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A Comparative Study of the Glenohumeral Joint in New World Monkeys

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Dr. Karen Weinstein, Advisor

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Abstract

The functional use of a primate's body greatly influences its skeletal morphology. Previous morphological studies include analyses of the glenohumeral joint as a reflection of the locomotion distinct to each Old World monkey. In addition, anthropologists examine the shoulder of hominoids to study the shift in locomotor behaviors towards bipedalism. The glenohumeral joint of hominoids, particularly those taking part in brachiation, is rounder and more globular in shape compared to other ancestral apes, indicative of a greater range in motion of the shoulder (Chan 2007a, 1; Green 2013, 253). However, little research examines the locomotion of New World monkeys, broadly described as arboreal quadrupedalism. In this study, I hypothesize that the morphology of the glenoid fossa and humeral head largely reflect the functional use of the shoulder. I examine the glenohumeral joint of 10 genera of Platyrrhini to assess whether *Ateles*, a brachiating New World monkey, displays the specific morphological features indicative of increased shoulder mobility. I also analyze the relative effects of phylogeny and body size on the variation in glenohumeral morphology. I calculate four indices, examining the breadth-length ratio of the humeral head and glenoid fossa, degree of curvature of the glenoid fossa and the location of the maximum glenoid breadth. The results of this study show that *Ateles* is distinct from other platyrrhine genera in having the roundest and widest humeral head and glenoid fossa. The unique morphology of the glenohumeral joint of *Ateles* compared to other New World monkeys suggests that there was a directional change related to an adaptation towards brachiation.

Introduction

The skeletal structure of all animals plays an important role in the protection of inner organs and the attachment of muscles. Different primates exhibit variation in their skeletal structure based on species, body size and use of habitat. In addition, the functional behavior of each mammal

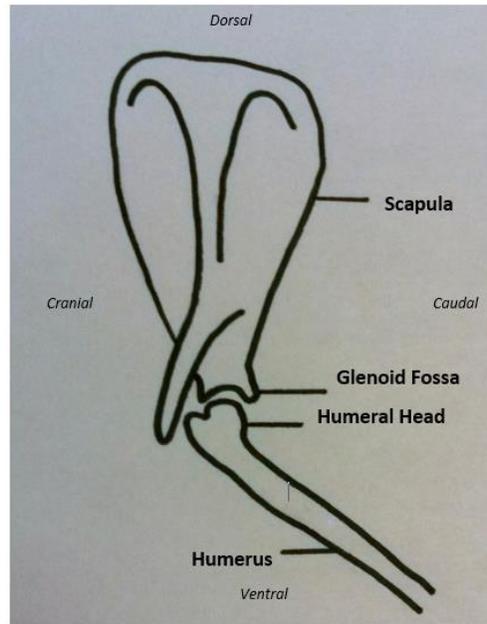
largely influences its skeleton. While researchers observe extant primates moving throughout their natural habitat, they study extinct primates based on their skeletal remains. Therefore, understanding the relationship between locomotion and skeletal morphology is vital to infer the locomotor behaviors used by extinct primates. Anthropologists often study the skeletal remains of hominoids and Old World monkeys in an effort to trace the evolutionary lineage towards modern humans (Strasser, 1992; Nakatsukasa, 1994; Larson, 1998). However, since New World monkeys, or Platyrrhini, take part in a large variety of locomotor behaviors, I am interested in the variation of skeletal morphology of the platyrrhines based on their vast locomotor repertoire.

The glenohumeral joint is one of the most important joints in the primate body, allowing for the movement and rotation of the forelimb in relation to the trunk (Veegar and van der Helm 2007, 2121). Broadly categorized as arboreal quadrupeds, New World monkeys use their shoulder in a different manner than bipedal modern humans (Chan 2007a, 2). I hypothesize that the platyrrhines will exhibit different morphology of the shoulder based on their distinct locomotor behaviors. To begin my study, I first provide an overview of the elements comprising the glenohumeral joint. I next introduce the phylogenetic divisions and associated traits of primates used when referring to New World monkeys. I define each specific locomotor behavior and group the platyrrhine genera based on their locomotion. Finally, I detail various methodologies utilized by previous researchers when analyzing skeletal remains. While I predominantly examine the influence of locomotion on glenohumeral morphology, I also analyze the effects of confounding variables of phylogeny and body size. Although this study examines extant New World monkeys, the assumed relationship between function and morphology is also useful when inferring locomotor behaviors of extinct primates.

Overview of Glenohumeral Joint

The glenohumeral joint is an important anatomical region of the primate body that exhibits a large degree of morphological variation. The shoulder joint is unique in that it allows primates the range of mobility to raise and rotate the forelimb while also maintaining stability to support the weight of the animal. The glenohumeral joint is skeletally comprised of the scapula and humerus, as seen in Figure 1. However, full shoulder mobility also involves the clavicle, thorax and a large range of muscles that aid in the movement of the forelimb (Chan 2007a, 2; Michilsens et al. 2009, 336). In addition to the position of the bones, the ligaments and the alignment of the articular surfaces greatly affect the stability of the shoulder. Veeger and van der Helm (2007, 2121) find that primates with a more stable joint have a higher amount of control of the rotator cuff muscles, which help to reduce the dislocation of the humeral head from the joint surface. Deeper curvature and rounder articular surfaces of the humeral head and glenoid fossa allow for increased control of the shoulder muscles. Primates exhibit advanced stability of the shoulder joint with this additional muscle control, indicative of higher functionality and mobility (Chan 2007a, 2; Green 2013, 253). While the functional use of the shoulder joint varies based on the locomotion of the primate, other additional factors affect the glenohumeral morphology, including phylogeny and body size.

Figure 1: Glenohumeral Joint of Quadrupedal Primates



Primate Phylogeny

The phylogenetic history of primates is important to functional studies. Primates who are more closely related share many traits, including diet, body size and habitat use. Two subdivided infraorders comprise the larger scientific order of Primates: Catarrhini, consisting of the hominoids (superfamily Hominoidea) and Old World monkeys (superfamily Cercopithecoidea), and Platyrrhini (Sussman 2003, 1). Evidence of Platyrrhini, or New World monkeys, dates back to 25 million years ago in Bolivia (Sussman 2003, 1). Three families comprise the infraorder of Platyrrhini: the Callitrichidae, Cebidae and Atelidae. Even further, the Cebidae and Atelidae families divide into four subfamilies: the Cebinae, Aotinae, Atelinae and Pitheciinae (Figure 2). These three larger families break into sixteen genera of New World monkeys, each sharing specific preference of habitat, diet and locomotion (Sussman 2003, 4).

Figure 2: Phylogenetic Tree of Platyrrhini (Sussman 2003)

Infraorder: Platyrrhini

Superfamily: Ceboidea

Family: Callitrichidae

Callimico (Goeldi's monkey)

Saguinus (Tamarin)

Leontopithecus (Lion tamarin)

Callithrix (Marmoset)

Cebuella (Pygmy marmoset)

Family: Cebidae

Subfamily: Cebinae

Cebus (Capuchin monkey)

Saimiri (Squirrel monkey)

Subfamily: Aotinae

Aotus (Owl monkey)

Callicebus (Titi monkey)

Family: Atelidae

Subfamily: Atelinae

Ateles (Spider monkey)

Lagothrix (Woolly monkey)

Brachyteles (Woolly spider monkey)

Alouatta (Howler monkey)

Subfamily: Pitheciinae

Pithecia (Saki)

Chiropotes (Bearded saki)

Cacajao (Uakari)

*Highlighted genera used in this study

New World Monkeys

The first family of New World monkeys is that of Callitrichidae. This family is unique, consisting of mostly small-bodied monkeys who have long tails, a dental formula of 2.1.3.2 and often give birth to twins (Table 1). One genus, *Callimico*, differs from the other four genera of Callitrichidae in that it has a third molar on each side, similar to all other New World monkeys (Sussman 2003, 8). The Callitrichidae retain many primitive features, such as claw-like nails, that allow for feeding on tree gum (Sussman 2003, 52).

Table 1: Characteristics of Callitrichidae (Sussman 2003)

Genus	Common Name	Number of Species	Location	Forest Use	Body Size (grams)	Diet	Group Composition
<i>Saguinus</i>	Tamarin	12	Central and South America	Undergrowth or mid-level canopy	300-600	Insects, fruit, floral nectar, tree sap	1-19 individuals
<i>Callithrix</i>	Marmosets	10	South America	Middle to upper canopy	300-500	Insects, fruit, floral nectar, tree sap	8-12 individuals
<i>Cebuella</i>	Pygmy marmoset	1	South America	Middle and lower canopy	100	Insects, fruit, floral nectar, tree sap	6-10 individuals
<i>Leontopithecus</i>	Lion tamarin	4	South America through Brazil	Middle and lower canopy	500-600	Plant gum, small vertebrates	5-8 individuals
<i>Callimico</i>	Goeldi's monkey	1	Upper Amazon through Brazil	Dense forest undergrowth	360	No tree sap	6-9 individuals

The second family of New World monkeys is the Cebidae. Two subfamilies create this larger family of Cebidae: the Cebinae and Aotinae (Tables 2, 3). The Cebidae have digits with flat nails instead of claws and a dental formula of 2.1.3.3. In contrast to the previous family of Callitrichidae, the Cebidae generally give birth to one young at a time.

Table 2: Characteristics of Cebinae (Sussman 2003)

Genus	Common Name	Number of Species	Location	Forest Use	Body Size (grams)	Diet	Group composition
<i>Cebus</i>	Capuchin monkey	4	South and Central America	Every type of forest	3,000-4,000	Insects, fruits, small vertebrates, invertebrates	6-35 individuals
<i>Saimiri</i>	Squirrel monkey	3	South and Central America	Lower canopy	700-900	Insects, fruits	20-75 individuals

Table 3: Characteristics of Aotinae (Sussman 2003)

Genus	Common Name	Number of Species	Location	Forest Use	Body Size (grams)	Diet	Group composition
<i>Aotus</i>	Owl monkey	1	Panama through Argentina	Dense undergrowth	800-1250	Fruits, flowers, leaves	2-4 individuals
<i>Callicebus</i>	Titi monkey	3	Amazon basin and Brazil	Dense low canopy	1,000	Fruits, insects, seeds	2-6 individuals

The subfamilies of the Atelinae and Pitheciinae belong to the final family of Platyrrhini: the Atelidae (Tables 4, 5). The dental formula for these two subfamilies is 2.1.3.3, similar to that of the Cebidae and one genus of Callitrichidae, *Callimico*. However, the physical characteristics of the Atelinae subfamily vary from other platyrrhines. The Atelinae all have prehensile tails with a region of naked skin toward the end of the tail, indicative of grasping on surfaces (Sussman 2003, 125; Table 4). Only *Ateles* and *Brachyteles* lack a thumb and use their hands to serve as hooks.

Table 4: Characteristics of Atelinae (Sussman 2003)

Genus	Common Name	Number of Species	Location	Forest Use	Body Size (grams)	Diet	Group Composition
<i>Ateles</i>	Spider monkey	4	Southern Mexico to Amazon	Middle and upper canopy	7,000-9,000	Fruits, buds, flowers, wood, leaves	2-8 individuals
<i>Lagothrix</i>	Woolly monkey	2	Upper Amazon to Andes	Middle and upper canopy	7,000-8,000	Fruits, seeds, leaves, flowers, wood	4-60 individuals
<i>Brachyteles</i>	Woolly spider monkey	1	Brazil	Upper canopy	8,000-10,000	Leaves, fruits, seeds, flowers	13-65 individuals
<i>Alouatta</i>	Howler monkey	7	Southern Mexico to Argentina	Middle and upper canopy	4,000-11,000	Leaves	8-21 individuals

Table 5: Characteristics of Pitheciinae (Sussman 2003)

Genus	Common Name	Number of Species	Location	Forest Use	Body Size (grams)	Diet	Group Composition
<i>Pithecia</i>	Saki monkey	5	Amazon	Lower canopy	1,800-2,400	Seeds, leaves, insects, fruit	2-9 individuals
<i>Chiropotes</i>	Bearded saki monkey	2	Amazon through Brazil	Upper canopy	2,500-3,200	Fruits, seeds, insects	8-30 individuals
<i>Cacajao</i>	Uakari	2	Amazon	Middle to upper canopy	2,500-3,500	Fruits, seeds, insects, flowers	15-100 individuals

Locomotor Definitions

The different forms and frequencies of locomotor behaviors greatly varies with primate phylogeny, specifically at the genus level. These positional behaviors allow the primate to access substantial food, potential mates and escape from predation. Even further, this variation in locomotion has lasting effects on skeletal morphology. In the realm of primatology, anthropologists apply numerous definitions to different forms of locomotion. Previous research focuses on defining the locomotor categories of Old World monkeys as they relate to the bipedalism used by modern humans (Hunt et al. 1996; Nakatsukasa, 1994; Larson, 1998). However, New World monkeys take part in a wide range of locomotor behaviors, more diverse than Old World monkeys (Sussman 2003, 4). While the specific definitions of each locomotion vary, the six most common locomotor behaviors exhibited in the Platyrrhini are quadrupedalism, climbing, leaping, bridging, brachiation and bipedalism (Hunt et al. 1996, 375; Arms et al. 2002, 247).

