Contr. Biol. Lab. Kyoto Univ., 25(3), 1978

Correlation between Relative Weights of Hindlimb Muscles and Locomotor Patterns in Japanese Anurans

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Abstract

The correlation between the relative weights of the hindlimb muscles and the locomotor patterns was examined in four species of Japanese anurans, *Bufo bufo japonicus* (terrestrial walker), *Rana catesbeiana* and *R. rugosa* (amphibious jumpers), and *Rhacophorus arboreus* (arboreal climber). The relative weight is represented as a percentage of each muscle weight to the total weight of the thigh and shank muscles. In *Rana catesbeiana* and *R. rugosa*, the relative weights of the same muscles are nearly equivalent, whereas those of *Bufo b. japonicus* are fairly different from the two *Ranas*. For example, distinct differences occur in the ratio of the muscle weight of the thigh to that of the shank and in the relative weights of three muscle groups acting on the hip, the knee, and the ankle joints. Arboreal *Rhacophorus arboreus* is intermediate between *Rana* and *Bufo* in the thigh muscle weights, whereas in the shank muscles, the characteristics of *Bufo* are amplified, and, therefore, *Rh. arboreus* is considered to have a hindlimb musculature different from *Bufo* and *Rana*. Each locomotor movement is discussed with reference to the mechanism of jumping with sepcific assumptions on the action of the three muscle groups. These assumptions are supported by the weight composition of the hindlimb musculature, and the locomotor patterns seemed to correspond with the characteristics of musculature.

The order Anura, as its alternative name, 'Salientia' indicates, is a group of amphibians generally characterized by the saltatory mode of locomotion. Most species are amphibious as adults, but some, such as *Xenopus* and *Pipa*, remain completely aquatic. Others, e.g. bufonids, are terrestrial and move chiefly by walking. Further, some tree-frogs are well adapted to the arboreal life and climbing is dominant in their life. These modes of locomotion, however, are deviations from the typical mode, i.e. jumping.

Remarkable morphological specializations, such as shortening of the trunk, are noted in every part of the anuran's body. Among these, the modifications of the hindlimbs, including its musculature, are particularly conspicuous.

Since the last century, the morphology of the anuran hindlimbs has been studied not infrequently (cf. GAUPP, 1896–1899 among others). NOBLE (1922) developed a classification of anurans on the basis of the morphological characters of the hindlimb musculature. Subsequent reports on the hindlimb musculature were more or less based on Noble's standpoint (BIGALKE, 1926; DUNLAP, 1960; LIMESES, 1964). On the other hand, few studies have been made on the functional aspects of the locomotor apparatus. Only studies on the relation between jumping distance and body proportions (WERMEL, 1934; RAND, 1952; STOKELY and BERBERIAN, 1953; ZUG, 1972), on the pelvic girdle (GREEN, 1931; WHITING, 1961), and on the mechanical analysis of the leg extensor muscles (CALOW and ALEXANDER, 1973) can be enumerated from the vast literature of morphological studies. No attempt has hitherto been made to investigate the functional aspects of the morphology of the hindlimb musculature, however.

The purpose of the present work is to determine the relationship between the hindlimb musculature and locomotor patterns in several species of anurans by comparing the relative weights of the thigh and shank muscles.

The Japanese common toads, *Bufo bufo japonicus*, mainly live on land and move by walking, though they occasionally hop. The bullfrogs, *Rana catesbeiana*, and the rugose frogs, *R. rugosa*, are amphibious, and they jump frequently. The green treefrogs, *Rhacophorus arboreus*, live usually in trees, and their main locomotor movements consist of climbing and walking. Since these species can be regarded as representing the three main patterns in anuran locomotion, observations and analyses were focussed on them.

Material and Methods

All the frogs and toads used in this study were adults and captured in the city of Kyoto. The number and sex of materials are as follows: *Bufo bufo japonicus* (3 males and 3 females), *Rana catesbeiana* (4 males and 2 females), *Rana rugosa* (1 male), and *Rhacophorus arboreus* (2 females).

Most of the specimens were preserved in 70% ethanol, although a few were fixed first in 10% formalin and later transferred to 70% ethanol. After skinning, each muscle was carefully separated, and the connective tissue and blood vessels attached to the surface of muscles were removed as carefully as possible. Only the fleshy portions were

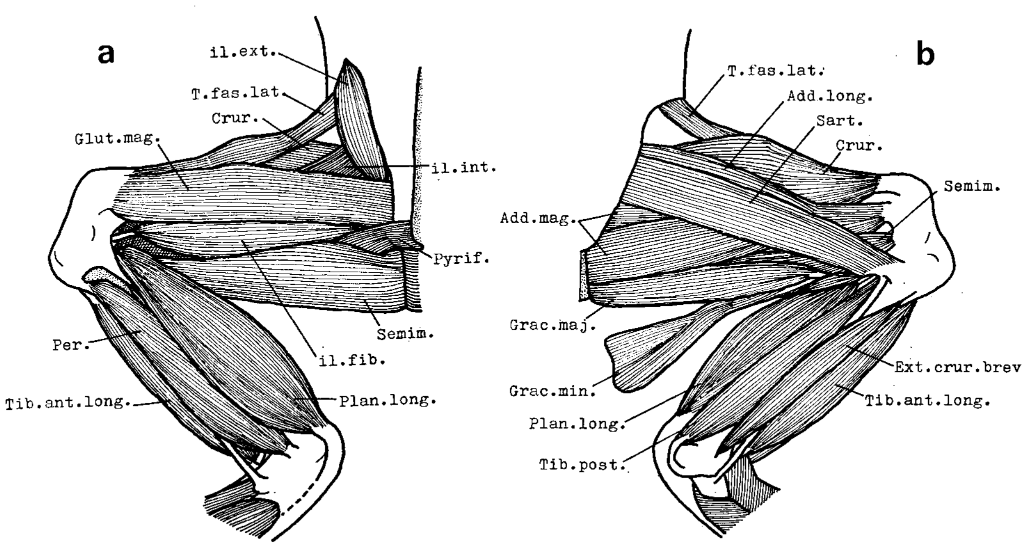

Fig. 1. Superficial muscles of the left leg of *Bufo bufo japonicus*; dorsal (a) and ventral (b) view. ×1.

removed; the tendons were excluded. Where necessary, the dissections were made under a binocular microscope. Muscles, thus separated, were stored in 70% ethanol, and consequently all the muscles were in the same condition with regard to preservation. Prior to weighing, the alcohol on the surface of a muscle was wiped off with a filter paper. The weight of the muscle was measured to an accuracy of 10 mg with a Chyo Jupiter balance, Model C3 200-D. The thigh and shank muscles weighed are listed in Table 1. Since anuran muscles have not yet been homologized with those of man, the human anatomical names cannot be applied to the anurans. Therefore, the terminology used in the present work is that proposed by GAUPP (1896–1899) and later adopted by DUNLAP (1960), which is currently universal.

