In 1969 I submitted a dissertation (Stern, 1971)[1] on the anatomy of the hip and thigh musculature of cebid monkeys.[2] Prior to my work, George Erikson had collected specimens of *Brachyteles* during various trips to South America, but these specimens were not available to me for study. In 2010, John Fleagle acquired from the estate of George Erikson many of the wet specimens he had collected in South America. Five yeas later, when I announced my intention to retire, John suggested that I close my career as it had begun it, by dissecting the hip and thigh musculature of the one ateline genus not previously available to me. I did so in the Spring of 2015, and now in the Summer of 2018 I am closing the circle by reporting the findings of these dissections. You may ask why I waited three years to do so. The answer is that in 2015 I told John we could jointly publish a genuine paper on my dissections of the hip and thigh of *Brachyteles* if he were to write the Introduction and Discussion with proper citation of previous publications on the taxonmic status and behavior of this genus. It now seems clear this will not happen in my lifetime. Hence, I present my results in this less-than-academically-proper manner so they will be available to the very few people who might be interested.

Erikson (1963)[3] published some anatomic information about the wooly spider monkey, but limited this to a presentation of certain body proportions, followed by the statements (p. 146) that on the basis of the forelimb length "and an array of detailed anatomical data that cannot be summarized here", *Brachyteles* "is not an annectant form between *Lagothrix* and *Ateles*, as has so often been stated, but resembles the latter much more closely". Erikson's observations of live captive wooly spider monkeys led him to assert that it "is just as truly a brachiator" as *Ateles*. I have been told by my colleagues that more recent studies suggest that the similarities in behavior and morphology between *Brachyteles* and *Ateles* are homoplasies rather than synapomorphies.

Material and Methods

Fixed cadavers of three female *Brachyteles* were dissected. Judging from their sizes, the specimens represent one juvenile, one young adult, and one mature adult. Since the hip and thigh musculature of *Brachyte*les shares with other atelines all those traits that differentiate this group from nonateline New World monkeys, detailed observations were confined to muscular traits known to distinguish *Lagothrix* from *Ateles* (Stern, 1971) in the hope of finding taxonomic or functional similarities between *Brachyteles* and one or the other of these genera.

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[1] Stern JTJr. 1971 Functional Myology of the Hip and Thigh of Cebid Monkeys and Its Implications for the Evolution of Erect Posture. Bibliotheca Primatologica. No. 14. Basel: Karger, 318 pp.

[2] In those days, all New World Monkeys excluding marmosets and tamarins, were assigned to the family Cebidae. Today, the genera of New World monkeys are partitioned among two families - Cebidae (*tamarins, marmosets, Aotus*, *Saimiri*, *Cebus*) and Atelidae (*Callicebus*, *Cacajao*, *Chiropotes*, *Pithecia*, *Alouatta*, *Lagothrix*, *Brachyteles*, *Ateles*).

[3] Erikson GE. 1963 Brachiation in New World monkeys and in anthropoid apes. Symp Zool Soc Lond, No. 10, The Primates, pp. 135-163.

Results

Table 1 presents a list of 16 traits in which the hip and thigh musculature of woolly monkeys (*Lagothrix*) differs from that of spider monkeys (*Ateles*). For each such trait the difference is described, as is the status of the trait in *Brachyteles*.

For 11 of the enumerated traits (1-11) the differences between *Lagothrix* and *Ateles* would seem to be of little functional importance, or at any rate Stern (1971) had no functional explanation for them. For six of these 11 nonfunctional traits (1-6), *Brachyteles* more closely resembles *Lagothrix* than *Ateles*. For the remaining five (7-11), *Brachyteles* more closely resembles *Ateles*.

The last five of the enumerated traits in Table 1 (12-16) were given functional interpretations by Stern (1971). For two of these, *Brachyteles* more closely resembles *Lagothrix* than *Ateles*. For one such trait the resemblance to *Atele*s is closer. For two of the functionally significant traits, *Brachyteles* is uniquely different from any other ateline genus.