The category of quadrupedalism differs based on substrate, or the surfaces on which the primates move. Generally, there are two forms of quadrupedalism: arboreal quadrupedalism, which occurs when primates maneuver in trees, and terrestrial quadrupedalism, which takes place on the ground. Arms et al. (2002, 247) describe quadrupedalism as the symmetrical movement of

limbs during a period in which at least two or three limbs are in contact with a substrate. Hunt et al. (1996, 375) consider quadrupedalism to be any locomotion on top of a support with an angle of less than 45°. However, Hunt et al. (1996, 375) also divide quadrupedalism based on speed and gait. Arboreal quadrupedalism, as described by Rein et al. (2011, 564), refers to the movement along an arboreal surface, generally those of horizontal inclination. Within this thesis, the definition of arboreal quadrupedalism includes cyclical limb movement only along a horizontal substrate, with an angle less than 45°.

While Cant (1986, 3) describes arboreal quadrupedalism as encompassing the activity of climbing, many other anthropologists separate quadrupedalism from climbing (Hunt et al. 1996, 381). Two specific studies define climbing as symmetrical limb movements on vertical or inclined surfaces (Arms et al. 2002, 247; Hunt et al. 1996, 378). In addition, climbing involves no interruption of brachiation or leaping (Chan 2007a, 2). For the purposes of this study, I define climbing as repetitive limb movement only along a substrate at an angle greater than 45°.

Another common locomotor behavior is that of leaping. Within my study, I adopt the commonly accepted definition of leaping as the movement across a discontinuous surface in which the hind limbs push off one substrate and accelerate the animal into a moment of aerial flight and then land on a second substrate (Arms et al. 2002, 247; Wright 2007, 740). In contrast, bridging involves a primate grasping one substrate with its hind limbs or tails and a second surface with its forelimbs, closing the gap between two substrates (Hunt et al. 1996, 381). I distinguish bridging as a unique locomotor behavior in which the primate is always in contact with at least one surface, without a phase of aerial movement.

New World monkeys rarely exhibit brachiation. Various authors describe brachiation as the bimanual movement along an overhead substrate for a set distance with no interruption of other

positional behaviors and without the use of other limbs (Michilzens et al. 2009, 335; Bertram 2004, 103). In addition, brachiation involves the rotation of the trunk along with the bimanual movement of the forelimbs (Cant et al. 2003, 668). However, numerous subdivisions apply to the broader locomotor category of brachiation. Cant et al. (2003, 668) define full-stride brachiation as a complete cycle of grasping one hand over another while rotating the trunk. Half-stride brachiation involves the use of the initial trailing forelimb to swing forward while the second hand remains in place as the trunk rotates. Ricochet brachiation then includes an aerial phase of movement (Cant et al. 2003, 668). The traditional definition of brachiation does not include the support of hind limbs or tail. However, for the purposes of this study, I include all subdivisions of brachiation within the broader category of this locomotion (Bertram 2004, 103; Turnquist et al. 1999, 264).

Bipedalism is the final, and rarest, form of locomotion among platyrrhines. Bipedalism is the repetitive movement of the hind limbs in an alternating pattern on a substrate while in an upright position (Demes 2002, 147). Only the hind limbs provide the support for the animal with no assistance of any other parts of the body (Hunt et al. 1996, 377). While bipedalism is more common among human primates, New World monkeys occasionally adopt this locomotion. Although the primary types of locomotor behaviors of New World monkeys include quadrupedalism, climbing, leaping, brachiation and bipedalism, many platyrrhine genera frequently use more than one locomotor behavior.

Categorization of Primates based on Locomotion

When categorizing the overall locomotion of each primate, anthropologists generally use the most common behavior to define the broader locomotor category of that genus. For example, Strasser (1992, 204) categorizes all Old World monkeys as arboreal quadrupeds. Comprised of two subfamilies, the Cercopithecinae and Colobinae, the Old World monkeys occasionally take

part in other locomotor behaviors. Previous scholars found that the cercopithecines use additional climbing while the colobines exhibit leaping, climbing and even limited brachiation (Strasser 1992, 203; Nakatsukasa 1994, 133; Gebo and Chapman 2005, 73; Bryon and Covert 2004, 105). However, since Old World monkeys predominantly use arboreal quadrupedalism, they are categorized based on this one locomotion.

Multiple studies also focus on grouping hominoids and apes based on locomotion. Gebo (1996, 55) describes the genera of *Gorilla* and *Pan* as terrestrial quadrupeds, *Pongo* as climbers and brachiators and *Hylobates* as brachiators. Although Thorpe and Crompton (2006, 384) refer to the suspensory behavior of *Pongo*, the majority of the literature cites the hylobatids as the most advanced brachiators (Larson 1998, 91; Takahashi 1990, 78; Young 2003, 454). While *Hylobates* exhibit other locomotor behaviors in addition to brachiation, the overarching category assigned to each of these primates is the most frequent type of locomotion. Contrary to the focus of previous literature, my thesis examines the vast locomotive repertoire of the Platyrrhini.

The platyrrhines take part in a combination of distinct locomotor patterns. Previous literature separates the New World monkeys into the following three categories: springers, climbers and brachiators (Erikson 1963, 143). Another study by Michilsens et al. (2009, 340) divide the brachiating animals further into groups of specialized brachiators, modified brachiators, semi-brachiators. However, Michilsens et al. (2009, 340) also combine all primates who do not brachiate into one large category of non-brachiating monkeys. Chan (2007a, 3) and Rein et al. (2011, 566) provide a more accurate separation of primates, representing the large variety of locomotor behaviors across the Platyrrhini. These two studies include a division of arboreal quadrupeds, terrestrial quadrupeds, climbers and brachiators (Chan 2007a, 3; Rein et al. 2011, 566). For the purposes of this study, I group the platyrrhines based on their most frequent forms

of locomotion. I include categories based on the six most common locomotor behaviors of New World monkeys: quadrupedalism, climbing, leaping, bridging, brachiation and bipedalism (Table 6).

Table 6: Locomotion of New World Monkeys

Genus	Common Name	Locomotion	Source
<i>Saguinus</i>	Tamarin	Arboreal quadrupedalism (AQ), leaping	Porter 2004, 1; Garber and Leigh 2001, 21
<i>Callithrix</i>	Marmosets	AQ	Erikson 1963, 143
<i>Cebuella</i>	Pygmy marmosets	AQ	Erikson 1963, 143
<i>Leontopithecus</i>	Lion tamarin	AQ	Rosenberger and Stafford 1994, 1
<i>Callimico</i>	Goeldi's monkey	AQ, leaping	Garber and Leigh 2001, 21; Rosenberg and Stafford 1994, 1
<i>Cebus</i>	Capuchin monkey	AQ, climbing	Erikson 1963, 143, Wright 2007, 1
<i>Saimiri</i>	Squirrel monkey	AQ, climbing	Arms et al. 2002, 260; Erikson 1963, 143
<i>Aotus</i>	Owl monkey	AQ	Sussman 2003
<i>Callicebus</i>	Titi monkey	AQ	Sussman 2003
<i>Ateles</i>	Spider monkey	AQ, brachiation	Cant 2003, 685; Schmitt et al. 2005, 435; Turnquist et al. 1999, 264
<i>Lagothrix</i>	Woolly monkey	AQ, brachiation	Cant 2003, 685; Schmitt et al. 2005, 435; Turnquist et al. 1999, 264
<i>Brachyteles</i>	Woolly spider monkey	AQ, brachiation, climbing	Sussman 2003, 149
<i>Alouatta</i>	Howler monkey	Slow AQ	Schon and Schon 1987, 70; Cant 1986, 1
<i>Pithecia</i>	Saki monkey	AQ, climbing, leaping	Sussman 2003, 155
<i>Chiropotes</i>	Bearded saki monkey	AQ, leaping	Sussman 2003, 155
<i>Cacajao</i>	Uakari	AQ, leaping	Sussman 2003, 159

Functional Morphology of the Glenohumeral Joint

Many anthropologists argue that the skeletal morphology of a primate reflects its locomotor behavior (Chan 2007b, 23; Green 2013, 257; Michilsens et al. 2009, 342; Rein et al. 2011, 570). Studies examining the functional morphology of the glenohumeral joint attribute the variation in morphology to two theories: adaptation towards slow climbing or adaptation towards brachiation. The first hypothesis centers on the idea that slow vertical climbing demands a greater range of motion of the shoulder (Gebo 1996, 57). The brachiation theory then argues that the morphological

features of the shoulder adapted to provide a greater range in mobility for primates using brachiation (Chan 2007b, 20). A common assumption with both hypotheses is that the morphological features of a round humeral head and wide glenoid fossa represent a larger range of shoulder mobility (Chan 2007a, 1; Erikson 1963, 155; Green 2013, 253; Rein et al. 2011, 565).

Most scholars favor the brachiation theory, claiming that the primates who take part in brachiation have a larger range of motion in the shoulder joint than those who perform other locomotive behaviors (Chan 2007b, 23; Erikson 1963, 159; Green 2013, 257; Michilsons et al. 2009, 342; Rein et al. 2011, 570). The mobility necessary for a fluid form of brachiation requires movement of the forelimb in the craniodorsal direction, which is rare among many quadrupedal animals (Chan 2008, 269). Various morphological traits associated with this increased shoulder mobility also reflect the use of brachiation: a round humeral head with a large degree of torsion, a wide and cranially oriented glenoid fossa as well as a dorsal scapula with an obliquely oriented spine (Chan 2007a, 1; Erikson 1963, 155; Green 2013, 253; Rein et al. 2011, 565).

The first skeletal element of the glenohumeral joint is the humeral head, which varies in shape and degree of torsion. Humeral torsion refers to the orientation of the humeral head in relation to the shaft and lower end of the humerus (Rein et al. 2011, 572). Different orientations of the humeral head allow for improved connection of the humeral articular surface with the glenoid fossa, varying with the position of the forelimb in relation to the trunk of the primate. Erikson (1963, 156) and Rein et al. (2011, 570) found that the primates that take part in brachiation have a larger and more globular humeral head as well as a higher degree of torsion of the humeral neck toward the medial direction. Erikson (1963, 137) discovered that extreme brachiators had the most globular humeral head, semi-brachiators had a moderately round and wide humeral head while quadrupedal primates displayed the least globular humeral head. In addition, a small degree

of medial torsion was only evident in the extreme brachiators. Rein et al. (2011, 570) confirmed these results, finding quadrupedal primates with a posteriorly oriented humeral head and a low degree of torsion. Both Erikson (1963) and Rein et al. (2011) argue that medial torsion of the humeral head is an adaptation found in brachiating primates, which allows for a fuller rotation of the shoulder joint and, thus, increased mobility.

Articulating with the humeral head, the glenoid fossa should also be adapted towards brachiation. Green (2013) analyzed scapulae of modern humans and apes throughout stages of growth. He found that all species who took part in suspensory behaviors had cranially oriented glenoid fossae in comparison to species of other locomotor categories. Since the humeral head of brachiators is larger and rounder, the glenoid fossa should also be round in order to align properly and provide a smoother range of shoulder mobility. Veeger and van der Helm (2007, 2125) agree that proper alignment and congruence of the glenoid fossa and humeral head allow for an increase in shoulder stability and mobility.

