Leg muscle architecture in primates and its correlation with locomotion patterns

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Title: Leg muscle architecture in primates and its correlation with locomotion patterns

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Abstract

Bone biomechanical studies indicate that leg bone structure can be related to different locomotor patterns. The osteological correlates of extant primates' locomotion patterns and substrate use are important to consider when estimating corresponding behaviors of extinct primates. Here, we test if these same patterns are seen in the differences in leg muscular architecture. Muscle mass, fascicle lengths (FL), physiological cross-sectional area (PCSA), reduced PCSA (RPCSA) and tendon-to-muscle belly ratio were studied in 33 primate species (6 strepsirrhines, 14 platyrrhines and 13 catarrhines). Muscles were grouped into toe and ankle flexors and extensors and studied for phylogenetic and functional signals. All variables strongly correlate with body mass: strength variables (mass, PCSA and RPCSA) scale with positive allometry, whereas the speed/stretch measure (FL) trend toward negative allometry. Thus, larger primates are relatively stronger than smaller species, but they have relatively shorter leg muscle fibers than smaller primates. The strongest functional signal emerged when comparing belly-muscle tendon unit (MTU) length ratio in leaping and non-leaping primates. Leapers show significantly larger plantarflexor belly-MTU ratio. Surprisingly, no significant results reflect a correlation between muscle architecture and substrate and locomotor groups. However, several trends suggest that a larger sample and more fine-grained defined categories could produce significant results. These results show the complex relation between leg bone biomechanics and muscle architecture and demand for further studies on this topic.

Key words: Arboreal, Terrestrial, Phylogeny, PCSA, Tendon

INTRODUCTION

Primates are adapted in many ways for moving primarily on arboreal substrates (Cartmill, 1992). However, the degree of arboreality differs throughout the Order; some, like baboons, spend the majority of their foraging time on the ground, while others rarely leave the tree canopy (Fleagle, 2013). The locomotor modes by which primates traverse their environments vary between and within species. Though primates' primary locomotor pattern is quadrupedalism, locomotor specializations are present within the order depending on the taxon, diet, body size, and general ecology of a species (Fleagle, 2013). Functional morphologists have already generated a large body of work devoted to understanding the relationship between morphology, substrate use, and locomotion in primates (Ward and Sussman, 1979; Glassman, 1983; Schaffler et al., 1985; Fleagle and Meldrum, 1988; Ruff, 1988; Burr et al., 1989; Meldrum, 1991; Demes and Jungers, 1993; Rose, 1993; Gebo and Sargis, 1994; Nakatsukasa, 1996; Runestad, 1997; Strasser et al., 1998; Kimura, 2002; Ruff, 2002; Marchi, 2005; Wright, 2007; DeSilva, 2009; Kikuchi and Hamada, 2009; Marchi et al., 2016; Orr, 2016; Leischner et al., this volume). The majority of these studies focus on the bony morphology of the hands and feet – the parts of the body in direct contact with the substrate during locomotion – and the humerus and femur – the skeletal components that bear the greatest load in locomotion.

Recent studies have also been conducted that focus on the structural properties of primate leg bones and their correlation with activity patterns of human and nonhuman primates, especially in relation to arboreal vs. terrestrial adaptations (Marchi and Borgognini-Tarli, 2004; Marchi 2007, 2015a,b; Marchi and Shaw, 2011). In these studies, we have found that the structure of the leg bones (tibia and fibula), in particular their cortical bone geometry and distal articular structure, are correlated with the different loading patterns the leg is subjected to when moving on arboreal and terrestrial substrates (Schmitt, 2003a; Carlson et al., 2005). While results obtained by the study of the structural properties of leg bones are of functional relevance, we should not underestimate the importance of foot actuators that originate on the leg bones. In fact, locomotor capabilities of primates are determined by different factors including the morphology of the skeleton and the properties of muscles.

The general properties of whole muscles are determined by the arrangement of their muscle fibers (Brinckmann, 2002). Their functional characteristics are, in part, determined by the proportion of fibers that are oriented parallel to each other. Muscles with a large number of sarcomeres, which are basic functional units within muscles, within fibers that run parallel to each other have the capacity to generate high force. Conversely, muscles with longer fibers, and therefore a greater number of sequential sarcomeres in each fiber, can generate force over a wider range of motion. Additionally, these muscles can contract more quickly than those with shorter fibers as the shortening rate of a muscle is a function of fascicle length. Fibers can also insert onto a central tendon (or multiple tendons), which allows for more fibers in a muscle than would be present in one without a central tendon—muscles with this fiber orientation are 'pennate.' However, pennate muscles have shorter fibers than a muscle with no pennation of the same muscle volume. This results in a trade-off between muscles of the same volume that need to contract quickly and provide flexibility (with fewer longer fascicles) and those that need to be stronger (with a greater number of shorter fascicles).

To estimate the force production capabilities of a pennate muscle, its cross section (which can be used as a general estimate of muscle power) must be altered to account for the change in muscle fiber orientation. Instead of using the anatomical cross section of pennate muscles, the physiological cross-sectional area (PCSA) is measured as the cross-sectional area perpendicular to the axis of orientation of the fibers (Maughan et al., 1983; Brinckmann, 2002). A variation of this, the reduced physiological cross-sectional area (RPCSA), is a calculation of force production that removes the amount of force perpendicular to the directional pull of a muscle that results from the angle of fibers that attach to the central tendon in a pennate muscle (Anapol and Barry, 1996; Perry et al., 2011).

Previous studies that evaluated the masticatory muscle architecture of felids and lemurs (Perry and Hartstone-Rose, 2010; Hartstone-Rose and Perry, 2011; Hartstone-Rose et al., 2012, 2015) found that architecture changes according to different dietary requirements. The regular ingestion of large food items coincided with the presence of relatively longer masticatory muscle fibers, yet the force production of muscles scaled with isometry or positive allometry with body mass. This suggests that fascicle length (FL) can signal particular dietary behaviors across body sizes, whereas PCSA and muscle mass (MM) follow more regular patterns within clades. Because of this pattern in the masticatory muscles, we have been led to suspect that muscle fiber architecture plays an important role in other anatomical regions and may indicate, for instance, different locomotor behaviors – particularly whether or not groups of muscles are adapted for stretch/speed or strength. Correlations may also be present between muscle fiber structure and substrate use (e.g., terrestrial vs. arboreal) or phylogeny (between the three suborders). A study performed on forearm muscles (Leischner et al., this issue) provides support to these hypotheses. We must however keep in mind that in some locomotor behaviors, such as leaping, high mechanical power is required (Aerts, 1998). Power is defined as the rate over which work is done and is therefore equal to the product of force and velocity (where velocity is displacement over time). Therefore, muscle architecture optimized for leaping should require both high force (i.e. PCSA) and displacement (i.e. FL).

The muscular architecture and geometry of leg muscles have been well described for humans (Friederich and Brand, 1990; Fukunaga et al., 1992; Narici et al., 1992) and nonhuman apes (Vereecke et al., 2005; Payne et al., 2006). However, remarkably little information exists concerning the mechanical capabilities of leg muscles in other primates. In a study on foot and ankle myology in primates, Langdon (1990) combined the observations from original dissections and from the literature to investigate the variation in cruropedal musculature of strepsirrhines and haplorrhines (14 families) and compared their discrete variations in attachments. In his analysis, the author found high variability across the order, and did not find significant correlation between locomotor behavior and muscle form. In another work, Rauwerdink (1993) measured fiber dimension and tendon length of leg muscles in ten different primate species to determine whether or not primate locomotor specialization is reflected in muscle architecture. The author divided the species in four locomotor categories: leapers, quadrupeds walking or running on the ground, climbing quadrupeds and brachiators. The author found some differences among the species concerning fiber and tendon length, but they were not conclusive enough to differentiate between locomotor categories. Moreover, he did not find any correlation between muscle mass and locomotor specialization.

In another paper Payne et al. (2006) analyzed muscle mass, fascicle length and ratios of muscle belly-muscle total unit (MTU) length ratio for all major hind limb muscles in hominoids including humans. They found similarity between gibbons and humans in hind limb muscle anatomy, in particular FL were short. They also found that in gibbons tendons comprised a greater proportion of the MTU for leg muscles, especially for the triceps surae muscles. On the other hand, non-human great apes were characterized by long FL with short tendons. Spring-like leg MTU are exemplified by the cursorial ungulates. Cursorial terrestrial animals move on a stable substrate, while the same does not hold for arboreal primates. The substrate where primates move is constituted by branches which have a high magnitude of compliance resulting in net loss of energy to locomotor support (Alexander, 1991). Payne et al. (2006) suggested that their results may be due to the particular arboreal locomotion of gibbons between rigid supports (e.g., tree trunks), which may allow internal energy stored in tendons to be used.

