Short Report

Comparative Anatomy of Caudal Musculature Attachments in Catarrhines with Different Tail Length

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INTRODUCTION

Tail length in primates greatly varies and is considered an important feature for understanding primate adaptations and phylogeny. Especially in some catarrhines, tails have become extremely reduced.

Previous studies suggested that some sacral morphology reflects tail length to reconstruct the process of tail reduction in catarrhines (Ankel, 1965, 1972; Ward et al., 1991; Russo & Shapiro, 2011; Tojima, 2013), but the reason why such morphology reflects tail length variation was not clarified. Generally, the muscles attached to bones must change together with the skeletal morphology. Thus, the musculoskeletal morphological variation in the sacro-caudal region must reflect differences of tail function, and it could be linked to the process of and the reason for tail reduction.

In catarrhines, however, there have been few studies of caudal musculature (Howell & Straus, 1965; Swindler & Wood, 1982; Tojima, 2010) and the anatomical musculature data with different tail lengths are still incomplete.

Therefore, this study aimed to provide an updated overview of caudal muscles in catarrhines and to clarify the relationships among caudal muscles, sacro-caudal skeletal morphology, and tail length variation.

MATERIALS AND METHODS

Materials

In this study, I performed comparative dissection of both the dorsal and ventral side of the lumbo-sacro-caudal region in five individuals of five catarrhine species with different tail length (*Macaca fascicularis*, *Papio hamadryas*, *M. fuscata*, *M. arctoides*, and *Pan troglodytes*) (Table 1) and compared the results with Tojima (2010), which dissected the caudal musculature of *M. cyclopis* and *M. mulatta*. A chimpanzee individual used in this study was a GAIN (Great Apes Information Network) specimen housed at the Primate Research Institute, Kyoto University, Inuyama, Japan. The other specimens used in this study were housed at the Primate Research Institute.

Nomenclature and definitions of the caudal muscles

In this study, the following nomenclature was used with the aim of consistency with previous studies that investigated primate caudal muscles (Howell & Straus, 1965; Swindler & Wood, 1982; Lemelin, 1995): ventral caudal muscles (*m. iliocaudalis*, *m. pubocaudalis*, *m. ischiocaudalis*, *m. flexor caudae longus*, and *m. flexor caudae brevis*), and dorsal caudal muscles (*m. extensor caudae lateralis*, *m. extensor caudae medialis*, *m. abductor caudae lateralis*, and *m. abductor caudae medialis*). The homologies of these muscles were judged from their positions of origin (which are much less varied than their positions of insertion) and location relative to the other muscles, and the muscles were categorized and defined as follows.

Pelvocaudal muscles (*m. iliocaudalis*, *m. pubocaudalis*, and *m. ischiocaudalis*) originate from the ilium, pubis, and ischium respectively.

The flexors are bilaterally symmetric muscles, which originate from the ventral side of the last lumbar vertebra or

Table 1. Specimens used in this study

Taxon	Sex	N	Tail length (mm)
<i>Macaca fascicularis</i>	M	1	575
<i>Papio hamadryas</i>	M	1	422
<i>Macaca fuscata</i>	M	1	65
<i>Macaca arctoides</i>	M	1	52
<i>Pan troglodytes</i>	F	1	absent

the sacrum. The lateral and more deeply located one is *m. flexor caudae longus* and the medial and shallower one is *m. flexor caudae brevis*.

As for the dorsal side, the muscles that originate from the mammillary processes of lumbar vertebrae and are distributed along the entire tail along the medial line are defined as the extensors. The lateral extensor is *m. extensor caudae lateralis*, and the medial one is *m. extensor caudae medialis*.

Abductors originate from the dorsal area of the sacro-iliac joint and insert on the lateral side of the caudal vertebrae. *M. abductor caudae lateralis* locates laterally and *m. abductor caudae medialis* locates medially.

Through the dissection in this study, I realized that some caudal muscle definitions in Tojima (2010) should be revised because the definitions in former study was more ambiguity and could not explain all the caudal muscle attachments observed in this study. Following the latest definitions, some caudal muscle attachments of *M. cyclopis* in Tojima (2010)

could be redefined as follows: *m. abductor caudae medialis* should be *m. extensor caudae medialis*, *m. extensor caudae medialis* should be *m. intertransversarii*, and *m. abductor caudae lateralis* should be *m. abductor caudae medialis*.