The position of the scapula is an important factor for the orientation of the forelimb. Anthropologists argue that a dorsally situated scapula allows for a greater range of motion (Chan 2007b, 20). While Green (2013, 240) agrees that a dorsal scapula signifies greater mobility, he also states that the scapular spine is obliquely oriented in primates with greater mobility. Both Chan (2007b) and Green (2013) found distinct differences of the scapula related to the locomotor repertoire of the primate. Chan (2007b, 32) discovered that arboreal quadrupeds have a more dorsally located scapula than terrestrial quadrupeds, as defined by a longer clavicle and shorter scapula. Even further, brachiating hominoids and one platyrrhine, *Ateles*, displayed more dorsal scapulae than other species. While Green (2013, 255) did not find a significant correlation between the length of the scapular spine and form of locomotion, he did confirm that suspensory species

have an obliquely oriented spine, connected with higher shoulder mobility. In sum, previous research of the morphology of the humerus and scapula support the brachiation theory, finding that primates who take part in brachiation have a larger degree of shoulder mobility than those of other locomotor behaviors.

Interplay of Phylogeny, Locomotion and Glenohumeral Morphology

Researchers have found convergence in shoulder morphology based on similarities in locomotion across phylogenetic suborders (Larson 1998, Young 2003). One particular platyrrhine, *Ateles*, is occasionally included when examining Old World monkeys and hominoids due to its common use of brachiation. In a comparison of various morphological traits of hominoids, Old World and New World monkeys, Larson (1998, 94) found eleven shared traits between hominoids and *Ateles*, all located along the proximal region of the upper forelimb. Furthermore, anthropologists such as Cant (1986, 9) and Young (2003, 451) argue that the morphology of *Ateles* most resembles that of the *Hylobates*, with both frequently utilizing brachiation.

The prevalent use of brachiation distinguish *Hylobates* and *Ateles* as outliers from their broader phylogenetic suborders (Larson 1998, 94; Cant 1986, 9). *Hylobates* are the most advanced brachiators compared to all primates, using brachiation as up to 84% of its locomotion. In comparison, *Ateles* only uses brachiation between 20-45% of its overall locomotor repertoire (Young 2003, 454). One scholar, Cant (1986, 9), discovered that the skeletal morphology of *Ateles* was closely linked with that of the hominoid *Hylobates* more so than the morphology of other non-brachiating platyrrhines. However, the frequency of brachiation also influences the shoulder morphology. *Hylobates*, the most renowned brachiator, had a more globular humeral head and longer forelimb length in comparison to *Ateles*, the intermittent brachiator (Larson 1998, 91; Takahashi 1990, 81).

While functional studies most commonly include *Ateles* as a comparative New World monkey due to its use of brachiation, other Platyrrhini, such as *Brachyteles* and *Lagothrix*, exhibit lesser frequencies of brachiation (Gebo 1996, 68; Schmitt et al. 2005, 442). One study by Gebo (1996, 68) found the shoulder morphology of both *Ateles* and *Brachyteles* to reflect that skeletal traits displayed in hominoids. While I do not examine the skeletal morphology of hominoids in this thesis, the link between skeletal morphology and functional use across phylogenetic suborders is important. Particularly, the functional use of the shoulder has a more prominent effect on the morphology than the phylogenetic relationship (Cant 1986, 9; Larson 1998, 94; Takahashi 1990, 78; Young 2003, 451). In addition, the shoulder morphology reflects variation in the frequency of locomotor behavior. Although the platyrrhines do not take part in frequent brachiation such as the hylobatids, *Ateles* is the most common brachiator of the Platyrrhini. Therefore, *Ateles* should exhibit the roundest and widest humeral head and glenoid fossa.

Methodologies for Examining Skeletal Remains

There are a variety of methodologies used in the discipline of biological anthropology to examine the skeletal remains of primates, including shape ratios and geometric morphometrics. While the methodology of geometric morphometrics is recently growing in popularity among anthropologists, researchers traditionally use shape ratios (Mamatha 2011; Rajput et al. 2012). Geometric morphometrics is a complex method of analyzing skeletal remains that generally involve a digital scan of the bone. This technique examines the overall shape of particular elements by gathering two or three-dimensional coordinates in the form of landmarks, which serve as a reference points to attain lengths and angles. On the other hand, shape ratios include the measurement of specific skeletal features, scaled by a common denominator or second measurement across specimens (Terhune 2013, 1265). While both techniques have certain

advantages and disadvantages, Kagaya (2006) used a combination of the two techniques to examine the interplay between the glenoid fossa and the humeral head. In order to conceptualize the resulting variation in shapes, Kagaya (2006, 19) calculated nine indices, concluding with findings that were easy to understand and visualize. The two methodologies of shape ratios and geometric morphometrics pose various complications. Geometric morphometrics produce complex outputs that are hard to decipher while shape ratios cannot capture the high complexity of certain shape elements. For my study, I utilize the methodology of shape ratios to examine general trends in morphology while including indices of the breadth-length ratio of the humeral head and glenoid fossa, degree of glenoid curvature and location of the maximum glenoid breadth to compare the morphological data across specimens.

Hypothesis

This study examines the relationship between locomotion and the skeletal morphology of the humeral head and glenoid fossa. If the functional use of the shoulder and forelimb greatly influences the morphology of the glenohumeral joint, then the platyrrhines who take part in similar forms of locomotion will exhibit convergent morphology of the humeral head and glenoid fossa. In addition, previous research found that brachiation demands the largest amount of shoulder mobility, as seen in a rounder and wider humeral head and glenoid fossa (Chan 2007a, 1; Green 2013, 253). Therefore, I hypothesize that *Ateles*, the New World monkey known for brachiation, will display the roundest and widest humeral articular surfaces and glenoid fossae compared to other non-brachiating platyrrhines.

Confounding Variables

While my study focuses on the effects of locomotion on the skeletal morphology of the shoulder, I include two other variables in my analyses: phylogeny and body size. My central

hypothesis includes the analysis of phylogenetic genera, categorizing platyrrhine genera based on locomotor category. However, since primates of close phylogenetic relatedness share in many traits, such as diet and habitat preference, it is also important to examine the role of phylogeny on skeletal morphology at a broader level. Therefore, I examine the humeral head and glenoid fossa based on the phylogenetic level family and subfamily.

I also include the variable of body size in this study. The body weight of the primate can affect many different aspects of the animal's life including diet, habitat choice and locomotion. Body size also varies based on phylogenetic relationship. When examining specific skeletal elements across a wide sample of primates from different genera, anthropologists need to account for this fluctuation in size, which may skew comparative skeletal measurements (Arias-Martorell et al. 2015, 4; Green 2013, 224). With this caution in mind, I include body size as a potential factor when comparing the variation in morphology of the humeral head and glenoid fossa.

Materials and Methods

For this study, I examined 172 specimens from 10 different genera of New World monkeys. The analyzed genera include specimens of *Alouatta* (*A. caraya*, *A. fusca*, *A. palliata*, *A. seniculus*), *Aotus* (*A. trivirgatus*), *Ateles* (*A. fusciceps*, *A. geoffroyi*, *A. sp.*), *Callimico* (*C. goeldii*), *Callithrix* (*C. argentata*, *C. geoffroyi*, *C. jacchus*), *Cebus* (*C. albifrons*, *C. paella*, *C. capucinus*), *Lagothrix* (*L. lagothrica*), *Leontopithecus* (*L. rosalia*), *Saguinus* (*S. fuscicollis*, *S. labiatus*, *S. oedipus*) and *Saimiri* (*S. sciureus*). The number of specimens from each genus ranged from 8-26, with the specific primates sharing close phylogenetic relationships and residing in similar habitats, but taking part in different forms of locomotion (Table 7). I chose the selected species due to their state of preservation and availability from the mammals collection at the Smithsonian National Museum of Natural History in Washington, DC. I gathered measurements on only adult skeletons,

determined by the fusion of the coracoid process on the scapula and the epiphyses of the humeral head. I examined only right scapulae and humeri that were fully intact.

I used eleven distinct skeletal markers (Figure 3) to gather six linear measurements of the glenoid fossa and humeral head across all specimens (Table 8). Two measurements focused on the shape humeral head and four examined the glenoid fossa. I used sliding calipers to record all measurements to the precision of 0.01 millimeters. I then calculated the four indices based on the six linear measurements (Table 9). I hypothesized that *Ateles* would display morphological characteristics indicative of a larger range of shoulder motion due to their frequent use of brachiation. The skeletal traits associated with a higher degree of glenohumeral mobility include a large breadth-length ratio of the humeral head and glenoid fossa, a higher degree of glenoid curvature and a centrally located maximum glenoid breadth.

To analyze the data, I calculated the average of each index using Microsoft Excel 2016. I further examined the data using SPSS to compute analysis of variance (ANOVA) and Bonferroni post-hoc tests on the resulting indices based on the genus, family and subfamily, body mass and locomotor group (Table 7). The phylogenetic categorization follows Sussman (2003). However, the estimation of body mass posed a larger problem. Various anthropologists assume a correlation between a specific weight-bearing skeletal elements and the overall body mass (Auerbach and Ruff 2004, 331). A regression equation can then use one specific bone measurement to calculate and estimate body mass. Unfortunately, no regression equation currently exists that encompasses the range of body weights exhibited in all Platyrrhini. Since the Smithsonian collection did not list any known body weights for each specimen, I assigned body weights to the examined species based on those published in Sussman (2003). The final variable of locomotor categories followed those described in previous literary sources (Table 6).

When interpreting the ANOVA tests, a P value of less than 0.05 represents a statistically significant difference. The ANOVA F value then represents the amount of variance among groups, with a larger F value representing a higher degree of variance. Finally, the Bonferroni post-hoc test shows which groups are significantly different from others. In addition, I analyzed each index using an error bar graph in SPSS to visualize the variation between means. With each error bar graph, the center black dot represents the mean of that group. The whiskers then signify twice the standard error above and below the mean.

Table 7: Examined Specimens by Genus

Subfamily	Genus	Common Name	Number of Specimens	Body Size, grams (Sussman 2003)	Locomotor Categories
Aotinae	<i>Aotus</i>	Owl monkey	26	500-1,000	Arboreal quadrupedalism (AQ)
Atelinae	<i>Alouatta</i>	Howler monkey	25	7,000-9,000	AQ
Atelinae	<i>Ateles</i>	Spider monkey	11	7,000-9,000	AQ and brachiation
Atelinae	<i>Lagothrix</i>	Woolly monkey	8	7,000-9,000	AQ and brachiation
Callitrichidae	<i>Callimico</i>	Goeldi's monkey	8	Under 500	AQ
Callitrichidae	<i>Callithrix</i>	Marmoset	17	Under 500	AQ
Callitrichidae	<i>Leontopithecus</i>	Lion tamarin	15	500-1,000	AQ
Callitrichidae	<i>Saguinus</i>	Tamarin	26	Under 500	AQ and leaping
Cebinae	<i>Cebus</i>	Capuchin monkey	22	3,000-5,000	AQ and climbing
Cebinae	<i>Saimiri</i>	Squirrel monkey	14	500-1,000	AQ and climbing

Figure 3: Skeletal Markers on Humeral Head and Glenoid Fossa

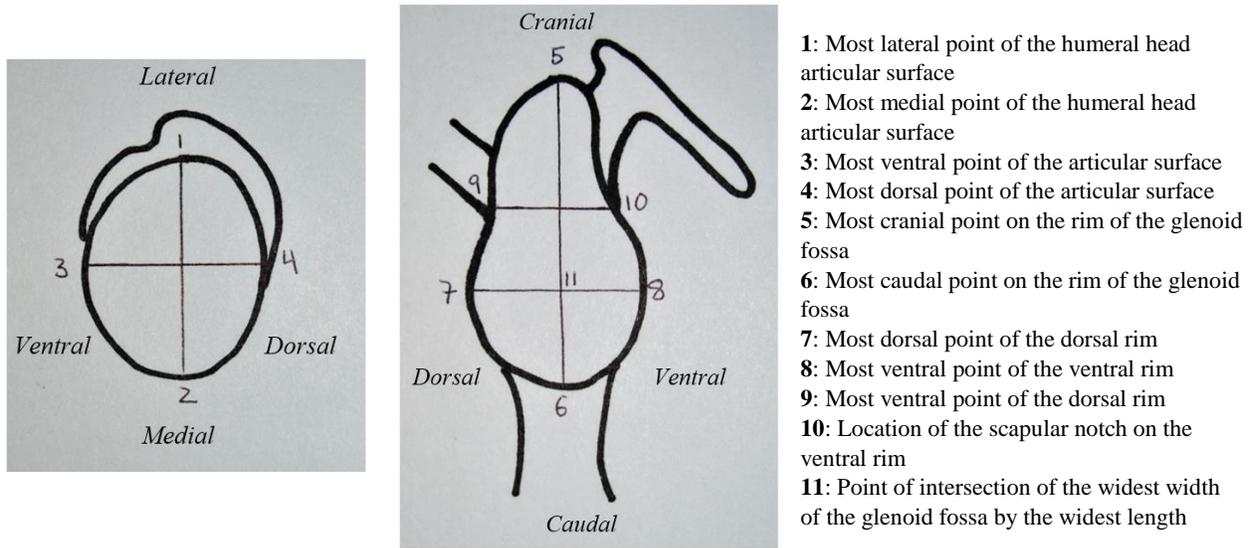


Table 8: Linear Measurements

Measurement Number	Morphological Significance	Skeletal Markers
M1	Length of the humeral head	1-2
M2	Width of the humeral head	3-4
M3	Length of the glenoid fossa	5-6
M4	Widest breadth of the glenoid fossa	7-8
M5	Minimum breadth of the glenoid fossa	9-10
M6	Length from the most cranial points to the cross-section of the maximum breadth of the glenoid fossa	5-11