Discussion

If one were to consider the traits for which no functional interpretation has been offered as being of systematic significance, then the fact that *Brachytele*s shares half of them with *Lagothr*ix and half with *Atele*s in no way contributes to resolving any lingering controversy about the taxonomic affinities of the woolly spider monkey. For two of the functionally interpretable traits (distal extent of attachment of the adductor longus, distal extent of the crural attachment of the short head of biceps femoris), the similarity of *Brachyteles* to *Lagothrix* conforms to the suggestion that these serve the purpose of facilitating use of the hind limb during suspensory postures of a large bodied monkey (Stern, 1971). Both *Brachyteles* and *Lagothri*x are said to use their hind limbs during suspensory postures more so than does *Ateles*, and both are heavier than *Ateles*

In *Brachyteles* the insertion of the ascending tendon of the gluteus superficialis resembles that of *Ateles* by being more distally positioned on the femoral shaft. Stern (1971) considered this trait as part of a suite of changes that transformed the muscle from a propulsive organ to a deltoid-like muscle important in positioning the hind limb to grasp various supports while the animal was suspended. Another component of this suite was the development of a caudal tendon of origin of gluteus superficalis that freed the posterior fibers of the muscle from their link to the tail. *Brachyteles* shares these traits with *Ateles*, but is unique in the fact that the caudal tendon of origin actually reaches the ischial tuberosity, with some fibers of the muscle actually arising from the ischial tuberosity. It might be viewed that the gluteus superficialis of *Brachyteles* has simply undergone a more extreme development of the changes characterizing *Atele*s. However, this view is contradicted by the fact that in *Ateles* the posterior fibers of the gluteus superficialis have migrated proximally in their femoral attachment, whereas those of *Brachytele*s insert even further distally along the femoral shaft than in *Lagothrix*. The more distal insertion in *Lagothrix* was interpreted by Stern (1971) to reflect either a greater propensity to quadrupedalism in this genus than in spder monkeys, or the need in the heavier *Lagothrix* for a more powerful limb retractor in both quadrupedalism and climbing. The yet greater weight of *Brachyteles* may explain why the

the posterior portion of its gluteus superficialis inserts even further down the thigh than in the woolly monkey.

The overall structure of the gluteus superficialis in *Brachyteles* has converged on a structure not terribly different from that seen in gibbons and African apes, although these taxa have an even greater degree of muscular origin from the ischial tuberosity and also a greater distal extent of the femoral insertion. Stern (1971) was puzzled by the development of a sacrotuberous ligament in some apes, suggesting the possibility that this structure might have developed if the ancestors of these creatures engaged in hind limb suspension more so than do their living representatives. However, Stern (1971) acknowledged both the speculative nature of this suggestion and fretted over the inability to apply to apes the reasoning that led to his conclusions about evolution of the gluteus superficialis in platyrrhines.

Conclusion

The hip and thigh musculature of *Brachyteles* is is no way intermediate between that of *Lagothrix* and *Ateles*, nor does it align more closely with one of these genera than the other. The gluteus superficialis of *Brachyteles* is fascinating.

Table 1

Some Muscular Traits of the Hip and Thigh Compared Between *Lagothrix*, *Brachyteles* and *Ateles*[1]
(similarities between any two of the genera are indicated by similar typeface)

		Lagothrix	***Brachyteles***	***Ateles***
1.	Any origin of gluteus medius from deep surface of the caudal tendon of origin of gluteus superficialis	no in five specimens, yes in one	no	*yes*
2.	Origin of pars posterior of gluteus minimus from dorsal surface of ischial spine	no, this area being occupied by origin of ischiocaudalis	no, this area being occupied by origin of ischiocaudalis	*yes, the origin of ischiocaudalis being confined to edge of ischial spine*
3.	Presence of superior gemellus	present	present (and well developed)	*present in only one of six specimens*
4.	Insertion of fused gracilis/semitendinosus tendon	onto anterior tibial crest in four specimens, lateral to the crest in one specimen, medial to the crest in one specimen	most of the tendon inserts lateral to the anterior tibial crest, but the distalmost fibers insert onto the crest	*medial to the anterior tibial crest*
5.	Origin of gracilis	entirely fleshy, not (or only slightly) overlapping that of adductor longus	entirely fleshy, not overlapping that of adductor longus	*partly tendinous, completely overlapping that of adductor longus in the majority of specimens*

[1] Based on dissections of six specimens each of *Lagothrix* and *Ateles* (Stern, 1971), and three of *Brachyteles*.

