 14.0		2.5 $\pm$ 0.7	3.0, 2.0	

Sex-specific samples consisting of 1 individual are not mean values. *mean, standard deviation, maximum, and minimum values were calculated with one less animal than the total N listed. SD= standard deviation, N/A= not applicable.

Table 3.7 Species-specific pairwise comparisons for flexion-extension

	Gorilla		Pongo	Symphalangus	Hyllobates	Ateles	Colobus	Trachypithecus	M. fascicularis	M. mulatta	Papio	Cebus
Pan	2	1		2		3	2		2,3		2,3	2,3
Gorilla		2			2,3	2	2		2,3	2,3	2,3	2
Pongo				2	1	2	2,1	2	2,3	2,3	2,3	1,2
Symphalangus					3		2		2,3	2,3	2,3	2
Hyllobates						1,3	2,3	2,3	1,2,3	1,2,3	2,3	2,3
Ateles							2,1,	2	2,3	2,3	2,3	1,2
Colobus												
Trachypithecus												
M. fascicularis												1,2,3
M. mulatta												1,2,3
Papio												2,3

Significant Tukey HSD pairwise comparisons ($p \leq 0.05$) are shown. Each number represents a significant difference in the motion indicated by that value. The comparisons coded in light gray cells represent comparisons between suspensory and non-suspensory species. Dark gray cells are redundant species comparisons, and blank cells have no significant comparisons. 1=flexion, 2=extension, 3=range of flexion-extension.

Table 3.8 Species-specific pairwise comparisons for adduction-abduction

	Gorilla	Pongo	Symphalangus	Hylobates	Ateles	Colobus	Trachypithecus	M. fascicularis	M. mulatta	Papio	Cebus
Pan	1,3							1		2,3	
Gorilla			1,3	1,3	1	1,3	1	1,3	1,3	1	1,3
Pongo			1		1		2	1	1	2	1
Symphalangus										3	
Hylobates							2			2,3	
Ateles											
Colobus											
Trachypithecus											2
M. fascicularis										3	
M. mulatta										3	
Papio											2,3

Significant Tukey HSD pairwise comparisons ($p \leq 0.05$) are shown. Each number represents a significant difference in the motion indicated by that value. The comparisons coded in light gray cells represent comparisons between suspensory and non-suspensory species. Dark gray cells are redundant species comparisons, and blank cells have no significant comparisons. 1=adduction, 2=horizontal abduction, 3=range of abduction-adduction.

Table 3.9 Species-specific pairwise comparisons for rotation

	Gorilla	Pongo	Symphalangus	Hylobates	Ateles	Colobus	Trachypithecus	M. fascicularis	M. mulatta	Papio	Cebus
Pan		2				2	2	1,2	2,3	1,2	2,3
Gorilla			1	1			2	1,2	2	1,2	2
Pongo			1,2	1,2			2	1,2	2,3	1,2,3	2,3
Symphalangus										2,3	1,3
Hylobates						1				2,3	1,3
Ateles						2	2	2	2,3	2,3	3
Colobus										2	
Trachypithecus											
M. fascicularis									1	2,,3	1,3
M. mulatta										2	
Papio											1

Significant Tukey HSD pairwise comparisons ($p \leq 0.05$) are shown. Each number represents a significant difference in the motion indicated by that value. The comparisons coded in grey cells represent comparisons between suspensory and non-suspensory species. Stippled cells are redundant species comparisons, and blank cells have no significant comparisons. 1=internal rotation, 2=external rotation, 3=range of internal-external rotation.

Table 3.10 Additional measures of abduction

Species	Sex	n	Abduction in extension		Abduction in flexion		Abducted knee position (cm)	
			Mean $\pm$ SD	Max, Min	Mean $\pm$ SD	Max, Min	Mean $\pm$ SD	Max, Min
<i>Pan troglodytes</i>	F	10	74.8 $\pm$ 5.1	80.0, 65.0	75.2 $\pm$ 4.3	84.0, 69.0	69.2 $\pm$ 5.4	76.0, 58.0
<i>Gorilla gorilla</i>	M	13	70.7 $\pm$ 3.5	79.0, 64.0	69.5 $\pm$ 2.6	73.0, 65.0	72.1 $\pm$ 4.9	81.0, 61.0
	F	2	71.0 $\pm$ 1.4	70.0, 72.0	ND	ND	66.5 $\pm$ 5.0	70.0, 63.0
<i>Pongo pygmaeus</i>	M	4	9.4 $\pm$ 25.2	62.0, 6.0	ND	ND	71.5 $\pm$ 3.5	75.0, 68.0
	F	3	82.0 $\pm$ 2.7	85.0, 80.0	82.0 $\pm$ 2.7	85.0, 80.0	63.0* $\pm$ 4.2	66.0, 60.0
	M	3	85.0* $\pm$ 4.2	88.0, 82.0	76.7 $\pm$ 5.5	82.0, 71.0	65.5* $\pm$ 6.4	70.0, 61.0
<i>Symphalangus syndactylus</i>	F	2	59.0 $\pm$ 12.7	68.0, 50.0	51.0 $\pm$ 12.7	60.0, 42.0	51.0*	N/A
	M	2	70.0 $\pm$ 7.1	75.0, 65.0	65.0 $\pm$ 0.0	65.0, 65.0	55.0*	N/A
<i>Macaca fascicularis</i>	F	8	20.4 $\pm$ 3.2	23.0, 14.0	20.3 $\pm$ 4.1	26.0, 15.0	21.3 $\pm$ 2.8	26.0, 18.0
	M	8	18.5 $\pm$ 5.7	26.0, 10.0	21.9 $\pm$ 6.4	32.0, 11.0	24.1 $\pm$ 3.0	28.0, 19.0
<i>Macaca mulatta</i>	F	8	21.5 $\pm$ 6.2	35.0, 15.0	24.0 $\pm$ 4.9	32.0, 16.0	28.1 $\pm$ 3.4	34.0, 24.0
	M	8	18.9 $\pm$ 3.7	21.0, 10.0	18.9 $\pm$ 5.2	26.0, 10.0	31.3 $\pm$ 3.6	36.0, 26.0

Units for abduction in extension and flexion are degrees. No data were collected for *Gorilla* in positions of abduction during flexion as the large abdomen prevented accurate placement of the goniometer. *mean, standard deviation, maximum, and minimum values were calculated with one less animal than the total N listed. SD= standard deviation, N/A= not applicable, ND=no data.

Table 3.11 Species-specific pairwise comparisons for additional measures

	<i>Gorilla</i>	<i>Pongo</i>	<i>Symphalangus</i>	<i>M.fascicularis</i>	<i>M.mulatta</i>
<i>Pan</i>	1		2,3	1,2,3	1,2,3
<i>Gorilla</i>		1	3	1,2,3	1,2,3
<i>Pongo</i>			1,2,3	1,2,3	1,2,3
<i>Symphalangus</i>				1,2,3	1,2,3
<i>M.fascicularis</i>					3

Significant Tukey HSD pairwise comparisons ($p \leq 0.05$) are shown. Each number represents a significant difference in the motion indicated by that value. The comparisons coded in light grey cells represent comparisons between suspensory and non-suspensory species. Dark gray cells are redundant species comparisons, and blank cells have no significant comparisons. 1=range of abduction in flexion, 2=range of abduction in extension, 3=abducted knee position.

Table 3.12 Species-specific Spearman correlations and OLS regressions

	rho	P _{rho}	<u>non-suspensory</u>			<u>suspensory</u>			P _{slope}	P _{intercept}
			r ²	slope	intercept	r ²	slope	intercept		
flexion	0.74	<0.01	0.44	16.46	17.87	0.67	19.04	11.55	0.76	0.50
extension	0.06	0.80	0.10	-55.81	196.19	0.08	-31.45	182.30	0.07	0.34
flex-extension range	-0.43	0.04	0.33	-72.27	178.32	0.55	-50.48	170.76	0.16	0.65
adduction	0.16	0.46	0.13	18.34	65.05	0.02	10.79	54.44	0.65	0.57
abduction	0.31	0.15	0.42	-18.53	1.44	0.02	-11.44	38.02	0.58	0.02
add-abduction range	0.24	0.26	0.32	-36.87	66.49	0.05	-22.23	92.46	0.28	0.48
internal rotation	-0.18	0.40	0.36	49.18	-12.75	0.49	15.86	26.59	<0.01	<0.01
external rotation	0.43	0.04	0.35	-62.85	88.73	0.19	-27.12	76.43	<0.01	0.29
rotation range	0.30	0.17	0.01	-13.67	75.98	0.20	-11.27	103.02	0.82	0.03

Three variables (flexion, range of flexion-extension, external rotation) were found to be significantly correlated with body mass (bold p_{rho} value). OLS results are provided as a supplement to phylogenetic regression (PGLS) results. Significant differences in slope (p_{slope}) or intercept (p_{intercept}) between locomotor groups are indicated in bold.

Table 3.13 Phylogenetic regressions (female-specific data only)

	non-suspensory			suspensory			P _{slope}	P _{intercept}	lambda
	r ²	slope	intercept	r ²	slope	intercept			
flexion	0.12	6.43	23.84	0.58	11.71	14.84	0.63	0.44	0.00
extension	0.54	-16.80	165.18	0.06	11.29	164.53	0.52	0.97	0.00
flex-extension range	0.64	-23.24	141.33	0.33	-17.22	149.69	0.76	0.69	0.00
adduction	0.21	-13.25	56.64	0.18	-14.06	58.72	0.97	0.94	0.00
abduction	0.06	-3.15	32.00	0.04	5.66	60.84	0.67	0.20	0.00
add-abduction range	0.17	-16.40	88.64	0.03	-8.40	119.56	0.84	0.46	0.00
internal rotation	0.62	19.04	24.51	0.91	-29.07	83.10	<0.01	<0.01	0.00
external rotation	0.22	-12.98	64.93	0.32	15.87	53.07	0.19	0.59	0.00
rotation range	0.03	6.06	89.44	0.26	-13.20	136.17	0.40	0.08	0.00

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The phylogenetic regressions did not detect significant differences in slope (p_{slope}) or intercept (p_{intercept}) between locomotor groups for most variables. The Pagel's lambda (λ) values calculated using a maximum likelihood approach are reported for each phylogenetic regression. Although r² values are reported, PGLS r² values are not directly comparable to those in traditional OLS and have less inferential utility (see supplemental materials in Lavin et al. 2008).

Figure 3.1 Measures

Adduction, abduction, internal rotation and external rotation were measured from the “horizontal” posture, which was defined as when the femur was 90° (perpendicular) to the examination table. Adduction and abduction were measured relative to the horizontal surface of the examination table for accuracy but the angles were then adjusted to the midline (indicated in grey). Although best illustrated from a caudal view (shown above), adduction and abduction were measured cranially between the abdomen and thigh.

Figure 3.2 Cleveland dot plots of extension and flexion

Mean and interquartile ranges are indicated by the boxplots. Angles are significantly different between locomotor groups ($p < 0.05$). Note that smaller values for flexion reflect a higher range of motion (see Figure 3.1). Dark dots indicate suspensory data points and light dots indicate non-suspensory data points.

Figure 3.3 Cleveland dot plots for abduction-adduction

Mean and interquartile ranges are indicated by the boxplots. Abduction, but not adduction, is significantly different between locomotor groups ($p < 0.05$). Dark dots indicate suspensory data points and light dots indicate non-suspensory data points.

Figure 3.4 Cleveland dot plots for internal-external rotation

Mean and interquartile ranges are indicated by the boxplots. Angles are significantly different between locomotor groups ($p < 0.05$). Dark dots indicate suspensory data points and light dots indicate non-suspensory data points.

Figure 3.5 Cleveland dot plots for ranges of flexion-extension, adduction-abduction, and internal-external rotation

Mean and interquartile ranges are indicated by the boxplots. Dark dots indicate suspensory data points and light dots indicate non-suspensory data points.

Figure 3.6 Abduction ability tied to lateral rotation

Examples of passive positions of abduction for (a) *Pongo pygmaeus*, (b) *Gorilla gorilla*, and (c) *Macaca mulatta*. The patella is indicated by blue arrows to highlight the external rotation that accompanies abduction in suspensory species. Note the lateral knee orientation (externally rotated thigh) in *Pongo* and *Gorilla* and the anterior orientation (non-rotated thigh) in *Macaca*.

CHAPTER 4: *IN SILICO* MODELS OF HIP JOINT ABDUCTION ABILITY

Abduction was found to discriminate suspensory and non-suspensory taxa more than any other movement at the hip in a sample of live animals (Chapter 3). This finding, using empirical data, provides a basis for reconstructing anthropoid range of femoral abduction.

A model for quantifying hip abduction was developed following work of MacLatchy (1995, 1996, 1998), MacLatchy and Bossert (1996), Jenkins and Camazine (1977), and Kapandji (1970). Simulations of hip abduction were performed here on a large sample of anthropoids, following the principles outlined in these previous works for how a joint should be positioned during normal loading. The novel modeling approach integrates laser scans, microscribe landmark data, and shape analysis software to digitally articulate the hip joint. Anthropoid range of femoral abduction and the functional outcome of hip abduction, the abducted knee position, were reconstructed using 3D polygonal models of primate pelves and femora.

The *in silico* models were validated in a subset of taxa for which *in vivo* data were also available (Chapter 3), allowing quantification of how far models of joint movement deviate from empirical measurements collected on primates *in vivo*. This research design makes it possible to assess how closely digitally articulated hip joints reflect the limits imposed by surrounding soft tissues and provides a validated method of inferring functional abilities when only the bones are present (as in fossil hominoids).

OBJECTIVES

First, extant suspensory anthropoids were tested for significantly increased ranges of abduction *in silico* compared to non-suspensory anthropoids. The ability to discriminate between locomotor groups by measures of abduction was tested by means of discriminant function analysis, and allometric scaling of hip joint abduction was assessed by standard major axis regression. Second, the hypothesis that there is a predictable relationship between hip abduction modeled *in silico* and that measured *in vivo* is tested. Analysis of variance (ANOVA) and pairwise multiple comparisons measure the relationship between data types at the locomotor and species levels.

SAMPLE

The *in silico* sample described here was used in analyses in both Chapter 4 and Chapter 5. Microscribe landmark data and laser scan data were collected for the pelves and femora of 252 extant anthropoid primates (Table 4.1). All individuals were judged to be adults based on femoral epiphyseal fusion. All individuals were wild shot specimens with the exception of 22 individuals (see specimens listed in Appendix B), which were included to supplement the sample sizes for high priority taxa for which wild specimens were unavailable. This total sample used in this project is comparable in size and diversity to other laser scan projects (Tocheri et al. 2005; Marzke et al. 2010). An ideal sample would include 20 sex-matched individuals per species but sample sizes are constrained by the known postcranial skeletal samples available in domestic and international museums. However, the sample included an independent test of the morphology-behavior association proposed for hominoids by including *Ateles-Cebus*. All taxa in the sample have locomotor behavioral data (see Chapter 2).

The laser scan and landmark coordinate data used in this study were collected by multiple researchers (discussion of intra- and inter-observer error below). The author collected most of the data from specimens at the United States National Museum (USNM), Museum of Comparative Zoology at Harvard (MCZ), Cleveland Museum of Natural History (CMNH), American Museum of Natural History (AMNH), Naturalis Leiden (ZMA), Bavarian State Zoological Collections (ZSM), and the National Museums of Kenya (KNM). To increase the sample size, laser scan data collected by Dr. J. Michael Plavcan (Department of Anthropology, University of Arkansas) were included in the sample. In addition, some microscribe landmark data collected by Dr. Carol Ward (Pathology and Anatomical Sciences, University of Missouri) were used (data from Ward 2009). The data collected by Plavcan and Ward were collected at locations listed above, as well as at the Royal Museum for Central Africa (MRAC), University of Zurich (UZIA), Powell Cotton Museum (PCM), and Field Museum of Natural History (FMNH).

LASER SCAN METHODS

Scanning and Polygonal Model Rendering

The left hipbone, or os coxa, and femur were scanned for each specimen. Right hipbones and femora were substituted when the left was damaged, as there was no systematic asymmetry in hipbone shape when the original specimens were examined. Scan data collected by the author and Carol Ward were collected with a Next Engine Desktop 3D Scanner (NextEngine, Malibu, CA, USA) and scan data collected by J. Michael Plavcan were collected with a Konica-Minolta Vivid 9i (Konica-Minolta, Tokyo, Japan). Laser scan data collected using different scanners, scan protocols, and even data point density are equivalent in volume and surface area (Guidi et al. 2008; Aguilar et al. 2009; Sholts et al. 2010; Slizewski et al. 2010). The low level of difference

observed between Konica-Minolta and Next Engine scanners is comparable to differences achieved within scanning trials of the same scanner (Sholts et al. 2011).

Multiple NextEngine scan protocols were necessary for this project because NextEngine scanners have optimal settings for objects of different sizes, opacities, colors, and densities. The scan protocol was determined on a case by case basis, with priority given to scan mode determined by object size. Large bones (>12 cm in any dimension), which comprised the majority of the sample, were scanned in the Wide Mode. Clean, non-greasy bones were usually scanned in a single 360° iteration followed by single-shots of the ends of the bone. Greasy specimens, such as many platyrrhine skeletons, required additional 360° scans to compensate for the laser diffraction that occurs as a result of the grease. In some cases, it was necessary to scan very large bones (>25 cm, such as *Gorilla* pelves) in Extended Mode. Small bones (<12 cm in all dimensions, such as *Cebus* pelves) were scanned in the Macro Mode. However, these small bones were often partially transparent due to their thinness, requiring multiple 360° iterations to capture the object and possibly talc coating to increase opacity of the specimen (if permitted by curatorial staff). Prior to scanning, all pelves were oriented on the NextEngine turntable in a safe, steady position using casting putty and the assistance of the NextEngine part gripper. Unless it was considered unstable, the preferred position for 360° iterations was with the iliac blade down for pelves and with the femoral head oriented up for femora. All scans were collected using high-definition settings (HD). Additional detail can be found on NextEngine scan setting options from the manufacturer (NextEngine 2012) and scan methodology publications (Tocheri 2009; Friess 2012).

NextEngine laser scan point cloud data for each hipbone and femur were aligned in the Next Engine ScanStudio HD Pro proprietary software, and exported as a polygonal model (wavefront or .obj format). Scan processing was done during downtime at museums to ensure quality data were collected and to allow re-scanning of specimens, if necessary. Further scan processing, or “cleaning” to remove irregular topographies produced during scanning, was completed using the IMEdit module of PolyWorks V 11.0 software (InnovMetric, Québec, Canada). As in other studies using NextEngine data (e.g., Tocheri et al. 2011; Garvin and Ruff 2012), the laser scan data were edited in an external software program due to the limited options for cleaning the polygonal model in Scan Studio.

The following Konica-Minolta scan protocol has been provided by J. Michael Plavcan. Most specimens were scanned with the telephoto lens, although larger specimens were scanned with the medium lens. Most specimens were positioned between 600-900 mm from the lens and scanned in two overlapping halves, which could then be aligned. Konica-Minolta point cloud data collected by Plavcan were first manually assembled using the Konica-Minolta Polygon Editing Tool software. Alignments were then fine-tuned to produce maximum convergence and 1:1 point sampling between scans using the IMAlign module of PolyWorks. Overlap was reduced and point clouds merged with medium smoothing to produce a 3D polygonal model using the IMMerge module. The polygonal models of each pelvis were imported into the IMEdit module of PolyWorks for final processing and cleaning.

MICROSCRIBE LANDMARK METHODS

Pelvis articulation methods and landmarks

Microscribe landmark data eliminated the need to laser scan both halves of the pelvis and sacrum by providing 3D landmarks that can be used to align the hipbone in the PolyWorks virtual environment. This step substantially reduced the time and costs of this project, and accuracy can be quantified in this method of digital articulation, unlike most other methods of digital articulation.

First, the left and right hipbones and sacrum were articulated using putty and rubberbands. The thickness of the putty at the pubic symphysis and sacroiliac joints is approximately 3 mm, following Li (2002) and Ward (2009). The 14 landmarks used in this analysis (Table 4.2) were indicated on the pelvis by a single pencil point. The microscribe data supplies 5 landmark coordinates of the left os coxa (ASIS, PIIS, dorsal acetabulum, center of acetabular fossa, and ischial spine) and 9 points used to establish the lumbosacral, midline, and sacral planes (Figure 4.1). These landmarks were selected because they provide information about anatomical planes and because they are easily observed on most pelves. The pelvis was then propped up by foam blocks and/or putty so that the landmarks were fully accessible from the ventral surface. Microscribe landmark data were then collected on the articulated pelvis using an Immersion (San Jose, California) MicroScribe 2GX. After completion of microscribe data collection, landmarks were removed using a white eraser.