Table 9: Computed Indices

Index Number	Morphological Significance	Calculation
I1*	Breadth-length ratio of humeral articular surface	M1/M2
I2*	Breadth-length ratio of glenoid fossa	M4/M3
I3	Degree of curvature of glenoid fossa	M5/M4
I4*	Location of maximum breadth of glenoid fossa	M6/M3

*Indices calculated according to the methodology utilized by Kagaya 2007

Results

Phylogenetic Genera

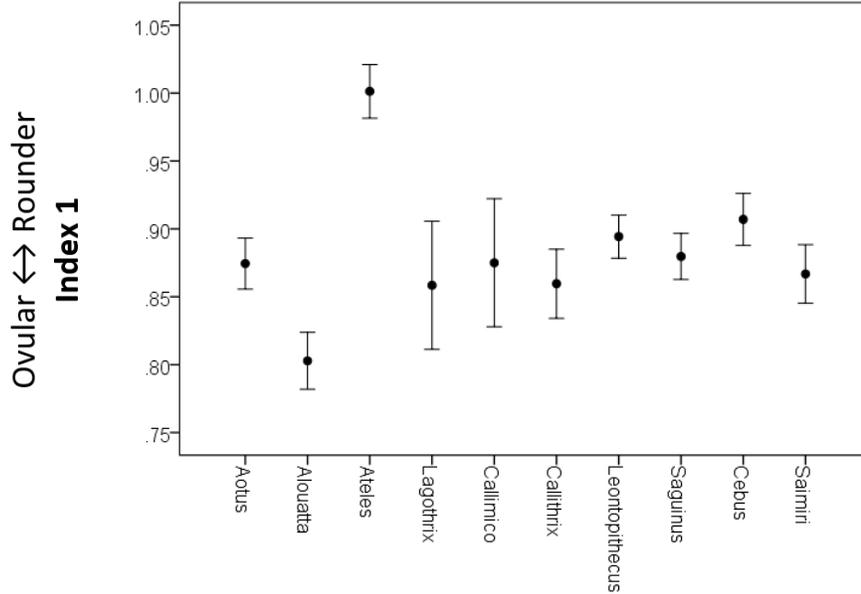
Index 1: Breadth-Length Ratio of the Humeral Articular Surface

This study finds that *Alouatta* has the lowest average first index while *Ateles* has the highest average index (Table 10). A lower mean index represents a more ovular articular surface of the humeral head, as seen in *Alouatta*. A higher index signifies a rounder humeral articular surface, with 1 being the most round. The findings of the ANOVA show that the results of the first index are significantly different between each genus (Table 10). While the Bonferroni post-hoc test shows that each genus is unique, the humeral head distinguishes only *Ateles* from all other examined monkeys (Table 10, Figure 4).

Table 10: Statistics for Index 1 based on Genera

Genus	Locomotion	Average Index 1	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
<i>Alouatta</i>	Arboreal quadrupedalism (AQ)	0.8	Ovular humeral articular surface  Rounder humeral articular surface	16.87	>0.001	All genera except <i>Lagothrix</i>
<i>Lagothrix</i>	AQ and brachiation	0.86				<i>Ateles</i>
<i>Callithrix</i>	AQ	0.86				<i>Alouatta, Ateles</i>
<i>Aotus</i>	AQ	0.87				<i>Alouatta, Ateles</i>
<i>Saimiri</i>	AQ and climbing	0.87				<i>Alouatta, Ateles</i>
<i>Callimico</i>	AQ and leaping	0.88				<i>Alouatta, Ateles</i>
<i>Saguinus</i>	AQ and leaping	0.88				<i>Alouatta, Ateles</i>
<i>Leontopithecus</i>	AQ	0.89				<i>Alouatta, Ateles</i>
<i>Cebus</i>	AQ and climbing	0.91				<i>Alouatta, Ateles</i>
<i>Ateles</i>	AQ and brachiation	1				All genera

Figure 4: Error Bar Graph of Index 1 based on Genera



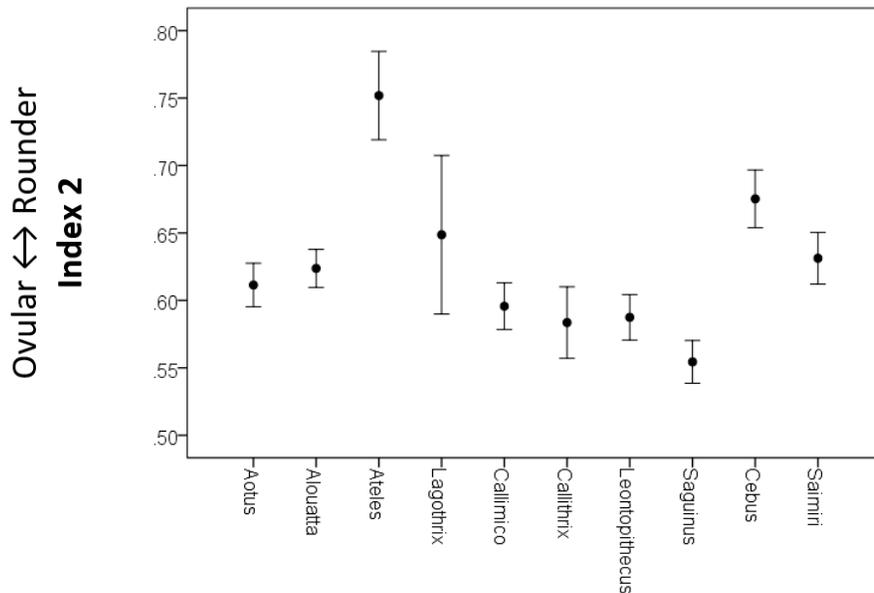
Index 2: Breadth-Length Ratio of the Glenoid Fossa

The lowest average of the second index belongs to *Saguinus* while the largest average is that of *Ateles* (Table 11). In a similar pattern to the findings of the first index, the smaller second index represents an ovular glenoid fossa, most notably that of *Saguinus*. The larger mean index signifies a rounder glenoid fossa, attributed to *Ateles*. The ANOVA test found that results of the second index vary significantly based on genus (Table 11). The Bonferroni post-hoc test and the error bar graphs also show that *Ateles* is the only genus significantly different between all other genera of monkeys in regards to the breadth-length ratio of the glenoid fossa (Table 11, Figure 5).

Table 11: Statistics for Index 2 based on Genera

Genus	Locomotion	Average Index 2	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
<i>Saguinus</i>	AQ and leaping	0.55	Ovular glenoid fossa ⇕ Round glenoid fossa	23.32	>0.001	All genera except <i>Callithrix</i> , <i>Callimico</i> , <i>Leontopithecus</i>
<i>Callithrix</i>	AQ	0.58				<i>Ateles</i> , <i>Cebus</i> , <i>Lagothrix</i>
<i>Leontopithecus</i>	AQ	0.59				<i>Ateles</i> , <i>Cebus</i>
<i>Callimico</i>	AQ and leaping	0.6				<i>Ateles</i> , <i>Cebus</i>
<i>Aotus</i>	AQ	0.61				<i>Ateles</i> , <i>Cebus</i> , <i>Saguinus</i>
<i>Alouatta</i>	AQ	0.62				<i>Ateles</i> , <i>Cebus</i> , <i>Saguinus</i>
<i>Saimiri</i>	AQ and climbing	0.63				<i>Ateles</i> , <i>Saguinus</i>
<i>Lagothrix</i>	AQ and brachiation	0.65				<i>Ateles</i> , <i>Callithrix</i> , <i>Saguinus</i>
<i>Cebus</i>	AQ and climbing	0.68				All genera except <i>Lagothrix</i> , <i>Saimiri</i>
<i>Ateles</i>	AQ and brachiation	0.75				All genera

Figure 5: Error Bar Graph of Index 2 based on Genera



Index 3: Degree of Curvature of the Glenoid Fossa

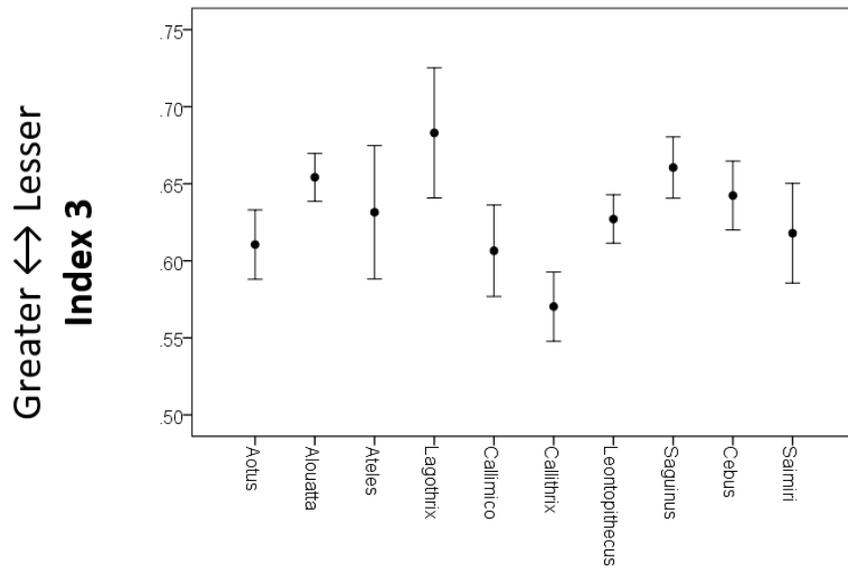
The degree of glenoid curvature, or the difference between the minimum and maximum breadth, show the smallest range of averages, spanning from 0.57-0.68. *Callithrix* has the smallest average index while *Lagothrix* shows the largest mean index. The greatest degree of curvature of

the glenoid fossa, as seen in *Callithrix*, indicates the largest variation between the maximum breadth and minimum breadth. The larger third index, present in *Lagothrix*, signifies the least amount of curvature of the glenoid fossa. The curvature of the glenoid fossa of *Ateles* falls within the mid-range of the average third index (Table 12). The results of the ANOVA test show that the findings of the third index do vary significantly between genera (Table 12). However, the Bonferroni post-hoc test finds that most genera have few significantly different degrees of curvature compared to other monkeys included in this study. Notably, no platyrrhine is significantly different compared to all other genera (Table 12, Figure 6).