The relative weight is represented by percentage of the weight of each muscle to the total weight of thigh and shank muscles. Mean (M) and standard deviation (SD) were calculated. For the purpose of analyzing variations, such as bilateral, sexual, and interspecific differences, the Student *t* test is given at the 95% confidence level.

Results

General Remarks

Except for *Rhacophorus arboreus*, the frogs and toads studied herein have 20 muscles

Table 1. List of thigh and shank muscles examined. Each figure indicates number of joints on which each muscle acts.

		Muscle	No. of joint
Thigh			
	1	M. cruralis	2
	2	M. tensor fasciae latae	2
	3	M. glutaeus magnus	2
	4	M. sartorius	2
	5	M. adductor longus	1
	6	M. adductor magnus	1
	7	M. gracilis major	2
	8	M. gracilis minor	2
	9	M. ileo-fibularis	2
	10	M. semimembranosus	2
	11	M. semitendinosus	2
	12	M. iliacus internus	1
	13	M. iliacus externus	1
	14	M. ileo-femoralis	1
	15	M. pyriformis	2
	16	M. pectineus	1
	17	M. obturator externus	1
	18	M. quadratus femoris	1
	19	M. gemellus	1
	20	M. obturator internus	1
Shank			
	21	M. plantaris longus	2+
	22	M. tibialis posticus	1
	23	M. peroneus	2
	24	M. tibialis anticus longus	2
	25	M. extensor cruris brevis	1
	26	M. tibialis anticus brevis	1

in the thigh and 6 in the shank (Table 1 and Figs. 1–3). In *Rhacophorus* the adductor longus is absent, apparently lost in the course of evolution (DUNLAP, 1960). The origin and insertion of each of these muscles vary more less in the four species. The muscles of *R. catesbeiana* and *R. rugosa* are very similar, but they are slightly different from those of *Rhacophorus* and clearly different from those of *Bufo*. For example, the

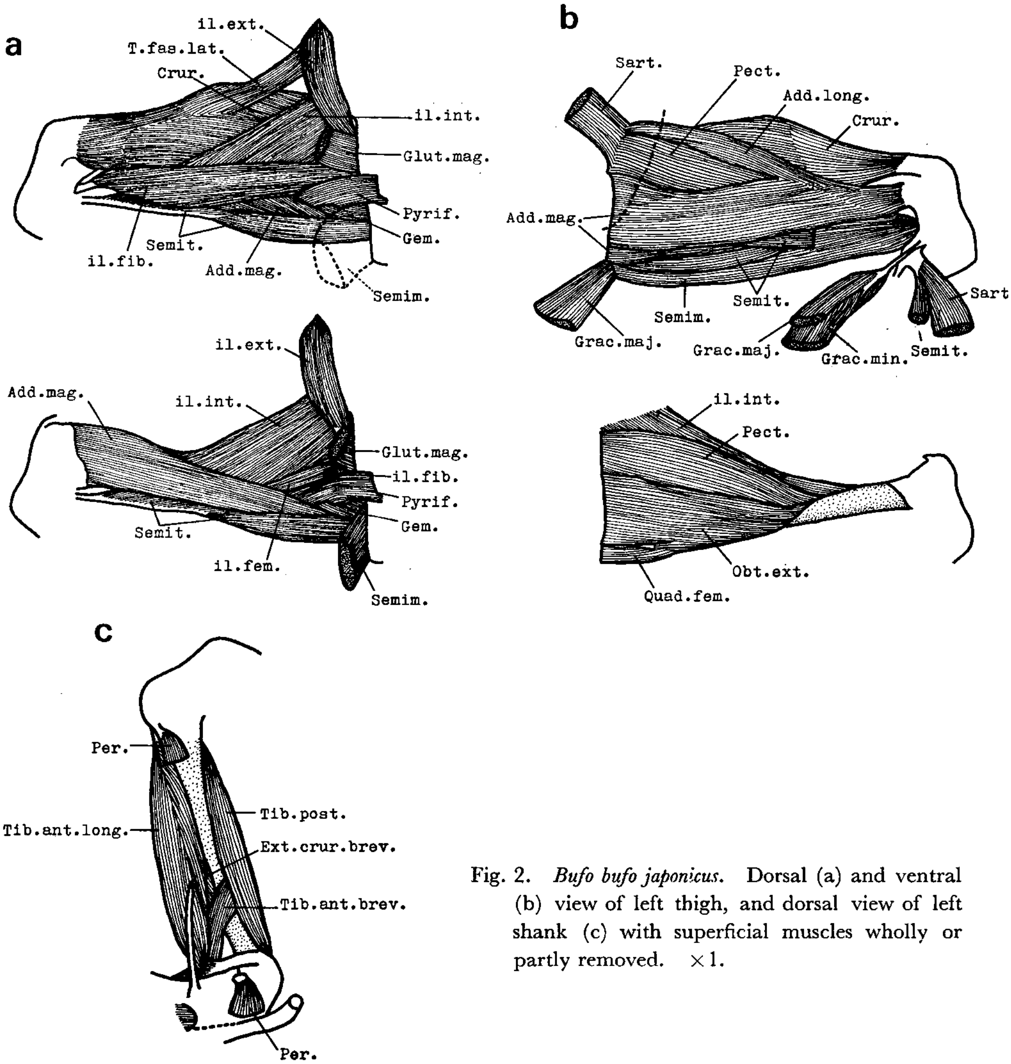

Fig. 2. *Bufo bufo japonicus*. Dorsal (a) and ventral (b) view of left thigh, and dorsal view of left shank (c) with superficial muscles wholly or partly removed. ×1.

origin of the tensor fasciae latae is fleshy in *Bufo*, while it originates as a tendon in *Rana* and *Rhacophorus*. This situation is the converse for the origin of the glutaeus magnus. The sartorius and the semitendinosus attach separately to the femur in *Rana*, whereas they attach to it with rather long common tendon in *Rhacophorus*, and so on. As a result, the origin and insertion of each muscle in the four species studied herein is essentially in agreement with the descriptions by previous authors on the same or closely related species of the same genera (*Bufo vulgaris* [=*B. bufo*]; BIGALKE, 1926; *B. boreas, Rana catesbeiana, Polypedates* [=*Rhacophorus*] *leucomystax*; DUNLAP, 1960). These previous observations will be referred to in later descriptions.