6.	Fusion of tendons of vastus laterlis and vastus medialis to tendon of vastus intermedius	no fusion	no fusion	*fusion present*
7.	Caudal vertebrae giving origin to gluteus superficialis	caudals 1 and 2 in five specimens, caudals 2 and 3 in one specimen	*caudal 1 alone in two specimens, caudals 1 and 2 in one specimen*	*caudal 1 alone in two specimens caudals 1 and 2 in four specimens,*
8.	Separability of adductor longus and pectineus	clearly separate	*closely adjacent but separable in two specimens, inseparable in one specimen*	*closely adjacent but separable*
9.	Separation of insertion of pars brevis of adductor brevis from insertion of pars longa of adductor brevis	two portions of adductor brevis always insert far from one another	*two portions of adductor brevis sometimes insert close to one another*	*two portions of adductor brevis sometimes insert close to one another*
10.	Relationship of femoral artery and vein to presemimembranosus	vessels pierce presemimembran-osus to reach the popliteal fossa	*vessels pass proximal to insertion of presemimembranosus to reach the popliteal fossa*	*vessels pass proximal to insertion of presemimembranosus to reach the popliteal fossa*
11.	Insertion of short head of biceps femoris into tendon of the long head	little or no insertion of short head fibers into the tendon of long head	*obvious insertion of proximal fibers of short head into tendon of long head*	*obvious insertion of proximal fibers of short head into tendon of long head*
12.	Length of caudal tendon of origin of gluteus superficialis (Fig. 1)	may be short or long, but in no case reaches the ischial tuberosity	**long and clearly attaching to the ischial tuberosity, which also gives rise to some actual fleshy fibers of the muscle**	*always long, but in no case reaching the ischial tuberosity*
13.	Location of insertion of ascending tendon of gluteus superficialis on femur (Fig. 2)	more proximal that in the spider monkey	*more distal than in the woolly monkey*	*in five of six specimens, more distal than in the woolly monkey*

14.	Most distal extent of muscular fibers of gluteus superficialis (Fig. 3)	about one-third down the thigh	**about two-fifths down the thigh**	*about one-quarter down the thigh*
15.	Location of adductor longus insertion on the femur (Fig. 4)	femoral attachment more distal than in the spider monkey	femoral attachment more distal than in the spider monkey	*femoral attachment more proximal than in the wooly monkey*
16.	Distalmost extent of the insertion of short head of biceps femoris into the fascia cruris (Figs. 5, 6)	> 65% down the leg	> 65% down the leg	*< 60% down the leg, usually < 40% down the leg*

