AMERICAN MUSEUM
Novitates
PUBLISHED BY
THE AMERICAN MUSEUM
OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET
NEW YORK, N.Y. 10024 U.S.A.
NUMBER 2615 APRIL 12, 1977

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Number 2615, p. 1-10, figs. 1, 2, table 1 April 12, 1977

Bodily Proportions of Uruguayan Myomorph Rodents

LYNNE M. MILLER[1] AND SYDNEY ANDERSON[2]

ABSTRACT

Sixteen external and skeletal measurements in 10 species of cricetine rodents from Uruguay have been compared.

Differences in measurements and proportions are sufficient to distinguish the species that are most alike, *Oryzomys delticola* from *O. flavescens*, *Akodon azarae* from *A. kempi*, *Holochilus brasiliensis* from *H. magnus*, and *Scapteromys* from *H. brasiliensis*.

Proportional differences reveal possible functional adaptations. *Oryzomys delticola* and *O. flavescens* are climbers: their tails and front and hind feet are long and both front and hind claws are short. *A. azarae*, *A. kempi*, and *Oxymycterus* are fossorial: their tails are short, their hind claws are long, and their scapula is long proportional to both humerus and ulna lengths. *Calomys* and *Reithrodon* are saltatorial: their hind feet are relatively long. *Scapteromys* is a good swimmer and climber: its hind feet are long, its front feet are small, and its front claws are long. Proportional differences among the segments of the hind limb are less variable among the 10 cricetines than are other proportions.

INTRODUCTION

Most studies of the proportions of limb segments and other bodily parts of Recent mammals have focused on certain specializations, such as for arboreal or bipedal locomotion in the primates (Erikson, 1963; Oxnard, 1963; Schultz, 1973) or for fast cursorial locomotion in perissodactyls or carnivores (Hildebrand, 1959). Some more general summaries that relate to mammalian proportions and their functions are those of Dagg (1973), Gambarian (1974), and Gray (1968) on locomotion; Duerst (1926) on methods of measurement; and Howell (1944) on speed. Limb proportions in bipedal marsupials have been compared with those of bipedal rodents and primates by Lessertisseur (1971). There are comparatively few studies of proportions in rodents. Among these are comparisons of pelvis, scapula, femur, and humerus in four European myomorphs by Hecht (1971); proportions and allometry in the gray squirrel by Thorington (1972); proportions of pelvic limb segments in more than 40 species of mammals, including five rodents (none myomorphs) by Kotak and Manzy (1973); and ontogenetic changes in proportions in three rodents (one muroid, two heteromyids) by Van de Graaf (1973).

Many data are scattered in taxonomic

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 ISSN 0003-0082 / Price 95 cents

descriptions and monographs on a few dimensions such as the standard lengths of the total animal, the tail, the hind foot, and the ear. In no case, to our knowledge, has anyone gone much beyond that and, at the same time, dealt with other skeletal proportions in a group not outstandingly specialized.

The muroid rodents comprise a group that is diverse in living species (about 1050 of some 4000 living species of mammals), but which in skeletal features, other than the highly specialized gnawing dentition and accompanying cranial features that characterize all rodents, are usually regarded as relatively unspecialized among mammals.

Hershkovitz (1962, 1965), more than any other author, has commented upon some proportions in external measurements and their possible significance in South American myomorphs. Our work includes these external dimensions and extends to some internal skeletal dimensions.

Studying specialization and variation within and between populations is fundamental to systematics. Variation may be related to geographic place, habitat, sex, age, food habits, and other factors. An adequate sample representing a population should be available for studying variation. An expedition in 1962 from the American Museum of Natural History to Uruguay provided a large series of rodents. Dr. Alfredo Langguth has provided some additional specimens recently. General ecological data, sex, breeding condition, and some external measurements were recorded in the field. Sizes and proportions of measurements were compared among 10 of the 13 species of cricetine rodents found in Uruguay.

The problem of identification and the possible occurrence of functional adaptations are two aspects of variations that were examined.

ACKNOWLEDGMENTS

The National Science Foundation supported the work of the first author as an Undergraduate Research Participant from Wellesley College in the summer of 1971 at the American Museum of Natural History. This was one of four studies participated in.

The United States Army Medical Research and Development Command supported the expedition in Uruguay in 1962 (Grant no. DA-MD-49-193-63-G82).