At any rate, it is difficult to detect the direct relation between the various anatomi-

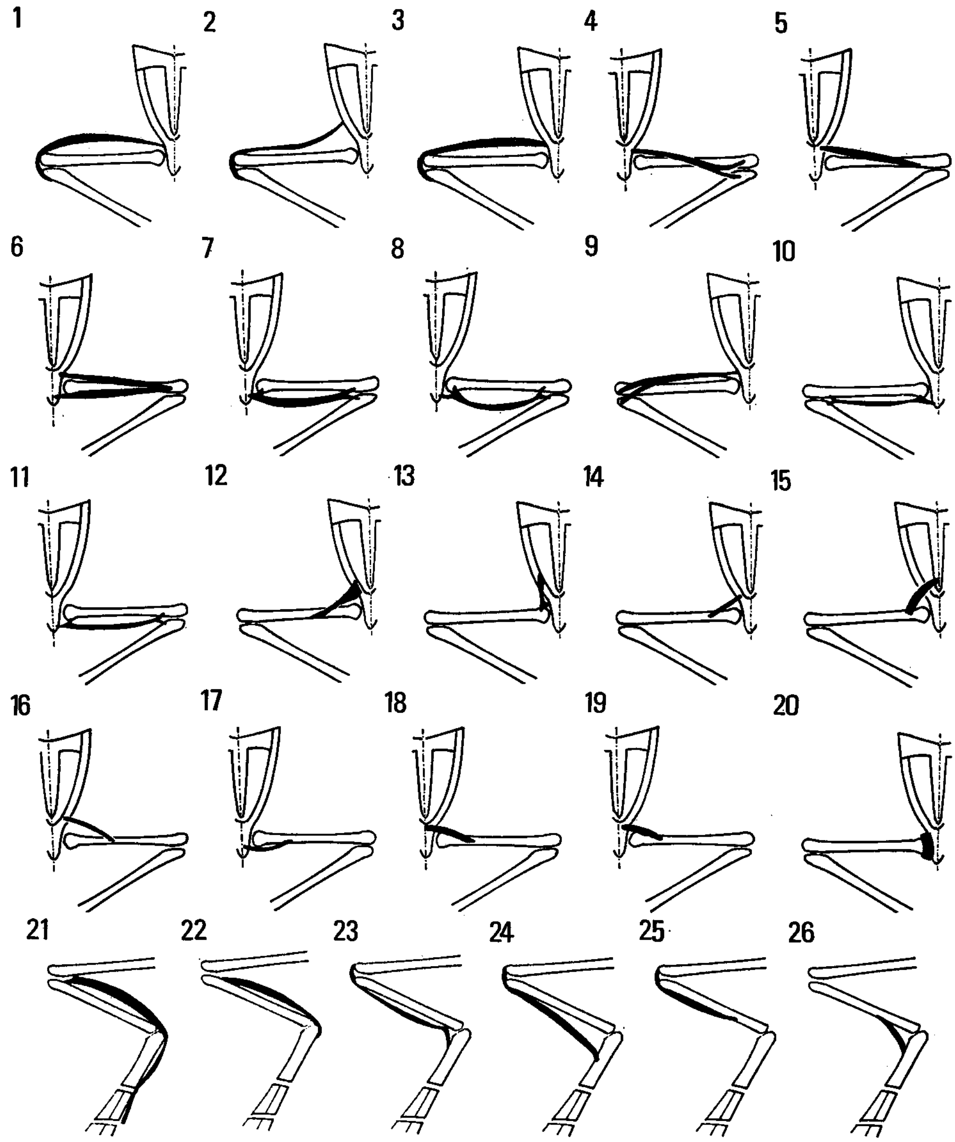

Fig. 3. Schematic representations of thigh and shank muscles showing the relations between each muscle and the hip, knee, and ankle joints. Each numeral corresponds to the muscle number listed in the Table 1.

cal arrangement of each muscle and the various locomotor patterns. Therefore, a quantitative analysis was pursued as a method of finding the correlation of the musculature and locomotor pattern.

Intraspecific variations in the relative wieght of each muscle were examined first. An increase of the total weight of the thigh and shank muscles does not affect the relative weight of each muscle, as is seen in the cruralis and the semimembranosus of *Bufo bufo japonicus* and the plantaris longus and the glutaeus magnus of *Rana catasbeiana* (Fig. 4a and b). Although the sample size is fairly small, this constancy holds for all the

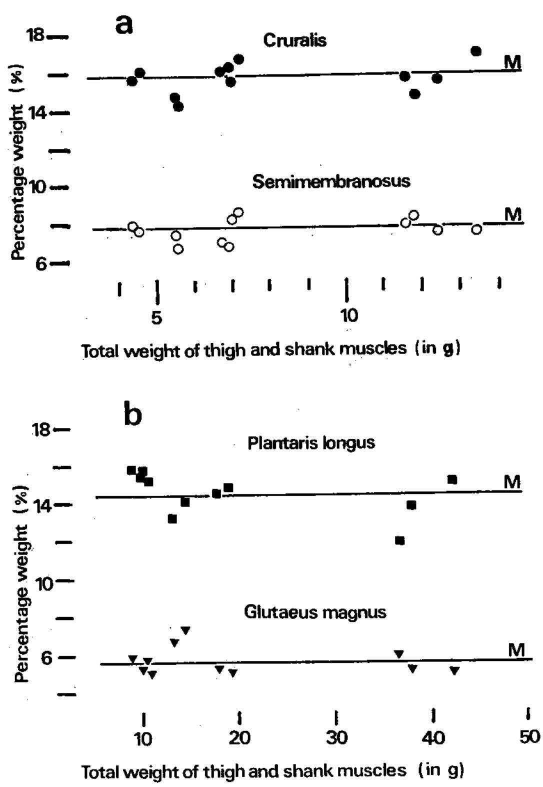

Fig. 4. Scatter diagrams of percentage weight of cruralis and semimembranosus to total weight of thigh and shank muscles in *Bufo bufo japonicus* (a) and that of plantaris longus and glutaeus magnus to total weight of thigh and shank muscles in *Rana catesbeiana* (b).

remaining muscles, and each relative weight seems to be almost invariable in individuals of different age of the same species. Also, as the result of the examinations of bilateral and sexual differences, no significant differences are found in either case in any of the muscles of *Bufo* (Tables 2 and 3). In *Rana catesbeiana*, a statistically significant sexual differences are found in the gemellus (Table 4), but this difference is minor in comparison to the interspecific differences.

From these rseults, there seems to be minor, if any, age, bilateral, or sexual difference in the relative weight of the specific muscles used herein. Thus, all the samples of any specific muscle are treated without discrimination hereafter.

