

Anuran Locomotion: Structure and Function. I. Preliminary Observations on Relation between Jumping and Osteometrics of Appendicular and Postaxial Skeleton

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The jumping abilities of *Bufo marinus*, *Bufo terrestris*, *Hyla crucifer* and *Rana clamitans* were determined by averaging the distances jumped in two trials, each of five successive jumps. The smallest absolute and relative jumping abilities were possessed by *Bufo*, the greatest absolute jumping ability by *Rana*, and the greatest relative jumping ability by *Hyla*. Each frog jumped was skeletonized in order to test the correlation of jumping ability and osteological characteristics.

Approximately 30 measurements taken of the postaxial and appendicular skeleton were converted into a series of proportions to reflect functional complexes. The proportions, in the main, possess low variability and, thus, high stability within each genus. By associating jumping abilities with proportions, several morphological and functional trends are disclosed. Notably, strong jumpers share a rectangular presacral platform, short forelimbs, large forefeet, short scapulae, long hindlimbs, and tibiofibula longer than femur.

ANURAN systematics is highly dependent upon the diversity of the locomotor apparatus. This dependence is particularly apparent at the familial level. In their recent systematic study, Kluge and Farris (1968) used six character sets, and three of these sets were derived from the locomotor apparatus. Similarly, Griffiths (1963) considered three character sets as basic for the definition of anuran families; two of these were from the locomotor apparatus. Inger (1967) used ten character sets. Of the five sets taken from adult morphology, four are related to locomotion. Characters from the locomotor apparatus are not excluded from use in the low levels of classification, for such characters as limb proportions appear commonly in specific and generic keys.

Constant use of these characters in classification has brought about an assumed reliability that has yet to be tested, consequently I have begun a long term investigation into the relationship between locomotion and the morphology of the anuran locomotor apparatus. The knowledge of a character's function allows critical evaluation of its importance in an animal's biology, thereby

establishing its probable importance in phylogeny. Character convergences and parallelisms are more evident when the relationship between function and structure is known.

The purpose of this preliminary report is to describe my research methods, to test the association of osteology and locomotion at an elementary level, and to establish a framework for my continuing investigation. This article presents an osteometric analysis of representatives of the three major locomotor types, i.e., arboreal, aquatic-terrestrial, and terrestrial, in the United States, in order to determine if there is any correlation between jumping ability and the osteology of the locomotor apparatus. The species selected to represent the three locomotor types are *Hyla crucifer*, *Rana clamitans*, and *Bufo terrestris*, respectively. *Bufo marinus* is utilized to compare the jumping data with published data.

MATERIALS AND METHODS

Jumping Tests.—All jumping tests were performed in the laboratory at an ambient temperature of 22–24 C. The jumping arena

was a 1½ m × 6 m open-ended corridor. The sides of the arena were 1 m high. No frogs were able to jump over the sides. The floor of the arena was covered with several layers of wrapping paper.

The technique used in the standard jumping trial was to blot the frog's venter in non-toxic ink, set it down on the paper at one end of the arena, and have it make a series of jumps. Usually the frogs jumped without being touched, for contact stimulation was kept to a minimum. After jumping, the frog was placed in a moist container, and the lengths of five consecutive jumps were measured. Soon after, a second trial was performed. The average of the 10 jumps was used as an estimator of jumping ability. Each jump was measured in millimeters from the posterior end of one ink blotch to the posterior end of the succeeding one. The first jump of each trial was normally excluded, because it tended to be made from an abnormal posture. After jumping, the frog was anesthetized in a chlorotone solution, and the sex, snout-vent length (SV), and weight were recorded. Small frogs were preserved and later cleared and stained (Zug and Crombie, 1970). Large frogs were skinned, eviscerated, and skeletonized by dermestid beetles.

Osteological Characters.—Dry skeletons were measured to the nearest tenth of a millimeter with a Helios dial caliper. The cleared and stained specimens were measured through an ocular micrometer, and these mensural units converted to millimeters. The mensural methods described below were selected to achieve the greatest equivalence of the measurements between the two types of skeletal specimens. Only the osseous part of each skeletal element was measured. All measurements are straight line measurements and taken on the dextral side unless the element of that side was missing or damaged.

Vertebrae widths (VW): The distance between the lateral edges of the left and right diapophyses of each vertebra. The measurement is recorded from the dorsal surface and is perpendicular to the anteroposterior body axis.

Vertebrae lengths (VL): The distance between the anterior and posterior edges of a centrum of each articulated vertebra. The measurement is recorded from the ventral surface of the vertebra along the anteroposterior body axis and only from the visible part of each centrum.

Vertebral column length (VCL): Sum of the individual vertebra lengths.

Sacral diapophysis breadth (SD): The distance between the anterior and posterior edges of the diapophysis. Two measurements recorded from the dorsal surface of the diapophysis and parallel to the longitudinal axis of the centrum. The proximal measurement was made adjacent to the centrum, distal one at the greatest breadth of iliosacral articular surface.

Urostyle length (UL): The distance from the anterior edge of neural ridge to the posterior edge of the urostyle. The measurement is recorded from the dorsal surface along the anteroposterior body axis. This measurement is not the total length of the urostyle.

Scapula length (SL): The distance along the midline of the scapula from its distal to proximal end.

Clavicle length (CLL): The distance from the proximal end to the distal end of the clavicle. The proximal end of the clavicle is considered to be its point of contact with the coracoid at the glenoid fossa.

Coracoid length (COL): The distance along the midline of the coracoid from its distal to proximal edge.

Clavicle-coracoid separation (CCS): The distance parallel to the anteroposterior body axis from anterodistal corner of the coracoid to the posterior edge of the clavicle. This measurement and the two preceding ones are taken on the ventral surface of the elements.

Humerus length (HUL), radioulna length (RUL), metacarpal length (MCL), proximal phalanx length (FPL), penultimate phalanx (FPP), ultimate phalanx length (FUP): The distance from the proximal to the distal articular surface of each element of the forelimb. Humerus length is taken along the ventral surface, whereas all others from the dorsal surface. The metacarpal and phalangeal lengths are those of the third digit.

