

UNIVERSIDADE FEDERAL DE ALFENAS

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**ESTUDO ANATÔMICO COMPARATIVO DO MEMBRO PÉLVICO - MÚSCULOS DA
REGIÃO ANTERIOR DA COXA DO PRIMATA *Sapajus* sp (MACACO-PREGO)
ASSOCIADO AO USO DE FERRAMENTAS E BIPEDALISMO**

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Orientador: Prof. Dr. Tales Alexandre Aversi-Ferreira

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SYLLA FIGUEREDO DA SILVA**“ ESTUDO ANATÔMICO COMPARATIVO DO MEMBRO PÉLVICO – MÚSCULOS DA REGIÃO ANTERIOR DA COXA DO PRIMATA *SAPAJUS SP.* (MACACO-PREGO) ASSOCIADO AO USO DE FERRAMENTAS E BIPEDALISMO ”**

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RESUMO

A ordem Primatas é uma importante radiação de mamíferos com uma rica diversidade de adaptações morfológicas, comportamentais e ecológicas. Os antropoides, cujo grupo de primatas do estudo fazem parte, são os primatas mais difusos e com maior diversidade morfológica. Os primatas neotropicais macacos-prego (*Sapajus* sp) e saguis (*Callithrix*) devido às suas características morfológicas, comportamental, fisiológicas e filogenéticas semelhantes com chimpanzés são bons modelos para pesquisas científicas. No entanto, os dados anatômicos e funcionais sobre os seus músculos anteriores da coxa são escassos ou inexistentes. O estudo desses primatas, em termo evolucionário poderá contribuir com áreas relacionados à taxonomia e ao entendimento da evolução do bipedalismo. O objetivo desse trabalho foi estudar a anatomia dos músculos da região anterior da coxa pela dissecação dos primatas neotropicais *Sapajus* e *Callithrix*, e da literatura para *Macaca cyclopes*, *Macaca fascicularis*, *Papio*, *Hylobates*, *Pongo*, *Gorilla*, *Pan* e *Homo* para fins comparativos em termos anatômicos e funcionais relacionados ao comportamento locomotor. Foram dissecados dez espécimes adultos *Sapajus* sp e três de *Callithrix* sp. A dissecação da coxa foi realizada com ênfase no quadríceps femoral. Para fins estatísticos utilizou-se o método comparativo não-paramétrico para associação entre diferentes espécies aos conceitos anatômicos de normalidade e variação. Dados alométricos foram coletados para avaliar a força muscular. O quadríceps femoral de *Sapajus* e *Callithrix* com relação aos parâmetros anatômicos foram idênticos. O reto femoral apresentou uma cabeça de origem apenas para os primatas *Macaca fascicularis*, *Hylobates* e *Pongo*. De acordo com a Lei dos cossenos uma cabeça de origem para esse músculo gera maior força muscular. Já as duas cabeças de origem permite uma melhor estabilidade da articulação coxo-femoral. O tensor da fáscia lata foi o músculo com maior divergência entre os primatas do estudo. Considerando o conjunto dos músculos anteriores da coxa, *Pongo* apresentou maior divergência comparado a *Sapajus*, o que pode ser explicado por uma especialização particular deste primata na evolução da sua locomoção. Anatomicamente, a maior semelhança entre os músculos da região anterior da coxa de *Sapajus* foi com os de *Callithrix*, possivelmente por ambos serem primatas neotropicais e compartilharem um ancestral mais próximo comparado aos demais primatas investigados e por serem quadrúpedes. Humanos modernos apresentaram a maior força do quadríceps, seguidos por *Sapajus* e *Callithrix*, demonstrando uma relação importante entre força proporcional desse músculo e o comportamento bípede e quadrúpede daqueles primatas. Entre os apes, *Hylobates* foi o que apresentou maior força do quadríceps comparado a *Pan*,

Gorilla e Pongo. O modelo área/volume demonstrou ser o mais adequado para a avaliação da força muscular que corroborou com a Lei dos cossenos e a Teoria do corpo-livre. Mais estudos anatômicos com primatas, abordando o membro posterior e sua força muscular se fazem necessários, uma vez que a ausência desses dados foi um dos fatores limitantes desse estudo e caso estivessem presente poderiam fornecer uma melhor compreensão do comportamento locomotor de primatas.

Palavras-chaves: Primatas; Bipedalismo; Comportamento locomotor; Músculos anteriores da coxa; Força muscular.

ABSTRACT

The order Primates is an important mammalian radiation with a rich diversity of morphological, behavioral and ecological adaptations. The anthropoids, which the group of primates in the study are part of, are the most diffused primates with the greatest morphological diversity. The neotropical primates capuchin monkeys (*Sapajus* sp) and marmosets (*Callithrix* sp) due to their morphological, behavioral, physiological, and phylogenetic characteristics similar to chimpanzees are good models for scientific research. However, anatomical and functional data on their anterior thigh muscles are scarce or non-existent. The study of these primates, in evolutionary terms, may contribute to areas related to taxonomy and the understanding of the evolution of bipedalism. The objective of this work was to study the anatomy of the muscles of the anterior region of the thigh by the dissection of the neotropical primates *Sapajus* and *Callithrix*, and of the literature for *Macaca cyclopes*, *Macaca fascicularis*, *Papio*, *Hylobates*, *Pongo*, *Gorilla*, *Pan* and *Homo* for comparative purposes in terms of anatomical and functional aspects related to locomotor behavior. Ten adult specimens of *Sapajus* sp and three of *Callithrix* sp were dissected. Thigh dissection was performed with emphasis on the quadriceps femoris. For statistical purposes, the non-parametric comparative method was used to associate different species with the anatomical concepts of normality and variation. Allometric data were collected for the assessment of muscle strength. The quadriceps femoris of *Sapajus* and *Callithrix* in terms of anatomical parameters were identical. The rectus femoris presented only one head of origin in *Macaca fascicularis*, *Hylobates* and *Pongo*. According to the Law of Cosines, a head of origin for that muscle generates greater muscle force. Already the two heads of origin a better stability of the hip joint. The tensor fascia lata was the muscle with the greatest divergence among the primates in the study. Considering the set of anterior thigh muscles, *Pongo* showed greater divergence compared to *Sapajus*, which can be explained by a particular specialization of this primate in the evolution of its locomotion. Anatomically, the greatest similarity between the muscles of the anterior region of the thigh of *Sapajus* was with those of *Callithrix*, possibly because both are neotropical primates and share a closer ancestor compared to the other primates investigated and because they are quadrupeds. Modern humans had the greatest quadriceps strength, followed by *Sapajus* and *Callithrix*, demonstrating an important relationship between proportional strength of this muscle and the bipedal and quadrupedal behavior of those primates. Among the apes, *Hylobates* was the one that showed greater quadriceps strength compared to *Pan*, *Gorilla* and *Pongo*. The area/volume model proved to be

the most suitable for the assessment of muscle strength, which corroborated the Law of Cosines and the Free-Body Theory. More anatomical studies with primates, addressing the hindlimb and its muscle strength are necessary, since the absence of these data was one of the limiting factors of this study and, if they were present, they could provide a better understanding of the locomotor behavior of primates.

Keywords: Primates; Bipedalism; Locomotor behavior; Anterior thigh muscles; Muscle strength.

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1 INTRODUÇÃO GERAL E APRESENTAÇÃO DO TEMA

A ordem Primatas é uma importante radiação de mamíferos com uma rica diversidade de adaptações morfológicas, comportamentais e ecológicas (ANKEL-SIMONS, 2007; FLEAGLE; SEIFFERT, 2020; POZZI *et al.*, 2014). De acordo com estudos baseados em evidências moleculares, esses animais divergiram dos demais mamíferos entre 63,7 e 87,2 milhões de anos (CHATTERJEE *et al.*, 2014; DI FIORI *et al.*, 2015; JAMESON *et al.*, 2011; PERELMAN *et al.*, 2011; POZZI *et al.*, 2014; SPRINGER *et al.*, 2012). Nessa ordem estão inclusas cerca de 80 gêneros, 521 espécies e 709 espécies e subespécies de primatas não-humanos. Atualmente, os primatas não humanos estão restritos principalmente às regiões tropicais ou subtropicais da Ásia, América Central e do Sul e África (ANKEL-SIMONS, 2007; POZZI *et al.*, 2014).

Além da grande flexibilidade de comportamento entre os indivíduos, a presença de unhas nas falanges distais das mãos e pés em substituição às garras, usadas para segurar em galhos e manipular objetos com melhor destreza, visão estereoscópica, cérebros relativamente maiores em relação à massa corporal, são algumas das características morfológicas que os distinguem dos demais mamíferos (ANKEL-SIMONS, 2007; BYRNE, 2000; FLEAGLE; SEIFFERT, 2020).

Os primatas objetos desse estudo, ou seja, *Sapajus* (macaco-prego), *Callithrix* (sagui), *Macaca Cyclopis* (Macaco de Taiwan), *Macaca fascicularis* (cinomolgo), *Papio* (babuíno), *Hylobates* (gibão), *Pongo* (orangotango), *Gorilla* (gorila), *Pan* (chimpanzé) e *Homo* (humanos modernos) fazem parte do grupo denominado antropoides, e são os primatas mais difusos e com maior diversidade morfológica, apresentam tamanho e cérebros relativamente maiores do que os demais existentes. Subdividem-se em dois importantes subgrupos: os catarrinos e os platirrininos (FLEAGLE; SEIFFERT, 2020).

Atualmente os catarrinos são encontrados apenas na África e na Ásia, com exceção dos humanos. Morfológicamente, comparados com os platirrininos, têm dois dentes pré-molares, possuem asas nasais e narinas próximas cujas aberturas correm inferiormente, um estreito septo nasal, e cauda, quando presente, é reduzida (ANKEL-SIMONS, 2007; DEFLER, 2009; FLEAGLE; SEIFFERT, 2020). Dividem-se em primatas do Velho Mundo, Apes e Humanos modernos.

Morfológicamente os primatas do Velho Mundo divergem dos apes quanto a forma bilofodonte de seus dentes, por apresentarem membros superiores geralmente iguais ou mais

curtos que os inferiores, e por todos possuírem cauda (embora possa estar bem reduzida) (FLEAGLE; SEIFFERT, 2020). Dos primatas aqui estudados fazem parte desse grupo a *Macaca Cyclopis*, *Macaca fascicularis* e *Papio*. Quanto ao comportamento locomotor desses animais são classificados como quadrúpedes andadores e corredores no solo (ANKEL-SIMONS, 2007).

Já o apes dividem-se em dois grupos principais, os pequenos apes (os do gênero *Hylobates*) e grandes apes (*Pongo*, *Gorilla* e *Pan*). O comportamento locomotor de *Hylobates* é caracterizado pela braquiação verdadeira. *Pongo* possui como atividade locomotora principal a escalada deliberada e dos grandes apes é o mais braquiador. No entanto, quando vem ao solo utiliza a caminhada andar com punhos quadrúpedes. Enquanto *Gorilla* e *Pan* são quadrúpedes que andam com os nós dos dedos. Todos os apes realizam bipedalismo intermitente. Sendo o bipedalismo verdadeiro observado somente em humanos modernos e reflete uma alta especialização na evolução da pelve e membro posterior (ANKEL-SIMONS, 2007; FLEAGLE; SEIFFERT, 2020). Os apes (exceto *Hylobates*) mostram quantidades variadas de uso de ferramentas e outras habilidades culturais. Têm cérebros relativamente maiores do que outros primatas, sendo que o cérebro de humanos modernos, em relação à sua massa corporal, está entre os maiores do reino animal (ANKEL-SIMONS, 2007; FLEAGLE; SEIFFERT, 2020).

Em relação aos platirrinos, também conhecidos como primatas do Novo Mundo ou primatas neotropicais, encontram-se amplamente distribuídos na América Central e do Sul. São dispersores de sementes, exercendo grande importância ecológica para o equilíbrio do meio ambiente (BICCA-MARQUES *et al.*, 2008; KIERULFF *et al.*, 2015). São primatas de pequeno a médio porte, com massa corporal variando entre 50 g e 10 kg. Todos, exceto o *Aotus* (macaco noturno), são diurnos, possuindo visão de cores tricromática polimórfica, com exceção do *Alouatta*, que tem tricromacia de rotina e *Aotus* que não tem visão de cores (FLEAGLE; SEIFFERT, 2020). Apresentam fórmula dentária, com a retenção de três pré-molares, largas cartilagens, septo nasal e presença de cauda semi-preênsil nos grupos de grande porte (ANKEL-SIMONS, 2007; DEANE *et al.*, 2014; DEFLER, 2009). *Sapajus* (macaco-prego) e *Callithrix* (sagui), primatas que foram dissecados nesse estudo, fazem parte desse grupo e são quadrúpedes arborícolas que caminham, correm e saltam, com o macaco-prego apresentado o comportamento locomotor de bipedalismo intermitente associado ao forrageamento, inesperado para um primata do Novo Mundo (ABREU *et al.*, 2021; ANKEL-SIMONS, 2007).

Devido a características morfológicas, organização comportamental e semelhanças fisiológicas e filogenéticas com chimpanzés os primatas neotropicais, especificamente os

macacos-prego (*Sapajus* sp) e saguis (*Callithrix* sp) têm sido bastante utilizados como modelo animal em investigações científicas. Além disso, esses primatas apresentam facilidade de reprodução em cativeiro, o que lhes confere mais uma vantagem no que diz respeito à sua utilização como modelo (ABREU *et al.*, 2021; MELO; MATI; MARTINS, 2012).

Os *Callithrix* sp são os menores primatas neotropicais, possuindo cerca de 20 centímetros de altura e peso variando entre 350 e 500 gramas, são arborícolas, diurnos, apresentam uma série de características anatômicas adaptativas como unhas em garra (essas garras são consideradas unhas modificadas e, portanto, não são garras verdadeiras) (ANKEL-SIMONS, 2007), apresentam especializações dentárias e comportamentais para arrancar cascas de árvores e se alimentar de exsudato, e insetos, além de possuir um ceco intestinal aumentado e complexo que facilita a digestão de polissacarídeos. Devido ao seu hábito alimentar generalista, flexibilidade comportamental e cuidado parental, a espécie pode se adaptar facilmente em diferentes habitat e tipos de alimentação (ANKEL-SIMONS, 2007; ARRUDA *et al.*, 2019; GARBINO, 2015; KORTE; EVERITT, 2019; RYLANDS; COIMBRA-FILHO; MITTERMEIER, 2009).

O *Sapajus* sp, comparado a outros primatas neotropicais possui porte médio, com peso corporal dos indivíduos adultos variando entre 2,5 a 5 Kg. Seus pelos, com coloração variando entre preto e tons de castanho, formam na região da cabeça um topete semelhante a uma crista. Possui calda semi-preênsil que o auxilia durante seu deslocamento arbóreo e na sustentação do seu corpo quando em posição bípede. No entanto, sua locomoção é essencialmente quadrupedal (AVERSI-FERREIRA *et al.*, 2007a; DEFLER, 2009; FRAGASZY; VISALBERGUI; FEDIGAN, 2004; FRAGASZY *et al.*, 2010; RUSSO; YOUNG, 2011).

Dentre os primatas neotropicais os macacos-prego do gênero *Sapajus* tem sido objeto de diversos estudos por apresentarem comportamento semelhante a primatas como os chimpanzés. Esses animais apesar de passarem a maior parte do tempo na marcha quadrúpede, são os únicos primatas do Novo Mundo que realizam bipedalismo intermitente em momentos de forrageamento e fazem uso de ferramentas envolvendo a obtenção e captura de alimentos da sua dieta, o que exige alta cognição para realização. Esses animais em termos comportamentais apresentam alta flexibilidade social. A facilidade com que alteram entre as posições quadrúpede e bípede os tornam bons modelos para estudos sobre a evolução do comportamento locomotor ligado à força muscular entre os primatas (ABREU *et al.*, 2021; AVERSI-FERREIRA *et al.*, 2010a; AVERSI-FERREIRA *et al.*, 2013; AVERSI-FERREIRA *et al.*, 2021; DEANE *et al.*, 2014; DEMES, 2011; DEMES; O'NEILL, 2013; DUARTE *et al.*, 2012; JONES; FRAGASZY,

2020). Desta forma, é de grande importância o estudo anatômico e comparativo dos músculos da região anterior da sua coxa, tanto em termos morfológicos quanto fisiológicos, para servir como base para a filogenia, evolução, comportamento e taxonomia e outras áreas afins. Em termos evolucionário poderá contribuir para a elucidação de lacunas relacionados à taxonomia e ao entendimento da evolução do bipedalismo em primatas não humano (ABREU *et al.*, 2021).