Weight Composition of the Hindlimb Musculature in Bufo bufo japonicus

The relative weights of the muscles that compose the hindlimb musculature were calculated (Table 5). The total weight of the 20 thigh muscles (75.45%) is far greater than that of the six shank muscles (24.55%), the ratio being 3.07:1. The largest muscle is the cruralis of the thigh (15.87%), and the plantaris longus of the shank ranks next. Other large muscles exceeding 5% in weight are the adductor magnus, the semimembranosus, and the iliacus internus in the thigh, and the tibialis anticus longus in the shank. The smallest muscle is the tibialis anticus brevis (0.20%) in the shank, and the quadratus femoris in the thigh is next. The tensor fasciae latae, the ileo-femoralis, and the adductor longus of the thigh are also small muscles under 1%.

Table 2. Comparison of relative weights (in %) of thigh and shank muscles between right and left sides in *Bufo bufo japonicus* (males and females combined).

Muscle	Right (n=6)		Left (n=6)	
	M	SD	M	SD
Thigh muscles				
Cruralis	16.179	0.872	15.569	0.674
Tensor fasciae latae	0.757	0.187	0.704	0.118
Glutaeus magnus	5.175	0.391	4.728	0.762
Sartorius	2.270	0.197	2.309	0.253
Adductor longus	0.879	0.383	0.922	0.346
Adductor magnus	11.709	0.704	11.531	1.211
Gracilis major	4.541	0.652	4.698	0.784
Gracilis minor	2.944	0.210	3.188	0.444
Ileo-fibularis	2.333	0.212	2.232	0.071
Semimembranosus	7.783	0.644	7.888	0.620
Semitendinosus	2.805	0.373	2.764	0.349
Iliacus internus	5.197	0.402	5.176	0.814
Iliacus externus	2.679	0.346	2.520	0.352
Ileo-femoralis	0.794	0.210	0.783	0.232
Pyriformis	1.104	0.110	0.981	0.077
Pectineus	2.756	0.620	2.785	0.675
Obturator externus	2.485	0.582	2.664	0.434
Quadratus femoris	0.695	0.245	0.668	0.164
Gemellus	1.105	0.226	1.172	0.205
Obturator internus	1.676	0.313	1.773	0.499
Shank muscles				
Plantaris longus	12.493	0.678	13.177	1.347
Tibialis posticus	1.991	0.155	2.108	0.265
Peroneus	2.629	0.187	2.750	0.192
Tibialis anticus longus	5.646	0.383	5.555	1.054
Extensor cruris brevis	1.175	0.224	1.170	0.192
Tibialis anticus brevis	0.202	0.045	0.203	0.032

Since the movements of each part of the hindlimb are performed around joints and the muscles act for these movements, the relation between each muscle and the joints was examined. All the 20 muscles of the thigh act on the hip joint, and among them, the cruralis, tensor fasciae latae, glutaeus magnus, sartorius, gracilis major, gracilis minor, ileo-fibularis, semimembranosus, and semitendinosus are two-joint muscles, since they arise from the ilium and attach to the tibiofibula, acting on the hip and knee joints (these muscles are indicated as "2" in Table 1); the other thigh muscles are one-joint muscles extending from the ilium or urostyle to the femur (indicated as "1"). All the six muscles on the shank act on the ankle joint; among them, three superficial muscles, the plantaris longus, peroneus, and tibialis anticus longus, are two-joint muscles that run from the knee to the foot and act on the knee and ankle joints (Table 1). Therefore, 75.47 per cent of the total weight is related to the hip joint, and 65.56 per cent to the knee joint, and 24.54 per cent to the ankle joint. As the plantaris longus fans out on the planter surface of the foot with a stout tendon, it is related to more than

Table 3. Comparison of relative weights (in %) of thigh and shank muscles between male and female in *Bufo bufo japonicus* (right and left sides combined).

Muscle	Male (n=6)		Female (n=6)	
	M	SD	M	SD
Thigh muscles				
Cruralis	15.957	0.672	15.792	0.965
Tensor fasciae latae	0.664	0.039	0.796	0.055
Glutaeus magnus	5.000	0.293	4.904	0.867
Sartorius	2.441	0.114	2.137	0.205
Adductor longus	0.720	0.303	1.081	0.313
Adductor magnus	11.931	1.287	11.309	0.303
Gracilis major	4.425	0.490	4.814	0.849
Gracilis minor	2.996	0.330	3.136	0.395
Ileo-fibularis	2.335	0.200	2.230	0.100
Semimembranosus	8.032	0.237	7.640	0.800
Semitendinosus	2.866	0.297	2.702	0.406
Iliacus internus	4.886	0.686	5.487	0.370
Iliacus externus	2.601	0.432	2.598	0.268
Ileo-femoralis	0.653	0.303	0.923	0.192
Pyriformis	1.027	0.077	1.058	0.145
Pectineus	2.824	0.554	2.718	0.722
Obturator externus	2.253	0.406	2.896	0.366
Quadratus femoris	0.588	0.100	0.775	0.237
Gemellus	1.089	0.210	1.188	0.214
Obturator internus	1.585	0.437	1.865	0.335
Shank muscles				
Plantaris longus	13.156	1.191	12.514	0.943
Tibialis posticus	2.138	0.130	1.960	0.266
Peroneus	2.790	0.200	2.589	0.130
Tibialis anticus longus	5.700	0.127	5.509	0.277
Extensor cruris brevis	1.144	0.228	1.201	0.184
Tibialis anticus brevis	0.213	0.045	0.192	0.032

two joints in strict sense, and is indicated as 2+ in Table 1.

Weight Composition of Hindlimb Muscluature in Rana catesbeiana

The relative weight of each muscle composing the hindlimb musculature is shown in Table 5.

The total weight of thigh muscles accounts for 78.13% of the sum total and that of shank muscles, 21.87%. The ratio of the two groups is 3.57: 1. As in the case of *Bufo*, the cruralis of the thigh is the largest (18.05%) and the plantaris longus of the shank is second. Muscles showing comparatively large value are all in the thigh: the semimembranosus, adductor magnus, gracilis major, and glutaeus magnus. The smallest is the quadratus femoris of the thigh, and the extensor cruris brevis of the shank is next. Small muscles less than 0.5% are the gemellus, ileo-femoralis, and pyriformis, all lying in the thigh.

The total values of relative weights of the muscles related to each joint are as follows: hip, 78.12%; knee, 73.99%; and ankle, 21.86%.

Table 4. Comparison of relative weights (in %) of thigh and shank muscles between male and female in *Rana catesbeiana* (right and left sides combined).