Forelimb length (FL): Sum of the lengths of the individual limb elements.

Forefoot length (FFT): Sum of the lengths of the metacarpal and phalanges.

Pelvic girdle length (PGL): Distance from the distal end of the ischium to the anterodistal end of the ilium.

Ilium length (IL): Distance from anterodistal end of the ilium to the anterodorsal edge of the acetabulum.

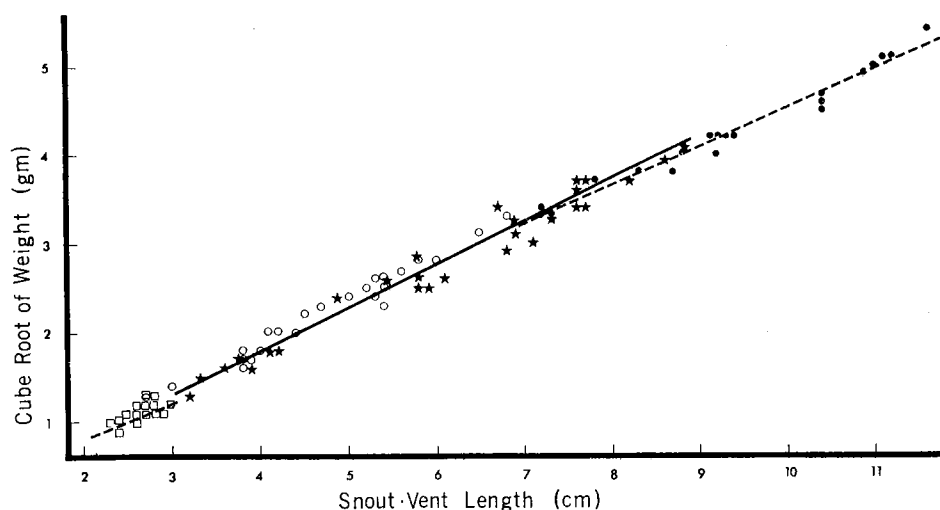


Fig. 1. The relation of snout-vent length to the cube root of weight in four species of anurans. Solid circles, *Bufo marinus*; open circles, *Bufo terrestris*; squares, *Hyla crucifer*; stars, *Rana clamitans*. The regression equations for the lines of the four species are $Y = 0.437 X + 0.150$, $Y = 0.529 X - 0.317$, $Y = 0.403 X + 0.041$, and $Y = 0.474 X - 0.102$, respectively. The regression line for *B. terrestris* is not plotted.

Femur length (FEL), tibiofibula length (TFL), calcaneum length (CAL), metatarsal length (MTL), proximal phalanx length (HPL), postproximal phalanx length (HPOP), penultimate phalanx length (HPP), ultimate phalanx length (HUP): The distance from the proximal to the distal articular surface of each element of the hindlimb. All measurements were taken along the dorsal surface of the hindlimb. The metatarsal and phalangeal lengths are those of the fourth digit.

Hindlimb length (HL): Sum of the lengths of the individual elements.

Hindfoot length (HFT): Sum of the lengths of the metatarsals and phalanges.

Data Analysis.—Two statistical methods are utilized to compare the osteometric characters with one another and with the jumping data: 1) Least-squares regression analysis and linear correlation coefficient; 2) Ratios and their standard deviations and standard error.

Specimens Examined.—All specimens used in this study are in the reptile and amphibian collection of the National Museum of Natural History (USNM). *Bufo marinus* 192818, 192820 (14), 192822 (6); *Bufo terrestris* 192326 (6), 192819 (2), 192823, 192824 (3), 192825-27, 192828 (6), 192829, 192830 (3), 192831 (2); *Hyla crucifer* 192343 (2), 192378, 192423 (12), 192424 (12), 192836 (8); *Rana clamitans*

192521, 192832 (4), 192833 (6), 192834 (5), 192835 (2), 192837 (3), 192838 (2), 192839 (2), 192840.

RESULTS AND DISCUSSION

Jumping Data.—Data on absolute or relative jumping distance of anuran species tend to be non-existent or anecdotal. Only four investigations (Wermel, 1934; Rand, 1952; Stokely and Berberian, 1953; Rand and Rand, 1966) provide real data on jumping ability. Wermel documented the jumping ability of 10 species of European anurans, in order to test his hypotheses on the effect of functional divergence of fore- and hindlimbs on simple heterotypy. Rand studied the jumping ability and endurance of 7 species of North American anurans. Stokely and Berberian analyzed the jumps of 101 *Rana pipiens* and concluded that the jumping performance is not noticeably affected by a change in the relative proportion of hindlimb segments. Rand and Rand showed that the relationship between jumping distance and snout-vent length or hindlimb length is linear in *Bufo marinus*.

The regression of snout-vent length to the cube root of weight is plotted in Fig. 1 for four species. The two parameters are linearly related, i.e., the linear correlation coefficient is 0.99 for *Bufo marinus*, 0.93 for *Bufo ter-*

