Evolution of the tail in the genus *Macaca*

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Introduction

A tail is an external part of an animal's body that aligns at the extension of the spine from the sacrum and is a shared trait of vertebrates. Most mammals have tails and the morphology varies among species. In most mammals, the number of vertebrae is under strong developmental constraint. However, the number of caudal vertebrae seems to be released from such developmental constraint. Due to this, the tail is considered as a unique feature, and its morphology can help understand the evolution of different species. Tails serve three functions in mammals: mechanical, behavioral, and physiological. To better elucidate how tail morphology has evolved, detailed and comprehensive study of caudal vertebral morphology with closely related species is preferable. The genus *Macaca* (macaques) is one of the most successful primate clades, representing a large number of species with wide geographical range and variation in morphology and types of sociality. The tail of macaques' ranges from 2% to 124% in relative tail length (RTL). Macaques are divided into four species groups and the tail length variations are seen in each species group. The present study aimed to investigate the proximate factor of macaques' tail length variation, the tail function-related morphology of caudal vertebrae, and the evolutionary process of the tail.

Materials and Methods

In Chapter 2, I investigate the number and the length of the bony particle of the tail (caudal vertebrae) for 15 macaque species to reveal tail length-related morphological characteristics and to evaluate phylogenetic constraints on this pattern. In Chapter 3, I investigate the morphology that relates to tail movement and function, focusing on the *fascicularis* group, and particularly on species with similar RTLs (*M. mulatta*, *M. a. assamensis*, and *M. nemestrina*). The RTL of these three species is between 35~38%, making them medium tailed, but they belong to different species groups. I measure inter-transverse process width, height, width, and spinous process length of caudal vertebrae, and caudal vertebral body angle. I also calculate the center of gravity to evaluate the effect of moment of inertia of the tail. In Chapter 4, I describe observations made during field surveys to identify the mechanical and social signaling function of the tails of three macaque species. The field observations targeted the three medium-tailed species and were conducted in Thailand. The observations were carried out through focal animal sampling and ad lib sampling, and ethograms of tail carriage and positional behavior were recorded.

Results

In Chapter 2, I found that the caudal vertebral length profiles show upward convex patterns for macaques with RTL ≥ 15% and flat to decreasing patterns for those with RTL ≤ 12%. There is significant variation between species groups in the lengths of proximal vertebra, the position and length of the longest vertebra, the numbers and lengths of distal vertebrae, and the total number of vertebrae. In the *silenus* and *sinica* groups, vertebral length was the major determinant of tail length. In contrast, vertebral number was the major determinant of tail length in the *fascicularis* group. These findings suggest that the mechanisms underlying tail length evolution are strongly controlled by phylogenetic constraint.

In Chapter 3, I found that tails were tapered in shape and longer-tailed species had a more robust structure to compensate for the requirement of stiffness in the bones. The relative center of gravity of *M. nemestrina* was more proximal than the other species, which suggests that the tail of *M. nemestrina* serves less as a balancing aid. The cumulative angle of sacral and caudal vertebrae was likely related to tail carriage and tail flexibility; however, the negative degrees seen in *M. fascicularis* and *M. cyclopis* probably mitigate the load on the intervertebral discs. Considering the greater length of the sacral crests and spinous processes, *M. nemestrina* is predicted to have a larger volume of muscles than the other medium-tailed species. The muscles attached to the sacral crests and spinous processes might control the dorsal extension of the tail.

In Chapter 4, the use of the tail as a balancing aid was observed more frequently in *M. assamensis* than *M. mulatta* and *M. leonina*. On the other hand, tail use for social signaling (i.e., communication) was observed in all species. Among the three species, *M. leonina*'s tail was more frequently used for social signaling than for balancing. The tail was not only used for swinging or rotating to obtaining the moment of inertia, but also for touching, hanging from, or hooking onto a substrate. Such types of tail usage are effective for maintaining body posture and were observed in *M. mulatta* and *M. assamensis*.

Discussion

Traditionally, tail length evolution has been considered to occur through reduction from long to short in macaques. In contrast, based on phylogenetic comparative analyses suggested that the tail length variation of macaques has occurred through both elongation and reduction. Though the ancestral state of tail length is still controversial, some morphological features, such as the sacrum and proximal caudal vertebral angle, could be the trait from the medium-tailed ancestors. In medium-tailed species, the sacrum and proximal caudal vertebrae angle is positive. The angles might change from positive to negative as the tail length increased in species like *M. cyclopis* and *M. fascicularis*, or decreased in *M. fuscata*. When the tail length increased, the negative angles of sacrum and proximal caudal vertebrae are considered to be effective to protect the intervertebral discs and to prevent herniation.

Conclusion

The determinants of tail length were different between the species groups in macaques. This finding suggests that the evolution of the tail is strongly controlled by phylogenetic constraints. Long-tailed species have a stiff structure to the caudal vertebrae which is lacking in short-tailed species, and medium-tailed species display variation in caudal vertebrae morphology. Therefore, the functions of the tail are probably different, even among species with similar tail lengths. Field observations revealed the relationship between tail carriage and positional behaviors. The RTL at which the tail functions as a balancing aid is around 35% and greater. Along with RTL, the skeletal morphology of the tail, such as the height and width of caudal vertebrae, is strongly linked with the function of tail. In macaques, the morphology and usage of the tail are related to social systems (despotic or egalitarian), habitat utility, and breeding systems.