Hipoteticamente, o aparato locomotor de *Sapajus* e *Callitrix* poderia ser um passo intermediário na evolução do bipedalismo entre Apes e Humanos modernos, como para os primatas do Velho Mundo.

O conhecimento da anatomia do macaco-prego (*Sapajus* sp) e saguis (*Callithrix* sp) além de contribuir para a conservação dessas espécies pode também auxiliar profissionais médicos veterinários quando da realização de procedimentos cirúrgicos, assim como na clínica quando do atendimento a esses primatas, visto que são frequentemente vítimas de atropelamentos em ambientes urbanos. Além de ser base para estudos filogenéticos, taxonômicos, evolutivos e etológicos (ABREU *et al.*, 2012; ALVES *et al.*, 2012; AVERSI-FERREIRA; NISHIJO; AVERSI-FERREIRA, 2018; AVERSI-FERREIRA *et al.*, 2011a; PFRIMER *et al.*, 2012; JÚNIOR *et al.*, 2019).

Estudos anatômicos comparativos realizados sobre a anatomia do membro anterior de *Sapajus* sp comparando esse primata com *Papio*, *Gorilla*, *Pan* e *Homo* trazem uma maior similaridade das estruturas anatômicas com babuíños, um primata do Velho Mundo que não faz uso de ferramentas e não realiza bipedalismo intermitente (ABREU *et al.*, 2012; AVERSI-FERREIRA *et al.*, 2005a, 2005b, 2006a, 2006b, 2007a, 2007b, 2007c, 2009; 2010, 2011a, 2011b, 2013, 2014, 2016; FIGUEREDO-DA-SILVA *et al.*, 2021; VASCONCELOS-DA-SILVA *et al.*, 2017), em termos comportamentais quanto ao uso de ferramentas, tolerância social e cognição esse primata demonstrou maior semelhança com os chimpanzés (ABREU *et al.*, 2021; FRAGASZY; VISALBERGHI; FEDIGAN, 2004; OTTONI; IZAR, 2008).

Há poucas informações anatômicas disponíveis na literatura sobre a anatomia comparativa dos músculos da região anterior da coxa de *Sapajus* sp. Os estudos que foram realizados são referentes aos seus nervos e vasos (AVERSI-FERREIRA *et al.*, 2011a, AVERSI-FERREIRA *et al.*, 2013) e sobre *Callitrix* sp não foi localizado nenhum com essa abordagem.

Desta forma, esse estudo referente a anatomia comparativa dos músculos anteriores da coxa de *Sapajus*, tem grande importância para a geração de dados anatômicos para ciências como a fisiologia, filogenia, taxonomia, medicina veterinária e uma melhor compreensão da evolução do bipedalismo. Com relação aos vasos do membro posterior de *Sapajus* o padrão

encontrado por Aversi-Ferreira *et al.* (2013) não permitiu inferir esse entendimento, sendo necessário estudos relacionados à morfologia e fisiologia muscular desse membro para uma melhor compreensão (ABREU *et al.*, 2021; AVERSI-FERREIRA *et al.*, 2013).

2 OBJETIVOS

2.1 OBJETIVO GERAL

Estudar a anatomia dos músculos da região anterior da coxa de macaco-prego (*Sapajus* sp), em termos morfológicos e fisiológicos, e comparar os resultados com os dados dessas estruturas com o primata do Novo Mundo sagui (*Callithrix* sp), primatas do Velho Mundo (*Papio*, *Macaca cyclopis* e *Macaca fascicularis*), Apes (*Hylobates*, *Pongo*, *Gorilla* e *Pan*) e Humanos modernos.

2.2 OBJETIVOS ESPECÍFICOS

- a) Dissecar os músculos da região anterior da coxa (reto femoral, vasto lateral, vasto medial, vasto intermédio, sartório e tensor da fáscia lata) de macaco-prego e sagui, com ênfase nos seguintes parâmetros: origem, inserção, inervação e vascularização;
- b) Coletar dados alométricos para os Primatas do Novo Mundo do estudo com ênfase nos parâmetros: massa e comprimento muscular do quadríceps e sartório, comprimento do fêmur e área da cabeça do fêmur;
- c) Descrever o comportamento locomotor dos primatas citados;
- d) Verificar a relação entre a força muscular do quadríceps e sartório e o comportamento locomotor dos primatas estudados.

3 ARTIGO DA PESQUISA QUE FOI SUBMETIDO

3.1 MATHEMATICAL MODELS TO ANALYZE THE COMPARATIVE GROSS ANATOMY AND THE PCSA OF THE QUADRICEPS, SARTORIUS AND TENSOR FASCIAE LATAE MUSCLES FROM NEW WORLD PRIMATES (*Sapajus* and *Callithrix*), OLD WORLD PRIMATES, APES, AND MODERN HUMANS

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ABSTRACT

The locomotor apparatus of *Sapajus* and *Callithrix* monkeys could be an intermediate step in the evolution of bipedalism between apes and modern humans. A detailed anatomical analysis of the anterior thigh muscles of *Sapajus* and *Callithrix monkeys* was performed through dissection to obtain data on morphology, allometry, strength, and locomotor behavior. The aim of this study was to compare the relationship between *Sapajus* and *Callithrix* muscles, with published data from *Macaca cyclopis*, *Macaca fasciculata*, *Papio*, apes, and modern humans. Muscle strength was calculated using the free-body cosine theory and measurements were obtained to calculate the Physiological Cross Section Area [PCSA]. The comparative non-parametric method was applied to associate the different species with their anatomical concepts

of normality and variation as nominal variables. Our results indicate that the proportional strength in the quadriceps femoris muscle is directly linked to bipedalism and quadrupedal locomotion in general. The mathematical model associating the area/volume ratio to calculate the force of the anterior thigh muscles was found to be the best suited to compare the proportional strength of the quadriceps of the primates studied here. The quadriceps strength IS association with the animal's weight and locomotor behavior. The bipedalism feature, plus large and heavy bodies in modern humans, indicated stronger quadriceps. Lighter primates with quadrupedal locomotion and jumping features also had stronger quadriceps. Among the apes, weight is associated with quadriceps strength, with lighter animals, such as the *Hylobates*, had stronger quadriceps than the heavier apes. The present study tested different mathematical models to estimate quadriceps strength. The area/volume model seemed to be more adequate for muscles strength analysis, corroborated by the free-body cosine theory, in comparison to other models found in the literature. This model indicated that bipedalism is linked to the quadriceps femoris strength and to the weight of animals: corroborating that modern humans present true bipedalism and that weight is inversely proportional to weight in primates.

Keywords: Primates; quadriceps muscles; PCSA; mathematical models; bipedalism.

INTRODUCTION

Most studies about fleshy tissue on ancient species are carried out by analyzing clues as to the insertions and muscle origins in preserved bones (Aversi-Ferreira et al., 2020). As such, the study of modern animals allows us to create a relationship between past and present species, or specimens, for evolutionary correlations (Zihlman & Bolter, 2015), and, at least, as a data source for taxonomy.

With regard to evolution, morphological and physiological data from primates indicate the phylogenetic path followed by humans; in fact, features such as manual skills and bipedalism are notable human skills that depend on muscle actions and morphological adaptations (Aversi-Ferreira, Vieira, Tomaz, & Aversi-Ferreira, 2014; Visalberghi & Fragaszy, 1995; Westergaard & Suomil, 1995). Data on the evolution of muscle adaptations still do not fully and correctly explain these very well-developed human features. Morphological data from a few primates studied, such as Neotropical ones (Aversi-Ferreira, Marin, Carneiro-e- Silva, & Aversi-Ferreira, 2011, Aversi-Ferreira et al., 2011), could generate more evidence to understand and corroborate, or not, the modern hypothesis of the evolution of locomotion in primates (Ankel-Simons, 2007).

True bipedalism, without large tails, only occurs in humans when considering the evolution of the pelvis and hindlimbs (Zihlman & Bolter, 2015), whereas other non-human primates show only intermittent bipedalism (Aversi-Ferreira et al., 2010; Fragaszy, Visalbergh, & Fedigan, 2004; Haslam et al., 2009).

The evolution of bipedalism represents, at least, an increase in the specialization of the hindlimbs, pelvic and dorsal muscles in humans (Ankel-Simons, 2000). To achieve the complex human morphology that allows for bipedalism to evolve, it starts mainly in primates. Apes are studied in more detail for this proposal. However, data from Old and New World primates are scarce (Aversi-Ferreira et al., 2010), or cover only such things as muscle weight or simple morphology, without taking evolution, taxonomic or locomotor behavior into account (Ogihara et al., 2017). The muscle strength needed for leaping could also provide data for an analysis of bipedalism (Bobbert, 2014).

Studies over the past 20 years have addressed *Sapajus*' intermittent bipedalism and its importance for tool use (Fragaszy, Visalbergh, & Fedigan, 2004). These primates hold stones with their hands and use about 40% of their weight to break open coconuts (Fragaszy et al., 2013; Fragaszy et al., 2010; Liu et al., 2009; Moraes, Souto, & Schiel, 2014; Souto et al., 2011).

They exhibit intermittent bipedalism for foraging (Demes, 2011), despite spending most of their time on a quadrupedal gait, which is their locomotor behavior (Ankel-Simons, 2000; Fragaszy, Visalbergh, & Fedigan, 2004).

Accordingly, a specific study carried out in apes and other primates, as this propose deals with comparative anatomy could provide more data for understanding locomotor behavior linked to muscle strength (Payne et al., 2006; Thorpe et al., 1999).

Hypothetically, the locomotor apparatus of *Sapajus* and *Callithrix*, or other New World primates, could be an intermediate step in the evolution of bipedalism between apes and modern humans, as for the Old World primates.

To make a detailed anatomical analysis of the quadriceps (vastus lateralis, vastus medialis, vastus intermedius, rectus femoris), sartorius and tensor fasciae latae of *Sapajus* and *Callithrix*, muscles were dissected and studied to generate data on morphology, allometry, strength, and behavior. The aim of the study is to explain the relationship between these primate muscles, using published data from *Macaca cyclopis*, *Macaca fasciculata*, *Papio*, apes, and modern humans.

As such, comments were made about bipedalism and locomotor behavior. In addition, muscle strength was calculated using the free-body cosine theory and measurements were obtained to calculate the Physiological Cross Section Area [PCSA] for *Callithrix* and *Sapajus*. Data was also taken from the literature on PCSAs of modern humans, *Pan*, *Gorilla*, *Pongo*, and *Hylobates*, and then, the combined statistical data on quadriceps strength among these primates were compared to be associated with locomotor behavior.

This type of analysis promotes data collection to verify the movement of primates (Bock & Winkler, 1978; Cartmill, 1974), mainly associating it with an environmental substrate, morphology, and locomotor behavior (Ankel-Simons, 2007).

MATERIAL AND METHODS

Samples – Ten adult specimens of capuchin monkeys (*Sapajus* sp) were used, weighing from 2.0 to 3.5 kg. The laboratory received mostly muscle carcasses, so the gender could not be identified, that is, except for one male. No animals were killed for the purposes of this study: they all suffered accidental deaths in their natural habitats and were acquired from the anatomical collection of the Museum of Morphology of the Federal University of Tocantins. The three specimens of *Callithrix* sp used for dissection were donated by Tocantins Nature Institute - NATURATINS -TO and were also acquired from the anatomical collection of the Museum of Morphology of the Federal University of Tocantins. Research on these primates was approved by the Ethics Committee of the Federal University of Goiás (CoEP-UFG 81/2008, with authorization from IBAMA No. 15275), and by the Federal University of Tocantins (CoEP-UFT 23101.003220 / 2013-85).

Preparation of animals for dissection – All procedures on the animals were performed in compliance with the guidelines of the Brazilian Society of Animal Experimentation (COBEA). After trichotomy using a razor blade, the animals were incubated in water at room temperature for 10-12 hours; and then received 10% formaldehyde with 5% glycerin perfusion through the femoral vein for fixation. The animals were preserved in 10% formaldehyde in covered opaque cubes to prevent light penetration and formaldehyde evaporation.

To carry out anatomical observations in this study, after receiving the specimens from the anatomical collection of the Federal University of Tocantins, each one was processed as follows: (1) they received an injection of 601-A latex (Dupont), stained with red Wandalax diluted in ammonium hydroxide, in the abdominal aorta, to facilitate the visualization of small arteries; (2) they were incubated in water, at room temperature, for 10–12 h; and then (3) they received 10% formaldehyde perfusion with 5% glycerin via the femoral vein for fixation. The animals were preserved in 10% formaldehyde in covered opaque cubes to prevent light penetration and formaldehyde evaporation.

Dissection and documentation – Thigh dissection was performed with emphasis on the quadriceps, and the procedure was recorded using a digital camera. Muscle nomenclature is, whenever possible, the same as used in human anatomy (Federative International Programme for Anatomical Terminology, 2019), including the anatomical position, and the book by Swindler and Wood (1973). When such a parallel was not possible, the muscles were named following the standards of the international nomenclature of the Human Anatomical Nominal.

The collected data were analyzed and compared with the patterns described for humans, apes, baboons, *Macaca cyclopis*, and *Macaca fascicularis*.

Anatomical Statistical Analysis – Based on the studies of Aversi-Ferreira (Aversi-Ferreira, 2009; Aversi-Ferreira et al., 2011, Aversi-Ferreira et al., 2014, Aversi-Ferreira et al., 2016), the comparative non-parametric method was applied to associate the different species with their anatomical concepts of normality and variation as nominal variables. This model, here called Model 1, allows the correlation of muscle characteristics with numbers, as explained below.

Table 1. General methods for calculating similarities between the quadriceps and sartorius muscles of *Sapajus* sp and of other species.

Species		<i>Sapajus</i> sp (control species) (i = 1)				<i>Hylobates</i> (i = 6)				...	<i>Pan</i> (i = 9)			
Investigated structures		Rectus femoris	Vastus intermedius	...	Sartorius	Rectus femoris	Vastus intermedius	...	Sartorius	...	Rectus femoris	Vastus intermedius	...	Sartorius
P_{ijk}	Specific weights given to variation													
Innervation (k = 1)	$w_1(=3)$	P_{111}	P_{121}	...	P_{1m1}	P_{211}	P_{221}	...	P_{2m1}	...	P_{s11}	P_{s21}	...	P_{sm1}
Origin (k = 2)	$w_2(=2)$	P_{112}	P_{122}	...	P_{1m2}	P_{212}	P_{222}	...	P_{2m2}	...	P_{s12}	P_{s22}	...	P_{sm2}
Insertion (k = 3)	$w_3(=2)$	P_{113}	P_{123}	...	P_{1m3}	P_{213}	P_{223}	...	P_{2m3}	...	P_{s13}	P_{s23}	...	P_{sm3}
Vascularization (k = 4)	$w_4(=1)$	P_{114}	P_{124}	...	P_{1m4}	P_{214}	P_{224}	...	P_{2m4}	...	P_{s14}	P_{s24}	...	P_{sm4}
Weighted averages for single muscle (PAF = $P_{w(ij)}$)		$P_{w(11)}$	$P_{w(12)}$...	$P_{w(1m)}$	$P_{w(21)}$	$P_{w(22)}$...	$P_{w(2m)}$...	$P_{w(s1)}$	$P_{w(s2)}$...	$P_{w(sm)}$
Weighted averages for multiple muscles (mean of $P_{w(ij)}$) ($P_{w(i)}$)		$P_{w(1)}$				$P_{w(2)}$...	$P_{w(s)}$			
GCAI = $ P_{w(i)} - P_{w(t)} $						$ P_{w(1)} - P_{w(2)} $...	$ P_{w(1)} - P_{w(s)} $			

Note: P_{ijk} = proportion of normal muscles, where i represents individual species, j represents individual structures, and k represents individual parameters of the muscles.