Methods

Before the dissection, the tail lengths of all specimens were measured using a tape measure (Table 1). However, most of the specimens were not intact and their conditions showed wide variation and other somatometric measurements, including sitting height and body weight, were not available.

After the tail length measurements, the specimens described above were dissected. In this study, nine caudal muscles were exposed, and the locations of their origin, insertion, and tendonization were observed. Additionally, *m. piriformis*, which originates ventral side of the sacrum, was also exposed, and its origin and insertion places were observed.

		Pan troglodytes M. arctoides M. fuscata M. mulatta** Papio hamadryas M. cyclopis# M. fascicularis						
Names of the muscles	level of...							
1, M. iliocaudalis	origin	pubic symphysis; iliac brim (caudal edge of sacro-iliac joint - ilio-pubo border)						
	insertion	coccyx	1st to 3rd CaV	1st to 2nd CaV	1st to 2nd CaV	last SV to 2nd CaV	3rd to 5th CaV	3rd to 5th CaV
2, M. pubocaudalis	origin	pubic symphysis; ischio-pubic symphysis (internal side)						
	insertion	coccyx	2nd CaV & rectum	1st to 2nd CaV	1st to 2nd CaV	2nd CaV	3rd to 5th CaV	3rd to 5th CaV
3, M. ischiocaudalis	origin	ischial spine						
	insertion	last SV to coccyx	last SV to 1st CaV	1st to 2nd CaV	last SV to 1st CaV	1st to 2nd CaV	1st to 4th CaV	2nd to 4th CaV
4, M. flexor caudae longus	origin		1st SV	1st SV	last LV	5th or 6th LV	last LV	
	tendonization		b/w 2nd & 3rd CaV	5th CaV	b/w 4th & 5th CaV	4th or 5th CaV	b/w 5th & 6th CaV	
5, M. flexor caudae brevis	origin				1st SV	1st SV	1st SV	
	tendonization				3rd CaV	2nd CaV	3rd CaV	
6, M. piriformis	origin	2nd to 4th SV	1st SV to 4th CaV	2nd SV to 1st CaV	2nd to 3rd SV	2nd to 3rd SV	2nd to 3rd SV	2nd to 3rd SV
	insertion	great trochanter						

Figure 1. Attachments of ventral caudal muscles

M. flexor caudae brevis of *M. cyclopis* was observed in only one individual (Tojima, 2010).

Abbreviations LV, SV, CaV, and b/w meant lumbar vertebra, sacral vertebra, caudal vertebra, and between, respectively.

* The description about *m. piriformis* was cited from Sugiyama (1960).

** The description about *m. piriformis* was from Howell & Straus (1965).

The descriptions about *M. cyclopis* and *M. mulatta* were from Tojima (2010).

RESULTS

Pelvocaudal muscles (Fig.1)

In all tailed species, these three muscles originated from the same place (*m. iliocaudalis*: on the iliac brim, from the caudal edge of the sacro-iliac joint to the ilio-pubic border; *m. pubocaudalis*: internal side of the ischio-pubic symphysis; *m. ischiocaudalis*: the ischial spine)(Fig. 1).

Similarly to *M. cyclopis* and *M. mulatta* (Tojima, 2010), the muscle bellies of *m. iliocaudalis* and *m. pubocaudalis* fused together near the anus in *M. fascicularis* and *M. fuscata*. This fused muscle inserted on the transverse processes (lateral side) and the vertebral bodies (ventro-lateral side) from the third to fifth caudal vertebrae in *M. fascicularis* (similarly to *M. cyclopis* (Tojima, 2010), and on the lateral side of the transverse processes of the first to second caudal vertebrae in *M. fuscata*, as well as in *M. mulatta* (Tojima, 2010).

P. hamadryas and *M. arctoides* had independent *m. iliocaudalis* and *m. pubocaudalis*. In *P. hamadryas*, *m. iliocaudalis* and *m. pubocaudalis* inserted on the lateral side of the transverse processes from the last sacral vertebra to the second caudal vertebra and on the lateral side of the second caudal vertebra, respectively. In *M. arctoides*, *m. iliocaudalis* inserted on the lateral side of the vertebral bodies from the first to the third caudal vertebrae, and the insertion of *m. pubocaudalis* was on the lateral side of the transverse process of the second caudal vertebra, and some muscle fibers attached to the rectum.