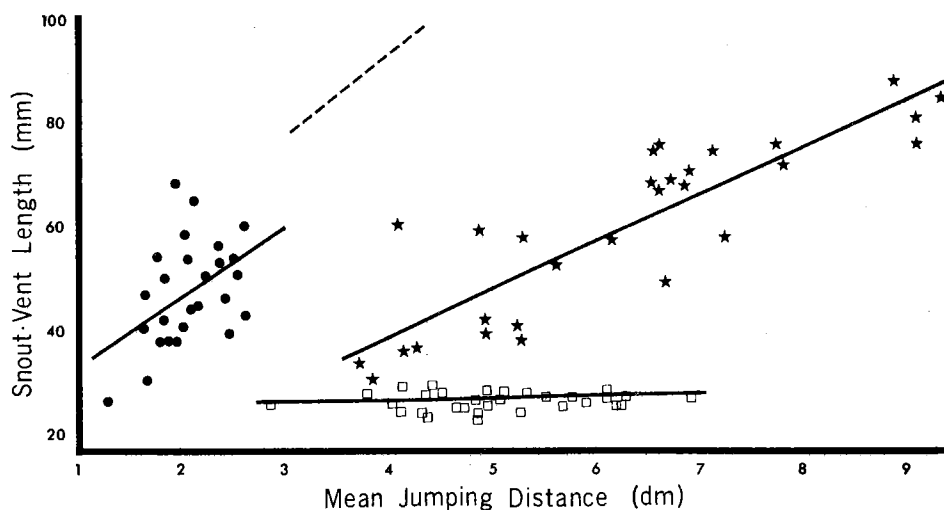


Fig. 2. The relation of mean jumping distance to snout-vent length in four species of anurans. Circles, *B. terrestris*; squares, *H. crucifer*; stars, *R. clamitans*. Only the regression line (broken line) for *B. terrestris* is plotted and not the actual points.

restris, 0.72 for *Hyla crucifer*, and 0.99 for *Rana clamitans*. The slopes and y-intercepts of the regression lines (see the legend of Fig. 1) are similar in all four species and appear to match those of Rand and Rand (1966). Similar slopes and y-intercepts would be expected between *B. terrestris* and *B. terrestris*, since they possess similar body proportions. Although the different body proportions of *Bufo*, *Hyla*, and *Rana* might be expected to produce different linear regres-

sion lines, my data indicate that most anurans will possess similar regression equations. Mosimann's data (1958) on chelonian carapace length and volume produced similar results, and leads to the hypothesis that members of an animal group sharing a single habitus will possess similar linear regression equations for longitudinal body lengths to body weight or volume.

The linear relationships of snout-vent length to either mean or maximum jumping

TABLE 1. THE SLOPES, INTERCEPTS, CORRELATION COEFFICIENTS, AND SAMPLE SIZES FOR THE RELATION BETWEEN JUMPING DISTANCE AND SNOUT-VENT LENGTH IN FOUR SPECIES OF ANURANS. X, JUMPING DISTANCE (MM), MEAN OR MAXIMUM; Y, SNOUT-VENT LENGTH (MM).

		X = bY	+ a	X = bX	+ a	Corr. Coef.	Sample Size
<i>B. terrestris</i>	Mean	2.354	183.629	0.151	32.781	0.596	21
	Max.	2.783	208.107	0.160	18.704	0.668	
<i>B. terrestris</i>	Mean	1.628	131.874	0.131	20.220	0.462	27
	Max.	2.006	153.695	0.094	24.420	0.433	
<i>H. crucifer</i>	Mean	8.383	285.107	0.003	25.121	0.153	35
	Max.	15.363	202.264	0.005	23.252	0.287	
<i>R. clamitans</i>	Mean	8.238	132.501	0.090	3.362	0.863	29
	Max.	9.527	173.478	0.075	4.446	0.843	

distance is not as precise (Fig. 2 and Table 1). *R. clamitans* has the highest linear correlation between jumping distance and body size. The high linear correlation of the *R. clamitans* sample is, at least in part, related to the size range of the animals tested, for a decrease in correlation is associated with a decrease in size range, i.e., the *H. crucifer* sample has a size range of 6 mm and the lowest correlation coefficient. The jumping ability of a species might also affect the correlation. If such an assumption is correct, there are two possible alternative effects: 1) Weak jumpers display a sequence of jumps of subequal length similar to the nearly equivalent stride lengths of a walking gait, because equivalent muscular effort tends to be applied to each jump in order to obtain maximum progress with a minimum of muscular fatigue. 2) Weak jumpers exhibit a sequence of jumps of variable length, since their jumping is not a means of rapid escape and there has been no selection for the same muscular effort with each jump. The first hypothesis implies that for the jumping series of weak jumpers, individuals of a similar size have equivalent means or maximum jumping distances. The second hypothesis implies that similar sized individuals of weak jumping species will have different means or maximum jumping distances, owing to the sampling of a highly variable sequence of events. The converse interpretations of these hypotheses would apply to the strong jumpers. My present data do not permit the acceptance or rejection of either hypothesis. *R. clamitans* jumped the greatest absolute distance and had the highest linear correlation. Yet smaller specimens of *H. crucifer* jumped farther than larger *R. clamitans* and have a low correlation coefficient. In contrast, *B. marinus* is a stronger jumper than *B. terrestris* and also has a higher correlation coefficient than *B. terrestris*. My data on maximum jumping distance agree with the previous remarks concerning the mean distances. The data of Rand and Rand (1966) on *B. marinus* appear to deviate less from a regression line than any of my jump data and thus support the first hypothesis. Although Rand and Rand (1966: Fig. 2) plotted hindlimb length against jumping distances, comparison of their results with mine is possible, because of the small dispersion of points from their regression line for hindlimb to snout-vent length. Unfortunately, they did not provide a correlation coefficient for the

values plotted in their Fig. 2, but I suspect it would be greater than mine for *B. marinus*. Their correlation appears to be greater, because they tested a greater size range of specimens, and the specimens with snout-vent lengths less than 70 mm have less scatter. Those greater than 70 mm appear to be dispersed similar to my data. Since Rand and Rand tested their toads on a natural substrate and our data are equivalent, my tests on a hard floor yield an accurate estimate of natural jumping ability.

Rand's (1952) earlier investigation on several North American anurans provides another data set for proving the accuracy and naturalness of my data. Rand's *Hyla crucifer* specimens (SV length, 24-28 mm) jumped between 62-552 mm on a smooth floor and 300-375 mm on a forest floor. His *Rana clamitans* (SV length, 69-75 mm) jumped from 400-830 mm on a grassy lawn. The data from both species are comparable to mine. The *Rana pipiens* used by Stokely and Berberian (1953) had mean jumps of 241 mm and were obviously slipping with each jump. The paper used in my test arena provided sufficient traction and slipping was rarely observed. Any jumps in which slipping occurred were not recorded.

