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A SYNOPSIS OF THE RODENT GENUS *SCOTINOMYS*

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RODENTS of the genus *Scotinomys* are small terrestrial inhabitants of the mountains of Central America. They occur principally above 1000 meters elevation in wet premontane (subtropical) and montane belts, which include the "coffee and dairy cattle zones" of the region. They also are found further upslope at least to 3300 meters on "paramo" which caps some of the cold, wind-swept peaks. The animals utilize runways through grass or other low-growing vegetation and among logs and tree roots on the forest floor (Fig. 1).

They are of greater interest to the biologist than their mundane vernacular name "brown mouse" would seem to indicate. They communicate vocally, produce a powerful scent, obviously use the olfactory sense in seeking food, are insectivorous, and are mainly or exclusively diurnal. Moreover, the species of the genus apparently differ considerably in behavior and reproductive strategies, and for these and other reasons qualify as excellent subjects for the study of speciation in the tropics. Some of these aspects of their biology are now being investigated and will be the subject of subsequent reports.

This paper summarizes morphological variations observed in these rodents. The basic data are from conventional study skins with accompanying skulls, together with examples in fluid and bolstered by information on habits of the animals and on the environments in which they live. The genus has not previously been reviewed.

MATERIALS AND METHODS

The 643 specimens examined are contained in the following institutions: Academy of Natural Sciences of Philadelphia (ANS); American Museum of Natural History (AM); Field Museum of Natural History (CM); Los Angeles County Museum (LA); Louisiana State Uni-



FIG. 1. Photograph of an example of *S. xerampelinus* from Volcán Turrialba, Costa Rica.

versity (LSU); University of California, Berkeley, Museum of Vertebrate Zoology (MVZ); University of California, Los Angeles (UCLA); University of Michigan Museum of Zoology (MZ); University of Kansas Museum of Natural History (KU); U.S. National Museum (US).

My thanks are due the curators of those collections for the use of the specimens. I also gratefully acknowledge the assistance of Ernesto Barriga B., Michael D. Carleton, David J. Klingener and Guy G. Musser in collecting data and specimens in Central America. Dr. Musser also kindly reviewed for me the six holotypes of *Scotinomys* contained in the American Museum, and solicited information on the type of *teguina* in the British Museum. Michael Eckardt and Arnold G. Kluge graciously gave advice and aid in use of a computer. The text figures are the work of Martha Lackey, artist of the Museum of Zoology. Financial support is provided by the National Science Foundation (G-6379, GB-5801).

Eighteen characters receive special attention in these analyses. These are the ones that, out of more than forty utilized at some stage of the study, are quantified to illustrate the variation observed in the skins and skulls. These eighteen are listed below and in Table 1.

Most of them are conventional in systematic mammalogy and require no detailed descriptions. Measurements of *total length*, *tail vertebrae*, *hind foot* (to tip of claws), and *ear* (from notch) were recorded by various collectors and are subject to considerable error, much more than are those of cranial parts. In measuring the crania I used an "Anderson craniometer" which employs a calibrated movable stage on a binocular microscope and yields direct readout in millimeters on photoelectric counters (Anderson, 1968).

*Length of skull* is the greatest length on the longitudinal axis. *Cranial breadth* indicates maximum breadth of brain case dorsal to the zygomatic arches. *Length of nasals* is the greatest length of either nasal, *interorbital breadth* the least breadth of the frontal bone between the orbits, and *length of molar row* the distance along the alveoli of the upper row.

*Maxilla, dorsally* indicates the distance on the dorsal face of the maxilla from the zygomatic notch (superior lip of infraorbital canal) posteriorly to lateral limit of the lacrimal bone.

Size of the *optic foramen* (Fig. 3) is compared with the occlusal width of  $M^3$  and indexed as: 1, when its transverse diameter equals, or is greater than, the occlusal width of  $M^3$ ; and 2, when its transverse diameter is much less than the tooth's width.

Posterior limits of the anterior *palatine foramina* relative to the upper tooth row are indexed as: 1, limits anterior to  $M^1$ ; 2, even with anterior border of  $M^1$ ; and 3, posterior to anterior border of the tooth. The skull rests dorsal-side-down on the stage of the microscope.

Position of the *masseteric process*, or tubercle (Fig. 3), is indicated relative to (a) plane of alveolus of molar row—specifically the distance dorsal to that plane and (b) anterior limit of alveolus of  $M^1$ —specifically the distance from alveolus to a dorso-ventral plane through the center of the tubercle. Position of the tubercle is indexed as a ratio of  $a/b \times 100$  in units of 25: index 1, ratio 0–25; 2, ratio 26–50; 3, ratio 51–75; 4, 76–100; 5, 101–125; and 6, ratio over 125.

*Nasals, posteriorly*, refers to the shape of the posterior border of the two nasal bones: index 1, the border of the two V-shaped; index 2, the border U-shaped.

*Nasals, laterally*, indicates whether the lateral borders of the nasal bones taper gradually posteriad (index 1) or (index 2) are bowed mediad about midway in their length.

There are either two or three pair of *mammae*. They are indexed: 1, a pectoral pair present in addition to the two inguinal pairs; and 2, no pectorals—two inguinal pair only.

Seventeen series of specimens, representing various parts of the

range of *Scotinomys*, provide most of the data for statistical purposes and illustrations (Figs. 2 to 11 and Table 1). These samples, or OTUs (Operational Taxonomic Units, cf. Sokal and Sneath, 1963), abbreviated in the figures and table as indicated, represent the following localities:

Guatemala (*Guat*): Cotzal, Tamahú, Coban, El Chol, Tukurú, and Injerto; elevations, 1070–2135 m.

El Salvador (*Salv*): Los Esesmiles, 2165–2440 m.

Honduras: *Hond 1*, Humuya, 1370 m; *Hond 2*, Cerro Puca, 2000 m.

Nicaragua (*Nic*): Santa María de Ostuma, 1300 m.

Costa Rica: *CR 1*, Los Higuerones, 1370 m; *CR 2*, Volcán Irazú, 2850 m; *CR 3*, Volcán Turrialba, 2600 m; *CR 4*, Volcán Irazú, 2350–3200 m; *CR 5*, vicinity of Cerro de la Muerte, 3000 m; *CR 6*, Volcán Chirripó Grande, 3200 m; *CR 7*, mountains south of Cartago, 1400–2100 m (Figs. 10, 11 only).

Panama: *Pan 1*, Río Chiriquí Viejo valley, 1720–1950 m; *Pan 2*, Santa Clara and Siola, 1200–1300 m; *Pan 3*, Río Gariché, 975 m; *Pan 4*, Finca Lerida, 2135 m; *Pan 5*, vicinity of Volcán Chiriquí, 2600–3200 m.

## INTERRELATIONSHIPS OF POPULATIONS

Interrelationships of populations from various parts of the range of *Scotinomys* are suggested in Figure 2. In that diagram, 11 of the larger samples are clustered in a Prim Network (Prim, 1957) on the basis of amount of dissimilarity of characters of skin and skull. The characters used in the computations are the 18 listed above and in Table 1. All characters are considered equal; the distribution of each is standardized to the distribution of mean 0 and standard deviation of  $\pm 1$  so that each character contributes equally to the dissimilarity matrix. The coefficient of dissimilarity was computed as:

$$d_{jk} = \sum_{i=1}^n \left| X_{ij} - X_{ik} \right|,$$

where  $X_{ij}$  is the character state (the standardized sample mean) of the  $i$ th character of species  $j$  and  $X_{ik}$  is the character state of the  $i$ th character of species  $k$ . The Prim Network results from an algorithm which progressively links each sample or OTU (see above) to the sample most like it. The resulting diagram (Fig. 2) is unidimensional so that only distances along the network are meaningful. Width of

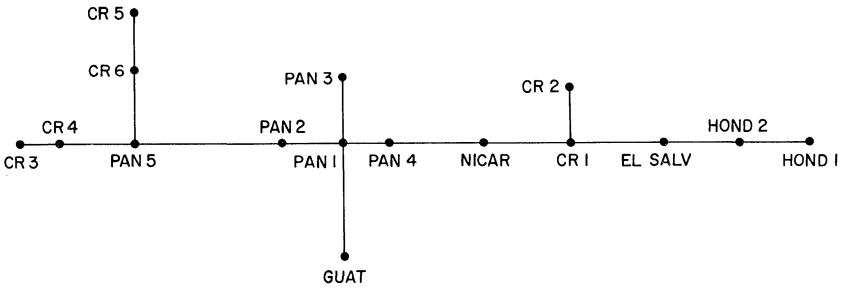


FIG. 2. Prim Network of 16 samples (OTUs) of *Scotinomys* based upon 18 characters. Localities and characters indicated in text.

gap between OTUs on the network indicates the relative amount of dissimilarity over all characters.

Though all of the character states have equal weight in the computation most of them are size-related; therefore, the influence of size is paramount in the diagram. Largeness is characteristic of the OTUs to the left, and there is more or less progressive decrease toward the right to minimum size in the OTUs of Honduras and El Salvador. The OTUs of the right and left extremes have attenuate nasals and three pair of mammae. OTUs between those extremes have truncate nasals and two pair of mammae.

Of several clusters in the diagram, the one at the extreme left, consisting of the highland samples from Panamá and Costa Rica, is set well apart from the others. The highland units (CR 3, 4, 5, 6, and Pan 5) are characterized by large dimensions, long tail, long tapering nasals, small optic foramen, three pairs of pectoral mammae, and other features. They are unlike lowland samples (to the right in the diagram) from the same region and localities.