The values for the statistics shown in Table 1 were based on the following formulas:

$$P_{ijk} = \frac{r_{v(ijk)}}{N}$$

where \mathbf{P} is the relative frequency, N is the total number of structures analyzed in the samples, and r_v is the number of normal structures.

$$PAF = P_{w(ij)} = \frac{\sum_{k=1}^q w_k \cdot P_{ijk}}{\sum_{k=1}^q w_k}$$

where P_{ijk} is the relative frequency and w_k is the weighted coefficient attached to a given parameter (i.e., innervation, origin, insertion, vascularization, number of heads),

$$P_{w(i)} = \frac{\sum_{j=1}^{m_j} P_{w(ij)}}{m_j}$$

where m_j is the number of structures studied for each thigh; in this study, $m = 5$ (five muscles). The tensor fasciae latae was not used for this propose [see below].

The $CAI_{ii'}$ represents the absolute difference of weighted averages ($P_{w(ij)}$) of a single structure between the **control species** (i) and other non-control (i') species. To compare one structure ($j = 1$) with one parameter ($k = 1$) between the control ($i = 1$) and non-control ($i' = 2$) species, the formula can be modified, as follows:

$$CAI_{12} = |P_{w(11)} - P_{(21)}|$$

where $i = 1$, and $i' = 2$.

Note that the $CAI_{ii'}$ ranges from 0 to 1, i.e., $0 \leq CAI_{ii'} \leq 1$. This is because the maximum value of $P_{w(ij)}$ is 1 and the minimum is 0.

$$P_{w(i)} = \frac{\sum_{j=1}^{m_j} P_{w(ij)}}{m_j}$$

where m_j is the number of studied structures; in this study, $m = 5$ (five muscles).

$$GCAI_{ii'} = |P_{w(i)} - P_{w(i')}|$$

or

$$GCAI_{ii'} = \left| \frac{\sum_{j=1}^{m_j} P_{w(ij)}}{m_j} - \frac{\sum_{j=1}^{m_j} P_{w(i'j)}}{m_j} \right|$$

GCAI represents a value that indicates the anatomical differences of the five thigh muscles of each species, using *Sapajus* sp as a reference. For GCAI, values closer to 1 indicate more similarities with the reference species.

Values of *i* for the different species were given as follows: *Sapajus* [*i* = 1], *Callithrix* [*i* = 2], *Macaca cyclopis* [*i* = 3], *Macaca fascicularis* [*i* = 4], *Papio* [*i* = 5], *Hylobates* [*i* = 6], *Pongo* [*i* = 7], *Gorilla* [*i* = 8], *Pan* [*i* = 9], *Homo* [*i* = 10].

To calculate the differences between the origins and insertions of the muscles, a logical arrangement of numbers was executed. For the rectus femoris, two heads on the origin were considered and when was taken as such since two of the heads had not completely separated, so it was considered as two. Thus, the origins were 1] two heads, plus the specific origin, such as the iliac spine or greater trochanter; and 2] one head, plus the specific origins for each case. For instance, 5% of the muscles of *Macaca cyclopis* had two heads, so the P_{ijk} was 0.5 for each. This number was divided by two, as one origin was cited as different from the *Sapajus*, so the value was changed to 0.25. However, for the 5% mentioned, the proportion of two heads is similar to *Sapajus*, because $P_{ijk} = [0.25 + (0.25 \times 0.05)] / 1$. This is a complex analysis, however, it is necessary to detail.

Regarding the case of the vastus lateralis, six detailed muscle origin possibilities were observed, i.e., 1] the inferolateral portion of the greater trochanter, 2] the inferoanterior portion of the greater trochanter, 3] the mediolateral portion of the greater trochanter, and the lateral surface of the proximal femur; 4] the lateral portion of the greater trochanter and the lateral surface of the femur; 5] the superior portion of the greater trochanter and the intertrochanteric line; 6] the inferoanterior portion of the greater trochanter and the intertrochanteric line. However, for safety reasons, due to the subjectivity of the observations, only three possibilities of relative frequency were considered, so all citations gathered for the greater trochanter were considered as one. The other different origins were the intertrochanteric line and the proximolateral portion of the femur. For clarification, the origin of the vastus lateralis in *Sapajus* is found in the inferior portion of the greater trochanter, and in *Macaca cyclopis*, it is

found in the mediolateral portion of the greater trochanter and the proximolateral portion of the femur. Thus, P_{ijk} was considered $\frac{1}{2}$, since they share a similar origin in two possibilities. However, *Papio* has the greater trochanter, linea aspera, and diaphysis of the femur, so the P_{ijk} value was defined as $\frac{1}{3}$.

Four possibilities for muscle origin were observed for the vastus intermedius, i.e., 1] the diaphysis of the anterior, lateral, and medial femur; 2] the anterior (only); 3] the anterior and lateral; and 4] the anterior and medial. Number 8 is the vastus medialis; 7 is sartorius; and 3 is the tensor fasciae latae.

Furthermore, the tensor fasciae latae innervation shows two possibilities for muscle origin and six for insertion. However, specific data for this muscle were not mentioned in the reference literature for *Macaca cyclopis* and *Macaca fascicularis*. Since GCAI values will not be calculated considering all the data, the CAI value was not calculated for the tensor fasciae latae.

Vascularization was rarely mentioned by the authors, except in modern humans. As such, given the region and understanding of the general vascular supply of the extensor muscles of the leg, the femoral artery was considered the artery that supplied the muscles in this study.

For cases where there were no data available for nerves, predominant data for other species were given due consideration, i.e., the femoral nerve, for the purposes of the statistical method.

Measurements and PCSA models - Regarding the quantitative analysis of muscle strength, the law of cosines was used, and a vector mechanical analysis was performed. For the quantitative aspects, the formula for the physiological cross-sectional area (PCSA) was calculated:

$$PCSA = \frac{m}{\rho \cdot \ell}$$

where m is the muscle mass, ρ is the muscle density (1.060 kg / m^3), and ℓ is the muscle length. For the purposes of calculating the PCSA, the average of the masses and lengths of the dissected primates was given due consideration, and, when possible, data taken from the literature.

The formulas for the mechanical analysis of components of a force, as determined by the law of cosines, were used for a qualitative analysis, using angle variations only for two heads of the rectus femoris muscle.

A caliper, a goniometer, and a set of scales were used to obtain PCSA data for *Sapajus* and *Callithrix*. Measurements were performed on three specimens of each species, in order to preserve the others for further studies. Muscle lengths were measured before and after the removal of the tendons from origin to insertion. The length of the femur and the muscle fascicles, along with the diameter of the femoral head, were obtained directly using a digital Niigara Seiki caliper model DN-150. Total muscle mass was measured using a Bioprecisa balance (Electronic Balance Fa-2104).

The length of the muscle fascicles was also measured since this part is responsible for the force of contraction. The entire muscle mass was weighed, as complete extension undergoes a contraction movement.

PCSA data were found in the reference literature on modern humans, *Pan*, *Gorilla*, *Pongo*, *Hylobates*, and *Callithrix*. However, data obtained were not sufficient to make a reliable comparison for *Papio*, *Macaca cyclopis*, and *Macaca fascicularis*. Data obtained, mainly from human cadavers, were used for a better and more accurate comparison to analyze the PCSA of *Sapajus* and *Callithrix*.

For a more reliable, feasible, and proportional comparison, three models were used for PCSA data in this study. One of them, Model 2, was used previously (Thorpe et al., 1999), as follows:

$$\frac{\text{muscles mass}}{\text{femur length}^3} [\text{model 2}].$$

The third model proposed in this study is to divide the PCSA by the femoral head area:

$$\frac{\text{PCSA}}{\text{femur head area}} [\text{model 3}].$$

For *Sapajus* and *Callithrix*, the diameter of the head of the femur was obtained directly. However, for other species, except for *Papio*, *Macaca cyclopis*, and *Macaca fascicularis*, data were taken from the literature [modern humans, *Pan*, *Gorilla*, *Pongo*, *Hylobates*].

A fourth model was also proposed in this study to analyze a proportional relationship using PCSA data, based on body growth linked to an area/volume ratio:

$$\frac{\text{PCSA}}{\text{weigh}} [\text{model 4}].$$

In qualitative terms, Models 2, 3, and 4 were utilized to associate quadricep strength and locomotor behavior in the primates studied in this study.

The values obtained to build the models were scrutinized using a trendline analysis to attain the best fit with the data, according to the taxonomy and gross anatomy of the groups. The best model should be able to demonstrate the morphological similarities between the groups, bundling the species together.

Due to a lack of data for comparison, the PCSA was calculated for quadriceps and sartorius and no calculation was performed for the tensor fasciae latae. In this case, only a crude comparative analysis was performed.

RESULTS AND DISCUSSION

1. Model 1 and gross anatomical descriptions

Gross anatomical and statistical data were compiled into two tables (Tables 2a and 2b), containing muscle data from the literature for *Macaca cyclopis*, *Macaca fascicularis*, *Papio*, apes, and modern humans. CAI and GCAI values of dissected *Sapajus* sp were included as a reference species and *Callithrix* as a dissected species (Tables 2a and 2b).

A more detailed comparison was performed on the *Sapajus* and *Callithrix* specimens dissected in this study. The general description taken from the literature was applied to the other primates mentioned.

The **rectus femoris** (figures 2 and 4) in *Sapajus* has two heads in its origin. The reflected head originates from the superior and posterior border of the ilium, above the acetabulum, next to the aponeurosis of the head of the rectus. The head of the rectus originates from a slender tendon of the sartorius, and a tendon from the inferior portion of the anteroinferior iliac spine. It inserts into the quadriceps tendon, is innervated by the femoral nerve, and is supplied by the femoral artery.

Similarly, in *Callithrix*, the rectus femoris also has two heads in its origin. The reflected head originates from the lateral border and the posterior ilium in the acetabulum. The straight head originates from the inferoanterior iliac spine and the lateral margin of the ilium. It inserts into the patellar tendon and is innervated by the femoral nerve. The CAI₁₂ in relation to *Sapajus* is 0.0000.

The rectus femoris is identical in *Sapajus*, *Callithrix*, *Papio*, *Gorilla*, *Pan*, and modern humans [CAI = 0.0000]. However, some differences were observed between *Sapajus* compared to *Macaca cyclopis* [CAI = 0.1313] and *Macaca fascicularis* [CAI = 0.1875] and *Pongo* [CAI = 0.8125]. Muscle origins varied regarding the number of heads, i.e., *Macaca cyclopis*, *Hylobates*, and *Pongo* (Ferrero, 2011; Fukuda & Sakuma, 1962; Gibbs, 1999; Kimura, Takahashi, Konishi, & Iwamoto, 1983) have only one head in the rectus femoris, (Fukuda & Sakuma, 1962; Kimura, Takahashi, Konishi, & Iwamoto, 1983; Swindler & Wood, 1973), while in *Sapajus*, *Callithrix*, *Papio*, *Gorilla*, *Pan*, and modern humans, it has two separate heads (Ferrero, 2011; Gibbs, 1999; Kimura, Takahashi, Konishi, & Iwamoto, 1983; Raven, 1950; Sonntag, 1924; Standring, 2008; Swindler & Wood, 1973).

Since the origin of the rectus femoris head is in deep association with the acetabulum capsule, the division of the tendons by the iliac border was considered two heads in order to

avoid interpretation problems. As for the *Papio*, the presence of two heads, which were not completely separated, was observed (Swindler & Wood, 1973). However, the two heads of the rectus femoris are not completely separated for all primates. Thus, the observation that the head is not completely separated (Swindler & Wood, 1973) may be difficult to understand, but it was considered here as a different standard for the purposes of a statistical analysis.

For all primates studied, it was found that the insertion, innervation and vascularization (Ferrero, 2011; Fukuda & Sakuma, 1962; Gibbs, 1999; Kimura, Takahashi, Konishi, & Iwamoto, 1983; Raven, 1950; Sonntag, 1924; Standring, 2008; Swindler & Wood, 1973) were identical: for the patella next to the quadriceps tendon, the femoral nerve and the femoral artery, respectively.

The **vastus lateralis** (figure 2) in *Sapajus* originates from the inferolateral portion of the greater trochanter of the femur and exchanges fibers with the vastus intermedius; it inserts into the tibial tuberosity forming the lateral part of the quadriceps femoris tendon. It is innervated by the femoral nerve and supplied by the femoral artery.

Similar to the case of the *Sapajus*, the *Callithrix*' vastus lateralis originates from the proximolateral and inferior portion of the greater trochanter and inserts into the patellar tendon. It has the same innervation, i.e., the femoral nerve. The value of CAI₁₂ equaled 0.000.

The CAI values were 0.000 for *Callithrix* and *Papio* compared with *Sapajus*, but it differed for *Macaca cyclopis* [CAI₁₃ = 0.1250], *Macaca fascicularis* [CAI₁₄ = 0.1250], *Hylobates* [CAI₁₆ = 0.1667], *Pongo* [CAI₁₇ = 0.1667], *Gorilla* [CAI₁₈ = 0.1250], *Pan* [CAI₁₉ = 0.1875], and modern humans [CAI₁₁₀ = 0.1875]. The main causes of differences were the muscle origins, such as the greater trochanter, the intertrochanteric line, and the proximal lateral femur, for instance. Furthermore, the association with other muscle origins also differed, such as the gluteus maximus in humans and the iliofemoral ligament in *Pongo* (Ferrero, 2011).

As for the quadriceps muscles of all primates studied, the insertion, innervation, and vascularization were identical: for the patella next to quadriceps tendon, femoral nerve, and femoral artery, respectively (Ferrero, 2011; Fukuda & Sakuma, 1962; Gibbs, 1999; Kimura, Takahashi, Konishi, & Iwamoto, 1983; Raven, 1950; Sonntag, 1924; Standring, 2008; Swindler & Wood, 1973).

The description of another quadriceps muscle, the **vastus intermedius** (figure 1) is identical between *Sapajus* and *Callithrix* [CAI₁₂ = 0.000]. In both, the muscle originates from the anterior, lateral, and medial portions of almost the entire length of the femur and inserts into

the quadriceps femoris tendon in the patella. It is innervated by the femoral nerve and supplied by the femoral artery.

The CAI values were identical for *Sapajus* when compared to *Pongo* [CAI₁₇ = 0.0000], *Gorilla* [CAI₁₈ = 0.0000], *Pan* [CAI₁₉ = 0.0000] and modern humans [CAI₁₁₀ = 0.0000], but differed for *Macaca cyclopis* [CAI₁₃ = 0.1667], *Macaca fascicularis* [CAI₁₄ = 0.1667], *Papio* [CAI₁₅ = 0.1250], and *Hylobates* [CAI₁₆ = 0.1250].

As previously mentioned, the insertion, innervation, and vascularization were identical for the quadriceps muscles in this study, but differed in their origin, placed on different portions of the femur, namely lateral and medial [*Gorilla*] (Ferrero, 2011; Gibbs, 1999; Raven, 1950); lateral, anterior, and medial [*Sapajus*, *Callithrix*, *Pan*, and modern humans] (Ferrero, 2011; Gibbs, 1999; Kimura, Takahashi, Konishi, & Iwamoto, 1983; Standring, 2008; Swindler & Wood, 1973); and anterior only [*Macaca cyclopis*, *Macaca fascicularis*, and *Papio*] (Fukuda & Sakuma, 1962; Kimura, Takahashi, Konishi, & Iwamoto, 1983; Swindler & Wood, 1973).

The **vastus medialis** muscle (figure 1), from the intertrochanteric line of the femur to the insertion into the tibial tuberosity, as the medial part of the quadriceps femoris, is identical for *Sapajus* and *Callithrix* [CAI₁₂ = 0.000]. In both, the **vastus medialis** is innervated by the femoral nerve and supplied by the femoral artery.