Rand's (1952) average length of jump (AJL) is the mean of the total of the greatest leaps in a series of jumps of a series of specimens of a single species. I have not used this value for two reasons: 1) Jumping distance is a function of body size, and the ALJ value includes individuals of different body size in the same sample, and 2) ALJ estimates the maximum jumping ability of anurans, not their average jumping ability. The latter point is particularly evident in Rand's data. Rand calculated the mean jumping distance for 10 consecutive jumps of each specimen in each species. The ALJ value exceeds these means in all specimens of *Hyla crucifer*, *Rana clamitans*, and *Rana pipiens*. One specimen each in *Acris crepitans*, *Bufo fowleri* and *Rana catesbeiana* has a mean greater than the ALJ. The ALJ is, therefore, not an accurate estimate of the jumping ability of an individual or species.

Wermel's (1934) data are not directly comparable to those presented herein. His average jumping distances for similar sized specimens of *Bufo*, *Hyla*, and *Rana* are approximately half the mean jumping distances of my specimens. I attribute this difference to his use of an average of 50 more or less con-

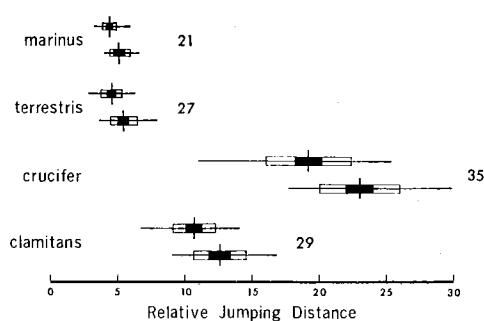


Fig. 3. A comparison of the ranges, means, standard deviations, and two standard errors of the relative jumping distance of four anuran species. The relative jumping distance equals the jumping distance divided by snout-vent length. The top diagram of each pair is calculated from the mean jumping distance, the bottom one from the maximum jumping distance. The number to the right of the diagrams is the sample size.

secutive jumps. I have observed in sequences of 25 jumps that the frogs begin to tire and do not jump as far.

The relative mean jumping distance (Fig. 3) is calculated by dividing the mean jumping distance by the snout-vent length. The three genera have significantly different relative jumping distances. *Hyla crucifer* has a relative jumping ability four times that of *Bufo marinus* and *B. terrestris* and two times that of *Rana clamitans*. The relative maximum jumping distances are also significantly dif-

ferent between the genera, even though the specimens compared are the same length. Within a genus they usually are not significantly different from the relative mean jumping distances. As the relative jumping ability increases, the difference between the mean and maximum jumping distances also increases.

Osteometric Data.—Similar animals of different size will jump similar distances (Hill, 1950). The previous jumping data do not negate this generalization, rather the data indicate that *Bufo* and *Rana* are not similar animals. Shape, not size, is affecting jumping ability, and the following discussion will deal with body proportions, which reflect differences in shape, and not with absolute size.

Of the specimens examined, all the *Hyla crucifer* had nine vertebrae anterior to the urostyle. The specimens of *Bufo terrestris* and *Rana clamitans* possessed eight or nine vertebrae. Only one *B. terrestris* had eight as a result of fusion of the first and second presacral vertebrae. The fusion did not affect the relative length of the column. The VCL/SV of this specimen was identical to the mean for the species (Table 2). Four specimens of *Rana clamitans* had fusion of adjacent vertebrae, i.e., three with fusion of eight presacral and sacral and one with fusion of third and fourth presacrals. The VCL/SV's were .30, .31, and .32 with no apparent affect on relative length of column.

The relative vertebral column length

TABLE 2. INTRAMEMBERAL PROPORTIONS OF THE VERTEBRAL COLUMN AND THE FORELIMB. ABBREVIATIONS OF THE DIFFERENT SKELETAL ELEMENTS LISTED IN THE TEXT; CV, COEFFICIENT OF VARIATION; N, SAMPLE SIZE; SD, STANDARD DEVIATION; \bar{x} , MEAN.

	<i>Bufo terrestris</i> (N 23)				<i>Hyla crucifer</i> (N 27)				<i>Rana clamitans</i> (N 23)			
	\bar{x}	Range	SD	CV	\bar{x}	Range	SD	CV	\bar{x}	Range	SD	CV
VCL/SV	.33	.29-.38	.02	6.8	.34	.29-.37	.02	5.4	.32	.29-.38	.02	5.5
UL/VCL	.89	.71-1.05	.07	8.0	.82	.72-.97	.06	6.8	.90	.71-1.11	.11	11.8
SD Exp.	1.61	1.23-2.14	.24	15.1	1.20	.95-1.50	.14	11.8	.83	.62-1.08	.11	13.6
FL/SV	.68	.60-.76	.04	5.7	.59	.54-.67	.03	4.7	.59	.51-.71	.05	8.1
HUL/FL	.43	.41-.47	.01	3.1	.39	.37-.42	.01	2.6	.41	.38-.45	.01	3.5
RUL/FL	.27	.25-.31	.01	3.7	.24	.21-.26	.01	4.0	.23	.21-.26	.02	6.6
MCL/FL	.13	.12-.14	.01	4.1	.14	.13-.15	.01	3.8	.14	.12-.16	.01	6.9
FFT/FL	.29	.27-.33	.01	4.9	.36	.34-.39	.01	3.6	.35	.32-.37	.01	3.8
RUL/HUL	.62	.55-.74	.04	5.6	.61	.54-.67	.03	5.2	.57	.50-.69	.05	9.3
SL/CLL	1.57	1.37-1.73	.10	6.2	1.14	.96-1.32	.09	8.0	1.15	.87-1.34	.11	9.7
CLL/COL	1.19	1.04-1.38	.09	7.6	1.22	1.05-1.39	.08	6.9	1.05	.92-1.25	.10	9.7
SL/FL	.25	.22-.28	.01	5.7	.19	.17-.21	.01	4.7	.20	.16-.24	.02	8.1
CLL/FL	.16	.14-.18	.01	5.7	.16	.14-.18	.01	6.1	.18	.16-.20	.01	6.8