The remainder of the OTUs are spaced rather evenly. The four lowland Panamanian ones (Pan 1, 2, 3, 4) perhaps form a cluster, and the two from Costa Rica (CR 1, 2) are also close together, but CR 1 and 2 are not far separated from Nicar (Nicaragua) and El Salv (El Salvador) which, in turn, is near Hond 1 and 2 (Honduras). The unit from Guatemala stands apart. Thus, on the basis of the 18 character states treated with equal weight, there are three or more OTU clusters: (1) a distinct one, representing highland localities of Panamá and Costa Rica, set well apart from (2) a group representing (a) lowland Panamanian sites, (b) another from Guatemala, and (c) a series of six approximately equally differentiated units along the scale from Costa Rica northwestward to El Salvador and Honduras.

In interpreting the diagram together with data from other samples I see clear evidence that two species are represented, to which the names *xerampelinus* and *teguina* will apply. Secondly, in my view, no more than four of the several geographic variants of *teguina* warrant recognition by technical name. These are from (1) Panamá; (2) Costa Rica and Nicaragua; (3) El Salvador and Honduras; and (4) Guatemala and southern México (Fig. 5).

#### Genus *Scotinomys* Thomas

*Hesperomys*, Alston, 1876:755. Description of *H. teguina*.

*Akodon*, Bangs, 1902:40–42. Description of *A. t. apricus* and *A. xerampelinus*.

*Scotinomys* Thomas, 1913:408–9. Type species: *Hesperomys teguina* Alston.

RELATIVES.—Although kinships of *Scotinomys* are not yet precisely known, several of many New World murids anatomically resemble the two species and likely are phylogenetically close relatives. Thomas (1913) and other authors have ranked the two forms near species of *Akodon*, and there is no question that some of those (e.g., *A. urichi*) superficially are much like forms of *Scotinomys*. Similarities with Nearctic species have also been pointed out. Hooper (1960) and Hooper and Musser (1964) in discussing structure of the male phallus drew attention to resemblances of *Scotinomys* to *Baiomys*, *Ochrotomys* and *Peromyscus* and suggested that close affinities of the genus may be with peromyscines.

Herskovitz (1962:85) listed *Scotinomys* with a group of cricetines characterized by plicidont molars (topography typified by infolds of enamel) in which the mesoloph (id) is never locked with the mesostyle (id). Forms of the group are “phyllostines of this monograph, sigmodonts, akodonts, and pastoral peromyscines (*Podomys*, *Haplomyomys*, *Onychomys*, *Baiomys*, *Reithrodontomys s.s.*, *Neotomodon*, *Scotinomys*, *Nelsonia*, *Neotoma*, *Xenomys*, *Ototylomys* and *Tylomys*).” These are viewed as predominately pastoral in habits.

Schaub (Stehlin and Schaub, 1951:171, 325) commented on the elongate shape of M<sup>1</sup> and M<sup>2</sup> of *Scotinomys* and saw resemblances in configuration of those teeth between that genus and *Pliotomodon primitivus* and *Cricetodon decedens*. Lower molars of those forms were less similar. The Pliocene *Pliotomodon* may be near the ancestral stock which led to *Scotinomys*.

Vorontsov (1967:72) indicated similarities of *Scotinomys* and *Lenoxus* in structure of upper molars, and suggested that the peculiar

pattern in *Scotinomys* perhaps was derived from something like that in *Lenoxus*. He also compared the upper molars of *Scotinomys* with those of the Oligocene forms *Scottimus* (North America) and *Selenomys* (Mongolia) and Pliocene *Pliotomodon* (North America). He submits those four genera as evidence, however, that the "selenodont" pattern seen in them may have originated repeatedly in the phylogeny of the "Cricetidae." He views this tooth pattern, rare in cricetids, to be a phyletically dead-end side line.

These patterns may or may not provide reliable clues to kinships of *Scotinomys*. Certainly they are functionally related to mastication and to kind of food. Perhaps the elongate piercing and crushing molars of *Scotinomys* are fitted for a mixed diet which includes a high percentage of chitinous invertebrates, which evidence suggests are in their diet. Data from the teeth may be useful in assessing affinities of *Scotinomys*, but those from many other sources also are essential. A more comprehensive coverage of data relating to propinquity of *Scotinomys* is the basis for another report, to follow.

EXTERNAL FORM.—Members of the genus externally resemble a small *Peromyscus*, *Akodon*, *Oryzomys*, or other scampering mouse-like rodent. Shape of head as in those taxa; muzzle moderately long, not blunt as in microtines or fossorial forms. Body correspondingly elongate, the combined length of head and body usually greater than that of tail (Table 1). Tail sparsely haired; scutellation as in other cricetines. Eyes small, partially hidden in fur. Pinnae moderate in size (Table 1), long enough to cover the eyes when laid forward, and sparsely covered with vari-colored hairs both within and outside. Forefoot with five digits, the outer four free from each other, without webbing; middle two of that four equal in length and outer two of that four equal in length and each tipped with a claw. Digit one (*D1*) short, reaching only to the base of *D2* and tipped with a nail, not a claw; appearance of that digit resembles the terminal segment of a human thumb. Five large plantar tubercles present, three of these at the base of the digits and two on the palm. No hair on underside of feet; sides and upper parts with a sparse cover of monocolored hair.

Hind feet with five independent (unwebbed), claw-tipped digits, the three medium ones about equal in length, *D1* shorter, and *D5* shortest. Six plantar tubercles present, four at the bases of the digits and two more proximal in position; a few hairs present between them throughout the sole of the foot.

The moderately long pelage consists of essentially unicolored guard hairs and multi-banded cover hairs, the buffy band a deep pink-

ish cinnamon. Overall effect of the upper parts and underparts is of a blackish-brown or dark cinnamon mouse.

Variations observed in coloration are mostly those associated with age and freshness of the pelage, as is typical of most tropical and subtropical New World murids. The young are uniformly blackish or sooty with little or no buffy hue. Buffy bands, appearing in the subadults, become wider in adults and give the deep cinnamon hue to those pelages. These buffy colors and the blacks of the overhairs fade with use and, as a result, a series of specimens from a given locality and representing different times of year typically varies noticeably in hue and tone.

In addition, there are differences in color which seem to be related to wetness or amount of cloud cover, rain, or mist. Specimens from wet, cloud-enshrouded areas (for example, Moravia de Chirripó, Tapanti, and Monte Verde, Costa Rica) are darker and the buffy band is a deeper cinnamon than in examples from nearby areas (e.g., parts of Volcán Poas, Volcán Irazú, Villa Quesada, and Escazú) where it is dryer most of the year and there is a pronounced dry season. These local differences in coloration were observed in several samples representing various parts of the range of the genus, and there well may be a mosaic distribution of pelage coloration corresponding to the elaborate pattern of moisture distribution in Central America.

**DIMENSIONS OF EXTERNAL PARTS.**—*S. xerampelinus* is the larger of the two species and has a longer tail and possibly larger ears (Table 1). Within each species there are slight geographic differences in external size—as indicated by total length and hind foot length—but because body length varies little or none at all geographically, some of the observed differences in total length (Fig. 6) and hind foot length (Table 1) may be attributable to collectors' techniques rather than being characteristics of populations.

**NUMBER OF MAMMAE.**—The number of pairs of mammary glands varies interspecifically, and also geographically within one of the species but not the other. Two inguinal pairs appear to be characteristic of all females; they were observed on all well-preserved specimens. A pectoral pair is present or absent, and the pattern of its occurrence is of particular interest.

Three pair of mammae are characteristic of *S. xerampelinus*, and the samples suggest that this number is constant in females throughout the range of the species. The pectoral pair is present in each of the 22 examples preserved in fluid (representing localities from Volcán



Turrialba southward to Volcán Chirripó Grande, Costa Rica) and in all well-prepared study skins. Rates of occurrence in dried material are as follows: 15 of 25 females from Cerro de la Muerte and Volcán Chirripó, 13 of 22 from Irazú and Turrialba volcanos; and 29 of 40 females from Volcán Chiriquí. The pectoral pair, thus, was observed in 79 of the 109 females examined. The 30 specimens in which the pectoral pair was not seen were either young, and no mammae were evident, or were poorly preserved such that the pectoral pair, if present, likely could not be seen. Although on the basis of these data the possibility cannot be excluded that either two or three pair may occur in *xerampelinus*, the evidence strongly suggests that three pair have become fixed in this species.

In *S. teguina* mammae count varies geographically (Table 1). Three pair of mammae appear to be characteristic of populations from the northwestern part of the range of the species (Honduras to México, Fig. 5) and two pair in the southern part (Nicaragua to Panamá). The possibility that mammary number varies within each of these two regions certainly can not be ignored because the samples are small, particularly from the northwestern region. There are only 45 females from that region: México, 1; Guatemala, 4; El Salvador, 18; Honduras, 22. There are more (78) females from the southern region: Nicaragua, 13; Costa Rica, 30; and Panamá, 35. Nonetheless, the samples give no positive evidence that number of mammae is other than that indicated—three pair in the north, two pair in the south. No pectorals were seen in the 69 examples from the region Nicaragua to Panamá. Of the 45 females from the region Honduras to México, a pectoral pair was observed in 28; and of the 17 in which they were not seen, most of the specimens were young or ill-prepared. The data thus suggest that in the northwestern segment of its range, *teguina* has six mammary glands, the same number as in *xerampelinus*. In the southern part, where it is partly sympatric with *xerampelinus* (Figs. 5, 12) it has only four of these.