Though the aforementioned works are informative, a detailed description of the primate leg muscle architecture, and in particular its correlation with different locomotor habits and substrate use, is still warranted.

Locomotion of primates shows a considerable amount of variation among species (Fleagle, 2013). Since the early attempts, to classify primate locomotion into categories has been a difficult task (Prost, 1965): it is therefore important to provide a classification of the primates studied concerning their locomotion. Those who use biomechanical approaches to understand primate locomotion and posture have long recognized that a complete understanding of primate musculoskeletal system should rely on quantitative primate positional behavior data (Hunt et al., 1996). Here we have assigned locomotor and substrate use categories to each species studied on the basis of data available in literature (see Material and Methods section).

The aim of this study is to quantify the overall leg muscle architecture and muscle belly-MTU length ratio in a wide array of extant strepsirrhines, platyrrhines and catarrhines and discuss the findings in relation to their phylogeny, locomotor habits and substrate use to test the following hypotheses:

1. prevalently arboreal primates will have relatively high PCSA and RPCSA compared to terrestrial primates. This is expected because of their reliance on highly propulsive movements through their arboreal habitat (Fleagle, 2013). In particular, because of the importance of grasping with both hands and feet in an arboreal substrate, prevalently arboreal primates (i.e., arboreal quadrupeds, climbers and suspensory primates) are expected to rely more on foot-grasping than terrestrial primates (Rauwerdink, 1993; Hunt et al., 1996; Lemelin, 1999). Therefore, we predict that prevalently arboreal primates will have high digital flexor muscle PCSA and RPCSA compared to prevalently terrestrial primates;
2. leapers will have relatively high plantarflexor PCSA and RPCSA, and because of the elasticity and speed that take-off requires, they will have longer FL compared to non-leaping primates. This is expected because leaping is associated with exceptionally high mechanical power (Demes et al., 1999; Aerts, 1998) and because primates that move by leaping are characterized by the predominance of muscles for hind limb joint extensions (Demes et al., 1998).
3. quadrupedal leaper primates will have larger muscle belly-MTU ratio in plantarflexor muscles than primates less involved in leaping behaviors. This is expected on the basis of previous studies: Payne et al. (2006) suggested that in hylobatids, which locomote primarily

by swinging through the trees, a larger muscle belly-MTU ratio in leg muscles could allow for energy storage in long tendons that would be used during their movements between points in the tree canopy. Moreover, a study conducted on *Galago* (Aerts, 1998) has proved that energy is stored in the internal connective tissue sheets and attachment structures of the vastus medialis and that such energy is released in the last phase of the extension of the muscle to amplify the mechanical power of the jump.

MATERIALS AND METHODS

The sample

The sample includes 35 adult specimens representing 33 species, six of which are strepsirrhines, 13 are platyrrhines, and 14 are catarrhines (Table 1). They were all obtained from captive facilities located throughout the United States and Spain, and were dissected at either the University of South Carolina or the Universidad de Valladolid. None of the specimens in this study were chemically fixed; all were frozen when fresh and dissected after thawing. All of the muscles of the leg (popliteus excluded) were excised via gross dissection in one hind limb for each specimen. The muscles of interest were all placed into one of two categories based on their function, similarly to Leischner et al. (this issue): plantar flexors and dorsiflexors. Plantar flexors move the dorsum of the foot away from the anterior surface of the leg and the toes towards the sole of the foot, and include the following muscles: gastrocnemius (both medial and lateral bellies), soleus, plantaris, flexor hallucis longus, flexor digitorum longus, tibialis posterior, fibularis longus, and fibularis brevis. Dorsiflexors do the opposite by bringing the dorsum of the foot and toes closer to the anterior surface of the leg, and include the rest of the muscles in the leg: tibialis anterior, extensor hallucis longus, extensor digitorum longus, and tibiofibularis. We then divided some muscles into more specific functional groups (digital flexor, digital extensors, evertors, invertors). The only muscles not present in every specimen were tibiofibularis and fibularis tertius, both of which are ankle flexors. The latter was present only in *Macaca sylvanus,* and the former was found in *Sapajus apella*, *Saimiri sciureus*, *Colobus guereza*, *Cercopithecus hamlyni*, and *Miopithecus talapoin*. These variations had no problematic effect on the analyses as individual muscles were not included in the present analyses, which were instead performed in broad groups.

Muscle analysis

All the muscles of the leg of each specimen were isolated and removed systematically by sharp dissection. For those muscles crossing the tibiotalar joint, the tendons were uniformly cut at the level of the flexor and extensor retinacula rather than excised from their insertion point within the foot. The length of each muscle with its associated tendon (if present) was recorded to the nearest 0.01 mm using digital calipers. The external tendon was cut from the muscle at the point where muscle fibers stopped inserting on the tendon (Stern, 1971). The muscle belly length, width, and thickness were then recorded with respect to their anatomical placement within the leg to the nearest 0.01 mm using digital calipers and then weighed to the 0.001g using a digital scale. Belly thickness was a measurement taken perpendicular to the direction of contraction of each muscle.

Methods used for chemical dissection were identical to Leischner et al. (this issue) and Hartstone-Rose et al. (this issue), and are a modification of Rayne and Crawford’s (1972) methods. Each muscle was covered in enough of a 10% sulfuric acid solution to allow for changes in shape while cooking, and then placed inside of a chemical laboratory oven set to 60°C. Cooking time depended on the size of each muscle and varied between 30 minutes for the smallest specimen (*Cebuella pygmaea*) and 6 hours for the largest (*Gorilla gorilla*). Muscle fibers were ready to be measured when the sulfuric acid had sufficiently dissolved enough of the connective tissue holding fascicles together to allow for their careful isolation with forceps. Ideally, ~40 fascicles that could serve as a representative sample for the whole muscle would be separated and measured to the nearest 0.01mm with digital calipers. In relatively larger or smaller muscles, more or fewer fascicles were measured, respectively. The mean of all fascicles lengths for each muscle was calculated.

To calculate the PCSA (in the equation below q) of each muscle, the muscle mass (in the equation below m) and mean FL (in the equation below l) were used along with the constant representing the specific density of a muscle (p; 1.0564 g/cm^3; Murphy and Beardsley, 1974) in an equation modified from Schumacher (1961):

$$q=m/lp$$

The units for the equation are as follows: PCSA (cm^2), MM (g), and FL (mm).

To then determine whether pennation affected the cross-sectional area of each muscle, the pennation angle (θ) and RPCSA were calculated using equations from Anapol and Berry (1996). Muscle thickness (a) and mean FL (l) were first used to calculate the pennation angle:

$$sin\theta = a/l$$

This value was then used for the final RPCSA (q_r) calculation:

$$q_r = \mathrm{m}(cos\theta)/lp$$

After FL and PCSA were recorded, calculations were done according to each muscle functional group (plantar flexors, dorsiflexors, digital flexors, digital extensors, invertors and evertors). The PCSA, RPCSA, and MM of each group were calculated by adding together the values for all muscles in each functional group for individual specimens. A weighted average FL was then calculated for each group by dividing the sum of the product of the MM and average FL for each muscle in a functional group by the sum of the MM of every muscle in the same group.

Ratios of muscle belly-MTU length (see Fig. 1 for measurements) were calculated by dividing muscle belly length by the length of the total MTU. This way, the closer the ratio is to 1, the larger is the contribution of the muscle belly to the whole MTU. As explained above, the tendons of muscles that crossed the tibiotalar joint were cut at the level of the flexor and extensor retinacula rather than excised from their insertion point within the foot. Therefore, the ratio we obtain is an overestimation of the real muscle belly-MTU ratio.

Before analyses, the square root of all area variables (PCSA, RPCSA) and the cube root of all volumetric variables (MM) were taken to ensure that the slopes for logged data in our regressions would be 1.