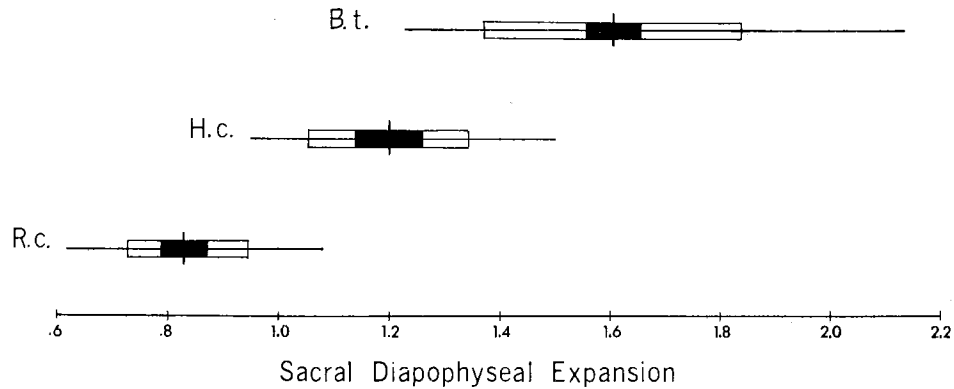


Fig. 4. A statistical comparison of relative sacral diapophyseal expansion in *Bufo terrestris* (B. t.), *Hyla crucifer* (H. c.) and *Rana clamitans* (R. c.). Sample sizes listed in Table 2.

(Table 2) is one-third of the snout-vent length in all three species. The relative length of the urostyle (UL/VCL in Table 2) is also nearly one-third of the snout-vent length. Although the UL/VCL of *Hyla crucifer* might be considered significantly different (no overlap of means ± 2 standard errors) from the other two species, the range for *H. crucifer* is included in that of each of the other species. The amount of the sacral diapophyseal expansion is expressed as the area of a sacral diapophysis, i.e., (one half width of sacral vertebra times one half the sum of the proximal and distal sacral diapophyseal breadth) \div (one half width of the third presacral vertebra times the proximal sacral diapophyseal breadth). This proportion attempts to illustrate both the relative length and dilation of a sacral diapophysis with a single value. Although it does show that the surface areas of the sacral diapophyses are significantly different (Fig. 4), the proportion does not show how they differ in shape. *Bufo terrestris* has the largest amount of distal dilation and a sacral diapophyseal width slightly shorter than that of the third vertebra. In *Hyla crucifer*, the dilation is nearly equal to that of *B. terrestris* but with the sacral diapophyseal width appreciably less than that of the third vertebra. The dilation of the sacral diapophysis of *Rana clamitans* is small or absent; the width of the sacral diapophyseal is similar to that of *H. crucifer*. The same proportions could have been obtained in different ways: longer sacral diapophysis relative to the third vertebral one with less dilation for both *terrestris* and *crucifer* or shorter sacral diapophysis

with more dilation for *clamitans*. Perhaps it is sufficient to show dilation by the ratio of proximal to distal sacral diapophyseal breadths.

The proportional widths of the vertebrae (VW) are shown in Fig. 5. Similar width trends of the column are seen in the three species. The third vertebra is the widest and the succeeding presacral vertebrae gradually narrow. In *B. terrestris*, the narrowing of vertebrae width is progressive with an abrupt enlargement of the sacral vertebrae. In *H. crucifer* and *R. clamitans*, the last four presacral and the sacral vertebrae retain the same relative size and form a rectangular platform, in contrast to an hour glass-shaped platform in *B. terrestris*. I suspect that the shape of the platform is related to specific arrangements of the axial musculature.

B. terrestris has the greatest relative length of the forelimb (FL/SV); *H. crucifer* and *R. clamitans* are similar (Table 2). The last two species are significantly different in relative forelimb length from *terrestris*. The difference in relative forelimb length is reflected in all three segments (Table 2 & Fig. 6). The proportional lengths of humerus (HUL/FL) and radioulna (RUL/FL) are greatest in *terrestris* whereas the proportional length of the forefoot (FFT/FL) is smallest in *terrestris*. The difference in foot length results from differences in phalangeal length, since the proportional lengths of the metacarpals (MCL/FL) are similar in all three species. The relationship between the humerus and radioulna (RUL/HUL) is similar in all three species.

Two of the pectoral girdle proportions

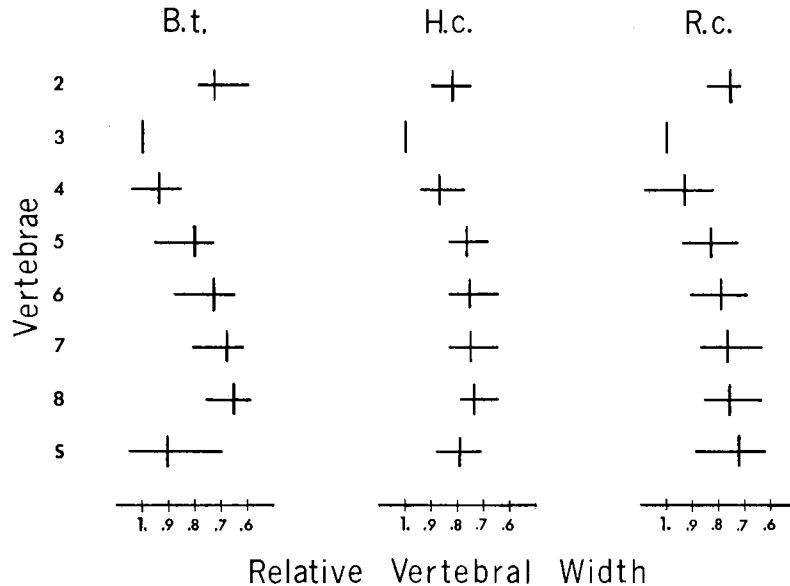


Fig. 5. The ranges and means of the relative vertebral widths for vertebrae with diapophyses in *B. terrestris* (B. t.), *H. crucifer* (H. c.) and *R. clamitans* (R. c.). Each vertebral width is divided by the width of the third vertebra to obtain the relative width.