If these distributional patterns of mammae prove to be characteristic of the populations, they may well provide important clues to the evolution of the two species and to mechanisms of competition between them. The two species very probably compete where they meet, and this difference in mammary formula between them may be an instance of character displacement associated with competitive exclusion of one from the other's *lebensraum*. What mammary formulae mean in terms of number of young per litter and per year and in terms of survival rates needs to be known. It is the subject of studies now underway both in the laboratory and in the field.

SKULL.—In appearance of the whole and in proportion of many of its parts, the skull resembles that of peromyscines, for example *Peromyscus crinitus*, *Reithrodontomys mexicanus* and *Baiomys musculus*. It is less like those of microtines, sigmodonts and some other South American groups. The upper surface is smooth, without prominent ridges. There is little or no zygomatic notch (Fig. 3), so that the anterior keel of the zygomatic plate is scarcely or not at all visible when the skull is viewed from above. The interparietal is anteroposteriorly narrow, that dimension is less than half of the interorbital breadth. Shape of nasals, frontals, maxillae, parietals, and squamosals are as in peromyscines.

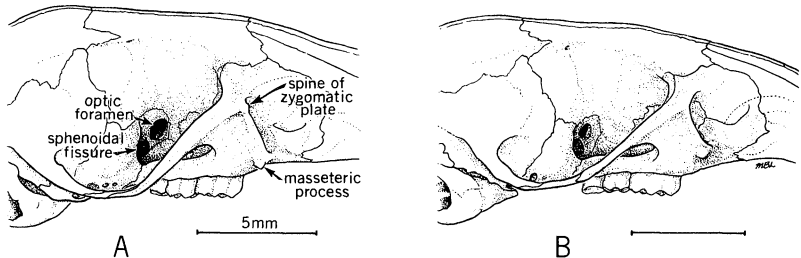


FIG. 3. Lateral view of skull showing characters of (A) *S. teguina*, MZ No. 112234, Moravia, Costa Rica and (B) *S. xerampelinus*, MZ No. 112243, Volcán Irazú, Costa Rica.

Shape and arrangement of ventral parts of the skull also are like those in peromyscines. This applies to the palate and pterygoid, occipital, auditory and mastoid areas. The incisive foramina terminate near the anterior limit of  $M^1$ . Each ectopterygoid fossa is wider than the mesopterygoid fossa. Sphenopalatine vacuities are long and moderately wide. There are no post-palatal pits or cavities as seen in oryzomyines, microtines and some other New World groups.

Inter- and intra-specific differences in cranial parts are mentioned on following pages. Of the several cranial features distinguishing *S. teguina* and *S. xerampelinus* (Table 1), breadth of brain case, length and shape of the nasals (Figs. 10, 11), position of the masseteric process of the maxilla, and diameter of optic foramen are impressive. What most of these differences mean in terms of function in the living animals is unknown and can only be surmised. Size of nasal bones may in some way relate to olfaction. Again, since the masseteric process is the site of origin of the slender tendon of *M. masseter superficialis pars*

*anterior*, presumably the two positions of the process in the species indicate different forces and stresses in the action of the masseter muscle system.

More clues are available for inferences regarding the size of the optic foramen. In *teguina* the foramen is a large opening not much smaller than the orbital fissure (Fig. 3). The size is similar to those seen in several other peromyscines inspected for this character, for example *Baomys musculus*, *Reithrodontomys mexicanus* and *Peromyscus crinitus*. In *xerampelinus* the optic foramen is smaller; its diameter much less than that of  $M^3$ . This interspecific difference in size suggests that additional tissues—blood vessels or nerves—may be transmitted through the larger foramen. In ten specimens dissected (5 *teguina* from two localities and 5 *xerampelinus* from two localities) however, I found no differences in content of the foramina. In both I saw only the optic nerve.

There was a difference in the size of the nerve; diameter of foramen apparently reflects diameter of nerve. In each of the five examples of *teguina* the nerve was larger in cross-section than in each of the five specimens of *xerampelinus*. The eyeball also averaged larger in *teguina* (10 specimens from Moravia de Chirripó compared with eight examples of *xerampelinus* from Cerro de la Muerte).

Reliability of these observations leaves something to be desired because of the differential states of preservation of the specimens. More complete and reliable data on the subject are being accumulated, and at the same time the possibility is being explored that differences in size of nerve and size of eye may reflect distinctions between the species in activity times or some behavioral or physiological function associated with vision. King (1965) indicated differences in weight of lens among taxa of *Peromyscus*, and suggested possible behavioral patterns which may be associated therewith. These kinds of data would seem to be exceedingly important in understanding differential behavior, possible competitive exclusion, and evolution of the two species.

**TEETH.**—The teeth provide principal generic characters. The incisors are ordinary, like those in *Peromyscus* and related forms without longitudinal grooves. The anterior face, beveled in young animals, may become flat with increasing age.

The upper cheek teeth are unusual among New World murids. The basic pattern of four cusps separated by labial and lingual folds is modified, especially in  $M^1$  and  $M^2$  (Fig. 4). The enamel folds are shallow and the teeth appear as four angular dentine-exposed cusps enclosing two crescentic pits. The arrangement recalls a high-crowned

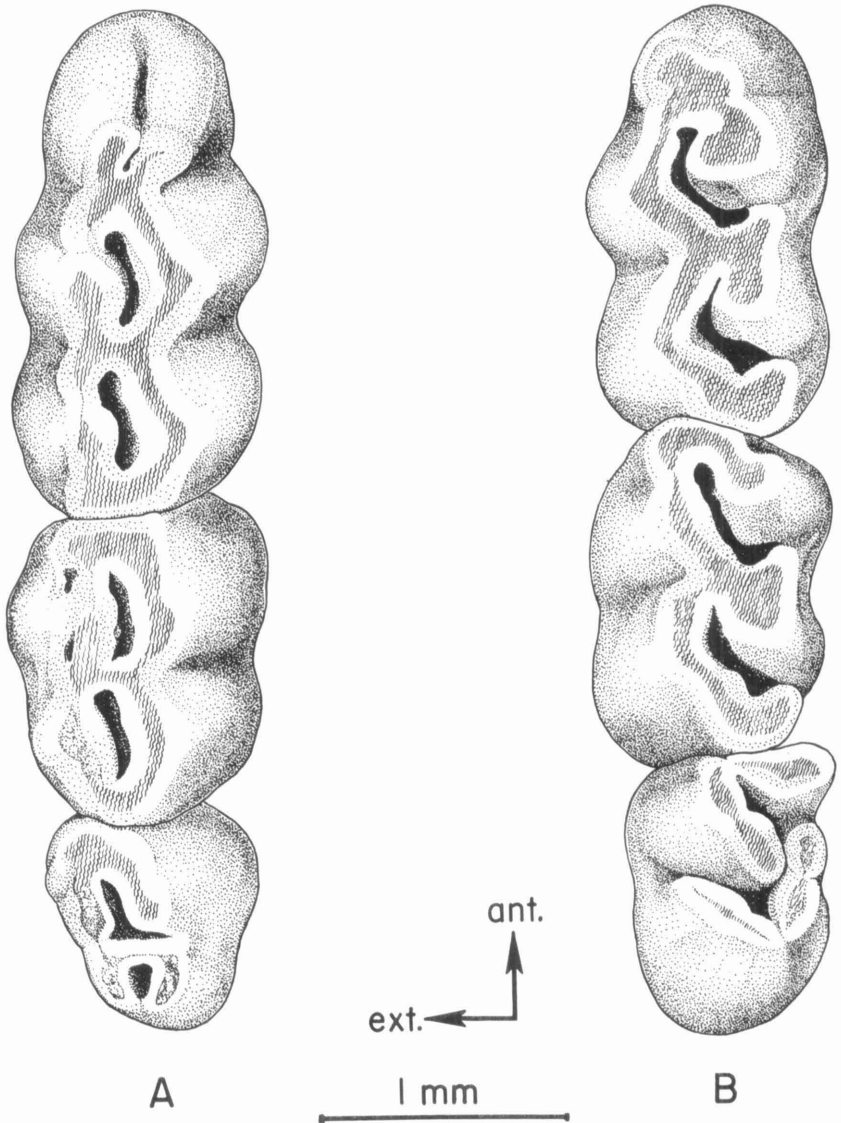


FIG. 4. Occlusal views of right upper (A) and left lower (B) molar rows in *S. xerampelinus*, MZ No. 112247, Volcán Irazú, Costa Rica. For names of folds and cusps see text and Hooper (1952).

selenodont tooth as Vorontsov (1967:72) suggested. The teeth erode to enamel-surrounded pools of dentine in which there are two enamel islands (figured by Stehlen and Schaub, 1951:171, 325 and Vorontsov loc. cit.). Closure of the labial and lingual valleys, which are broader and more open in most peromyscines, appears to be the result, evolutionally, of fusion of (a) a large mesostyle with paracone and hypocone and (b) the anterior cingulum with paracone, thus making a continuous enamel ridge with shallow indentations which are the major and secondary folds. Details of young teeth (Fig. 4) are mentioned below; the nomenclature follows Hooper (1952).

