A SYSTEMATIC STUDY OF THE RODENT GENUS *OTOTYLOMYS*

TIMOTHY E. LAWLOR

ABSTRACT.—The genus *Ototylomys* is revised taxonomically. One species and three subspecies are recognized. Generic and intraspecific relationships are analyzed and discussed. Size and color of venter seem related to altitude or differential gene flow between populations. Ecologic and zoogeographic factors influencing distribution of *Ototylomys* are discussed.

The rodent genus *Ototylomys* ranges from Tabasco, Mexico, southeastward to Costa Rica. The genus was originally defined by Merriam (1901: 561–2) on the basis of specimens from the Mexican states of Campeche and Yucatan.

In the course of this study, I examined 327 specimens. External measurements used were those recorded on specimen labels. Cranial measurements (in millimeters) were taken in the manner described by Hooper (1952: 9–11). Fourteen external and cranial measurements were recorded, but only three are discussed beyond, because the geographic trends observed in the latter were similar to those displayed by the other measurements not included in this report. Bacula were extracted from dried skins, cleared, stained, and preserved in the manner described by Anderson (1960: 185). Only those from adults were compared. Color of pelage was indexed by means of a Photovolt Photoelectric Reflection Meter, Model 610, on which measurements are recorded as a percentage of pure white. Sample sizes generally are small. Thus, sample means are assumed to adequately estimate population means.

GENERIC RELATIONSHIPS

Ototylomys is most closely related morphologically to *Tylomys*. Both are known in the vernacular as climbing rats and are endemic to Middle America. The two resemble each other in such features as flattened braincase, elongate skull, highly developed supraorbital ridges, large incisive foramina, and morphology of the accessory reproductive glands. Characters that serve to distinguish *Ototylomys* from *Tylomys* are: size smaller, both externally and cranially; tail uniformly brownish or blackish, without a white tip; ears much larger relative to length of body; auditory bullae larger, much more inflated, and without anterior protuberances; rostrum narrower, more elongate; interorbital region relatively narrower; zygomatic notch deep (contrasting with shallow or absent); coronoid process of lower jaw reduced, rami slenderer; dental topography more complex, the primary folds of molars less prominent owing to numerous accessory ridges and cusps; anterior cingulum, endostyles, and endostylids of molars well developed; baculum much longer and narrower relative to size of animal; dorsal face deeply concave proximally (instead of flat or slightly concave); distal end of baculum with small rounded head (rather than none); glans penis with baculum extending into a large internal crater at distal end of urethra; dorsal prostate and ampullary glands absent.

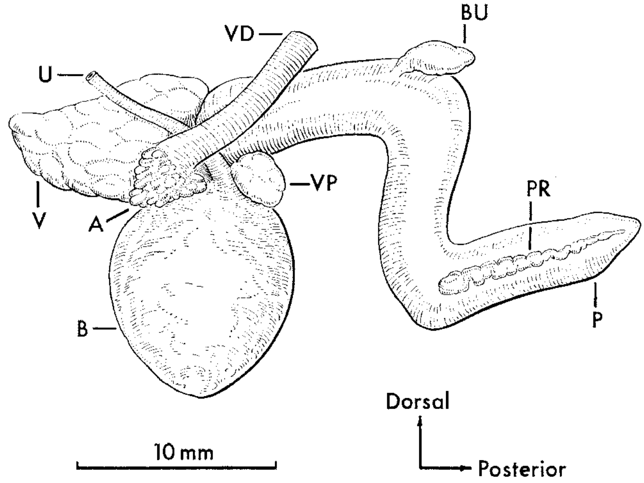

FIG. 1.—Male reproductive tract of *Ototylomys phyllotis*: A—ampullary gland; B—bladder; BU—bulbo-urethral gland; P—phallus; PR—preputial gland; V—vesicular gland; VD—vas deferens; VP—ventral prostate gland. Terminology after Arata (1964: 3–8, 34–38).

Ototylomys is allied also to *Neotoma*, as indicated by similarities of male phalli (Burt, 1960: 62; Hooper, 1960: 14, 19). The anatomy of the accessory reproductive glands in male *Ototylomys* (Fig. 1) also suggests a close relationship with *Neotoma*; a position between *Neotoma* and *Tylomys* is indicated (Table 1). Hooper and Musser (1964: 54–56) placed *Ototylomys* among the neotomine rodents, which also include *Neotoma, Nelsonia,* and *Tylomys.* The neotomine rodents were incorrectly called "neotomyines" by Hooper and Musser (*loc. cit.*). "Neotomyine" is properly derived from the South American genus *Neotomys*, not from *Neotoma.* Precedence for use of the name neotomine stems from the subfamilial name Neotominae (Merriam, 1894: 228).

TABLE 1.—*Comparison of accessory reproductive glands in males of* Ototylomys, Tylomys, *and* Neotoma floridana. *Data for* Tylomys *and* Neotoma *are taken from Arata (1964: 15–17, 36).*

Gland	*Neotoma*	*Ototylomys*	*Tylomys*
Ampullary	Large, diffuse, no ampulla	Large, diffuse, no ampulla	Minute diverticulum, ampulla present
Dorsal prostate	Absent	Absent	Present, filiform
Ventral prostate	Large, filiform	Small, compact	Small, compact
Vesicular	Absent	Present, large, lobate	Present, large, lumpy
Preputial	Absent	Present, tubular	?

TAXONOMY OF THE SPECIES

Three species, *O. phyllotis* Merriam (1901), *O. connectens* Sanborn (1935), and *O. brevirostris* Laurie (1953), currently are recognized.