are shared by *clamitans* and *crucifer*. The scapuloclavicular index (SL/CLL) and the relative length of scapula (SL/FL) of *crucifer* and *clamitans* are significantly different from those of *terrestris* (Table 2 & Fig. 6), and demonstrate that the scapula is distinctly longer in *terrestris*. The relative clavicular lengths (CLL/FL) are identical for *terrestris* and *crucifer*, and *clamitans* is significantly different or nearly so (Table 2). In this case, the proportionately longer forelimb of *ter-*

restris appears to be hidden by the proportionate difference in clavicular length. The coracoclavicular index (CLL/COL) of *terrestris* and *crucifer* are also similar and significantly different from *clamitans*. The coracoclavicular index provides a rough estimate of the angle (secant) between the two bones, i.e., approximately 18°, 33°, and 35° for *clamitans*, *terrestris*, and *crucifer*. The secant tends to be an overestimate of the coracoclavicular angle, because a line drawn

TABLE 3. INTRAMEMBRAL PROPORTIONS OF THE HINDLIMB AND PELVIC GIRDLE. ABBREVIATIONS OF THE DIFFERENT SKELETAL ELEMENTS LISTED IN THE TEXT; OTHER ABBREVIATIONS AND SAMPLE SIZES ARE THE SAME AS THOSE OF TABLE 2.

	<i>Bufo terrestris</i>				<i>Hyla crucifer</i>				<i>Rana clamitans</i>			
	\bar{x}	range	SD	CV	\bar{x}	range	SD	CV	\bar{x}	range	SD	CV
HL/SV	1.26	1.13-1.44	.07	5.7	1.52	1.40-1.75	.08	5.0	1.57	1.44-1.78	.08	5.4
FEL/HL	.28	.26-.29	.01	2.6	.26	.25-.28	.01	1.9	.26	.24-.27	.01	3.2
TFL/HL	.28	.26-.29	.01	2.8	.30	.29-.31	.01	1.5	.29	.28-.30	.01	2.4
CAL/HL	.15	.14-.16	.01	3.5	.18	.17-.19	.00	2.1	.14	.14-.15	.01	3.7
MTL/HL	.13	.12-.14	.01	3.9	.11	.10-.12	.00	3.4	.12	.11-.13	.00	3.6
HFT/HL	.29	.27-.31	.01	3.6	.25	.24-.26	.01	2.5	.31	.29-.33	.01	2.9
TFL/FEL	.99	.93-1.05	.03	2.8	1.14	1.07-1.19	.03	2.7	1.13	1.06-1.27	.06	5.1
CAL/TFL	.56	.50-.59	.03	5.3	.60	.57-.64	.02	2.8	.49	.45-.53	.02	5.1
PGL/HL	.33	.25-.38	.03	8.4	.25	.23-.26	.01	4.1	.24	.22-.27	.02	8.6
IL/PGL	.78	.73-.81	.02	2.7	.80	.76-.84	.02	2.2	.78	.66-.90	.05	6.8

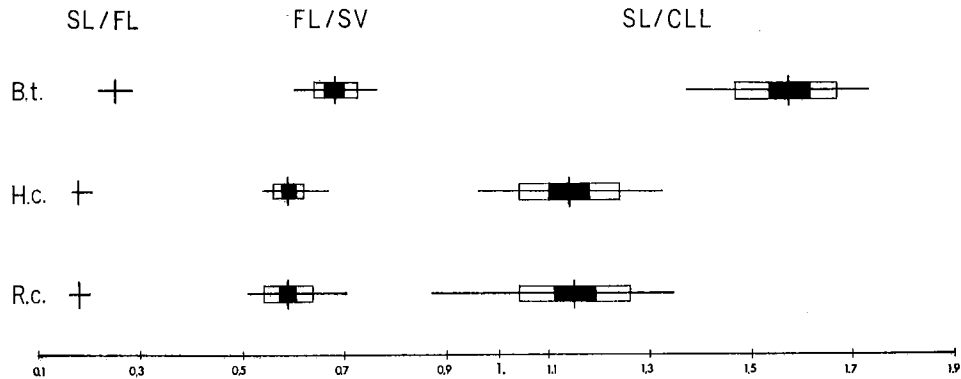


Fig. 6. A statistical comparison of the relative scapula (SL/FL) and forelimb (FL/SV) lengths and the scapuloclavicular indices (SL/CLL) of *B. terrestris* (B. t.), *H. crucifer* (H. c.) and *R. clamitans* (R. c.). Sample sizes listed in Table 2.

parallel to the longitudinal body axis from the medial end of the clavicle rarely intercepts the medial end of the coracoid. Nonetheless this estimate provides a uniform method for angle determination in all genera possessing clavicles and coracoids. Both *crucifer* and *terrestris* have arciferal girdles and large angles; *clamitans* is firmisternal.