Muscle	Male (n=7)		Female (n=4)	
	M	SD	M	SD
Thigh muscles				
Cruralis	17.697	1.198	18.656	0.778
Tensor fasciae latae	1.246	0.089	1.074	0.055
Glutaeus magnus	5.780	0.869	5.503	0.382
Sartorius	2.508	0.148	2.668	0.126
Adductor longus	1.711	0.241	1.622	0.686
Adductor magnus	11.306	0.812	11.047	0.409
Gracilis major	9.669	0.979	8.927	0.321
Gracilis minor	1.450	0.118	1.172	0.118
Ileo-fibularis	2.189	0.173	2.232	0.105
Semimembranosus	11.947	1.429	11.175	0.528
Semitendinosus	2.703	0.523	2.748	0.055
Iliacus internus	3.831	0.158	3.769	0.192
Iliacus externus	1.424	0.318	1.418	0.063
Ileo-femoralis	0.434	0.100	0.418	0.032
Pyriformis	0.494	0.105	0.446	0.055
Pectineus	1.301	0.138	1.288	0.071
Obturator externus	1.297	0.110	1.201	0.063
Quadratus femoris	0.331	0.095	0.219	0.045
Gemellus	0.483	0.100	0.311	0.018
Obturator internus	1.029	0.122	0.926	0.207
Shank muscles				
Plantaris longus	13.964	1.155	15.545	0.350
Tibialis posticus	1.560	0.207	1.683	0.114
Peroneus	2.617	0.257	2.760	0.095
Tibialis anticus longus	1.931	0.239	2.053	0.026
Extensor cruris brevis	0.445	0.141	0.370	0.066
Tibialis anticus brevis	0.649	0.114	0.684	0.018

Comparison between Bufo bufo japonicus *and* Rana catesbeiana

The two ratios mentioned above, i.e., 3.07:1 in *Bufo* and 3.57:1 in *Rana*, indicate that in both species the total weight of the thigh muscles is far greater than that of the shank muscles and that the difference is greater in *Rana*. Form the percentages of the muscles related to each of the three joints in the two species, it is clear that the muscles related to the hip and knee joints are greater in *Rana*, whereas those related to the ankle joint are larger in *Bufo* than in *Rana*. Moreover, the relative weight of muscles related to the knee joint is especially greater in *Rana* than that of *Bufo*.

For a comparison of each corresponding muscle, the differences in relative weight between *Rana* and *Bufo* were examined (Figs. 5–7). As is evident from Fig. 7 and Table 5, the following muscles greatly differ in weight between the two species: the cruralis, gracilis major, and semimembranosus in the thigh; the tibialis anticus longus in the

Table 5. Comparison of relative weight (in %) of thigh and shank muscles in four species of Japanese anurans, with males and females, right and left sides combined.

Muscles	*Bufo bufo japonicus* (n=12)		*Rana catesbeiana* (n=11)		*Rana rugosa* (n=1)	*Rhacophorus arboreus* (n=3)	
Thigh	M	SD	M	SD		M	SD
Cruralis	15.874	0.809	18.045	1.142	19.526	17.771	0.409
Tensor fasciae latae	0.730	0.155	1.183	0.122	0.878	0.258	0.077
Glutaeus magnus	4.952	0.620	5.679	0.721	5.046	4.538	0.020
Sartorius	2.289	0.221	2.566	0.160	2.016	2.635	0.026
Adductor longus	0.900	0.351	1.711	0.239	0.960		
Adductor magnus	11.620	0.949	11.212	0.683	11.367	8.063	1.190
Gracilis major	4.620	0.688	9.399	0.863	11.422	10.462	2.621
Gracilis minor	3.066	0.355	1.349	0.181	1.220	2.292	0.452
Ileo-fibularis	2.282	0.167	2.205	0.151	1.851	1.828	0.089
Semimembranosus	7.836	0.598	11.667	1.207	11.244	10.145	1.486
Semitendinosus	2.784	0.349	2.719	0.410	2.249	2.693	0.385
Iliacus internus	5.186	0.616	3.808	0.175	2.962	2.611	0.245
Iliacus externus	2.600	0.339	1.422	0.248	0.974	2.274	0.145
Ileo-femoralis	0.788	0.212	0.428	0.079	0.302	0.562	0.045
Pyriformis	1.043	0.105	0.477	0.084	0.425	0.359	0.032
Pectineus	2.771	0.616	1.296	0.117	1.522	2.999	0.077
Obturator externus	2.575	0.495	1.262	0.106	0.836	1.847	0.716
Quadratus femoris	0.682	0.197	0.290	0.096	0.411	0.512	0.130
Gemellus	1.138	0.212	0.421	0.117	0.507	0.475	0.105
Obturator internus	1.725	0.397	0.991	0.157	0.878	1.067	0.228
Total	75.461		78.130		76.595	73.391	
Shank							
Plantaris longus	12.835	1.078	14.539	1.213	14.164	10.558	0.049
Tibialis posticus	2.049	0.221	1.605	0.185	1.920	2.052	0.028
Peroneus	2.689	0.200	2.669	0.224	3.908	7.148	0.255
Tibialis anticus longus	5.600	0.762	1.975	0.200	2.249	4.365	0.141
Extensor cruris brevis	1.712	0.202	0.418	0.212	0.507	1.133	0.316
Tibialis anticus brevis	0.202	0.045	0.662	0.089	0.658	1.357	0.498
Total	24.547		21.868		23.406	26.613	