As the previous study reported, these two muscles fused completely and formed *m. levator ani* in chimpanzee (Swindler & Wood, 1982). This muscle originated from the dorsal side of the pubic symphysis and inserted on the tip of the coccyx.

As for *m. ischiocaudalis*, it inserted on the tips of the transverse process of the second to fourth caudal vertebrae in *M. fascicularis*. In *P. hamadryas* and *M. fuscata*, it inserted on lateral edge of the transverse processes of the first and second caudal vertebrae. In *M. arctoides*, it inserted on lateral edge of the transverse processes from the last sacral vertebra to the first caudal vertebra. As Swindler & Wood (1982) reported, *m. ischiocaudalis* was changed to *m. coccygeus* in chimpanzee, which originated from the ischial spine and inserted on the anterior side of the last sacral vertebra and coccyges.

Flexors (Fig.1)

In *M. fascicularis*, *m. flexor caudae longus* originated from the ventral aspect of the last lumbar vertebra just caudal to the intervertebral disc. It became tendinous between the fifth and sixth caudal vertebrae, and the tendon was distributed until

the tip of the tail, with some fibers attaching to the apex of the hemapophyses in the proximal region and the ventro-lateral aspect of the cranial articular surface of each distal caudal vertebra. *M. flexor caudae brevis* in *M. fascicularis* originated from the ventral edge of the cranial articular surface of the first sacral vertebra and became tendinous at the level of the third hemapophysis. Its tendon combined with that of *m. flexor caudae longus* and ran to the tip of the tail.

P. hamadryas possessed both of the flexors. *M. flexor caudae longus* originated from the same place as in *M. fascicularis* and became tendinous between the fourth and fifth caudal vertebrae. *M. flexor caudae brevis* also originated and inserted at the same place as in *M. fascicularis*.

As well as in *M. mulatta* and most of *M. cyclopis* (Tojima, 2010), *m. flexor caudae brevis* was not observed in *M. fuscata*; instead, only *m. flexor caudae longus* existed. In this species, *m. flexor caudae longus* originated from the ventral edge of the sacral cranial articular surface, and became tendinous at fifth, and the second and third, caudal vertebrae, respectively. In *M. arctoides* and *Pan troglodytes*, neither of the flexors was observed.

Instead, *m. piriformis* expanded the region of its origin to the ventral side of the sacrum in both species (Fig. 1). It inserted at the great trochanter in all specimens, but the range of the origin varied. *M. piriformis* of *M. fascicularis* and *P. hamadryas* originated from the lateral edge of the sacrum (from the second to third sacral vertebrae) and the ventral side of the last sacral vertebra. In *M. fuscata*, it originated from the ventral side of the last sacral vertebra and the first caudal vertebra. In *M. arctoides*, it arose from middle of the first sacral vertebra to the last sacral vertebra. Chimpanzee had the most expanded origin, which extended from the second to the fourth sacral vertebra. Tojima (2010) did not examine the origin of *m. piriformis* in *M. cyclopis* and *M. mulatta*, but according to Sugiyama (1960) and Howell & Straus (1965) respectively, their *m. piriformis* seems to arise from the same place, transverse process of the second and third sacral vertebrae.

Extensors (Fig.2)

In *M. fascicularis*, *m. extensor caudae lateralis* originated from the mammillary processes, the basement of prezygapophyses, and the vertebral arches of all lumbar vertebrae and the median sacral crest, and it became tendinous at the level of the third, fourth, and fifth caudal vertebrae. Its tendon attached to prezygapophyses of every caudal vertebra and was distributed until the tip of the tail. *M. extensor caudae medialis* originated from the articular processes of the first to third sacral vertebrae, and became tendinous at the

Figure 2. Attachments of dorsal caudal muscles

Abbreviations LV, SV, CaV, and b/w meant lumbar vertebra, sacral vertebra, caudal vertebra, and between, respectively.