M<sup>1</sup>. Long and narrow, the tooth, excluding the anterocone, about the same size as M<sup>2</sup>. Anterocone, the size of the protocone, with a deep anteromedian fold which with wear cuts off to form an anterointernal enamel island. Anterior cingulum small and joined to the paracone, thereby separating the first primary fold from the first internal fold which is a crescentic enamel island. Second primary fold a broad shallow valley between the paracone and metacone. No second secondary fold, distinct posterior cingulum, or secondary lophos or styles in the tooth. The opposing enamel ridges on protocone, and on hypocone as well, do not meet on the occlusal surface; dentine thus is exposed continuously over those cones, around the enamel island, and onto the paracone and metacone. On the unworn paracone and metacone the dentine is mostly, but not entirely, covered by enamel.

M<sup>2</sup>. Like that of M<sup>1</sup> without anterocone. A shallow first primary fold outlines a trace of an anterior cingulum. Two enamel fossettes sometimes present on (a) anterior and (b) posterior inner faces of the paracone (Fig. 3) may be remnants, respectively, of (a) a part of the first primary fold that has been cut off from the exterior and (b) an isolated segment of the large first internal fold. No second secondary fold or secondary lophos or styles on the tooth.

M<sup>3</sup>. Much like that of moderately complex-toothed peromyscines, the anterior half similar to the comparable part of M<sup>2</sup>, and the posterior half a compacted and contorted version of its counterpart in M<sup>2</sup>. In the unworn tooth all cones and crests are enamel-covered; little or no dentine is exposed. Protocone largest; paracone second in size, with a trace of an indentation of the first primary fold; hypocone smaller, separated from the protocone by an indentation; metacone low, essentially a ridge on the postero-external part of the tooth connecting the hypocone and the paracone, and bordering a second internal fold. First internal fold, approximately as large as its counterpart in M<sup>2</sup>, constitutes the single enamel island in a pool of dentine in the well worn tooth.

Lower cheek teeth much like those in simple-toothed *Peromyscus* and other peromyscines, but relatively narrower and with a differently shaped anteroconid. Because the lower teeth tend to be evolutionally more conservative than the uppers (Hooper, 1957), their configurations in *Scotinomys* possibly provide clues to the ancestral condition from which the bizarre pattern of the upper molars was derived. In each of the three teeth a large mesostylid, joined to the entoconid, closes the second primary fold and thus allows for a continuous enamel ridge on the lingual side in the worn tooth; it cuts off a large internal fold. The second internal fold is formed by a corresponding closure: the posterior cingulum merges with the entoconid. The result is an obscure "selenodont" pattern in  $M_1$  and  $M_2$ , less distinct than in  $M^1$  and  $M^2$  (Fig. 3).

$M_1$ . Anteroconid, about the size of protoconid, with a shallow anteromedian fold which with wear does not form an enamel peninsula or island. Protoconid and hypoconid about equal in size. Metaconid and entoconid, also similar in size, demarked lingually by a shallow first primary fold and mesially by the first internal fold. Each of the two internal folds becomes isolated from its lingual valley (primary folds) early in wear.

$M_2$  and  $M_3$  are dissimilar, as is usual in peromyscines.  $M_2$  is like  $M_1$  without an anterocone.  $M_3$  is a contracted copy of  $M_2$  in which three folds—the major, second primary, and second internal—are continuous in the unworn tooth. Entrance to first internal fold is blocked by a large mesostylid attached to the entoconid. Entoconid, the smallest of the four cusps, separated from the hypoconid by a shallow secondary primary fold which is continuous with the major fold and thus in an unworn tooth separates the hypoconid from the other cusps and lophs (Fig. 4). Wear results in two enamel islands. The architecture of this tooth in particular suggests that closure of the primary folds on both the upper and lower teeth is effected by a large mesostyle (id) which merges with the cones anterior and posterior to it and thus helps to form a continuous enamel ridge on one side of the tooth—labial in upper row and lingual in lower.

I found no dental characters which will distinguish any taxa of the genus.

GENITALIA.—The glans penis of *S. teguina* and of *S. xerampelinus* is figured and described by Hooper (1960) and Starrett (1960), respectively. The glandes at hand, 21 of *xerampelinus* and 7 of *teguina*, are closely similar. The base of the baculum, however, is more deeply concave ventrally in the examples of *xerampelinus*, and the tip is

evenly truncate in ventral view, in contrast to being lightly cleft or bilobed in 6 of the 7 *teguina*.

*Scotinomys teguina teguina* Alston

*Mus Tegulina* Gray 1843:79. *Nomen nudum*.

*Hesperomys teguina* Alston, 1876:755.

*Akodon teguina*, Bangs, 1902:40; Allen, 1904:46.

*Scotinomys teguina*, Thomas, 1913:409.

*Scotinomys teguina subnubilis* Goldman, 1935:141. Mexico, Chiapas, 10 mi NW Ocozocoautla (25 mi W Tuxtla Gutiérrez), Ocuilapa, 3500 ft.

TYPE.—Adult, sex unknown, skin and partial skull; British Mus. Nat. Hist. No. 43.6.13.2 (also 1843a) (*vide*, J. E. Hill, *in litt.*, 17 July 1970); Guatemala, Alta Verapaz, Cobán (Alston, 1876).

DISTRIBUTION.—Mountains of southeastern México and Guatemala (Fig. 5). Known range from the vicinity of Zanatepec, Oaxaca, southeastward to Tamajú and Cobán, Guatemala; altitude span from 1070 m near Tamajú to 2135 m near Cotzal.

CHARACTERS.—Moderate size of body and skull (Figs. 6, 7, Table 1), posteriorly truncate nasals (Fig. 10), and three pair of mammae.

REMARKS.—Alston's description of *teguina* (1876) was preceded by Gray's presentation (1843) to the Royal Society of London of the then mounted specimen to which the name *teguina* was applied. Because Gray did not characterize the new form, such as to satisfy Articles 12 and 16 of the International Code of Zoological Nomenclature, his *teguina* is a *nomen nudum*. Alston retained it with his description. I have not seen the type specimen.

The type of *subnubilis* Goldman fits well in the series from Oaxaca and Guatemala. Viewed in the light of known variances within single populations of the species, the type of *subnubilis* provides no sound reason for assuming that the populations in the vicinity of Ocuilapa are differentiated, as indicated by Goldman (1935), from those to the west or east of that locality. It is clear, however, that an entirely satisfactory appraisal of relationships of the populations in México, Guatemala and Honduras must await larger samples representing adequate geographic coverage of the region.

SPECIMENS EXAMINED.—Thirteen from the following localities:

Guatemala. Alta Verapaz: near Cobán, 4200 ft, 3 (CM); 2 mi W Tamajú 3500 ft, 2 (US); near Tukurú, Finca Concepción, 1100 m, 1.

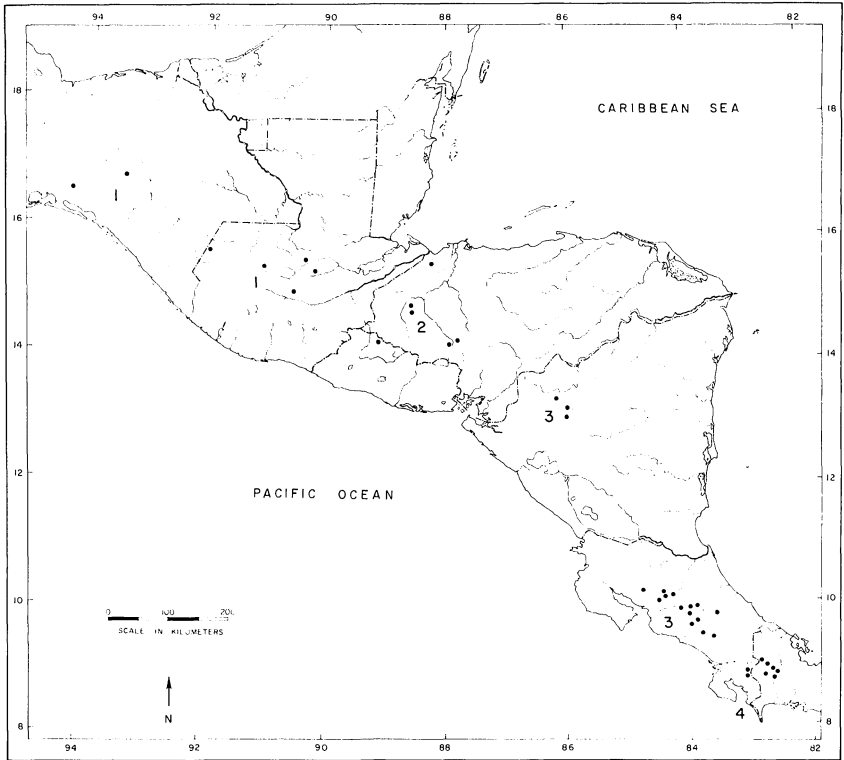


FIG. 5. Geographic distribution of *S. teguina* as indicated by specimens examined (filled circles): 1, *S. t. teguina*; 2, *S. t. rufoniger*; 3, *S. t. irazu*; 4, *S. t. apricus*.

Baja Verapaz: 5 mi N, 1 mi W El Chol 6000 ft, 1 (KU). Huehuetenango: Hacienda El Injerto, 1600 m, 1. Quiché: Cotzal, 7 mi E Río Cotzal, 4600 ft, 1 (US).