Pelvis landmarking error study

The author conducted a repeatability study of 10 landmarking trials to calculate (intraobserver) precision in measuring 3D landmark location. A chimpanzee pelvis

housed in the Ward Lab (University of Missouri) was articulated following methods described above. The landmarks (Table 4.2) used in this study were digitized 10 times on August 2, 2011. Following the methods described in Singleton (2002), the distance of each landmark from the landmark centroid was calculated for each trial. The average distance for all trials for each landmark was also calculated. Mean deviations for each landmarking trial were calculated and the root mean square error (RMSE) was calculated for each landmark (Table 4.3). Singleton (2002) uses the quadratic mean, or root mean square error, to represent the intraobserver error. The author's mean RMSE is 0.89, which is considered acceptable given the large size of the primate pelvises. The author's microscribe precision averaged 0.35 mm across landmarks, and did not exceed 1.67 mm deviation from the centroids, a level of precision similar to other landmark-based studies (Singleton 2002; Frost et al. 2003). The values reported in Table 4.3 suggest that the author has a very high level of repeatability in selection of landmarks⁸.

Pelvis articulation error study

The author conducted a similar repeatability study to calculate (intraobserver) precision in articulating pelvises. The biggest source of error in articulating pelvises is almost certainly variation in the putty thickness, which is necessary to hold the two hipbones and sacrum together. The previously described chimpanzee pelvis housed in the Ward Lab was articulated 5 times during a 12 hour period on August 2, 2011. After each articulation session, the 14 landmarks used in this analysis were digitized and recorded. Because it was necessary to move the pelvis between articulations, the percent difference between 4 interlandmark distances were examined (Table 4.4). The

⁸ Some landmark data used in this study were provided by Ward (2009), who has also verified her high levels of precision in landmark selection in an independent error study (personal communication).

distances were selected because they span both the sacrum and pelvis, which is necessary to gauge the precision with which the bones were aligned to each other. A comparison of the interlandmark distances (Table 4.5) found less than 1.2% difference between all maximum and minimum interlandmark distances in the 5 articulation trials. These values suggest a very high level of intraobserver repeatability in articulation technique.

DIGITAL ALIGNMENT METHODS

Pelvis alignment to landmark coordinate data

For each specimen, the laser scanned os coxa was aligned to its matching microscribe landmark coordinates in the PolyWorks IMInspect module. First, the microscribe x, y, z landmark coordinate data were saved as tabular data in text files (.txt) and imported into the IMInspect workspace. The PolyWorks virtual environment also works within an x, y, z system and can recognize the numeric data as coordinates within its environment. The landmarks were manually identified as point objects, one of the PolyWorks geometrical primitives, giving the landmarks a three-dimensional anchor in the virtual environment. Midline and lumbosacral planes were then established using these point objects (Figure 4.2). A best-fit plane was established to point objects created from landmarks 6-10 (Table 4.2), corresponding to the pubic symphysis and sacral midline. A best-fit plane was also established from point objects created from landmarks 11-14, collected on the cranial surface of the first sacral vertebra, and corresponding to the lumbosacral plane. A third plane was from landmarks 10, 13 and 14, roughly corresponding to the ventral surface of the sacrum, to facilitate viewer orientation in images but is not used in this study.

The hipbone polygonal model belonging to the landmarks was then imported into the IMInspect workspace. The model loads with 3D coordinates assigned by the scanner and so it must be aligned to the landmark coordinate data manually. Points were anchored on the pelvis model at the ASIS, PIIS, center of the acetabular fossa, ischial spine, and dorsal border of the acetabulum, in the same locations as microscribe landmarks 1-5 collected on the original specimen. The IMInspect center point alignment operation was then used to align the 5 points on the polygonal model to the points established from the landmark data, dragging the polygonal model into alignment along the midline plane in the process. It is worth noting that the midline landmarks collected on the pubic symphysis were collected with putty (approximately 3 mm thick) in between the two innominates, and so the midline plane should be just slightly medially off-set from the innominate.

Femoral abduction constraints

Maximum abduction was determined by digitally manipulating the femur within the acetabulum following a set of boundary conditions, which are largely based on biological and theoretical constraints outlined by MacLatchy (1995).

Center of movement

All movements of the femur were constrained around the hip joint center. For a ball and socket joint like the hip, the center of rotation of the hip joint is the center of the femoral head, which is the same as the center of the acetabulum (Pauwel 1980; Brinckmann et al. 2002a). The hip joint center was calculated numerically using a digital sphere-fitting approach (described in “femoral abduction methods” below).

Boundary constraints on mobility

The fovea capitis was restricted to the confines of the acetabular fossa. Since the fovea is hypothesized to be confined to the acetabular fossa during normal joint loading (see extensive discussion in Chapter 2, as well as Kapandji 1970; Jenkins and Camazine 1977), the simulated movements of the femoral head within the acetabulum are limited by keeping the fovea capitis within the internal boundaries of the lunate surface (Figure 4.3). This constraint did not apply to *Pongo*, which does not typically have a subchondral ligamentum teres insertion.

In addition, the subchondral borders of the acetabular margin and femoral head were kept relatively congruent. Attention to the subchondral borders was the only subjective constraint but is an extremely important one because it was the primary method for assessing positions of the femoral head within the acetabulum in *Pongo*. This limit on movement can be influenced by joint geometry (personal observation), with more shallow or loose-packed joints being more difficult to estimate when the subchondral borders were not congruent. MacLatchy (1995) allowed “slight overlap” of non-articular surfaces with subchondral surfaces until one of the other constraints on movement had been met, although MacLatchy’s study limited femoral movement before the acetabular margin would have impinged the femoral neck. In this study, this constraint was rarely met, as the maximum fovea position within the acetabular fossa was typically met before the subchondral borders overlapped.

A final boundary constraint on mobility was that bony elements cannot intersect other bony elements. Special attention was paid to the femoral neck and greater trochanter, which cannot intersect the bony pelvis during movements of the hip *in vivo*. This constraint was never met within this study or MacLatchy’s (1995; 1996; 1998) study.

Femoral abduction methods

After aligning each pelvic polygonal model to its corresponding landmarks, the matching femur model was imported into the IMInspect workspace. IMInspect geometrical objects, or shape primitives, were necessary to establish certain landmarks for abducting the femur. All shape objects were established by a single observer (the author), reducing the potential for error. The following eight objects were created in the IMInspect workspace in order to align the femur within the acetabulum and to measure femoral abduction:

(1) A best-fit sphere was fit to the acetabular lunate surface by selecting the surface of the entire C-shaped subchondral lunate surface, making sure not to select surface points in the acetabular fossa or beyond the external acetabular borders, using the least squares sphere-fitting option. Data points that were more than 2.5 standard deviations from the average used to compute the sphere were rejected, and the sphere was recomputed without outlier points. This option was selected for all sphere-fitting procedures used in this thesis. Best-fit spheres following a pure least squares approach using PolyWorks operations can be fit with less than 1% error within and between observers to both the acetabular lunate surface and the femoral head articular surface (Hammond et al. 2012; Plavcan et al. 2012; Hammond et al. 2013b).

(2) A point object was created at the numerical center of the acetabular sphere, representing the center of the hip joint.

(3) A best-fit sphere was fit to the femoral head by selecting the entire subchondral surface, making sure not to select surface points in the fovea capitis or beyond the external borders, using the least squares sphere-fitting option (Figure 4.5).

(4) A point object was created at the numerical center of the femoral head sphere (Figure 4.5).

(5) A point object was anchored at the center of the fovea capitis, based on visual inspection. Because foveae are irregular and not necessarily deepest at their central point, it was not possible to use automated methods to identify the central point.

(6) A point object was anchored at the posterior intercondylar notch of the distal femur.

(7) A vector was fit to the femoral shaft by selecting the entire cylindrical diaphysis, beginning below the lesser trochanter and ending above initial flaring for the femoral condyles, using the least squares vector-fitting option (Figure 4.6). Data points that were more than 2.5 standard deviations from the average used to compute the vector were rejected, and the vector was recomputed without outlier points. Best-fit vectors can be fit with a high level of precision in PolyWorks, with a maximum difference $<2^{\circ}$ in orientation between vectors in an error study conducted for this thesis (Table 4.8).

(8) A plane was set perpendicular to the long axis of the ischium manually. It was not possible to identify a long axis using automated methods in species with very short ischia (e.g., *Hylobates*) and in most fossil specimens which have damage to the caudal ischium, and so it was necessary to use a manual technique for setting the plane through the ischium. From a lateral view, the long axis of the ischium was positioned left to right and then set an orthogonal plane through the ischium. The angle formed between the diaphyseal vector and the ischial plane was monitored using IMInspect measurement features.

After the creation of the shape primitives, the femur and pelvis contained all necessary components to begin abduction simulations. First, the best-fit spheres for the femoral head and lunate articular surfaces were made coincident via the IMInspect point

alignment operation, positioning the femoral head within the acetabulum. The fovea point on the femoral head was then aligned to the point anchored to the center of the acetabular fossa to ensure the femoral head was positioned medially, and the point alignment operation was repeated for the femoral head and acetabular sphere center points. The femoral head was then rotated from the center of movement in the center of the hip joint to a position of maximum abduction where all other boundary constraints had been met.

During abduction simulations, the femoral shaft was kept in a neutral “horizontal” posture in an attempt to match the *in vivo* and *in silico* measures as closely as possible. The horizontal posture is intermediate in the flexion-extension range for quadrupeds⁹ (Figure 4.4), and was achieved by keeping the least squares best-fit vector of the diaphysis parallel to a transverse plane set through the ischium. More specifically, the horizontal posture is 90° (varying by less than +/-1°) to the long axis of the ischium (e.g., perpendicular). Thus, the horizontal posture is based on the position described in Chapter 3 but is measured relative to the long axis of the ischium rather than a horizontal examination Tabletop. The ischium was selected as the best approximation of the horizontal because it usually runs cranio-caudally and because it is present in multiple fossil primates. It is worth noting that there is variation in the dorsal flexion of the ischium, with colobine monkeys and hylobatids having a moderately flexed ischium and (non-human) hominids and atelines having straight ischia (Fleagle and Simons 1979; Fleagle and Anapol 1992; McCrossin and Benefit 1992). There could be some interspecific influence on the model from dorsal flexion of the ischium but it is not

⁹ MacLatchy's (1995) study examined 2 femoral postures, highly extended (0°, or parallel, to the long axis of the ischium) and flexed (135° to the long axis of the ischium). According to MacLatchy (1996), however, she also examined a position 90° and 45° to the long axis of the ischium, finding the same results in both these positions.

expected to be greater than that resulting from comparisons between *in vivo* and *in silico* data.

Femoral abduction measures

Maximum abduction was measured by (a) angular abduction of the femur relative to the midline plane and (b) by the physical distance between the knee and the midline plane (Figure 4.7). The angle of abduction was measured by calculating the angle formed between the diaphyseal vector (primitive #7) and the midline plane. The physical distance spanned by the knee was measured as the shortest distance from the intercondylar notch point (primitive #6) to the midline plane.

QUANTITATIVE METHODS

Differences between suspensory and non-suspensory primates

Angular abduction and knee position determined *in silico* were compared between suspensory and non-suspensory primates (full sample in Table 4.1) by locomotor group. Significant differences in abduction and abducted knee position were tested between suspensory and non-suspensory species by means of one-way analysis of variance (ANOVA). Boxplots were used to visualize differences between taxa. *Gorilla beringei*, *Alouatta caraya*, and *Pygathrix nemaeus* were plotted alongside extant taxa in figures but are not included in ANOVAs where suspensory and non-suspensory locomotor categories were used. Quantitative analyses were performed in R (version 3.0.1, R Core Team 2012).

Classification accuracy

Linear discriminant function analyses (DFA) were used to find the accuracy in classifying *in silico* data by locomotor group (suspensory vs. non-suspensory). DFA is important for later analyses because it measures the strength of predictions for fossil group membership. First, the percentage of correct classifications by locomotor group for abduction (degrees) and abducted knee position (mm) were calculated when sampling all individuals in both locomotor groups. Second, discriminant function analysis was then used to find the accuracy in classifying *in silico* data into a refined category (i.e., hylobatids, *Gorilla gorilla*, *Pan*, *Pongo*, *Ateles*, *Cebus*, cercopithecoids), in the case that this might provide additional specificity for fossil predictions. These refined categories were selected because they broadly correspond to taxonomic groups of more refined locomotor categories. That is, hylobatids are specialized brachiators, *Gorilla gorilla* and *Pan* frequently use terrestrial knuckle-walking, *Pongo* uses slow quadrumanous clambering, *Ateles* uses clambering and semi-brachiation, with *Cebus* and cercopithecoids using quadrupedalism. *Gorilla beringei*, *Alouatta caraya*, and *Pygathrix nemaeus* were excluded from DFA analyses, as in other analyses requiring extant species to be *a priori* assigned to a specific locomotor category. The DFAs included iterative jackknife reclassification techniques, and were performed in R using the MASS package (Venables and Ripley 2002).

Allometric Scaling

The influence of size on measures of abduction and abducted knee position was assessed using standard major axis (SMA) regression. Log-transformed femoral head diameter was selected as the size proxy because MacLatchy (1995) found that joint diameter is the functional scaling unit of the hip joint and a more appropriate size

surrogate than other measures, particularly areal measures. In addition, males and females have equivalent scaling relationships between femoral head size and mass (Jungers 1991), minimizing the potential for estimation error. Angular data were not transformed but the femoral head sphere diameter was log-transformed prior to regression. Regression models were calculated using species sex-specific means, excluding *Gorilla beringei*, *Alouatta caraya*, and *Pygathrix nemaeus* due to the difficulties in assigning these taxa to a locomotor group.

SMA models were implemented in the *smatr* package of R (Warton et al. 2012). SMA is preferable to least squares methods when testing the similarity of regression slopes between groups (Aiello 1992; Smith 2009). The suspensory and non-suspensory locomotor groups were tested for common slopes using a likelihood ratio test compared to a chi square distribution (Warton et al. 2006). If the slope tests were significantly different ($p \leq 0.05$), individual regressions were fitted for the suspensory and non-suspensory groups. A slope of 1 for linear and angular measures is considered isometric. If the isometric slope falls within the 95% confidence limits of the predicted slope, the two are not statistically different ($p \leq 0.05$) (Goldman et al. 1990). Positive and negative allometry are indicated when the isometric slope falls beyond the 95% confidence intervals.

Model validation

In silico models of abduction and abducted knee position were compared to *in vivo* data in order to quantify how well the models represent the values from live animals. *In vivo* and *in silico* angle of abduction and abducted knee position were compared by percent difference, two-way ANOVA, and Tukey's post-hoc pairwise comparisons within taxa.

In silico data were statistically compared to *in vivo* measures of angular abduction (Chapter 3) in order to evaluate the level of error in the modeling process, which is typically referred to as model validation (see review in Hutchinson 2011). In comparing *in vivo* and *in silico* data for angular abduction, taxa were compared at the genus level because taxa in the same genus are assumed to generally have the same locomotor adaptation (validation sample included in Table 4.13). The one exception to this was the mountain gorilla (*G. beringei*), which may differ substantially from the western lowland gorilla (*G. gorilla*) (see Chapter 2) in locomotor behaviors. In this case, comparisons between *in vivo* and *in silico* measures of abduction were restricted to *G. gorilla*.

In silico and *in vivo* data for abducted knee position were also compared. Whereas abduction is not expected to vary significantly within a genus (except perhaps in *Gorilla*), the abducted knee position could vary substantially when genera have different body masses. Because the abducted knee position has the potential to be greatly influenced by body size, validation statistics were considered at the species level instead.

RESULTS

Differences between suspensory and non-suspensory groups in full extant sample

Femoral angular abduction

Sex-specific species means for abduction are reported in Table 4.7. Suspensory taxa have significantly larger abduction (one-way ANOVA $p < 0.01$) *in silico* than non-suspensory taxa. Boxplots show that the two locomotor groups have substantial overlap between 35-55° abduction (Figure 4.8). In particular, the low abduction ability of *Gorilla*

gorilla results in suspensory taxa encompassing much of the range of non-suspensory taxa, although the suspensory taxa have increased abduction ability as a group compared to non-suspensory taxa (see also Figure 4.11).

Knee position

Sex-specific species means for abducted knee position are reported in Table 4.9. Suspensory taxa have significantly increased abducted knee positions (one-way ANOVA $p < 0.01$) *in silico* than non-suspensory taxa. Boxplots show substantial overlap in abducted knee position between the locomotor groups, particularly between 175-225 mm from the midline (Figure 4.9).

Classification accuracy

Femoral angular abduction

Linear discriminant function analysis (DFA) was used to evaluate how well *in silico* abduction classifies group membership and at what level of specificity. This step is important for showing the reliability of locomotor predictions generated from models of abduction. DFA first compared locomotor groups (suspensory, non-suspensory), followed by very broad taxonomic groups with similar locomotor behaviors (hylobatids, *Pongo*, *Gorilla gorilla*, *Pan*, *Ateles*, *Cebus*, cercopithecoid). The DFA results show that broad locomotor categorization is a better classifier than the refined categories (Table 4.8). Overall, abduction ability cannot accurately predict taxonomic membership (59% overall correct classification) but does accurately predict locomotor membership (80% overall correct classification). The DFA results suggest that degree of abduction cannot classify an anthropoid beyond broad locomotor group (i.e., suspensory vs. non-suspensory), and that different locomotor groups are more disparate in their abduction ability than the taxonomic groups. In addition to showing that locomotor categories are

more accurate classifiers, the DFA results show that non-suspensory taxa are correctly classified with slightly higher frequency (83%) than suspensory species (78%), which is probably due to the low abduction values for *G. gorilla*.

Knee position

Discriminant function analysis (Table 4.8) shows that data for abducted knee position can be reasonably classified using broad locomotor categories (73% correct classification in suspensory, 91% non-suspensory). As in abduction ability, sorting the *in silico* data by taxonomic unit returned low correct classification values (68% correct).

Allometric Scaling

Femoral angular abduction

There is not a significant relationship between abduction and femoral head diameter ($p > 0.05$; see Figure 4.12). This is consistent with the live animal measures of abduction regressed on body size in Chapter 3.

Knee position

There is a significant relationship between the abducted knee position and femoral head diameter (Figure 4.12). Significant differences in slope were detected between locomotor groups ($p = 0.025$). The isometric slope is contained within the 95% confidence intervals for the predicted slope in non-suspensory primates (95% CI: 0.671-1.080). The slope for non-suspensory primates is therefore not significantly different from isometry, and so it can be inferred that abducted knee position scales isometrically in this group. However, the isometric slope is not contained within the 95% confidence intervals for suspensory primates (95% CI: 0.508-0.728). The predicted slope for abducted knee position scales with negative allometry in suspensory taxa.

It is important to note that hylobatids and *Ateles* have an abducted knee position that is larger than non-suspensory taxa of equivalent femoral head size (Figure 4.12). Although there are no extant large-bodied non-suspensory taxa to compare to the great apes, the negatively allometric slope in suspensory taxa indicates that great apes and similarly-sized non-suspensory taxa would converge on similar abducted knee positions. Why suspensory taxa scale with negative allometry in this measure has yet to be explored but probably relates to great apes having relatively shorter femora for their body size compared to cercopithecoids (see Discussion).

Validation of *in silico* models with *in vivo* data

Femoral angular abduction

In vivo and *in silico* measures of abduction were compared broadly and then compared at the taxonomic level. First, the two kinds of data were compared to each other, finding that the means of the *in silico* and *in vivo* data were not significantly different (ANOVA $p=0.43$, Table 4.10; see also Table 4.11 for means). This non-significant difference appeared to be a function of the *in silico* and *in vivo* data being differently distributed by locomotor category *in vivo* (e.g., *in silico* data was generally intermediate between the significantly different suspensory and non-suspensory *in vivo* data). Specifically, the *in vivo* data showed higher ranges of abduction for suspensory taxa and lower ranges of abduction for the non-suspensory taxa than was detected *in silico*. A two-way ANOVA comparing the interaction of locomotor group (suspensory versus non-suspensory) and data type (*in silico* versus *in vivo*) confirmed this observation, finding a significant interaction between these variables ($p<0.01$, Table 4.10). Examining the means of the data show that the *in silico* data overestimate range

of *in vivo* abduction in non-suspensory primates, whereas the *in silico* data conservatively estimate range of *in vivo* abduction in suspensory primates (Table 4.11).