Unlike *Sapajus* and *Callithrix*, this muscle has different CAI values for all other primates, i.e., *Macaca cyclopis* [CAI₁₃ = 0.1500], *Macaca fascicularis* [CAI₁₄ = 0.1250], *Papio* [CAI₁₅ = 0.1250], *Hylobates* [CAI₁₆ = 0.2500], *Pongo* [CAI₁₇ = 0.2500], *Gorilla* [CAI₁₈ = 0.2500], *Pan* [CAI₁₉ = 0.1875], and modern humans [CAI₁₁₀ = 0.2143].

Differences were caused by variations of the muscle origin on the lesser trochanter and lateral edge of the greater trochanter [*Macaca cyclopis*] (Fukuda & Sakuma, 1962); the intertrochanteric line of the medioanterior portion of the proximal part of the femur connected to the pectineal line [*Macaca fascicularis*] (Kimura, Takahashi, Konishi, & Iwamoto, 1983); the intertrochanteric line and the medial lip for 1/3 of the femur [*Papio*] (Swindler & Wood, 1973); the iliofemoral ligament and the posteromedial portion of the femoral diaphysis at the linea aspera [*Hylobates*] (Ferrero, 2011; Gibbs, 1999); the internal lip of the linea aspera, the iliofemoral ligament, and the intermuscular septum of the thigh [*Pongo*] (Ferrero, 2011); the posteromedial zone of the femoral diaphysis and the medial lip of the linea aspera [*Gorilla*] (Ferrero, 2011; Gibbs, 1999; Raven, 1950); the iliofemoral ligament, the intertrochanteric line, the entire femoral neck, the posteromedial surface of the femoral diaphysis, and the medial lip of the linea aspera [*Pan*] (Ferrero, 2011; Gibbs, 1999; Sonntag, 1924; Swindler & Wood, 1973);

the inferior portion of the intertrochanteric line, the spiral line, the medial lip of the linea aspera, the proximal part of the supracondylar line, the long adductor magnus tendon, and the medial intermuscular septum [modern humans] (Standring, 2008; Swindler & Wood, 1973). As such, this muscle has a different origin for each primate shown in this study.

For the **sartorius** (figure 2), muscle origin and insertion differ for both *Sapajus* and *Callithrix* [$CAI_{12} = 0.08334$]. However, the portion of the bones of origin, namely, the ilium in the iliac crest and the iliac spine, respectively, are considerably close. The insertion occurs in the identical portion of the proximal tibia. During dissection, the arterial supply to the *Callithrix*' sartorius could not be determined easily, however, due to the location of the muscle and the femoral artery, it was considered that this artery supplied the muscle.

Specifically, and in more detail, the sartorius in *Sapajus* originates from the external oblique abdominal fascia and the anterior portion of the iliac crest; it inserts into the tibial tuberosity and exchanges fibers with the gracilis muscle; it is innervated by the femoral nerve and supplied by the femoral artery. For *Callithrix*, the sartorius originates in the anterosuperior iliac spine and is inserted on the medial portion of the proximal tibia. It is innervated by the femoral nerve.

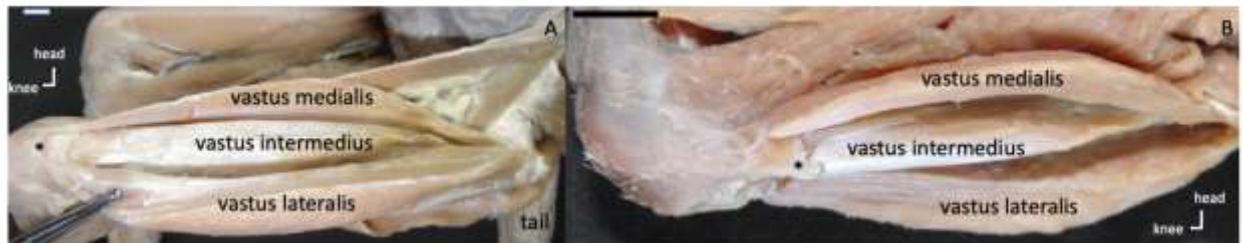


Figure 1: Photos of the left thighs, anterior view, of the *Sapajus* (A) and *Callithrix* (B). The muscles are identified as shown on the structures. * indicates the tendon of the rectus femoris muscle that was removed. Scales: A [1:1.5]; B [1:3].

Sapajus and other primates differed due to the different muscle origins for each of them (Beddard, 1893; Ferrero, 2011; Gibbs, 1999; Kimura, Takahashi, Konishi, & Iwamoto, 1983; Raven, 1950; Sigmon, 1974; Sonntag, 1924; Standring, 2008; Swindler & Wood, 1973), resulting in different CAIs: *Macaca cyclopis* [$CAI_{13} = 0.22222$], *Macaca fascicularis* [$CAI_{14} = 0.2222$], *Papio* [$CAI_{15} = 0.2222$], *Hylobates* [$CAI_{16} = 0.08334$], *Pongo* [$CAI_{17} = 0.08334$], *Gorilla* [$CAI_{18} = 0.1250$], *Pan* [$CAI_{19} = 0.250$] and modern humans [$CAI_{10} = 0.1250$].

The CAI was not calculated for the **tensor fasciae latae** (figure 2) since there was no anatomical description found for this muscle for both genera of *Macaca* studied here. The CAI

was not calculated due to its minor importance for the general function of the anterior region of the thigh.

Thus, only a morphological description was given. This muscle had considerable differences between *Sapajus* and *Callithrix* regarding insertion and innervation. In *Sapajus*, it originates from the anterior margin and lateral portion of the ilium and inserts into the fasciae latae laterally; it is innervated by the cranial gluteal nerve and supplied by the femoral artery. In *Callithrix*, the tensor fasciae latae originates from the anterosuperior portion of the iliac spine and the fascia of the gluteus maximus; it inserts into the fasciae latae, and is innervated by a branch of the sciatic nerve.

Differences regarding the other primates were due to the three different origins, namely the anterior portion of the anterosuperior iliac spine and fascia of the gluteus maximus [*Callithrix*, *Hylobates*] (Ferrero 2011; Sigmon, 1974); the lateral portion of the greater trochanter [*Papio*] (Swindler & Wood, 1973); the iliac spine [*Pongo* (when present)] (Ferrero, 2011; Kaplan & Meier, 1958; Sigmon, 1974); and the superoanterior iliac spine and fasciae latae [*Gorilla*, *Pan*, and modern humans] (Ferrero, 2011; Gibbs, 1999; Kaplan & Meier, 1958; Miller, 1952; Raven, 1950; Sigmon, 1974; Standring, 2008; Swindler & Wood, 1973). There are two types of innervation: the femoral nerve and the superior gluteal nerve [*Sapajus*, *Callithrix* (ischiatric branch), *Pongo*, *Gorilla*, *Pan*, and modern humans] (Ferrero, 2011; Gibbs, 1999; Kaplan & Meier, 1958; Miller, 1952; Raven, 1950; Sigmon, 1974; Standring, 2008; Swindler & Wood, 1973). There are six different insertions, namely, the fascia latae [*Sapajus*, *Callithrix*]; the lateral patella [*Papio*] (Swindler & Wood, 1973); the iliotibial tract [*Hylobates*] (Ferrero, 2011; Sigmon, 1974); the iliotibial tract fused with gluteal muscles [*Pongo* (if present)] (Ferrero, 2011; Kaplan & Meier, 1958; Sigmon, 1974; Gibbs, 1999); the iliotibial tract, femoral diaphysis, patella, and upper leg fascia [*Pan*] (Ferrero, 2011; Gibbs, 1999; Miller, 1952; Sigmon, 1974; Swindler & Wood, 1973); the two layers of the iliotibial tract of the fascia lata, where it usually ends 1/3 of the way down the thigh, but occasionally extends to the lateral femoral condyle [modern humans] (Standring, 2008; Swindler & Wood, 1973).

The tensor fasciae latae is very different among the primates studied, perhaps because the diameter is smaller and they are shorter compared to the quadriceps and sartorius muscles, acting with little force on the knee joint.

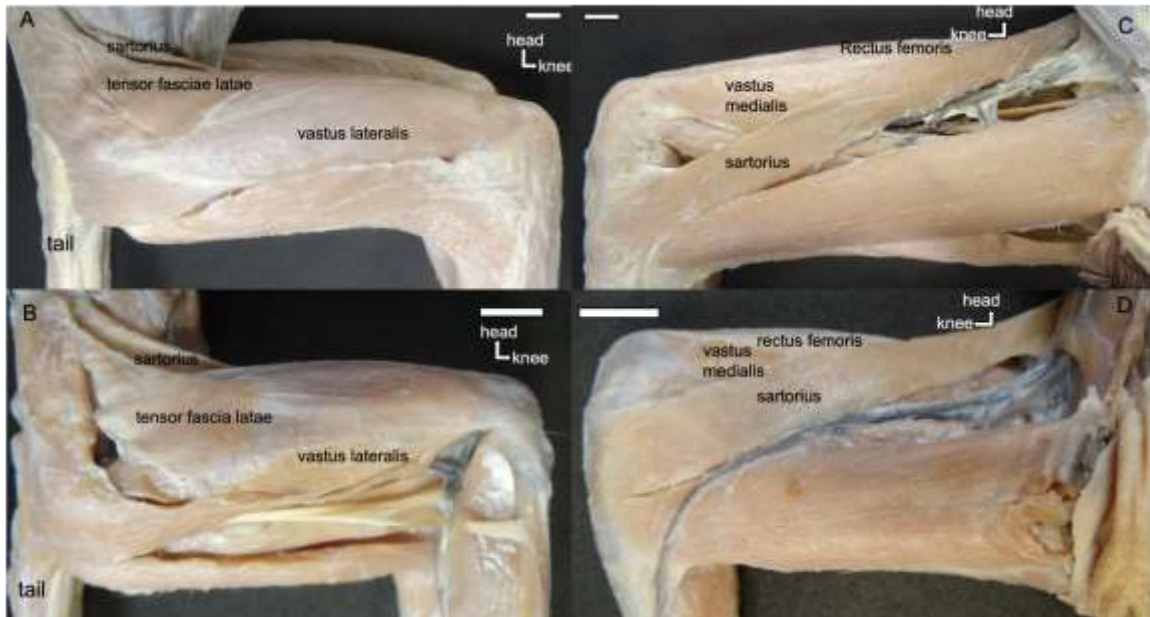


Figure 2: Photos from the right thighs of *Sapajus*, lateral aspect (A), medial aspect (C) and *Callithrix* lateral aspect (B), medial aspect (D). The muscles are identified as shown on the structures. Scales: A [1:1.3]; B [1:2]; C [1:1.44]; D [1:3.3].

Generally, the quadriceps and sartorius muscles of the primates studied here are very similar for *Sapajus* and *Callithrix*, (figure 3) with $GCAI_{12} = 0.9834$. There were some differences observed for the other primates, namely, $GCAI_{13} = 0.8680$, $GCAI_{14} = 0.8347$, $GCAI_{15} = 0.9056$, $GCAI_{16} = 0.8750$, $GCAI_{17} = 0.68754$, $GCAI_{18} = 0.8834$, $GCAI_{19} = 0.8750$, $GCAI_{110} = 0.8946$ (figure 3).

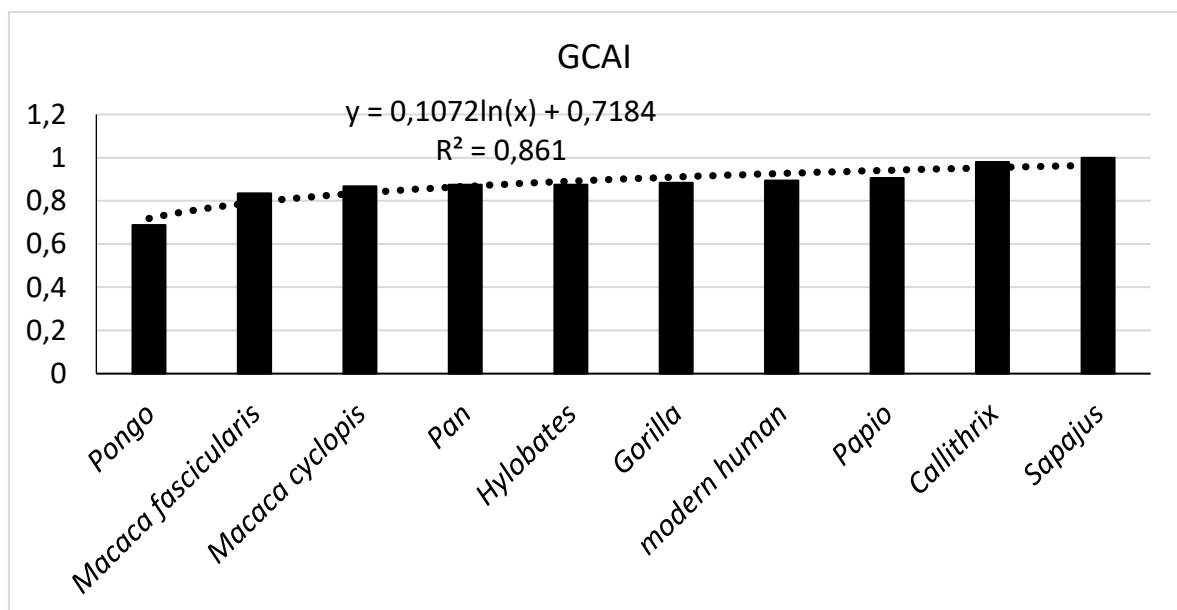


Figure 3. GCAI values [model 1] for primates studied here in relation to reference specie *Sapajus*. From left to right, the anatomical distance for GCAI, as calculated, increases.

The greatest difference was shown with *Pongo* [GCAI₁₇ = 0.68754] and *Macaca fascicularis* [GCAI₁₄ = 0.8347] which could be explained by a particular specialization this primate in evolutionary locomotion and because the geographic isolation of the *Macaca fascicularis*, which is endemic in Japan.

As such, the greatest similarity, as expected, occurred between *Sapajus* and *Callithrix* [GCAI₁₂ = 0.9834] (figure 3) which could be explained by both being neotropical primates with closer ancestry. As observed in other studies on the muscles of the thoracic limbs and vascularization of the lower limbs, a high similarity was found between *Sapajus* and *Papio* [GCAI₁₅ = 0.9056]. This could be explained by the closer ancestry and/or identical locomotor behavior, however, the migration of ancestral primates from the Old to the New World is very controversial (Cartmill, 1974; Seiffert et al., 2020).

The morphological gross anatomy analysis, using Model 1 for the quadriceps and sartorius muscles, is similar for New World primates grouped to the right on the *x*-axis (figure 3), with the *Pongo* being the furthest away from *Sapajus*. Since *Sapajus* is the reference species, the data show the gross anatomical distance from this primate, so the taxonomy cannot be considered for this analysis, specifically for the quadriceps. In fact, the Pan's forearm was more similar to *Sapajus* than to *Papio* and modern humans, in an analysis using GCAI (Aversi-Ferreira et al., 2010).

Table 2a. Comparative data features from the dissected *Sapajus* sp and *Callithrix* sp and Old-World Primates from literature with CAI and GCAI values in comparison with *Sapajus* (reference specie).