Mexico. Chiapas: 10 mi NW Ocozocoautla, Ocuilapa, 3500 ft, 1 (US). Oaxaca: Juchitán, Zanatepec, 5000 ft, 3 (US).

*Scotinomys teguina rufoniger* Sanborn

*Scotinomys teguina rufoniger* Sanborn, 1935:84.

*Scotinomys teguina teguina*, Goodwin, 1942:170.

TYPE.—Skin and skull; Field Mus. Nat. Hist. No. 22387; Honduras, Cortés?, mountains west of San Pedro Sula, 4500 ft; collected 1 April 1923 by Karl P. Schmidt and Leon L. Walters; orig. No. 51.

DISTRIBUTION.—Wet-forest uplands of Honduras and El Salvador (Fig. 5). Known range from the mountains west of San Pedro Sula



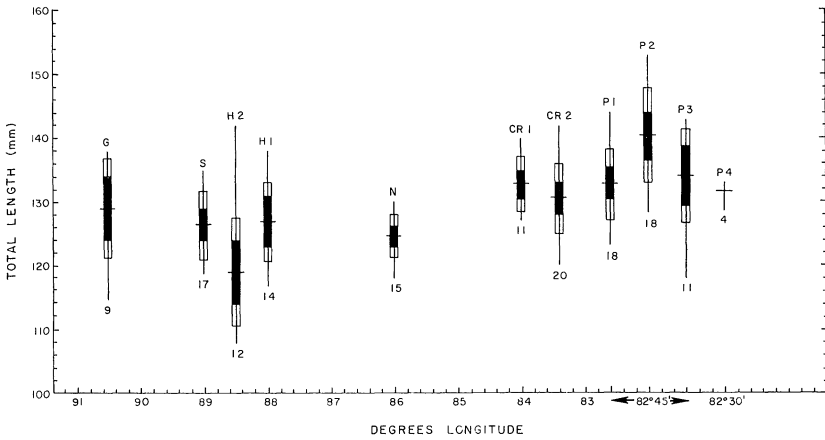


FIG. 6. Diagrams of total length in samples of *S. teguina* from Guatemala (G), El Salvador (S), Honduras (H 1, 2); Nicaragua (N); Costa Rica (CR 1, 2); and Panamá (P 1, 2, 3, 4). In each diagram the vertical line indicates range of sample, with mean (cross bar) and two standard errors (vertical bar) and one standard deviation (open rectangle) above and below the mean; numeral indicates sample size.

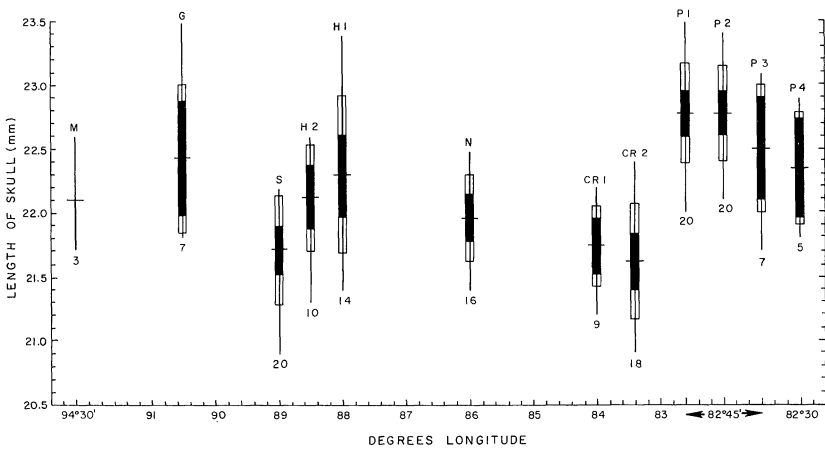


FIG. 7. Diagrams of length of skull in *S. teguina*. See Fig. 6 for explanation.

southward to Monte Linderos, Honduras and Los Esesmiles, El Salvador; vertical range from 1000 m at Lepaera to 2620 m on Monte Linderos, Honduras.

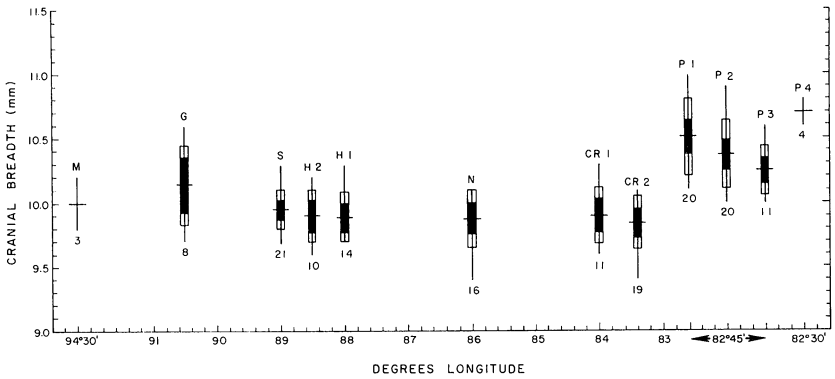


FIG. 8. Diagrams of cranial breadth in *S. teguina*. See Fig. 6 for explanation.

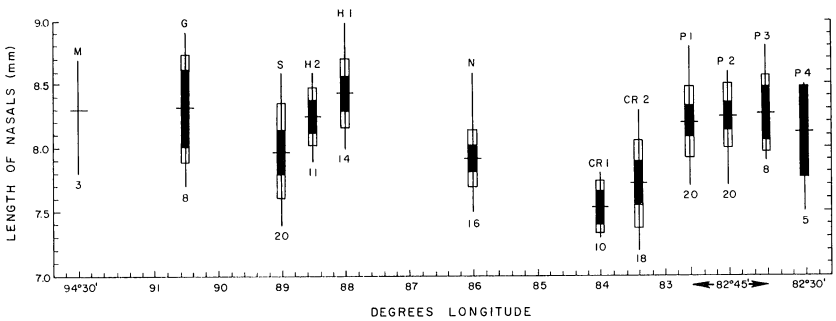


FIG. 9. Diagrams of length of nasals in *S. teguina*. See Fig. 6 for explanation.

**HABITAT AND FOOD.**—Examples from Los Esemiles were obtained in montane “oak rain forest” or “cloud” forest in situations as follows: under rotten logs; among moss and ferns at base of a tree; beside a hole in moss; in holes in logs among ferns.

Specimen tags indicate stomach contents as follows: starchy pulp; seeds and insects; fruit pulp; green pulp; insects and starchy pulp.

**CHARACTERS.**—Long relatively narrow cranium (Figs. 7, 8) with long, posteriorly attenuate nasals (Figs. 9, 10); three pair of mammae.

**REMARKS.**—The slimmer appearing skull with its narrow brain case (Fig. 8) and posteriorly V-shaped nasals (Fig. 10) constitute principal features distinguishing the samples from El Salvador and Honduras (*rufoniger*) from those to the north (*teguina*). These two sets

differ little, or not at all, in color or in size of other external or cranial parts (Figs. 6 to 9, Table 1). The dark pelage and "flat" cranial profile said to characterize *rufoniger* (Sanborn, 1935) also obtain in samples to the west (*teguina*) and southeast (*irazu*).

The specimens from El Salvador resemble those from Honduras externally and cranially, but on the average are smaller in length of skull and nasals (Figs. 7, 9); in size they are like examples from Nicaragua.

In samples from localities to the southeast, to which the name *irazu* may be applied, the nasals are shorter and truncate posteriorly (Figs. 9, 10) and there are two pair of mammae. There are no records of pectoral mammae in the specimens of *S. teguina* south of Honduras and El Salvador. Relationships of *rufoniger* and *teguina* should be re-examined when additional samples providing better geographic representation are available.

SPECIMENS EXAMINED.—Ninety-nine from localities as follows:

El Salvador. Chalatenango: Los Esesmiles, 7100–8000 ft, 35 (29 MVZ, 6 MZ).

Honduras. Cortés?: mts. west of San Pedro Sula, 4500 ft, 3 (CM). La Paz: Cerro Linderos, 8700 ft, 1 (AM); Humuya, 36 (AM). Lempira: Cerro Puca, 6600 ft, 23 (AM); Lepaera, 3300 ft, 1 (AM).

#### *Scotinomys teguina irazu* Allen

*Akodon irazu* Allen, 1904:46.

*Scotinomys irazu*, Thomas, 1913:409.

*Scotinomys teguina cacabatus* Goodwin, 1945:1. Costa Rica, Alajuela, near Villa Quesada, Lajas, 5000 ft.

*Scotinomys teguina escazuensis* Goodwin, 1945:2. Costa Rica, San Jose, upslope from Escazú, Los Higuerones, 5000 ft.

*Scotinomys teguina irazu*, Goodwin, 1945:2.

*Scotinomys teguina stenopygius* Buchanan and Howell, 1967:414. Nicaragua, Matagalpa, 12 km N Matagalpa, Santa María de Ostuma, 1250 m.

TYPE.—Adult female, skin and skull; Amer. Mus. Nat. Hist. No. 18128; Costa Rica, Cartago, Volcán Irazú; collected 23 Feb. 1902 by M. A. Carricker, Jr.

DISTRIBUTION.—Humid montane areas of Nicaragua and Costa Rica (Fig. 5). Known range from the vicinity of San Rafael del Norte and Río Coco, Nicaragua southeastward into the Cordillera de Talamanca east of San Isidro del General, Costa Rica; altitudinal span

from approximately 1100 m near Escazú to 2940 m on Volcán Irazú, Costa Rica.