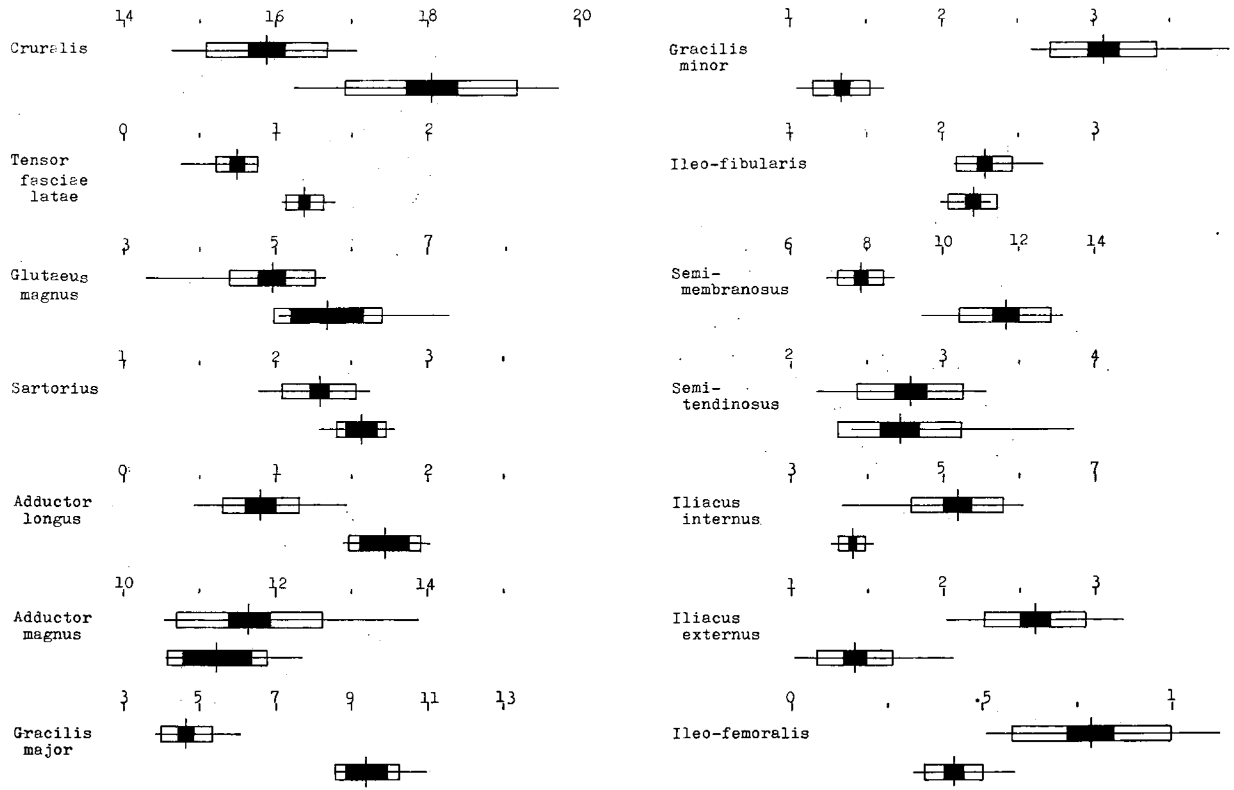

Fig. 5. A comparison of the ranges, means, standard deviations, and standard errors of the relative weight (%) of thigh muscles of *Bufo bufo japonicus* (above) and those of *Rana catesbeiana* (below).

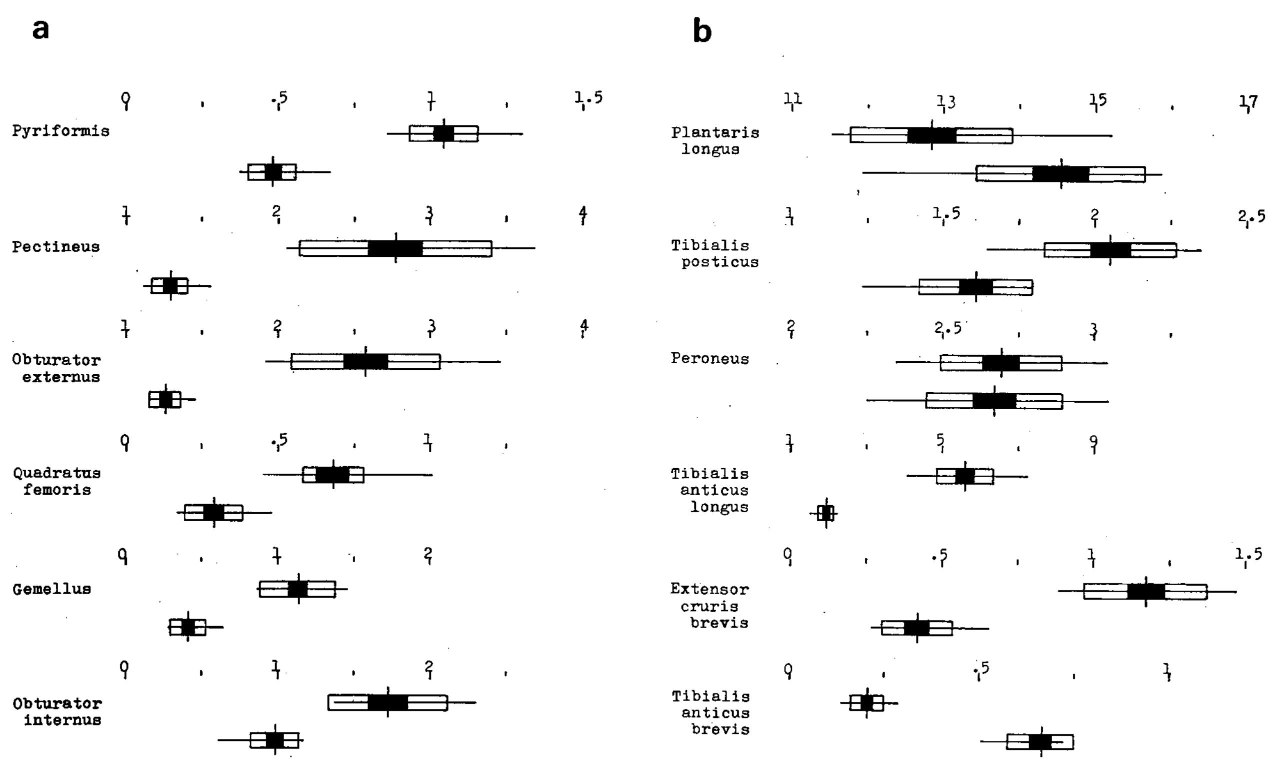

Fig. 6. A comparison of the ranges, means, standard deviations, and standard errors of the relative weight (%) of thigh (a) and shank (b) muscles of *Bufo bufo japonicus* (above) and those of *Rana catesbeiana* (below).

shank. Of the muscles showing statistically significant differences ($p<0.05$), the muscles with larger values in *Bufo* than in *Rana* are the gracilis minor, iliacus internus, iliacus externus, ileo-femoralis, pyriformis, pectineus, obturator externus, quadratus femoris, gemellus, obturator internus, tibialis posticus, tibialis anticus longus, and extensor cruris brevis; those with larger values in *Rana* than in *Bufo* are the cruralis, tensor fasciae latae, glutaeaus magnus, sartorius, adductor longus, gracilis major, semimembranosus, plantaris longus, and tibialis anticus brevis.

A further examination was made on the morphology and the action of the muscles that somewhat differ between the two species by comparing the sites of origin and in-

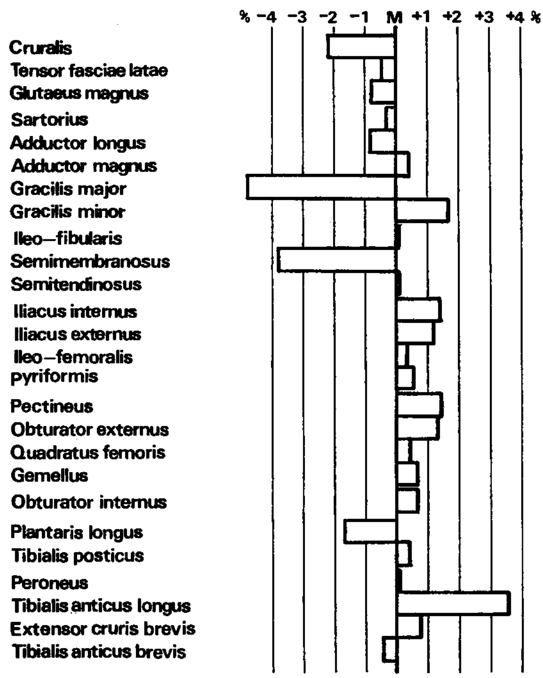

Fig. 7. Differences in relative weight of thigh and shank muscles between *Bufo bufo japonicus* and *Rana catesbeiana*. "M" indicates mean of *Bufo bufo japonicus*.