O. brevirostris was based on two specimens (one damaged) taken at Kate's Lagoon, British Honduras (Laurie, 1953: 389). The species was defined as being similar to *O. phyllotis* in general appearance "but a little smaller," the skull having a much shorter rostrum and shorter palatine (incisive) foramina. Laurie (1953: 390) also described a subspecies, *O. b. affinis*, on the basis of five individuals from Chichen-Itza, Yucatan. It was characterized by being "a little larger" than, but otherwise resembling, *O. b. brevirostris.*

After examining two paratypes of *affinis* and considerable additional material from the Yucatan Peninsula, and after perusing the original descriptions of *brevirostris* and *affinis*, I am convinced that the reported differences between *brevirostris, affinis*, and *phyllotis* are attributable to age, and that *affinis* and *brevirostris* are synonymous with *O. phyllotis.* The two specimens of *O. b. affinis* closely resemble young adult *O. phyllotis* from the Yucatan region in all external and cranial dimensions and in features of dental topography, tooth wear, and pelage. Moreover, recent collections made in the vicinity of Chichen-Itza, Yucatan, and in British Honduras, have yielded only *O. phyllotis.*

Ototylomys connectens evidently represents a geographic variant of *phyllotis* and is at best only subspecifically distinct. Sanborn (1935: 82) described *connectens* from specimens collected in the highlands of Guatemala. They were characterized by large size and gray ventral coloration owing to plumbeous basal color of the hairs. Differences in external and cranial dimensions and color of pelage between highland and lowland populations of *Ototylomys* often is quite striking. However, detailed study of the mor-

TABLE 2.—*External and cranial measurements of adult* Ototylomys *(11 males, 10 females) from San Antonio, Nicaragua.*

Measurement	*N*	Mean	Range	95% C.L.	C.V.
Total length	19	309.32	284.00–337.00	± 7.32	4.91
Tail length	19	156.11	142.00–174.00	± 4.24	5.64
Length of hind foot	21	27.29	26.00– 28.00	± 0.25	2.06
Greatest length of skull	18	40.53	39.00– 41.80	± 0.40	1.97
Zygomatic breadth	21	19.48	18.45– 20.40	± 0.22	2.44
Interorbital breadth	21	6.25	5.85– 6.75	± 0.11	3.81
Breadth of supraorbital ridges	21	15.62	14.90– 16.50	± 0.21	2.90
Length of rostrum	21	14.80	13.75– 15.70	± 0.28	4.07
Breadth of rostrum	21	6.23	5.85– 6.80	± 0.11	3.91
Breadth of mesopterygoid fossa	21	2.63	2.25– 3.00	± 0.09	7.77
Length of maxillary toothrow	21	6.95	6.35– 7.30	± 0.10	3.22
Length of incisive foramen	21	7.55	6.90– 8.10	± 0.16	4.57
Palatal length	20	5.88	5.40– 6.10	± 0.10	3.57
Mastoidal breadth	18	14.76	14.30– 15.50	± 0.18	2.49

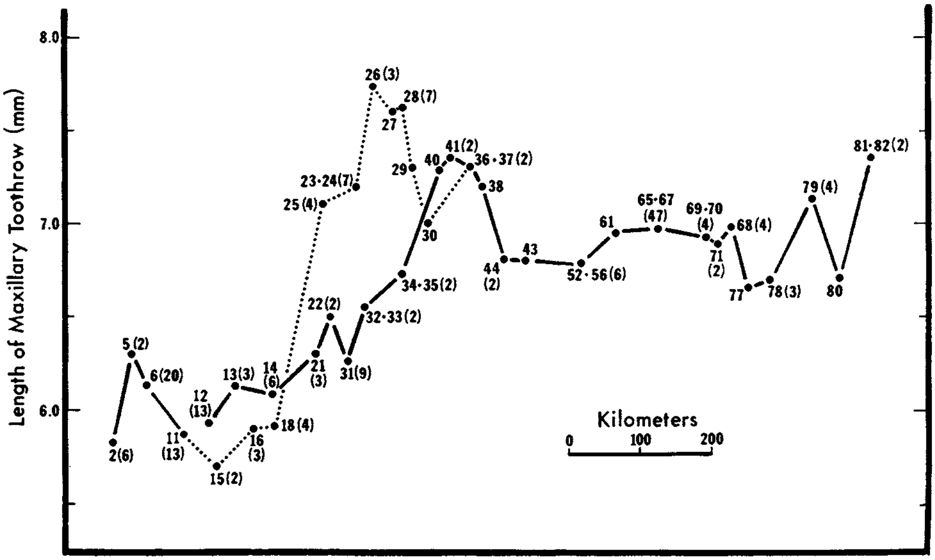

FIG. 2.—Geographic change of mean length of maxillary toothrow in *Ototylomys phyllotis*. Unbracketed numbers identify the localities discussed in text and presented in the list of specimens examined and in Fig. 5; bracketed numbers denote sample sizes (when greater than one). Solid and broken lines represent two transects of different areas; distances between different localities measure horizontally.

phology of individuals from these and geographically intermediate localities provides evidence for retention of only *phyllotis* as a valid species.

INTRASPECIFIC VARIATION

Nongeographic Variation

A sample of 11 adult males and 10 females from San Antonio, Nicaragua, was tested by use of Student's *t*-test for variation owing to secondary sexual characteristics. There were no significant differences between sexes ($P > 0.05$) in the 11 cranial characters examined. Consequently the sexes were treated jointly for purposes of studying geographic variation. Intralocality variation was examined in the same sample (Table 2).

An individual was considered adult if the dentine islands of the six major cusps of the M1 were connected by dentine troughs. These troughs and islands become larger with increased wear, and some individuals exhibit molars with enormous dentine islands and correspondingly broad troughs.

All individuals excepting juveniles with newly or incompletely erupted M3 were used for the analysis of geographic variation in length of maxillary toothrow (Fig. 2). No significant difference ($P > 0.05$) was noted for this character between adults and subadults in the sample from San Antonio, Nicaragua. Only adults were used in the treatments of other measurements.