**HABITAT AND FOOD.**—Most or all of the localities of record lie in premontane (“subtropical”) to montane wet or rain forest zones of Tosi (1969). Reduced insolation by cloud cover, moderate temperatures, and high humidity typify these zones; in the wettest of them the epiphyte-draped forests are bathed in clouds or drenched by daily rains through the year.

Listed below are a few specific situations where specimens were obtained. Santa María de Ostuma, Nicaragua: in runways beneath ferns and forbs on a wet cut-bank; beneath logs in a dense, stream side, second-growth forest; in runways beneath logs and among ferns and other low-growing plants on a hillside covered with virgin forest. Volcán Irazú: in runways beneath a dense mat of native grasses beside a fence and a ditch, the area of native grasses and shrubs bordered by pastures of kikuyu (*Pennisetum clandestinum*) and other introduced grasses; under roots and brush among trees in pastures; in runways in a grassy and weedy fencerow. Moravia de Chirripó: runways at base of stumps and beside logs among grass and weeds at edge of wet forest. Monte Verde: in runways among grass, ferns, forbs and cultivated flowers in and around a greenhouse in recently cleared premontane rain forest.

Insects are a principal food of *S. teguina*. Of 16 stomachs from Panamá and Costa Rica examined under a microscope all contained insect parts; in 13 of the 16 those parts amounted to 80 per cent or more of the volume. These and other data will appear in greater detail in a subsequent report.

**CHARACTERS.**—Comparatively short cranium with narrow brain case (Figs. 7, 8) and short, posteriorly truncate nasals (Fig. 10); two pair of mammae. Distinguishable from *apricus* by its shorter narrower skull (Figs. 7, 8) with shorter nasals that are gradually tapered, rather than having the margins bowed mediad about midway in their length (Fig. 11). Like *rufoniger* in size (Figs. 6, 7), but nasals shorter and truncate, rather than acuminate posteriorly, and mammae in two pairs rather than three.

**REMARKS.**—The samples indicate that in Nicaragua and Costa Rica as well as elsewhere in the range of *S. teguina* there are local differences in size and pelage coloration associated with terrain and climate. Samples from perennially cloud-covered wet areas may have

darker pelage than others from nearby and more sunny altitudinal belts. Similarly, size of skull may vary geographically over short distances, suggesting demic patterns in the populations. Some of these have been formally recognized under the names *cacabatus*, *escazuensis*, and *stenopygius*. If the objective is to point to local variants, the number of named populations of *teguina* may be increased many fold in recognition of the complicated mosaics in terrain and characteristics of populations of the region. But there are not yet adequate samples from enough areas to permit that detailed analysis, and only broader variational patterns, as that designated here under the name *irazu*, are now adequately documented.

The specimens from Santa María de Ostuma, the type locality of *stenopygius*, are small on the average, like examples from Costa Rica and El Salvador. The other characters ascribed to the form (Buchanan and Howell, 1967) simply do not hold as taxonomically distinctive population attributes on the basis of the larger, more nearly adequate samples now at hand. This is also true of the features said to characterize *cacabatus* and *escazuensis* (Goodwin, 1945).

**SPECIMENS EXAMINED.**—One hundred and ninety from the localities listed below.

Costa Rica. Alajuela: Lajas, 9 (AM); San Ramón, 4 (CM); Tapezco, 3 (AM); Volcán Poas, 2400 m, 1 (MZ); Zarcero, 1 (CM). Cartago: La Carpentera, 1 (AM); vicinity of Cartago, 4500–4800 ft, 8 (MZ); Moravia de Chirripó, 1116 m, 15 (MZ); Tapanti, 1200 m, 1 (MZ); Volcán Irazú, hwy. #8, 2800–2940 m, 40 (18 AM, 21 MZ, 1 CM). Heredia: 1.2 mi N Angel Falls, 5000 ft, 2 (LA). Puntarenas: Monte Verde, 1430 m, 14 (12 MZ, 2 LA). San José: 3 km E Canaan, 6600 ft, 5 (LSU); El Copey de Dota, 6000 ft, 4 (MZ); Escazú, 3000 ft, 4 (AM); S of Escazú, Los Higuerones, 1370 m, 42 (AM); 9–10½ N San Isidro del General, 4800–5200 ft, 3 (1 LA, 2 MZ).

Nicaragua. Jinotega: Hacienda La Trampa, 1 (KU); San Rafael del Norte, 6 (AM). Jinotega?: Río Coco, 5100 ft, 1 (AM). Matagalpa: 9 km N Matagalpa, Santa María de Ostuma, 1300–1400 m, 25 (3 UCLA).

*Scotinomys teguina apricus* Bangs

*Akodon teguina apricus* Bangs, 1902:40.

*Scotinomys teguina apricus*, Thomas, 1913:409.

*Scotinomys teguina episcopi* Enders and Pearson, 1939:1. Panamá, Chiriquí, 10 mi WNW El Volcán Post Office, Río Colorado (tributary of Río Chiriquí Viejo), Siola, 4100 ft.

- Scotinomys teguina garichensis* Enders and Pearson, 1939:2. Panamá, Chiriquí, 5 mi SW El Volcán Post Office, Río Gariché, 3200 ft.
- Scotinomys teguina leridensis* Enders and Pearson, 1939:3. Panamá, Chiriquí, near Boquete, Finca Lerida, Casita Alta, 7000 ft.
- Scotinomys teguina endersi* Goodwin, 1946:409. Costa Rica, Puntarenas, Aqua Buena, 3500 ft.

TYPE.—Adult female, skin and skull; Mus. Comp. Zool., Harvard Univ., No. 10236; Panamá, Chiriquí, vicinity of Boquete; collected 24 February 1901 by W. W. Brown.

DISTRIBUTION.—Mountains of eastern Costa Rica and western Panamá (Fig. 5). Known range from the vicinity of San Vito de Java, Costa Rica to localities near Boquete, Panamá; vertical span from 975 m on the Río Gariché to 2135 m on Finca Lerida, Panamá.

HABITAT AND FOOD.—Listed below are a few places of capture of examples in montane moist and wet forest zones of the valley of the Río Chiriquí Viejo, Panamá: under shrubs and logs bordering a soggy grassy pasture and a steep hillside covered with second growth forest; runway at base of cutbank below overhanging vegetation; within primary forest in runways at base of trees near a brook and among shrubs; runways through grass along a fence between pastures; within a 10-foot wide fence-row of grass, weeds, blackberry, bamboo and shrubs separating a pasture and a corn field; on rocky floor of dry oak forest adjoining grassland.

CHARACTERS.—Large body and skull (Figs. 6, 7, Table 1); nasals posteriorly truncate and their lateral margins bowed mediad about midway in their length (Figs. 10, 11); two pair of mammae.

REMARKS.—The populations here known by the name *apricus* are well differentiated from the others of *S. teguina*. They are among the largest in external size (Fig. 6), but it is in cranial rather than external features that they are set apart as an extreme in the observed range of variation in the species. The long skull with broad brain case and long peculiarly shaped nasals (Figs. 7 to 11) are unique. The nasals appear unusually broad distally and instead of becoming gradually narrow posteriad they remain comparatively broad in their distal half, then abruptly constrict and gradually taper to a truncate base.

These features characterize all samples of Panamá and eastern Costa Rica and provide a sound basis for the recognition of *apricus*. Giving formal attention to this apparently natural grouping of the samples and the populations they represent, however, overrides minor

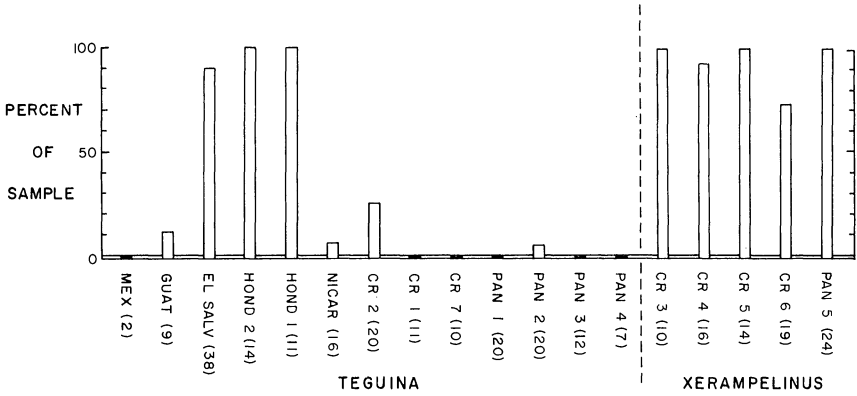


FIG. 10. Frequencies (per cent of each sample) of posteriorly attenuate, in contrast to truncate, nasal bones in 18 samples of *Scotinomys* from México (Mex) southeastward to Panamá (Pan). Numbers of specimens in parentheses.