Table 12: Statistics for Index 3 based on Genera

Genus	Locomotion	Average Index 3	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
<i>Callithrix</i>	AQ	0.57	Greatest degree of curvature  Least degree of curvature	6.01	>0.001	<i>Alouatta, Cebus, Lagothrix, Saguinus</i>
<i>Aotus</i>	AQ	0.61				<i>Lagothrix, Saguinus</i>
<i>Callimico</i>	AQ and leaping	0.61				None
<i>Saimiri</i>	AQ and climbing	0.62				None
<i>Ateles</i>	AQ and brachiation	0.63				None
<i>Leontopithecus</i>	AQ	0.63				None
<i>Cebus</i>	AQ and climbing	0.64				<i>Callithrix</i>
<i>Alouatta</i>	AQ	0.65				<i>Callithrix</i>
<i>Saguinus</i>	AQ and leaping	0.66				<i>Aotus, Callithrix</i>
<i>Lagothrix</i>	AQ and brachiation	0.68				<i>Aotus, Callithrix</i>

Figure 6: Error Bar Graph of Index 3 based on Genera



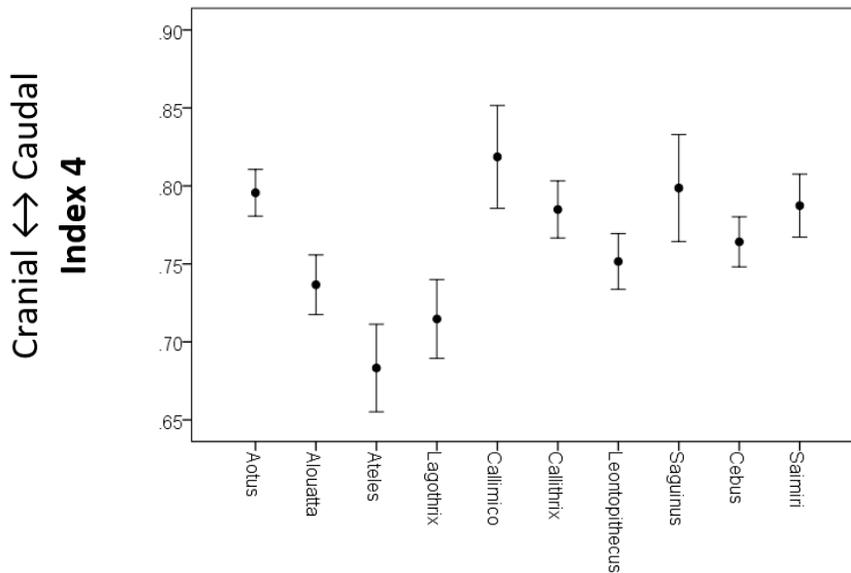
Index 4: Location of the Maximum Breadth of the Glenoid Fossa

The ANOVA test shows that the location of the maximum breadth of the glenoid fossa is significantly different between each species (Table 13). *Ateles* has the smallest average fourth index, representing a more cranially located maximum breadth. An index of 0.5 represents a centrally located maximum glenoid breadth. The largest average fourth index, found in *Callimico*, signifies a caudally located maximum breadth of the glenoid fossa (Table 13). The Bonferroni post-hoc test confirms that the fourth index of all genera are uniquely different to at least one other genus. However, no one platyrrhine is significantly different compared to all other genera (Table 13, Figure 7).

Table 13: Statistics for Index 4 based on Genera

Genus	Locomotion	Average Index 4	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
<i>Ateles</i>	AQ and brachiation	0.68	Maximum breadth of glenoid fossa cranially located \updownarrow Maximum breadth of glenoid fossa caudally located	8.88	>0.001	All genera except <i>Alouatta</i> , <i>Lagothrix</i>
<i>Lagothrix</i>	AQ and brachiation	0.71				<i>Aotus</i> , <i>Callimico</i> , <i>Saguinus</i>
<i>Alouatta</i>	AQ	0.74				<i>Aotus</i> , <i>Callimico</i> , <i>Saguinus</i>
<i>Leontopithecus</i>	AQ	0.75				<i>Ateles</i>
<i>Cebus</i>	AQ and climbing	0.76				<i>Ateles</i>
<i>Callithrix</i>	AQ	0.78				<i>Ateles</i>
<i>Saimiri</i>	AQ and climbing	0.79				<i>Ateles</i>
<i>Aotus</i>	AQ	0.8				<i>Alouatta</i> , <i>Ateles</i> , <i>Lagothrix</i>
<i>Saguinus</i>	AQ and leaping	0.8				<i>Alouatta</i> , <i>Ateles</i> , <i>Lagothrix</i>
<i>Callimico</i>	AQ and leaping	0.82				<i>Alouatta</i> , <i>Ateles</i> , <i>Lagothrix</i>

Figure 7: Error Bar Graphs of Index 4 based on Genera



Locomotor Category

Index 1: Breadth-Length Ratio of the Humeral Head

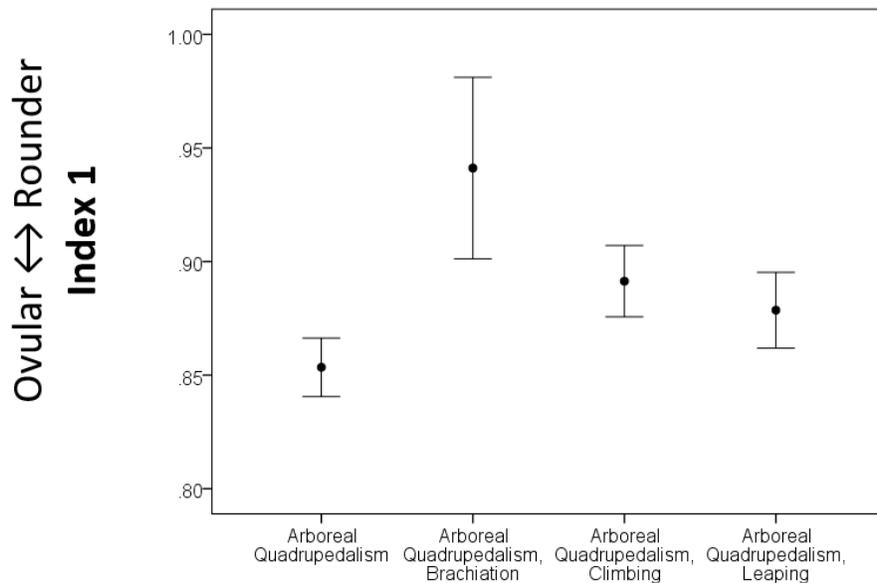
The results show that the first index, the shape of the humeral articular surface, is statistically different between locomotor categories. Notably, the humeral head of the arboreal quadrupeds that take part in brachiation vary significantly from all other forms of locomotion

(Table 14). The strict arboreal quadrupeds have the most ovular humeral articular surface while those that take part in brachiation have the roundest articular surface (Table 14, Figure 8).

Table 14: Statistics for Index 1 based on Locomotion

Locomotor Category	Genera	Average Index 1	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
AQ	<i>Aotus, Alouatta, Callithrix, Leontopithecus</i>	0.85	Ovular humeral articular surface ⇕ Rounder humeral articular surface	12.83	>0.001	AQ and brachiation, AQ and climbing
AQ and leaping	<i>Callimico, Saguinus</i>	0.88				AQ and brachiation
AQ and climbing	<i>Cebus, Saimiri</i>	0.89				AQ, AQ and brachiation
AQ and brachiation	<i>Ateles, Lagothrix</i>	0.94				All locomotor categories

Figure 8: Error Bar Graph of Index 1 based on Locomotion



Index 2: Breadth-Length Ratio of the Glenoid Fossa

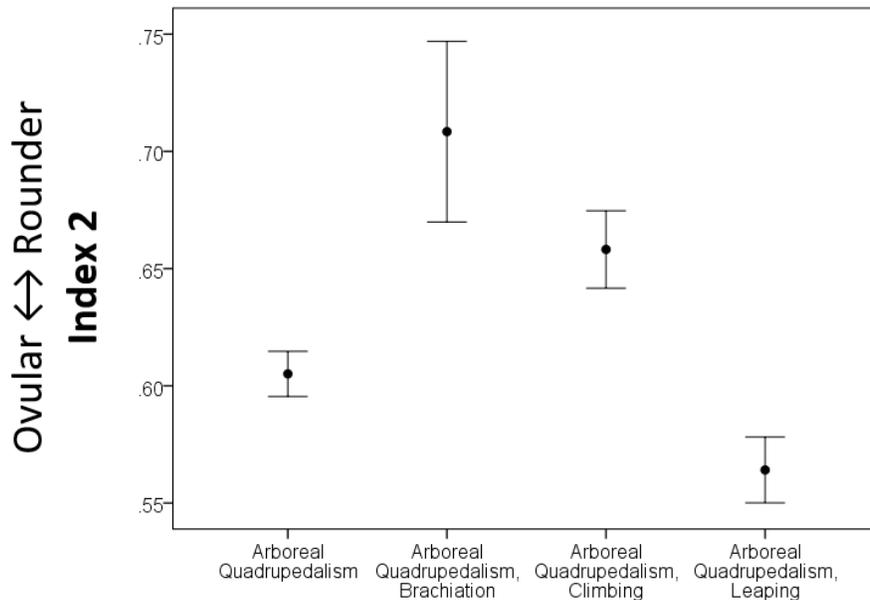
The shape of the glenoid fossa, index 2, is statistically different between all forms of locomotion (Table 15). The arboreal quadrupeds and leapers have the most ovular glenoid fossa while the arboreal quadrupeds and brachiators have the roundest glenoid fossa (Table 15). In a similar pattern of the first index, the arboreal quadrupeds who take part in brachiation display a

notably higher average value for the second index compared to all other locomotor categories (Figure 9).

Table 15: Statistics for Index 2 based on Locomotion

Locomotor Category	Genera	Average Index 2	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
AQ and leaping	<i>Callimico, Saguinus</i>	0.56	Ovular glenoid fossa ↕ Rounder glenoid fossa	42.80	>0.001	All locomotor categories
AQ	<i>Aotus, Alouatta, Callithrix, Leontopithecus</i>	0.61				All locomotor categories
AQ and climbing	<i>Cebus, Saimiri</i>	0.66				All locomotor categories
AQ and brachiation	<i>Ateles, Lagothrix</i>	0.71				All locomotor categories

Figure 9: Error Bar Graph of Index 2 based on Locomotion



Index 3: Degree of Curvature of the Glenoid Fossa

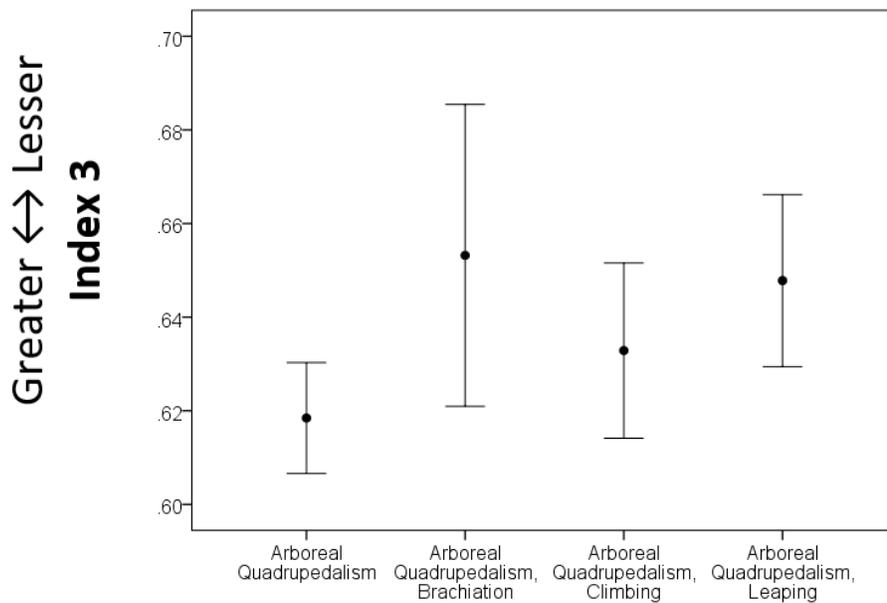
The strictly arboreal quadrupeds display the greatest degree of curvature while the leapers and brachiators both have the least degree of curvature (Table 16). While the ANOVA shows that the degree of curvature of the glenoid fossa varies significantly between monkeys based on locomotion, the Bonferroni post-hoc test does not reflect this calculation (Table 16). However, the

error bar graph shows the noticeably lower mean value of the third index of the arboreal quadrupeds (Figure 10).