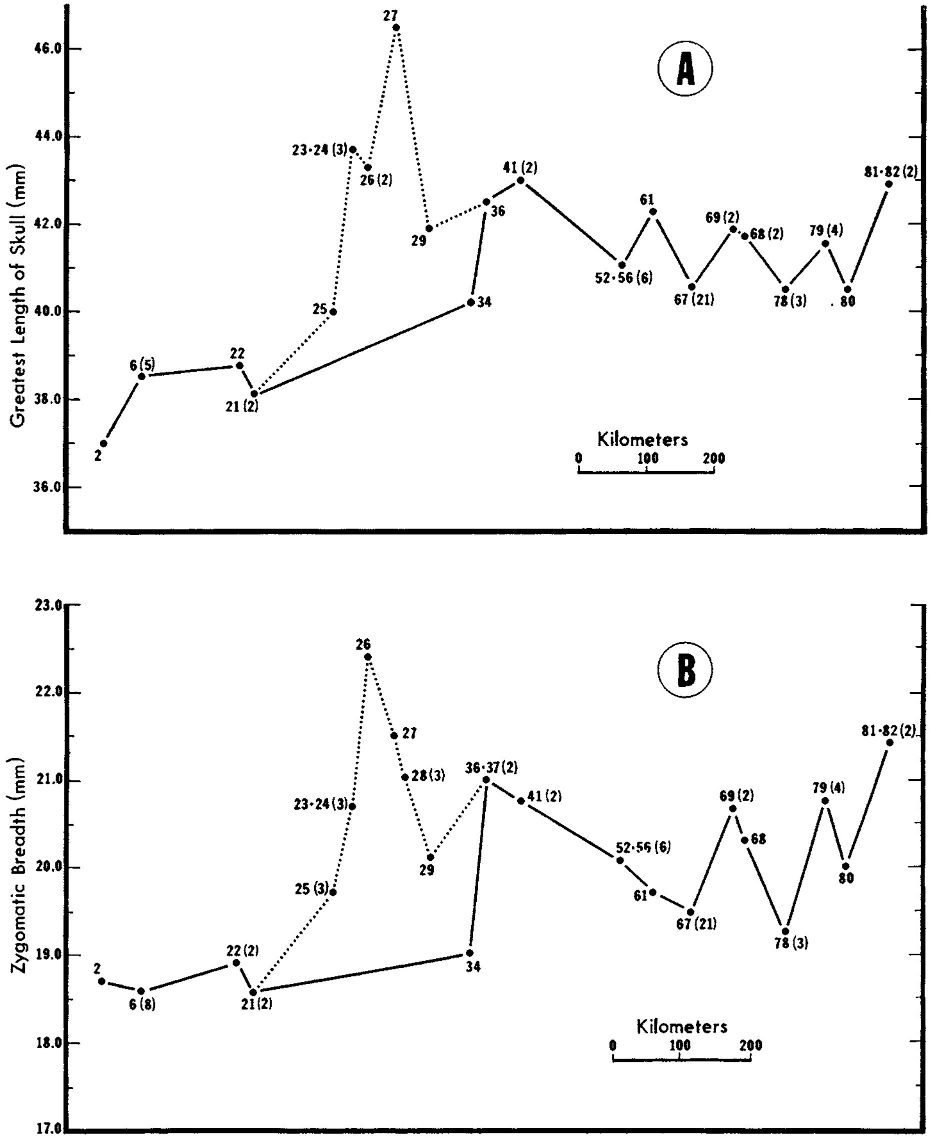

FIG. 3.—Geographic change (expressed as mean values) of greatest length of skull (A) and zygomatic breadth (B) in *Ototylomys phyllotis*. For explanation of numerals, lines, and measure of distance, see Fig. 2.

Geographic Variation

Size.—Two major trends of geographic variation in size were noted (Figs. 2 and 3). First, size, particularly as indexed by length of maxillary toothrow (Fig. 2), varies gradually from small in the lowlands of the Yucatan Peninsula south and east to large in Costa Rica. A second and somewhat more complex situation was noted between large individuals from Tabasco (localities 23, 24) and the highlands of Chiapas and Guatemala (localities 26 to 28, and 36 to 41) and small individuals from the adjacent lowlands to the east and south. The size gradient steepens along the margin of the highlands, from northeastern Chiapas south to the state of Alta Verapaz in central Guatemala and east to the Santa Cruz Mountains near Lake Izabal. Specimens intermediate in size are from 6 km SSE Palenque (25) and Laguna Ocotal (29), Chiapas, and 20 km NW Chinaja, Guatemala (34). The largest are from north-central Chiapas, Mexico. There also is a gradation in size between rats inhabiting the highlands of central Guatemala and those to the south and east.

The abrupt shifts of dimensions on the graphs, particularly among highland samples, may be somewhat misleading. Distances taken from maps are linear and do not take into account altitudinal changes that result in greater actual distances. If distances were certainly known, the changes would likely be more gradual.

Pelage.—Color of dorsum and venter also varied geographically. Variation in color of venter is particularly evident owing to differences in the width of gray and white bands on the hairs. Individuals from Tabasco and the highlands of Chiapas and Guatemala exhibit slate-colored venters as a result of a wider, proximal gray band on the hairs. Individuals from elsewhere generally are characterized by creamy white to dull white bellies. Specimens from 6 km SSE Palenque, Chiapas (25), and 20 km NW Chinaja (34), Tucuru (38), and Concepcion (39), Guatemala, were intermediate. Geographic variation of ventral color is presented in Fig. 4.

The dorsum of specimens from highland areas and Tabasco generally are dark, grayish-brown with an admixture of cinnamon. The reddish tinge is especially noticeable in specimens from north-central Chiapas and Tabasco. Elsewhere color of the dorsum varied from dusky brown (Yucatan Peninsula) to grayish-brown (Costa Rica) except on the Rio Curinguas (74), in the wet lowlands of eastern Nicaragua, where two blackish-brown specimens were taken. Only slight geographic differences in color reflection were observed.

In addition to the differences in color, the length of hair is greater in pelages of highland individuals from Chiapas and Guatemala than it is in specimens from adjacent lowlands. The numbers of hairs per unit area appears greater in the highland specimens. No direct measurements were taken of density and length of hairs.

