NOTE *Anatomy*

Dimensions of the Foot Muscles in the Lowland Gorilla

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ABSTRACT. We dissected the hindlimb of a female western lowland gorilla and determined the muscle dimensions (mass, fascicle length, and physiological cross-sectional area: PCSA). Comparisons of the muscle parameters of the measured gorilla with corresponding reported human data demonstrated that the triceps surae muscles were larger and had more capacity to generate force than the other muscle groups in both species, but this tendency was more prominent in the human, probably as an adaptation to strong toe-off during bipedal walking. On the other hand, PCSAs of the extrinsic pedal digital flexors and digiti minimi muscles were larger in the western lowland gorilla, suggesting that the foot, particularly the fifth toe, has a relatively high grasping capability in the lowland gorilla.
KEY WORDS: foot, gorilla, muscle architecture.

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Gorillas are generally regarded as the most terrestrial of the extant hominoids. However, the degree of arboreality is known to vary among subspecies. Mountain gorillas (*G. gorilla beringei*) living in eastern central Africa seem to be the least arboreal, and the amount of time they spend above ground is only 7% in females and 2% in males [1]. On the other hand, western lowland gorillas (*G. g. gorilla*) in western central Africa are observed to be more arboreal and are frequently found in trees higher than 20 m [1, 9]. Such differences in the degree of arboreality among the subspecies are correlated with foot anatomy. The foot of the western lowland gorilla has a relatively longer free portion of the first toe capable of opposing to the other four toes for grasping, whereas that of the mountain gorilla is relatively more humanlike and adapted for terrestrial locomotion [10, 11]. Therefore, understanding subspecies variations in the muscular characteristics of the gorilla foot is important for interpreting functional adaptations of the foot in hominoids. However, although Payne *et al.* [8] have reported the muscle architecture of the gorilla's hindlimb, no studies so far have provided complete quantitative data on all of the foot muscles, including the intrinsic muscles.

In this study, we dissected the left hindlimb of a female western lowland gorilla to provide complete quantitative

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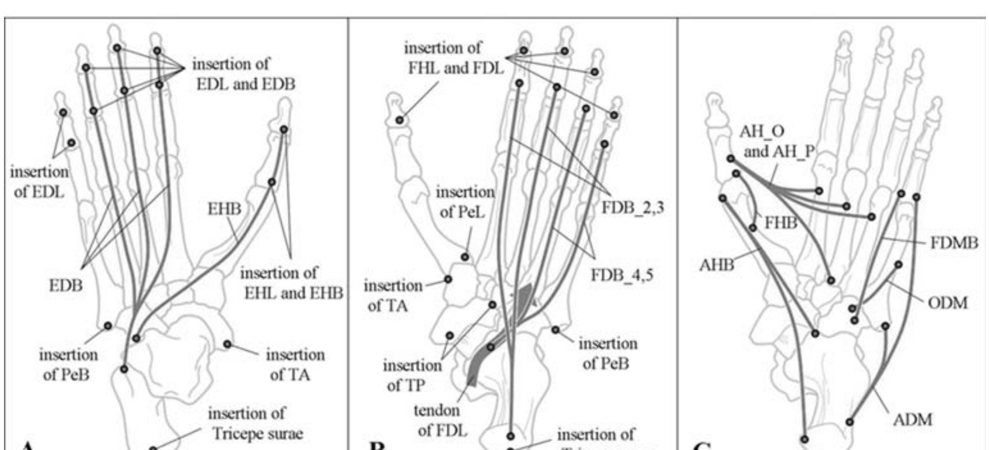

Fig. 1. Schematic diagram of the foot muscles of the lowland gorilla in dorsal (A) and planter (B, C) views. The ankle dorsiflexor (TA, EHL, EDL), extrinsic digital flexor (FHL, FDL) and digital minimi muscles (ADM, FDMB, ODM, FDB_5) were well-developed in the lowland gorilla. *Mm. lumbricals* and *Mm. interossei* are not included. Muscle name abbreviations are as detailed in Tables 1 and 2.