Locomotor and substrate categories

The locomotion, posture, and substrate primarily preferred by each species were taken from the literature (Table 1; Supplementary online material). Although degrees of variability in locomotion exist between and within species, each species was assigned one of three broad locomotor categories that they fall into the majority of the time (Table 1):

1. “quadrupedal” primates move primarily on horizontal surfaces (arboreal and/or terrestrial) with a consistent gait using both their hands and feet (Gebo 1987);
2. “quadrupedal-leaper” primates use their lower limbs to propel themselves over gaps between two points (Gebo 1987). Vertical clingers and leapers (i.e. *Galago senegalensis*) and leaping anthropoids (like callitrichines and *Miopithecus talapoin*) were included in this category as finer subdivision within this category may have precluded any significant results;
3. “suspensory” primates use up to four limbs to move between points while hanging underneath a substrate (Gebo 1987). Primates with prehensile tails (*Ateles fusciceps*, in this sample) use them in addition to their limbs to locomote. Though *Gorilla gorilla* (the specie included in this study, Table 1) is predominantly a terrestrial species, it is more arboreal than *G. beringei* and females and juveniles normally feed and rest on trees (Remis, 1995; Doran, 1997). We therefore included this species in the suspensory category, to avoid further subdivisions which may have precluded any significant results.

Arboreality is the main characteristic of primates as an order. However, many primates spend some time on the ground foraging and moving from a foraging site to the next, while other are mainly terrestrial, climbing up trees only to escape predators or to sleep (Fleagle, 2013). As it is for locomotion and posture, also for substrate use the broad subdivision between arboreal and terrestrial primates does not fully take into account the complexity of substrate use patterns. Arboreal primates, for example, use different strategies to cope with their environment on the basis of their body size and branch diameter (Cant, 1992; Stevens, 2008). As a consequence the degree of terrestriality of different primates can change considerably also in species that are phylogenetically strictly related (Gebo, 1987; McGrew, 1998, 2000). We recognize that many species of guenons, for example, spend different amount of times on the ground (Gebo and Sargis, 1994). Each species used in the present study was categorized as either arboreal or terrestrial based on the substrate that they primarily locomote on. Similarly to the locomotor categories, many primates maneuver between both arboreal and terrestrial substrates. We categorized as "terrestrial" those primates who spend most of their feeding time on the ground, while "arboreal" are those who spend most of their feeding time in the trees. For this reason, *L. catta* was grouped in the terrestrial category differently from all other lemurs (Table 1).

Statistical analysis

In order to test the prediction that there are differences in leg muscle architecture across primates based on phylogeny, locomotor/posture pattern, and substrate use, Reduced Major Axis (RMA) regressions of each functional variable (MM, FL, PCSA, RPCSA organized into their functional groups) with body size were analyzed in JMP13 (SAS) and evaluated for allometry. RMA regressions were applied across the entire primate sample, and within-group patterns were assessed via RMA of subsets of data (suborder-infraorder, locomotor pattern, and substrate use).

Residuals were taken as the distance from data points to the regression line when following a path perpendicular to the x-axis and used to evaluate the significance of leg muscle architecture in the suborders, locomotor groups, and substrate groups free from the influence of body mass. Multiple pairwise comparisons were also applied to the muscle belly-MTU length ratios among each of the subgroups. All analyses were performed in PAST (Hammer et al., 2001) and STATISTICA10 (StatSoft), using a significance criterion of alpha < 0.05.

RESULTS

Isometry/Allometry across the sample

All MM correlate strongly with body mass ($r^2 \geq 0.83$) and scale with isometry trending toward positive allometry for all muscle groups (Table 2). This suggests that larger primates may have relatively larger leg muscles than smaller primates. PCSA scales with body mass with significant positive allometry for all muscles combined ($r^2 \geq 0.74$) and for each muscle sub-group (slopes range from 1.26-1.51) except the digital extensors, which however trend towards positive allometry (slope ranges from 0.93 to 1.64) (Table 2). This suggests that larger primates will also have relatively stronger leg muscles than smaller primates. RPCSA, however, scales with significant positive allometry for only the digital flexors and invertors, while all other groups scale with isometry trending towards positive allometry (slopes range from 1.11 to 1.18; Table 2). Interestingly, correcting for pennation suggests that the strength of the leg muscles of larger primates may be relatively stronger than those of smaller primates, but not as much as it appears before correcting for pennation.

FL scales with isometry across the sample for several muscle groups: dorsiflexors, digital flexors, digital extensors, invertors, and evertors (slopes range from 0.90 to 1.09). However, for all leg muscles combined (slope = 0.91, range = 0.77 to 1.07) and for plantar flexors (slope = 0.90, range = 0.76 to 1.06), FL scales with isometry trending toward negative allometry (Table 2) suggesting that larger primates may have relatively shorter FL than smaller primates.

The trend of strength proxies (MM, PCSA, RPCSA) towards positive allometry indicates that there is a scaling relationship between these variables—larger primates are expected to have relatively larger and stronger leg muscles than smaller primates. Leg FL trending toward negative allometry suggests that larger primates will have relatively shorter FL, and therefore less flexible and quick leg muscles, than smaller primates.

Analyses of the residuals by phylogenetic, substrate, and locomotor groupings

When individuals are grouped by phylogeny, the only significant findings involve leg evertors and only for FL digital flexors (Table 3). The evertor PCSA and RPCSA of platyrrhines and strepsirrhines are significantly different from one another, with strepsirrhines having higher PCSA and RPCSA than platyrrhines. Strepsirrhines display significantly higher evertor and digital flexor FL than catarrhines, and significantly higher evertor MM than catarrhines and platyrrhines.

Surprisingly, no significant differences were found among primates grouped by substrate use (Table 4). Only dorsiflexor FL of arboreal primates were nearly significantly longer than those of terrestrial primates ($p = 0.09$) and a trend toward relatively longer FL for digital extensors and invertors was observed for arboreal primates. No significant differences were found either when primates in the sample were grouped by locomotor pattern (Table 5).

Ratios of muscle belly-MTU length are shown in Table 6. Ratios ranged from 1 (no discernable tendon, peroneotibialis in quadrupedal and in terrestrial primates, and gastrocnemius lateral belly, soleus, flexor hallucis longus, flexor digitorum longus, peroneus brevis and peroneus longus in suspensory primates) to 0.59 (tendon represent almost half the length of the muscle-tendon unit, plantaris in platyrrhines) (Table 6).

No differences among phylogenetic groups concerning muscle belly-MTU length ratio were found (Table 7). The comparison among locomotor groups shows some differences for various muscle groups. Suspensory primates have significantly larger plantarflexor belly-MTU proportions than both quadrupedal and quadrupedal leaper primates (Table 7). In general, though significance is not reached for all comparisons (Table 7), suspensory primates exhibit shorter tendons than the other locomotor groups. Moreover, though significance is never reached (Table 7), quadrupedal-leapers primates show a tendency toward relatively longer tendons than quadrupedal primates. When substrate use is taken into consideration, no significant differences are found, though terrestrial primates show nearly significantly ($p = 0.07$, Table 7) higher plantarflexor belly-MTU proportions than terrestrial primates, suggesting that arboreal primates may have relatively longer plantarflexor tendons than terrestrial primates.

DISCUSSION

The aim of this work was to provide a description of leg muscle architecture and belly-muscle total unit length ratios of a vast array of primates from different taxa (strepsirrhines, platyrrhines and catarrhines) involved in different locomotor behaviors (quadrupedal, quadrupedal leapers and suspensory) and found on different substrates (arboreal and terrestrial). We hypothesized that prevalently arboreal primates will have in general relatively high PCSA and RPCSA and in particular high digital flexors muscle PCSA and RPCSA compared to prevalently terrestrial primates; that primates that are more involved in leaping behavior will have relatively higher plantar flexor PCSA and RPCSA and longer FL; and that leaping primates will have longer plantarflexors tendons and shorter bellies compared to quadrupedal primates. The results of our analyses only partially support these hypotheses.

The regressions of leg muscle architecture properties on body mass show that larger primates have relatively larger (MM) and stronger (PCSA and RPSA) muscles than smaller primates. Fiber length, on the other hand, scales with isometry for almost every muscle category and trends toward negative allometry for the combined muscle category. Thus larger primates have larger and stronger muscles, and they do not have longer FL and may have relatively shorter FL for their body size. A similar result was obtained in a study on the muscle architecture of the primate forearm (Leischner et al., this issue). The results may suggest that larger primates have more need for larger and stronger muscles than faster-moving muscles for both the forearm and the leg—particularly in the leg, where more numerous shorter fascicles would allow for higher force generation. Previous studies have consistently found the same relationship for masticatory muscles (Perry and Hartstone-Rose, 2010; Hartstone-Rose et al., 2012, 2015). It was proposed that the isometry of FL may not be a consequence of the fact that stretch/speed ability of muscles scales directly with body size, but rather because FL tends to be where a stronger functional signal is found – thus, there is more scatter around the line based on function, reducing the strength of the correlation which increases the confidence intervals of the slope, reducing the likelihood of statistical significance beyond isometry. In other words, the variation of FL in masticatory muscles between species could be caused by differences in diet (e.g. frugivory and folivory) or locomotion pattern and substrate use, which would reduce any allometric signal to isometry.