Comparisons were also made at the genus level. *In vivo* and *in silico* measures of abduction were found to overlap within each taxon (Figure 4.13), although there was only a small amount of overlap between *in vivo* and *in silico* data for *Pan*. Percent differences between data types by genus confirms this pattern on a finer scale (Table 4.13), although it is worth noting that percent differences maximize the appearance of differences between means with smaller values. For instance, for species with absolutely smaller angular abduction, a difference as small as 1° will be a relatively larger percent difference compared to a species with an absolutely larger amount of angular abduction.

In addition, Tukey's honest significance test (Tukey's HSD) multiple comparisons between *in silico* and *in vivo* data types were performed between taxa (Table 4.14). Significant differences between means of data types were found in *Pan*, *Macaca*, *Papio*, and *Ateles*, consistent with the observations regarding percent differences.

Knee position validation

First, abducted knee position was broadly compared between *in vivo* and *in silico* data types. Means of the *in silico* and *in vivo* data were significantly different ($p < 0.01$ in Table 4.12, see also Table 4.11 for means). Next, *in vivo* and *in silico* data were divided into their locomotor groups and a two-way ANOVA was used to test for a significant interaction between locomotor group and data type. The two-way ANOVA found a significant interaction between these variables ($p < 0.01$, Table 4.12). A comparison of the mean values shows that *in silico* data for suspensory primates conservatively

estimates knee position, although *in vivo* and *in silico* means for non-suspensory taxa are virtually the same (Table 4.11).

The abducted knee position was also compared at the species level. The *in vivo* and *in silico* data for knee position were found to overlap when visually examined (Figure 4.14). The species-specific means between the two data types differ in some species, however. Percent differences in mean knee position were relatively large in *Pan* (female=15%, male=21%), *Symphalangus* (female=20%, male=23%), and *Cebus* (male=20%) (Table 4.13). However, as previously noted, there are certain limitations to examining differences by percentage. A more specific comparison between the two data types are through Tukey's HSD pairwise comparisons between data types for each species (Table 4.15). All taxa were found to have means that were not statistically different between *in silico* and *in vivo* data for knee position, except *Pan troglodytes*. *Pan troglodytes* was statistically significant ($p < 0.01$, Table 4.15). It is probable that this difference in *P. troglodytes* is responsible for the difference between *in silico* and *in vivo* suspensory means in Table 4.11. However, *in silico* and *in vivo* knee position show a very strong relationship in the other species, indicating a high correspondence between *in vivo* and *in silico* data for knee position.

DISCUSSION

As anticipated, the *in silico* models indicate that there are significant differences between suspensory and non-suspensory species, particularly in regards to the more highly suspensory species (*Pongo*, *Pan*, hylobatids) (see Figure 4.10). Interestingly, *Gorilla* has a lower simulated range of angular abduction than other suspensory species and overlaps with non-suspensory species in this measure. In particular, *Gorilla beringei* has a range of abduction between 21-39° (Table 4.7, Figure 4.11), which is at the low

range even for non-suspensory monkeys. Of particular relevance here is that gorillas are the largest of the extant primates, with male *G. gorilla* and *G. beringei* averaging 170 kg and 163 kg, respectively (Smith and Jungers 1997). It is suggested here, as suggested by others (Rubin and Lanyon 1982; Biewener 1983; Rubin and Lanyon 1984; Alexander 1985; Polk et al. 2009; Zihlman et al. 2011), that very large-bodied species such as *Gorilla* may operate their joints in a narrower range of positions and/or at slower speeds in order to maintain acceptable joint safety factors. However, both species are similarly large and so this does not fully explain why *G. beringei* has an even lower range of abduction than *G. gorilla*. These differences probably relate to different locomotor behaviors and associated habitual limb postures. As discussed in Chapter 2, *Gorilla beringei* is substantially more terrestrial than any of the suspensory species (Schaller 1963; Reynolds 1965; Doran 1996; Doran and McNeillage 1998), including its co-generer *Gorilla gorilla* (Doran and Hunt 1994; Remis 1995; Doran 1997; Remis 1998). *Gorilla beringei* uses terrestrial quadrupedalism for 97% of locomotor behaviors (Doran 1996) whereas *Gorilla gorilla* is only quadrupedal 64% of the time (Hunt 2004) (see Table 2.1).

Abducted knee posture is a proxy for the hindlimb spatial envelope, or range of foot positions relative to the body (Figure 4.15), and is the additive result of hip mobility, body size, and morphology. Large animals have absolutely long thighs and so, not surprisingly, the *in silico* models show that range of abducted knee positions are significantly larger in suspensory primates, especially in the large-bodied great apes. This finding was anticipated based on results in Chapter 3, but this chapter shows that the abducted knee position is influenced by morphology in addition to body size and range of motion. The importance of morphology is inferred because the abducted knee

position does not scale isometrically in suspensory taxa, with great apes having a lower value than would be predicted based on size alone. This almost certainly results from the proportions of the hindlimbs in great apes, specifically that great apes have relatively short femora for their size (Jungers and Susman 1984; Jungers 1985).

This chapter also confirms that certain taxa have similar abducted knee positions but different ranges of abduction, indicating body size is an important factor in abducted knee position. A clear example of this is for instance *Pongo* and *Gorilla* (Figure 4.15). Although *Gorilla* and *Pongo* have the ability to position their knee equally far lateral relative to the midline of the body (Figure 4.9), the angle at which they do this is different (Figure 4.8), resulting in somewhat different functional abilities. Although the range of knee positions possible conveys basic information about locomotor behavior (e.g., "suspensory" vs. "non-suspensory") and what range of supports are directly available to an animal, abducted knee position cannot provide information about the more subtle aspects of locomotor behavior that distinguish different taxa. That is, *Gorilla* and *Pongo* are quite different in their specific locomotor adaptations and hindlimb capabilities but this is not detected from abducted knee position alone. In short, the spectrum of locomotor behaviors known to exist in anthropoids (see Chapter 2) is not distinguished in this metric without additional information about range of abduction.

The findings in this study are compatible with those reported by MacLatchy (MacLatchy 1995; 1996; MacLatchy and Bossert 1996), who modeled joint mobility in *Pongo pygmaeus*, *Pan troglodytes*, *Mandrillus sphinx*, and *Macaca fascicularis*. In abduction during extension¹⁰, MacLatchy found significantly different abduction in *M.*

¹⁰ MacLatchy's (1995) dissertation simulated abduction from an extended posture (parallel or 0° to the ischial ramus) and a flexed posture (135° to the ischial ramus). Her subsequent works (1996, 1998) also reference a "neutral posture", when the fovea capitis is centered in the acetabular fossa and the shaft of the femur is flexed 90° to the ischial ramus. The neutral posture used in MacLatchy's study is the most comparable to

fascicularis and *M. sphinx* with abduction in *P. troglodytes* and *P. pygmaeus* (1995; 1996). In abduction during flexion, MacLatchy was unable to detect significant differences between *M. fascicularis*, *M. sphinx*, and *P. troglodytes* but did find *P. pygmaeus* to have a significantly greater range of motion (1995; 1996). Overall, her work indicated there is a spectrum of mobility, with Old World monkeys having the lowest range of motion and *P. pygmaeus* having the greatest, with *P. troglodytes* being intermediate between the two. It was previously unclear whether the patterns observed in MacLatchy's study were related to a limited taxonomic sample, phylogenetic influences, and/or allometric effects, but this work demonstrates that hip abduction varies with locomotor behavior. The spectrum of hip mobility evinced in MacLatchy's work is present here, with *Pongo* having the greatest range of abduction in the hominoids, followed by hylobatids and *Pan*, and *Gorilla gorilla* being lower and overlapping with some non-suspensory monkeys (Figure 4.13).

This study can be more specific than MacLatchy's study regarding hip mobility in cercopithecoids and clarifies some of her findings. This study sampled a much larger number of cercopithecoids and found that most colobine monkeys and macaques generally have increased range of abduction than terrestrial cercopithecines (*Papio*, *Theropithecus*, *Erythrocebus*). This finding presumably reflects the increased arboreality of colobines and macaques. *Macaca fascicularis* is unusual among cercopithecine monkeys in more frequently being arboreal (Rodman 1979; Cannon and Leighton 1994) and is apparently capable of more mobility than many other cercopithecine monkeys, explaining why MacLatchy's study did not detect significant differences between *Pan* and *Macaca* when abducting from flexed hip postures.

the shaft orientation in this study. Unfortunately, very limited data are provided on the neutral posture in anthropoids (see MacLatchy 1996) but it is said to yield the same results as the flexed posture.

Cebus, *Alouatta*, and *Ateles* show that increased arboreal versatility is also associated with an increased range of abduction in the platyrrhines. *Cebus* has the smallest range of abduction, followed by *Alouatta*, and with *Ateles* having the largest range of the three platyrrhines (see Figure 4.8). The ranges for *Cebus* and *Ateles* are consistent with the behavioral data for these taxa (see Chapter 2). The behavioral data for *Alouatta* emphasized arboreal quadrupedalism (Grand 1968; Mendel 1976; Fleagle and Mittermeier 1980) but there are reports that *Alouatta* occasionally uses prehensile tail-assisted suspensory behaviors (Grand 1968; Fleagle and Mittermeier 1980; Ybarra 1984; Gebo 1992; Prates and Bicca-Marques 2008), making a discrete locomotor classification difficult for this genus. However, range of abduction for *Alouatta* falls between quadrupedal *Cebus* and frequently suspensory *Ateles*, which seems to fit with the intermediate behavioral data for *Alouatta*. Not surprisingly, the influence of higher abduction ability in *Ateles* is reflected in the abducted knee position. *Ateles* has a larger span at the knee than *Alouatta* (see Figure 4.9), despite both taxa having similar reported body masses (~6 kg, Smith and Jungers 1997), and both *Ateles* and *Alouatta* have a larger span at the knee than *Cebus*.

The results for cercopithecoids show a few unexpected results. Asian colobine *Pygathrix nemaeus* has been reported to use some suspensory behaviors in captive settings (Workman and Covert 2005; Wright et al. 2008) but the hip morphology does not necessarily promote high levels of hip abduction as would be expected in a suspensory species. Instead, *P. nemaeus* has hip abduction consistent with most other non-suspensory arboreal cercopithecoids. This would suggest that either additional behavioral data is needed on free-ranging *P. nemaeus*, or that the moderate level of hip mobility is adequate and/or necessary for locomotor behaviors used by *P. nemaeus*. *Colobus guereza*, however, has somewhat low range of abduction compared to the

arboreal cercopithecoids (e.g., *Nasalis*, *Rhinopithecus*, *Trachypithecus*, *Ptilocolobus*) and falls within the range of the more terrestrial cercopithecoids (e.g., *Papio*, *Erythrocebus*). Although there is a spectrum of abduction within the cercopithecoids, one possibility raised by these taxa is that monkeys, perhaps even arboreal ones, need a more limited range of abduction for their quadrupedal locomotor behaviors. Lateral joint excursions might be detrimental to powerful flexion-extension movements at the hip, and so taxa that do propulsive leaping (e.g., *Colobus*) or cover large distances by moving terrestrially (e.g., *Papio*, *Theropithecus*) might be especially likely to have less abduction possible at their hip joints. Additional work evaluating morphological and biomechanical trade-offs associated with different hindlimb usage are necessary to test this hypothesis.

This study found that *in silico* measures of abduction and abducted knee position can be used to predict locomotor category with some accuracy, which is an important criterion for reconstructing locomotor behaviors in fossil taxa. Discriminant function analyses were used to predict categorical group membership (suspensory vs. non-suspensory) from the measures of abduction and abducted knee position. *In silico* measures of abduction correctly predicted locomotor category 80% of the time in DFA, and knee position correctly predicted locomotor category 81% of the time. However, the models of abduction and abducted knee position cannot correctly predict taxonomic groups that broadly correspond to more refined locomotor classifications (i.e., specialized brachiation in hylobatids, terrestrial knuckle-walking in *Gorilla* and *Pan*, quadrumanous anti-pronograde clambering in *Pongo*, clambering and semi-brachiation in *Ateles*, and quadrupedalism in *Cebus*). The DFA results found a low overall prediction accuracy for abduction (59% correct classification) and abducted knee position (68% correct classification) when divided into smaller groups. These results

make it seem unlikely that the *in silico* models can be used to achieve higher levels of specificity beyond the broad locomotor categories (i.e., suspensory vs. non-suspensory).

The validity of the interpretations garnered from this model entirely depends on how well the model matches some form of empirical data. Quantifying how closely a model matches empirical data is referred to as model “validation” (Hutchinson 2011), and this study has given particular attention to quantifying the relationship between models of hip abduction and abduction in living anthropoids. This work does not intend to prove that the modeling approach is exact, as models can only approximate reality and many validation tests produce extremely high error rates (review in Hutchinson 2011). The comparisons between the two kinds of data highlight certain differences that exist between the two samples and it is imperative to be aware of how the two kinds of data differ (discussed below). Fortunately, the *in silico* and live animal data quantified for this study have a predictable relationship, suggesting that the modeling approach outlined here has utility for paleobiological reconstructions of hip joint abduction in extinct anthropoids.

Angular abduction displays differences between the *in silico* and *in vivo* approaches in certain taxa. The two forms of data are congruent in *Symphalangus*, *Pongo*, *Gorilla*, and *Cebus* in abduction, with substantial overlap between *in vivo* and *in silico* data (Figure 4.13) and non-significant species-specific pairwise comparisons between data (Table 4.14). It is more difficult to evaluate *Trachypithecus*, *Colobus* and *Hylobates* due to sample sizes, but the limited *in silico* and *in vivo* data also overlap (Figure 4.13). The *in vivo* and *in silico* data for *Macaca*, *Papio*, *Ateles*, and *Pan* display little overlap (Figure 4.13) and are significantly different in pairwise comparisons (Table 4.14). This shows that there is some variability in which species will deviate *in silico*

from the values expected based on the live animal data; differences between the two forms of data are not limited to a single locomotor group or a single species.

Despite some of these observed differences between the *in silico* and *in vivo* data for angular abduction, the way the data differ are consistent. Modeled abduction is underestimated in suspensory species compared to live animal data, and overestimated in the non-suspensory species. Because the models of abduction are based on positions assumed during loading, it might be expected that the models would underestimate passive range of motion, although this does not explain why non-suspensory models overestimate abduction. Differences between the two locomotor groups are diminished *in silico* but predictions that fall in the suspensory range are likely to conservatively estimate the true range of abduction whereas predictions that are in the range of non-suspensory taxa are likely to be an overestimate of abduction ability.

The abducted knee position *in silico* closely tracks the *in vivo* data at the species level. This result indicates that the functional outcome of hip mobility—the abducted knee position—is approximated with a high degree of accuracy in the modeling approach, despite some differences between the two data types observed in angle of abduction. Pairwise comparisons show that only *Pan troglodytes* is significantly different in abducted knee position between data types (Table 4.15). However, none of the other comparisons between *in silico* and *in vivo* data were significantly different and there is nearly complete overlap between the two data for the other species (Figure 4.14). Because the models of hip abduction during loading closely approximate the abducted knee position measured in anesthetized primates, this suggests that the modeling approach developed here actually is converging on the overall hindlimb capabilities of the animals.

Of course, it is important to keep in mind that the models of hip abduction are meant to represent the most abducted position of the joint under loading, whereas the live animal data are the maximum positions allowed by the joint when overlying soft tissues are present. This is a fundamental distinction to be made between these two kinds of data. Models of hip abduction are limited by the bony morphology, and so the bony morphology clearly determines the range of abduction in these models. Hip mobility is not primarily determined by bony morphology in living animals, however, and is instead limited by the surrounding soft tissue structures. When soft tissues are not present, the bones of the non-suspensory taxa overestimate the range of abduction at the joint, indicating that the overlying soft tissues structures are important for limiting joint mobility in these taxa. In suspensory taxa, the models of maximum hip abduction underestimate the range of abduction possible.

The differences between live animal and digital measures of abduction in this study are clarified by MacLatchy's results for strepsirrhines, which suggest that models of maximum hip abduction usually underestimate passive range of abduction. Although limited to strepsirrhines, MacLatchy (1995) also found that angle of abduction in digital models was typically less than passive abduction measured *in vivo*. MacLatchy (1995) measured a small number of strepsirrhines both *in silico* (*Microcebus* n=8, *Galago* n=8, *Cheirogaleus* n=3, *Periodicticus* n=5) and *in vivo* (*Microcebus* n=1, *Galago* n=2, *Cheirogaleus* n=2, *Periodicticus* n=2). Maximum angle of abduction during flexion and extension was compared between digital and live animal data, although the small sample limited the statistical tests that could be performed. All *in vivo* data were within a single standard deviation of the mean for maximum angles of abduction during flexion, and the *in vivo* angles were usually larger than the mean in the digital models (see

MacLatchy 1995, p. 122). Similarly, maximum angles of abduction during extension were usually within a single standard deviation of the *in silico* means, although one *Galago* and one *Cheirogaleus* individual were closer to two standard deviations above the *in silico* means (see MacLatchy 1995, p. 123). MacLatchy's results suggest that passive abduction measured in strepsirrhines slightly over-estimates abduction measured *in silico*, similar to what was observed in suspensory anthropoids in this study. In short, the digital modeling technique used by MacLatchy (1995) and further developed in this study conservatively estimates the total range of femoral abduction in strepsirrhines, hominoids, and *Ateles*. What remains unexplained is why this study overestimates abduction in non-suspensory cercopithecoids, particularly for *Macaca*.

There are several possibilities for why live animal abduction measurements for *Macaca* are lower than predicted by the models. An untested possibility which cannot be currently excluded is that abduction measured in the *in vivo* macaque sample does not accurately reflect wild-shot range of motion. The macaques sampled in this study (Chapter 3) were housed in cages and not allowed to roam like the *Papio* sample, which was housed in a large outdoor colony. However, the possibility that the *in vivo* measures are under-estimates is somewhat unlikely given the other similarly low values found in the other cercopithecoids. In addition, past studies on anthropoid joint mobility have found captive animals to have larger range of motion than wild counterparts (Turnquist 1983; 1985). Although it seems unlikely that captive macaques would have a substantially reduced range of abduction, the influence of caging could be tested by digitally modeling range of abduction using models derived from captive macaques.

A more likely possibility proposed here is that external (lateral) rotation is limited *in vivo* by soft tissues in non-suspensory species but these limits on movement are

absent from the digital model. The work in Chapter 3 supported previous inferences made by Stern and Larson (1993) that highly abducted hip postures in primates involve concomitant external rotation. High levels of external rotation were found to be an important factor in passive range of hip abduction in suspensory taxa, and it was hypothesized that external rotation *in vivo* was limited by soft tissue structures surrounding the hip joint in non-suspensory taxa. In particular, interspecific differences in the strength of hip joint capsule ligaments, the size of the acetabular labrum, and differences in muscle extensibility, tone, and attachments were hypothesized to affect passive range of external rotation (Chapter 3). Because the models here cannot incorporate soft-tissue limits on external rotation, abduction simulations in the non-suspensory taxa may have had a higher level of external rotation occurring *in silico* than would have occurred *in vivo*. If this occurred, the increased external rotation could have facilitated an increased level of abduction in the non-suspensory models.

CONCLUSIONS

Extant suspensory taxa have a significantly greater range of hip joint abduction *in silico* than non-suspensory taxa. Importantly, the inclusion of *Ateles* and *Cebus* shows that the patterns observed within suspensory hominoids and non-suspensory cercopithecoids are not just related to phylogeny. Discriminant function analysis can classify taxa as suspensory or non-suspensory using *in silico* estimates of abduction, although given the overlap in degrees of abduction between suspensory and non-suspensory taxa there must be some caution when estimates are intermediate between the two groups. Only fossil taxa that are found well within the suspensory (>55°) or non-suspensory (<35°) ranges can be easily attributed to one of these locomotor groups. The abducted knee position is significantly different as well but, as in degrees of

abduction, there is some overlap between locomotor groups. The abducted knee position is related to body size and so this metric is most appropriately considered along with hip abduction (degrees) in order to make inferences about arboreal versatility in fossil anthropoids.