Discussion of Variation

Body size in *Ototylomys* seemingly increases with altitude. In addition to the large highland forms of *Ototylomys* from Chiapas and Guatemala noted previously, other, though less demonstrative, examples of the trend include populations from the highlands of central Nicaragua (11 km SE Dario, 68, and Matagalpa, 69) and Costa Rica (San Ignacio de Acosta, 82, and Monte Rey, 81). Individuals from those places average larger than those from

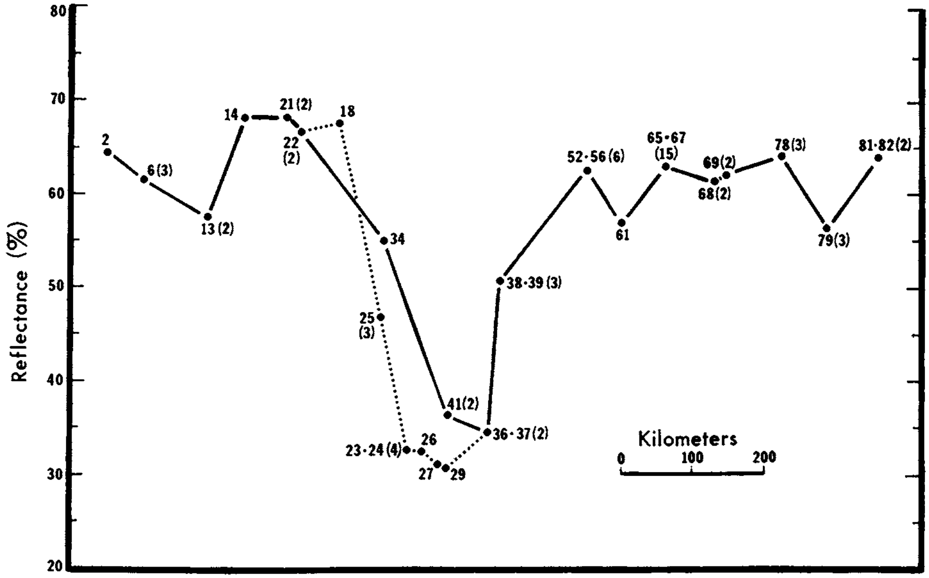

FIG. 4.—Geographic variation of mean color reflectance (red filter) of the venter in *Ototylomys phyllotis*, recorded as a percentage of pure white. Only adult individuals were used in this analysis. Blue and green filter readings differed from reflected red in their respective values but showed similar geographic changes.

nearby lowlands. In fact, the size contrast between individuals from the highlands of Costa Rica and lowlands of Costa Rica and Nicaragua is similar to that observed between rats of the highlands of Chiapas and Guatemala and the peninsular lowlands to the north. However, there are two exceptions to this trend. Individuals from Tabasco clearly resemble the large highland variant to the south in all size characters, but they were taken at altitudes of less than 200 meters; and the large rats from 8 mi. S Santa Cruz, Cerros de San Juan, Costa Rica (79), where the climate is similar to the surrounding semiarid flatlands, closely resemble highland individuals from central Costa Rica.

Geographic variation in color of venter only broadly parallels the trend in size. Typically, dark venters are found in individuals from highland areas (e.g., in Chiapas and Guatemala), and white venters are observed in lowland individuals, except that: (1) highland individuals of large size from Nicaragua and Costa Rica have white venters usually characteristic of lowland rats; and (2) large rats from the lowlands of Tabasco have slate-colored bellies characteristic of their highland counterparts nearby. The latter two examples suggest that there is no direct correlation of geographic change in ventral color and body size at those places.

The factors responsible for the geographic changes in size and color are not clear. Cool climates associated with altitudinal changes may have resulted in selection favoring large body size (and perhaps dark color) in highland populations, but this phenomenon has not been fully demonstrated in this study. The large individuals from Tabasco and 8 mi. S Santa Cruz, Costa Rica, suggest that temperature was not the factor favoring selection of large individuals at those places. It is possible that certain geographic similarities in characters of size and color are the fortuitous result of relationships between populations brought about by gene flow. That is, the local character of individuals may have come about partly from their genetic affinities via gene flow with populations geographically adjacent and in slightly different habitats rather than as a direct result of local selection. This is suggested by the lowland Tabascan and Costa Rican individuals (see above) that exhibit characteristics of those from nearby highland populations, and also by individuals of the Costa Rican and Nicaraguan highland populations that exhibit the same ventral coloration of nearby lowland populations. Large size and dark color may be adaptive to the lowlands of Tabasco, for example, but it seems likely that interchange of genes from nearby highland populations may be dampening the effects of selection there. Certainly the clinal effects of variation noted herein also resulted partly from phenomena of this sort, although selection must be responsible for differences in the extremes.

Selection favoring large body size at high altitudes seemingly is evidenced by the occurrence of large individuals in widely separated highland areas (see above). Intervening areas are inhabited by smaller animals.

The variation among populations located in the area of the steep gradient in size in Chiapas, Tabasco, and Guatemala is suggestive of secondary intergradation at some places. First, not all samples from the margin of the highlands were intermediate in all features. For example, only individuals from 6 km SSE Palenque, Chiapas, and 20 km NW Chinaja, Guatemala, were intermediate in features of size and pelage among the five localities where intermediate rats are represented (cranial measurements could not be obtained for specimens from Concepcion, Guatemala). This suggests that there is restricted gene exchange at the other intermediate localities. Second, there is a marked difference in the clinal nature of the variation at different places. It does not appear, for example, that intergradation occurs directly between populations from southwestern Campeche and northwestern Tabasco, because of the great differences in the character of the samples from those two areas; a more circuitous route is indicated. Also, the character shift in northwestern Chiapas is much more abrupt than elsewhere along the zone of intergradation. The gradual nature of the cline in variation in populations from the lowlands of the Yucatan Peninsula southward through northern and eastern Guatemala to the highlands of central Guatemala is more suggestive of primary intergradation.

It seems evident on the basis of the geographic trends of variation in size and color that there is gene flow between northern highland and lowland populations of *Ototylomys*. Although complete data concerning this intergradation are wanting, the available information strongly suggests that the genus consists of a single species that is characterized by considerable local and geographic variation. Additional data are required to determine the extent of gene flow between the subspecies here called *O. p. connectens* and *O. p. phyllotis* (see below). The following synopsis lists the subspecies of *Ototylomys phyllotis* that are most discernable to me:

Ototylomys phyllotis phyllotis Merriam. Type locality, Tunkas, Yucatan, Mexico. The names *O. phyllotis phaeus* Merriam, *O. p. fumeus* Allen, *O. p. guatemalae* Thomas, *O. brevirostris brevirostris* Laurie, and *O. b. affinis* Laurie, are synonyms. The range probably encompasses (1) areas to the east and north of the highlands of eastern Chiapas and central Guatemala, including El Peten of Guatemala, British Honduras, and the Yucatan Peninsula, and (2) areas to the south and east of the central Guatemalan highlands, including southern and extreme eastern Guatemala, and Honduras, El Salvador, and Nicaragua.