Analyses of the residuals grouped by suborder suggest that strepsirrhines have significantly higher evertor PCSA and RPCSA than platyrrhines, and that they also have significantly larger (MM) and faster (FL) leg evertor muscles than catarrhines. A possible explanation for the first finding could lie in the different morphology of the ankle joint in strepsirrhines and platyrrhines — foot orientation after landing on a vertical support may differ between the suborders and, in turn, place different demands on the leg muscles. Interestingly, the finding that strepsirrhines would have relatively larger and faster evertors than catarrhines challenges our results obtained on masticatory muscle architecture, i.e. that a muscle would lean towards either greater strength or speed depending on the behavior of the animal it belonged to. As there are only six strepsirrhines in our sample, however, a larger number would be beneficial for further evaluation—there is a notable lack of overlap in the body sizes of primates in each taxonomical category analyzed here (i.e. strepsirrhines, platyrrhines and catarrhines), and a larger sample could help to address this issue.

Contrary to our expectations (i.e. Hypothesis 1) we did not find any consistent significant difference between the leg muscle architecture of prevalently arboreal and prevalently terrestrial primates. A closer look at the data, however, presents a pattern that partially agrees with our expectations; FL of dorsiflexors are nearly significantly longer in arboreal than in terrestrial primates and we observe a pattern of relatively longer FL for digital extensors and invertors of arboreal primates, suggesting that arboreal primates require faster dorsiflexion and inversion of the foot and extension of the toe than terrestrial primates. Arboreal primates are characterized by more agile locomotion when compared to terrestrial primates implying rapid movements through the trees, for which having longer FL in the limbs may be advantageous. Furthermore, in our sample almost half of the arboreal primates are involved in frequent leaping; therefore, speed and lightness of the leg muscles may constitute an advantage for their locomotion. Arboreal primates are also involved in greater range of motion of the hind limb segments and that could also select for longer FL in those primates.

One possible explanation for the lack of significance in these results may lie in the breadth of the two substrate categories included in this study. As previously pointed out, almost all primates have an arboreal component in their substrate use habits, though the percentage is highly variable between species and environments where different populations of a species may live (Gebo and Sargis, 1994; Gebo, 1987; Cant, 1992; McGrew, 1998, 2000; Stevens, 2008; Fleagle, 2013). For example, it is recognized that the degree of arboreality among the species included within the guenon group is highly variable. *Cercopithecus campbelli* is reported as a frequent user of the terrestrial environment, though not being habitually committed to life on the ground (Gebo and Sargis, 1994; McGrew, 2000). On the other hand, *C. petaurista* is reported as prevalently arboreal (Gautier-Hion, 1988; McGraw, 2000; Jaffe and Isbell, 2011). The purpose of this study was to provide a first analysis of leg muscle architecture and investigate its possible association with behavioral observations concerning substrate use. Given the exploratory nature of this study, we deemed it sufficient to categorize the species included into two broad categories (i.e. arboreal and terrestrial). The results seem to indicate that a weak leg muscle architecture signal is present, though not at the significant level.

Interestingly, the comparison of muscle architecture among different locomotor groups did not produce any significant results. Thus, we found no support for Hypotheses 2. As we have explained above, primates are a very eclectic group of mammal when it comes to locomotion. The locomotory classification used here is very broad and there is overlap among different species included in different categories which may in part be responsible for the lack of significant results of this study. Moreover, only two species (*Gorilla gorilla* and *Ateles paniscus*) were included in the suspensory category (see Table 1) which may play a role in the lack of significance in the results.

Hypothesis 3 is partially validated by our results. Though plantarflexor muscles do not show significantly larger belly-MTU length ratio in quadrupedal leapers as hypothesized, results show a clear pattern in that direction. Therefore, tendons comprised the lowest portion of the muscle-tendon unit in primates that include a considerable amount of leaping in their habitual locomotor behavior. As explained above, only rarely the problem of tendon storage function has been addressed in primates (Aerts, 1998). However, it appears that energy is stored in the internal connective tissue sheets and attachment structure of the vastus medialis of *Galago* which is released in the last phase of the extension of the muscle to amplify the mechanical power of the jump. We suggest that the same mechanism may be present in the plantarflexor muscles of the leg.

Our results also show smaller relative tendon length in the plantarflexors of suspensory primates than in the other locomotor groups. In a previous study, Payne et al. (2006) found that muscle fibers comprised a greater proportion of the MTU in great apes than in gibbons and explained the results as a consequence of their particular arboreal locomotion, i.e. brachiation. The suspensory group included in our study is comprised by only two species: *G. gorilla* and *A. paniscus*. Though the sample is very small, and therefore any consideration must be tentative, the two species are very close in every functional comparison. Our results for *G. gorilla* are in agreement with Payne et al.'s (2006) results. *Ateles paniscus* is an arboreal, suspensory primate whose anatomy resembles apes and which is usually broadly classified as semi-brachiator (Youlatus and Meldrum, 2011; Fleagle, 2013). Therefore, we may expect some similarities with gibbons in their muscle belly-MTU length ratio. However, *A. paniscus* locomotion differs from that of gibbons in many aspects: *A. paniscus* mainly moves between small branches, leaping behavior does not occupy a large percentage of its locomotion repertoire, and it is involved in tail-assisted brachiation (Jones, 2008; Youlatus and Meldrum, 2011). All the above mentioned differences may be responsible for the differences in the muscle belly-MTU proportions found here compared to what Payne et al., (2006) found in gibbons. Further studies on the kinetics and kinematics of atelids are necessary to clarify the reason for the results found in the present study.

The main limitation of this study is the small sample size of some of the categories included in the analysis. For example, only four species constitute the terrestrial group in the comparison among substrate use, and only two species constitute the suspensory group in the comparison among locomotion repertoires and substrate use (Table 1). Another limitation, as we have noted above, is the breadth of the categories included in the study. Primates are characterized by their lack of specialization. Therefore, the degree of terrestrial locomotion and especially the locomotor repertoires are highly variable among species even at the genus level. Our results show some patterns that move into the direction of proving the hypotheses formulated though significance is not reached in as many cases as we would have liked. In future studies, it would therefore be highly advantageous to include more species for each locomotor and substrate use category analyzed and to provide more fine-grained definitions of both locomotor repertoires and substrate use of the species included in order to test the results obtained by this study. Studies on the mechanical function of tendons in leg muscles in leaping primates are also needed in order to test our suggestion that the tendon storage function found for the vastus medialis of *Galago* is also present in the plantarflexor muscles. Finally, the kinetics and kinematics of atelids (and other suspensory primates) need to be further investigated to clarify why the muscle belly-MTU proportions found in this study for atelids (i.e. semi-brachiators) are different from those found in other studies for true brachiators (i.e. gibbons). However, we believe that this preliminary study represents the most in-depth analysis of leg muscle fiber architecture of a relatively broad sample across the primate order and it is a clear step toward understanding the functional significance of this morphology.

CONCLUSIONS

In this study we provided muscle architectural information for a sample of primates made up by 33 species including strepsirrhines, platyrrhines and catarrhines. To the extent possible based on this large and yet constrained sample, we interpreted the results in the context of phylogeny, locomotion and substrate use. In agreement with other studies conducted on muscle architecture, our results show that larger primates have larger and stronger leg muscles, and a tendency toward shorter fascicles, than those of smaller primates. This suggests that larger primates have more need for stronger muscles than faster-moving muscles for the leg. Moreover:

1. strepsirrhines have relatively higher evertor PCSA and RPCSA than platyrrhines, and relatively higher MM and FL than catarrhines;
2. dorsiflexor, digital extensor, and invertor FL show a pattern of higher values (though not significant) in arboreal primates than in terrestrial primates, but there are no trends or statistical evidence suggesting that locomotor category (quadrupedal, quadrupedal leapers and suspensory) is reflected in primate leg muscle architecture based on our sample;
3. plantarflexors show larger belly-MTU length ratio in quadrupedal leapers than in the other categories and in arboreal than in terrestrial primates, indicating a possible energy storage function of longer tendons depending on substrate and locomotion.