Table 16: Statistics for Index 3 based on Locomotion

Locomotor Category	Genera	Average Index 3	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
AQ	<i>Aotus, Alouatta, Callithrix, Leontopithecus</i>	0.62	Greatest degree of curvature ⇕ Least degree of curvature	3.38	0.020	None
AQ and climbing	<i>Cebus, Saimiri</i>	0.63				None
AQ and brachiation	<i>Ateles, Lagothrix</i>	0.65				None
AQ and leaping	<i>Callimico, Saguinus</i>	0.65				None

Figure 10: Error Bar Graph of Index 3 based on Locomotion



Index 4: Location of the Maximum Breadth of the Glenoid Fossa

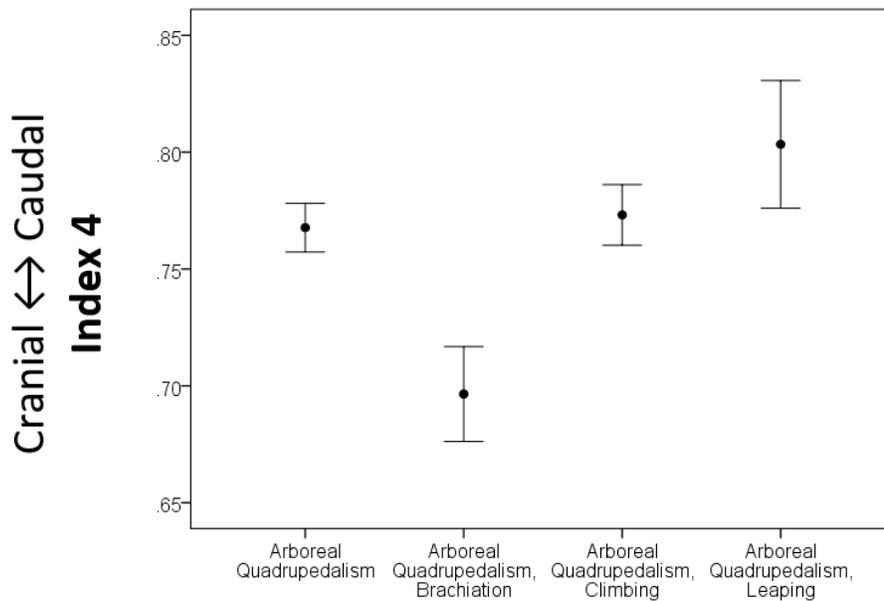
The fourth index is also significantly different based on locomotion. The Bonferroni post-hoc test shows that the location of the maximum breadth of the glenoid fossa, is unique between arboreal quadrupeds who take part in brachiation in comparison to all other forms of locomotion (Table 17). The brachiators have the most cranially located maximum breadth while the leapers have the most caudally located maximum breadth (Table 17). Figure 11 displays the large

difference in mean values between the arboreal quadrupeds and brachiators compared to all other locomotor categories.

Table 17: Statistics for Index 4 based on Locomotion

Locomotor Category	Genera	Average Index 4	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
AQ and brachiation	<i>Ateles, Lagothrix</i>	0.70	Maximum breadth of glenoid fossa cranially located \updownarrow Maximum breadth of glenoid fossa caudally located	16.36	>0.001	All locomotor categories
AQ	<i>Aotus, Alouatta, Callithrix, Leontopithecus</i>	0.77				AQ and brachiation, AQ and leaping
AQ and climbing	<i>Cebus, Saimiri</i>	0.77				AQ and brachiation
AQ and leaping	<i>Callimico, Saguinus</i>	0.80				AQ, AQ and brachiation

Figure 11: Error Bar Graph of Index 4 based on Locomotion



Phylogenetic Family and Subfamilies

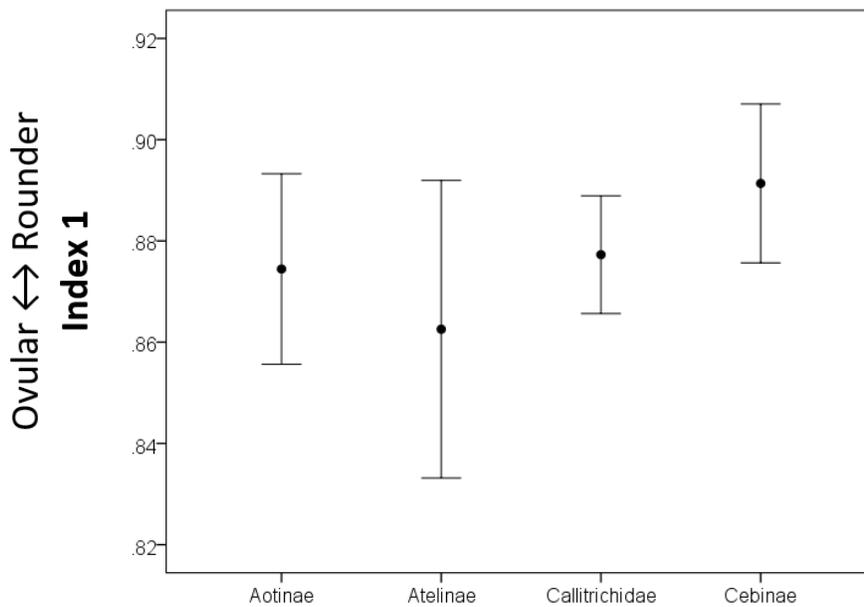
Index 1: Breadth-Length Ratio of the Humeral Head

There is no significant difference in the morphology of the humeral head based on the family Callitrichidae and subfamilies Atelinae, Aotinae and Cebinae (Table 18). While the Atelinae have the lowest average first index and the Cebinae the highest, Table 18 and Figure 12 show the close mean values for each family and subfamily.

Table 18: Statistics for Index 1 based on Family, Subfamilies

Subfamily	Genera	Average Index 1	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
Atelinae	<i>Alouatta, Ateles, Lagothrix</i>	0.86	Ovular humeral articular surface \updownarrow Rounder humeral articular surface	1.35	0.26	None
Aotinae	<i>Aotus</i>	0.87				None
Callitrichidae	<i>Callimico, Callithrix, Leontopithecus, Saguinus</i>	0.88				None
Cebinae	<i>Cebus, Saimiri</i>	0.89				None

Figure 12: Error Bar Graphs of Index 1 based on Family, Subfamilies



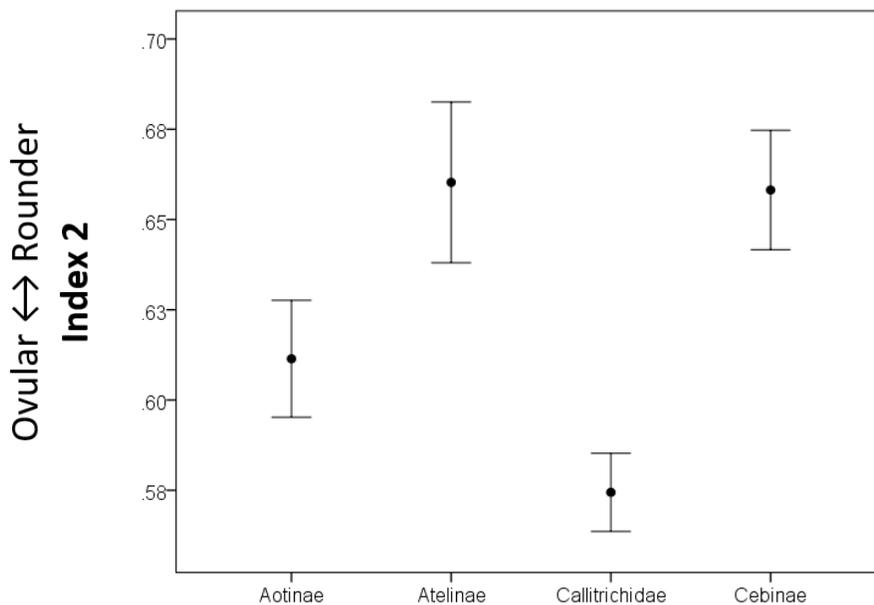
Index 2: Breadth-Length Ratio of the Glenoid Fossa

The second index varies significantly based on family and subfamilies. The Callitrichidae have the lowest average second index, indicative of the most ovular glenoid fossa. The Atelinae and Cebinae both have the highest average index, significant of a rounder glenoid fossa (Table 19). Notably, the Bonferroni post-hoc test shows that the Atelinae and Cebinae are significantly different from both the Callitrichidae and Aotinae, but not from each other (Table 19). The error bar graph, Figure 13, shows that the mean of the Callitrichidae is noticeably less than that of any other subfamily.

Table 19: Statistics for Index 2 based on Family, Subfamilies

Subfamily	Genera	Average Index 2	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
Callitrichidae	<i>Callimico, Callithrix, Leontopithecus, Saguinus</i>	0.57	Ovular glenoid fossa \updownarrow Rounder glenoid fossa	30.11	>0.001	All subfamilies
Aotinae	<i>Aotus</i>	0.61				All subfamilies
Atelinae	<i>Alouatta, Ateles, Lagothrix</i>	0.66				Callitrichidae, Aotinae
Cebinae	<i>Cebus, Saimiri</i>	0.66				Callitrichidae, Aotinae

Figure 13: Boxplot Graph of Index 2 based on Family, Subfamilies



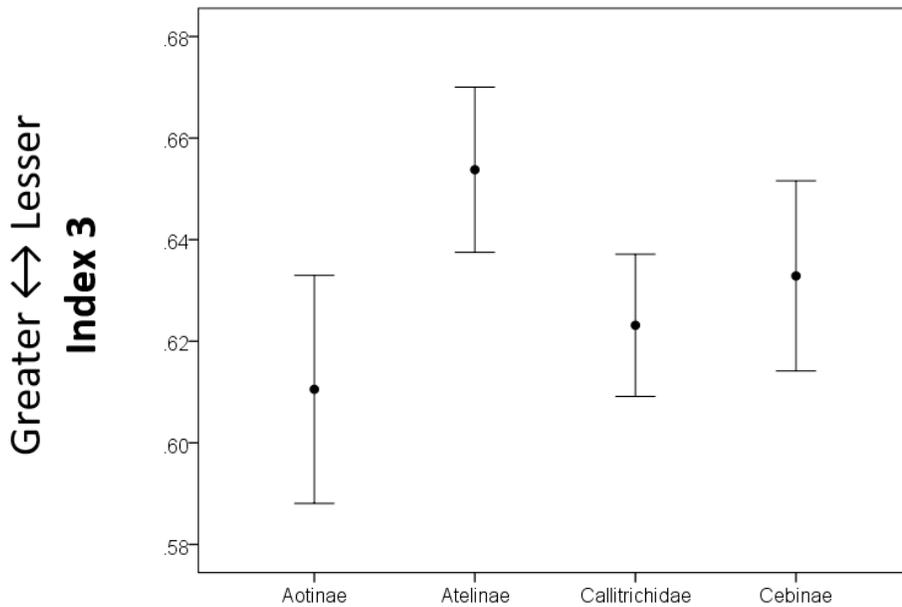
Index 3: Degree of Curvature of the Glenoid Fossa

The third index also differs significantly based on family and subfamilies. The Aotinae have the lowest average third index, representative of a larger degree of curvature. The Atelinae display the least amount of curvature with the largest average third index (Table 20). The Bonferroni post-hoc test shows that the Atelinae are significantly different from the Callitrichidae and Aotinae in morphology. Figure 14 clearly displays the higher mean of index 3 belonging to the Atelinae and the lower mean attributed to the Aotinae.