<i>Sapajus</i> sp	<i>Callithrix</i> sp	<i>Macaca cyclopis</i> (Fukuda & Sakuma, 1962)	<i>Macaca fascicularis</i> (Kimura, Takahashi, Konishi, & Iwamoto, 1983)	<i>Papio</i> (Swindler & Wood, 1973)
Rectus femoris muscle				
Two heads of origin. The reflected head originates from the superior and posterior border of ilium above the acetabulum together with the aponeurosis of rectus straight head. The rectus straight head originates from a thin tendon in the sartorius and a tendon from the inferior portion of the anterior inferior iliac	Two heads of origin. The reflected one originates from the lateral border and posterior body of ilium on the acetabulum and the rectus straight head originates from the anterior aspect of the anterior inferior iliac spine and lateral border of ilium. It inserts onto the patellar tendon. Innervation: femoral nerve	Originates from iliac spine and acetabulum border and ilium. 5% of them originate with two heads; inserts onto patella base together other vasti muscles. Innervation: femoral nerve CAI ₁₃ = 0.1313	It has one head. Originates from a robust tendon from the anterior border of the ilium and the surface of the acetabulum. Inserts on the tibia tuberosity. Innervation: femoral nerve. CAI ₁₄ = 0.1875	Originates from ante-acetabular process of ilium. The heads are not completely separated. Inserts onto base of patella. Innervation: femoral nerve CAI ₁₅ =0.0000

spine. Inserts onto the quadriceps tendon. Innervated by the femoral nerve. Supplied by the femoral artery.	CAI ₁₂ = 0.0000			
Vastus lateralis muscle				
		(Fukuda & Sakuma, 1962)	(Kimura, Takahashi, Konishi, & Iwamoto, 1983)	(Swindler & Wood, 1973)
Originates from lateral-inferior aspect the greater trochanter of femur and exchanges fibers with vastus intermedius. Inserts onto tuberosity tibiae forming the lateral part of the quadriceps femoris tendon. Innervated by the femoral nerve. Supplied by the femoral artery.	Originates from the proximal lateral and inferior to the greater trochanter and inserts onto the patella tendon. Innervation: femoral nerve CAI ₁₂ = 0.000	Originates from the middle lateral aspect of the greater trochanter and lateral proximal surface of the femur. It inserts onto the patella base together with tendon of the vastus intermedius. Innervation: femoral nerve CAI ₁₃ = 0.1250	Originates from the lateral aspect of the greater trochanter and proximal lateral of the femur. Inserts onto tuberosity of tibia and patella retinaculum. Innervation: femoral nerve. CAI ₁₄ = 0.1250	Originates from lateral aspect of the greater trochanter. Inserts onto lateral patella. Innervation: femoral nerve CAI ₁₅ =0.0000
Vastus intermedius muscle				
		(Fukuda & Sakuma, 1962)	(Kimura, Takahashi, Konishi, & Iwamoto, 1983)	(Swindler & Wood, 1973)
Mainly originates from the anterior, but also the lateral and medial faces of almost the entire length of the femur. Inserts onto quadriceps femoris tendon. Innervated by the femoral nerve. Supplied by the femoral artery.	Originates from the anterior, lateral, and medial proximal in the femur shaft and inserts onto patella tendon. Innervation: femoral nerve CAI ₁₂ =0.0000	Originates from the anterior aspect of the lower femur shaft and inserts onto the anterior surface of the patella together other tendons of the quadriceps. Innervation: femoral nerve CAI ₁₃ = 0.1667	Originates from anterior surface of the femur and inserts onto patella base. Innervation: femoral nerve. CAI ₁₄ =0.1667	Originates from anterior surface of the femur. Inserts onto base patella. Innervation: femoral nerve CAI ₁₅ =0.1250
Vastus medialis muscle				
		(Fukuda & Sakuma, 1962)	(Kimura, Takahashi, Konishi, & Iwamoto, 1983)	(Swindler & Wood, 1973)
Originates from the intertrochanteric line of the femur and inserts in the tuberosity of tibiae as the medial part of the quadriceps femoris. Innervated by the femoral nerve. Supplied by the femoral artery.	Originates from the intertrochanteric line and inserts onto patella tendon. Innervation: femoral nerve CAI ₁₂ = 0.0000	Originates from medial aspect of the lesser trochanter and lateral border of the greater trochanter (intertrochanteric line); 6% originates from ½ or 1/3 proximal shaft of the femur. It inserts onto the medial border of the patella.	Originates from the intertrochanteric line to the anterior medial aspect of the proximal part of the femur linked to pectineal line. Inserts onto tibial tuberosity. Innervation: femoral nerve. CAI ₁₄ = 0.1250	Originates from intertrochanteric line and medial lip for 1/3 of the femur Inserts onto medial patella. Innervation: femoral nerve CAI ₁₅ =0.1250

		Innervation: femoral nerve CAI ₁₃ = 0.0150		
Sartorius muscle				
		(Fukuda & Sakuma, 1962)	(Kimura, Takahashi, Konishi, & Iwamoto, 1983)	(Swindler & Wood, 1973)
Originates from the obliquus externus abdominal fascia and anterior facies of the crista iliaca. Inserts onto tuberositas tibiae and exchanges fibers with gracilis muscle. Innervated by the femoral nerve. Supplied by the femoral artery.	Originates from the anterior superior iliac spine and inserts onto the medial aspect of the proximal tibia. Innervation: femoral nerve CAI ₁₂ = 0.08334	Originates from the middle part of the anterior border of the ilium together the origin of the tensor fasciae latae. Inserts onto the proximal tibia together the tendon of gracilis and semitendinosus. Innervation: femoral nerve CAI ₁₂ = 0.2222	Originates from the border of the ilium between acetabulum and iliac crest; it is fused with tensor of fasciae latae and with the aponeurosis of the obliquus externus abdominis. Inserts onto anterior surface of the tibia. Innervation: femoral nerve. CAI ₁₃ = 0.2222	Originates from middle 1/3 of margo acetabuli of ilium Inserts onto proximal tibia. Innervation: femoral nerve CAI ₁₄ = 0.2222
Tensor fasciae latae muscle				
		(Fukuda & Sakuma, 1962)	(Kimura, Takahashi, Konishi, & Iwamoto, 1983)	(Swindler & Wood, 1973)
Originates from anterior margin and lateral aspect of the ilium. Inserts onto laterally fasciae latae. Innervated by the gluteus cranialis nerve. Supplied by the femoral artery.	Originates from the anterior aspect of the anterior superior iliac spine and fasciae of the gluteus maximus. Inserts onto fascia lata. Innervation: branch of the ischiatic nerve	-----	-----	Originates from lateral aspect of the greater trochanter. Inserts onto lateral patella. Innervation: femoral nerve
GCAI [except for tensor fasciae latae]	GCAI ₁₂ = 0.9834	GCAI ₁₃ = 0.8680	GCAI ₁₄ = 0.8347	GCAI ₁₅ = 0.9056

*m_j=5

Table 2b. Comparative data features from the dissected *Sapajus* and for apes and modern humans from literature indicating the CAI values for comparison with *Sapajus* (reference specie).

<i>Sapajus</i> sp	<i>Hylobates</i> (Ferrero, 2011; Gibbs, 1999)	<i>Pongo</i> (Ferrero, 2011)	<i>Gorilla</i> (Ferrero, 2011; Gibbs, 1999; Raven, 1950)	<i>Pan</i> (Ferrero, 2011; Gibbs, 1999; Sonntag, 1924; Swindler & Wood, 1973)	<i>Homo</i> (Standing, 2008; Swindler & Wood, 1973)
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Rectus femoris muscle					
<p>Two heads of origin. The reflected head originates from superior and posterior border of acetabulum together with the aponeurosis of rectus straight head. The rectus straight head originates from a thin tendon of the sartorius and a tendon from the inferior portion of the anterior inferior iliac spine. Inserts onto tendon of the quadriceps. Innervated by the femoral nerve. Supplied by the femoral artery.</p>	<p>Possesses only one head, the rectum, that originates from the distal portion of the anterior inferior iliac spine, immediately superior to acetabulum. Inserts onto superior border of the patella and by patellar ligament onto tibial tuberosity.</p> <p>Innervation: femoral nerve.</p> <p>CAI₁₆ = 0.1250</p>	<p>Possesses only one head, the rectum, that originates from anterior inferior iliac spine, between the iliac portion of the iliopsoas and scansorius, distal to arise of the sartorius, and some fibers originates from acetabular fossa. Inserts onto superior border of the patella base and by patellar ligament onto tibial tuberosity. Is more related with vastus lateralis than others vastus.</p> <p>Innervation: data not available.</p> <p>CAI₁₇ = 0.1875</p>	<p>It has two heads. The rectum head originates from anterior inferior iliac spine, and the reflexum head originates from acetabular fossa. Inserts onto patellar base and capsule of the knee.</p> <p>Innervation: femoral nerve.</p> <p>Comments: according to the Gibbs (1999), the caput rectum and caput reflexum are present as distinct structures in 2/3 of <i>Gorilla</i>.</p> <p>CAI₁₈ = 0.0000</p>	<p>Originates from ante-acetabular process of ilium (heads not completely separated). The present head is the reflexum that originates distally from anterior inferior iliac spine and from ilium surface upper to acetabular fossa. Inserts onto superior portion of the patella. Is fused with vastus lateralis and medialis.</p> <p>Innervation: femoral nerve (saphenous branches (Sonntag, 1924).</p> <p>CAI₁₉ = 0.0000</p>	<p>It has a double origin on the ilium; the straight tendon originates from the anterior inferior iliac spine, and a thinner, flatter reflected tendon from a groove above the acetabulum and from the fibrous capsule of the hip joint. Rectus straight femoris may originates from the anterior superior iliac spine and its reflected head may be absent. Inserts onto base of the patella.</p> <p>Innervation: femoral nerve.</p> <p>CAI₁₁₀ = 0.0000</p>
Vastus lateralis muscle					
	(Ferrero, 2011)	(Ferrero, 2011)	(Ferrero, 2011; Gibbs, 1999; Raven, 1950)	(Ferrero, 2011; Gibbs, 1999; Swindler & Wood, 1973)	(Standring, 2008; Swindler & Wood, 1973)
<p>Originates from lateral-inferior aspect of the greater trochanter of femur and exchanges fibers with vastus intermedius. Inserts onto tuberosity tibiae forming the lateral part of the quadriceps femoris tendon.</p> <p>Innervated by the femoral nerve. Supplied by the femoral artery.</p>	<p>It runs from the lateral and inferior part of the greater trochanter to 1/3 proximal part of the lateral aspect of the femur diaphysis together linea aspera. Inserts onto superior external border of the patella and by patellar ligament onto tibial tuberosity.</p> <p>Innervation: by femoral nerve.</p> <p>CAI₁₆ = 0.1667</p>	<p>Originates from lateral aspect of the greater trochanter, 2/3 distal of the external lip of the linea aspera and iliofemoral ligament. Inserts onto superior external border of the patella and by patellar ligament onto tibial tuberosity.</p> <p>Innervation: Data are not available.</p> <p>CAI₁₇ = 0.1667</p>	<p>Originates from lateral aspect of the greater trochanter and 2/3 proximal of the lateral aspect of the femoral diaphysis. Inserts onto base of the patella and capsule of the knee joint and by patellar ligament onto tibial tuberosity.</p> <p>Innervation: by femoral nerve.</p> <p>CAI₁₈ = 0.1250</p>	<p>Originates from the anterior inferior border of the greater trochanter, intertrochanteric line, gluteal tuberosity and 2/3 distal of the lateral lip of the linea aspera of the femur.</p> <p>It divides the insertion tendon of the gluteus medius. Inserts onto superior lateral border of the patella. Is associated with vastus intermedius and medial.</p> <p>Innervation: by femoral nerve.</p> <p>CAI₁₉ = 0.1875</p>	<p>Originates from a broad aponeurosis from upper part of the intertrochanteric line, the anterior and inferior borders of the greater trochanter, the lateral lip of the gluteal tuberosity, the proximal half of the lateral lip of the linea aspera, many fibers originate from deep surface of its aponeurosis, few fibers originate from tendon of origin of the gluteus maximus and the lateral intermuscular septum between vastus lateralis and the short head of the biceps femoris. Inserts onto base and lateral border</p>

					of the patella and blends into the compound quadriceps femoris tendon; it contributes an expansion to the capsule of the knee joint which descends to the lateral condyle of the tibia and blends with the iliotibial tract. Innervation: femoral nerve. CAI ₁₁₀ = 0.1875
Vastus intermedius muscle					
	(Ferrero, 2011)	(Ferrero, 2011)	(Ferrero, 2011; Gibbs, 1999; Raven, 1950)	(Ferrero, 2011; Gibbs, 1999; Swindler & Wood, 1973)	(Gibbs, 1999; Standring, 2008; Swindler & Wood, 1973)
Mainly originates from in the anterior, but also, lateral and medial faces of almost the entire length of the femur. Inserts onto quadriceps femoris tendo. Innervated by the femoral nerve. Supplied by the femoral artery.	Originates from proximal femur diaphysis, medial, lateral and anteriorly and inserts onto superior external border of the patella and by patellar ligament and inserts onto tibial tuberosity. Innervation: femoral nerve. CAI ₁₆ = 0.0000	Originates from femoral diaphysis in anterior, medial and lateral aspects extending distally, insert onto superior external border of the patella and by patellar ligament onto tibial tuberosity. Innervation: Data are not available. CAI ₁₇ = 0.0000	Originates from the anterior femoral diaphysis extending medially and may include the capsule of the femoral neck. Inserts onto base of the patella and capsule of the knee joint and by patellar ligament onto tibial tuberosity. Innervation: femoral nerve. CAI ₁₈ = 0.08325	Originates from anterior, medial and lateral aspects of the proximal half of the femoral diaphysis. Inserts onto the superior aspect of the patella and the capsule of the knee joint. Innervation: femoral nerve. CAI ₁₉ = 0.00000	Originates from the anterior and lateral surfaces of the upper 2/3 of the femoral shaft and the lower part of the lateral intermuscular septum. Inserts onto lateral border of patella and lateral condyle of the tibia. Appears to be inseparable from vastus medialis. Innervation: femoral nerve. CAI ₁₁₀ = 0.0000
Vastus medialis muscle					
	(Ferrero, 2011)	(Ferrero, 2011)	(Ferrero, 2011; Gibbs, 1999; Raven, 1950)	(Ferrero, 2011; Swindler & Wood, 1973)	(Gibbs, 1999; Standring, 2008; Swindler & Wood, 1973)
Originates from linea intertrochanterica of femur and inserts in tuberositas tibiae forming the medial part of the quadriceps femoris. Innervated by the femoral nerve.	Originates from iliofemoral ligament and posteromedial part of the femoral diaphysis at linea aspera, to superior internal border of the patella and by patellar ligament inserts onto tibial tuberosity.	Originates from the internal lip of the linea aspera, ligament iliofemoral and intermuscular septum of the thigh. Inserts onto superomedial border of the patella and by patellar ligament	Originates from the posteromedial zone of the femoral shaft and medial lip of the linea aspera, to base and the medial aspect of the patella and by patellar ligament onto tibial tuberosity. Innervation: by femoral nerve.	Originates from iliofemoral ligament, intertrochanteric line, all femur neck, posteromedial surface of the femur shaft and medial lip of the linea aspera. Inserts onto medial supracondylar line, to medial patella and medial zone of the	Originates from lower part of the intertrochanteric line, spiral line, medial lip of the linea aspera, proximal part of the supracondylar line, the tendon of the adductor longus and magnus and the medial intermuscular septum. Inserts by