Ototylomys phyllotis connectens Sanborn. Type locality, Coban, Alta Verapaz, Guatemala. Specimens from Tabasco, Chiapas, and the central highlands of Guatemala are assignable to this subspecies. This name is used instead of *O. p. guatemalae* for individuals from the highlands because *guatemalae* was named on the basis of specimens that are intermediate between *O. p. phyllotis* and *O. p. connectens*. *O. p. guatemalae* is placed in synonomy with *O. p. phyllotis* because it more closely resembles *phyllotis* than *connectens*.

Ototylomys phyllotis australis Osgood. Type locality, San Geronimo, near Pozo Azul de Pirris, San Jose, Costa Rica. This name is tentatively retained for climbing rats from Costa Rica. I have seen no topotypes of this race.

Natural History

Ototylomys occurs in a wide variety of habitats within its geographic range. Investigators have reported that members of the genus exhibit a preference for tropical forest underlain with fragmented rock or possessing rocky ledges (Laurie, 1953: 389–390; Ingles, 1959: 395; Ryan, 1960: 14; Felten, 1958: 7; and Goodwin, 1934: 59). Murie (1935: 27) reported 15 specimens collected "under logs and among the roots of fallen trees." The species also inhabits rocky slopes and mine tunnels (Burt and Stirton, 1961: 59). In Nicaragua, I trapped and observed climbing rats in dense second-growth shrubs and small trees consisting chiefly of *Cordia diversifolia* (family Boraginaceae) and two unidentified species of the Rubiaceae, and in litter on the forest floor. At night the animals commonly were observed perched or running on creepers and branches of the vegetation. One specimen was trapped on a grassy slope about 20 yards from the nearest tree or shrub. On the Yucatan Peninsula, *Ototylomys* commonly was taken near rocky outcroppings, quarries, sink holes, and in forest.

Climbing rats inhabit areas of diverse climatic extremes. The species occurs in the semiarid scrub forest of northern Yucatan, Mexico; in semi-rainforest, with its characteristic high rainfall, along the coastal lowlands; and in the cool highlands of Chiapas, Guatemala, and elsewhere. *O. phyllotis* has an altitudinal distribution from near sea level to above 6000 feet in the Sierra Madre del Sur of Chiapas.

In Nicaragua the range of the species is restricted principally to second-growth vegetation along streams, roads, and fences, where it may be abundant locally. Extensive cultivation in many areas of Central America has resulted in the replacement of mature forest with second-growth vegetation and discontinuous distributions of many tropical rodents, including *Ototylomys*. It is possible that evolutionary change within the genus has occurred partly as a response to new habitats produced by cultivation.

Species of rodents that have been observed or captured in the same habitats with climbing rats are *Oryzomys palustris*, *Sigmodon hispidus*, *Mus musculus*, *Heteromys gaumeri*, *Peromyscus leucopus*, *P. yucatanicus*, and *Nyctomys sumichrasti*. The closest ecologic counterpart of *Ototylomys* in Nicaragua may be *Nyctomys sumichrasti*. Both are arboreal, forest-dwelling rodents. At San Antonio, Nicaragua, where the two species occur in the same habitat, the activity of *Nyctomys* is restricted to the upper levels of trees, generally 10 feet or more above ground. Conversely, *Ototylomys* forages on creepers and branches in places generally below the area of activity of *Nyctomys*. Occasionally climbing rats were observed on the ground. When frightened, they consistently moved laterally in the trees rather than upward. In one instance, individuals of the two species were observed occupying the same branch. Both species were common in the summers of 1964 and 1966 at San Antonio, where 85 *Nyctomys* and 56 *Ototylomys* were collected and others were observed. It appears that the two species are closely related ecologically but that competition is minimal. No information is available concerning interactions between *Ototylomys* and *Tylomys* in areas of sympatry. To my knowledge, the two genera have not been taken at the same locality.

The Isthmus of Tehuantepec marks the northern limit of distribution of *Ototylomys*, and may provide a barrier to the northwestward dispersal; the southeastern boundary of the range of the genus, however, is less well defined. The reason for the failure of *Ototylomys* to invade or cross the Isthmus is not clear. On the northern (Gulf) side of the Isthmus, generally a humid tropical environment, are found tropically-adapted inhabitants (Baker, 1963: 232). Perhaps *Ototylomys* does exist there at present, but none has been recorded. *Tylomys* also has a geographic range that is principally southeast of the Isthmus, but one species, *T. gymnurus*, inhabits areas of Veracruz and northern Oaxaca in, and to the northwest of, the Isthmus. *T. nudicaudus* also has been recorded from the Isthmus of Tehuantepec (Goodwin, 1955: 1).

Available evidence suggests that *Ototylomys* breeds throughout the year. Pregnant females and juvenal animals among specimens I examined were

TABLE 3.—*Geographic change in number of young (in utero) per female.*

Place	*N*	Mean	Range
Southern Tabasco	4	2.75	1–4
Yucatan Peninsula	16	2.25	1–3
Central British Honduras; El Peten, Guatemala*	13	2.00	1–3
Western Nicaragua	7	1.83	1–3

* Data for Guatemala from Murie (1935: 27).

taken in January, February, March, April, May, July, August, and December. Burt and Stirton (1961: 59) recorded similar data for the species in El Salvador. Of particular interest is the apparent geographic variation in the number of young (in utero) per female (Table 3).

Nesting habits of *Ototylomys* are poorly known. Goodwin (1934: 50) concluded from few data that the animals live in well-drained soil among rocks. A lactating female with three young was taken 20 km NW Chinaja, Guatemala, from beneath a log in forest (field notes of J. Knox Jones, Jr.). Percy L. Clifton (University of Kansas field collector) took a female "from a hole in a tree about 3 ft. above ground in a dense forest. . ." 103 km SE Escarcega, Campeche. Newborn rats are well developed and decidedly precocious (Murie, 1935: 27).