Table 1. Foot and shank muscle dimensions in the lowland gorilla

	Abbrevition	Mass (g)	PCSA (cm^2)	FL (cm)
Gastrocnemius and Plantaris	Gas + Pla	88.3	11.80	7.1
Soleus	Sol	102.3	21.98	4.4
Popliteus	Pop	4.9	0.93	5.0
Flexor hallucis longus	FHL	58.1	7.42	7.4
Flexor digitorum longus	FDL	22.1	2.67	7.8
Tibialis posterior	TP	19.4	4.16	4.4
Tibialis anterior	TA	58.2	7.16	7.7
Extensor hallucis longus	EHL	10.9	1.12	9.2
Extensor digitorum longus_2,3	EDL_2,3	9.4	0.97	9.1
Extensor digitorum longus_4	EDL_4	7.6	0.84	8.5
Extensor digitorum longus_5	EDL_5	13.5	1.35	9.4
Peroneus longus	PeL	44.0	7.40	5.6
Peroneus brevis	PeB	21.6	4.02	5.1
Peroneus tertius	PeT	7.6	0.96	7.5
Extensor hallucis brevis	EHB	4.7	1.29	3.4
Extensor digitotrum brevis_2	EDB_2	4.0	0.63	6.1
Extensor digitotrum brevis_3	EDB_3	2.9	0.65	4.2
Extensor digitotrum brevis_4	EDB_4	3.0	0.73	3.8
Flexor digitorum brevis_2	FDB_2	4.8	0.99	4.6
Flexor digitorum brevis_3	FDB_3	6.3	0.98	6.0
Flexor digitorum brevis_4	FDB_4	1.4	0.75	1.8
Flexor digitorum brevis_5	FDB_5	0.7	0.48	1.4
Abductor hallucis brevis	AHB	20.7	4.93	4.0
Flexor hallucis brevis	FHB	10.9	5.31	1.9
Adductor hallucis, caput obliquum	AH_O	7.8	2.53	2.9
Adductor hallucis, caput transversum	AH_T	12.5	4.19	2.8
Abductor digiti minimi	ADM	15.6	8.98	1.6
Flexor digiti minimi brevis	FDMB	3.7	2.26	1.5
Opponens digiti minimi	ODM	0.8	0.52	1.4
Dorsal interosseus_1	DI_1	3.8	1.99	1.8
Dorsal interosseus_2	DI_2	2.3	1.91	1.1
Dorsal interosseus_3	DI_3	3.5	2.15	1.5
Dorsal interosseus_4	DI_4	4.3	3.26	1.3
Plantar interosseus_1	PI_1	3.2	2.60	1.1
Plantar interosseus_2	PI_2	1.6	0.73	2.1
Plantar interosseus_3	PI_3	1.5	1.08	1.3
Lumbricalis_1	Lu_1	0.4	0.10	4.0
Lumbricalis_2	Lu_2	0.9	0.21	4.1
Lumbricalis_3	Lu_3	0.7	0.16	4.3
Lumbricalis_4	Lu_4	0.6	0.14	4.2

PCSA = physiological cross-sectional area. FL = fascicle length.

data on the gorilla foot musculature. The cadaver (Museum No.: NSMT-M35965) was obtained from Ueno Zoological Gardens through the National Museum of Nature and Science, Tokyo, Japan. The gorilla died at the approximate age of 40 years, with a body mass of 69 kg at the time of death. The specimen was stored frozen until dissection.

A schematic diagram of the foot muscles in the lowland gorilla is provided in Fig. 1. The foot musculature of the lowland gorilla is essentially similar to that of the human and other great apes, although some structural variations are noted. For example, *M. quadratus plantae*, running from the calcaneus to the tendon of the extrinsic pedal digital flexor muscles, is known to occur in only 30% of the lowland gorilla [12]. This muscle was absent in the present specimen. Moreover, *M. flexor digitorum brevis* was separated into the superficial and deep heads in the present specimen as also observed in other great apes [10, 12]; the superficial head arose from the calcaneus and inserted to the second and third toes, and the deep head arose from the tendon of *M. flexor digitorum longus* and inserted to the fourth and fifth toes (Fig. 1B). However, this muscle consists of only the superficial head and sends its tendons to the lateral four toes in the human [4].

During dissection, the muscles listed in Table 1 were exposed and removed from the foot and hindlimb bones. Muscle mass was determined using an electronic balance. Each muscle belly was immersed in 10% formalin. Thereafter, the fascicle length was measured at three to six places using a caliper. The PCSA was calculated by dividing the muscle volume by the fascicle length. The muscle volume was obtained by dividing the muscle mass by the muscle density (1.0597 g/cm^3) [5]. We did not include the penna-

Table 2. Comparisons of mass ratios and PCSA ratios in shank muscles with those of published gorilla (Gm and Gj) and human data

	Mass ratios				PCSA ratios			
	This study	Gm	Gj	Human (SD)	This study	Gm	Gj	Human (SD)
Triceps surae	43.2	42.5	40.9	54.3 (3.55)	49.8	39.7	39.6	61.7 (6.84)
Extrinsic pedal digital flexors	18.2	19.2	17.0	7.7 (1.47)	14.9	18.9	15.8	8.5 (1.89)
Dorsiflexors	22.6	23.7	21.4	17.5 (2.74)	16.9	27.9	17.2	10.4 (1.88)
Other muscles	16.1	14.6	20.7	20.4 (1.16)	18.4	13.6	27.4	19.4 (4.11)

Gm and Gj are cited from reported gorilla data [8]. The two values for human are given as the means and standard deviations (SD) of data from two published studies [2, 13]. Mass and PCSA ratios were calculated as subtotal of the constituent muscles of muscle groups. Muscle name abbreviations are as detailed in Table 1. Muscle groups: Triceps surae (Gas+Pla, Sol), Extrinsic pedal digital flexors (FHL, FDL), Dorsiflexors (TA, EHL, EDL), Other muscles (TP, PeL, PeT). *M. popliteus* and *M. peroneus brevis* are not included in other muscle group because complete data for the gorilla [8] and the human [2].