Dr. Alfredo Langguth (then a student at the University in Montevideo) worked with the expedition in the field in 1962 and 1963, was consulted by us in 1971 (while in New York on a Guggenheim Fellowship), and sent us some needed specimens in 1975.

Dr. Edwin Hudson voluntarily rechecked our original computations, made some additional measurements and computations, and prepared figure 1.

Drs. Langguth, Hudson, and Guy G. Musser provided helpful suggestions on the manuscript.

We are grateful to these persons and agencies (and to the taxpayers who provided the funds for the agencies).

MATERIALS AND METHODS

Data were obtained from dry study skins and prepared skeletons of adult male cricetines. The species and the catalogue numbers of specimens studied in the American Museum of Natural History follow:

Oryzomys delticola (205931, 205935, 205964, 205967, and 205975)
Oryzomys flavescens (205986, 205988, 205995, 206001, and 206004)
Akodon azarae (206046, 206072, 206073, 206081, and 206085)
Akodon kempi (206111, 206126, 206141, 206148, and 206158)
Oxymycterus rutilans (206181, 206186, 206189, 206196, and 206198)
Scapteromys tumidus (206230, 206244, 206259, 206263, 206275, and 206511)
Calomys laucha (206332, 206334, 206335, 206338, and 206337)
Reithrodon auritus (206347, 206352, 206354, 206355, and 206356)
Holochilus brasiliensis (206362, 206375, 206377, 206382, and 206390)
Holochilus magnus (206381 and 206393)

Names are as in Ximenez, Langguth, and Praderi (1972).

Specimens of greatest total length and greatest weight were selected for each species.

Males only were studied to eliminate the influence of sexual dimorphism, except that a few measurements of females were used where there were few or no data available for males. The occurrence of data from females is noted where used. From specimen labels were taken total length (measurement 1 of table 1 and figs. 1 and 2), tail length (2), weight (4), and length of the hind foot (5); length of head and body (3) was derived by subtracting 2 from 1; length of claw of third digit of pes (6) and of third digit of manus (8), and length of manus (7) were measured with dial calipers to nearest tenth of a millimeter. Claw lengths were taken on

TABLE 1
Measurements (means) in Millimeters (except Weight is in Grams) of Samples of 10 Cricetine Rodents from Uruguay[a]

		O.d.	*O.f.*	*A.a.*	*A.k.*	*O.r.*	*S.t.*	*C.l.*	*R.p.*	*H.b.*	*H.m.*
1.	total	241.5	207.6	178.2	178.0	217.4	311.6	122.5	248.6	397.8	476.0
		(4)	(5)	(4)	(4)	(5)	(5)	(5)	(5)	(5)	(2)
2.	tail	131.8	114.0	74.8	82.8	85.8	137.8	53.0	106.8	198.8	239.5
		(4)	(5)	(4)	(4)	(5)	(5)	(5)	(5)	(5)	(2)
3.	head and body	109.8	91.6	103.5	95.2	131.6	173.8	69.5	141.8	199.0	236.5
		(4)	(5)	(4)	(4)	(5)	(5)	(5)	(5)	(5)	(2)
4.	weight	35.1	21.2	29.3	26.4	73.2	139.1	12.6	86.8	220.8	369.1
		(2)	(4)	(4)	(4)	(5)	(4)	(5)	(4)	(0)	(0)
5.	hind foot	24.3	23.8	19.5	20.2	24.5	36.3	16.0	32.2	51.4	60.5
		(4)	(5)	(4)	(4)	(5)	(5)	(5)	(5)	(5)	(2)
6.	hind foot claw	1.35	1.36	1.72	1.90	2.94	3.42	0.94	2.14	3.58	4.85
		(4)	(5)	(4)	(4)	(5)	(5)	(5)	(5)	(5)	(2)
7.	front foot	7.55	7.08	5.70	5.92	7.44	9.88	4.82	7.22	11.94	13.95
		(4)	(5)	(4)	(4)	(5)	(5)	(5)	(5)	(5)	(2)
8.	front foot claw	0.78	0.46	1.12	1.22	3.16	3.44	0.50	1.04	1.74	2.40
		(4)	(5)	(4)	(4)	(5)	(5)	(5)	(5)	(5)	(2)
9.	skull	26.73	23.94	25.28	24.87	33.95	39.08	20.34	36.16	40.34	45.12
		(5)	(5)	(5)	(4)	(4)	(5)	(5)	(4)	(4)	(2)
10.	scapula	12.20	11.33	12.66	12.66	17.67	20.82	10.53	20.22	22.78	25.92
		(4)	(5)	(4)	(5)	(4)	(6)	(2)	(3)	(5)	(2)
11.	humerus	13.20	11.59	12.53	11.79	16.07	20.88	9.78	20.25	25.00	26.62
		(5)	(6)	(5)	(5)	(5)	(4)	(5)	(5)	(3)	(2)
12.	ulna	15.45	14.56	14.23	15.44	21.65	28.0	13.0	26.4	30.0	31.9
		(1)	(1)	(1)	(1)	(1)	(3♂,1♀)	(2)	(1)	(1)	(1♀)
13.	innominate	20.61	18.20	19.23	18.32	27.39	35.02	12.88	29.83	42.13	50.68
		(5)	(6)	(5)	(5)	(5)	(6)	(3)	(4)	(5)	(2)
14.	femur	19.57	17.43	17.18	15.85	23.73	31.74	12.81	28.97	39.20	43.82
		(5)	(6)	(5)	(4)	(5)	(5)	(5)	(5)	(5)	(2)
15.	tibio-fibula I	13.37	12.53	11.00	11.15	15.07	20.98	8.25	20.28	26.46	29.98
		(3)	(5)	(4)	(2)	(3)	(5)	(4)	(2)	(4)	(2)
16.	tibio-fibula II	23.16	21.42	18.08	19.41	26.44	35.9	14.4	34.5	41.3	46.8
		(1)	(1)	(1)	(1)	(1)	(4♂,1♀)	(2)	(0)	(1)	(1♀)