Supplied by the femoral artery.	Innervation: by femoral nerve. CAI ₁₆ = 0.2500	onto tibial tuberosity. Innervation: Data are not available. CAI ₁₇ = 0.2500	CAI ₁₈ = 0.2500	capsule of the knee joint. Innervation: by femoral nerve. CAI ₁₉ = 0.1875	an aponeurosis onto medial border of the patella and quadriceps tendon; an expansion from this aponeurosis reinforces the capsule of the knee joint and is attached below to the medial condyle of the tibia. Innervation: by femoral nerve. Comments: the lowest fibers of the vastus medialis are nearly horizontal and form a bulge in the living beings, medial to the upper half of the patella, this part of the vastus medialis is called vastus medialis obliquus, with fibers that originate largely from the tendon of the adductor magnus and insert into the medial border of the patella; it plays an important role in the function of the patellofemoral joint. CAI ₁₁₀ = 0.2143
Sartorius muscle					
	(Ferrero, 2011; Sigmon, 1974)	(Beddard, 1893; Ferrero, 2011; Sigmon, 1974)	(Ferrero, 2011; Gibbs, 1999; Raven, 1950)	(Ferrero, 2011; Gibbs, 1999; Sigmon, 1974; Swindler & Wood, 1973)	(Standring, 2008; Gibbs, 1999; Swindler & Wood, 1973)
Originates from of the obliquus externus abdominal fascia and anterior face of the crista iliaca. Inserts onto tuberositas tibiae and exchanges fibers with gracilis muscle. Innervated by the femoral nerve. Supplied by the femoral artery.	Originates from the anterior iliac border (Hepburn 1892; Beddard 1893), (region of the anterior superior iliac spine) as well as from the lateral iliac border. The muscle courses obliquely over the thigh dorsal to the medial femoral condyle. Insertion is onto the medial border of the tibial shaft superficial to	Originates from the ventral (anterior) iliac border, often including the anterior superior iliac spine, and occasionally also from the lateral iliac border to the medial border of the femoral shaft. The insertion of the sartorius is superficial to those of gracilis and semitendinosus.	Originates from lateral border of the ilium. Inserts onto proximal and medial border of the tibia diaphysis and medial crural fascia. Innervation: femoral nerve. CAI ₁₈ = 0.1250	Originates from aponeurosis of the entire length of margo of the acetabuli of ilium, below of the anterior superior iliac spine. Inserts onto medial border of the proximal extremity of the tibia diaphysis, with an aponeurotic expansion from sartorius to sural fascia; this insertion is superficial to insertion of the gracilis and	Originates from anterior superior iliac spine and upper ½ of iliac notch. Inserts by aponeurosis onto proximal part of the medial surface of the tibia in front of gracilis and semitendinosus, together forming the 'pes anserinus'. Innervation: femoral nerve.

	the insertion of the gracilis and of the semitendinosus Innervation: femoral nerve. CAI ₁₆ = 0.08334	Innervation: femoral nerve. CAI ₁₇ = 0.08334		semitendinosus muscles and extend around 0.5cm proximally and 3cm distally to these insertions. Innervation: femoral nerve. CAI ₁₉ = 0.2500	CAI ₁₁₀ = 0.1250
Tensor fasciae latae muscle					
	(Ferrero, 2011; Sigmon, 1974).	(Kaplan & Meier, 1958; Ferrero, 2011; Sigmon, 1974)	(Ferrero, 2011; Raven, 1950)	(Ferrero, 2011; Gibbs, 1999; Miller, 1952; Sigmon, 1974; Swindler & Wood, 1973)	(Standring, 2008; Swindler & Wood, 1973)
Originates from anterior margin and lateral aspect of the ilium. Inserts onto laterally fasciae latae. Innervated by the gluteus cranialis nerve. Supplied by the femoral artery.	Originates from anterior surface of the anterior superior iliac spine and gluteal fascia, inserts onto iliotibial tract. Innervation: the mediodorsal part of the tensor fasciae latae is innervated by the superior gluteal nerve, while the anterolateral part is innervated by the femoral nerve.	This muscle is present in all hominoids, but it is usually missing or rather small in <i>Pongo</i> . The muscle runs from the anterior superior iliac spine to the iliotibial tract, being often fused proximally with the gluteus maximus and laterally with the gluteus medius and the gluteus minimus. Innervation: when present, it is innervated by the superior gluteal nerve.	Originates from anterior superior iliac spine and fascia lata just distal to it, to iliotibial tract, specifically to fascia lata lateral to vastus lateralis (Ferrero 2011) according to Raven (1950). Innervation: by superior gluteal nerve.	Originates from the anterior superior iliac spine and the gluteal fascia. Inserts to iliotibial tract to femoral shaft, patella, fascia of upper leg. Innervation: by superior gluteal nerve.	Originates from the anterior 5cm of the outer lip of the iliac crest, from the lateral surface of the anterior superior iliac spine and part of the border of the notch below it, between gluteus medius and sartorius, and from the deep surface of the fascia lata. Inserts onto two layers of the iliotibial tract of the fascia lata and, usually ends 1/3 of the way down the thigh, but occasionally extend to lateral femoral condyle. Innervation: superior gluteal nerve.
GCAI [except for tensor fasciae latae]	GCAI ₁₆ = 0.8750	GCAI ₁₇ = 0.68754	GCAI ₁₈ = 0.8834	GCAI ₁₉ = 0.8750	GCAI ₁₁₀ = 0.8946

2. Models, PCSA strength and locomotor behavior

2.1. The law of Cosines applied to two heads of the rectus femoris

One of the problems that should be addressed concerns the strength associated with the presence of one or two heads of the rectus femoris muscle in the quadriceps. This muscle crosses two joints, the pelvis and the knee, as it stabilizes both and has the function of extending the

leg and contracting (flexing) the pelvis when the leg is static (Standring, 2008; Testut & Latarjet, 1959). In this case, some primates might need the action of this muscle, mainly to stabilize the joints, or as a basis for locomotion.

In fact, the difference between one and two muscle heads has evolutionary, physiological, and locomotor behavior importance, since the strength of this muscle generates more balance and/or more strength in the joints where it acts. For two heads, the muscle strength can be calculated by the law of cosines using the theory of vector mechanics.

As such, for one head, the reflected one is the main one (Standring, 2008; Swindler & Wood, 1973). Using forces F_x for the x component and F_y for the y component, for each head of the two; F_x could be made parallel and coincident to the x -axis (figure 4), and F_y becomes perpendicular to x , coincident and parallel to the y axis, so the value of F_y is zero (figure 4).

$$F_{r1} = \sqrt{F_x^2 + F_y^2 - 2 \cdot F_x \cdot F_y \cdot \cos(\theta)} = \sqrt{F_x^2 + 0^2 - 2 \cdot F_x \cdot 0 \cdot \cos(\theta)} = \sqrt{F_x^2} = F_x.$$

Where F_{r1} is the resultant of the strength for the analysis of two heads with an angle of 90° .

Setting the angles between the heads $0^\circ < \theta < 90^\circ$, i.e., possible angles for the reflected head in relation to the straight head, and for the maximum and minimum possible values for the tension of the rectus, we have:

$$F_{r2} = \sqrt{F_{x'}^2 + F_{y'}^2 - 2 \cdot F_{x'} \cdot F_{y'} \cdot \cos(\theta)}.$$

Where F_{r2} is the resultant of the strength for both heads for angles $0^\circ < \theta < 90^\circ$.

However, assuming, for comparison purposes, that the total force (tension supported by the tendons) could be divided exactly by two heads, i.e., both heads giving the same force for muscle action, and using $F_{x'}$ coincident with F_x , i.e., $F_x = F_{x'}$, because the position of the head of the rectum has not changed, then,

$$F_{r2} = \sqrt{F_{x'}^2 + F_y^2 - 2 \cdot F_{x'} \cdot F_y \cdot \cos(\theta)} = \sqrt{F_x^2 + F_y^2 - 2 \cdot F_x \cdot F_y \cdot \cos(\theta)} = \sqrt{F_x \cdot -(2 \cdot F_y \cdot \cos(\theta) + F_y^2)}.$$

For $\theta = 0^\circ$, we have $F_{y'} = 0$, i.e., the reflex head is parallel to the straight head.

$$F_{r2} = \sqrt{F_{x'}^2 + F_y^2 - 2 \cdot F_{x'} \cdot F_y \cdot \cos(0)} = \sqrt{F_x^2 + F_y^2 - 2 \cdot F_x \cdot 0 \cdot 1} = \sqrt{F_x^2} = F_x.$$

For $\theta=90^\circ$, we have:

$$F_{r2} = \sqrt{F_{x'}^2 + F_y^2 - 2 \cdot F_{x'} \cdot F_y \cdot \cos(90^\circ)} = \sqrt{F_x^2 + F_y^2 - 2 \cdot F_x \cdot F_y \cdot 0} = \sqrt{F_x^2 + F_y^2}.$$

In the first case, the primate has only one head and, in the second, the anatomical arrangement is not observed.

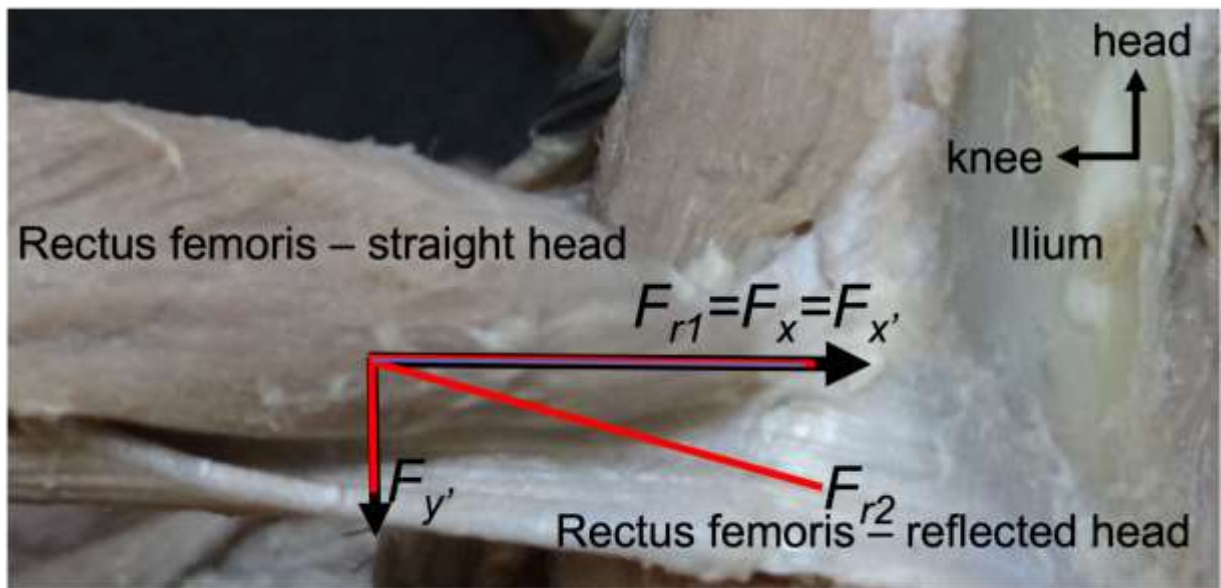


Figure 4. Photograph of the origins of the rectus femoris in the left thigh of the *Sapajus*. Vectors were drawn on the muscle to show the relationship between the strength of these two heads in the thigh movement.

Thus, the rectus femoris containing one head exerts more strength for a specific action than with two heads, and, considering the angle of separation of the tendon, both heads of the rectus femoris could allow more stabilization in the pelvis-femur joint.

In fact, to prove, using geometry, how the PCSA is directly proportional to the cross-sectional area of the muscle, suppose that for a head with a cross-sectional area of radius 1, the sum of both heads is 2; and giving a single head an area of radius 2, the calculation will show that the area of one head (A_2) is twice the sum of the areas of each head (A_1):

$$A_1 = \pi \cdot 1^2 + \pi \cdot 1^2 = 2\pi;$$

$$A_2 = \pi \cdot 2^2 = 4\pi.$$

Therefore, the indirect PCSA for one head is twice the sum of the two heads working together.

In summary, considering only splitting heads and other constant variables, the rectus femoris is stronger with one head than that with two, but splitting two origins into tendons can give greater balance to the pelvis or knee joints. In all primates, for the pelvis-femur joint, by having two heads of a proximal origin from the rectus femoris, both the ilium and part of the joint capsule will receive muscle action (figure 4).

To perform an individual analysis of the muscles using the law of cosines, the values of the angle of each muscle in relation to the axis of the femur, which is the x -axis referential for F_x , is necessary. However, according to our research, the data on all primates needed for this study was not found in the literature. For *Pongo*, *Hylobates*, *Gorilla*, and *Pan*, PCSA values for rectus femoris and quadriceps were shown separately, but not for other individual muscles (Payne et al., 2006; Thorpe et al., 1999).

Sapajus, *Callithrix*, *Gorilla*, and modern humans are shown as having a separate head, *Papio* and *Pan* are mentioned as not having completely separate heads. For the other primates studied here, namely, *Macaca*, *Hylobates*, and *Pongo*, they have only one muscle head.

Modern human locomotion, due to the pelvis-femur stabilization required for bipedalism, justifies the two heads in the rectus femoris muscle, but the *Gorilla*'s heavy weight cannot justify the two heads. In the case of *Callithrix* and *Sapajus*, which have large proportional areas and small volume, two muscle heads provide pelvis-femur stabilization, because the large area, it allows greater muscle strength. An unseparated head mentioned for *Papio* and *Pan* is not relevant if the origins of the head are different, because the separated tendons will provide the stabilization mentioned for the pelvis-femur joint. Its strength seems to be the main adaptation for the rectus femoris for *Macaca*, *Hylobates*, and *Pongo*.

Considering different locomotion behaviors, *Papio*, *Sapajus*, and *Callithrix* are quadrupedal, walkers and runners; *Gorilla* and *Pan* are quadrupedal knuckle-walkers (Ankel-Simons, 2000), while modern humans are bipedal. *Pongo* and *Hylobates* are more arboreal than the others mentioned here, therefore, strength is the main utility for the rectus femoris. But that is not a reasonable explanation for *Macaca*.

Accordingly, no detailed anatomical data were found to explain the difference between the one or two heads for the rectus femoris. However, in this study, we carried out an individual analysis for the heads, so the action of the adjacent muscles was not considered.

2.2. Model 2

Initially, when using published data for *Pan* and modern humans, specific PCSA values were compared using values from the relationship (Thorpe et al., 1999) (figure 6).

For a better view, absolute data were plotted and a trendline analysis was carried out (figure 3). These absolute data for PCSA and the primate's weight were a good fit (figure 5), showing a good sequence for an anatomical and taxonomical analysis, including similar curves built from the values of the exponents. However, for a proportional analysis, the absolute PCSA values do not show the primate's real strength, as they do not consider proportional size and weight.

A power function for the weights was expected, since weight is proportional to volume, and volume increases to the power of 3. In fact, a value close to 3 in the exponent x was obtained, namely 3.2793 ($R^2_{Pd} = 0.9371$), the best trendline for this data.

There was no complete correspondence between all primate data for absolute PCSA values and weights. The best trendline analysis for absolute PCSA values was an exponential function ($R^2_E = 0.9857$), which was also expected since the PCSA formula gives the final value squared. As the weight, to the power of 3, and the squared PCSA values increased, some discrepancies for more heavy primates were expected since the increase in a powered variable is proportionally greater than its linear value, and the difference depends on the power to which the variable has undergone.

A reasonable correlation between primates, regarding the x -axis, is seen in Figures 5A and 5B, indicating that increased body weight and absolute PCSA values are partially linked and that heavier animals need more quadriceps strength.

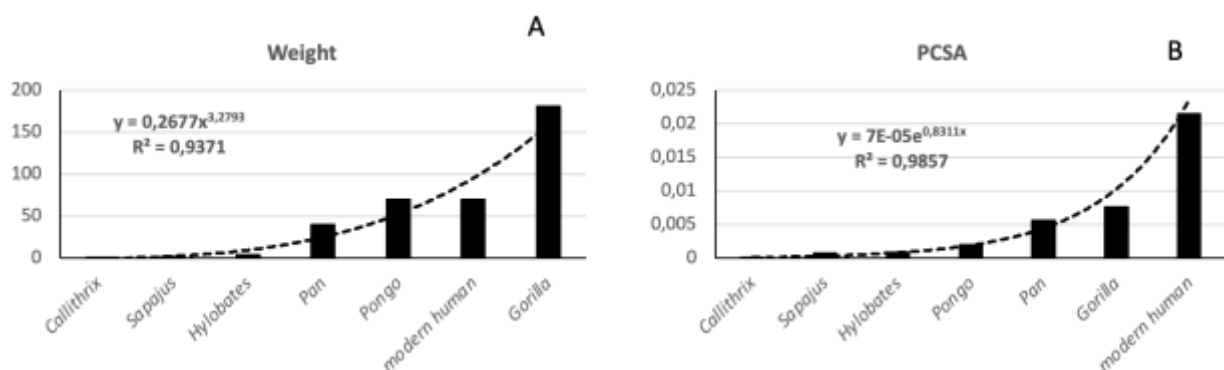


Figure 5. A] Values for weight and B] absolute PCSA for primates studied here. Note that the best regression for weight comparison was a powered regression and for absolute PCSA, it was an exponential regression.