Table 20: Statistics for Index 3 based on Family, Subfamilies

Subfamily	Genera	Average Index 3	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
Aotinae	<i>Aotus</i>	0.61	Greatest degree of curvature ⇕ Least degree of curvature	4.02	0.009	Atelinae
Callitrichidae	<i>Callimico, Callithrix, Leontopithecus, Saguinus</i>	0.62				Atelinae
Cebinae	<i>Cebus, Saimiri</i>	0.63				None
Atelinae	<i>Alouatta, Ateles, Lagothrix</i>	0.65				Callitrichidae, Aotinae

Figure 14: Error Bar Graph of Index 3 based on Family, Subfamilies



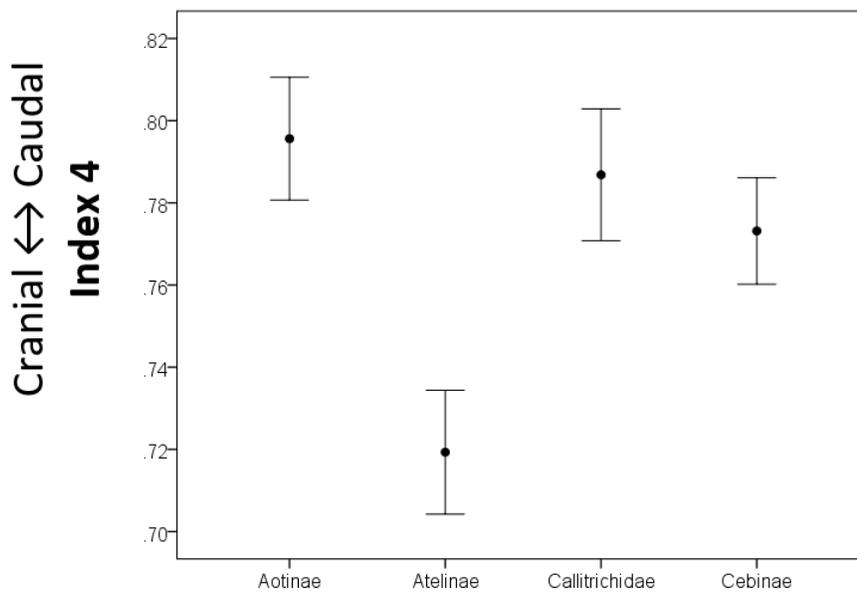
Index 4: Location of the Maximum Breadth of the Glenoid Fossa

The position of the maximum breadth of the glenoid fossa also varies significantly between the Callitrichidae and phylogenetic subfamilies. The Atelinae have the most cranially oriented maximum breadth while the Aotinae have the most caudally located maximum breadth (Table 21). The Bonferroni post-hoc test finds that the Atelinae are significantly different from all other groups (Table 21). This difference in morphology reflects the vastly lower mean value of the fourth index of the Atelinae compared to all other families and subfamilies (Figure 15).

Table 21: Statistics for Index 4 based on Family, Subfamilies

Subfamily	Genera	Average Index 4	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
Atelinae	<i>Alouatta, Ateles, Lagothrix</i>	0.72	Maximum breadth of glenoid fossa cranially located ⇕ Maximum breadth of glenoid fossa caudally located	17.56	>0.001	All subfamilies
Cebinae	<i>Cebus, Saimiri</i>	0.77				Atelinae
Callitrichidae	<i>Callimico, Callithrix, Leontopithecus, Saguinus</i>	0.79				Atelinae
Aotinae	<i>Aotus</i>	0.80				Atelinae

Figure 15: Error Bar Graph of Index 4 based on Family, Subfamilies



Body Size

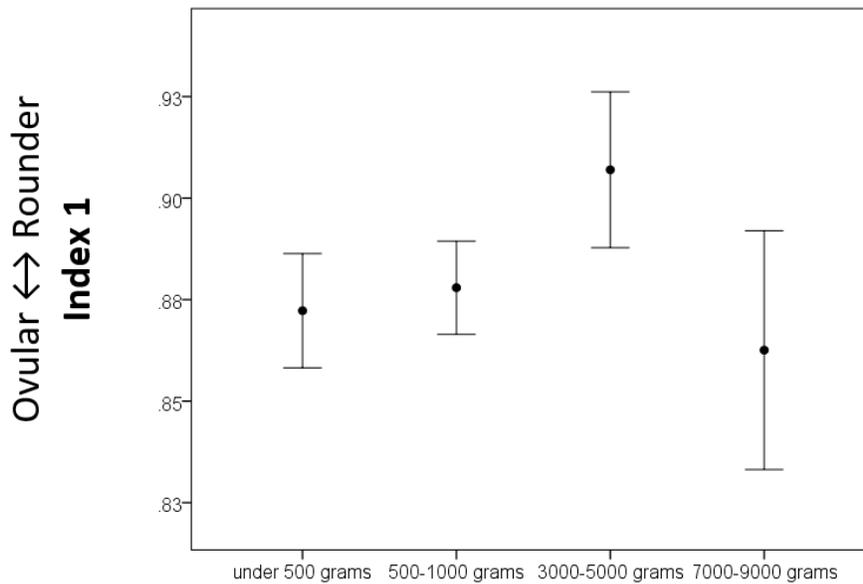
Index 1: Breadth-Length Ratio of the Humeral Head

The ANOVA test shows that the shape of the humeral articular surface does not vary significantly based on body size (Table 22). While the primates weighing between 7,000-9,000 grams have the most ovular humeral articular surface, the morphology of the monkeys weighing between 3,000-5,000 grams reflects the roundest shape (Table 22). Figure 16 displays the lower average first index belonging to the larger bodied platyrrhines, while the majority of the mean values overlapped across body size.

Table 22: Statistics for Index 1 based on Body Size

Body Size, grams (Sussman 2003)	Genera	Average Index 1	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
7,000-9,000	<i>Alouatta, Ateles, Lagothrix</i>	0.86	Ovular humeral articular surface ⇕ Rounder humeral articular surface	2.49	0.063	3,000-5,000
Under 500	<i>Callimico, Callithrix, Saguinus</i>	0.87				None
500-1,000	<i>Aotus, Leontopithecus, Saimiri</i>	0.88				None
3,000-5,000	<i>Cebus</i>	0.91				7,000-9,000

Figure 16: Error Bar Graph of Index 1 based on Body Size



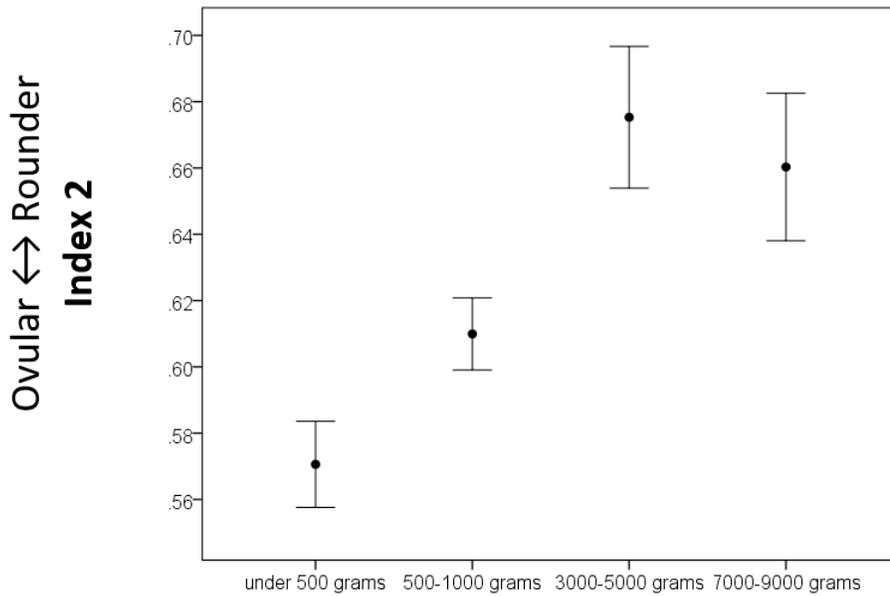
Index 2: Breadth-Length Ratio of the Glenoid Fossa

The shape of the glenoid fossa, index 2, differs greatly with the variation of body size. The primates under 500 grams displayed the most ovular glenoid fossa while those of 3,000-5,000 grams have the most round glenoid fossa (Table 23). The Bonferroni post-hoc test also shows that the Platyrrhini under 500 grams and between 500-1,000 grams vary significantly from all other body sizes (Table 23). The mean values of the two groups of larger New World monkeys are notably higher than the average of the smaller monkeys (Figure 17).

Table 23: Statistics for Index 2 based on Body Size

Body Size, grams (Sussman 2003)	Genera	Average Index 2	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
Under 500	<i>Callimico, Callithrix, Saguinus</i>	0.57	Ovular glenoid fossa \updownarrow Rounder glenoid fossa	31.15	>0.001	All body sizes
500-1,000	<i>Aotus, Leontopithecus, Saimiri</i>	0.61				All body sizes
7,000-9,000	<i>Alouatta, Ateles, Lagothrix</i>	0.66				Under 500, 500-1,000
3,000-5,000	<i>Cebus</i>	0.68				Under 500, 500-1,000

Figure 17: Error Bar Graph of Index 2 based on Body Size



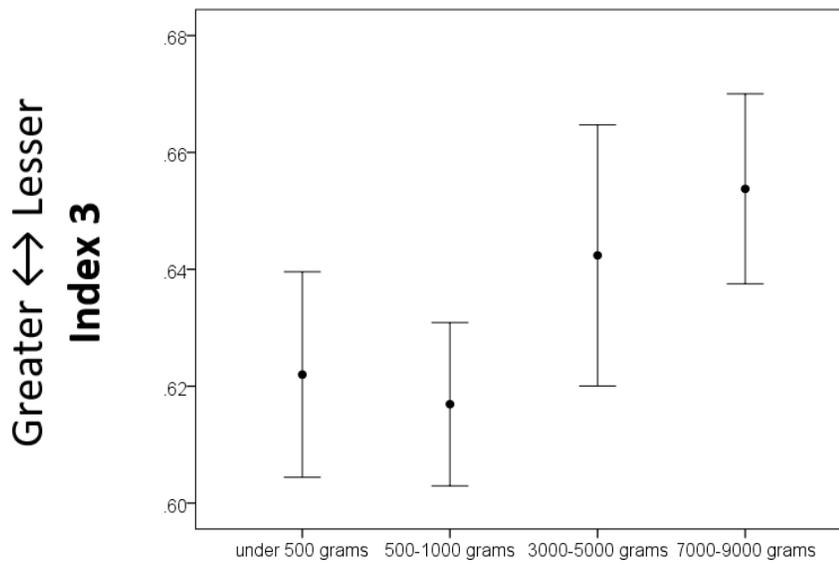
Index 3: Degree of Curvature of the Glenoid Fossa

Index 3, the degree of curvature of the glenoid fossa, is also statistically different from the primates under 500 grams and between 500-1000 grams to those of 7000-9000 grams in weight (Table 24). The primates with the greatest degree of curvature have body weights under 500 grams. The monkeys ranging from 7,000-9,000 grams display the least degree of curvature, as reflected in Table 24 and Figure 18.

Table 24: Statistics for Index 3 based on Body Size

Body Size, grams (Sussman 2003)	Genera	Average Index 3	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
Under 500	<i>Callimico, Callithrix, Saguinus</i>	0.62	Greatest degree of curvature ⇕ Least degree of curvature	4.34	0.006	7,000-9,000
500-1,000	<i>Aotus, Leontopithecus, Saimiri</i>	0.62				7,000-9,000
3,000-5,000	<i>Cebus</i>	0.64				None
7,000-9,000	<i>Alouatta, Ateles, Lagothrix</i>	0.65				Under 500, 500-1,000

Figure 18: Error Bar Graph of Index 3 based on Body Size



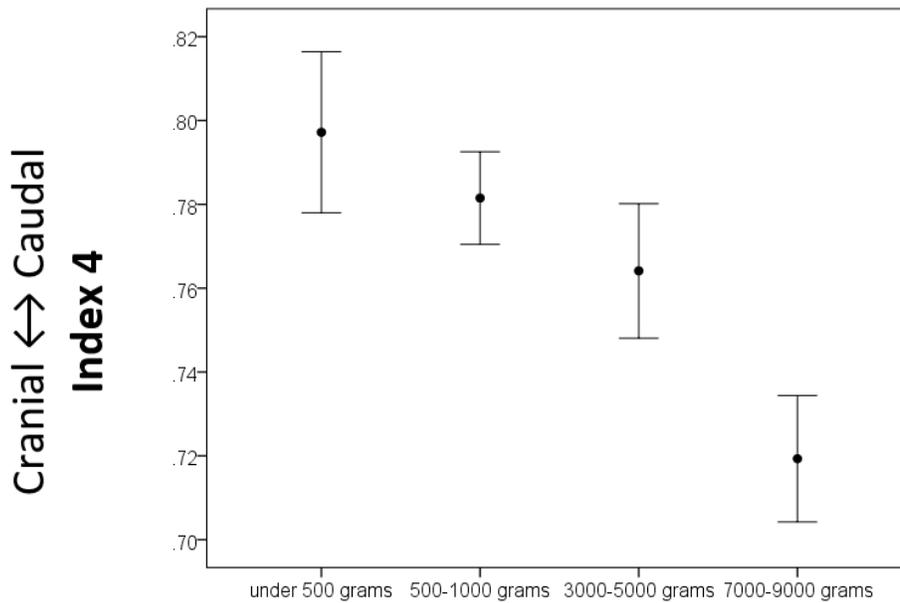
Index 4: Location of the Maximum Breadth of the Glenoid Fossa

There are also significant differences of the fourth index based on body size. In particular, the location of the maximum breadth of the glenoid fossa, index 4, is different from primates with body weights of 7000-9000 grams compared to all other categories (Table 25). The larger primates have the most cranially located maximum breadth while the smallest monkeys have the most caudally located (Table 25, Figure 19).