[a]Measurements are explained in text. Specimens and samples are also listed in text, initials only are used here and in figure 2. Where this is zero the value given is an estimate.

ventral surface. The entire length of the manus could not be measured owing to methods used in preparing the skin. The wire through the front feet was not placed consistently so that a posterior point could not be found that was distinct in each specimen. The measurement of the front foot was, therefore, taken in ventral view from the base of the fifth finger (an indentation can be felt) to the tip of the third finger, not including the claw.

Other dimensions (numbers 9 to 16 in table 1 and explained below) were measured to the nearest hundredth of a millimeter with Anderson's craniometer (1968) attached to a Wild stereomicroscope (a few measurements were later taken with dial calipers). Measurements are taken along one axis by aligning a baseline or reference line with the vertical line of the microscope cross-hair, aligning one of the two points of the measurement with the horizontal cross-hair, zeroing the counter, moving the stage until the second point of the measurement is aligned with the horizontal cross-hair, and recording the distance the stage has traveled.

Measurements made on the craniometer (refer to fig. 1) were: length of skull (9), distance from the anterior tip of nasal bones to the posterior margin of the occiput, baseline is midsagittal plane; length of scapula (10), distance from the tip of acromion to the posteriormost point on vertebral border, baseline is spine of scapula; length of humerus (11), greatest length, baseline through the outermost point of deltoid tuberosity and outermost point of lateral epicondyle; length of ulna (12), greatest length measured in lateral aspect, baseline through proximal and distal points on the side opposite the semilunar notch; length of innominate (13), distance from anteriormost point of crest of ilium to posteriormost point of ischium in lateral view, baseline through dorsalmost point of ischium and dorsalmost point of ilium; length of femur (14), greatest length, baseline through the outerpoint of third trochanter and the outerpoint of lateral condyle; length of tibiofibula I (15), distance from proximal point of tibia to distal notch of interosseous opening, baseline through proximal and distal points of interosseous opening; length of tibiofibula II (16), greatest length, same baseline as in 15.

Means were calculated for each dimension measured in each species (see table 1). It was not possible to measure the length of the ulna or total length of the tibiofibula for all species. These bones were broken when the skins were prepared. When the skeleton only was preserved, the ulna and tibiofibula could be measured. In a few cases (dimension 12 for five species and 16 for four species), specimens obtained later enabled us to fill gaps where data were absent at first. In three cases (dimension 16 for one species and 4 for two species), we had no direct measurement and have inserted estimates.