Table 3. Comparisons of mass ratios and PCSA ratios in foot muscles with those of published human data

	Mass ratios		PCSA ratios	
	Gorilla	Human	Gorilla	Human
Hallucal muscles	46.2	40.1	36.8	38.3
Digiti minimi muscles	16.9	14.6	24.7	13.4
Intrinsic pedal digital extensors	8.1	2.9	4.1	3.8
Intrinsic pedal digital flexors	10.2	20.7	5.5	16.4
Interossei	16.4	19.3	27.7	25.7
Lumbricals	2.2	2.4	1.2	2.3

Human data are cited from Kura *et al.* [4]. Mass and PCSA ratios were calculated as subtotal of the constituent muscles of muscle groups. Muscle name abbreviations are as detailed in Table 1. Muscle groups: Hallucal muscles (EHB, AHB, FHB, AH_O, AH_T), Digiti minimi muscles (ADM, FDMB, ODM, FDB_5), Intrinsic pedal digital extensors (EDB_2–4), Intrinsic pedal digital flexors (FDB_2–4, *M. quadratus plantae*), Interossei (DI_1–4, PI_1–3), Lumbricals (Lu_1–4).

tion angle in our calculation of PCSA, because, in the two-dimensional muscle model, it was difficult to correctly measure the angle of the three-dimensional fascicle within a muscle. For comparisons of muscle architecture, the mass and PCSA of each foot muscle were divided by the total foot muscle mass and PCSA to calculate mass and PCSA ratios, respectively. The mass and PCSA ratios of the shank muscles were calculated in the same manner.

To confirm the consistency of our measurements, the mass and PCSA ratios of the shank muscles were compared with those reported by Payne *et al.* [8] (two male western lowland gorillas, Gm and Gj). Although a certain degree of variability exists, Table 2 indicates that the data acquired in the present study were generally in accordance with the previously reported data, suggesting that the described gorilla muscle architectural patterns appear to be reasonably representative.

Table 2 also shows compares the mass and PCSA ratios of gorilla and human shank musculature. The human data are taken from Wickiewicz *et al.* [13] and Friederich and Brand [2]. In both species, the triceps surae muscles were larger and had more capacity to generate force than the other muscle groups, but this tendency was found to be more prominent in the human, probably as an adaptation to strong toe-off during bipedal walking. On the other hand, the mass and PCSA ratios of the ankle dorsiflexor and extrinsic digital flexor muscles were larger in the gorilla (Table 2).

With respect to the intrinsic foot muscles (Table 3), the digital flexor muscles were relatively smaller in the gorilla because *M. quadratus plantae* is relatively large in the human foot [4], whereas this muscle is rudimentary in the gorilla's foot [3, 12]. Instead, the PCSA ratio of the digital minimi muscles was relatively larger in the gorilla, possibly indicating that the lowland gorilla has a greater grasping capability of the fifth toe (Table 3).

This study is the first complete report on the muscular dimensions of the foot in the lowland gorilla. The mass, PCSA, and fascicle length of the thigh muscles from the same specimen are also presented in the Appendix. Such complete data of the muscle dimensions are essential for understanding the form-function relationship of musculature in hominoids [e.g., 6, 7]. We hope to have more opportunities to dissect the feet of both lowland and mountain gorillas for comparative analysis of the intra- and inter-subspecies variations in muscle architecture in gorillas, which might reflect differences in their habitats and locomotor behaviors.

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Appendix. Thigh muscle dimensions in the lowland gorilla

	Mass (g)	PCSA (cm^2)	FL (cm)
Psoas major and Psoas minor	73.3	8.57	8.1
Iliacus	79.8	11.58	6.5
Tensor fascia latae	25.7	1.58	15.4
Gluteus maximus	328.2	31.97	9.7
Gluteus medius	391.0	36.04	10.2
Prifoermis	37.5	6.07	5.8
Gluteus minimus	57.3	8.99	6.0
Quadratus femoris	10.5	2.24	4.4
Superior gemellus	2.7	0.96	2.6
Inferior gemellus	1.4	0.33	3.9
Biceps femoris, caput longum	103.0	7.06	13.8
Biceps femoris, caput breve	44.6	4.86	8.7
Semimembranosus	19.4	1.25	14.6
Semitendinosus	100.9	7.00	13.6
Gracilis	91.1	3.40	25.3
Sartorius	19.2	0.55	32.9
Adductor longus	40.7	3.57	10.8
Adductor brevis	51.8	7.70	6.4
Adductor magnus	442.8	23.88	17.5
Pectineus	15.1	2.01	7.1
Obturatorius internus	35.3	6.61	5.0
Obturatorius externus	37.2	5.69	6.2
Rectus femoris	79.6	7.36	10.2
Vastus lateralis	174.7	19.23	8.6
Vastus medialis	105.3	12.95	7.7
Vastus intermedius	117.8	14.07	7.9

PCSA = physiological cross-sectional area. FL = fascicle length.

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