These models aim to demonstrate the strongest quadriceps, comparing the species in an identical analysis, i.e., calculate data to obtain a proportional analysis, avoiding differences such as primate weight and size, at least.

Accordingly, values used from different articles in the literature generate errors. Errors can also arise from problems linked to different methods of obtaining data from different people (e.g. human error), discrepancies between animal weight regarding captivity, or variations in wildlife and health. Also, the number of subjects, namely, small samples or the different number of subjects for each sample, and dehydration of cadavers. In fact, these errors formed the main limitation of this study.

For a comparison between PCSA values, for model 2, values found by Thorpe et al. (1999) for femur length [FL] were taken for *Pan* and modern humans. For *Hylobates*, *Pongo* and *Gorilla*, the comparison was calculated from values found by Payne et al. (2006), and, for *Callithrix* and *Sapajus*, data were obtained directly from the subjects in this study.

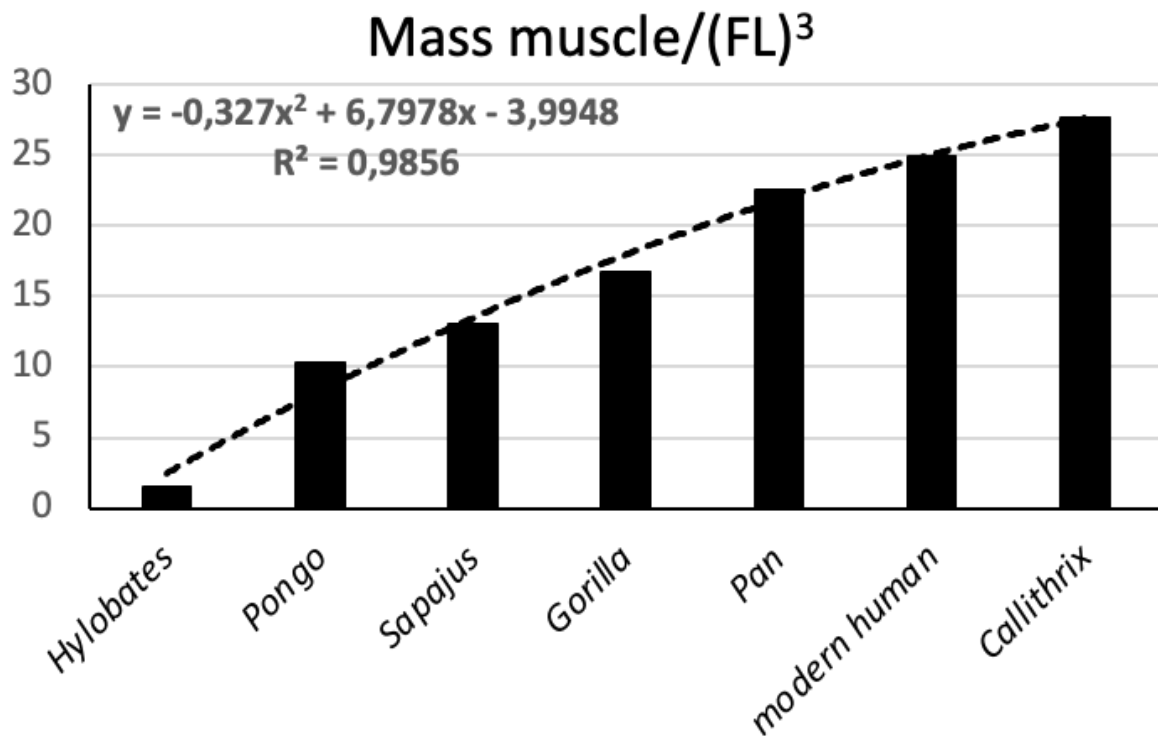


Figure 6. A comparison of the relationship [muscle mass/(FL³)] taken from literature for *Pan* and modern humans (Thorpe et al.,1999), and calculated through the literature for *Hylobates*, *Pongo* and *Gorilla* (Payne et al., 2006), and calculated directly for *Callithrix* and *Sapajus*. The best trendline among the data was given by a logarithmic one. FL is femur length.

Note that in Figure 6, the best trendline analysis for the data was polynomial with $R^2_P = 0.98567$. It is greater than the other trendlines analyzed as linear, logarithmic, exponential, polynomial, and power.

For this analysis, *Callithrix* had proportionally stronger quadriceps among the primates studied in Model 2, while *Hylobates* had the weakest. The presence of *Sapajus* among the apes made it difficult to provide a reasonable explanation, using this model, to associate this genus with morphological and taxonomic data, and locomotor behavior.

2.3. Model 3

For the next models, values obtained from articles were utilized to calculate the femoral head area and body weights for modern humans (Kuo, Skedros, & Bloebaum, 1998; Pick, Stack, & Anson, 1941; Rashid et al., 2019; Thorpe et al., 1999), *Pan*, *Gorilla*, *Pongo*, and *Hylobates* (Payne et al., 2006; Plavcan et al., 2005; Thorpe et al., 1999), and direct measurements were taken on *Sapajus* and *Callithrix*.

To obtain a more reliable model, a dimensionless relationship could be a better solution, to avoid variations in the dimensions of variables, as previously tried when using Model 2 (Thorpe et al., 1999), when the values of the variables were linked with a physiological approach for the muscle actions.

Therefore, the area of the femur head that generates a squared value was chosen as a variable to divide the absolute PCSA values, also squared (figure 7A). Other data, such as mid-femur diaphysis cross-sectional area or total thigh middle cross-sectional area, might be a better choice. However, this choice was hampered by the data found for the femur area in the literature. Therefore, the area of the femur head may not be the best choice. However, bone and muscle strength is proportional to the cross-sectional area (Gould, 1966), but a relationship was made for different organs, namely, for muscles associated with bones.

Nevertheless, maintaining a physiological approach, the femur head is associated with the action of quadriceps, and it increases according to the muscle strength, which acts on the pelvis-femur joint to support the animal's weight (figure 5A). The relationship (PCSA/femoral head area) in model 3, shows a better polynomial trendline ($R^2_P = 0.9812$) compared to other trendlines, but with a different array of primates compared to Models 2 and 3 on the x -axis in which the species are placed (figures 6 and 7A).

2.4. Model 4

Body size increases for both individuals of the same or different species, to the power of two, and to the power of 3 in relation to weight [volume]. As such, the relationship [PCSA/weight] in model 4 could indicate that the information is more reliable for muscle strength (figure 7B) due to, inter alia, body growth [inanimate, organic beings], which is to the power of $2/3$, i.e., maintaining the area/volume ratio (Aversi-Ferreira, 2018; Aversi-Ferreira, Freitas-Ferreira, & Aversi-Ferreira, 2021; Gould, 1966; Huxley, 1950).

In fact, an increase in size requires, or allows, changes in shape and, a geometric similarity to be maintained, where bodies will have decreasing surface [area]/volume [weight] ratios (Gould, 1966).

Polynomial trendline analysis was the best fit for the data from Model 4, but the linear trendline shows values for $R^2_L = 0.9633$ and the polynomial $R^2_P = 0.9725$ (figure 7).

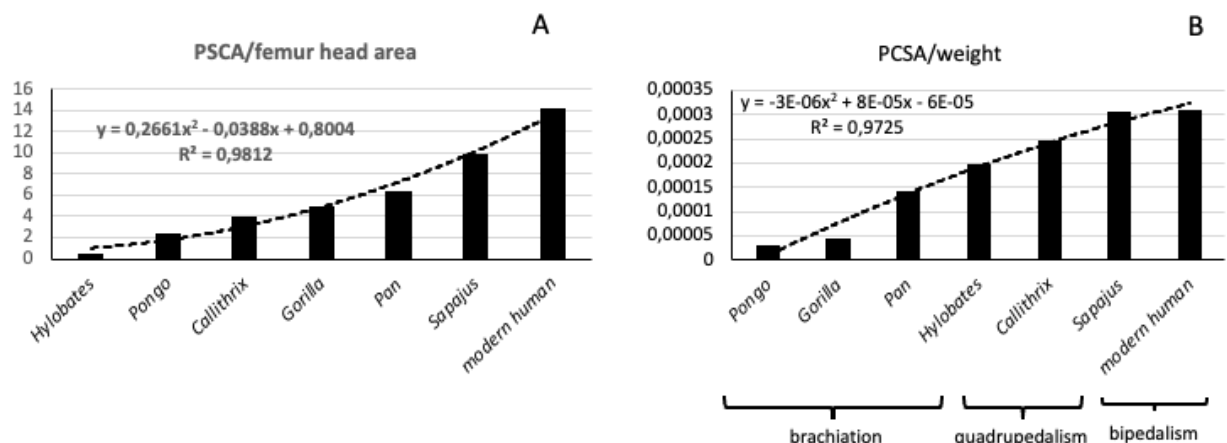


Figure 7. A) Relationship for quadriceps (PCSA/head femur area) where B) the relationship (PCSA/weight) for primates studied in these models shows the best polynomial regression; however, the order of primates in the axis x is different for each model.

After analyzing the aforementioned relationships in Models 2, 3, and 4, more discrepancy was found in *Callithrix* for [muscle mass/ FL^3], indicating that its quadriceps were proportionally stronger in relation to the other primates. However, in general, *Sapajus* and modern humans had stronger quadriceps using Model 3, and apes had the weakest.

Modern humans must have stronger quadriceps because of the locomotor behavior of bipedalism. Considering the anatomical similarities between *Sapajus* and *Callithrix* (table 2a, vide GCAI), and placing the apes in a single group, Model 4 seems to be the most reliable model to show the strongest quadriceps, considering a proportional analysis for primate weight and size.

2.5. Association, in model 4, for gross anatomy, and locomotor behavior

Furthermore, considering locomotor behavior combined with taxonomy and anatomical data, the primates that use brachiation locomotion [modified brachiation subtype] are the great apes [*Pongo*, *Gorilla*, and *Pan*], and *Hylobates*, which have a true brachiation subtype (Napier & Napier, 1967). They were grouped in the model 4 graph (figure 7B).

Callithrix and *Sapajus* are classified under the same type of quadrupedalism [walkers, runners, and leapers], with the features of climbing, springing, and jumping. Furthermore, they were grouped in the Model 4 graph. Modern humans exhibit bipedalism as locomotor behavior (Ankel-Simons, 2000; Wright et al., 2019). They were placed in the right portion of the graph (figure 7B). Keeping this group separate in the classification of locomotor behavior, the [PCSA/weight] model fits the data better than the others (figure 7B), considering the very strong quadriceps expected for modern humans due to bipedalism, which requires the support of a large part of the body's weight.

On the other hand, data from *Macaca* and *Papio* could improve this study making it more consistent. However, adequate data were not found for the calculations for these genera. In fact, *Macaca* and *Papio* have the same subtype of quadrupedalism, i.e., ground running and walking (Ankel-Simons, 2000). The values for comparison could indicate important information for the analysis of the locomotor strength-behavior relationship, placing Old World primates in this model [PCSA/weight] supposedly between apes and New World primates.

2.6. Models and sartorius PCSA

Specifically for the sartorius, the PCSA value was calculated and models were performed separately on the quadriceps data of the other primates (figure 8), due to the different actions of this muscle in relation to the other muscles from the quadriceps muscles, inter alia.

The primate array on the x -axis for Model 4 showed the groups divided, namely, the great apes on the left, modern humans in between the great apes and quadrupeds, and the *Hylobates*, showing stronger sartorius, on the right (figure 8B). The data show a polynomial function of the trendline $R^2_p = 0.9665$ for Model 3, the same trendline for the same model for quadriceps.

Regarding the quadriceps (figure 7B), *Hylobates* are in the place of modern humans, which indicates that *Hylobates* compete with the quadrupedal jumpers, namely, *Callithrix* and *Sapajus*. A stronger sartorius for modern humans compared to that of the great apes can be justified by the stabilization of the pelvis-knee joints required by bipedalism, which expends great muscle strength. Also, this muscle crosses two joints, namely the pelvis-femur and the knee.

Great apes have brachiation and are intermittent bipedal (Wright et al., 2019) with triple support, mainly for gorillas and chimpanzees, so a strong sartorius seems not to be as necessary as it is for human bipedalism.

Some similarities are found in Model 4 for the sartorius, regarding the distribution of the groups of primates on the x -axis, but not in Model 2 (figures 6 and 8D). This could represent one more indication that the best model for this study was the fourth model.

However, the following consideration must be addressed: one of the *Gorillas* used by Payne et al. (2006) showed a large discrepancy from the other two for the PCSA value, so this outlier was not used for sartorius calculations.

Due to large variations and insufficient data, calculations were not made for the tensor fasciae latae. In these cases, only one anatomical analysis was performed.

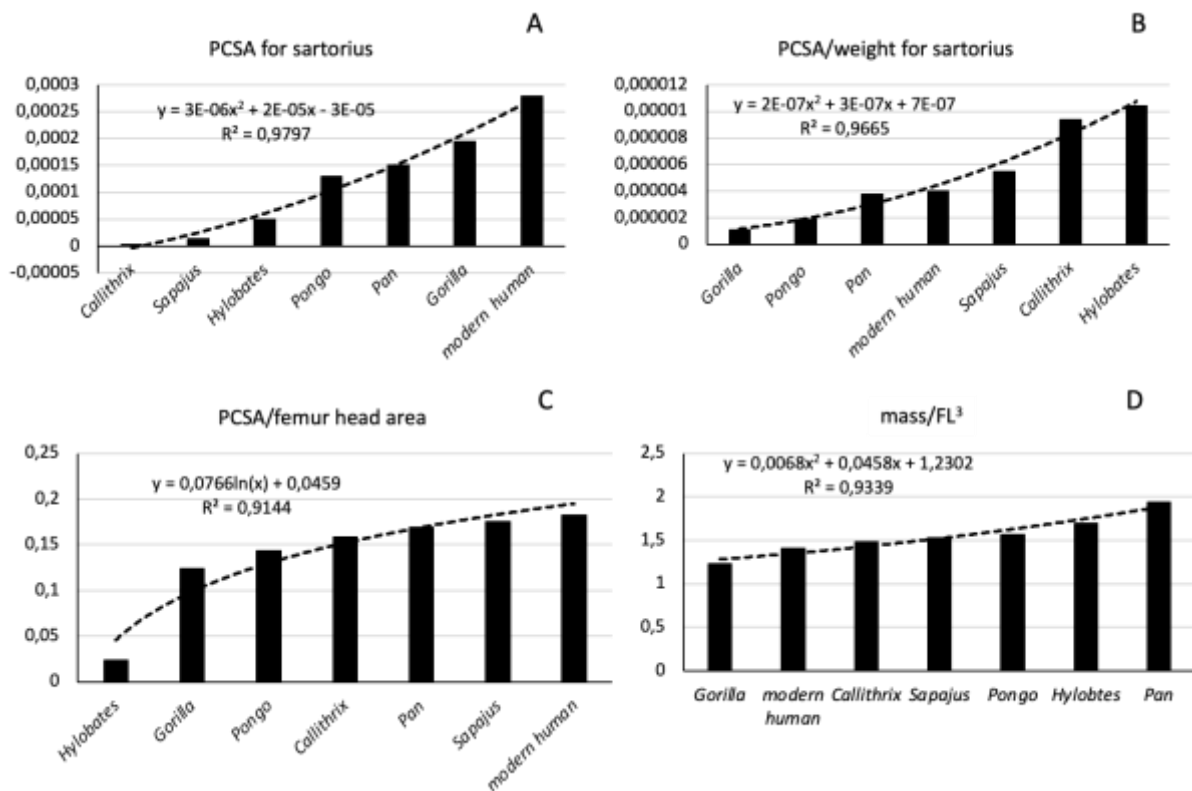


Figure 8. Studies the relationship for the sartorius. A) data for the absolute PCSA with best polynomial trendline; B) Relationship [PCSA/weight], model 4 showing a best polynomial trendline; C) model 3, [PCSA/head femur area] with best logarithmic trendline; D) model 2, [mass/FL³] with best polynomial trendline.