METHODS OF COMPARISONS

A ratio diagram was constructed to show proportional relationships between the samples of cricetines (see Simpson, Roe, and Lewontin [1960, p. 358]). All means in table 1 were converted to logarithms. An arbitrary value near the midpoint of the range among the species was chosen as the standard. For each dimension, the difference between the log (base 10) value of the standard and each of the other cricetines was calculated and plotted (see fig. 2). Measurements larger than those for the standard are represented on the graph as positive values; measurements smaller than those of the standard are represented as negative values. Samples with the same proportions as the standard will be represented by a series of points on a line parallel to that of the standard. Any two cricetines that have similar proportions will be represented by parallel lines (lines are not necessarily parallel to the standard).

To provide a basis for judging the magnitude of variation, the following are the coefficients of variation for the measurements of the 16 dimensions in *Oryzomys flavescens* (in numbered order as in table 1; external measurements rounded to integers, skeletal measurements rounded to two digits): 7, 9, 7, 5, 8, 21, 9, 33, 1.4, 3.6, 3.4, dimension 12 no data, 3.8, 4.3, and 4.5 (dimension 16 no data). To provide a rough basis for visual estimation of the significance of differences shown in figure 2, at the left are drawn boxes showing the magnitude of the range of plus and minus two standard errors of the