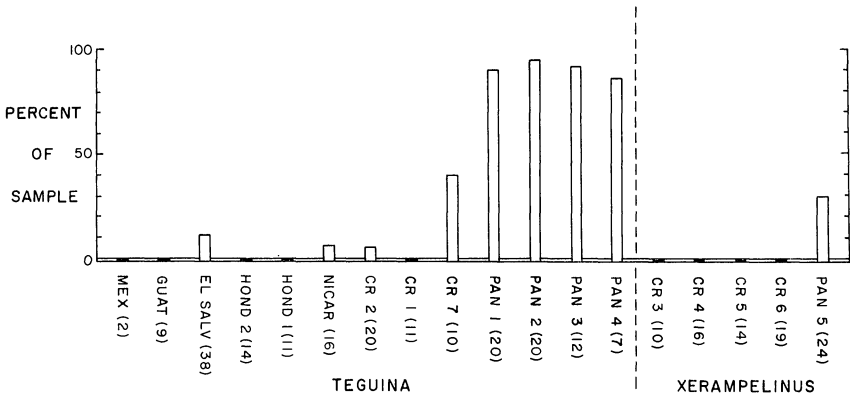


FIG. 11. Frequencies (per cent of each sample) of bowed, in contrast to gradually tapered, lateral margins of nasal bones in *Scotinomys* from México (Mex) southeastward to Panamá (Pan). Numbers of specimens in parentheses.

variations among samples in pelage coloration or in size of some external or cranial part. Most of these minor differences between samples in color and size will not hold as population characteristics when they are judged in the light of the variance observed in large recently-obtained series of specimens representing the gamut of ages and seasons at a locality. The characters ascribed to *episcopi*, *garichensis* and *endersi* appear to be local variations of this sort, and by the stand-

ards employed here provide inadequate basis for the recognition of those forms.

SPECIMENS EXAMINED.—One hundred and fifty-six from the following localities.

Panamá. Chiriquí: Cotito Hot Springs, 4900 ft, 13 (ANS); Cerro Pando, 4800 ft, 8 (ANS); vicinity Volcán de Chiriquí: El Banco, 1 (CM); "Camp 1," 2 (ANS); Casita Alta, 2 (ANS); Cerro Punta, 3 (ANS); Finca Lerida, 5000 ft, 10 (ANS); Río Chebo, 4 (ANS); Río Chiriquí Viejo, Wald, 3800 ft, 2 (ANS); Río Chiriquí Viejo, 1700–1880 m, 32 (MZ); Río Gariché, 3200 ft, 16 (ANS); Río Santa Clara, 18 (ANS); Siola, 4100 ft, 42 (ANS).

Costa Rica. Puntarenas: Cañas Gordas, 2 (AM); 5 km S San Vito de Java, Finca Las Cruces, 1200 m, 1 (MZ).

*Scotinomys xerampelinus* Bangs

*Akodon xerampelinus* Bangs, 1902:41.

*Scotinomys xerampelinus*, Thomas, 1913.

*Scotinomys longipilosus* Goodwin, 1945:2. Costa Rica, Cartago, Volcán Irazú, 9400 ft.

*Scotinomys harrisi* Goodwin, 1945:3. Costa Rica, Cartago, Las Vueltas, 8000 ft.

TYPE.—Adult male, skin and skull; Mus. Comp. Zool., Harvard Univ., No. 10240; Panamá, Chiriquí, Volcán de Chiriquí, 10,300 ft; collected 26 May 1901 by W. W. Brown.

DISTRIBUTION.—From montane wet and rain forest belts upslope into dwarf forest or "heath" ("paramo") zones of Costa Rica and Panamá (Fig. 12). Known range from Volcán Irazú and Volcán Turrialba southeastward in the Cordillera de Talamanca to Volcán Chiriquí; altitudinal range from 2150 m at Casita Alta near Chiriquí at least to 3300 m on Cerro de la Muerte, Costa Rica and 3200 m on Volcán Chiriquí, Panamá.

HABITAT AND FOOD.—The species occurs under appropriate cover on the floor of forests, in mixed growth in ecotones between forests and open situations, under dense grass or forbs on "potreros," and under low shrubs and "heath-type" growth on cold windswept summits of peaks and ridges. Examples of specific places of capture follow. Vicinity of Cerro de la Muerte: beneath logs and tree roots among moss, liverworts, and ferns on cloud-drenched wooded hillsides; runways in tall grass and shrubs in second-growth forest; among rocks, moss, ferns,



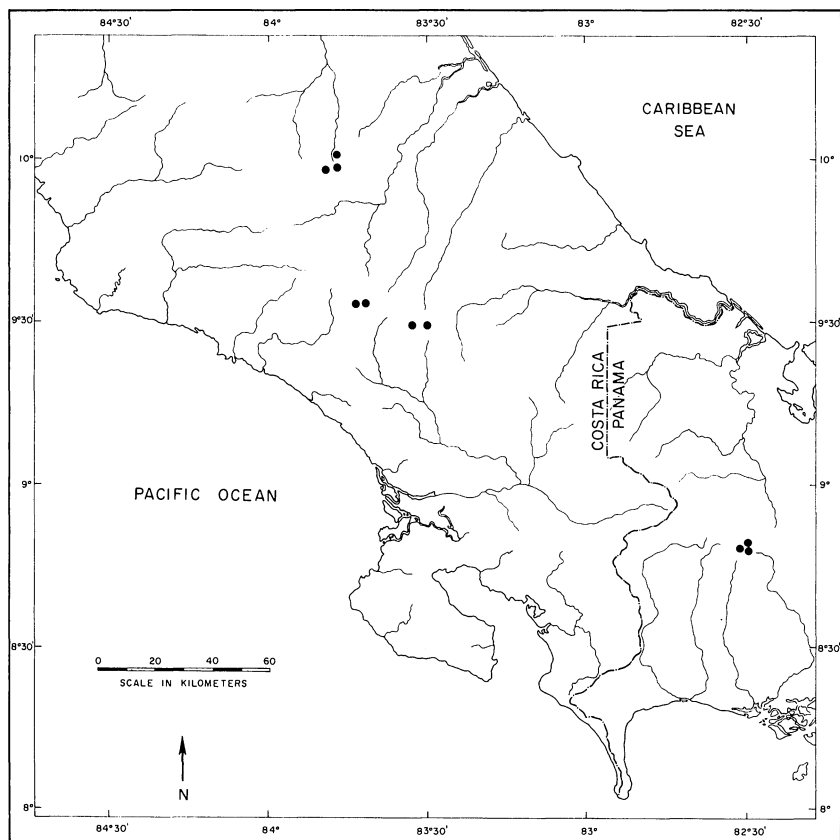


FIG. 12. Part of Central America showing distribution of *S. xerampelinus* as indicated by specimens examined (filled circles).

grass and low shrubs; under brush and rocks on cloud-enshrouded second-growth-covered hillside. Volcán Irazú and Volcán Turrialba: in runways in tangles of grass, weeds, blackberry, and exposed roots of trees (oaks and other); in runways beside logs in grassy pasture; in runways under matted grass on "cleared" hillsides and potreros; among grass, forbs, blackberry and other vines at border between an alder thicket and grassland.

Insect parts were present in each of 20 stomachs examined and amounted to 100 per cent of the volume in 17 of the 20.

CHARACTERS.—Averages slightly larger than *S. teguina* in most measurements (Table 1); tail disproportionately longer; nasals typically

gradually tapered, acuminate basally (Figs. 10, 11); optic foramen much smaller than orbital fissure (Fig. 3, Table 1), its transverse diameter much less than that of the occlusal surface of  $M^3$  (foramen  $> M^3$  in *teguina*); masseteric process situated more dorsally relative to molar row (Fig. 3, Table 1); two pair of mammae.

REMARKS.—The species *xerampelinus* and *teguina* are for the most part allopatric, *xerampelinus* occurring above 2100 meters and *teguina* ranging in premontane and lower montane belts (Figs. 5, 12). The two are known to occur together at three localities, however, and I would expect a narrow band or discontinuous pockets of sympatry along much of the lower edge of the range of *xerampelinus*. To judge from current records these areas of overlap or contiguity are in the altitudinal range 2200–2800 meters, and usually in upper parts of it. Factors, now unknown, which control the lower limit of *xerampelinus* and upper boundary of *teguina* are the subject of a concurrent laboratory and field project and will be reported elsewhere. Preliminary information indicates that perennial moisture and cloud cover importantly influence the occurrences of the species.

Following are examples of sympatry or close contiguity of range. In discussing distribution of *Scotinomys* in Chiriquí Province, Panamá, Enders and Pearson (1939:4) indicate that “a single specimen of *xerampelinus* was obtained near the same location” where four of the five examples of *S. t. leridensis* were trapped. This was “in or near an abandoned planting of fruit trees near Casita Alta at approximately 7000 feet.” The authors provide no further information regarding sympatry of the species.

We have found both species within 100 meters of one another at two localities near the highway (No. 8) on Volcán Irazú. One of these is in and adjoining the canyon that opens out at Hotel Robert; the trapping locality is upslope,  $\frac{1}{8}$  mile north of the Hotel at 2850 meters. In 1962 we obtained *teguina* on the rather dry brush-and-tree-covered slopes of the canyon, and *xerampelinus* in fencerows of grass with a few shrubs on the adjoining steep pasturelands. In 1969 I found neither form in this same area, but located *teguina* in a similar fencerow about an eighth of a mile to the east and 25 meters higher (2875 m *vide* topographic map, 1:50,000, Instituto Geografico de Costa Rica, 1961).

The second area on Irazú where the two species occurred close to each other and likely were in contact is on La Pastora, a “lechería” (dairy farm) along Highway 8 higher on the mountain. Both species were trapped in the vicinity of the headquarters houses and barns, ele-

vation 2940 meters. Only *teguina* was obtained slightly lower near the highway (2900 m) and only *xerampelinus* at 3000 meters upslope along the highway. A zone of contact and sympatry, thus, on southern flanks of Irazú is within 2850 and 2950 meter levels.