The relative hindlimb lengths (HL/SV) are greater in *H. crucifer* and *R. clamitans* than in *B. terrestris* (Table 3 & Fig. 7) and significantly different from the latter species. However, the proportional contribution of the femur (FEL/HL) and the tibiofibula (TFL/HL) are nearly identical in the three species. The relative lengths of these two segments, FEL/SV and TFL/SV (not included in Table 3, but can be calculated by multiplying the appropriate intramembral

proportion and the relative hindlimb length), will also be greater for the former pair of species. The calcaneal (CAL/HL) and hind-foot (HFT/HL) proportional contributions to hindlimb length are similar, yet form distinct groups which are clearly significantly different. The proportional length of the calcaneum is the lowest in *terrestris* and *clamitans* and proportional length of hind-foot lowest in *crucifer*. In terms of relative length (CAL/SV and HFT/SV), *crucifer* possesses a calcaneum 1 1/3 to 1 1/2 times larger than the other species and *clamitans* has a larger hindfoot than either *terrestris* or *crucifer*. The increase in foot length appears to result from longer phalanges, because the metatarsal proportion (MTL/HL) is similar in all three (Table 3). Even though *crucifer* and *clamitans* have similar relative hindlimb

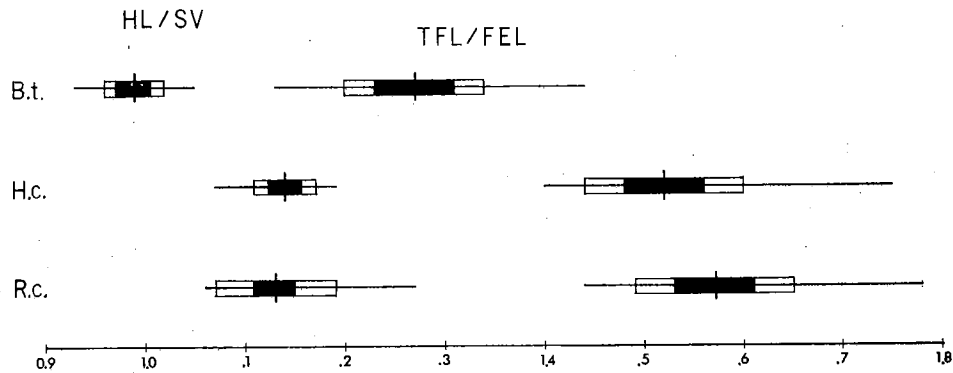


Fig. 7. A statistical comparison of the relative hindlimb lengths (HL/SV) and crural indices (TFL/FEL) of *B. terrestris* (B. t.), *H. crucifer* (H. c.) and *R. clamitans* (R. c.). Sample sizes listed in Table 2.

TABLE 4. INTERMEMBRAL PROPORTIONS OF VERTEBRAL COLUMN AND APPENDICULAR SKELETON AND THE RELATION BETWEEN MEAN JUMPING DISTANCE AND VARIOUS HINDLIMB UNITS. ABBREVIATIONS OF THE DIFFERENT SKELETAL ELEMENTS LISTED IN THE TEXT; OTHER ABBREVIATIONS AND SAMPLE SIZES ARE THE SAME AS THOSE OF TABLE 2.

	<i>Bufo terrestris</i>				<i>Hyla crucifer</i>				<i>Rana clamitans</i>			
	\bar{x}	range	SD	CV	\bar{x}	range	SD	CV	\bar{x}	range	SD	CV
VCL/PGL	.80	.65-1.24	.12	14.8	.90	.78-1.04	.05	5.8	.83	.71-.93	.06	7.5
UL/PGL	.70	.62-.88	.05	7.7	.74	.68-.81	.04	4.8	.75	.64-.83	.06	7.4
FL/HL	.54	.52-.57	.01	2.1	.39	.37-.41	.01	3.2	.38	.35-.42	.02	4.7
FFT/HFT	.54	.51-.59	.02	3.6	.56	.52-.61	.02	4.3	.43	.39-.50	.02	5.3
JUMP/HL	3.6	2.3 - 5.1	0.7	20.3	12.6	7.2 -16.6	2.2	17.7	6.7	4.6 - 8.3	1.0	14.5
JUMP/TFL	12.8	8.5 -18.2	2.4	18.6	41.7	23.8 -54.8	7.5	18.0	23.1	15.3 -27.6	3.3	14.1
JUMP/CAL	23.2	15.1 -33.9	5.0	21.7	69.9	41.8 -89.2	11.6	16.6	47.0	33.7 -57.6	7.1	15.2

lengths, they have obtained these lengths by separate adaptive pathways. The calcaneum has lengthened proportionately in *crucifer* and the hindfoot in *clamitans*.

In *terrestris*, the femur and tibiofibula (TFL/FEL) are of the same length, and in *crucifer* and *clamitans* the tibiofibula is longer than the femur (Table 3 & Fig. 7). The calcaneotibiofibular index (CAL/TFL) shows a different relationship among the three species. Although all three have similar tibiofibular proportions (TFL/HL), and *crucifer* differs from the other two in the calcaneal proportion (CAL/HL). The calcaneotibiofibular index is significantly different in the three, but the indices of *terrestris* and *crucifer* are closer to one another than either is to that of *clamitans*.

The relative length of the pelvic girdle (PGL/HL) shows the effect of the relatively longer legs in *crucifer* and *clamitans* (Table 3). The girdle length relative to body length (PGL/SV = PGL/HL times HL/SV) does not have the girdles significantly different in length, i.e., .41, .38, .37 for *terrestris*, *crucifer*, and *clamitans*. The ilial contribution (IL/PGL) to the girdle length is similar in the three species.

The relations of vertebral column and the urostyle to the pelvic girdle (VCL/PGL and UL/PGL) are the same in all three species (Table 4). The pelvic girdle is slightly more than a third of the body length. The fore- to hindlimb index (FL/HL) illustrates the disproportionate shortening of the forelimbs in *crucifer* and *clamitans*. This index is affected by the relatively longer hindlimbs of these two species; nonetheless, their forelimbs are still proportionately shorter than those of *terrestris*. Both *crucifer* and *ter-*

restris possess similar fore- to hindfoot indices.

The samples of frogs used in this investigation were not restricted to a specific size class. In fact, I attempted to include all sizes and both sexes. The *B. terrestris* sample included nearly equal numbers of males and females and ranged from 27.3 to 67.9 mm in snout-vent length. The *H. crucifer* sample included a predominance of males and ranged from 23.4 to 29.9 mm, viz., all taken from breeding choruses. The *R. clamitans* sample included a predominance of females and ranged from 31.5 to 88.2 mm.