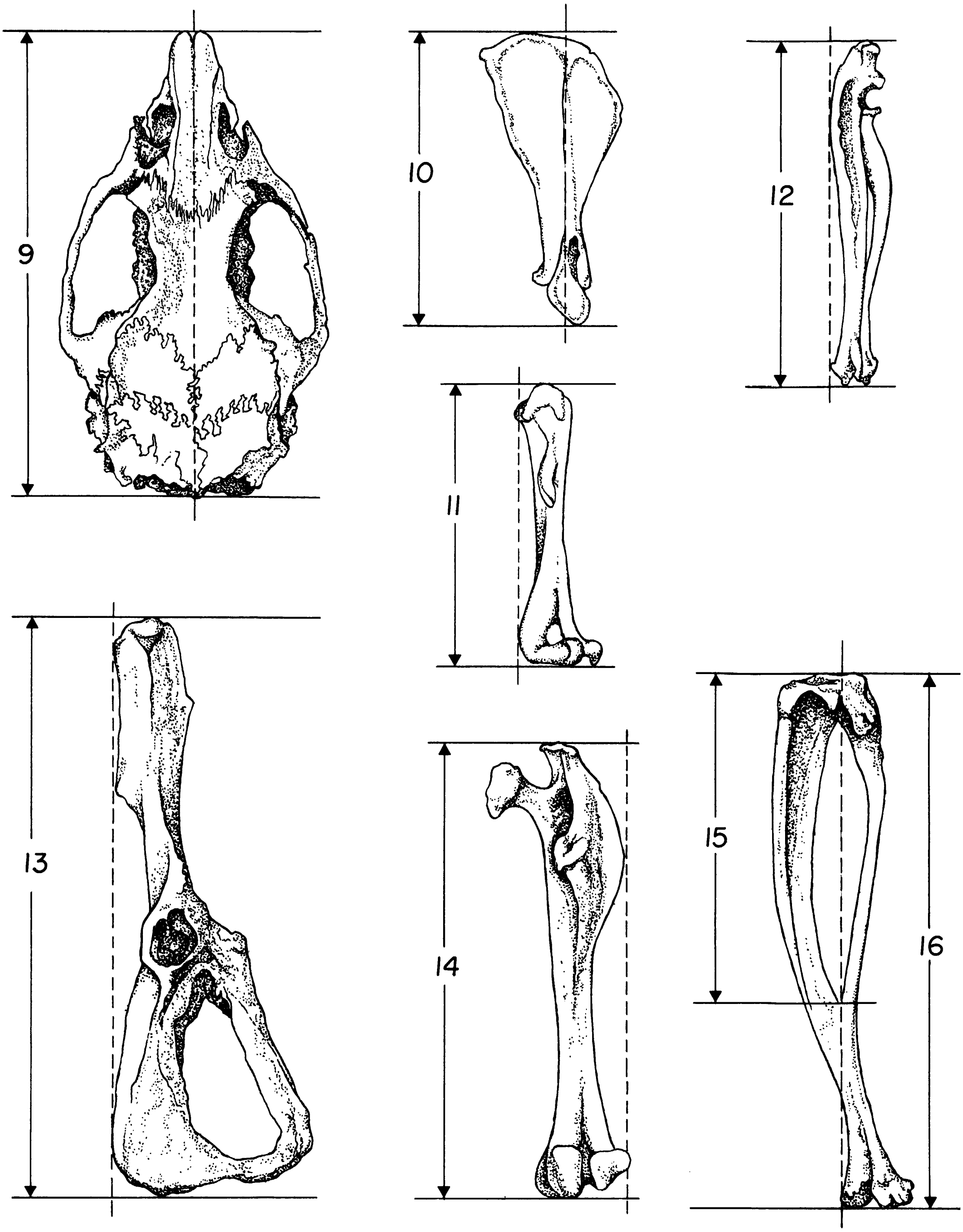

FIG. 1. Skeletal dimensions measured (explained in text).

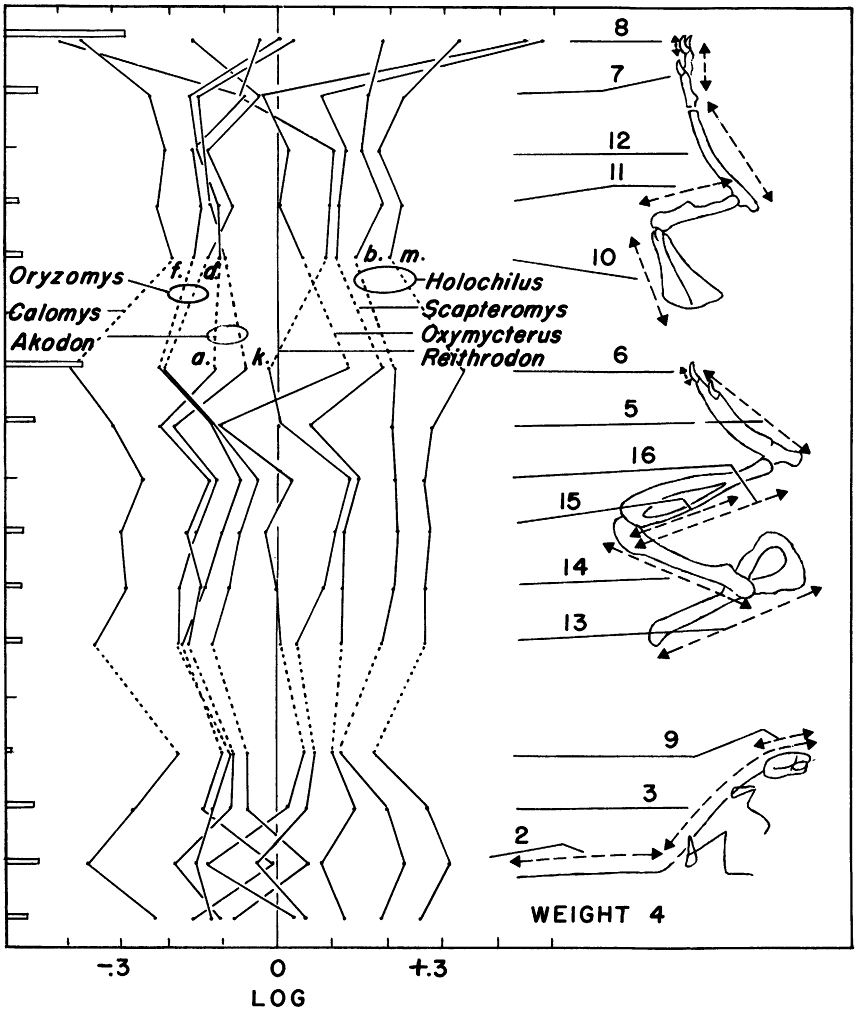

FIG. 2. Ratio diagram showing proportions of various external and skeletal dimensions (illustrated at the right) in ten species of cricetines. Numbers refer to the numbered list of dimensions in text. Boxes at the left indicate variability of measurements (see text).

mean of the sample of *Oryzomys flavescens*. If two species differ in a measurement by more than twice the range shown by the box for that measurement, then the difference probably is approaching significance at the 95 percent level.