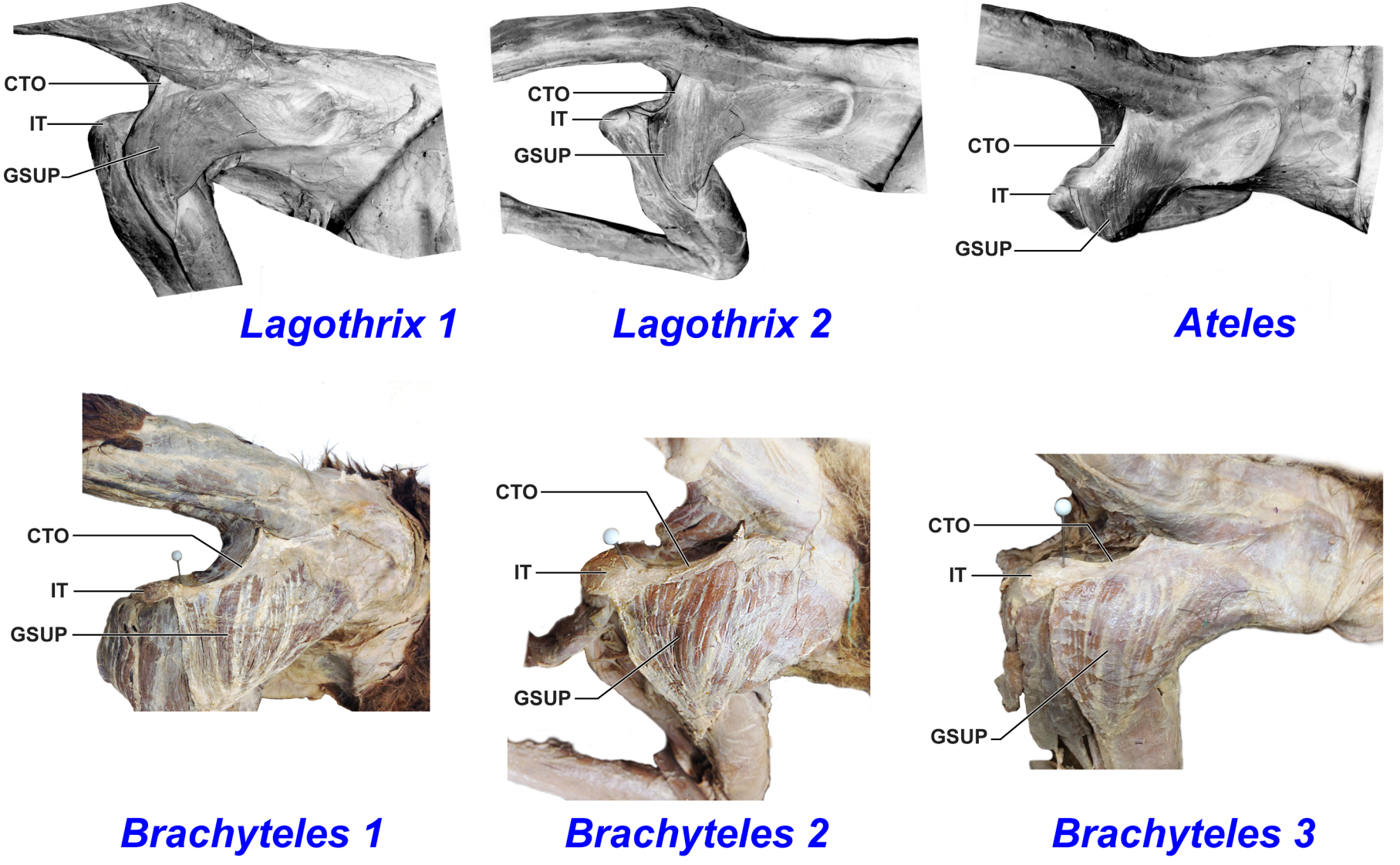


Fig.1: Development of the caudal tendon of origin (CTO) of the gluteus superficialis (GSUP) in atelines. This structure is variably developed in *Lagothrix*. The CTO is well developed in *Ateles*, but never reaches the ischial tuberosity (IT). In *Brachyteles*, the CTO is well developed and consistently attaches to the IT, from which some fibers of the GSUP actually arise. The white-headed pin marks the cranial edge of the IT in *Brachyteles*.