[#] The descriptions and figures of *M. cyclopis* and *M. mulatta* were cited from Tojima (2010) and partly modified following the muscle definition of this study.

prezygapophyses of the third caudal vertebra. The tendon combined with that of *m. extensor caudae lateralis*, and they were distributed to the tip of the tail together.

M. extensor caudae lateralis of *P. hamadryas* had an origin at the same places as that in *M. fascicularis*, but it became tendinous at the third caudal vertebra. *M. extensor caudae medialis* originated from the sacral prezygapophyses and its basement and became tendinous at the third caudal vertebra.

In *M. fuscata*, only one muscle was observed, and its origins were located at the places where *m. extensor caudae lateralis* or *m. extensor caudae medialis* might originate. The muscle originated from the mammillary process, prezygapophyses and its basement, and vertebral arch of the third lumbar vertebra, and also from the prezygapophyses and its basement of the second sacral vertebra. Then, it became tendinous at the last sacral vertebra.

Similarly to *M. fuscata*, only one caudal abductor muscle was present in *M. arctoides*. It originated from the mammillary process, base of prezygapophyses, vertebral arch of the last lumbar vertebra, and became tendinous at the caudal end of the last sacral vertebra.

In *Pan troglodytes*, one muscle originated tendinously from the vertebral arch of the third lumbar vertebra, and inserted

fleshly at the transverse process of the last sacral vertebra. From its places of origin and insertion, this muscle seemed to correspond to *m. extensor caudae lateralis* in rudimentary form.

Abductors (Fig.2)

The two abductors were observed independently and had the same respective origins in all tailed species (Fig. 2).

In *M. fascicularis*, *m. abductor caudae lateralis* and *m. abductor caudae medialis* inserted at the same place (the base of the transverse process of the fourth or fifth caudal vertebra).

In *P. hamadryas*, the insertions were at the base of the transverse process of the fourth caudal vertebra for *m. abductor caudae lateralis* and at the base of the transverse process of the third caudal vertebra for *m. abductor caudae medialis*, respectively.

In *M. fuscata* and *M. arctoides*, the insertions of *lateralis* and *medialis* were at the bases of the transverse processes of the third and second caudal vertebrae, respectively.

In tailless *Pan troglodytes*, any muscles, which could be considered as caudal abductors, were not observed.

DISCUSSION

Ventral caudal muscle attachments

Both in pelvicaudal and flexor muscles, the places of insertion and tendonization tended to be more cranial in shorter tailed species. The pelvicaudal muscles existed even in tailless species, because they play an important role in the maintenance of pelvic viscera as well as in tail movement. In tailless hominoids, the muscles might change their major function from tail movement to maintenance of the pelvic viscera (Elftman, 1932).

However, the flexors largely varied with tail length variation. In the relatively long tailed species (except *M. cyclopis* (Tojima, 2010)), both of the flexors were observed, but in shorter tailed species than *M. mulatta* (Tojima, 2010), *m. flexor caudae brevis* was lost and only *m. flexor caudae longus* was present. Thus, the function of ventral tail flexion is gradually reduced in shorter tailed species and almost completely lost in *M. arctoides* with diminished tail.

M. piriformis seemed to extend its origin to the ventral side of the sacrum while the flexors became reduced with tail reduction. But the functional meaning of this variation is obscure.

Dorsal caudal muscle attachments

In shorter tailed species (*M. fuscata* and *M. arctoides*), only one kind of caudal extensor muscle was present and their origins tended to be more caudal. So far, it is hard to judge if this muscle is *m. extensor caudae lateralis* or *medialis*. However, considering the tendencies of the caudal musculature observed in this study (shorter tailed species tended to have more caudally originating muscles with some exceptions, and the lateral muscles tended to be lost when two muscles with similar function were present like ventral caudal flexors), these muscles are likely *m. extensor caudae lateralis*. The abductors did not change their places of origin very much, but their insertions became more cranial. However, both of dorsal caudal muscles were present and never completely lost in all tailed species (Fig. 2), while ventral flexors were lost in relatively short tailed species (Fig.1). The reason of why the variations of the attachment places of ventral and dorsal caudal muscles were not consistent is still obscure.