Fifteen proportions were calculated for each species. These proportions seemed to express most general external and skeletal relationships. The ratio diagram shows, with a little study, which proportions are similar. The information in both the ratio diagram and our chart of calculated proportions is used to interpret differences between the samples.

IDENTIFICATION

First, the data are examined for characters that may be useful for distinguishing pairs of species. Other observable differences, such as pelage or shapes of structures, are not examined;

only the measured differences are here considered. By applying the means in table 1 it would be difficult, for example, to confuse *Calomys* with *Holochilus*. However, species within the same genus, or species from different genera with similar measurements, could be confused. We are seeking differences that can be used to distinguish between such species.

The differences between the means of samples of *Oryzomys delticola* and *O. flavescens* are significant at the 95 percent level (based on t-tests) for the following measurements: total length, tail length, head-body length, weight, front foot claw length, skull length, scapula length, humerus length, innominate length, and femur length. *Oryzomys delticola* is larger in all these dimensions. Not only size differences, but also proportions may help to distinguish between two species. The two species of *Oryzomys* differ significantly in the following proportions: The front foot claw length is a greater proportion of the length of the front foot in *O. delticola* than in *O. flavescens*. The scapula in *O. flavescens* is a greater percentage of the length of the humerus. The humerus is a greater proportion of the length of the ulna in *O. delticola*. Langguth (1963) discussed characters in which these two species of *Oryzomys* differ.

Samples of *Akodon kempi* are significantly different in size from the samples of *A. azarae* only in that *A. kempi* has a longer front foot. Three proportions are significantly different. *Akodon kempi* has a smaller ratio of humerus to ulna and larger ratios of scapula to humerus and tibiofibula I to femur than does *A. azarae*.

Holochilus magnus is significantly larger than *H. brasiliensis* in all measurements except for the front foot claw length. There are two significant differences in proportions. The front claw expressed as a proportion of the front foot length is greater in *H. magnus* and the proportion of the femur to innominate is greater in *H. brasiliensis*.

A large *Scapteromys* could be confused with a small *H. brasiliensis*. A determination of the proportion of tail length to head-body length, and front claw length to front foot length should separate them. In the *Holochilus*, tail and head-body length are equal. In *Scapteromys*, the tail is 79 percent the length of the head and body. The front foot claw of *Scapteromys* is 35 percent the length of the front foot, and of *Holochilus*, 15 percent the length of the front foot.

FUNCTIONAL ADAPTATIONS

For the second aspect of this study, the measurement data are related to knowledge of species habitat and behavior. The focus is on what kind of external and skeletal proportions are found among the primarily swimming or climbing or digging or jumping cricetine species studied.

General distribution and behavior of the 10 species follow:

Oryzomys delticola, a climbing rodent, is the common woodland mouse of Uruguay (Barlow, 1969, p. 10). It is found in dense and open woodland. Barlow reported (1969, p. 11) observing them climbing in trees and over rocks. The degree of specialization for climbing and the time spent climbing are not known.

Oryzomys flavescens. Barlow (1969, p. 14) found *O. flavescens* to frequent "stands of tall grass in marshes." Langguth (personal commun.) has observed *O. flavescens* climbing in tall grass. Hershkovitz (1962, p. 21) said that *Oryzomys* is not a digger. Langguth (personal commun.) considered both species of *Oryzomys* to be agile climbers.

Akodon azarae is found in a variety of habitats: open woodland, grassland, and dry places in marshes (Barlow, 1969, p. 18).

Akodon kempi is found in grasslands and wet habitats (Barlow, 1969, p. 22). Langguth (personal commun.) considered both species of *Akodon* to be potentially fossorial.

Oxymycterus rutilans. Barlow reported (1969, p. 24) that *O. rutilans* "occurs in wet meadows with stands of bunch grass (*Paspalum* sp.); tall grass adjacent to streams and rivers; and drier parts of marshy areas among clumps of pampas grass. . . ." *Oxymycterus rutilans* will not go to water unless as a means of self-defense (Hershkovitz, 1965, p. 106). Langguth (personal commun.) considered *O. rutilans* to be an efficient digger.

Scapteromys tumidus is found in marshy places (Barlow, 1969, p. 27). Massoia and Fornes

(1964) said that *Scapteromys* traps prey by rooting and digging. The long claws are used to dig for food and are helpful in climbing. Barlow (1969, p. 28) said that *Scapteromys* is an excellent swimmer and has agility in climbing.