While previous structural studies of the leg bones found clear relationships between locomotor patterns and bone structure, the results of the present myological study show the complex relationship between leg bone biomechanics and muscle architecture—and the need for further studies on this topic.

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Figure legends

Fig. 1 – In figure a drawing of tibialis anterior of a *Cebus apella* is shown. The proximal insertion of the muscle is on the right. The figure shows how total muscle unit length and muscle belly length were taken.

Table 1 - Body mass, locomotor category and substrate of the species included in this study

Species	Family[a]	Body Size (g)[b]	Locomotor Category[c]	Substrate[c]
Eulemur fulvus albifrons	Lemuridae	1810*	Quadrupedal	Arboreal
Eulemur macaco	Lemuridae	1730	Quadrupedal	Arboreal
Lemur catta	Lemuridae	2210	Quadrupedal	Terrestrial
Microcebus murinus	Cheirogaleidae	72	Quadrupedal	Arboreal
Galago senegalensis	Galagidae	213*	Quad-Leaper	Arboreal
Otolemur crassicaudatus	Galagidae	1150	Quadrupedal	Arboreal
Aotus nancymaae	Aotinae	874	Quadrupedal	Arboreal
Aotus azarae	Ceboidea	1190	Quadrupedal	Arboreal
Callithrix jacchus	Cebidae	320	Quad-Leaper	Arboreal
Callithrix geoffroyi	Cebidae	359	Quad-Leaper	Arboreal
Mico argentata	Cebidae	300	Quad-Leaper	Arboreal
Cebuella pygmea	Cebidae	116	Quad-Leaper	Arboreal
Saguinus labiatus	Cebidae	539	Quad-Leaper	Arboreal
Saguinus oedipus	Cebidae	404	Quad-Leaper	Arboreal
Saguinus imperator	Cebidae	682	Quad-Leaper	Arboreal
Saguinus midas	Cebidae	515	Quad-Leaper	Arboreal
Saimiri sciureus	Cebidae	723*	Quadrupedal	Arboreal
Sapajus apella	Cebidae	3085*	Quadrupedal	Arboreal
Ateles fusciceps	Atelidae	8890	Suspensory	Arboreal
Macaca sylvanus	Cercopithecidae	8900	Quadrupedal	Arboreal
Cercocebus atys	Cercopithecidae	12100	Quadrupedal	Arboreal
Cercocebus torquatus	Cercopithecidae	6230	Quadrupedal	Arboreal
Cercopithecus hamlyni	Cercopithecidae	3360	Quadrupedal	Arboreal
Cercopithecus cephus	Cercopithecidae	4290	Quadrupedal	Arboreal
Cercopithecus mona	Cercopithecidae	5100[d]	Quadrupedal	Arboreal
Cercopithecus neglectus	Cercopithecidae	10635	Quadrupedal	Arboreal
Cercopithecus petaurista	Cercopithecidae	2900	Quadrupedal	Arboreal
Cercopithecus campbelli	Cercopithecidae	1505	Quadrupedal	Arboreal

Chlorocebus aethiops	Cercopithecidae	3620*	Quadrupedal	Terrestrial
Miopithecus talapoin	Cercopithecidae	1380	Quadrupedal	Arboreal
Mandrillus sphinx	Cercopithecidae	6900	Quadrupedal	Terrestrial
Colobus guereza	Cercopithecidae	6730	Quadrupedal	Arboreal
Gorilla gorilla	Hominidae	120950	Suspensory	Terrestrial

[a] Fleagle, 2013.

[b] Fleagle, 2013 except as noted. Average mass for sex if sex was known. Average for species if sex was unknown (annotated "*").

[c] Data compiled from: Napier and Walker, 1967; Thorington, 1967; Jones and Sabater, 1968; Kinzey et al., 1975; Mittermeier and Fleagle, 1976; Morbeck, 1977; Rose, 1979; Ward and Sussman, 1979; Fleagle and Mittermeier, 1980; Garber, 1980; Fleagle et al., 1981; Gebo, 1987; Ford, 1988; Gautier-Hion, 1988; Snowdown and Soini, 1988; Stevenson and Rylands, 1988; Wright, 1989; Oxnard et al., 1990; Ansorge et al., 1992; Dodson et al., 1992; Garber 1992; Janson and Boinski, 1992; Gebo and Sargis, 1994; Hammerschmidt et al., 1994; Taylor, 1994; Remis, 1995; Digby and Barreto, 1996; Nakatsukasa, 1996; Rogers et al., 1996; Doran, 1997; Meldrum, 1998; Dagosto and Yamashita, 1998; McGraw, 1998; Youlatos, 1999; McGrew, 2000; Arms et al., 2002; Fleagle and McGraw, 2002; McGraw and Bshary, 2002; Schmitt, 2003b; Shapiro, 2007; Wright, 2007; Veracini, 2009; Polk et al., 2010; Jaffe and Isbell, 2011; Youlatus and Meldrum, 2011; Fleagle, 2013.

[d] Anandam et al., 2013.

Table 2: Descriptive statistics for analyses of muscle architecture variables.

Y-variable	Slope (β) ^b	Y-intercept	r^2	Lower β CL	Upper β CL
		Log Fiber Length (mm)			
Total	0.91	0.26	0.85	0.77	1.07
Plantar Flexors	0.90	0.23	0.85	0.76	1.06
Dorsiflexors	0.96	0.33	0.77	0.78	1.19
Digital Flexors	0.90	0.22	0.77	0.73	1.11
Digital Extensors	1.02	0.21	0.74	0.81	1.29
Evertors	0.90	0.20	0.71	0.70	1.16
Invertors	1.09	0.12	0.55	0.76	1.57
		Log Muscle Mass (g) ^1/3			
Total	1.05	-0.67	0.92	0.94	1.17
Plantar Flexors	1.06	-0.72	0.92	0.95	1.19
Dorsiflexors	1.02	-0.86	0.92	0.91	1.14
Digital Flexors	1.11	-0.99	0.92	0.98	1.25
Digital Extensors	1.03	-1.00	0.85	0.87	1.23
Evertors	1.05	-0.99	0.83	0.88	1.26
Invertors	1.11	-1.00	0.92	0.99	1.26
		Log PCSA[a] ^1/2			
Total	1.38	-0.95	0.74	1.10	1.74
Plantar Flexors	1.43	-1.05	0.72	1.12	1.83
Dorsiflexors	1.26	-1.22	0.77	1.26	1.03
Digital Flexors	1.51	-1.47	0.74	1.20	1.90
Digital Extensors	1.24	-1.34	0.67	0.93	1.64
Evertors	1.48	-1.53	0.61	1.07	2.05
Invertors	1.50	-1.50	0.77	1.21	1.85
		Log RPCSA[b] ^1/2			
Total	1.12	-0.66	0.88	0.97	1.30
Plantar Flexors	1.14	-0.72	0.88	0.98	1.31
Dorsiflexors	1.11	-1.05	0.85	0.94	1.31
Digital Flexors	1.20	-1.12	0.86	1.03	1.41
Digital Extensors	1.15	-1.25	0.72	0.90	1.46
Evertors	1.18	-1.18	0.74	0.94	1.49
Invertors	1.24	-1.20	0.86	1.06	1.44

* $p \leq 0.15$;** $p \leq 0.05$

[a] PCSA = Physiological Cross-Sectional Area. See text for explanation.

[b] RPCSA = Reduced Physiological Cross-Sectional Area. See text for explanation.

Table 3: Comparison of muscle groups among taxa.