There is a predictable relationship between hip joint abduction and knee position modeled *in silico* and that measured *in vivo*. The *in silico* abduction simulations behave in a predictable way relative to the *in vivo* range of abduction, and there is an even stronger relationship between data in reference to knee position. It should be emphasized that *in vivo* angular abduction is the maximum range allowed by the joint when overlying soft tissues are present, whereas the models are built on criteria about how joints are expected to operate during conditions of loading. Given the inherent difference in what is being measured, we would not expect one-to-one correspondence between the two kinds of data. However, the results present a clear hypothetical framework for interpreting *in silico* abduction estimates derived for fossil taxa: fossil estimates that are consistent with extant suspensory taxa are conservative estimates of actual range of abduction allowed by the joint, whereas fossil estimates consistent with non-suspensory taxa are probably high estimates of possible range of angular abduction.

Table 4.1 Extant laser scan and microscribe landmark sample (n=252)

Taxon	♂ (♀)	Locomotion	Museum
<u>platyrrhines (n=33)</u>			
<i>Ateles belzebuth</i>	0 (2)	S	AMNH
<i>Ateles fusciceps</i>	2 (4)	S	USNM
<i>Ateles geoffroyi</i>	0 (3)	S	USNM
<i>Ateles paniscus</i>	1 (1)	S	ZMA, AMNH
<i>Alouatta caraya</i>	5 (5)	--	AMNH
<i>Cebus apella</i>	3 (6)	N	AMNH, USNM, ZMA
<u>colobines (n=52)</u>			
<i>Colobus guereza</i>	2 (3)	N	USNM, KNM
<i>Nasalis larvatus</i>	8 (9)	N	MCZ, USNM, ZSM
<i>Ptilocolobus badius</i>	0 (4)	N	PCM
<i>Rhinopithecus roxellana</i>	1 (2)	N	USNM, AMNH
<i>Trachypithecus cristatus</i>	8 (8)	N	MCZ, ZSM, USNM, ZMA
<i>Pygathrix nemaeus</i>	5 (2)	--	USNM, MCZ, AMNH
<u>cercopithecines (n=55)</u>			
<i>Cercopithecus mitis</i>	4 (4)	N	USNM
<i>Erythrocebus patas</i>	3 (2)	N	AMNH, USNM, ZSM
<i>Macaca fascicularis</i>	4 (6)	N	MCZ, USNM
<i>Macaca nemestrina</i>	1 (5)	N	MCZ
<i>Papio cynocephalus</i>	1 (7)		KNM, USNM
<i>Papio anubis</i>	4 (5)	N	USNM
<i>Theropithecus gelada</i>	3 (6)	N	UZIA, USNM, ZMA
<u>hominoids (n=112)</u>			
<i>Hylobates lar</i>	7 (10)	S	ZSM, MCZ
<i>Symphalangus syndactylus</i>	10 (11)	S	ZSM, USNM, ZMA, AMNH
<i>Pongo pygmaeus</i>	5 (10)	S	CMNH, USNM, MCZ, ZMA
<i>Pongo abelii</i>	3 (3)	S	USNM, MCZ
<i>Gorilla gorilla</i>	10 (8)	S	CMNH, USNM
<i>Gorilla beringei</i>	3 (3)	--	USNM
<i>Pan troglodytes</i>	8 (10)	S	CMNH, USNM
<i>Pan paniscus</i>	5 (6)	S	MRAC

Locomotor abbreviations: S, suspensory; N, non-suspensory; dashes (--), unassigned locomotor category. Institutional abbreviations are listed in text and Appendix C.

Table 4.2 Microscribe landmark coordinates

Landmark	Location	Used for
1	Left posterior	virtual alignment of scanned
2	Left anterior	virtual alignment of scanned
3	Left dorsal	virtual alignment of scanned
4	Left acetabular	virtual alignment of scanned
5	Left ischial spine	virtual alignment of scanned
6	Caudal pubic	midline plane
7	Cranial pubic	midline plane
8	Caudal S1	midline plane
9	Caudal S2	midline plane
10	Caudal S3	midline plane
11	Dorsal cranial	lumbosacral plane
12	Ventral cranial	lumbosacral plane
13	Right cranial border	lumbosacral plane
14	Left cranial border	lumbosacral plane

Table 4.3 Intraobserver mean deviation (mm) and error (RMSE) across landmarks

	Mean Deviations	RMSE
Mean	0.35	0.89
Max	1.67	1.30
Min	0.00	0.56

Table 4.4 Interlandmark distances used in pelvis articulation error study

Interlandmark Distances	
Distance 1	Left ASIS to dorsal S1
Distance 2	Left ASIS to inferior S1
Distance 3	Left acetabular center to dorsal S1
Distance 4	Left acetabular center to inferior S1

Table 4.5 Interlandmark distances (mm) and mean deviations (mm)

	Distance 1	Distance 2	Distance 3	Distance 4
Interlandmark Distances				
Max	141.9	136.73	151.68	127.62
Min	141.01	135.45	150.52	126.16
%Difference*	0.63%	0.94%	0.77%	1.15%
Mean Deviations				
Mean	0.26	0.4	0.4	0.4
Max	0.52	0.64	0.72	0.78
Min	0.09	0.15	0.21	0.08

*Percent difference represents the difference between the maximum and minimum interlandmark distances.

Table 4.6 Differences in 5 repeated trials of best-fit diaphyseal vectors for *Papio* and *Pan* specimens.

Specimen	Difference in orientation between vectors		
	Maximum	Minimum	Mean
<i>Pan troglodytes</i> (CMNH B1056 ♂)	0.52	0.07	0.26
<i>Pan troglodytes</i> (CMNH B1758 ♂)	0.47	0.04	0.25
<i>Pan troglodytes</i> (CMNH B1770 ♀)	0.45	0.11	0.26
<i>Pan troglodytes</i> (CMNH B1723 ♀)	1.16	0.03	0.52
<i>Pan troglodytes</i> (CMNH B1755 ♀)	0.34	0.01	0.18
<i>Papio anubis</i> (NMNH 483234 ♂)	0.43	0.10	0.24
<i>Papio anubis</i> (NMNH 394989 ♂)	0.96	0.16	0.53
<i>Papio anubis</i> (NMNH 395441 ♀)	0.39	0.03	0.19
<i>Papio anubis</i> (NMNH 397476 ♀)	0.35	0.08	0.18
<i>Papio anubis</i> (NMNH 395438 ♀)	0.48	0.02	0.29

Vectors from 5 repeated trials per individual compared equaling 10 comparisons per specimen.

Table 4.7 Sex-specific descriptive statistics for abduction (*in silico*)

	Sex	n	Abduction (°)	
			Mean $\pm$ SD	Max, Min
<i>Pan troglodytes</i>	F	10	54.96 $\pm$ 5.25	64.70, 47.55
	M	8	49.70 $\pm$ 6.71	61.99, 42.06
<i>Pan paniscus</i>	F	6	60.35 $\pm$ 2.10	62.67, 57.29
	M	5	62.89 $\pm$ 3.31	66.76, 59.56
<i>Gorilla gorilla</i>	F	8	50.02 $\pm$ 4.61	55.90, 41.57
	M	10	39.69 $\pm$ 6.40	48.73, 29.83
<i>Gorilla beringei</i>	F	3	33.74 $\pm$ 4.63	38.81, 29.73
	M	3	26.76 $\pm$ 7.38	35.12, 21.17
<i>Pongo pygmaeus</i>	F	10	75.66 $\pm$ 8.83	86.24, 60.34
	M	5	71.44 $\pm$ 1.68	73.30, 69.00
<i>Pongo abelii</i>	F	3	75.30 $\pm$ 5.36	81.49, 72.04
	M	3	75.11 $\pm$ 4.40	80.15, 72.06
<i>Symphalangus syndactylus</i>	F	11	57.12 $\pm$ 5.57	63.80, 45.50
	M	10	56.45 $\pm$ 7.56	66.70, 43.82
<i>Hylobates lar</i>	F	10	60.16 $\pm$ 7.26	68.00, 47.38
	M	7	55.50 $\pm$ 8.50	67.27, 44.58
<i>Colobus guereza</i>	F	3	34.16 $\pm$ 7.19	38.77, 25.87
	M	2	30.02 $\pm$ 4.44	33.16, 26.88
<i>Nasalis larvatus</i>	F	9	44.76 $\pm$ 5.75	55.47, 35.59
	M	8	46.12 $\pm$ 5.71	52.59, 36.74
<i>Ptilocolobus badius</i>	F	4	39.86 $\pm$ 6.18	48.58, 34.49
<i>Rhinopithecus roxellana</i>	F	2	40.45 $\pm$ 0.08	40.51, 40.40
	M	1	42.87	NA
<i>Trachypithecus cristatus</i>	F	8	46.38 $\pm$ 4.89	51.81, 39.97
	M	8	44.07 $\pm$ 5.59	53.43, 37.89
<i>Pygathrix nemaeus</i>	F	2	46.65 $\pm$ 4.11	49.56, 43.75
	M	5	52.09 $\pm$ 6.16	62.56, 47.63
<i>Cercopithecus mitis</i>	F	4	37.97 $\pm$ 6.60	46.91, 32.01
	M	4	38.81 $\pm$ 6.79	48.90, 34.19
<i>Erythrocebus patas</i>	F	2	36.27 $\pm$ 3.42	38.69, 33.85
	M	3	22.14 $\pm$ 6.49	29.57, 17.64
<i>Macaca fascicularis</i>	F	6	45.95 $\pm$ 5.58	52.51, 39.05
	M	4	44.22 $\pm$ 1.83	46.52, 42.34
<i>Macaca nemestrina</i>	F	5	48.68 $\pm$ 5.58	53.70, 40.77
	M	1	56.52	NA
<i>Papio cynocephalus</i>	F	7	37.23 $\pm$ 6.54	48.11, 29.71
	M	1	36.07	NA
<i>Papio anubis</i>	F	5	32.26 $\pm$ 8.04	43.53, 25.52
	M	4	37.99 $\pm$ 2.51	41.46, 35.77
<i>Theropithecus gelada</i>	F	6	39.38 $\pm$ 7.52	49.87, 28.31
	M	3	38.48 $\pm$ 6.80	45.15, 31.55
<i>Ateles belzebuth</i>	F	2	60.55 $\pm$ 0.63	60.99, 60.11
<i>Ateles fusciceps</i>	F	4	50.12 $\pm$ 8.79	62.49, 42.88
	M	2	45.14 $\pm$ 4.11	48.04, 42.24
<i>Ateles geoffroyi</i>	F	3	52.71 $\pm$ 0.92	53.41, 51.66
<i>Ateles paniscus</i>	M	3	54.95 $\pm$ 10.48	62.27, 42.95
<i>Alouatta caraya</i>	F	5	53.23 $\pm$ 7.53	60.98, 42.16
	M	5	48.46 $\pm$ 1.93	50.38, 45.63
<i>Cebus apella</i>	F	6	42.48 $\pm$ 5.31	48.19, 34.08
	M	3	41.18 $\pm$ 4.87	46.63, 37.24

Table 4.8 Percent correct classification in *in silico* models using discriminant function analysis

Locomotor Group	Abduction (degrees)	Abducted knee position (mm)
Suspensory (n=120)	78.33%	72.50%
Non-suspensory (n=109)	82.57%	90.83%
Total (n=229)	80.35%	81.22%
Taxonomic Group	Abduction (degrees)	Abducted knee position (mm)
hylobatid (n=38)	63.16%	84.21%
<i>Pongo</i> (n=21)	90.48%	0.00%
<i>G. gorilla</i> (n=18)	0.00%	61.11%
<i>Pan</i> (n=29)	0.00%	93.10%
<i>Ateles</i> (n=14)	0.00%	0.00%
<i>Cebus</i> (n=9)	0.00%	33.33%
cercopithecoid (n=100)	93.00%	82.00%
Total (n=229)	59.39%	67.69%

Alouatta caraya, *Gorilla beringei*, and *Pygathrix nemaeus* were excluded from the comparisons due to uncertain locomotor classification.

Table 4.9 Sex-specific descriptive statistics for abducted knee position (*in silico*)

	Sex	n	Abducted knee position (mm)	
			Mean $\pm$ SD	Max, Min
<i>Pan troglodytes</i>	F	10	301.59 $\pm$ 19.77	337.35, 272.70
	M	8	298.29 $\pm$ 20.16	335.03, 277.31
<i>Pan paniscus</i>	F	6	318.77 $\pm$ 11.07	330.83, 305.09
	M	5	310.23 $\pm$ 10.32	322.84, 294.51
<i>Gorilla gorilla</i>	F	8	324.02 $\pm$ 19.69	358.09, 298.97
	M	10	353.31 $\pm$ 24.97	393.74, 310.32
<i>Gorilla beringei</i>	F	3	274.18 $\pm$ 10.85	280.75, 261.66
	M	3	304.34 $\pm$ 33.53	336.06, 269.25
<i>Pongo pygmaeus</i>	F	10	293.87 $\pm$ 17.41	329.04, 267.54
	M	5	332.15 $\pm$ 10.54	345.61, 319.46
<i>Pongo abelii</i>	F	3	285.63 $\pm$ 4.02	288.49, 281.04
	M	3	353.84 $\pm$ 19.95	376.66, 339.71
<i>Symphalangus syndactylus</i>	F	11	212.20 $\pm$ 13.95	238.90, 196.42
	M	10	223.45 $\pm$ 16.88	259.41, 202.34
<i>Hylobates lar</i>	F	10	215.86 $\pm$ 13.51	240.29, 199.39
	M	7	200.80 $\pm$ 13.64	218.11, 176.516
<i>Colobus guereza</i>	F	3	148.56 $\pm$ 12.70	159.65, 134.70
	M	2	142.63 $\pm$ 13.42	152.12, 133.15
<i>Nasalis larvatus</i>	F	9	188.74 $\pm$ 20.44	217.45, 161.69
	M	8	216.37 $\pm$ 15.57	237.27, 189.26
<i>Ptilocolobus badius</i>	F	4	159.00 $\pm$ 12.13	175.08, 147.63
<i>Rhinopithecus roxellana</i>	F	2	126.76 $\pm$ 57.48	167.40, 86.12
	M	1	200.43	NA
<i>Trachypithecus cristatus</i>	F	8	152.88 $\pm$ 10.26	166.53, 134.22
	M	8	154.74 $\pm$ 12.52	173.76, 133.47
<i>Pygathrix nemaeus</i>	F	2	178.42 $\pm$ 7.97	184.06, 172.79
	M	5	218.27 $\pm$ 15.72	243.47, 202.74
<i>Cercopithecus mitis</i>	F	4	120.73 $\pm$ 15.78	142.29, 107.86
	M	4	143.42 $\pm$ 14.18	164.02, 131.57
<i>Erythrocebus patas</i>	F	2	131.30 $\pm$ 1.47	132.34, 130.26
	M	3	131.98 $\pm$ 25.74	161.70, 117.11
<i>Macaca fascicularis</i>	F	6	113.93 $\pm$ 10.88	128.53, 100.00
	M	4	124.06 $\pm$ 1.02	124.77, 122.58
<i>Macaca nemestrina</i>	F	5	156.16 $\pm$ 14.30	173.18, 139.24
	M	1	200.53	NA
<i>Papio cynocephalus</i>	F	7	171.36 $\pm$ 19.18	201.86, 145.44
	M	1	196.98	NA
<i>Papio anubis</i>	F	5	175.28 $\pm$ 30.69	215.16, 151.13
	M	4	210.50 $\pm$ 5.84	218.61, 205.45
<i>Theropithecus gelada</i>	F	6	156.97 $\pm$ 18.15	177.08, 127.42
	M	3	172.71 $\pm$ 15.94	186.62, 155.33
<i>Ateles belzebuth</i>	F	2	203.07 $\pm$ 8.91	209.37, 196.77
<i>Ateles fusciceps</i>	F	4	195.42 $\pm$ 11.97	212.54, 184.70
	M	2	176.85 $\pm$ 3.17	179.10, 174.61
<i>Ateles geoffroyi</i>	F	3	188.16 $\pm$ 3.35	190.81, 184.39
<i>Ateles paniscus</i>	M	3	210.60 $\pm$ 25.03	239.47, 194.94
<i>Alouatta caraya</i>	F	5	151.00 $\pm$ 12.12	162.65, 137.10
	M	5	158.75 $\pm$ 4.07	162.26, 152.44
<i>Cebus apella</i>	F	6	107.06 $\pm$ 12.73	120.55, 93.09
	M	3	112.37 $\pm$ 7.47	119.90, 104.96

Table 4.10 ANOVAs for angular abduction

Source	F	Sig.
Locomotor group (suspensory or non-suspensory)	526.76	<0.01
Data type (<i>in vivo</i> or <i>in silico</i>)	0.63	0.43
Locomotor group * Data type	115.14	<0.01

This comparison excludes *Trachypithecus* due to the *in vivo* sample size for this genus.

Table 4.11 Means by locomotor group and treatment type

Locomotor group	Data type	<u>Mean</u>	
		Abduction (degrees)	Abducted knee position (mm)
non-suspensory	<i>in silico</i>	40.41	115.36
	<i>in vivo</i>	25.43	115.54
suspensory	<i>in silico</i>	56.94	285.91
	<i>in vivo</i>	69.67	321.25

This comparison excludes *Trachypithecus* due to the *in vivo* sample size for this genus. Tables 4.8 and 4.11 provide statistical tests for these data.

Table 4.12 ANOVAs for knee position

Source	F	Sig.
Locomotor group (suspensory vs. non-suspensory)	754.85	<0.01
Data type (<i>in vivo</i> vs. <i>in silico</i>)	14.09	<0.01
Locomotor group * Data type	17.57	<0.01

Table 4.13 Percent difference between sex-specific means by data type

Taxon	sex	n <i>in silico</i>	n <i>in vivo</i>	mean		% difference between means
				<i>in silico</i>	<i>in vivo</i>	
Angular abduction (degrees)						
<i>Pongo</i>	f	13	3	75.58	82.33	-8.94
	m	8	3	72.82	81.00	-11.23
<i>Gorilla gorilla</i>	f	8	2	50.02	62.50	-24.95
	m	10	4	39.69	48.00	-20.94
<i>Pan</i>	f	16	13	56.98	75.38	-32.30
	m	13	18	54.77	70.06	-27.91
<i>Hylobates</i>	f	10	1	60.16	69.00	-14.69
	m	7	1	55.50	69.00	-24.32
<i>Symphalangus</i>	f	11	2	57.12	52.00	8.96
	m	10	2	56.45	67.50	-19.57
<i>Colobus</i>	f	3	1	34.16	30.00	12.18
	m	2	1	29.55	26.00	12.01
<i>Trachypithecus</i>	m	8	1	47.16	41.00	13.06
<i>Macaca</i>	f	11	16	47.19	25.83	45.27
	m	5	16	61.89	24.94	59.71
<i>Papio</i>	f	12	3	51.52	30.67	40.48
	m	5	5	37.60	18.40	51.06
<i>Ateles</i>	f	9	3	53.30	62.33	-16.95
	m	5	3	51.03	70.33	-37.83
<i>Cebus</i>	f	6	4	42.65	34.75	18.52
	m	3	2	41.18	49.00	-18.99
Knee position (mm)						
<i>Pongo</i>	f	10	2	293.87	315.00	-7.19
	m	5	2	332.15	327.50	1.40
<i>Gorilla</i>	f	8	2	324.02	332.50	-2.62
	m	10	4	353.31	357.50	-1.19
<i>Pan</i>	f	10	10	301.59	346.00	-14.73
	m	8	13	298.29	360.00	-20.69
<i>Symphalangus</i>	f	11	1	212.2	255.00	-20.17
	m	10	1	223.95	275.00	-22.80
<i>Colobus</i>	f	3	1	148.56	145.00	2.40
<i>Macaca</i>	f	6	8	113.93	106.56	6.47
	m	4	8	124.06	120.63	2.76
<i>Cebus</i>	f	6	4	107.06	116.25	-8.58
	m	3	2	112.37	135.00	-20.14

Percent difference was calculated here as $((in\ silico\ mean - in\ vivo\ mean) / in\ silico) * 100$.