Correlation between the variation of caudal muscle attachments and sacro-caudal skeletal morphology with different tail length

Caudal muscle variations observed in this study are probably related to the sacro-caudal skeletal morphological

variation (i.e. the number of proximal caudal vertebrae, morphology of sacral spinous processes, and the degree of sacral curvature).

First, the variation of the insertion and tendonization places might be related to the number of caudal vertebrae. Tojima (2014) revealed that the number of proximal caudal vertebrae, which provide insertion places to caudal muscles, correlated with relative tail length (the percentage of tail length against head and body length) in Papionini. Together with this insight, the result of this study suggested a possibility that the number of proximal caudal vertebrae and the insertion places of caudal muscles are highly related.

Loss of one caudal extensor muscle (perhaps *m. extensor caudae medialis*) is probably related to the morphology of spinous processes and sacral curvature. Tojima (submitted for publication) reported that shorter tailed Old World monkeys possessed more reduced spinous processes and ventrally curved sacrum. In most species, both of the extensors attach to the sacral crest. But in species whose tail length is at most very short, only one caudal extensor muscle attaches to the sacral crest. This result is in accord with the reduced height of the spinous processes, which provide attachment sites for the extensors. Reduction of the extensors may also be related to the sacral curvature. Loss of one caudal extensor muscle must cause decrease of the tension pulling the sacrum toward the dorsal side (Tojima, submitted for publication). As a result, the dorsal tension becomes lesser than the ventral one and the sacrum may curve ventrally.

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Summary

Comparative Anatomy of Caudal Musculature Attachments in Catarrhines with Different Tail Length

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In some catarrhines, tails have extremely reduced. In order to clarify the tail reduction process in the catarrhines, understanding the sacro-caudal musculo-skeletal morphological variations with different tail lengths is essential. Although previous studies revealed that skeletal morphology strongly reflected tail length variation, caudal musculature has scarcely been studied. Thus, this study aimed to increase the knowledge about caudal musculature in catarrhines. Comparative dissection of both the dorsal and ventral side of the lumbo-sacro-caudal region in five individuals of five catarrhine species was performed, and following findings were obtained: 1) All caudal muscles tended to insert or become tendinous more cranially in shorter tailed species, 2) Ventral caudal flexors were completely lost in catarrhines with shorter tails than *M. arctoides*, 3) Pelvocaudal muscles were present regardless of the tail length, 4) Only one kind of dorsal caudal extensor muscle was observed in very short tails species and were lost in tailless species, and 5) Dorsal caudal abductors existed independently in all of tailed species and were lost in tailless *Pan troglodytes*. Together with the skeletal morphological perspective, these findings will be helpful for understanding the tail reduction process in catarrhines in the future.

(要約)

霊長類における尾は、環境への適応や系統を反映する重要な形態のひとつである。特に一部の狭鼻猿類では尾が極端に短縮・喪失しており、その進化過程を解明するためこれまで尾長変異と骨格形態変異について研究がなされ、仙尾部骨格形態が尾長を反映して変異することが知られるようになった。こうした骨格形態変異は、尾長の変化に伴う尾の機能変異を反映していると考えられるが、尾の機能に重要な影響を及ぼす尾筋が尾長変異によりどのように変異するのかについては、知見が不足していた。そこで本研究では、狭鼻猿の尾筋に関する知見の更新ならびに尾長変異に伴う尾筋の形態変異の解明を目的とし、尾長の異なる狭鼻猿 5 種 5 体の腰部から尾部を剖検、尾筋付着部位を観察した結果、以下の知見を得た。1) 観察した全ての尾筋は、短尾な種ほど頭側で停止・腱様化する、2) 尾屈筋群はベニガオザルより短尾の種に存在しない、3) 骨盤尾筋群は尾が無い種にも存在する、4) 背側尾伸筋群は非常に短い尾をもつニホンザル、ベニガオザルでは 1 種類しか見られず、尾のないチンパンジーにはない、5) 背側尾外転筋群は尾を持つ全ての種で 2 種類独立に存在する。これらは、従来の骨格形態変異に関する知見と併せ、狭鼻猿の尾長短縮過程解明に重要な役割を果たすだろう。

Key words: catarrhine, tail length, caudal abductors, caudal extensors, caudal flexors, pelvocaudal muscles

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