Despite the variability of size and sex composition of the samples, most of the proportions show a low degree of variation (see coefficients of variation columns in Tables 2, 3, and 4). The smallest amount of variation is found in the intramembral proportions of the fore and hindlimb, particularly those proportions involving the pro- and epipodial segments of forelimb and the pro-, epi-, and mesopodial segments of the hindlimb. The low variation in these segments and their apparent isometric growth suggest that they are the critical segments for anuran locomotor behavior. Weight increases approximately to the cube of the linear dimensions, therefore allometry of the limb segments might be expected in order to increase the muscular power for jumping in larger animals. However, their isometry stresses the importance of maintenance of constant leverage relationship of adjacent segments for effective jumping.

Locomotor Behavior and Osteometric Proportions: Speculations.—The data presented in the preceding sections are preliminary. Nonetheless, certain trends are indicated

TABLE 5. SELECTED OSTEOLOGICAL CHARACTERS ILLUSTRATING DIFFERENCES BETWEEN THE THREE ANURAN SPECIES STUDIED. THE NUMERICAL VALUES ARE THE MEANS OF PROPORTIONS LISTED IN TABLES 2, 3, AND 4.

	<i>B.</i> <i>terrestris</i>	<i>H.</i> <i>crucifer</i>	<i>R.</i> <i>clamitans</i>
Presacral Platform	hour-glass	rectangular	rectangular
SD Expansion	1.61	1.20	.83
FL/SV	.68	.59	.59
FFT/FL	.29	.36	.35
Pectoral Girdle	arciferal	arciferal	firmisternal
SL/CCL	1.57	1.14	1.15
CCL/CO	1.19	1.22	1.05
SL/FL	.25	.19	.20
HL/SV	1.26	1.52	1.57
CAL/HL	.15	.18	.14
HFT/HL	.29	.25	.31
TFL/FEL	.99	1.14	1.13
CAL/TFL	.56	.60	.49

and will be discussed here to provide a direction for future investigations. Since these data are based on only one species of each of the three genera, the next step is to make an intrageneric comparison in order to determine the constancy of the proportions. I also plan to compare species with the same locomotor habits but from unrelated genera to determine whether the constancy is associated with specific locomotor habits, i.e., terrestrial, arboreal, etc. By investigating the mechanics of jumping and landing, the effect of different proportions on the locomotor mechanisms may be disclosed.

In Table 5, thirteen osteological characters are presented that differentiate the three species from one another or a pair of species from the other one. How do these characters relate to jumping ability? As shown earlier, *H. crucifer* possesses the greatest relative jumping ability, whereas *R. clamitans* the greatest absolute jumping ability. However, for my purpose of speculation, I will simply consider *Hyla* and *Rana* strong jumpers and *Bufo* a weak jumper.

The strong jumpers share a rectangular presacral platform. This platform may support a complex musculature which permits a more controlled flexion and extension of

the trunk during locomotion. I suspect that is important in the preparation for leaping, particularly during a sequence of rapid jumping. Strong jumpers tend to land with a splat. The forelimbs absorb the initial landing force but the chest and abdominal area still meet the ground forcefully. Such a landing leaves the hindlimbs, which have flexed upon touchdown, directly lateral to the body. There is an overt flexing immediately after landing and the limbs are drawn against the body. Perhaps the epaxial musculature is partly responsible for establishing the limb posture. Certainly *Bufo* lands with more grace and maintains a functional limb posture throughout landing.

Strong jumpers share similar proportions for FL/SV, FFT/FL, SL/CCL, SL/FL, HL/SV, and TFL/FEL. The first four of these proportions are probably also associated with landing. The relative shorter forelimbs in the strong jumpers may reflect the need for shorter but heavier segments to absorb the shock and not break upon landing. The proportionately bigger feet of strong jumpers may spread the touch-down force over a larger area thus reducing the weight per unit area. The shorter scapula (SL/CCL and SL/FL) of the strong jumper may be an adaptation to reduce the amount of landing shock transmitted from the girdle to the vertebral column. The strong jumpers have proportionately longer hindlimbs and longer tibiofibula (TFL/HL). Since the hindlimbs are the propulsive agent in jumping, these two characters must be responsible for the greater jumping ability.

Bufo and *Hyla* share arciferal pectoral girdles and coracoclavicle indices (CCL/CO). Differences in jumping ability and landing force prevent, at this time, any functional correlation with structure. The same lack of association exists for the characters (CAL/HL, HFT/FEL) shared by *Bufo* and *Rana*. Both genera, however, share terrestrial habits, so shorter calcanea and larger feet may be associated with locomotion on land. Certainly the larger foot of *Rana* is also associated with its swimming ability. The degree of sacral diapophyseal expansion and calcaneotibiofibular index (CAL/TFL) are different in the three genera. The trend in diapophyseal expansion is inversely related to the trend in absolute jumping distance. The trend of the indices does not follow any locomotor trend.

CONCLUSIONS

Both the absolute and relative jumping ability of the three generic representatives of anurans are different. *Bufo* is a weak jumper, whereas *Hyla* and *Rana* are strong jumpers. Although *Rana* can attain the greatest absolute jumping distance, *Hyla* has the greatest relative jumping ability. The occurrence of equivalent relative jumping distances in the two unequal-sized species of *Bufo* suggest that species within a single genus may possess nearly identical locomotor patterns. The previous facts do not negate Hill's (1950) generalization but emphasize the difference in body proportions of these three anurans.

The conversion of the osteometric data to proportions removes the variation resulting from size differences and permits direct comparison of different size species. The proportional data have low variability and clearly indicate osteological differences between the three genera. No specific hypotheses were made on the association between jumping ability and osteology owing to the preliminary nature of the data. A few speculations on such associations were suggested, but these comments were meant to direct further investigations and to show that the current direction of research had predictive potential for classification and morphological studies.

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