The food of *Ototylomys* consists chiefly of seeds, fruits, and other vegetative matter. Of the seven stomachs from Nicaraguan specimens that were examined, all contained finely masticated pulp of fruit and leafy vegetation; no insect remains were found. The fruit of madders (Rubiaceae) and the borage, *Cordia diversifolia*, may provide a substantial portion of the diet of the species in Nicaragua and elsewhere. Felten (1958: 7) noted the remains of "reddish fruit" in the stomach of a female from Laguna de Guija, El Salvador. A specimen reported by Pearse and Kellogg (1938: 303) from Chichen-Itza, Yucatan, "had eaten finely chewed vegetation."

External parasites that have been collected and identified from *Ototylomys* include ticks of the genera *Ixodes* and *Ornithodoras* (Yucatan Peninsula), and laelaptid and spinturnicid mites (Nicaragua, and Yucatan and Nicaragua, respectively).

Specimens Examined

Specimens examined during the course of this study are arranged by number (in parentheses preceding locality designations) according to the distribution map (Fig. 5). Abbreviations in parentheses refer to institutions cited in "Acknowledgments."

MEXICO. *Yucatan*: (1) Calcehtok, 55 km SSW Merida, 1 (USNM); (2) 66 km NE Merida, 7 (KU); (3) Tohil (= Xtohil), Chac Mol Cave, 1 (USNM); (4) 6 km N Tizimin, 2 (KU); (5) Tunkas, 5 (USNM); (6) 3 km N Piste, 10 (KU); (6) 2 km N Piste, 10 m, 1 (KU); (6) Piste, 10 m, 1 (KU); (6) Chichen-Itza, 10 m, 16 (2 BM, 5 KU, 9 USNM); (6) Cenote Seco, 2 km E Chichen-Itza, 4 (KU); (7) Valladolid, 1 (KU); (8) Peto, 1 (KU). *Quintana Roo*: (9) Pueblo Nuevo X-Can, 10 m, 7 (KU); (9) 2 km S Pueblo Nuevo X-Can, 1 (KU); (10) La Vega, 1 (USNM); (11) Esmeralda, 14 (UMMZ); (11) 1 km SW Esmeralda, 3 (UMMZ); (12) 4 km NNE Felipe Carrillo Puerto, 16 (KU); (13) 68 km N, 16 km E Chetumal, 1 (KU); (13) 60 km N, 16 km E Chetumal, 2 (KU); (14) 85 km W Chetumal, 2 (KU); (14) 83 km W Chetumal, 2 (KU). *Campeche*: (15) Dzibalchen, 2 (KU); (16) 5 km S Champoton, 10 m, 4 (KU); (17) San Jose Carpizo, 49 km S Campeche, 1 (UMMZ); (18) 7½ km W Escarcega, 8 (KU); (19) 7 km N, 51 km E Escarcega, 1 (KU); (20) La Tuxpena, 1 (USNM); (21) 103 km SE Escarcega, 3 (KU); (22) 65 km S, 128 km E Escarcega, 2 (KU). *Tabasco*: (23) 2 mi E Teapa, 4 (KU); (23) 5 mi SW Teapa, 2 (KU); (24) 5 mi SE Macuspana, 3 (KU). *Chiapas*: (25) Ruins near 6 mi SE Palenque, 5 (3 FMNH, 2 KU); (26) 8 mi (by road)