Table 25: Statistics for Index 4 based on Body Size

Body Size, grams (Sussman 2003)	Genera	Average Index 4	Morphological Significance	ANOVA F Value	ANOVA P Value	Bonferroni Significance
7,000-9,000	<i>Alouatta, Ateles, Lagothrix</i>	0.72	Maximum breadth of glenoid fossa cranially located \updownarrow Maximum breadth of glenoid fossa caudally located	19.009	>0.001	All body sizes
3,000-5,000	<i>Cebus</i>	0.76				7,000-9,000
500-1,000	<i>Aotus, Leontopithecus, Saimiri</i>	0.78				7,000-9,000
Under 500	<i>Callimico, Callithrix, Saguinus</i>	0.80				7,000-9,000

Figure 19: Error Bar Graph of Index 4 based on Body Size



Discussion

Index 1: Breadth-Length Ratio of the Humeral Head

The first index examined the overall shape of the humeral articular surface. The results of this study support my hypothesis, finding that *Ateles* displayed a significantly rounder and wider humeral head in comparison to all other platyrrhines. This trend in the morphology of the humeral head also reflects the findings of previous anthropologists. Arias-Martorell et al. (2015, 14) and

Kagaya (2006, 19) found that *Ateles* had more globular humeral articular surface, similar to that of one particular hominoid, *Hylobates*.

I also discovered that the humeral head of *Ateles* was significantly different from that of *Lagothrix*, who take part in limited brachiation. Although the humeral morphology of the two brachiating platyrrhines, *Ateles* and *Lagothrix*, was significantly different based on genera, an analysis of humeral morphology based on locomotor group found that arboreal quadrupeds who take part in brachiation were distinguished from all other forms of locomotion. In particular, the group of brachiators exhibited the roundest and widest humeral articular surface, traits associated with a higher degree of shoulder mobility. The morphology of the humeral head did not vary significantly based on either confounding variable of phylogenetic family and subfamily or body size. Thus, the overall analysis of the humeral head showed that the functional use of the forelimb and shoulder have a greater effect on the skeletal morphology than the broader phylogenetic history or body size of the primate.

Index 2: Breadth-Length Ratio of the Glenoid Fossa

When examining the breadth-length ratio of the glenoid fossa, my results show that *Ateles* has the roundest and widest glenoid fossa compared to all other genera, even *Lagothrix*. In a similar trend, previous research also found *Ateles* to have the roundest glenoid fossa, linked with the use of brachiation (Larson 1998, 92; Kagaya 2006, 19). When I analyzed the effects of locomotion on the glenoid morphology, all locomotor groups were significantly different. The arboreal quadrupeds associated with brachiation also displayed the largest breadth-length ratio of the glenoid fossa, indicative of a round and broad shape.

The glenoid morphology varied based on the two additional variables of phylogenetic family and subfamily as well as body size. The glenoid breadth-length ratio of the Callitrichidae

family and Aotinae subfamily were distinct from all other subfamilies. The glenoid morphology of the smaller primates, weighing under 500 grams and between 500-1,000 grams, were different from all other body size categories. However, since the glenoid morphology distinguished between all four locomotor categories, contrary to the differences of the two confounding variables, I conclude that the functional use of the shoulder has the largest effect on the overall glenoid shape.

Index 3: Degree of Curvature of the Glenoid Fossa

I hypothesized that *Ateles*, most known of brachiation, would exhibit the largest degree of curvature, which is indicative of a wider glenoid fossa. While the degree of curvature did vary based on genera, *Ateles* was not significantly different from other platyrrhines. When examining the effect of locomotion on this particular skeletal trait, the ANOVA test did show significant distinctions based on locomotor behavior. However, the Bonferroni post-hoc test did not reflect any significant morphological difference between specific locomotor groups. Thus, the functional use of the shoulder did not largely effect the degree of curvature of the glenoid fossa.

When including the two additional variables of phylogenetic family and subfamily as well as body weight, I found various significant differences. The Atelinae subfamily had the least degree of curvature, statistically different from the Callitrichidae family and Aotinae subfamily. However, the degree of glenoid curvature did separate the primates based on body size. By testing the two confounding variables, I found that the broader phylogeny and body size had a larger effect on the degree of glenoid curvature than the functional use of the shoulder and forelimb.

Index 4: Location of the Maximum Breadth of the Glenoid Fossa

The final index examined the morphological location of the maximum glenoid breadth. I anticipated that *Ateles* would exhibit the most centrally located maximum breadth, associated with a broader glenoid fossa of the brachiating hominoids. My results found that *Ateles* had the most

cranially located glenoid maximum breadth compared to other genera, falling the most towards the middle of the glenoid fossa compared to other platyrrhines. The location of the maximum glenoid breadth was statistically different between *Ateles* and all other genera except *Alouatta* and *Lagothrix*. My findings reflect the results of previous anthropologists, in which *Ateles* displayed the roundest and most cranially located maximum glenoid breadth (Larson 1998, 92; Kagaya 2006, 19). When examining the effect of locomotor behavior on shoulder morphology, all locomotor groups exhibited significantly different locations of the maximum glenoid breadth. Notably, the arboreal quadrupeds taking part in brachiation displayed the most cranially located maximum glenoid breadth.

The additional factors of broader phylogeny and body size also show morphological difference of the maximum glenoid breadth. The analysis of the phylogenetic family and subfamilies distinguished the location of the maximum glenoid breadth as more cranially located in the Atelinae when compared to the other family and subfamilies. In a similar manner, the larger bodied primates, weighing between 7,000-9,000 grams, had a significantly more cranially located maximum breadth than the smaller platyrrhines. While the location of the maximum glenoid breadth was affected by both confounding factors of phylogenetic family and subfamily as well as body size, the functional use based on locomotor behaviors also significantly affected the skeletal morphology of the shoulder.

Brachiation Theory

The findings of my study reflect the argument of previous scholarship that the functional use of a primate's body has a significant effect on its morphology. In particular, my results support the brachiation theory. *Ateles*, the most prominent brachiator among Platyrrhini, had the roundest humeral head while *Alouatta*, known for slow arboreal quadrupedalism, had the most ovular

humeral articular surface. In addition, *Ateles* displayed the widest and roundest glenoid fossa while *Saguinus*, a quadrupedal leaper, had the most ovular shape. Since the wide and globular humeral head and glenoid fossa are indicative of a larger range of motion and *Ateles* shows the most extreme of these morphologies, the results of this thesis supports the notion of morphological adaptation towards brachiation.

There are various reasons as to why the use of brachiation may be beneficial for a primate. Many anthropologists state that brachiation may provide a better route of travel for the primate and reduce the energy expenditure in travel (Gebo 1996, 75; Cant 1986, 9). In addition, brachiation may allow the primate access to more food sources (Cant 1986, 11). Another common assumption is that brachiation allows heavier primates to increase balance along smaller substrates (Gebo 1996, 75; Cant 1986, 10). While *Ateles* does average a body mass larger than other New World monkeys, between 7,000-9,000 grams, *Alouatta* represents the largest of the Atelinae primates, reaching a maximum of 11,000 grams (Sussman 2003, 142). If brachiation were to aid larger primates in balancing along substrates, it would be logical that *Alouatta* should also take part in brachiation. Instead, this genus of Platyrrhini takes part in slow climbing. Even further, the results of first and second index find statistical differences between the morphology of *Ateles* and *Alouatta*, with both falling at the opposite spectrums of glenohumeral morphology. While I do not fully explore all factors influencing the selection of this locomotion, my study finds evidence of glenohumeral adaptations to brachiation and suspension within the examined genera.

Varying Brachiation Forms of *Ateles* and *Lagothrix*

Both *Ateles* and *Lagothrix* are arboreal quadrupedal platyrrhines who partake in brachiation. However, the present study shows only *Ateles* as most adapted for such locomotor behaviors. *Ateles* exhibited a significantly rounder and wider glenoid fossa and humeral head as

well as a more cranially located maximum glenoid breadth when compared to the morphology of *Lagothrix*. In fact, the morphology of the humeral head of *Lagothrix* (index 1) most resembles that of *Alouatta*, falling on the opposite extreme as compared to *Ateles*. While the morphology of the glenoid fossa of *Lagothrix* shows more similarities to the morphology of *Ateles* in both the breadth-length ratio of the glenoid fossa and the location of the maximum glenoid breadth, *Ateles* is the sole outlier of all platyrrhines, even different in morphology compared to fellow brachiator *Lagothrix*. The differing morphology of two genera of Platyrrhini known to take part in brachiation suggest that either the frequency of brachiation plays a larger role in the morphology, or the two genera achieve this locomotor behavior through different functional means.

Previous literature argues that the brachiation of *Ateles* is unique from the locomotion utilized by *Lagothrix*. Cant et al. (2003, 688) found that *Ateles* takes part in a higher prevalence of brachiation than *Lagothrix*. In particular, *Ateles* utilized brachiation twice as much as the *Lagothrix* (Schmitt et al. 2005, 442). In addition to the frequency, the form and functional use of brachiation varies between the two genera. Turnquist et al. (1999, 264) state that the brachiation of *Ateles* is different from that of *Lagothrix* in the sequence of hand and tail use. *Lagothrix* also takes part in short, choppy strides of brachiation while the movements of *Ateles* are long and fluid. Overall, Turnquist et al. (1999, 264) argues that the brachiation of *Ateles* most closely resembles that locomotor behavior utilized by the hylobatids. The findings of the current study support the connection between the use of brachiation and associated morphological characteristics present in *Ateles* and the hylobatids. The study also confirms that the frequency of functional use influences the skeletal morphology. *Ateles*, the most prevalent brachiator examined in this study, displayed the roundest and widest humeral head and glenoid fossa.

Future Research

While my study found interesting trends among the humeral and glenoid morphology of a small group of New World monkeys, it was limited in scope. In the future, I hope to analyze the morphology of the glenohumeral joint of a larger sample of platyrrhine genera, including *Brachyteles* and other genera from the Pitheciinae subfamily. I anticipate that the glenohumeral joint of *Brachyteles* will reflect the morphology found in *Ateles* due to their frequent use of brachiation and similar physical characteristics. Though previous research has examined the skeletal morphology of Old World monkeys and hominoids, I would also examine the humerus and scapula of the catarrhines and hominoids known to take part in brachiation to have a more comparative and substantial collection. Finally, I would expand my measurements to analyze the depth of the glenoid fossa and humeral articular surface, capturing the location where the two skeletal elements interact. Even with the limitations of my current study, I found that *Ateles* exhibited unique shoulder morphology due to their specialized form of locomotion.

Conclusions

This study examined the glenohumeral joint of 10 platyrrhine genera to assess whether *Ateles*, known for frequent use of brachiation, displayed distinct morphology indicative of a greater range of shoulder mobility. I hypothesized that *Ateles* would exhibit the roundest and widest humeral head and glenoid fossa, the highest degree of glenoid curvature and the maximum glenoid breadth towards the middle range. I found that while *Ateles* displayed the roundest and widest humeral head and glenoid fossa and central maximum glenoid breadth, this genus did not exhibit the highest degree of glenoid curvature. Overall, the results of my study show *Ateles* to have unique glenohumeral morphology, even compared to the partial brachiator, *Lagothrix*. My study confirms the relationship between functional use and the morphology of the shoulder and upper limb of

extant platyrrhines. The morphology of the humeral head varied based on locomotor categories and genera associated with these functional behaviors. However, the shape of the glenoid fossa reflected morphological difference based on functional use and genera as well as the two confounding factors: phylogenetic family and subfamily and body size. This study was important in understanding how functional use of the primate body manifests itself within the skeletal structures of important joints, particularly the shoulder. Although a small selection of platyrrhines were included in this study, the impact of functional use on the skeletal structure of a primate's body can be applied when examining skeletal remains of both living and extinct Platyrrhines and Catarrhines.

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