	Catarrhine[a]	Platyrrhine	Strepsirrhine	p-value[b]
		Log Fiber Length (mm)		
Total	-0.01	0.00	0.03	0.14
Plantar Flexors	-0.02	0.01	0.03	0.11
Dorsiflexors	-0.02	0.00	0.04	0.14
Digital Flexors	-0.02_{S}[c]	0.01	0.05_{C}	0.03*
Digital Extensors	-0.02	0.01	0.04	0.17
Evertors	-0.03_{S}	0.01	0.06_{C}	0.03*
Invertors	-0.04	0.01	0.08	0.06
		Log Muscle Mass (g) ^1/3		
Total	0.00	-0.01	0.02	0.37
Plantar Flexors	0.00	-0.01	0.02	0.28
Dorsiflexors	0.00	-0.01	0.00	0.77
Digital Flexors	-0.01	-0.01	0.02	0.40
Digital Extensors	0.00	0.00	-0.02	0.70
Evertors	0.00_{S}	-0.02_{S}	$0.07_{C,P}$	0.00*
Invertors	0.00	-0.01	0.02	0.31
		Log PCSA[d]^1/2		
Total	0.00	-0.02	0.05	0.38
Plantar Flexors	0.00	-0.02	0.06	0.30
Dorsiflexors	0.00	-0.01	0.01	0.95
Digital Flexors	-0.01	-0.02	0.06	0.32
Digital Extensors	-0.01	0.00	0.02	0.90
Evertors	-0.01	-0.04_{S}	0.14_{P}	0.02*
Invertors	0.00	-0.02	0.05	0.37
		Log RPCSA[e]^1/2		
Total	0.00	-0.01	0.01	0.60
Plantar Flexors	0.00	-0.01	0.02	0.47
Dorsiflexors	0.00	0.00	-0.01	0.89
Digital Flexors	-0.01	0.00	0.02	0.61
Digital Extensors	0.00	0.01	-0.03	0.62
Evertors	0.00	-0.03_{S}	0.09_{P}	0.01*
Invertors	0.00	-0.01	0.01	0.81

[a] Values in table are residuals of the regression of the muscle architecture variables against body mass taken as the distance from data points to the regression line when following a path perpendicular to the x-axis.

[b] One-way ANOVA results. * $p < 0.05$.

[c] Results of post hoc Tukey test for all groups. Capital letters indicate $p < 0.05$ significant level (C = Catarrhines, P = Platyrrhines, S = Strepsirhines); lower case letters indicate a $0.05 < p < 0.10$ significant level (c = Catarrhines, p = Platyrrhines, s = Strepsirhines).

[d] PCSA = Physiological Cross-Sectional Area. See text for explanation.

[e] RPCSA = Reduced Physiological Cross-Sectional Area. See text for explanation.

Table 4 – Comparison of muscle groups among substrate use.

	Arboreal[a]	Terrestrial	p-value[b]
	Log Fiber Length (mm)		
Total	0.00	-0.03	0.27
Plantar Flexors	0.00	-0.02	0.48
Dorsiflexors	0.01	-0.05	0.09°
Digital Flexors	0.00	-0.03	0.29
Digital Extensors	0.01	-0.05	0.15
Evertors	0.00	-0.03	0.34
Invertors	0.01	-0.08	0.12
	Log Muscle Mass (g) ^1/3		
Total	0.00	0.00	0.91
Plantar Flexors	0.00	0.00	0.83
Dorsiflexors	0.00	0.00	0.94
Digital Flexors	0.00	-0.01	0.69
Digital Extensors	0.00	-0.02	0.56
Evertors	0.00	-0.01	0.84
Invertors	0.00	-0.01	0.65
	Log PCSA[c]^1/2		
Total	0.00	-0.05	0.30
Plantar Flexors	0.00	-0.06	0.30
Dorsiflexors	0.00	-0.04	0.29
Digital Flexors	0.00	-0.07	0.20
Digital Extensors	0.01	-0.07	0.14
Evertors	0.01	-0.07	0.27
Invertors	0.00	-0.05	0.30
	Log RPCSA[d]^1/2		
Total	0.00	-0.03	0.30
Plantar Flexors	0.00	-0.03	0.28
Dorsiflexors	0.00	-0.03	0.37
Digital Flexors	0.00	-0.04	0.14
Digital Extensors	0.01	-0.06	0.18
Evertors	0.00	-0.04	0.34
Invertors	0.00	-0.03	0.33

[a] Values in table are residuals of the regression of the muscle architecture variables against body mass taken as the distance from data points to the regression line when following a path perpendicular to the x-axis.

[b] Results of t-test for the two groups. ° $0.05 < p < 0.10$.

[c] PCSA = Physiological Cross-Sectional Area. See text for explanation.

[d] RPCSA = Reduced Physiological Cross-Sectional Area. See text for explanation.

Table5 – Comparison of muscle groups among locomotor modes.

	Quadrupedal[a]	Quad-leaper	Suspensory	p-value[b]
		Log Fiber Length (mm)		
Total	-0.00	0.00	-0.00	0.99
Plantar Flexors	-0.00	0.00	0.01	0.80
Dorsiflexors	-0.00	0.01	-0.02	0.79
Digital Flexors	-0.01	0.01	0.03	0.50
Digital Extensors	-0.00	0.01	-0.03	0.69
Evertors	-0.00	0.00	-0.00	0.95
Invertors	-0.01	0.02	-0.03	0.65
		Log Muscle Mass (g) ^1/3		
Total	0.00	-0.01	-0.02	0.51
Plantar Flexors	0.00	-0.01	-0.01	0.53
Dorsiflexors	0.00	0.00	-0.03	0.28
Digital Flexors	0.00	0.01	-0.03	0.38
Digital Extensors	0.00	0.01	-0.05	0.21
Evertors	0.01	-0.02	-0.00	0.57
Invertors	0.00	-0.01	-0.01	0.66
		Log PCSA[c]^1/2		
Total	0.01	-0.02	-0.05	0.51
Plantar Flexors	0.01	-0.02	-0.05	0.48
Dorsiflexors	0.00	0.01	-0.04	0.58
Digital Flexors	0.01	-0.00	-0.08	0.32
Digital Extensors	0.01	0.02	-0.09	0.20
Evertors	0.02	-0.03	-0.06	0.49
Invertors	0.01	-0.02	-0.04	0.58
		Log RPCSA[d]^1/2		
Total	0.00	-0.00	-0.02	0.80
Plantar Flexors	0.00	-0.01	-0.02	0.78
Dorsiflexors	-0.00	0.01	-0.03	0.52
Digital Flexors	-0.00	0.01	-0.05	0.27
Digital Extensors	-0.00	0.02	-0.07	0.17
Evertors	0.01	-0.01	-0.03	0.65
Invertors	-0.00	0.00	-0.01	0.95

[a] Values in table are residuals of the regression of the muscle architecture variables against body mass taken as the distance from data points to the regression line when following a path perpendicular to the x-axis.

[b] One-way Anova results. * $p < 0.05$.

[c] PCSA = Physiological Cross-Sectional Area. See text for explanation.

[d] RPCSA = Reduced Physiological Cross-Sectional Area. See text for explanation.

Table 6 – Ratio of muscle belly length to total muscle tendon unit length

	Suborder			Locomotion			Substrate[f]		
	Strepsirrhine[a]	Platyrrhine	Catarrhine	Quadrupedal	Quad-Leaper	Suspensory	Arboreal	Terrestrial	p-value
GasM[b]	0,61[c]	0.68	0.67	0.63[e]$_{S}$	0.66$_{S}$	0.91$_{Q\text{-}L,Q}$	0.65	0.75	0.07
GasL	0,69	0.73	0.70	0.69$_{S}$	0.72$_{S}$	1.00$_{Q\text{-}L,Q}$	0.70	0.78	0.22
Plant	0.75	0.59	0.65	0.67	0.62	-	0.64	0.73	0.31
Sol	0.83[d]$_{C}$	0.86$_{C}$	0.98$_{P,S}$	0.95$_{q\text{-}l}$	0.85$_{q}$	1.00	0.91	0.95	0.52
FHL	0.85	0.74	0.85	0.82	0.77	0.96	0.79	0.92	0.19
FDL	0.83	0.81	0.88	0.87	0.78	1.00	0.84	0.87	0.77
PB	0.86$_{C}$	0.91	0.98$_{S}$	0.95	0.88	1.00	0.92	0.95	0.63
PL	0.63	0.73	0.78	0.76$_{S}$	0.68$_{S}$	1.00$_{Q\text{-}L,Q}$	0.73	0.83	0.11
TA	0.94	0.94	0.85	0.88	0.92	0.97	0.90	0.88	0.65
EDL	0.93	0.93	0.95	0.94	0.93	0.99	0.93	0.98	0.41
EHL	0.92	0.82	0.87	0.88	0.80	0.96	0.88	0.76	0.22
TP	0.79	0.70	0.71	0.73	0.66	0.94	0.71	0.74	0.81
PT	-	0.97	1.00	1.00	0.97	-	0.99	1.00	0.74

[a] Values in table are calculated as muscle belly length / total muscle tendon unit length.