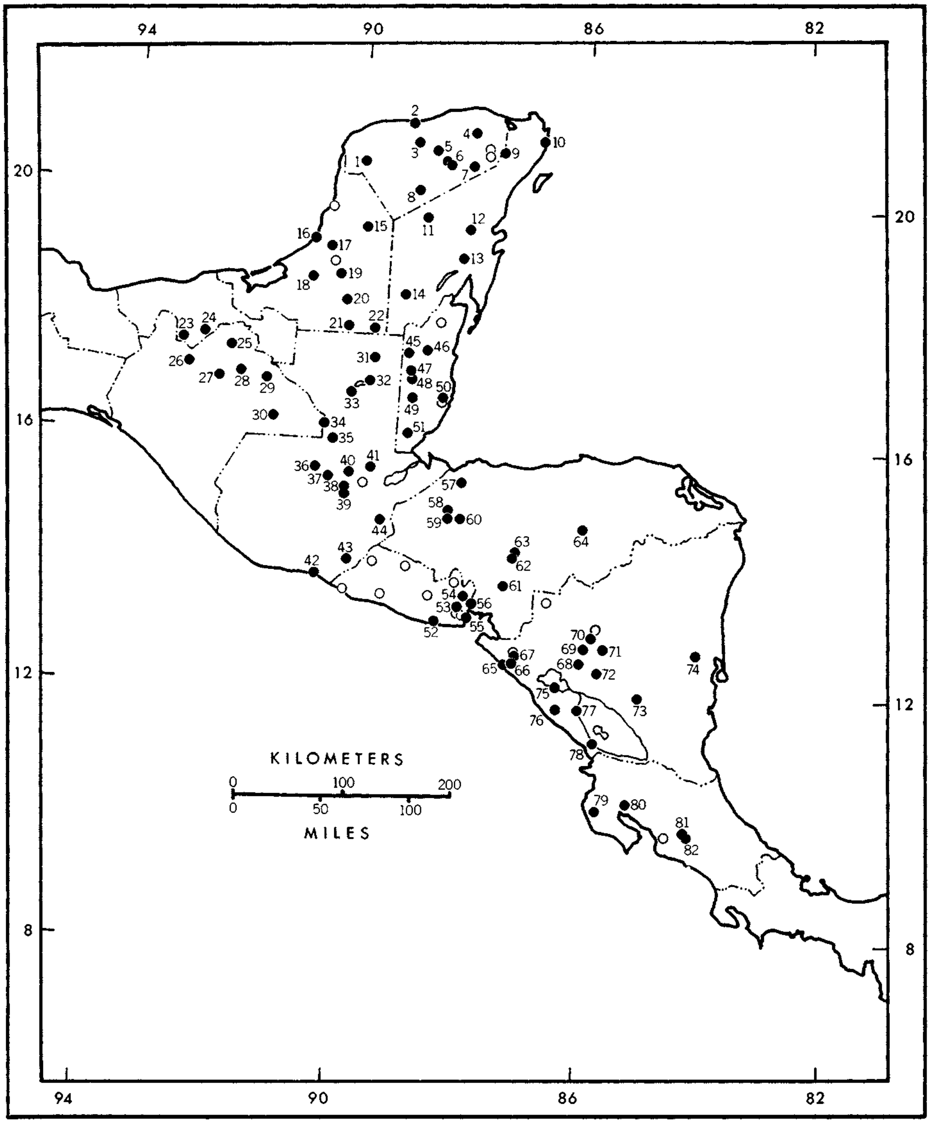

FIG. 5.—Geographic distribution of *Ototylomys phyllotis*. Numbers refer to localities discussed in text, presented in Figs. 2–4, and to the list of specimens examined. Solid circles denote localities from which specimens were examined; open circles represent published records.

NW Pueblo Nuevo, 6300 ft, 1 (KU); (26) 7½ mi (by road) NW Pueblo Nuevo, 6000 ft, 1 (KU); (27) Ruins of Tonina, 3300 ft, 1 (KU); (28) Finca El Paraiso, 4050 ft, 7 (KU); (29) Laguna Ocotal, 3 (MCZ); (30) Sabana de San Quintin, 215 m, 1 (KU).

GUATEMALA. *El Peten:* (31) Uaxactun, 16 (14 UMMZ, 2 USNM); (32) Remate, 1 (USNM); (33) Pacomon, 1 (USNM); (34) 20 km NW Chinaja, 5 (KU); locality unknown, 4 (3 UMMZ, 1 USNM). *Alta Verapaz:* (35) 4 km S Chinaja, 1950 ft, 1 (KU);

(36) Finca Chama, 1 (AMNH); (37) Coban, 1 (AMNH); (38) Tucuru, Polochic River, 1500 ft, 1 (BM); (39) Finca Concepcion, 3 (AMNH); (40) Lanquin Cave, 970 ft, 2 (KU); (40) 1/5 mi W Lanquin Cave, 1220 ft, 1 (KU); (41) Chimoxan, 4 (AMNH). *Santa Rosa*: (42) Astillero, 25 ft, 1 (KU). *Jutiapa*: (43) 1 mi SE Monogoy, 1 (KU). *Chiquimula*: (44) 3 mi E Jocotan, 1400 ft, 3 (KU).

BRITISH HONDURAS. *Orange Walk*: (45) Gallon Jug, 1 (LSU); (46) Hill Bank, 1 (LSU). *Cayo*: (47) Central Farm, 2 (USNM); (48) 8 mi from Georgeville on Chiquibul Road, 6 (USNM); (49) 12½ mi S Augustine, 1 (LSU). *Stann Creek*: (50) Pomona, 1 (LSU); (50) 1 mi S Pomona, 1 (LSU). *Toledo*: (51) 2 mi W San Pedro Colombia, 2 (LSU).

EL SALVADOR. *Usulutan*: (52) Triumfo, 2 (UMMZ). *Morazan*: (53) Monte Cristo, 1½ mi W Divisidero, 1 (UMMZ). *San Miguel*: (54) Volcan San Miguel, 1 (UMMZ). *La Union*: (55) Pine Peaks, Volcan Conchagua, 1 (UMMZ); (56) Rio Goascoran, 13° 30′ N, 1 (UMMZ).

HONDURAS. *Santa Barbara*: (57) Ilama, 1 (AMNH); (58) Santa Barbara, 1 (AMNH). *Cortez*: (59) Hda. Santa Ana, near San Pedro, 1 (FMNH); (60) Lago de Yojoa, Las Ventanas, 1 (AMNH). *Francisco Morazan*: (61) La Piedra de Jesus, Sabanagrande, 4 (AMNH); (62) La Flor Archaga, 1 (AMNH); (63) El Derrumbo, 1 (AMNH). *Olancho*: (64) Catacamas, 1 (AMNH); (64) El Boqueron, Catacamas, 1 (AMNH).

NICARAGUA. *Chinandega*: (65) Hda. San Isidro, 10 km S Chinandega, 10 m, 1 (KU); (66) San Antonio, 35 m, 56 (KU); (67) Volcan Casita, Finca Bellavista, 5 (KU). *Matagalpa*: (68) 11 mi SE Dario, 4 (KU); (69) Matagalpa, 3 (AMNH); (70) 10½ km N, 9 km E Matagalpa, 960 m, 1 (KU); (71) Uluce, 3 (AMNH). *Boaco*: (72) Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 4 (KU). *Chontales*: (73) 1 km N, 2½ km W Villa Somoza, 330 m, 3 (KU). *Zelaya*: (74) Rio Curinguas, 84° 03′ W, 12° 52′ N, 2 (USNM). *Chiltepe*: (75) Hda. Corpus Christi, 1 (USNM). *Managua*: (76) Azacualpa, 1 (USNM). *Granada*: (77) Mecatepe, 3 (1 KU, 2 USNM). *Rivas*: (78) Rio Javillo, 3 km N, 4 km W Sapoa, 40 m, 4 (KU).

COSTA RICA. *Guanacaste*: (79) Cerros de San Juan, 8 mi S Santa Cruz, 4 (UMMZ); (80) ½ mi E Finca Jiminez, 1 (UMMZ). *San Jose*: (81) Monte Rey, 22 km S San Jose, 1100 m, 1 (KU); (82) San Ignacio de Acosta, 1 (LSU).