Table 4.14 Tukey's HSD comparisons between data types (*in vivo* vs. *in silico*) for angle of abduction

	<i>in vivo</i> vs. <i>in silico</i> p-value
<i>Pongo</i>	0.74
<i>G. gorilla</i>	0.43
<i>Pan</i>	<0.01
<i>Hylobates</i>	0.21
<i>Symphalangus</i>	1.00
<i>Colobus</i>	1.00
<i>Macaca</i>	<0.01
<i>Papio</i>	<0.01
<i>Ateles</i>	<0.01
<i>Cebus</i>	1.00

Significance was assessed at $p \leq 0.05$.

Table 4.15 Tukey's HSD comparisons between data types (*in vivo* vs. *in silico*) for abducted knee position

	<i>in vivo</i> vs. <i>in silico</i> p-value
<i>P. pygmaeus</i>	0.99
<i>G. gorilla</i>	1.00
<i>P. troglodytes</i>	<0.01
<i>S. syndactylus</i>	0.10
<i>M. fascicularis</i>	1.00
<i>C. apella</i>	0.99

Significance was assessed at $p \leq 0.05$.

Figure 4.1 Microscribe landmarks are superimposed on a pelvis
PIIS (landmark 1) and the center of the acetabular fossa (landmark 4) are not visible due to the orientation of the pelvis.

Figure 4.2 Pelvis polygonal model alignment to landmark data is shown for *Papio cynocephalus* (OM7276) in the IMInspect module in PolyWorks

Points are created for the landmark coordinate data imported into IMInspect (a). Planes can then be established to the points (b). Corresponding points anchored to the pelvis are then aligned to the points for the ASIS, PIIS, center of the acetabular fossa, dorsal acetabular border, and ischial spine.

Figure 4.3 The fovea capitis is confined to the boundaries of the acetabular fossa
 An articulated model of *Pan troglodytes* (CMNH B1708 ♂), with transparent pelvis is shown (a). The acetabular fossa is outlined in green on the acetabulum (b) and superimposed over the corresponding femoral head (c).

Figure 4.4 The femoral diaphysis is oriented parallel to an orthogonal plane to the long axis of the ischium

Figure 4.5 Femoral head least squares sphere-fitting and centroid creation

The femoral head subchondral surface is selected, a least squares best-fit sphere is fit to the selected data points, and a sphere centroid is identified. *Symphalangus syndactylus* (ZSM 1905.60 ♀) is shown.

Figure 4.6 Femoral diaphysis least squares vector-fitting

The femoral diaphysis was selected beginning just inferior to the lesser trochanter and superior to the initial flaring for the femoral condyles. A least squares best-fit vector is then fit to the selected data points. The femur on the right has a section of the diaphysis removed to show the vector running inside the polygonal model. *Symphalangus syndactylus* (ZSM 1905.60 ♀) is shown.

Figure 4.7 Measures of abduction (degrees) and abducted knee position (mm) relative to the midline

(a) Angular abduction and (b) the span at the knee, a proxy for the hindlimb spatial envelope. The red dashed line indicates where the midline plane is when extended from its vertices. *Papio anubis* (NMNH 236976 ♀) shown.

Figure 4.8 In silico measures of abduction (degrees)

Suspensory taxa are indicated by the darker blue shaded boxplots and non-suspensory taxa are indicated by yellow boxplots. No shading indicates an unassigned locomotor category in fossils and certain extant taxa (*G. beringei*, *A. caraya*, *P. nemaeus*).

Suspensory and non-suspensory taxa are significantly different in abducted knee position (one-way ANOVA, $p < 0.01$), but there is substantial overlap between locomotor groups between 35-55° abduction.

Figure 4.9 In silico measures of abducted knee position (mm)

Suspensory taxa are indicated by the darker blue shaded boxplots and non-suspensory taxa are indicated by yellow boxplots. No shading indicates an unassigned locomotor category in fossils and certain extant taxa (*G. beringei*, *A. caraya*, *P. nemaeus*).

Although suspensory and non-suspensory taxa are significantly different in abducted knee position relative to the midline (one-way ANOVA, $p < 0.01$), there is some overlap between locomotor groups in between 175-225mm.

Figure 4.10 Visual comparison of *in silico* measures of abduction (degrees) and abducted knee position (mm) in a subset of female anthropoids
Specimen numbers are provided for the individuals figured. Different taxa are not shown to the same scale.

Figure 4.11 Visual comparison of *in silico* measures of abduction (degrees) and abducted knee position (mm) in female *Gorilla gorilla* and *Gorilla beringei*
Specimen numbers are provided for the individuals figured. Individuals are not shown to the same scale.

Figure 4.12 *In silico* measures of abduction (degrees) and abducted knee position (mm) on the femoral head sphere diameter using standard major axis regression

The relationship between abduction and the body size surrogate is not significant across anthropoids or within locomotor groups. The relationship between body size and abducted knee position is significant, with significant differences in slope ($p=0.025$) detected between locomotor groups. Regressions for suspensory (blue dashed line) and non-suspensory taxa (black dashed line) are indicated by dashed lines. *Gorilla beringei*, *Alouatta caraya*, and *Pygathrix nemaeus* were not included in the regression calculations but are also plotted. NS=non-significant.

Figure 4.13 Comparison of *in vivo* and *in silico* data points for angular abduction by locomotor group

Triangles represent *in silico* data, with circles positioned above indicating *in vivo* data points. Data have been color coded by data type and locomotor group to maximize visualization of the distribution. Data (both *in vivo* and *in silico*) for male *Trachypithecus* are shown in this figure but *Trachypithecus* was not included in the two-way ANOVA (Table 4.10) and descriptive statistics (Table 4.9) due to the small *in vivo* sample ($n=1$).

Figure 4.14 Comparison of *in vivo* and *in silico* data points for abducted knee position by locomotor group

Triangles represent *in silico* data, with circles positioned above indicating *in vivo* data points. Data have been color coded by data type and locomotor group to maximize visualization of the distribution. *In vivo* data for knee position were adjusted by dividing the gross span at the knee in half, which adjusts the values to be comparable to a midline plane.

Figure 4.15 Hypothetical examples of the hindlimb spatial envelope

The hindlimb spatial envelope is determined by, but not limited to, body size, hindlimb and pelvic morphology, as well as range of motion allowed at the hindlimb joints. Orangutans and gorillas have the same abducted knee position (distance from the midline), but the greater joint mobility in orangutans allows them to abduct their hindlimb laterally to the body rather than tucked under it, increasing the range of possible foot postures. Figure modified from Zihlman et al. (2011).

CHAPTER 5: RECONSTRUCTING HIP JOINT FUNCTION IN FOSSIL CATARRHINES

The goal of this chapter is to use the validated digital modeling approach developed in Chapter 4 to estimate hip abduction ability in fossil catarrhines. In doing so, this chapter will address the overarching goal of this dissertation, which is to test whether suspensory behaviors can be inferred in fossil nonhuman hominoids based on range of hip abduction modeled *in silico*. Taxa chosen for this analysis are fossil hominoids *Rudapithecus hungaricus* and *Proconsul nyanzae*, and fossil cercopithecoids *Paracolobus chemeroni*, *Paracolobus mutiwa*, and *Theropithecus oswaldi*.

The most critical taxon for this study is *Rudapithecus hungaricus*, which has been interpreted to be a highly suspensory Miocene hominoid. Because *Rudapithecus hungaricus* preserves a relatively complete femur (RUD 184) and pelvic innominate (undescribed) from the same individual, it provides an opportunity to test whether adaptations for suspensory behaviors can be inferred in fossil nonhuman hominoids based on range of hip abduction. If hip abduction in *Rudapithecus* is found to be exclusively within the range of extant suspensory species, this will provide corroborative evidence that at least one late Miocene crown hominoid used suspensory behaviors.

Although early Miocene hominoid *Proconsul nyanzae* (KNM-MW 13142) is one of the most well-studied fossil hominoids, hip morphology in *P. nyanzae* has been highly influential in the locomotor reconstruction for this taxon and all other early hominoids. *Proconsul nyanzae* displays many postcranial features consistent with arboreal quadrupedalism but has a hip joint that appears to confer high levels of mobility, leading to interpretations of clambering above-branch behaviors (see discussion and references

below). A re-examination of hip abduction ability in *P. nyanzae* will clarify whether the hindlimb postures in this species are consistent with its locomotor reconstruction or whether the abduction ability is consistent with generalized arboreal quadrupedalism.

In addition, abduction ability is estimated in three large fossil cercopithecoids. These fossil monkeys provide an opportunity to test whether cercopithecoids with a large body size also display more limited hip abduction abilities than suspensory taxa. In doing so, this will also allow us to test the published locomotor reconstructions for these fossil cercopithecoids. The locomotor reconstructions for these large fossil cercopithecoids typically emphasize a significant reliance on terrestrial behaviors, which contrasts with the locomotor reconstructions of *Rudapithecus hungaricus*, *Proconsul nyanzae*, and the majority of extant anthropoids.

Fossil taxa and hypothesized locomotor reconstructions

The locomotor reconstruction for late Miocene *Rudapithecus hungaricus* (10 Ma, Rudabánya, Hungary) involves a significant reliance on suspensory behaviors (Morbeck 1983; Begun 1992; 1993; Kivell and Begun 2009; Begun and Kordos 2011; Begun et al. 2012). Specifically, *Rudapithecus hungaricus* has been described as a “generalized suspensory arboreal quadruped” (Begun 1993, p. 373) based on forelimb morphology (Begun 1993; Kivell and Begun 2009; Begun and Kordos 2011; Begun et al. 2012). The distal humerus is described as promoting high elbow mobility (Morbeck 1983), and the scaphoid and capitate are qualitatively similar to *Pongo* and suspensory taxa (Kivell and Begun 2009). Manual proximal phalanges from Rudabánya also have features found in suspensory anthropoids, including a ventral median groove, well-developed flexor sheath ridges, highly curved shafts, and large round distal articular surfaces (Begun 1988; 1993). The manual proximal phalanges are described as most similar to

Symphalangus, although hylobatids tend to display higher curvature and more defined flexor ridges than is observed in *Rudapithecus* (Begun 1988). Little has been published about the Rudabánya pelvic innominate (Ward et al. 2008; Ward et al. 2010; Ward 2013) and femora (Begun and Kordos 2011; Begun et al. 2012), although they are described as having morphology similar to suspensory taxa (see also Chapter 2).

The only other Miocene ape with a relatively complete, undistorted pelvis and femur is *Proconsul nyanzae* (KNM-MW 13142) from Mfangano Island, Kenya. Early Miocene *Proconsul* (~18 Ma) has primitive torso morphology (Ward 1991; 1993; Ward et al. 1993) and lacked a tail (Ward et al. 1991; Nakatsukasa et al. 2004), but had long and powerful manual and pedal phalanges (Begun 1993; Begun et al. 1994) (see Chapter 2 for review). At odds with most aspects of the locomotor reconstruction is the hip joint, which has features thought to increase range of motion at the hip, including a shallow acetabulum, a wide acetabular notch, a spherical femoral head with even articular surface, and a high neck-shaft angle (Ward 1991; 1993; Ward et al. 1993). The combination of a cercopithecoid-like torso, mobile hip joint, and powerful grasping hands and feet has led to a reconstruction as a clambering quadruped using deliberate, cautious arboreal behaviors (Le Gros Clark and Leakey 1951; McHenry and Corruccini 1983; Walker and Pickford 1983; Beard et al. 1986; Ward 1993; Ward et al. 1993; Kelley 1997; Ward 2007). Early Miocene *Proconsul* and late Miocene *Rudapithecus* currently represent the extremes for primitive and derived locomotor reconstructions in Miocene hominoids.

Given that a relatively large femoral head might potentially increase the range of hip excursions (Ruff 1988), it is possible that *Proconsul* might have a high range of abduction *in silico* because it had a large femoral head. Because there are no extant

cercopithecoids that are as large as the great apes, incorporating large-bodied fossil cercopithecoids (27-58 kg, Table 5.1) controls for the possibility that abduction ability in extant non-suspensory species is related to their size rather than locomotor behaviors. Indeed, fossil *Theropithecus* and *Paracolobus* have been included as a comparative outgroup in past morphological analyses of *Proconsul* because *Proconsul nyanzae* (KNM-MW 13142) body mass estimates fall outside the range of extant monkeys (Ward 1991; 1993). Pelves and femora are preserved for large-bodied Plio-Pleistocene fossil cercopithecoid specimens of *Theropithecus oswaldi* (Olduvai-MCKII and KNM-ER 866), *Paracolobus chemeroni* (KNM-BC 3), and *Paracolobus mutiwa* (KNM-WT 16827). *Theropithecus oswaldi*, *Paracolobus chemeroni*, and *Paracolobus mutiwa* are all reconstructed as quadrupedal with little or no use of suspension, but perhaps using some arboreal behaviors (Table 5.1). Moreover, these large fossil cercopithecoids are hypothesized to use at least some terrestrial behaviors (see discussions below) since it can be difficult for large-bodied animals without suspensory adaptations to move in the canopy.

Theropithecus oswaldi is hypothesized to be a predominantly terrestrial cercopithecine associated with open habitats (Eck 1987; Krentz 1993; Elton 2002). This species has multiple features of the postcrania that indicate terrestrial quadrupedalism, including a dorsally-flexed olecranon process, projecting greater trochanter and tubercles of the humerus, a low neck-shaft angle of the femur, and a short femoral neck (Krentz 1993). Most of the forelimb and hindlimb anatomy is interpreted as aiding powerful protraction-retraction movements of the limbs, suggesting a highly terrestrial and stereotyped locomotor profile (Krentz 1993). *Theropithecus oswaldi* is known from sites throughout Africa and southern Europe, and is found with high frequency beginning

at the end of the Pliocene (Jolly 1972; Gibert et al. 1995; Elton 2002; Frost and Delson 2002; Rook et al. 2004). This species is the most widely-represented monkey in the late Pliocene-early Pleistocene fossil record and is usually considered the most terrestrial of the fossil cercopithecoids.

Paracolobus chemeroni is one of the better sampled colobines in East Africa but is primarily known from the KNM-BC 3 skeleton from Baringo, Kenya (Leakey 1969; Birchette 1982; Leakey 1982). *Paracolobus chemeroni* has been described as a “locomotory chimera” because it displays postcranial features common to both terrestrial and arboreal cercopithecines (Hlusko 2007, p. 73). The locomotor reconstruction for *Paracolobus chemeroni* includes both arboreal and terrestrial behaviors to accommodate the combination of terrestrially-adapted and arboreally-adapted morphologies (Birchette 1982; Leakey 1982; Ting 2001).

The closely related species *Paracolobus mutiwa*¹¹ is best known from the KNM-WT 16827 partial skeleton from Lomekwi, Kenya (Leakey 1982). *Paracolobus mutiwa* has been described as slightly more terrestrial in comparison to *P. chemeroni*, although not to the extreme observed in *Theropithecus oswaldi* (Harris et al. 1988; Ting 2001; Hlusko 2007). This derives from subtle postcranial differences between *P. chemeroni* and *P. mutiwa*, with *P. mutiwa* displaying slightly more cercopithecine-like features of the tarsus, pelvis, femur, glenoid fossa, and humerus (Harris et al. 1988; Ting 2001). Overall, the locomotor reconstruction for *P. mutiwa* is a mix of arboreal and terrestrial behaviors.

¹¹ Research in progress is examining the taxonomic status of *Paracolobus mutiwa* due to observed differences in craniodental morphologies with other *Paracolobus* fossils (Nina Jablonski, personal communication).

OBJECTIVES

The primary objective of this chapter is to estimate range of hip abduction for fossil hominoids *Rudapithecus hungaricus* and *Proconsul nyanzae*. These fossil apes are compared to extant anthropoids in order to test their published locomotor reconstructions. As previously discussed, *Rudapithecus hungaricus* is hypothesized to have been highly suspensory and so it is expected that this taxon would have had a range of abduction similar to extant suspensory taxa. *Proconsul nyanzae* is hypothesized to have been an ambling above branch quadruped that did not use forelimb-dominant behaviors (Le Gros Clark and Leakey 1951; McHenry and Corruccini 1983; Walker and Pickford 1983; Beard et al. 1986; Ward 1993; Ward et al. 1993; Kelley 1997; Ward 2007), and would therefore be expected to have had a more limited range of abduction similar to extant non-suspensory taxa. It is expected that *Rudapithecus hungaricus* will have a range of abduction that is greater than that estimated for *Proconsul nyanzae*.

A secondary objective of this chapter is to estimate range of hip abduction for several large-bodied fossil cercopithecoids. Earlier chapters in this dissertation indicated that abduction ability in suspensory taxa is not a consequence of body size. The extant non-suspensory sample¹² has a more limited range of body sizes than the suspensory taxa¹³, and so it is unknown whether hip abduction might actually vary in a wider range of body sizes in the non-suspensory group. Fossil hominoids *Rudapithecus hungaricus* and *Proconsul nyanzae* are compared to large-bodied fossil cercopithecoids (28-58 kg,

¹² The mean body masses in non-suspensory species range from a small of ~2 kg in female *Cebus* to a large of 21 kg in male *Papio anubis* (Smith and Jungers 1997). The size range of the non-suspensory species means is only ~19 kg.

¹³ The mean body masses in suspensory species range from a small of 5 kg in female *Hylobates lar* to a large of 170 kg in male *Gorilla gorilla* (Smith and Jungers 1997). The size range of the suspensory species means is ~165 kg.

see Table 1) as an additional test that abduction relates to locomotor behavior rather than body size in non-suspensory taxa. The fossil cercopithecoids examined are *Theropithecus oswaldi*, *Paracolobus mutiwa*, and *Paracolobus chemeroni*, which all have been reconstructed as non-suspensory taxa with varying amounts of terrestrial and arboreal behaviors. It is expected that large-bodied fossil cercopithecoids will have a low range of hip abduction due to their hypothesized non-suspensory behaviors, further demonstrating that body size is not a primary determinant of range of abduction (degrees) in non-suspensory taxa.

SAMPLE

The extant comparative sample is the laser scanned sample used for abduction simulations described in Chapter 4. Species, sexes, and sample sizes correspond to those in Table 4.1, following the locomotor classifications provided in Table 2.2.

A total of six fossil specimens are sampled (Table 5.1). The fossil sample includes *Proconsul nyanzae* (KNM-MW 13142), *Rudapithecus hungaricus* (unpublished pelvis and corresponding RUD 184 femur), *Theropithecus oswaldi* (Olduvai-MCKII and KNM-ER 866), *Paracolobus chemeroni* (KNM-BC 3), and *Paracolobus mutiwa* (KNM-WT 16827).

The *Rudapithecus hungaricus* pelvis and femur from Rudabánya, Hungary, are in the process of being formally described (Ward et al. 2008; Begun and Kordos 2011; Begun et al. 2012). The *Rudapithecus hungaricus* pelvis (undescribed, Figure 5.1) and femur (RUD 184, Figure 5.3) were found together during excavations in the summer of 2006 (Ward et al. 2008) and are associated with a female cranium (RUD200) (David Begun, personal communication). The original Rudabánya fossils are housed at the Geological Institute of Hungary (Budapest). Casts of the *Rudapithecus hungaricus*

(unpublished) materials were graciously loaned by David Begun (Department of Anthropology, University of Toronto) and scanned by the author using a NextEngine scanner.

The *Proconsul nyanzae* (KNM-MW 13142) femur and pelvis belong to a partial skeleton from Mfangano Island, Kenya. The femur and pelvis have both been extensively described (Ward et al. 1993) and are figured here (Figure 5.1-5.2). The *Proconsul nyanzae* (KNM-MW 13142) original specimens were scanned by J. Michael Plavcan at the National Museums of Kenya (Nairobi) using a Konica-Minolta Vivid 9i.

The fossil cercopithecoid sample includes *Theropithecus oswaldi* (Olduvai-MCKII and KNM-ER 866), *Paracolobus chemeroni* (KNM-BC 3), and *Paracolobus mutiwa* (KNM-WT 16827). The *T. oswaldi* (KNM-ER 866) and *P. chemeroni* (KNM-BC 3) original specimens were scanned using a Konica-Minolta Vivid 9i by J. Michael Plavcan at the National Museums of Kenya. *Theropithecus oswaldi* (Olduvai-MCKII) was scanned by the author using a NextEngine scanner from high quality casts owned by Carol Ward. All fossil laser scan data were imported into PolyWorks IMEdit software for polygonal model creation as described for the extant sample in Chapter 4.