[b] GasM: gastrocnemius medial belly; GasL: gastrocnemius lateral belly; Plant: plantaris; Sol: soleus; FHL: flexor hallucis longus; FDL: flexor digitorum longus; PB: peroneus brevis; PL: peroneus longus; TA: tibialis anterior; EDL: extensor digitorum longus; EHL: extensor hallucis longus; TP: tibialis posterior; PT: peroneotibialis.

[c] Ratios were calculated by dividing muscle belly length by total-muscle tendon unit. For those muscles crossing the tibiotalar joint, the tendons were uniformly cut at the level of the flexor and extensor retinacula.

[d] Results of post hoc Tukey test for all suborder groups. Capital letters indicate $p < 0.05$ significant level (S = Strepsirrhine, P = Platyrrhine, C = Catarrhine); lower case letters indicate a $0.05 < p < 0.10$ significant level (s = Strepsirrhine, p = Platyrrhine, c = Catarrhine).

[e] Results of post hoc Tukey test for all locomotion groups. Capital letters indicate $p < 0.05$ significant level (Q = Quadrupedal, Q-L = Quadrupedal-Leaper, S = Suspensory); lower case letters indicate a $0.05 < p < 0.10$ significant level (q = Quadrupedal, q-l = Quadrupedal-Leaper, s = Suspensory). For m. plantaris and m. peroneotibialis a t-test was used.

[f] Results of t-test for substrate groups.

Table 7 – Ratio of muscle belly length to total muscle tendon unit length by functional groups

	Taxon			Substrate			Locomotion		
	Strepsirrhine[a]	Platyrrhine	Catarrhine	Arboreal	Terrestrial	p-value[c]	Quadrupedal	Quad-Leaper	Suspensory
Plantarflexors	0.76[b]	0.76	0.80	0.77	0.84	0.07°	$0.78^{d}_{S,q\text{-}l}$	$0.74_{S,q\text{-}l}$	$0.97_{Q\text{-}L,\ Q}$
Dorsiflexors	0.92	0.91	0.90	0.91	0.88	0.50	0.91	0.88	0.97
Digital flexors	0.84	0.78	0.86	0.82	0.90	0.30	0.84	0.77	0.98
Digital extensors	0.92	0.89	0.91	0.91	0.87	0.50	0.92	0.85	0.97

[a] Values in table are calculated as muscle belly length / total muscle tendon unit length.

[b] Results of post hoc Tukey test for all suborder groups. Capital letters indicate $p < 0.05$ significant level (S = Strepsirrhine, P = Platyrrhine, C = Catarrhine); lower case letters indicate a $0.05 < p < 0.10$ significant level (s = Strepsirrhine, p = Platyrrhine, c = Catarrhine).

[c] Results of t-test for substrate groups. ° $0.05 < p < 0.10$.

[d] Results of post hoc Tukey test for all locomotion groups. Capital letters indicate $p < 0.05$ significant level (Q = Quadrupedal, Q-L = Quadrupedal-Leaper, S = Suspensory); lower case letters indicate a $0.05 < p < 0.10$ significant level (q = Quadrupedal, q-l = Quadrupedal-Leaper, s = Suspensory).

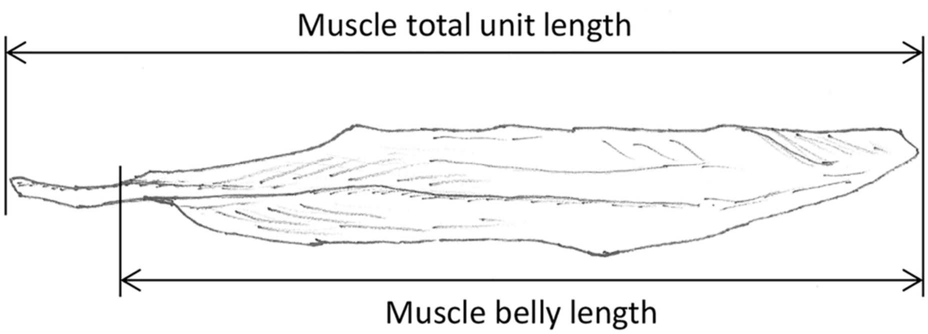

Fig. 1 – In figure a drawing of tibialis anterior of a Cebus apella is shown. The proximal insertion of the muscle is on the right. The figure shows how total muscle unit length and muscle belly length were taken.

46x17mm (600 x 600 DPI)

Supplementary Online Material

Leg muscle architecture in primates and its correlation with locomotion patterns

Damiano Marchi*, Carissa L. Leischner, Francisco Pastor, Adam Hartstone-Rose.

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LOCOMOTOR CATEGORIES OF THE PRIMATES STUDIED

Strepsirrhines

Eulemur fulvus: *E. fulvus* is almost totally arboreal and horizontal supports are used most frequently during travel (Dagosto, 1994). They move primarily by quadrupedal walking and running and by leaping. In the wild they are never observed suspending underneath branches (Dagosto and Yamashita, 1998). In a study of captive animals, Gebo (1987) found that *E. fulvus* leaped, climbed, and engaged in suspensory movements and postures more often than did *L. catta. E. fulvus* used quadrupedalism and suspension in the arboreal setting far more often than did *L. catta,* which tended to leap and climb when in trees.

Eulemur macaco: *E. macaco* can be defined as a generalist among lemurs involved in arboreal quadrupedalism, leaping and climbing (Gebo, 1987). Meldrum (1998) observed that *E. macaco* is particularly adept in hind limb suspension during feeding on horizontal supports of various diameters postures.

Lemur catta: it moves quadrupedally more than any other lemurid and also have high percentage of bipedalism consisting of hopping or walking when on the ground (Gebo, 1987). *L. catta* spends a considerable amount of time on the ground. Ward and Sussman (1979) estimate roughly 30% of its daily hours are spent terrestrially and 65% of group travel is done on the ground. Furthermore, Ward and Sussman (1979) never observed *L. catta* using vertical clinging postures.

Galago senegalensis: the bushbabies have relatively long legs and ankle bones and are all adept leapers (McArdle, 1981). In a study on wild animals, Crompton (1983) found that more than half of the displacements in *G. senegalensis* is leaping which overall accounts for two thirds of total travel distance. Walking and running account for about 20% while climbing around 18%. A singular characteristic of *G. senegalensis* is their ability to descent vertical trunks head-first (Curtis and

Feistner, 1994, and references therein). This mode of locomotion creates biomechanical problems to quadrupeds and especially to primates. Primates have a more caudal position of their center of gravity where the hindlimb carries more body weight than the forelimb. In head first descent this situation is reversed (Preuschoft, 1990). The rotation of the subtarsal and midtarsal joint to reverse the foot posture in *G. senegalensis* are functional to head first descent (Curtis and Feistner, 1994, and references therein).

Otolemur crassicaudatus: *Otolemur* is strictly related to *G. senegalensis* but it is also larger and body size is responsible of its different locomotor behavior. *O. crassicaudatus* combines leaping with an emphasis on horizontal postures, differently from *G. senegalensis*. It is an active quadrupedal arboreal primate which leaps from a pronograde posture (Oxnard et al., 1990; Shapiro, 2007).

Microcebus murinus: *Microcebus* are among the smallest of all living primates. Their limbs are short relative to the length of the trunk and their forelimbs are shorter than their hind limbs. Mouse lemurs are arboreal quadrupeds that involved mainly in walking and running along small branches (Dodson et al., 1992; Fleagle, 2013).

Aotus nancymaae and *Aotus azarae*: Owl monkeys are found in a variety of forest habitats and do not show any preference in the canopy level. They are arboreal quadruped primates but are adept leapers (Fleagle, 2013). Detailed data on the locomotion and postures of *Aotus* are not available, probably because it is mainly nocturnal. Anecdotal descriptions and predictions from postcranial traits suggest a mainly quadrupedal primate with moderate leaping activities (Wright, 1989). This piece of information is also supported by postcranial similarities with *Callicebus* (Ford, 1988), which exhibits such positional patterns.

Platyrrhines

Marmosets: there are several general of marmosets.

The genus *Callithrix* consists of five species including *C. jacchus*. All *Callithrix* move by a combination of quadrupedal walking and running and by leaping and engage in clinging behavior on vertical trunks (Fleagle, 2013). *Callithrix jacchus* is more frequently found gouging for exudates on large vertical trunks where they can engage their claws and climb in the manner of nonprimates (Stevenson and Rylands, 1988; Garber 1992; Digby and Barreto, 1996). The postcranial skeleton and postural behavior of *C. jacchus* has been explained as closer to squirrels than the ones of other callitrichines. In fact, even though all callitrichines have claw-like nails, only *C. jacchus* is characterized by gait mechanics with less protracted forearm and high forelimb forces, different from all other primates and more similar to non-primate mammals (Schmitt, 2003).