2.7. Locomotor behavior and PCSA approach

As such, in this session, Model 4 will be used to analyze proportional PCSA values and muscle strength, to address a comparison with locomotor behavior, associated with the quadriceps and sartorius muscles, as this model, and the morphological data from the taxonomy, provide a better relationship.

Some comments will show that the area/volume ratio appears to be a reliable approach for analyzing bodies and organs for different species with similar geometric structures, such as hindlimb muscles in humans being stronger than in *Pan* (Thorpe et al., 1999). [The *Pan* genera could be classified as similar due to the small difference in the PCSA value for the hindlimb muscles] (Payne et al., 2006).

It has been hypothesized that hindlimb muscles are stronger in modern humans than in *Pan* since free joint movement (mobility) is used, and compared to chimpanzees, which is due to their quadrupedal movement (Thorpe et al., 1999). However, two more reasons could be proposed such as 1] stiff-legged gait in humans (Smith, 2003) requiring strong muscles to balance the pelvis in order to support most of the bodyweight in bipedalism and, additionally, 2] larger bodies show weaker proportional support keeping similar geometric structure (Gould, 1966). In fact, Model 4 shows that the quadriceps muscles of the hindlimbs of modern humans are stronger than the other primates compared in this study (figure 7B).

All explanations suggested above fall under the area/volume explanation of the increase in body size. As a matter of fact, humans are heavier and bipedal, while *Pan* has a quadrupedal knuckle-walk (common to African great apes), and supports itself at the front of the body during locomotion (Tuttle, 1969), which does not result in a need for stronger hindlimb muscles to support their weight. For *Gorillas*, which are heavier than both *Pan* and modern humans, quadriceps muscles are weaker than those of chimpanzees and modern humans because of the quadrupedal gait (living predominantly on the ground), presumably because they are too heavy to swing in trees (Ankel-Simons, 2000).

However, when considering all the muscles of the body, *Pan* is about 1.35 times stronger than modern humans (O'Neill et al., 2017).

Another assertion regarding their weight is that *Pan paniscus* weighs an average of 40 kg, and they swing and jump in trees more than the *Pan troglodytes*, which weigh an average of 60 kg (Ankel-Simons, 2000).

Another great ape that had weaker quadriceps was the *Pongo*, also a quadrupedal knuckle-walker, and deliberate climber, weighing around 70kg. They compete with the average modern human weight, and another study indicated that, among the great apes, the proportional strength of the quadriceps of the hindlimbs is lower (Payne et al., 2006).

Interestingly, *Hylobates* (Fleagle, 1974), a true brachiator, shows stronger quadriceps than the great apes, but despite being more arboreal, they are versatile using ground locomotor modes, such as quadrupedal, tripedal, and bipedal locomotion, with the latter being a bonobo (Vereecke, D'Août, & Aerts, 2005). Putatively, a small body weight, maintaining a decrease in the area/volume ratio, could be a reasonable explanation for the proportional strength calculated in Model 4, as small bodies present proportionally larger areas of structures. Indeed, the proportional strength of hindlimbs in *Hylobates* competes with that of modern humans (Payne et al., 2006).

As such, this is why strengthened quadriceps were found in *Callithrix* and *Sapajus* in Model 4 rather than for the apes. The fact that *Sapajus* have stronger quadriceps muscles than *Callithrix*, can be explained by their locomotion behavior, as the former is more quadrupedal than the latter (Ankel-Simons, 2000). *Sapajus* are mainly quadrupedal walkers, climbers, and runners; they stay on the ground for foraging and make a specific action that requires great strength from their hindlimb muscles, i.e., they use stones weighing about 40% of their body weight to crack open nuts (Fragaszy, Visalberghi, & Fedigan, 2004; Wright et al., 2019). This indicates the need to rethink the evolution of tool use (Haslam et al., 2009). Meanwhile, *Callithrix* walk in a quadrupedal gait, jump over the tree branches (Ankel-Simons, 2000) and do not use tools like *Sapajus* and great apes.

Sapajus' adaptation to foraging on the ground is justification enough for having stronger quadriceps compared to other primates, except for modern humans.

Despite a lack of PCSA strength compared to *Macaca* and *Papio* in this study, note that they spend more time on the ground, so they are classified as terrestrial quadrupeds with a digitigrade walk (Ankel-Simons, 2000). As such, a lack of data needed to analyze the quadriceps in relation to other primates makes it difficult to associate these genera with the locomotion behavior.

CONCLUSIONS

Since there are restrictions for a reliable analysis, as mentioned in this study, i.e., the difference between the dehydrated species, genus, variances in bodyweight from different environments (captive or wild), different approaches to analysis, and difference in accuracy in muscle description, inaccuracy is expected for the tested models.

An individual study regarding the presence of one or two heads of the rectus femoris muscle is suitable. According to an analysis using the law of cosines, one head generates a stronger action, and two heads, a better stabilization of the pelvis-femur joint. However, it was not possible to fully explain the number of heads. The presence of two muscle heads in modern humans is very well justified by bipedal locomotion. The greater proportional area for the New World primates studied here could justify two heads for them, as strength is intrinsic over a large area and joint stabilization is always desirable.

For a PCSA analysis, the area/volume ratio (model 4) is better for comparing the proportional strength of the quadriceps of the primates studied, and for a plausible relationship between these data and locomotor behavior, and gross anatomy linked to taxonomy.

Thus, the strongest quadriceps were that of modern humans, followed by New World primates (*Callithrix* and *Sapajus*), *Hylobates*, and the great apes. Accordingly, quadriceps strength is associated with the animal's weight and locomotor behavior. The bipedalism feature, plus large and heavy bodies in modern humans, indicated stronger quadriceps. Lighter primates with quadrupedal locomotion and jumping features also had stronger quadriceps. Among the apes, the explanations are also linked to weight, i.e., the *Hylobates*, which are lighter in weight, had stronger quadriceps than the heavier apes.

GCAI values indicate structural similarity between primates. Specializations are noticeable in gross anatomy in this type of analysis, but a high level of similarity between *Sapajus* and *Callithrix* was expected, and found, for the quadriceps, which indicates a specialization for walking, running, and leaping in their locomotor behavior.

It was shown that, at least for the quadriceps, Model 4 (area/volume ratio) is more accurate for a strength analysis. However, the limited data on New and Old World primates make it difficult to carry out a more reliable analysis, indicating that the gross anatomy of these groups is scarce, and needs to be performed both for a morphological comparison, as well as for a taxonomic review.

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4 CONSIDERAÇÕES FINAIS

A partir desse estudo percebeu-se que, em termos anatômico, considerando a análise estatística utilizada como modelo 1, a maior semelhança entre os músculos da região anterior da coxa de *Sapajus* foi com os de *Callithrix*, possivelmente por ambos serem primatas neotropicais, compartilharem um ancestral mais próximo comparado aos demais primatas investigados e por serem quadrúpedes apresentando especializações para andar, correr e saltar. Já a maior divergência encontrada entre os músculos anteriores da coxa de *Sapajus* foi com os de *Pongo*, o que pode ser explicado pela especialização apresentada para a atividade locomotora desse primata. Quanto à divergência importante encontrada entre *Sapajus* com *Macaca fascicularis* supõe-se que seja devido à distância filogenética desse primata do Velho mundo comparado a *Sapajus* e ao seu isolamento geográfico.

Embora o músculo tensor da fáscia lata de *Sapajus* tenha apresentado divergência com os demais primatas investigados, é importante ressaltar que foi realizada apenas uma descrição anatômica e uma comparação considerando os parâmetros individualmente devido à ausência de dados anatômicos na literatura para o músculo citado, o que dificultou uma análise comparativa de modo mais robusto. Não sendo possível a realização da análise estatística comparada com os demais primatas do estudo.

O GCAI demonstrou ser um bom modelo para ser utilizado na anatomia comparativa, por permitir avaliar estruturas anatômicas únicas e múltiplas em diferentes espécies, utilizando conceitos anatômicos de normalidade e variação com associação a variáveis nominais, corroborando com Aversi-Ferreira *et al.*, (2015) e Aversi-Ferreira, Nishijo e Aversi-Ferreira (2017).

O modelo área/volume (PCSA/peso) demonstrou ser o mais adequado para a avaliação da força muscular relacionada ao comportamento locomotor, corroborando com a Lei dos cossenos e a Teoria do corpo-livre. Com humanos modernos apresentando a maior força do quadríceps, seguido por *Sapajus* e *Callithrix*, e por fim pelos apes (*Hylobates*, *Pongo*, *Gorilla* e *Pan*). Demonstrando uma relação importante entre força proporcional desse músculo e o comportamento bípede e quadrúpede daqueles primatas.

A avaliação da força muscular relacionada com o comportamento locomotor foi realizada apenas para *Sapajus* e *Callithrix* (animais dissecados), apes e humanos modernos. Não sendo realizada para os primatas do Velho Mundo *Macaca cyclopis*, *Macaca fascicularis*

e *Papio* em função da ausência de dados na literatura para o cálculo do parâmetro citado. Portanto, impossibilitando a apresentação de um modelo com maior robustez.

Diante o exposto, a ausência e/ou escassez de estudos anatômicos na literatura para os primatas do Velho Mundo e Novo Mundo denotam a relevância da realização de mais estudos musculares com abordagem morfofisiológica para uma melhor compreensão da evolução do comportamento locomotor em primatas.

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ANEXO A - Parecer consubstanciado do Comitê de Ética UFG



PROTOCOLO Nº
081/08

UNIVERSIDADE FEDERAL DE GOIÁS
PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO
COMISSÃO DE ÉTICA EM PESQUISA

PARECER CONSUBSTANCIADO

I - Finalidade do projeto (pesquisa/ensino)

PROJETO DE PESQUISA

II - Identificação:

Título do projeto:

- Localização de miosina-V e calmodulina no neocórtex de *Cebus libidinosus* (RYLANDS, 2000)

Pesquisador Responsável:

- Yandra Cássia Lobato do Prado - ICB/UFG

Pesquisadores Participantes:

- Prof. Dr. Eugênio Gonçalves de Araújo – EV/UFG
- Prof. Dr. Tales Alexandre Aversi Ferreira – ICB/UFG

Instituição onde será realizado:

- Universidade Federal de Goiás
- Centro de Triagem de Animais Silvestres (CETAS) - IBAMA

Data de apresentação ao CEP: 04/06/2008

III - Objetivos e justificativa do projeto:

O presente projeto tem como finalidade:

- Localizar por técnicas morfológicas e bioquímicas as proteínas calmodulina e miosina-V no neocórtex de *Cebus libidinosus*.
 - Localizar a miosina-V no encéfalo de macacos *Cebus*, pelo emprego de técnica imunistoquímica, imunofluorescência e *Western blot*;
 - Verificar a associação entre a miosina V e as moléculas de calmodulina nos neurônios, por meio de co-localização pela imunofluorescência e microscopia confocal.

IV - Sumário do projeto:

Discussão sobre a possibilidade de métodos alternativos:

- Não apresentada. A equipe justifica que a localização da miosina-V associada à calmodulina no encéfalo de macacos *Cebus* representará uma possível confirmação qualitativa/quantitativa dessas moléculas nos neurônios cerebrais de animais superiores, pela primeira vez em primatas. Além disso, afirma que as publicações que envolvem estudos com *Cebus* têm apresentado enorme repercussão mundial, sendo intenção da equipe abrir novas perspectivas para o uso dessa espécie como modelo experimental, não somente na neurociência, mas também para outras finalidades, como os estudos de efeitos de fármacos.

Descrição do animal utilizado (número, espécie, linhagem, sexo, peso, etc):

- Macacos (*Cebus libidinosus*)
 - Serão utilizados seis animais, adultos e saudáveis, cedidos pelo IBAMA (documentação apresentada).

Descrição das instalações utilizadas e número de animais/área/qualidade do Ambiente (ar, temperatura, umidade), Alimentação/hidratação:

- Os animais são provenientes do CETAS-Goiânia e serão utilizados pelo estudo após eutanásia.

Utilização de agente infeccioso/gravidade da infecção a ser observada:

- Não se aplica a este ensaio.

Adequação da metodologia e considerações sobre o sofrimento imposto aos animais:

CEP/UFG

PARECER CONSUBSTANCIADO

PROTOCOLO Nº 081/08

- A metodologia foi apresentada no corpo do projeto e no item 09 do protocolo. Em síntese:
 - Os animais serão capturados no recinto por meio de um puçá, imobilizados manualmente por pessoa experiente e qualificada para tal função. Em seguida, será feita a tranquilização com aplicação de quetamina (50mg/ml) na dose de 10mg/kg por via intramuscular. A veia cefálica será então acessada para aplicação de tiopental (1000mg) na dose de 50mg/kg. Após a constatação de parada cardio-respiratória e choque bulbar, os encéfalos serão imediatamente retirados por dissecação cuidadosa.
 - A separação dos lobos cerebrais será feita com lâmina de barbear, baseando-se nas principais fissuras e sulcos, correspondentes à anatomia do homem. Cada lobo será seccionado em vários cortes para fragmentação das técnicas de imunoistoquímica, *Western Blot*, imunofluorescência e microscopia confocal.
 - Método de eutanásia:**
 - Será realizada conforme descrito no item anterior.
 - Destino do animal:**
 - Esses animais serão destinados ao Núcleo de Estudos em Neurociências e Comportamento de Primatas do ICB/UFG onde serão utilizados para estudos descritivos de anatomia.
- IV – Comentários do relator frente às orientações do COBEA**
- Estrutura do protocolo:**
 - O protocolo atende às orientações pertinentes à experimentação animal. **Contém todos os documentos necessários à sua análise.**
 - Análise de sofrimento imposto, métodos alternativos e benefícios:**
 - Os animais serão utilizados na pesquisa após eutanásia. Antes disso permanecerão em recintos próprios para a espécie no CETAS.
 - Análise dos riscos aos pesquisadores/alunos:**
 - Os pesquisadores apontam que os riscos possíveis serão sanados pela presença de pessoal capacitado do CETAS para o manuseio dos animais, não havendo contato desses com os pesquisadores até o momento da anestesia.
 - Necessidade do número de animais:**
 - O número de animais é justificado no protocolo, entretanto o delineamento estatístico não foi apresentado.

V - Parecer do CEP:De acordo com a documentação apresentada a este comitê consideramos o projeto **APROVADO**.**VI - Data da reunião: 06/04/2009**


 Profª Drª Rita Goreti Amaral

ANEXO B – Parecer consubstanciado da Comissão de Ética em Pesquisa Animal**UNIVERSIDADE FEDERAL DO
TOCANTINS COMISSÃO DE ÉTICA NO
USO DE ANIMAIS CEUA-UFT**

O projeto intitulado “**Estudo anatômico comparativo do primata *Sapajus* (anteriormente *Cebus*) *libidinosus* (macaco-prego) (PRIMATAS, CEBIDAE) associados aos aspectos comportamentais cognitivos, de uso de ferramentas e evolução**”, processo nº 23101.003220/2013-85, sob a responsabilidade do **Professor Doutor Tales Alexandre Aversi-Ferreira**, está de acordo com as normas éticas estabelecidas pela lei de Procedimentos para o Uso Científico de Animais, de 8 de outubro de 2008, estando aprovado para a sua execução pelo parecerista da Comissão de Ética no Uso de Animais da Universidade Federal do Tocantins.

Araguaína, 14 de fevereiro de 2014.

Atenciosamente,

Alberto Yim Júnior

Presidente da Comissão de Ética em Pesquisa Animal da UFT

ANEXO C – Comprovante de submissão do artigo à revista The Anatomical Record

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Thank you for your submission

Submitted to Anatomical Record

Manuscript ID AR-22-0127

Title Mathematical models to analyze the comparative gross anatomy and the PCSA of the quadriceps, sartorius and tensor fasciae latae muscles from Primates (Sapajus and Callithrix), Old World Primates, apes, and modern humans

Authors Figueredo-da-Silva, Sylla
 Vasconcelos-da-Silva, Ediana
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 Aversi-Ferreira, Roqueline
 Tomaz, Carlos
 Vasconcelos, Carlos Augusto
 Aversi Ferreira, Tales

Date Submitted 31-Mar-2022

Author D

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