The abduction simulations described in Chapter 4 use digital best-fit techniques and relatively complete femora and pelves. The majority of fossil primate pelves and femora are incomplete and often cracked, crushed, abraded, weathered, or suffer from plastic deformation. Some of the fossils included in this study had pitting or abrasions that could be easily removed from the polygonal models. Because best-fit operations are known to be sensitive to surface irregularities (MacLatchy 1995; Hammond et al. 2013b), it was decided that small spot-cleaning of surface topography in the fossils would be more accurate than keeping the irregular surfaces. For instance, *Proconsul*

nyanzae (KNM-MW 13142) has a pit on the articular surface of the femoral head probably resulting from carnivore toothmarks (Ward et al. 1993), but this small pit can be removed from the polygonal model and filled in using the automated hole-filling and repair features of the PolyWorks IMEdit software. All polygonal models from fossil scan data are figured (Figures 5.1-5.6).

METHODS

Maximum abduction was measured by (a) angular abduction of the femur relative to the midline plane and (b) by the physical distance between the knee and the midline plane. Angular abduction was measured in all six specimens. The abducted knee position could only be measured in *Proconsul nyanzae* (KNM-MW 13142). Although three specimens (KNM-MW 13142, Olduvai-MCKII, KNM-BC3) preserve the knee distally, only *Proconsul nyanzae* (KNM-MW 13142) could be measured relative to an original midline (discussed below).

Digital abduction methods differed from the procedures outlined in Chapter 4 in several ways to accommodate the use of fossils. First, repeated trials of measurements were undertaken on all fossils. This option was selected for the fossils because averaging values is known to reduce the influence of error that can result from a single measure (Lee 1990; Yezerinac et al. 1992).

Second, additional procedures for aligning incomplete fossil pelves (Olduvai-MCKII, KNM-ER 866, KNM-WT 16827, KNM-BC3, *Rudapithecus* unpublished) to the midsagittal plane were required because these fossils do not preserve the midline symphyseal and sacral morphology. These additional procedures are detailed below.

Third, the *Rudapithecus hungaricus* acetabulum has some deformation cranially, with the lunate surface being broken or partially eroded in some places cranially and dorsally. Rather than using the entire lunate surface for sphere-fitting as described for the extant sample in Chapter 4, only the most caudal region of the lunate surface of the *R. hungaricus* hipbone was used for sphere-fitting (see Figure 5.8). The region used for sphere-fitting in *R. hungaricus* (Figure 5.8) corresponds to regions 6,7, and a portion of region 5 described in Hammond et al. (2013). Given that Hammond et al.'s study found mean percent prediction error of around 2% (maximum 8%) when using at least 2 regions of the lunate surface for sphere-fitting, it is expected that the *R. hungaricus* sphere-fitting technique has a similarly low potential for error in sphere fitting.

Lastly, *Rudapithecus hungaricus*, *Proconsul nyanzae*, and *Paracolobus mutiwa* preserve a pelvis but contralateral femur, so the femur of each was mirrored to match the same side as the pelvis. There is no known reason why substituting a right femur for a left femur would result in error, other than the potential for small differences in articular surface distribution within an individual, and thus the effects of substitution are expected to be minimal.

Fossils preserving midline morphology (Proconsul)

Proconsul nyanzae (KNM-MW 13142) preserves enough sacral and pubic morphology for microscribe landmark data to be collected on the midline by articulating the sacrum with the hipbone. These landmark data were collected from cast and were provided by Carol Ward. The *Proconsul nyanzae* (KNM-MW 13142) pelvis was aligned to landmark data and the femora articulated following the methodology described in Chapter 4. The femur of *Proconsul nyanzae* (KNM-MW 13142) was re-articulated and measurements were collected 21 times. Averaging repeated trials of measurements

should reduce the potential for error in a single measure (Lee 1990; Yezerinac et al. 1992), and 21 trials was selected to match the repeated sampling of the other fossil specimens (described below).

Fossils without midline morphology (Rudapithecus, Theropithecus, Paracolobus)

No sacra are preserved for *Rudapithecus hungaricus* (unpublished), *Paracolobus mutiwa* (KNM-WT 16827) and *Theropithecus oswaldi* (Olduvai-MCKII, KNM-ER 866), and therefore midline and lumbosacral microscribe landmark data cannot be acquired from these specimens directly. In addition, although a sacrum is preserved for *Paracolobus chemeroni* (KNM-BC 3), it is preserved in articulation with the right os coxa and shows evidence of deformation when the left os coxa is re-articulated. As such, midline and lumbosacral data for *P. chemeroni* (KNM-BC 3) were not acquired directly from the specimen. The scanned hipbones for *R. hungaricus* (unpublished), *T. oswaldi* (Olduvai-MCKII, KNM-ER 866), *P. mutiwa* (KNM-WT 16827) and *P. chemeroni* (KNM-BC 3) were alternatively aligned relative to a midline plane using scaled coordinate data from multiple extant species to provide a range of likely estimates of pelvic orientations.

A range of pelvic orientations based on extant species was created for each incomplete fossil pelvis. This additional process was necessary to align the incomplete pelvises to a midline plane. Five random females were selected from the extant sample of *Pongo pygmaeus*, *Pan troglodytes*, *Symphalangus syndactylus*, *Hylobates lar*, *Papio cynocephalus*, *Nasalis larvatus*, and *Alouatta caraya* (Table 5.4). These taxa were selected because they sample suspensory and non-suspensory taxa, which are thought to have different pelvic morphologies related to their different locomotor behaviors (see Ward 1991; 1993). Taxa were also selected specifically to sample different body sizes since it is currently unknown how certain portions of the pelvis change in response to

size. The mean body weights from these species run from a low of 4.33 kg in female *Alouatta caraya* and a high of 45.8 kg in female *Pan troglodytes* (Smith and Jungers 1997). Only females were selected to eliminate error that might result from mixing male and female landmark data.

Species mean landmark configurations were generated for the sample of extant species in MorphoJ software (Klingenberg 2011). Configurations were generated using all 14 landmarks, and then again using the reduced sample of four landmarks (PIIS, dorsal acetabulum, center of acetabular fossa, and ischial spine). Two centroids were calculated from the mean configurations in order to calculate the scaling factor for the extant landmark data. The first centroid ("Centroid 1") consists of the landmarks that are present in the fossil pelvises (PIIS, dorsal acetabulum, center of acetabular fossa, and ischial spine) whereas the second centroid ("Centroid 2") consists of all 14 landmarks collected from the extant species. The species, specimen numbers, and mean landmark centroid sizes are provided in Table 5.4.

The linear relationship between the mean size of all landmark data (14 landmarks) and the reduced number of landmarks preserved in fossils (4 of 14 landmarks) was then calculated. Centroid2 was plotted as a function of Centroid1 for extant species (Figure 5.7). Both a standard major axis (SMA) and least square regression (OLS) approach were used to estimate the linear relationship between centroids. The correlation coefficient is high ($r^2=0.939$) and both models produce similar functions (SMA $y=3.755x-9.315$; OLS $y=3.638x-3.079$).

Centroids of the fossils were then calculated so that the extant mean landmark configurations could be scaled to the appropriate size for each fossil specimen. First, a centroid size was established for each fossil pelvis using three-dimensional landmark

coordinates from the posterior inferior iliac spine (PIIS), dorsal acetabulum, center of acetabular fossa, and ischial spine. Microscribe landmark coordinates were collected by the author on *Rudapithecus hungaricus* (unpublished), *Theropithecus oswaldi* (Olduvai-MCKII, KNM-ER 866), *Paracolobus mutiwa* (KNM-WT 16827), and *Paracolobus chemeroni* (KNM-BC 3) from high quality casts housed in the Ward Lab (University of Missouri). Microscribe landmark coordinates were collected 5 times for each fossil. The anterior superior iliac spine was excluded from the landmark coordinates in the fossils as most fossils have a broken or damaged anterior ilium. These landmark coordinates were then imported into MorphoJ, where the mean landmark configuration was created using a procrustes fit algorithm (Table 5.2), and a centroid (Centroid1) was calculated for each specimen from mean from the 5 landmarking trials (Table 5.3).

Centroid2 for the fossils was estimated using both the SMA and OLS equations (Table 5.3), with predictions from both equations being virtually the same. The Centroid2 size predicted from SMA for each fossil was then used to numerically scale up the mean landmark configurations for each extant species. Mean landmarks for each fossil were multiplied by the predicted Centroid2 size estimated from SMA. In fossil cercopithecoids, pelvis landmark data for extant species was usually scaled up, whereas *Rudapithecus hungaricus* required scaling the landmarks down. Each scaled species mean landmark configuration was imported into IMInspect, where the midline and lumbosacral planes were created from the landmark data, as in Chapter 4.

Differences in the degree of femoral angular abduction could certainly result from different extant pelvic orientations (e.g., *Pan* vs. *Papio* vs. *Ateles*). However, different measures of angular abduction could also result from subtle differences in manual alignments of the femur within the acetabulum in a single species (e.g., trial 1 vs. trial 2

vs. trial 3). In order to minimize this type of error, femora were abducted and bound to the pelvis before being aligned to different species mean landmark configurations. Specifically, each fossil femur was abducted within the acetabulum and then locked into a position of maximum abduction prior to any pelvic alignment procedures. This was repeated three times using duplicated femur models, providing three possible abducted femoral positions for each pelvis. By locking the abducted femora into place, this step ensured that femur position was held constant during all subsequent pelvic alignments so that measurements exclusively reflect the influence of pelvic alignment and not variability in femur positioning.

Fossil pelves were aligned to the midline planes and associated scaled extant landmarks, moving the three femora with them. The *Rudapithecus*, *Paracolobus*, and *Theropithecus* fossil pelves were then aligned to the PIIS, dorsal acetabulum, center of acetabular fossa, and ischial spine landmarks as described for the extant sample in Chapter 4. In total, *Rudapithecus hungaricus* (unpublished), *Theropithecus oswaldi* (Olduvai-MCKII, KNM-ER 866), *Paracolobus mutiwa* (KNM-WT 16827), and *Paracolobus chemeroni* (KNM-BC 3) fossils were each aligned to 7 species mean landmark configurations based on 3 trials of articulation. As a result, 21 configurations for femoral abduction were measured for each of these fossils. The mean value and range of the 21 configurations are reported for each fossil (Table 5.5). The fossil pelves aligned to scaled landmark data represent different orientations relative to the midline but not necessarily accurate distances from the midline, as pelvic breadth varies between taxa. As such, abducted knee position could not be measured in pelves aligned to scaled landmark data.

Quantitative Analyses

Means, standard deviations, and ranges of angular abduction were calculated for the 21 repeated alignments for each fossil (Table 5.5). The abducted knee position could only be measured in *Proconsul nyanzae* (KNM-MW 13142). The means, standard deviations, and ranges of the *Proconsul nyanzae* (KNM-MW 13142) abducted knee position in the repeated trials were calculated. Fossil means were plotted alongside boxplots of extant data for visualization (Figures 5.3 and 5.4). Linear discriminant function analyses were used to predict locomotor classification for each fossil based on mean angular abduction value (from Table 5.6). Quantitative analyses were performed in R (version 3.0.1, R Core Team 2012), with DFA posterior probabilities calculated using the MASS package (Venables and Ripley 2002).

RESULTS

Angular abduction (degrees)

Angular abduction was higher in *Rudapithecus hungaricus* (unpublished) than all other fossil catarrhines examined. The mean estimated maximum hip joint abduction for *Rudapithecus hungaricus* (unpublished) is 56° (range 47-61°; Table 5.5 and Figure 5.9) and a discriminant function analysis predicts *R. hungaricus* is suspensory (78% posterior probability, Table 5.6). This estimate of abduction for *R. hungaricus* is larger than all non-suspensory extant specimens except a single *Macaca nemestrina* male (MCZ 35670, abduction = 57°). *Rudapithecus hungaricus* has lower abduction than observed in *Pongo* and probably *Pan paniscus*, and is most similar to that observed in *Ateles* and hylobatids.

Proconsul nyanzae (KNM-MW 13142) would have been capable of less abduction than most suspensory taxa. The mean estimated maximum hip joint abduction for *P. nyanzae* (KNM-MW 13142) is 43° (range 35-46°; Table 5.5 and Figure 5.9), a degree of abduction that overlaps with both locomotor groups. A discriminant function analysis finds a high likelihood that *P. nyanzae* (KNM-MW 13142) is non-suspensory (73% posterior probability, Table 5.6). The degree of angular abduction is consistent with above-branch quadrupedal locomotor behaviors in *P. nyanzae* (KNM-MW 13142), although not necessarily reconstructions that include highly abducted hindlimb postures. The results for horizontal abduction in *Proconsul nyanzae* (KNM-MW 13142) are also consistent with previous work by MacLatchy and Bossert (1996), who estimated the range of abduction during extension in KNM-MW 13142 to be approximately 49°.

The mean estimated maximum hip joint abduction for *Paracolobus chemeroni* (KNM-BC 3) is 37° (range 31-43°; Table 5.5). This value overlaps with suspensory *Gorilla gorilla* but is most consistent with non-suspensory cercopithecoids such as extant *Theropithecus* (i.e., geladas), *Papio*, and *Cercopithecus* (Figure 5.9). The linear discriminant function analysis finds a high likelihood that *P. chemeroni* (KNM-BC 3) is non-suspensory (88% posterior probability, Table 5.6).

The mean estimated maximum hip joint abduction for *Paracolobus mutiwa* (KNM-WT 16827) is 42° (range 36-49°; Table 5.5). This value is similar to that observed in *P. chemeroni* (KNM-BC 3) and, accordingly, the interpretations are similar. Like *P. chemeroni* (KNM-BC 3), *P. mutiwa* (KNM-WT 16827) overlaps with suspensory *Gorilla gorilla* but is most consistent with non-suspensory cercopithecoids such as *Theropithecus*, *Papio*, and *Cercopithecus* (Figure 5.9). The linear discriminant function

analysis finds a high likelihood that *P. mutiwa* (KNM-WT 16827) is non-suspensory (84% posterior probability, Table 5.6).

The mean estimated maximum hip joint angular abduction for *Theropithecus oswaldi* (KNM-ER 866, Olduvai-MCKII) is 37° (range 31-43°; Table 5.5). Abduction in specimen KNM-ER 866 (mean 28°) is low even for the non-suspensory taxa. Although both specimens technically overlap with *Gorilla gorilla*, they are most similar to non-suspensory taxa (Figure 5.9). A linear discriminant function analysis predicts that *T. oswaldi* specimen KNM-ER 866 has a 97% posterior probability of being non-suspensory, with *T. oswaldi* specimen Olduvai-MCKII having a 76% posterior probability of being non-suspensory.

The large-bodied fossil cercopithecoids have a low range of hip abduction, confirming that body size is not driving range of abduction (degrees) in extant non-suspensory taxa. The fossil cercopithecoids display lower ranges of angular abduction compared to *Rudapithecus hungaricus* and, to a lesser extent, *Proconsul nyanzae*.

Abducted knee position (mm)

As previously noted, the abducted knee position can only be measured in fossil taxa that preserve midline morphology because fossil pelvises aligned to scaled landmark data do not necessarily accurate distances from the midline, as pelvic breadth varies between taxa. Accordingly, only values for *Proconsul nyanzae* (KNM-MW 13142) can be reported and compared to extant taxa. The mean abducted knee position for *Proconsul nyanzae* (KNM-MW 13142) is 260 mm, which is intermediate between extant hylobatids and great apes for abducted knee position (Figure 5.10). In fact, a linear discriminant function analysis finds a 91% posterior probability that *P. nyanzae* (KNM-MW 13142) is suspensory. These results, which align *P. nyanzae* (KNM-MW 13142)

with large-bodied (i.e., suspensory) extant species, should be interpreted in consideration with both angular abduction and KNM-MW 13142 body size estimates (see discussion below).

DISCUSSION

Hip abduction in Miocene hominoids

The results of this study suggest that *Rudapithecus hungaricus* was probably capable of hip postures with a high degree of abduction, and thus may have been adapted for suspensory forms of locomotion similar to the types of locomotion found in extant apes. The degree of abduction predicted for *R. hungaricus* (mean 56°) suggests that it would have achieved abducted hip positions most similar to *Ateles* and hylobatids, two smaller-bodied and highly suspensory extant taxa. Given that the *in silico* models of abduction conservatively estimate passive range of abduction in suspensory taxa, it is likely that *Rudapithecus hungaricus* was actually capable of a larger range of abduction when alive. This study corroborates previous interpretations primarily from phalangeal and carpal bones that *R. hungaricus* was a suspensory species (Begun 1992; 1993; Kivell and Begun 2009; Begun and Kordos 2011; Begun et al. 2012). Finding a range of abduction similar to extant suspensory taxa in *Rudapithecus hungaricus* demonstrates that inferences about suspensory locomotion can be made by modeling hindlimb joint function in extinct hominoids.

This study finds that hip joint abduction in *Proconsul nyanzae* (KNM-MW 13142) is not necessarily greater than non-suspensory cercopithecoids, which differs from most of the previous interpretations of the KNM-MW 13142 femoral morphology. Past work on *P. nyanzae* (KNM-MW 13142) has usually emphasized that the hip joint appears to have been more mobile than cercopithecoids based on an apparently high neck-shaft

angle and spherical femoral head with even femoral head articular surface distribution (Ward 1991; 1993; Ward et al. 1993). If *Proconsul nyanzae* (KNM-MW 13142) did not have hip abduction like extant apes despite similarities in aspects of femoral morphology, this suggests that many of the features often used to infer higher hip mobility are not necessarily reflecting increased ranges of motion. Given the substantial variation in Miocene hominoid femora (see Chapter 2), identifying which morphologies are the best predictors of hip mobility is one of the most important next steps for interpreting functional abilities in isolated fossil hominoid femora. As proposed in Chapter 3, future work should directly quantify the relationship between hip joint mobility and hip morphologies, and explore what aspects of hip morphology are and are not related primarily to ROM or other functional factors.

Although apparently not capable of more acrobatic hip postures, *Proconsul nyanzae* (KNM-MW 13142) would have been capable of spanning gaps in the canopy by virtue of being large. At such a large body size (~35 kg for KNM-MW 13142) (Ruff et al. 1989), it is likely that *P. nyanzae* was using slow, deliberate movements with powerful manual and pedal grips for stability during transfer between supports (Cartmill and Milton 1977; Begun et al. 1994; Kelley 1997; Rose 1997; Ward 2007), and was almost certainly not bounding and leaping the way smaller-bodied arboreal Old World monkeys do when crossing gaps. Based on abduction ability, this study is in agreement with the studies that propose that *P. nyanzae* was a cautious above-branch quadruped. However, *Proconsul nyanzae* is within the range of suspensory species for abducted knee position, a metric which is heavily influenced by body size (see Chapter 4). Although *P. nyanzae* would have been able to reach supports across canopy gaps because of its size, it did not have joint mobility indicative of an adaptation for moving acrobatically below-branch like extant apes. Accordingly, if smaller-bodied *Proconsul* species such as

Proconsul heseloni had similar abduction ability as *P. nyanzae*, these would have been limited to less discontinuous canopy (i.e., smaller gaps) or would have been forced to cross gaps differently than *P. nyanzae*.

The intermediate abduction ability but large span at the knee in *Proconsul nyanzae* (KNM-MW 13142) underscores the discussion offered in Chapter 4, which emphasized the need to look at abduction (degrees) and abducted knee position relative to the midline (mm) in combination with each other. It is likely that the female *Rudapithecus hungaricus* studied here, with a high range of angular abduction possible at the hip joint, would have had a larger span at the knee than non-suspensory monkeys of similar size. However, this female *Rudapithecus hungaricus* individual would have a smaller span at the knee compared to larger-bodied *Proconsul nyanzae*, extant great apes, and maybe even male *Rudapithecus hungaricus* given the high levels of postcranial sexual dimorphism in this species (e.g., Morbeck 1983; Bernor et al. 2004; Begun and Kordos 2011). Non-suspensory taxa have an isometric relationship between size and knee position and large non-suspensory taxa are predicted to have an abducted knee position equal to suspensory taxa (Chapter 4, and Figure 4.12), which have a negatively allometric relationship. It is therefore probable that the large-bodied fossil cercopithecoids would have had a span at the knee overlapping with suspensory taxa simply because the fossil cercopithecoids are so large, yet clearly some of these specimens would not have been capable of abducted hindlimb postures like those possible in suspensory species. Both abduction (degrees) and abducted knee position relative to the midline (mm) should be used to inform interpretations regarding positional capabilities, and it should not be forgotten that having a large hindlimb spatial envelope by virtue of being large is quite different from having a large envelope due to high levels of hip joint mobility.