The genus *Mica* shows a locomotor repertoire similar to other marmosets that leave in the same habitats (Veracini, 2009).

Cebuella pygmea is the smallest anthropoid and is characterized by morphological adaptations to feeding on tree exudates and to frequent climbing, clinging and quadrupedalism and leaping on vertical supports (Youlatos, 1999). In a study in the wild, Kinzey et al. (1975) found that *C. pygmea* uses a wide range of locomotion behaviors including quadrupedal walking and running and leaping. The authors found that the major part of feeding time was spent clinging to vertical supports and also observed hogh frequency of leaps to and/or from a vertical supporting branch. On the basis on these observations, Kinzey et al. (1975) proposed to consider *C. pygmea* as a vertical clinger and leaper (Napier and Walker, 1967). A more recent study (Youlatos, 1999) has reported that quadrupedal walk and leaping dominates during both traveling and feeding in *C. pygmea*. Leaping between terminal supports is the main leaping way, while vertical leaps are rare. Climbing up and down trunks and claw clinging are used mainly in feeding activities (Kinzey et al., 1975; Youlatos, 1999).

Tamarins: there are more than 20 species of tamarins. Saguinus is the most widespread genus of callitrichine. Studies performed on several species of the genus *Sanguinus* have highlighted a consistent locomotor behavior for the group primarily characterized by quadrupedal walking and running, and by leaping between different types of supports (depending on the species, Fleagle and Mittermeier, 1980; Garber, 1980; Snowdown and Soini, 1988). When tamarins feed on exudates they adopt a stable vertical clinging posture by implanting their claw-like nails into the bark. In an experimental study performed on captive *S. aedipus* (Arms et al., 2002) it was found that *Sanguinus* prefers horizontal substrates (84% of time) to inclined or vertical substrates. Jumping constituted a good amount of the locomotor activity (22%) and the main locomotor modes were quadrupedal walking or running (74%).

Saimiri sciureus: squirrel monkeys are arboreal quadrupeds that leap frequently and live in the lower levels of riverine and secondary forests (Fleagle, 2013). Like all cebines *S. sciureus* use predominantly quadrupedal walking and running for locomotion with the only major difference being the frequency of leaping: squirrel monkeys are remarkably good leapers and leap more often than other cebines (Fleagle and Mittermeier, 1980; Janson and Boinski, 1992) especially when travelling in the lower forest levels. *Saimiri sciureus* only occasionally come to the ground in which occasion they walk quadrupedally (Fleagle et al., 1981). In studies conducted on wild animals, it has been noted that quadrupedal movements (55% of bouts) are more frequent than leaping (42% of bouts) during travel. Climbing accounts for only 3% of bouts (Fleagle and Mittermeier, 1980). When foraging for insects, the percentage of quadrupedal locomotion increases (75%) and of leaping decreases (22%). The greater adaptation to leaping might be the cause of the frequently found small amount of fusion between the tibia and fibula distally (Fleagle, 2013).

Sapajus apella: tufted capuchin monkey is predominantly an arboreal quadrupedal species as the squirrel monkey. However, it is less saltatory than *S. sciureus* and has a prehensile tail. Locomotion during feeding is much more quadrupedal (Fleagle et al., 1981). Quadrupedal walking and running account for the major part of the locomotor activities of *S. apella* (Youlatus and Meldrum, 2011). Wright (2007) found that *S. apella* walks 40% of the time and leaps 22% of the time. However, *S. apella* uses suspensory locomotion and postures more frequently than *S. sciureus* (Thorington, 1967).

Ateles fusciceps: *A. fusciceps* is part of the spider monkey group and has long limbs and a prehensile tail. Spider monkeys are the largest platyrrhines and in many aspect of their anatomy they resemble apes (Fleagle, 2013). Spider monkeys when travelling in the forest canopy use both quadrupedalism and suspensory behavior, including brachiation and climbing. Depending on the species they can spend up to 50% of their locomotion time in suspensory behavior (Youlatus and Meldrum, 2011). They occasionally leap and often move bipedally in the trees.

Catarrhines

Macaca sylvanus: the genus *Macaca* has the widest distribution of any nonhuman primate groups (Fleagle, 2013). All *Macaca* are quadrupedal but there is high variation as for the extent to which they are arboreal or terrestrial. *Macaca sylvanus* are largely terrestrial during the day but climb into trees or onto cliffs during the night. They also may climb into tree for resting during the day (Ansorge et al., 1992; Hammerschmidt et al., 1994).

Cercocebus atys and *C. torquatus*: the monkeys of the genus *Cercocebus* prefer the understory and are most commonly found on the ground when they are both travelling and feeding (Nakatsukasa, 1996; McGraw and Bshary, 2002; Fleagle, 2013). In a study on wild animals, McGraw (1998) found that *C. atys* spends the major part of its time moving and feeding on the ground (76% of the time) or in the shrub layer (around 13% of the time). Even though they spend the majority of their locomotor time on the ground, they frequently climb understory saplings to search for food. In another study, Jones and Sabater (1968) found that *C. torquatus* is terrestrial as well as arboreal and spends much time on the ground.

Guenons: The species of the genus *Cercopithecus* is usually referred to as guenons. There are 19 guenon species which are relatively uniform is size and body proportions (Fleagle, 2013). All species are arboreal quadrupeds, but some of them come frequently on the ground and others are good leapers.

Cercopithecus neglectus is one of the largest guenons (Fleagle, 2013). They live in flooded forests where they move primarily in the understory and on the ground (Gebo and Sargis, 1994). They are slow quadrupedal monkeys.

Cercopithecus hamlyni and *C. campbelli* are also frequent users of the terrestrial environment, though not being habitually committed to life on the ground (Gebo and Sargis, 1994; McGrew, 2000).

Cercopithecus cephus, and *C. petaurista* are prevalently arboreal (Gautier-Hion, 1988; McGraw, 2000; Jaffe and Isbell, 2011).

Miopithecus talapoin: the talapoin monkey is the smallest Old World monkey. They prefer the dense undergrowth of riverine forests where they move by leaping and quadrupedal walking and running. They are very good leapers (Fleagle, 2013, Polk et al., 2010).

Chlorocebus aethiops is a relatively terrestrial oriented monkey but still moves often in the arboreal environment (Rose, 1979; Fleagle, 2013). Terrestrial movement account for 20% of their locomotion. When on the ground grivets spend 95% of their time walking or running quadrupedally (Gebo and Sargis, 1994).

Mandrillus sphinx: the papionins of the genus *Mandrill* are large forest primates. *Mandrill* has forelimb and hindlimb of nearly equal length and is a predominantly terrestrial forest-dwelling cercopithecine, although they have been observed to regularly climb into trees in search of food

(Rogers et al., 1996; Fleagle and McGraw, 2002). Jolly (1970) noted that mandrills and drills both show anatomical signs of considerable greater adaptation to tree climb than what observed in baboons.

Colobus guereza: colobines are generally more arboreal and usually better leapers than cercopithecines (Fleagle, 2013). The locomotor repertoire of *C. gue*reza consists primarily of quadrupedal galloping and bounding, and leaping. It does not brachiate or walk bipedally and rarely performs arm-swinging (Mittermeier and Fleagle, 1976). *Colobus guereza* spends most of its time in above branch postural activities, primarily in sitting postures. Locomotion accounts for less than one-fifth of its positional behavior (Morbeck, 1977).

Gorilla gorilla: the western lowland gorilla is characterized by extreme sexual size dimorphism. Gorillas have relatively long forelimbs while hind limbs are relatively short (Fleagle, 2013). *Gorilla gorilla* is predominantly a terrestrial primate. However, compared to *G. beringei* it is more arboreal with females and juveniles normally feeding and resting on trees (Remis, 1995; Doran, 1997). Morphological studies indicate for *G. gorilla* more suspensory postcranial adaptations than for *G. beringei* (Taylor, 1994). On the ground, *G. g. gorilla* walks or runs quadrupedally using the characteristic hand posture called knuckle-walking. During arboreality, gorillas utilize vertical climbing with high frequency (Tuttle and Watts, 1985).

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