Fig. 2

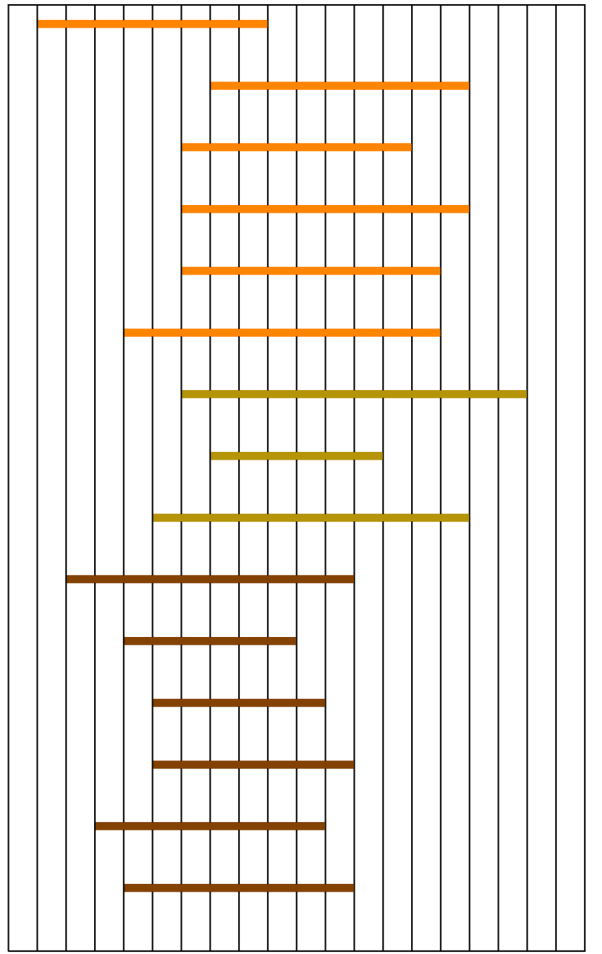

Ateles
Brachyteles
Lagothrix
10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
Level of Insertion of Ascending Tendon of Gluteus Superficilais Into Femur
(expressed as the percentage of the distance from the center of the femoral head to the distalmost point of the lateral femoral condyle)