sertion on the hindlimb skeleton and the number of joints on which these muscles act. Most of the muscles with larger values in *Bufo* are either related to the hip joint, lying superficially, on the anterior side of the femur or lying deeply around the latter (iliacus internus, iliacus externus, ileo-femoralis, pyriformis, obturator externus, quadratus femoris, gemellus, and obturator internus) or related to the ankle joint and lie on the anterior side of the tibia (tibialis anticus longus, and extensor cruris brevis). On the other hand, the muscles with larger values in *Rana* are either related to the hip and knee joints and lie superficially, on its posterior side (gracilis major and semimembranosus), or related to the ankle joint and run on the posterior side of the tibia (plantaris longus).

Since these notable differences between the two species were found in the quanti-

Table 6. Total relative weights (in %) of thigh and

	One-joint muscles						
	Thigh			Shank			Total of 1-joint muscles
	Deep	Supf. ant.	Total of thigh	ant. side	post. side	Total of shank	
Kind of muscles*	6, 14, 16–20	5, 12, 13		25, 26	22		
Bufo bufo japonicus	21.30	8.69	29.99	1.37	2.05	3.42	33.41
Rana catesbeiana	15.90	6.94	22.84	1.08	1.61	2.69	25.53
Rana rugosa	15.82	4.90	20.72	1.17	1.92	3.09	23.80
Rhacophorus arboeus	15.53	4.89	20.41	2.49	2.05	4.54	24.95

* Each figure corresponds to the muscle number shown in Table 1.

tative composition of the hindlimb musculature, further comparisons were made by classifying each muscle according to its location and the number of joints on which it acts (Table 6). A characteristic of *Bufo*, compared to *Rana catesbeiana*, is that the one-joint muscles related to the hip joint and lying in the deep of the thigh, and the two-joint muscles related to the ankle joint and lying on the anterior side of the tibia are remarkably large (Table 6). In *Rana catesbeiana*, on the other hand, the muscles related to the hip and knee joints and lying superficially on both anterior and posterior sides of the thigh are larger than those of *Bufo*, and the difference from *Bufo* is evident in the muscles on the posterior side. In addition, the muscle acting on the ankle joint and lying on the posterior side of the tibia, i.e. the plantaris longus, is larger in *Rana*, and thus the constructural differences between the two species becomes quite clear.

To sum up these results, it is postulated from the viewpoint of the relative weight that there are prominent differences between *Bufo bufo japonicus* and *Rana catesbeiana* in the ratio of the thigh muscles to the shank muscles, in the total weights of muscles related to the hip, knee, and ankle joints respectively, and in the composition by the muscles. Consequently, it is evident that the two species are clearly different from each other in the hindlimb musculature.

Quantitative Analysis of the Hindlimb Musculature in Rhacophorus arboreus *and* Rana rugosa

The remaining two species, *Rana rugosa* and *Rhacophorus arboreus*, are compared with reference to the characteristics of the hindlimb musculature. *Rana rugosa*, a relative of *R. catesbeiana*, moves by jumping, whereas *Rhacophorus arboreus*, a tree-dweller, usually walks on trunks and branches with the aid of finger discs but often jumps well. The relative weights of the hindlimb muscles in these two species, on which the following comparison was made, are listed on Table 5. Though the intraspecies variations were not examined because of the smallness of the sample size, the results obtained with *Bufo bufo* and *R. catesbeiana* may indicate that small sample size can possibly be used. In addition, *Rhacophorus arboreus* lacks the adductor longus as described before, but no correction was made and, consequently, the total of 25 muscles corresponds to 100%.

In the first place, the ratio of the total weight of muscles at the thigh to that of the shank was compared. In *Rhacophorus*, the total of thigh muscles accounts for 73.39%

shank muscles classified according to their positions.

Deep	Two-joint muscles: Thigh, Superficial, ant. side	post. side	Total of thigh	Shank: and. side	post. side	Total of shank	Total of 2-joint muscles
15	1–4, 9	7, 8, 10, 11		23, 24	21		
1.04	26.13	18.31	45.48	8.29	12.84	21.12	66.60
0.48	29.68	25.13	55.29	4.64	14.54	19.18	74.47
0.43	29.32	26.14	55.88	6.16	14.16	20.32	76.20
0.36	27.03	25.59	52.98	11.53	10.56	22.07	75.05

and that of the shank muscles 26.61%, hence the ratio being 2.8:1; in *R. rugosa*, they are 76.60% and 23.41%, respectively, the ratio being 3.3:1. Compared with the ratios in *Bufo* and *R. catesbeiana*, the ratio for *R. rugosa* is intermediate between *Bufo* and *R. catesbeiana*, whereas the ratio in *Rhacophorus* is somewhat smaller than that in *Bufo*.

Secondly, the totals of muscles related to each of the hip, knee, and ankle joints are as follows: 73.39%, 74.69%, and 26.61%, respectively, in *Rhacophorus*; and 76.60%, 75.78%, and 23.40%, respectively, in *R. rugosa*. The values of *R. rugosa* are approximate to those of *R. catesbeiana* (78.12%, 73.99%, 21.86%). By contrast, *Rhacophorus* resembles *Bufo* in muscles of the hip and ankle joints, though it approximates *R. catesbeiana* in those of the knee joint.

Thirdly, five aspects, in which remarkable differences were seen between *Bufo* and *R. catesbeiana*, were examined in *Rhacophorus* and *R. rugosa* (see the 1st, 9th, 10th, 12th, and 13th columns of Table 6). In *Rhacophorus*, the percentage of the muscles acting on the hip joint and lying deeply in the thigh (15.53%) is closer to that of *R. catesbeiana* (15.90%) than to *Bufo* (21.30%). Also, the value of the muscles related to the hip and knee joints and lying on the posterior side of the thigh (25.59%) is approximate to *R. catesbeiana* (25.13%), whereas that of the muscles acting on these joints and lying on the anterior side of the thigh (27.03%) is intermediate between those of *R. catesbeiana* (29.68 %) and *Bufo* (26.13%). Furthermore, the percentages of the muscles related to the knee and ankle joints and lying on both the anterior and posterior sides of the shank (11.51% and 10.56%, respectively) are closer to those of *Bufo* (8.29% and 12.84%) than to *R. catesbeiana* (4.64% and 14.54%).