Hip abduction in Plio-Pleistocene fossil cercopithecoids

The fossil cercopithecoids have a range of abduction most similar to non-suspensory taxa but still overlap with both locomotor groups. Range of abduction in *Theropithecus oswaldi* specimen KNM-ER 866 approaches the lowest range observed in extant terrestrial monkeys. *Theropithecus oswaldi* specimen Olduvai-MCKII, *Paracolobus chemeroni* (KNM-BC 3), and *Paracolobus mutiwa* (KNM-WT 16827) overlap with arboreal monkeys and even *Gorilla gorilla*. The discriminant function results indicate that these species would be most likely classified as non-suspensory, with a very low probability that they would classify with suspensory primates (12% probability in *P. chemeroni*, 16% in *P. mutiwa*, and 3-24% in *T. oswaldi* specimens).

There was a non-significant relationship between body size and hip abduction (degrees) reported in Chapter 4, but there was a small possibility that this result could have been affected by the size ranges available to be sampled within extant non-suspensory taxa. The fossil cercopithecoids are as large as great apes and corroborate that body size does not determine hip abduction (degrees) in large cercopithecoids. *Theropithecus oswaldi* is similar in size to *Pan* or *Pongo* yet has a limited range of abduction in comparison. *Paracolobus chemeroni* (KNM-BC 3), and *Paracolobus mutiwa* (KNM-WT 16827) are smaller than *T. oswaldi* but have a similar range of abduction as *T. oswaldi* specimen Olduvai-MCKII.

The fossil cercopithecoids display abduction that falls into in a zone of overlap between locomotor extant groups. Technically, all of the fossil cercopithecoids fall into the interquartile ranges of *Gorilla gorilla* for degrees of abduction, and all but KNM-ER 866 have ranges that overlap with the range for *Proconsul nyanzae* (KNM-MW 13142) (see Table 5.5). This does not necessarily indicate that the fossil taxa were using the

same locomotor behaviors as each other or even using the same behaviors as gorillas. One thing seems clear, however-- the range of hip abduction in the fossil cercopithecoids would not exclude suspensory behaviors but it would greatly reduce their arboreal versatility, particularly given their body size.

The estimates for hip abduction in these three large-bodied cercopithecoids seem in accord with other regions of the postcrania which suggest these species were adapted for terrestrial or semi-terrestrial behaviors. Rather than cross discontinuous gaps by suspension as in great apes, these large monkeys probably crossed gaps between trees by returning to the ground. This scenario is especially likely for KNM-ER 866, which displayed both limited abduction ability and large body size. Although *Proconsul nyanzae* (KNM-MW 13142) also was a large bodied species incapable of highly abducted hip postures, *Proconsul nyanzae* (KNM-MW 13142) had powerful manual and pedal grasping abilities which would have made above-branch transfer and bridging behaviors more stable at such a large body size.

Even though the abduction estimates for fossil cercopithecoids are low or only moderate at best, it is possible that the range of abduction estimated in the fossil cercopithecoids is actually too large. Abduction simulations in extant non-suspensory typically over-estimate the range of passive abduction measured *in vivo* (see Chapter 4), and so the fossil cercopithecoids simulations of abduction might be larger than they would have been in living animals. Additionally, *Theropithecus oswaldi* has a “reverse carrying angle of the femur” (Krentz 1993) which probably increased the angle formed between the femoral neck and the shaft in this species. Whether the abduction estimated for the fossil cercopithecoids is too large is unknown but it suggests that, if anything, the range of abduction in these species would have been even more restricted.

Evolutionary scenarios

Fossil hominoids seem to become specialized for either more arboreal or more terrestrial behaviors during their evolutionary history. A model of hominoid locomotor evolution proposed by Nakatsukasa and Kunimatsu (2009) proposed that the earliest apes relied on slow pronograde quadrupedalism and began incorporating vertical climbing and other antipronograde behaviors (e.g., orthograde clamber, transfer, and bridging), until eventually there was a significant reliance on suspension in late Miocene hominoids (Figure 5.11). The Nakatsukasa and Kunimatsu (2009) model is placed in the context of a global cooling event which begins in the middle Miocene, where multi-leveled canopy forests were replaced by more fragmented and single-canopied forests. In this scenario, arboreal hominoids would have either opted to become more terrestrial to cross gaps in the canopy (e.g., *Sivapithecus* and *Dryopithecus*) or they would have become specialized for suspensory behaviors to cross gaps in the canopy (e.g., *Rudapithecus*). Features of the forelimb and hindlimb that facilitate gap crossing and suspensory behaviors (e.g., antipronograde climbing, clambering, transfer, bridging, brachiation, etc.) would thus be selected for in the more arboreal middle and late Miocene apes. Moreover, it is proposed here that suspensory species routinely using the flexible, small-diameter supports found in the terminal branch environment would be particularly likely to show high joint mobility as compared to suspensory species using the center of the crown where supports are larger and more rigid.

Elongated limbs are hypothesized to facilitate climbing on large-diameter supports (Cartmill 1974; Fleagle et al. 1981b; Cartmill 1985; Isler and Thorpe 2003) and so the range of knee positions within suspensory anthropoids might very well reflect different substrate usage. It remains to be seen how the spatial envelope relates to use

of the environment, specifically how it might reflect preference for different forest canopy levels, types of arboreal supports, tree density, tree crown diameter, and/or continuity of the canopy (Figure 5.12). A horizontally continuous canopy is unlikely to necessitate antipronograde behaviors, where gaps can be crossed by simple reaching or short leaps, and high abduction ability and large spatial envelope could signify a shift towards more discontinuous canopy structure experienced by some Miocene hominoids.

Although locomotor behaviors and canopy usage are often discussed in extant species (e.g., Cannon and Leighton 1994), the environmental context of fossil taxa is usually poorly integrated into discussions of locomotor behavior. Future work should investigate the relationship between spatial envelope in extant species and the environmental composition (Figure 5.12), as it may give insight into the relationship between the changing climate in the middle and late Miocene and how that relates to the highly derived locomotor morphology in the surviving relict populations.

The findings regarding both the fossil cercopithecoids are important for scenarios regarding catarrhine evolution more broadly. Much work has favored a scenario where arboreal behaviors in cercopithecoids evolved in the Plio-Pleistocene because many fossil colobines and cercopithecines appear semi-terrestrial or even fully-terrestrial (Andrews 1982; Harrison 1989; Ciochon 1993; Benefit 1999; Leakey et al. 2003). However, it has been proposed that most fossil colobines were arboreal by the Pliocene (Hlusko 2006), with the more terrestrially-adapted fossil colobines potentially being secondarily derived for terrestrial behaviors. More recently, arboreal adaptations have been found in Miocene fossil colobines at Lemudong'o (6 Ma, Hlusko 2007) and Nakali (9.8 Ma, Nakatsukasa et al. 2010) in Kenya. It is hypothesized that monkeys and apes competed for resources during the course of their evolution, in part because this earlier timing for colobine diversification in the middle to late Miocene coincides with the decline

in Miocene hominoids in Africa (Nakatsukasa et al. 2010). Further research on both locomotor and dietary adaptations of both fossil hominoids and cercopithecoids should help identify how both groups might have directly competed during their evolutionary histories.

One of the biggest obstacles to developing and testing evolutionary scenarios about locomotor evolution is that we have yet to determine how different fossil taxa are related. Past workers attempting to resolve the Miocene phylogeny have found equally parsimonious tree topologies within a single analysis (Begun et al. 1997a; Rae 1999; Young and MacLachy 2004). In addition, the most informative taxa for the evolution of suspensory behaviors have undergone substantial generic revisions in the last decade (see discussion of *Hispanopithecus* and *Rudapithecus* in Chapter 2), and most of these taxa are not included or accurately represented in these past phylogenies. Although taxa like *Hispanopithecus* and *Rudapithecus* are almost certainly within crown hominoids, if not potentially pongines or hominines (see Chapter 2), how these taxa are related to each other and other Miocene hominoids is unclear. Several small-bodied catarrhines potentially have suspensory adaptations as well, and interpretations vary as to whether species such as *Dendropithecus* and *Limnopithecus* are hominoids (Andrews and Simons 1977; Harrison 2010). It could even be argued that we do not know which species are within the crown group because of uncertainties regarding the timing of hylobatid evolution (Raaum et al. 2005; Matsudaira and Ishida 2010; Chan et al. 2012). If hylobatids diverged greater than 18 Ma ago, it is possible that *Proconsul* could actually be an early hominid (i.e., stem great ape), which would require substantial re-interpretations of locomotor evolution in hominoids. Renewed investigations into the phylogenetic relationships between fossil catarrhines and extant hominoid taxa are needed.

Gaps in the hominoid fossil record also limit efforts to reconstruct how and when suspensory behaviors appear. The first suspensory behaviors in Miocene apes appear in the late Miocene in Europe but we still do not have conclusive evidence for how and when apes entered Europe, as well as which locomotor adaptations characterized the earliest apes out of Africa. The earliest hominoid taxon currently known in Europe, *Griphopithecus* (16.5 Ma per Heizmann and Begun 2001; Begun et al. 2003a; Begun et al. 2003b), has limited postcranial materials suggesting generalized quadrupedalism consistent with mixed semi-terrestrial and semi-arboreal behaviors (Ehrensberg 1938; Begun 2002; Ersoy et al. 2008; Alba et al. 2010b). This locomotor reconstruction for early European apes is not very different from the clambering quadrupedalism of early Miocene hominoids like *Proconsul*. Later *Pierolapithecus catalaunicus* (11.9 Ma) has morphology more advanced than *Proconsul*, having modifications to the lumbar vertebrae, ribs, and pelvis that suggest more anti-pronograde behaviors (Moyà-Solà et al. 2004; Begun and Ward 2005; Alba et al. 2010a; Susanna et al. 2010; Hammond et al. 2013a) but has phalangeal and carpal morphology that is inconsistent with suspension (Moyà-Solà et al. 2004; Almécija et al. 2007; Almécija et al. 2009; Alba et al. 2010a). The other middle Miocene fossils apes (e.g., *Equatorius*, *Sivapithecus* and *Dryopithecus*) appear terrestrial and were probably not suspensory. Identifying how and when great apes evolved suspensory locomotor behaviors will require the recovery of additional middle and late Miocene fossil hominoids. Filling in the gap in the European hominoid fossil record between more primitive hominoids (i.e., *Griphopithecus*) and highly specialized late Miocene hominoids (i.e., *Rudapithecus* and *Hispanopithecus*) is another critical step needed to testing evolutionary scenarios of locomotor evolution in hominoids.

CONCLUSIONS

The primary goal of this thesis is to determine whether adaptations for suspensory behaviors can be inferred in fossil hominoids based on hip joint abduction (see Chapter 1), and these results provide the first evidence of suspensory locomotor behaviors in a fossil ape based on hip joint mobility. *Rudapithecus hungaricus*, hypothesized to be highly suspensory based on forelimb elements, demonstrates that adaptations for suspensory behaviors can be inferred in fossil nonhuman hominoids from the hip joint based on range of abduction. The mean for angular abduction in *Rudapithecus hungaricus* was exclusively in the range of extant suspensory anthropoids and was found to have a high posterior probability of being suspensory in a discriminant function test. The abduction ability of *Rudapithecus hungaricus* was not within the range of highly acrobatic and quadrumanous *Pongo*, and instead fell closer to *Ateles* and hylobatids.

Proconsul nyanzae and the large fossil cercopithecoids *Theropithecus oswaldi*, *Paracolobus mutiwa*, and *Paracolobus chemeroni* have substantially lower hip abduction than *Rudapithecus hungaricus*. *Proconsul nyanzae* was most similar to non-suspensory taxa for angular abduction and was only within the range of a single suspensory species (*Gorilla gorilla*). *Proconsul nyanzae* had a high posterior probability of being non-suspensory. Despite a somewhat limited range of abduction, *Proconsul nyanzae* was able to position its knee relatively far from the midline by virtue of being large. *Proconsul nyanzae* would have reached across gaps in the canopy by virtue of being large but not necessarily through acrobatic hindlimb postures.

Rudapithecus hungaricus has an increased range of hip abduction relative to the other fossil species examined, potentially the result of directional selection for enhanced

hindlimb mobility associated with more antipronograde arboreal behaviors than in early hominoids like *Proconsul*. Additional work disentangling evolutionary relationships between taxa, as well as the recovery of additional middle and late Miocene hominoid postcranial materials, would help clarify the timing and trajectory of suspensory behaviors.

Table 5.1. Fossil sample used in simulations of abduction

Species	Accession number	Geological age (Ma)	Estimated body size (kg)	Locomotor reconstruction
<i>Rudapithecus hungaricus</i>	unpublished	~10.0 ¹	13.46 ²	orthograde with the frequent use of suspension ³
<i>Proconsul nyanzae</i>	KNM-MW 13142	17.8 ⁴	34.7 ⁵	arboreal quadruped that rarely would have used suspension ⁵
<i>Paracolobus chemeroni</i>	KNM-BC 3	2.0-5.4 ⁶	37.5 ⁷	arboreal quadruped that rarely would have used suspension ⁸
<i>Paracolobus mutiwa</i>	KNM-WT 16827	2.52-3.36 ⁹	27-52 ¹⁰	mixed terrestrial/arboreal quadruped that rarely would have used suspension ¹¹
<i>Theropithecus oswaldi</i>	KNM-ER 866	1.9-2.1 ¹²	49.0-57.9 ¹³	terrestrial quadruped that rarely would have used suspension ¹⁴
<i>Theropithecus oswaldi</i>	Olduvai-MCKII	0.4-1.85 ¹⁵	58.4 ¹⁶	terrestrial quadruped that rarely would have used suspension ¹⁴

Data from: 1 Begun et al. (2012); 2 Calculated from femoral head diameter (22.26mm) using the reduced major axis regression presented for non-hominins in Jungers (1991); 3 Begun et al. (2012), Kivell and Begun (2009); 4 Drake et al. (1988); 5 Ward (1993); 6 Birchette (1982), Leakey (1982); 7 Birchette (1982), and see also Ward (1991) and Delson et al. (2000), suggesting a range of 30-43 kg. for this specimen; 8 Birchette (1982), Ting (2001); 9 Harris et al. (1988); 10 Delson et al. (2000); 11 Leakey (1982); Ting (2001); 12 Feibel et al. (1989); 13 Ward (1991), DeSilva (2008); 14 Jolly (1972), Krentz (1993), Elton (2002); 15 Hay (1976) per Krentz (1993); 16 Ward (1991)

Table 5.2. Procrustes size-removed coordinates from 5 landmarking trials

Specimen	PIIS			dorsal acetabulum			acetabular fossa			ischial spine		
	x	y	z	x	y	z	x	y	z	x	y	z
<i>R. hungaricus</i> (unpublished)	-0.82	-0.02	-0.01	0.23	0.17	0.07	0.22	-0.15	0.11	0.37	0.01	-0.17
<i>P. chemeroni</i> (KNM-BC 3)	-0.72	-0.01	0.00	0.17	0.20	0.21	0.21	-0.19	0.22	0.34	0.00	-0.42
<i>P. mutiwa</i> (KNM-WT 16827)	-0.80	-0.02	-0.02	0.25	0.15	0.11	0.26	-0.16	0.17	0.28	0.03	-0.26
<i>T. oswaldi</i> (KNM-ER 866)	-0.79	-0.02	-0.07	0.32	0.24	0.18	0.33	-0.19	0.11	0.15	-0.03	-0.21
<i>T. oswaldi</i> (MCKII)	-0.79	-0.02	-0.03	0.25	0.21	0.13	0.27	-0.19	0.14	0.27	0.00	-0.25

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The mean landmark configurations for each taxon were transformed during the process of procrustes superimposition and represent “size-removed” variables. Values have been rounded to 2 decimal places. PIIS= posterior inferior iliac spine.

Table 5.3. Fossil Centroid1 and Centroid2 values from 5 landmarking trials

Specimen	Centroid1 size	Predicted Centroid2 size (SMA)	Predicted Centroid2 size (OLS)
<i>R. hungaricus</i> (unpublished)	56.56	203.07	202.69
<i>P. chemeroni</i> (KNM-BC 3)	56.90	204.35	203.92
<i>P. mutiwa</i> (KNM-WT 16827)	70.99	257.26	255.19
<i>T. oswaldi</i> (KNM-ER 866)	65.63	237.14	235.70
<i>T. oswaldi</i> (MCKII)	70.14	254.04	252.07

Centroid1 was calculated from 5 landmarking trials. Centroid2 was estimated by inputting Centroid1 into the standard major axis regression (SMA) equation for the extant species ($y=3.755x-9.315$). Centroid values have been rounded to 2 decimal places.

Table 5.4. Extant centroid sizes and specimens used to calculate centroids

Species	Centroid1 size	Centroid2 size	Specimens Used*
<i>Pan troglodytes</i>	79.88	284.11	CMNH 1748, 1766, 1843, 3539, 3551
<i>Pongo pygmaeus</i>	70.48	272.69	USNM 145308, 145309; CMNH 1443, 1055, 1167
<i>Symphalangus syndactylus</i>	51.23	175.16	USNM 141161, 141162, 271048; AMNH 106584; ZSM 1904.21
<i>Hylobates lar</i>	46.81	148.18	MCZ 41412, 41424, 41442, 41440, 41494
<i>Nasalis larvatus</i>	40.58	152.61	MCZ 37328, 37339, 37343, 41554, 41559
<i>Papio cynocephalus</i>	50.54	166.99	KNM 7264, 7262, 7254, 7276, 7277
<i>Alouatta caraya</i>	34.49	139.31	AMNH 211495, 211501, 211506, 211512, 215060

*All specimens are female. Values in table have been rounded to 2 decimal places.

Table 5.5. Hip function in fossils

Species	<u>Abduction (degrees)</u>			<u>Abducted knee position (mm)</u>		
	Mean	SD	Range	Mean	SD	Range
<i>R. hungaricus</i> (unpublished)	56°	4.6°	47-61°	NA	NA	NA
<i>P. nyanzae</i> (KNM-MW 13142)	43°	3.8°	35-48°	260	11.7	236-277
<i>P. chemeroni</i> (KNM-BC 3)	37°	3.5°	31-43°	NA	NA	NA
<i>P. mutiwa</i> (KNM-WT 16827)	39°	5.6°	28-49°	NA	NA	NA
<i>T. oswaldi</i> (KNM-ER 866)	28°	2.6°	23-32°	NA	NA	NA
<i>T. oswaldi</i> (Olduvai-MCKII)	42°	3.2°	36-49°	NA	NA	NA

Means, standard deviations, and ranges are reported for 21 trials. The hip joint in *Proconsul nyanzae* was aligned and abducted in 21 repeated trials. Other species were more fragmentary and aligned to alternate pelvic orientations from scaled landmark data in 7 species, with 3 articulations per species. Abducted knee position could not be measured in specimens aligned to scaled coordinate data and so only values for *P. nyanzae* are reported. NA=not applicable.

Table 5.6. Discriminant function percent classification of fossil means in extant suspensory and non-suspensory locomotor groups

	Suspensory taxa	Non-suspensory taxa
<u>Abduction (degrees)</u>		
<i>R. hungaricus</i> (unpublished)	78%	22%
<i>P. nyanzae</i> (KNM-MW 13142)	27%	73%
<i>P. chemeroni</i> (KNM-BC 3)	12%	88%
<i>P. mutiwa</i> (KNM-WT 16827)	16%	84%
<i>T. oswaldi</i> (KNM-ER 866)	3%	97%
<i>T. oswaldi</i> (Olduvai-MCKII)	24%	76%
<u>Abducted knee position (mm)</u>		
<i>P. nyanzae</i> (KNM-MW 13142)	91%	9%

Figure 5.1. Polygonal models of fossil hominoid and cercopithecoid pelves used in simulations.

Figure 5.2. Polygonal model of the femur of *Proconsul nyanzae* (KNM-MW 12142)
From left to right, posterior, anterior, medial, and superior views are shown. All views are not to the same scale.

Figure 5.3. Polygonal model of the femur of *Rudapithecus hungaricus* (RUD 184)
From left to right, posterior, anterior, medial, and superior views are shown. The RUD 184 femur is a right that has been digitally mirrored. All views are not to the same scale.