Calomys laucha is found in open grasslands, rocky hillsides, and sometimes marshes and swamps. *Calomys* jumps or runs on the hind legs, and often stands on its hind toes. Barlow (1969, p. 34) said that *Calomys* often jumps on its hind legs somewhat as does *Dipodomys*.

Reithrodon auritus is the single cricetine studied here that occurs only in grassland (Barlow, 1969, p. 35). Barlow (1969, p. 36) noted that *Reithrodon* digs burrows in the soil or uses the burrows of other mammals. Langguth (personal commun.) said *Reithrodon* often jumps on its hind legs.

Holochilus brasiliensis is found in swamps, grasslands, and other moist unforested situations (Hershkovitz, 1955, p. 48).

Holochilus magnus has the same habitat as mentioned for *H. brasiliensis*. Both are more aquatic than *Scapteromys*.

When the ratio diagram is examined, it can be seen that there are differences in proportions between genera. Some of these differences could reflect adaptations to different activities or habitats. Proportional differences will now be considered:

Tail Length/Head and Body Length. Only in *Oryzomys* is the tail longer than the head and body. Possibly this is a specialization for arboreal life. The longer or shorter the tail than head and body length, the greater is the specialization (Hershkovitz, 1960, p. 527). In *Holochilus* the tail length is approximately equal to the head and body. Hershkovitz (1960, p. 526) said this is typical of most cricetines. He believed that there is a general tendency for the tail to become longer in arboreal and aquatic cricetines, however. The typical tail of *Holochilus*, thus, could indicate that *Holochilus* is not greatly aquatic. The shortest tail occurred in *Oxymycterus* (65% of head and body length). Some thermoregulatory and locomotor functions of rodent tails have been studied by Thorington (1966).

Foot Length/Head and Body Length. In *Oryzomys delticola* and *O. flavescens* the hind foot length is approximately 24 percent of the head-body length. Hershkovitz (1960, p. 527) wrote, "In oryzomyines the longer the hind foot than 21%, the more specialized it is. In other cricetines, the critical proportions may be a little more or less." In *Holochilus*, the hind foot is 25 percent of the head and body length. In *Reithrodon* the hind foot is 23 percent of the head and body length.

The species of *Oryzomys* have the largest front foot (7.3% of head and body length). *Reithrodon* has the smallest front foot (5% of head and body length).

Claw Length/Foot Length. *Oxymycterus* has significantly longer hind claws (12% of hind foot length) and longer front claws (43% of front foot length) than the other cricetines. *Scapteromys* also has a large front claw (35% of front foot length). The long claws seem adapted for digging. The arboreal cricetines, *Oryzomys*, have the shortest front and hind claws.

Skull/Head and Body Length. *Calomys* has a significantly longer skull in proportion to head-body length (29%) than the other cricetines studied, and as the size of the animals studied increases, the head tends to be proportionally smaller. In *Holochilus* the skull is 20 percent of the head-body length.

Forelimb Proportions. *Calomys*, *Oxymycterus*, and *Akodon kempi* each have a longer scapula than humerus. The scapula is a functional part of the front limb; the immovable pelvis does not have the same relation to the hind limb (Howell, 1926, p. 141). In *Oryzomys delticola* the humerus is 85 percent the length of the ulna. In *Oxymycterus* the humerus is 74 percent the length of the ulna. The two species of *Akodon* and *Oxymycterus* have longer scapulae in proportion to the ulna than do the two *Oryzomys*.

Pelvis and Hindlimb Proportions. The proportion of the innominate to head-body length of the 10 cricetines varies less between species than other calculated proportions. There is little variation among the proportions of the lower leg.

The differences in external and skeletal proportions among the seven genera are not great. In general, there are trends for arboreal cricetines to have a relatively longer tail and longer feet. Aquatic cricetines tend to have longer hind feet. Fossorial cricetines seem to have longer claws. Saltatorial cricetines seem to have short front feet. In proportions other than these, the genera are similar.

Langguth suggested that an examination of our data for allometry in various ratios would be of interest. He plotted some data for us. Some graphs do seem reasonably linear on a log-log graph (and hence allometric). Other pairs of measurements are either more variable or suggest curvilinear or clumped distributions. We decided not to pursue these questions, which might better be examined with a larger suite of species later.

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