Additional records (arranged alphabetically in each country).—MEXICO. *Campeche*: Apazote (Merriam, 1901: 563); 2 mi S Campeche (Ingles, 1959: 395). *Quintana Roo*: 10 mi E Quintana Roo-Yucatan border on road between Valladolid and Puerto Morelos (*Ibid.*). GUATEMALA. *Alta Verapaz*: Senahu (Ryan, 1960: 13). *Izamal*: "on the coast" (not mapped) (Sanborn, 1935: 183). BRITISH HONDURAS (Laurie, 1953: 388). *Belize*: Kate's Lagoon. *Toledo*: Silkgrass. EL SALVADOR (Burt and Stirton, 1961: 59, unless otherwise noted). *Ahuachapan*: Barra de Santiago. *Chalatenango*: San Jose del Sacare. *La Paz*: Volcan de San Vicente. *Libertad*: Chilata. *Morazan*: Mt. Cacaguatique. *San Miguel*: Lake Olomega; Rio San Miguel. *Santa Ana*: Laguna de Guija (Felten, 1958: 7). NICARAGUA. *Chinandega*: Volcan de Chinandega (= Volcan Casita) (Allen, 1908: 658). *Jinotega*: Pena Blanca (Allen, 1910: 100). *Nueva Segovia*: Ocotal (Allen, 1908: 658). COSTA RICA. San Geronimo, near Pozo Azul de Pirris (Goodwin, 1946: 401).

Gaumer (1917: 126) also records *Ototylomys* from Nabalam, Yucatan, under the name *Neotoma ferruginea* (= *N. mexicana*). His description, probably taken from the literature, clearly does not describe a climbing rat, but this record is considered valid here on zoogeographic grounds and because Gaumer's illustration is apparently that of an *Ototylomys*. Additionally, Hatt *et al.* (1953: 66) reported remains of climbing rats from six cave deposits in northwestern Yucatan (not mapped).

Acknowledgments

I am indebted to the following persons for allowing me to examine specimens in their care: Sydney Anderson, American Museum of Natural History (AMNH); James Corbett, British Museum (Natural History) (BM); Joseph Moore, Field Museum of Natural History (FMNH); Barbara Lawrence, Museum of Comparative Zoology, Harvard University (MCZ); George Lowery, Museum of Natural History, Louisiana State University (LSU); J. Knox Jones, Jr., Museum of Natural History, University of Kansas (KU); and William H. Burt, Museum of Zoology, University of Michigan (UMMZ). I am especially grateful to J. Knox Jones, Jr., for assistance and counsel during the course of this study. William H. Burt and Emmet T. Hooper read the manuscript. Martha Lackey prepared the illustrations.

Research was supported in part by a grant to J. Knox Jones, Jr., from the U. S. Army Research and Development Command (DA-49-193-MD-2215).

Literature Cited

Allen, J. A. 1908. Mammals from Nicaragua. Bull. Amer. Mus. Nat. Hist., 24: 647–670.

———. 1910. Additional mammals from Nicaragua. Bull. Amer. Mus. Nat. Hist., 28: 87–115.

Anderson, S. 1960. The baculum in microtine rodents. Univ. Kansas Publ., Mus. Nat. Hist., 12: 181–216.

Arata, A. A. 1964. The anatomy and taxonomic significance of the male accessory reproductive glands of muroid rodents. Bull. Florida State Mus., 9: 1–42.

Baker, R. H. 1963. Geographical distribution of terrestrial mammals in Middle America. Amer. Midland Nat., 70: 208–249.

Burt, W. H. 1960. Bacula of North American mammals. Misc. Publ. Mus. Zool., Univ. Michigan, 113: 1–75.

Burt, W. H., and R. A. Stirton. 1961. The mammals of El Salvador. Misc. Publ. Mus. Zool., Univ. Michigan, 117: 1–69.

Felten, H. 1958. Nagetiere (Mammalia, Rodentia) aus El Salvador. Senckenbergiana Biol., 39: 1–10.

Gaumer, G. F. 1917. Monografía de los mamíferos de Yucatán. Dept. de Talleres Graficos de la Secretaría de Fomento, México, xii + 331 pp.

Goodwin, G. G. 1934. Mammals collected by A. W. Anthony in Guatemala, 1924–1928. Bull. Amer. Mus. Nat. Hist., 68: 1–60.

———. 1946. Mammals of Costa Rica. Bull. Amer. Mus. Nat. Hist., 87: 271–473.

———. 1955. New tree-climbing rats from Mexico and Colombia. Amer. Mus. Novit., 1738: 1–5.

Hatt, R. T., H. I. Fisher, D. A. Langebartel, and G. W. Brainerd. 1953. Faunal and archeological researches in Yucatan caves. Bull. Cranbrook Inst. Sci., 33: 1–119.

Hooper, E. T. 1952. A systematic review of the harvest mice (genus *Reithrodontomys*) of Latin America. Misc. Publ. Mus. Zool., Univ. Michigan, 77: 1–255.

———. 1960. The glans penis in *Neotoma* (Rodentia) and allied genera. Occas. Papers Mus. Zool., Univ. Michigan, 618: 1–20.

Hooper, E. T., and G. G. Musser. 1964. The glans penis in Neotropical cricetines (Family Muridae) with comments on classification of muroid rodents. Misc. Publ. Mus. Zool., Univ. Michigan, 123: 1–57.

Ingles, L. G. 1959. Notas acerca de los mamiferos mexicanos. Ann. Inst. Biol., 29: 379–408.

Laurie, E. M. O. 1953. Rodents from British Honduras, Mexico, Trinidad, Haiti and Jamaica collected by Mr. I. T. Sanderson. Ann. Mag. Nat. Hist., ser. 12, 6: 382–394.

Merriam, C. H. 1894. A new subfamily of murine rodents—the Neotominae—with description of a new genus and species and a synopsis of the known forms. Proc. Acad. Nat. Sci. Philadelphia, 1894: 225–252.

———. 1901. Seven new mammals from Mexico, including a new genus of rodents. Proc. Washington Acad. Sci., 3: 559–563.

MURIE, A. 1935. Mammals from Guatemala and British Honduras. Misc. Publ. Mus. Zool., Univ. Michigan, 26: 1–30.

PEARSE, A. S., AND R. KELLOGG. 1938. Mammalia from Yucatan caves. Publ. Carnegie Inst. Washington, 491: 301–304.

RYAN, R. M. 1960. Mamiferos colectados en Guatemala en 1954. Acta Zool. Mexicana, 4: 1–19.

SANBORN, C. C. 1935. New mammals from Guatemala and Honduras. Field Mus. Nat. Hist., Zool. Ser., 20: 81–85.

Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104. *Accepted 21 October 1968.*