(a) KNM-ER 866

(b) Olduvai MCK-II

Figure 5.4. Polygonal models of the femur of *Theropithecus oswaldi* (KNM-ER 866, Olduvai MCK-II)

From left to right, posterior, anterior, medial, and superior views are shown. The KNM-ER femur is a right that has been digitally mirrored to maintain consistency in measurement technique. All views are not to the same scale.

Figure 5.5. Polygonal models of the femur of *Paracolobus chemeroni* (KNM-BC 3)
From left to right, posterior, anterior, medial, and superior views are shown. All views are not to the same scale.

Figure 5.6. Polygonal models of the femur of *Paracolobus mutiwa* (KNM-WT 16827)

From left to right, posterior, anterior, medial, and superior views are shown. All views are not to the same scale.

Figure 5.7. Centroid 2 (using 14 landmarks) as a linear function of Centroid 1 (using 4 landmarks)

Reduced major axis (solid line, $y = 3.755x - 9.315$) and least squares regressions (dotted line, $y = 3.638x - 3.079$) are shown. Regression correlation coefficients are $r^2 = 0.939$.

Figure 5.8. The region of the *Rudapithecus* pelvis used for acetabular sphere-fitting

The region used for sphere-fitting in *R. hungaricus*, indicated in orange, corresponds to regions 6,7, and a portion of region 5 described in Hammond et al. (2013).

Figure 5.9. Mean abduction in fossil specimens plotted alongside boxplots of extant taxa

Suspensory taxa are indicated by the darker blue shaded boxplots and non-suspensory taxa are indicated by yellow boxplots. No shading indicates an unassigned locomotor category in certain extant taxa (*G. beringei*, *A. caraya*, *P. nemaeus*).

Figure 5.10. Abducted knee position of fossil specimens plotted alongside boxplots of extant taxa

Suspensory taxa are indicated by the darker blue shaded boxplots and non-suspensory taxa are indicated by yellow boxplots. No shading indicates an unassigned locomotor category in certain extant taxa (*G. beringei*, *A. caraya*, *P. nemaeus*).

Figure 5.11 Hypothesized sequence of evolution of suspensory behaviors in Miocene hominoids

Above branch behaviors become increasingly antipronograde until eventually suspension becomes the primary mode of locomotion. Image modified from Nakatsukasa and Kunitatsu (2009), original illustrations from Fleagle (1976a).

CHAPTER 6: SUMMARY AND FUTURE DIRECTIONS

The overarching goal of this dissertation is to address whether we can infer adaptations for suspensory behaviors in Miocene apes by modeling hip joint abduction. The results of two large studies were used to infer locomotor behaviors in fossil hominoids.

The first study tested was whether living suspensory and non-suspensory anthropoids differ in hip mobility, particularly in terms of abduction ability. Hominoids and atelines are known to use suspensory behaviors and have long been assumed to possess greater hip joint mobility than non-suspensory monkeys, an assumption that has greatly influenced how extant and fossil primate hip joint morphology has been interpreted, despite the fact that there are no data available on these taxa. Passive hip joint mobility was measured on a large sample of anesthetized captive anthropoids, and data were analyzed for significant differences by locomotor group (Chapter 3). The data demonstrate that suspensory anthropoids are capable of significantly greater hip abduction and external rotation. Degree of flexion and internal rotation were not larger in the suspensory primates, indicating that suspension is not associated with a global increase in hip mobility. Future work should consider the role of external rotation in abduction ability, how the physical position of the distal limb segments are influenced by differences in range of motion proximally, as well as focus on soft tissue differences that enable or restrict abduction and external rotation at the anthropoid hip joint. Excluding some published data for *Macaca* and *Erythrocebus*, the data presented in Chapter 3 represent the first known hip joint range of motion data for the anthropoids, and will

prove to be important for other researchers who would like to compare other kinds of simulations to empirical data (e.g., Ogiwara et al. 2009; Seth et al. 2011; O'Neill et al. 2013).

The second study developed a modeling technique to estimate range of hip abduction and then tested the accuracy of the modeling approach against the live animal data. Previous work by MacLachy (MacLachy 1995; 1996; MacLachy and Bossert 1996; MacLachy 1998) attempted to reconstruct anthropoid hip abduction by digitally articulating individual femora and matching pelvis based on hypotheses about how synovial joints function under normal loading (Kapandji 1970; Jenkins 1972; Jenkins and Camazine 1977; Latimer et al. 1987; Ward 1991; 1993; Ward et al. 1993). Elaborating on MacLachy's approach, hip joint abduction and the abducted knee position were reconstructed in a large sample of anthropoids (Chapter 4). These data were then compared to the *in vivo* data for passive range of abduction (Chapter 3) to see how well the models approximate empirical data.

The relationship between raw *in vivo* and *in silico* data for angle of abduction was shown to be predictable for most taxa. Abduction modeled in suspensory taxa *in silico* was slightly less than the passive range measured *in vivo*, as would be expected. Abduction modeled in non-suspensory taxa was usually slightly larger than the passive range. These results indicated that the modeling technique consistently conservatively estimated abduction in suspensory taxa but over-estimated abduction in non-suspensory taxa. Accordingly, the analyses provided a hypothetical framework for interpreting *in silico* abduction estimates for fossil taxa that fall at either ends of the spectrum of range of abduction. Only non-suspensory taxa had a range of abduction below 35° and only suspensory taxa had values above 55°, but the *in silico* models showed substantial

overlap in degrees of abduction between suspensory and non-suspensory taxa between 35° and 55° degrees. Although overlap between suspensory and non-suspensory taxa is not ideal for locomotor reconstructions in fossils, it is also not surprising given that different locomotor behaviors overlap in hindlimb postures. Even the most terrestrial monkeys will climb into trees to access foods or escape from predators, requiring basic arboreal competency and hip mobility in non-suspensory taxa such as *Theropithecus* and *Papio*. Modeling hip joint abduction is most useful in fossils that are found in the extreme ranges for the two locomotor groups (suspensory >55°, non-suspensory <35°), where adaptations for highly terrestrial or highly suspensory behaviors can be detected.

The relationship between raw *in vivo* and *in silico* data was shown to be especially predictable for abducted knee position. With the exception of *Pan troglodytes*, all *in silico* estimates of abducted knee position closely matched the *in vivo* measures. This indicates that the modeling approach usually converges on the functional outcome of hip mobility—the abducted knee position—even when angular abduction is slightly over- or under-estimated by the models. However, unlike angular abduction, the abducted knee position has a significant relationship with body size. Although certain species will have similar abducted knee positions (e.g., macaque and siamang, or gorilla and orangutan), their angular abduction exposes significantly different levels of hip mobility and presumably different levels of hindlimb versatility. The abducted knee position is therefore most informative when considered along with angular abduction measures.

The validated model provides a way to make inferences about hip abduction ability and therefore potentially about locomotor behavior in Miocene apes. It was possible to model hip joint function in early hominoid *Proconsul nyanzae* (KNM-MW

13142) using the same basic parameters as the extant sample. A modified approach that accommodated the preserved morphology was used in *Rudapithecus hungaricus* (undescribed pelvis and RUD 184 femur). *Rudapithecus hungaricus* had simulated abduction that was exclusively in the range of extant suspensory anthropoids, falling close to *Ateles* and hylobatids, but not within the range of *Pongo*. The results of the hip joint abduction simulations for *Rudapithecus hungaricus* are the first evidence for suspensory behavior in a Miocene ape based on joint function. Abduction simulations in *Proconsul nyanzae* yielded abduction similar to non-suspensory taxa and only within the range of a single suspensory species (*Gorilla gorilla*). When *R. hungaricus* and *P. nyanzae* are compared to each other, it is clear that *R. hungaricus* has a substantially larger range of abduction possible at its hip joint. Despite a somewhat limited range of abduction, however, simulations show that *P. nyanzae* would have been able to position its knee relatively far from the midline by virtue of being large.

This study has highlighted many aspects of hip function that remain to be explored. One of the most important next steps for assessing hip mobility and locomotor adaptation in Miocene hominoids involves identifying which hip morphologies actually relate to hip abduction ability. Most Miocene femora and pelves are incomplete, broken, or abraded, which limits our ability to estimate abduction ability by modeling. However, there are many fossil femora preserved for Miocene apes, including proximal femora from *Hispanopithecus*, *Dryopithecus*, *Nacholapithecus*, *Morotopithecus*, *Equatorius*, and *Oreopithecus*. If we understand which femoral morphologies can be used to predict abduction ability, we might be able to estimate hindlimb postures in a much broader sample of Miocene hominoids. This would allow us to chart the evolution of hip joint mobility in other taxa in addition to *Proconsul* and *Rudapithecus*, and extend inferences

about locomotor evolution to different time periods and different taxa in hominoid evolution.

It would also be worthwhile to consider whether certain femoral and pelvic morphologies promote abduction ability *per se* or promote a combination of external rotation and abduction. The role of external (lateral) rotation in hominoid hip function has been vastly underappreciated. It is proposed here that external rotation facilitates the highly abducted hip postures observed *in vivo* in hominoids and atelines, and probably was influential in the *in silico* measures of abduction as well. Unfortunately, external rotation could not be accessed in the models in this study due to difficulties in quantifying external rotation *in silico*. Rose (1983) and MacLatchy and Bossert (1996) hypothesized that some features routinely found in Miocene hominoid femora, such as a high neck-shaft angle and even articular surface distribution, also relate to external rotation. The modeling approach used in this study can be further developed to test the importance of these morphologies, not only on abduction, but on external rotation as well.

Moving forward, it would be useful to examine how the configurations, composition and mechanical properties of soft tissues around the hip joint affect mobility. For instance, size of the acetabular labrum and strength of the hip joint ligaments should limit hip mobility but have not been thoroughly characterized in anthropoids. Preliminary studies note qualitative differences in the hip joint capsular structure between monkeys and great apes (Keith 1894; Sonntag 1923; 1924; Howell and Straus 1933), although it is unclear how these qualitative differences reflect mechanical differences of the capsular ligaments (see also Chapter 2). Gluteal and thigh muscular structure are also expected to be influential in both active and passive range of hip motion but this musculature is poorly characterized beyond general patterns of muscle origin and

insertion in anthropoids (Sonntag 1923; 1924; Howell and Straus 1933; Raven 1950; Stern 1971; Diogo 2012). A few studies have quantified hindlimb muscle architecture, moment arms, and cross-sectional areas from just a few anthropoid taxa (Alexander 1981; Rauwerdink 1991; Thorpe et al. 1999; Payne 2001; Payne et al. 2006a; b), finding that suspensory anthropoids usually have muscular structure which should promote the production of force over a wider range of positions (Thorpe et al. 1999; Payne 2001; Payne et al. 2006a; b). However, it is still unclear how hip musculature *itself* limits hip mobility, much less how differences in structure or attachments in suspensory and non-suspensory taxa influence range of motion. Just the presence of musculature around joints will significantly limit range of motion of the joint (see Hutson and Hutson 2012; Hutson and Hutson 2013). A slow and detailed dissection of the layers of soft tissues of the hip joint and thigh in anthropoids is necessary to understand how different soft tissues specifically limit hip mobility.

Additional work should focus on identifying how the femoral head is positioned in the acetabulum for different hip postures. Many of the principles guiding the joint modeling in this study are based on how hips are positioned during routine loading, and in particular, how the fovea capitis and ligamentum teres are positioned within the acetabulum (Kapandji 1970; Jenkins and Camazine 1977; Ward et al. 1993; Notzli et al. 2001). Functional morphologists hypothesize that routine loading of the ligamentum teres will result in joint pathologies and osteoarthritis, but no systematic experimental work has been done to test this. Clearly, the live animal work here (Chapter 3) suggests that chimpanzees are capable of passive abducted postures beyond what would be expected for their articular structure (Chapter 4), although it is unclear whether chimpanzees actively use these highly abducted hip postures. Additional study of how the femoral head is positioned in the acetabulum during loading is imperative and now

possible with imaging technologies such as XROMM (e.g., Brainerd et al. 2010). Studies of *in vivo* joint configuration have applications beyond functional morphology. One such application is by incorporating the data in this thesis into models of how specific variation in human hip joint morphology affects hip mobility, which can be integrated into clinically relevant models of hip dysplasia, femoroacetabular impingement and joint congruence, and osteoarthritis.

Few field studies directly consider the role of hip postures during different anthropoid locomotor behaviors (Grand 1968; Fleagle 1976a), and additional field work characterizing the use of abduction and lateral thigh rotation in apes and atelines would be particularly useful for primate functional morphologists. With the exception of a single study on captive hominoid climbing (Isler 2003; 2005), there are no published kinematic data on hip abduction or external rotation in primates. Kinematic and behavioral data that quantitatively characterize hip postures during different locomotor behaviors will be integral to understanding how different hip abilities would have been selected for during the course of hominoid evolution. The hindlimb spatial envelope should also be investigated by behavioral and experimental researchers in order to have a gauge for how different ranges of foot postures reflect different substrate usage, environmental contexts, and different locomotor behaviors.

Testing the hypothesized link between hip morphology and abduction in other comparative taxa would serve to strengthen the functional inferences made in this study. With some additional work, this validated technique of measuring hip abduction can be made applicable to the study of any mammal. Limb abduction and posture (i.e., “sprawling” vs. “erect” postures) are also critical to models of locomotor evolution in early mammals (Kielan-Jaworowska and Hurum 2006), birds and reptiles (Gatesy 1991; Gatesy and Biewener 1991; Blob 2001; Farke and Alicea 2009; Hutchinson and Allen

2009), and this project will serve as a comparative model for other researchers to approach joint function outside of anthropoid primates. Testing the relationship between hip morphology and abduction ability in a comparative sample outside of primates is necessary for testing the application of these findings to other taxa.

Determining how different Miocene taxa are related to each other and extant taxa is critical for testing virtually all hypotheses regarding ape and human evolution, including locomotor hypotheses (see Chapter 5). This work provides information about behavioral capacities of Miocene fossil apes, providing critical data for parsimony-based reconstructions of the primitive crown hominoid condition and hominin ancestors, information which is critical for evolutionary scenarios (Simons 1967; Tuttle 1975; Moyà-Solà and Köhler 1993; Gebo 1996; Richmond and Strait 2000; Richmond et al. 2001; Thorpe et al. 2007b; Lovejoy et al. 2009b; Almécija et al. 2013). The postcrania of *Ardipithecus ramidus* has been used to argue that *Pongo*, *Gorilla*, and *Pan* independently evolved below-branch suspensory adaptations from a generalized ancestor (Lovejoy 2009; Lovejoy et al. 2009a; Lovejoy et al. 2009b), and some experimental evidence also suggests certain great ape-like adaptations independently evolved (Schmitt 2003; Kivell and Schmitt 2009). However, this study adds support to existing evidence for suspensory specializations in multiple European fossil apes thought to be crown hominoids, all of which predate the appearance of *Ardipithecus* (Moyà-Solà and Köhler 1993; 1996; Begun et al. 1997b; Moyà-Solà et al. 2004; Almécija et al. 2007; Begun 2010; Almécija et al. 2011; Begun and Kordos 2011). If the last common ancestor between *Pan* and humans was a primitive ape, not specialized for great ape-like locomotion, this would require that many fossil hominoids are homoplastic (review in Wood and Harrison 2011). Regardless of whichever phylogeny is ultimately

supported, accurate reconstructions of hominoid locomotor evolution require further research into the behavioral capabilities and positional adaptations of fossil taxa.

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VITA

Ashley Hammond attended Florida Atlantic University for her Bachelors and Masters degrees in Anthropology, discovering a strong interest in morphology and gross anatomy along the way. She moved to the University of Missouri's Department of Pathology and Anatomical Sciences for doctoral work. Her time in graduate school has allowed her to work in North America, Europe and Africa with many remarkable people, and these experiences have come to define her and her early career.

APPENDIX A

PHYLOGENETIC TREE WITH BRANCH LENGTHS USED IN PHYLOGENETIC REGRESSIONS

Consensus tree branch lengths:

((((Papio_cynocephalus:12.852525,(Macaca_fascicularis:5.045978, Macaca_mulatta:5.045978):7.806547):8.557849,(Colobus_guereza:15.435157, Trachypithecus_francoisi:15.435159):5.975217):8.589626,((Hylobates_lar:6.598361, Symphalangus_syndactylus:6.598362):13.007584,((Gorilla_gorilla_gorilla:8.652233, Pan_troglodytes_troglodytes:8.652232):6.480222, Pongo_pygmaeus:15.132455):4.473491):10.394055):16.811821,(Ateles_fusciceps:21.3 21300, Cebus_apella:21.321301):25.490521)

The *in vivo* consensus tree used for phylogenetic regressions (Chapter 3).

The tree topology based on a downloaded consensus tree from the 10k Tree Project (Arnold et al. 2010). *Papio cynocephalus* and *Ateles geoffroyi* were used for *Papio hamadryas-anubis-cynocephalus* and *Ateles fusciceps-geoffroyi-robustus* hybrids.

APPENDIX B

OSTEOLOGICAL SPECIMENS INCLUDED IN THIS STUDY FROM CAPTIVE OR UNKNOWN ORIGINS

All individuals in this study are confirmed wild-shot specimens except those listed here.

Species	Museum	Number	Sex	Origin
<i>Ateles belzebuth</i>	AMNH	259	F	no data
<i>Ateles belzebuth</i>	AMNH	202194	F	zoo
<i>Ateles paniscus</i>	AMNH	35449	M	zoo
<i>Erythrocebus patas</i>	USNM	257013	F	zoo
<i>Erythrocebus patas</i>	USNM	238072	M	zoo
<i>Erythrocebus patas</i>	USNM	399317	M	zoo
<i>Gorilla gorilla</i>	CMNH	B1057	M	no data
<i>Gorilla gorilla</i>	CMNH	B1431	M	no data
<i>Nasalis larvatus</i>	USNM	399070	M	zoo
<i>Pan troglodytes</i>	CMNH	B2746	M	no data
<i>Pongo abelli</i>	USNM	22937	F	no data
<i>Pygathrix nemaeus</i>	USNM	536409	F	zoo
<i>Symphalangus syndactylus</i>	USNM	519573	F	no data
<i>Symphalangus syndactylus</i>	USNM	395514	M	no data
<i>Theropithecus gelada</i>	USNM	319992	F	zoo
<i>Theropithecus gelada</i>	USNM	240885	M	zoo
<i>Theropithecus gelada</i>	USNM	305107	M	zoo
<i>Theropithecus gelada</i>	UZIA	8555	F	zoo
<i>Theropithecus gelada</i>	UZIA	9300	F	zoo
<i>Theropithecus gelada</i>	UZIA	10351	F	zoo
<i>Theropithecus gelada</i>	UZIA	12108	F	zoo
<i>Theropithecus gelada</i>	ZMA	11341	M	died immediately after import to zoo

Museums are the United States National Museum (USNM), Cleveland Museum of Natural History (CMNH), American Museum of Natural History (AMNH), Naturalis Leiden (ZMA), and University of Zurich (UZIA).

APPENDIX C

INSTITUTIONAL ABBREVIATIONS

Institutional abbreviations for extant specimens:

AMNH, American Museum of Natural History, New York, NY, USA
CMNH, Cleveland Museum of Natural History, Cleveland, OH, USA
FMNH, Field Museum of Natural History, Chicago, IL, USA
KNM, National Museums of Kenya, Nairobi, Kenya
MCZ, Museum of Comparative Zoology at Harvard, Cambridge, MA, USA
MRAC, Royal Museum for Central Africa, Tervuren, Belgium
PCM, Powell Cotton Museum, Birchington, Kent, United Kingdom
USNM, United States National Museum, Washington DC, USA
UZIA, University of Zurich, Zurich, Switzerland
ZMA, Naturalis Leiden and Zoological Museum Amsterdam collections, Leiden, Netherlands
ZSM, Bavarian State Zoological Collections, Munich, Germany

Institutional abbreviations for fossil specimens:

BA, Naturhistorisches Basel, Basel, Switzerland
BMNH, British Museum of Natural History, London, United Kingdom
IGF, Museo di Storia Naturale at the Università degli Studi di Firenze, Florence, Italy
IPS, Institut Català de Paleontologia Miguel Crusafont, Sabadell, Spain
KNM, National Museums of Kenya, Nairobi, Kenya
MUZ-M, Makerere University Zoology Museum (MUZ-M), Kampala, Uganda
RUD, the materials from the site of Rudabánya housed at the Geological Institute of Hungary, Budapest, Hungary.
YPM, Yale Peabody Museum housed at Peabody Museum at Harvard University, Cambridge, MA, USA