In *R. rugosa*, the conditions of the five aspects somewhat resemble those of *R. catesbeiana*. The percentages are shown in the above five columns of Table 6.

As mentioned above, the results of comparisons of the muscles of *Rhacophorus arboreus* and *R. rugosa* with those of *Bufo bufo japonicus* and *R. catesbeiana* indicate that the two species of the genus *Rana* have a hindlimb musculature similar to each other. On the other hand, *Rhacophorus* stands isolated from both *Bufo* and *R. catesbeiana* in the hindlimb musculature, because it is intermediate between *Bufo* and *R. catesbeiana*. *Rhacophorus* somewhat resembles the latter in the muscles of the thigh, but in the shank it amplifies still more the features of *Bufo*.

Discussion and Conclusions

In anurans, all of the hip, knee, and ankle joints are flexed in the normal resting posture. Jumping is begun from this squatting posture by a strong extension of these three jojnts. Muscle actions that may cause these extensions is no more than a surmise. However, as far as the results of the anatomy and relative weight analysis indicate, it would seem probable that the following three muscle groups act mainly for these movements: (1) muscles lying on the posterior side of the thigh and related to the hip and knee joints (*Rana catesbeiana* 25.13%, *Bufo bufo japonicus* 18.13%), (2) those lying on the anterior side of the thigh and related to the same joints (*R. c.* 29.68%, *B. b.* 26.13%), and (3) those lying on the posterior side of the shank and related to the ankle joint (*R. c.* 14.54%, *B. b.* 12.84%). In other words, the fundamental mechanism of jumping in anurans are presumed to be a simultaneous action of (1) two-joint muscles acting for hip extension–knee flexion and hip flexion–knee extension, and (2) those acting for knee flexion–ankle extension, at the three joints of the hindlimb.

On the other hand, the mechanism of walk differs somewhat from that of jumping. BARCLAY (1946) explained the amphibian walking movement from a kinetic point of view, in which he stressed that the walking of toads mainly depended on the propulsion by the hindlimbs. The body is first lifted by the limbs and then the walking posture follows. Therefore the maintenance of this sprawled posture is at first very important. This posture, in contrast to that of resting, needs moderate extension of the hip, knee, and ankle joints. Then a further gentle extension of these three joints will take place for the subsequent propulsive movement. In these movements, the adductor muscles will act to prevent the flexion at the hip joint. Furthermore, the extenosr muscles will also act for extension of the hip and knee joints. The fact that one-joint muscles lying deeply in the hip joint region are remarkably large in *Bufo* (*Bufo* 21.30%, *R. catesbeiana* 15.90%) and that the extensor muscles in the hip and knee joint region are large as well (*Bufo* 52.72%, *R. catesbeiana* 59.46%) seems to be consistent with the above supposition.

Thus, *Bufo bufo japonicus*, the walker, is characterized by the large values of one-joint adductor muscles acting chiefly on the hip joint and of extensor muscles acting on the hip and knee joints, though the latter value is smaller than that of *R. catesbeiana*, the jumper. The relative weight of muscles lying on the anterior side of the shank and related to the ankle joint, is different to some extent between the walker and jumper (*Bufo* 8.29%; *R. catesbeiana* 4.64%). These muscles act for the extension of the knee joint and for the fixation of the ankle joint.

Finally, the three muscle groups mentioned before, whose actions are thought to be important for jumping, will be examined in *Rhacophorus arboreus*, the climber. The percentage of muscles lying on the posterior side of the thigh and acting on the hip and knee joints is close to that of the jumper, while that of muscles on the anterior side of the thigh is intermediate between the jumper and walker. Further, the value of muscles lying on the posterior side of the shank and related to the ankle joint is closer to that of the walker. Although *Rhacophorus* may generally be regarded as a jumper, it is evident that it has a mode of locomotion considerably different from that type, and this fact is reflected to some extent in the above data. An examination of the hindlimb muscles in *Rhacophorus* other than the above three muscle groups, shows that the percentage of muscles lying on the anterior side of the shank and acting on the ankle joint (11.51%) is particularly large as compared with those of the jumpers and walkers (4.64% and 8.29 %, respectively). These data may possibly be related to the life habit of *Rhacophorus*, i.e. living in trees and climbing on the leaves and trunks with well-developed suckers.

Quantitative examinations of the hindlimb musculature in relation to locomotor patterns in the four species of Japanese anurans revealed that the differences in locomotor pattern, such as jumping, walking, and climbing, corresponded with the weight composition of the muscle groups. To summarize the results, in the jumpers the two-joint extensor muscles acting on the hip, knee, and ankle joints are developed in accordance with jumping, whereas in the walker the hindlimb musculature is essentially similar to that of the jumping type, with the exception of the remarkable development of one-joint adductor muscles in the thigh and of the flexor muscles acting on the ankle. Furthermore, the arboreal climber basically resembles the jumpers in its musculature, but the flexor muscles of the ankle joint are much more developed in the former.

There has been no valid theory on the origin and evolutionary process of locomotor specialization in anurans as yet, but it is doubtless that jumping is the essential element of the anuran locomotion. GANS and PARSONS (1966), in reviewing the previous opinions, considered that the riparian origin of jumping is the most probable, but they did not refer to the subsequent modifications of this jumping movement. If jumping is presumed as the most fundamental of the anuran locomotor patterns, the walking movement seen in *Bufo* should be a secondary modification, because, on the one hand, there is no essential difference in the number and kinds of muscles between *Rana* and *Bufo*, and on the other hand, the musculature of *Bufo* is quite different from that of walking urodeles (NOBLE, 1922) which are regarded as more primitive than the anurans.

The differentiation of locomotor patterns seems to be reflected upon the quantitative features presented above. *Rhacophorus* has been regarded as a close relative of *Rana* on the basis of the comparative myology (NOBLE, 1922; DUNLAP, 1960), but clear differences were found between them in the relative weights, which suggest the arboreal adaptation of the former.

In pursuing the phylogenetic problems from the viewpoint of the aspects of the hindlimb musculature, more appropriate conclusions may be drawn by combining such quantitative properties of each muscle as presented here with the qualitative ones and osteological characters hitherto reported.

Acknowledgements

The author wishes to express his heartfelt gratitude to Dr. Motoö TASUMI of the Department of Zoology, Faculty of Science, Kyoto University, for his continuous leadership and advice under which this study was carried out. He also wishes to extend his appreciation to Dr. Hidemi ISHIDA of the Laboratory of Physical Anthropology of the same Department for his valuable advice and encouragement, and to Mr. Hiromi

URABE of the same Department who kindly offered the author useful materials. Particular appreciation is extended to Dr. George R. ZUG of the United States National Museum who read an early draft of the manuscript and provided useful critiques for its improvement.

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