Fig. 3

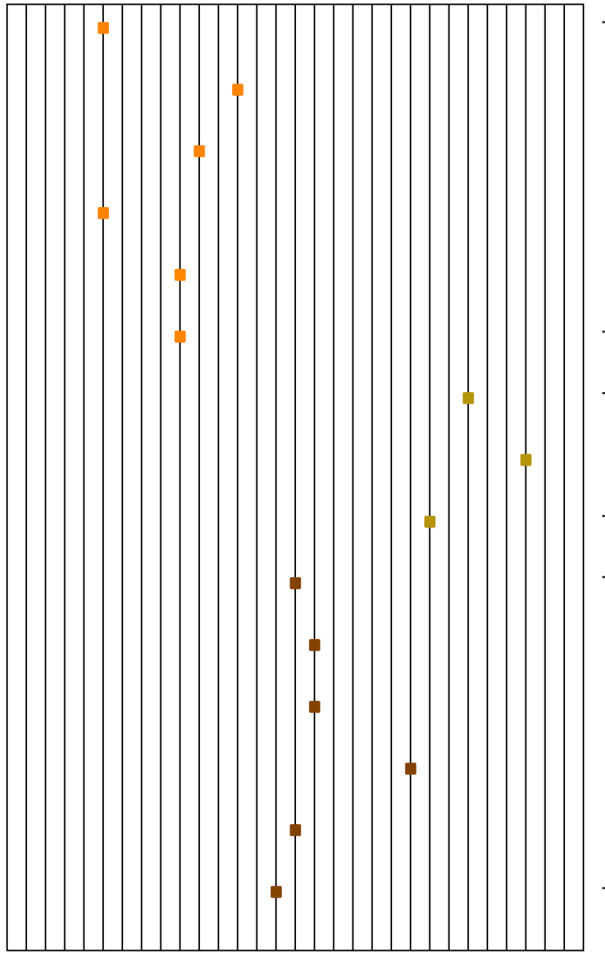
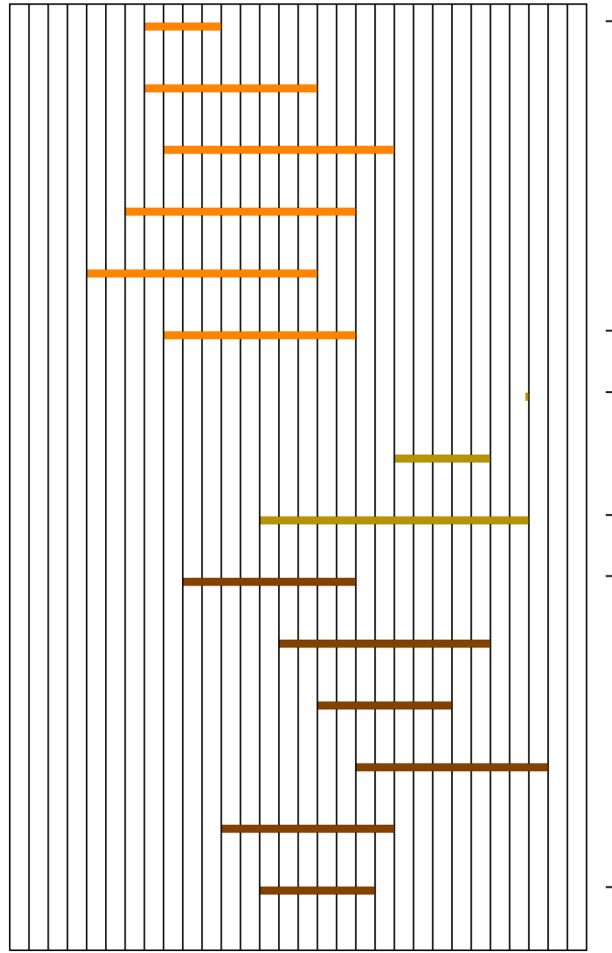
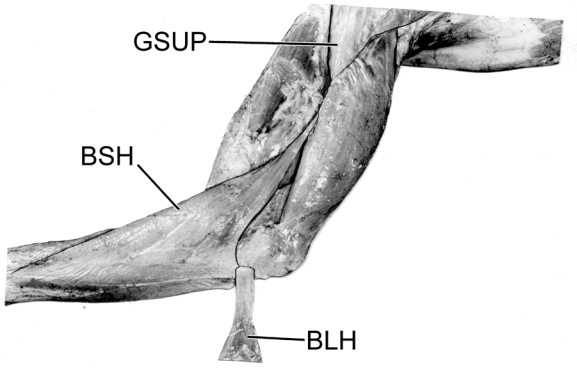
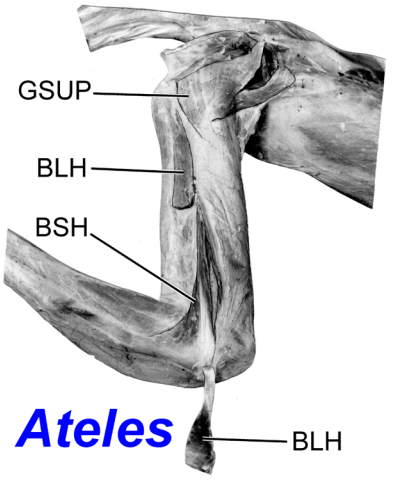

Ateles
Brachyteles
Lagothrix
15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45
Level of Most Distal Extent of Flesh of Gluteus Superficialis in the Thigh
(expressed as the percentage of the distance from the center of the femoral head to the distalmost point of the lateral femoral condyle)

Fig. 4

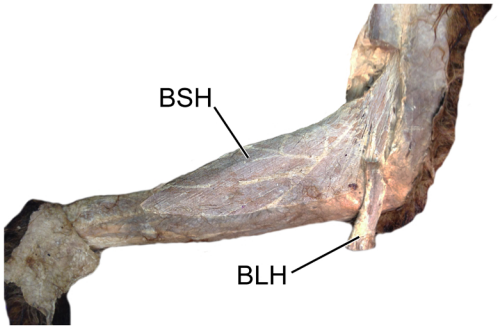

Ateles
Brachyteles
Lagothrix
15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45
Level of Insertion of Adductor Longus Into Femur
(expressed as the percentage of the distance from the center of the femoral head to the distalmost point of the lateral femoral condyle)