Altitudinal limits for the species must be quite different, however, around the mountain to the east where the slopes are more frequently bathed by moisture-laden winds from the Caribbean and, as a result, there is more lush and epiphyte-draped native vegetation. There in that wetter zone *xerampelinus* ranges to lower elevations, for example to 2350 m on Finca Coliblanco on Irazú and at least to 2600 m at El Retiro on the flanks of Volcán Turrialba. If the two species have different ecological preferences those preferences have yet to be precisely defined.

The five principal samples of *xerampelinus* at hand—from Volcán Turrialba, Volcán Irazú, Cerro de la Muerte, Volcán Chirripó Grande, and Volcán Chiriquí (see specimens examined)—are closely similar in all external and cranial characters. In the Chiriquí series, however, there is a dilution in some of the traits which contrast *xerampelinus* with *teguina* in Costa Rica. In the Chiriquí series, for example, there is more variance in the size of the optic foramen, such that in some specimens the contrast between the foramen's diameter and that of  $M^3$  diminishes, approaching that seen in *teguina* (coefficient of variation in foramen/ $M^3$  index is 29 in Chiriquí, 12 in Chirripó and 0 in the others). The position of the masseteric tubercle on the average also is lower on the skull in the Panamanian specimens and, in addition, the palatine foramina on the average terminate farther posteriorly relative to  $M^1$  than in all Costa Rican samples except that from Volcán Chirripó. These traits might be employed as the basis for treating the central Costa Rican populations and those from Panama as different subspecies.

By the criteria employed in this report, however, that basis is inadequate, and for this reason *longipilosus* and *harrisi* are treated as synonyms of *xerampelinus*. Both of those clearly are of the species *xerampelinus* and to judge from Goodwin's description of *longipilosus* (1945) that type together with the type of *harrisi* can be immersed without further recognition in the series from Irazú, Turrialba, Cerro de la Muerte and, through the Chirripó series into that of Chiriquí.

**SPECIMENS EXAMINED.**—One hundred and eighty-five from localities as follows:

Costa Rica. Cartago: vicinity of Cerro de la Muerte, 9700–11,000 ft, 36 (19 LSU, 14 MZ, 2 LA, 1 MVZ); Las Vueltas, 8000 ft, 1 (MZ);

Volcán Irazú, Hwy #8, 2850–3200 m, 13 (MZ); Finca Coliblanco, 2350 m, 17 (MZ); Volcán Turrialba, 2590–2800 m, 11 (MZ). San Jose: 7.5 km E Canaan, Fila La Maquina, 8700 ft, 2 (LSU); 4 km SW Cerro Chirripó Grande, La Piedra, 10,500 ft, 22 (LSU); Cerro Chirripó, headwaters Río Talari, 11,000 ft, 12 (LSU).

Panamá. Chiriquí, vicinity of Volcán de Chiriquí (ANS): Casita Alta, 7800 ft, 6; Copeta, 10,000 ft, 7; Cylindro, 8; Hortigal, 8; Sardinia, 4; Potrero, 10,200–10,600 ft, 38.

TABLE 1  
EXTERNAL AND CRANIAL DIMENSIONS AND INDEXES IN 5 SAMPLES OF *S. teguina*  
AND OF *S. xerampelinus*.<sup>1</sup>

Characters and Samples	n	Measurements (mm) and Indexes			Range
		$\bar{x}$	2SE $\bar{x}$	s	
Total length:					
Guat	9	129	4.94	7.41	115–138
Salv	17	126	2.56	5.27	119–135
Nic	15	124	1.77	3.42	118–130
CR 2	20	130	2.48	5.55	120–142
Pan 1	18	133	2.66	5.65	123–144
CR 4	15	149	4.99	9.67	136–164
CR 6	19	149	2.61	5.68	137–160
Pan 5	23	149	2.21	5.29	137–158
Tail vertebrae:					
Guat	9	53	3.07	4.60	46–58
Salv	19	51	1.15	2.51	47–56
Nic	15	48	.95	1.83	45–51
CR 2	20	54	1.73	3.87	45–63
Pan 1	18	55	1.26	2.68	50–62
CR 4	15	72	2.10	4.08	66–80
CR 6	19	69	1.39	3.04	65–76
Pan 5	23	69	1.19	2.84	65–75
Hind foot, length:					
Guat	9	18	.47	.71	17–19
Salv	21	18	.35	.81	15–19
Nic	16	17	.34	.68	16–18
CR 2	20	17	.32	.73	16–19
Pan 1	20	18	.37	.82	16–19
CR 4	16	19	.32	.63	18–20
CR 6	19	19	.28	.60	18–20
Pan 5	23	19	.31	.74	17–20

<sup>1</sup> For further explanation, see text.

Characters and Samples	n	Measurements (mm) and Indexes			Range
		$\bar{x}$	2SE $\bar{x}$	s	
Ear, length:					
Guat	5	16	1.47	1.64	14-18
Salv	9	13	.48	.73	12-14
Nic	14	13	.42	.83	12-14
CR 2	19	13	.32	.69	12-14
Pan 1	20	13	.32	.72	12-14
CR 4	16	14	.48	.97	12-15
CR 6	19	16	.30	.66	15-17
Pan 5	24	14	.29	.72	13-16
Skull, length:					
Guat	7	22.4	.44	.59	21.8-23.5
Salv	20	21.7	.19	.43	20.9-22.2
Nic	16	22.0	.17	.33	21.4-22.5
CR 2	18	21.6	.22	.47	20.9-22.4
Pan 1	20	22.8	.18	.40	22.0-23.5
CR 4	15	22.6	.41	.79	21.5-24.2
CR 6	19	23.3	.18	.40	22.5-24.2
Pan 5	23	22.8	.24	.57	21.2-23.7
Cranial breadth:					
Guat	8	10.1	.22	.31	9.7-10.6
Salv	21	10.0	.06	.14	9.7-10.3
Nic	16	9.9	.11	.21	9.4-10.1
CR 2	19	9.8	.10	.22	9.4-10.1
Pan 1	20	10.5	.13	.29	10.1-11.0
CR 4	16	10.5	.13	.27	10.0-10.8
CR 6	19	10.4	.09	.19	10.0-10.8
Pan 5	22	10.4	.09	.22	10.1-10.9
Nasals, length:					
Guat	8	8.3	.31	.43	7.7-8.9
Salv	20	8.0	.17	.39	7.4-8.6
Nic	16	7.9	.12	.24	7.5-8.6
CR 2	18	7.7	.17	.35	7.2-8.3
Pan 1	20	8.2	.12	.28	7.7-8.8
CR 4	15	8.5	.23	.45	7.6-9.3
CR 6	19	8.6	.12	.26	8.0-9.2
Pan 5	23	8.3	.18	.43	7.2-9.0
Interorbital breadth:					
Guat	8	4.4	.11	.16	4.2-4.7
Salv	21	4.2	.06	.13	4.0-4.5
Nic	16	4.2	.05	.10	4.0-4.4
CR 2	20	4.1	.05	.11	3.9-4.3
Pan 1	20	4.3	.06	.14	3.9-4.5
CR 4	16	4.5	.07	.13	4.2-4.7
CR 6	19	4.5	.07	.15	4.2-4.7
Pan 5	24	4.4	.06	.15	3.9-4.7

Characters and Samples	n	Measurements (mm) and Indexes			Range
		$\bar{x}$	2SE $\bar{x}$	s	
<b>Maxilla, dorsally:</b>					
Guat	9	.71	.08	.13	.57-.92
Salv	21	.68	.05	.12	.46-.91
Nic	16	.77	.05	.10	.56-.91
CR 2	20	.69	.05	.11	.43-.87
Pan 1	20	.79	.03	.07	.66-.90
CR 4	16	.48	.04	.08	.35-.68
CR 6	19	.63	.03	.07	.50-.76
Pan 5	24	.56	.03	.08	.41-.70
<b>Molar row, length:</b>					
Guat	9	3.9	.11	.16	3.7-4.1
Salv	21	3.9	.05	.12	3.7-4.2
Nic	16	4.0	.05	.10	3.9-4.2
CR 2	20	3.9	.05	.11	3.6-4.0
Pan 1	20	4.1	.06	.14	3.7-4.3
CR 4	16	4.0	.09	.18	3.8-4.3
CR 6	19	4.2	.06	.13	4.0-4.5
Pan 5	24	4.0	.06	.15	3.6-4.2
<b>Palatine foramina:</b>					
Guat	9	2.9	.22	.33	2-3
Salv	21	2.1	.40	.91	1-3
Nic	16	3.0	0	0	3
CR 2	20	2.8	.23	.52	1-3
Pan 1	20	2.6	.27	.61	1-3
CR 4	16	1.3	.22	.45	1-2
CR 6	19	1.7	.34	.73	1-3
Pan 5	24	1.7	.28	.69	1-3
<b>Masseteric process:</b>					
Guat	9	2.6	.35	.53	2-3
Salv	21	2.6	.29	.67	2-4
Nic	16	2.8	.20	.40	2-3
CR 2	20	2.0	.18	.39	1-3
Pan 1	20	2.4	.22	.49	2-3
CR 4	16	4.8	.43	.86	4-6
CR 6	19	3.8	.32	.69	3-6
Pan 5	24	3.6	.21	.50	3-4

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