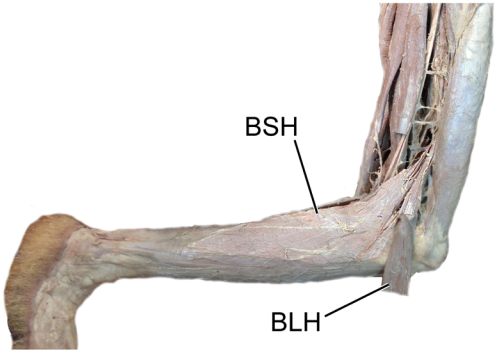
Lagothrix



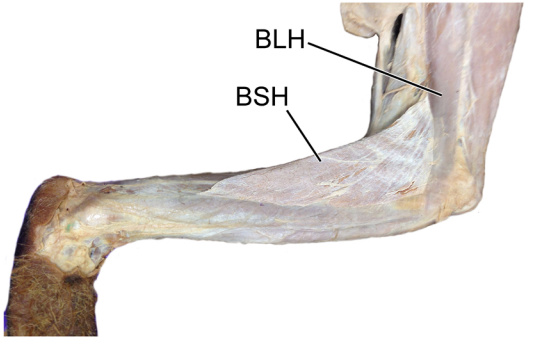
Ateles



Brachyteles 1



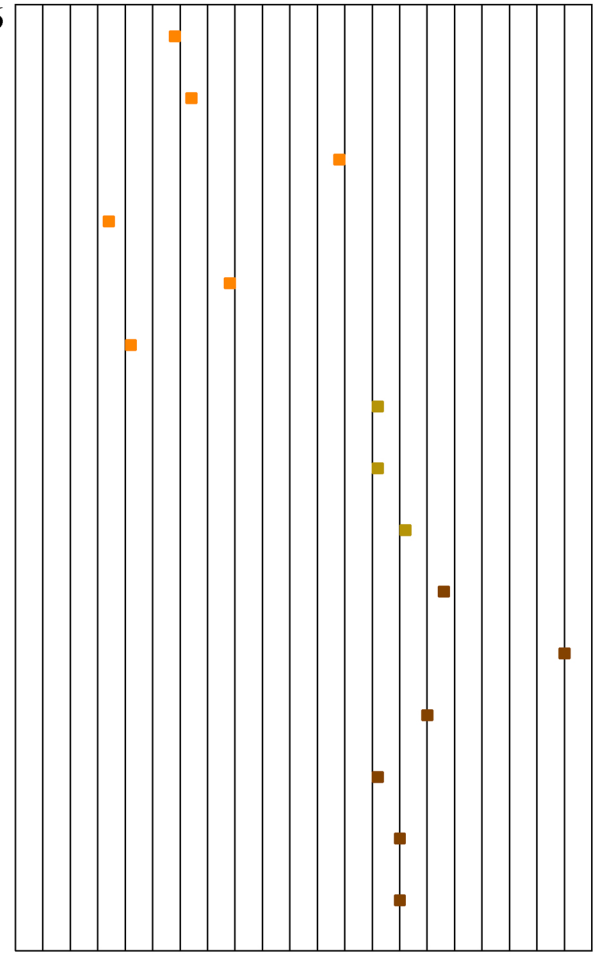
Brachyteles 2



Brachyteles 3

Fig. 5: The extent of the insertion of the short head of biceps femoris (BSH) into the fascia cruris is much greater in Lagothrix and *Brachyteles* than in *Ateles*. It can also be see that in *Ateles* and *Brachyteles* the BSH inserts into the deep surface of the tendon of long head of biceps femoris (BLH), whereas there is no such insertion in *Lagothrix*.

Fig. 6


Ateles
Brachyteles
Lagothrix
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100
Level of Most Distal Extent of Insertion of Short Head of Biceps Femoris Into Fascia Cruris
(expressed as a percentage of the length of the lower leg measured from the most medial point on the proximal rim of the medial tibial condyle to the tip of the medial malleolus)