ZOOGEOGRAPHY OF *SCOTINOMYS* IN MIDDLE AMERICA, WITH THE DESCRIPTION OF A NEW SUBSPECIES FROM NICARAGUA

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ABSTRACT.—The distribution of the cricetid rodent genus *Scotinomys* is briefly reviewed, and its distribution as a Middle American endemic is shown to coincide with the distribution of cloud forest, or upper humid montane forest. A new subspecies of *S. teguina* is described from north-central Nicaragua, and the significance of the Nicaraguan gap in the distribution of this mid-montane species is defined.

Few genera of cricetid rodents are restricted to tropical Middle America. Of these, only one, *Scotinomys* Thomas, 1913, is seemingly confined to the middle-montane regions—those areas lying predominately between 1000 and 3000 m, clothed in cloud forest, humid broadleaf forest, or wet montane savanna, i.e., regions that are frequently referred to as Upper Humid Tropical Zone (Goldman, 1920: 38), or Subtropical Wet Forest (Holdridge, 1947: 367–368). The genus *Scotinomys*, with four described species, ranges discontinuously from Boquete, Chiriqui, Panama, north through the Cordillera Central to Ocuilapa, 10 miles NW of Ocoyocoautla, Chiapas, Mexico. Despite the allegedly continuous distribution of the genus in Middle America inferred by interpolation of collecting localities (Hall and Kelson, 1959: 668–671), *Scotinomys* has not been heretofore reported from the 300-mile expanse bridging south-central Honduras (Goodwin, 1942: 169–170) and the Tapesco area of north-central Costa Rica (Goodwin, 1946: 408). In view of the approximately 100-mile stretch of lowlands in southern Nicaragua, it is of particular interest zoogeographically to delimit more precisely the distribution of montane species such as those comprising the genus *Scotinomys*.

One of the results of a series of collections made in Nicaragua in recent years by the authors was the discovery of a representative of the genus *Scotinomys* in a cloud forest in the north-central highlands of that country. Four specimens were obtained, which were expected to be referable to the species *teguina* on geographical grounds; comparison with a series of *teguina* from Honduras and Costa Rica showed that the Nicaraguan material represents an heretofore undescribed subspecies, which may be known as

Scotinomys teguina stenopygius, new subspecies

Holotype.—Univ. California (Los Angeles) no. 19,234; young adult female, skin and skull, in perfect condition; from Santa Maria de Ostuma, 12 km N Matagalpa, 1250 m, Departamento de Matagalpa, Nicaragua; collected 15 December 1961 by O. M. Buchanan, Jr., original no. 982. Santa Maria de Ostuma is a coffee finca located in the Cordillera Central of north-central Nicaragua, straddling the divide between the Pacific and the Caribbean drainages. The immediate locality represents a classic cloud forest, the understory of which has been cleared for coffee planting.

Diagnosis.—A small *Scotinomys*—not only the smallest of the races of *teguina*, but the smallest representative of the genus; wt 8.7 to 11.5 g (10.6); head and body relatively short (54.7% of total length); hind foot relatively long (ratio of hind foot to total length,

TABLE 1.—*Measurements of selected populations of* Scotinomys *from Middle America.*

Species or subspecies	Total length	Tail	Hind foot	Ear from notch	Greatest length of skull	Zygomatic breadth	Interorbital constriction	Length of maxillary toothrow	Length of mandibular toothrow	N
S. t. teguina	119.5 (116–126)	48.0 (45–52)	16.0 (15–17)	13.5 (12–14)	21.8 (21.1–22.5)	11.6 (11.3–12.2)	4.1 (3.9–4.2)	3.9 (3.8–4.0)	4.1 (3.8–4.2)	3 ♂♂, 2 ♀♀
S. t. stenopygius	115.7 (113–118)	50.3 (47–52)	17.8 (17–18)	13.8 (13–14.5)	21.9 (21.0–23.0)	11.0 (10.8–11.2)	4.3 (4.1–4.5)	4.0 (4.0–4.1)	4.1 (4.0–4.2)	1 ♂, 3 ♀♀
S. t. cacabatus	129.8 (125–135)	53.6 (51–55)	18.2 (17–19)	12.6 (12–13)	21.9 (21.5–22.2)	11.5 (11.5)	4.2 (4.2–4.3)	3.9 (3.6–4.0)	4.0 (3.9–4.1)	3 ♂♂, 2 ♀♀
S. t. endersi	128	57	18	12	22.6	11.0	4.0	3.5	3.6	1 ♀
S. harrisi	141	58	19	14	22.8	11.6	—	4.2	—	1 ♂ (a)
S. longipilosus	151	70	18	13	22.3	11.2	—	4.0	—	1 ♂ (b)
S. xerampilinus	145	65	17	14	21.7	11.7	4.7	4.2	4.1	1 ♂ (c)

(a) Measurements of type specimen, from Goodwin (1945: 4).
(b) Measurements of type specimen, from Goodwin (1945: 3).
(c) Measurements of type specimen, from Hall and Kelson (1959: 669); skull measurements provided by Charles W. Mack.

15.7%); ears long, the maximum length (14.5 mm) representing the greatest length known for the genus; pelvic region decidedly reduced (this character most striking in the flesh and evident in all study skins); pelage long (6.2 mm in middorsal region), and lax; color of dorsum almost uniformly dark, rich, reddish sepia, the rump region darker (i.e., fewer admixed reddish hairs) than the shoulders; underparts brownish ochre, the bases of the individual hairs dark brownish gray; ears very near the color of the dorsum, with several long (2 mm), reddish hairs emerging from the inner side of the pinna; skull of the type (a young adult) with the cranial sutures fully closed and the molars showing slight wear only; skull characteristic for the genus and species—large proportionate to body size, with broad interorbital constriction (broader in absolute measurement than any of the described subspecies of *teguina*). Measurements (mm) of the type specimen are: total length, 115; tail, 52; hind foot, 18; ear from notch, 14.5; greatest length of skull, 21.0; zygomatic breadth, 10.8; interorbital constriction, 4.4; maxillary toothrow, 4.1 mandibular toothrow, 4.2; wt, 8.7 gm.

Comparisons.—Externally, *stenopygius* may be readily distinguished from other subspecies of *S. teguina* by 1) smaller overall size, 2) proportionately longer tail, 3) proportionately longer hind foot, 4) more distinctly reduced pelvic region, 5) broad interorbital region, and 6) the exceedingly dark, rich coloration. Only one of the comparative specimens at hand, an example of *S. teguina endersi* from Canas Gordas, Costa Rica, approaches the depth and richness of coloration in *stenopygius*. However, the greater total length, shorter ear, dull overglaze of the pelage, and the narrow interorbital constriction distinguish this specimen of *endersi* from *stenopygius*. Measurements of the races of *teguina* examined, as well as the species *harrisi*, *longipilosus*, and *xerampelinus*, are given in Table 1.

Distribution.—Known only from the type locality, but probably occurs in suitable areas of cloud forest in adjacent parts of the Cordillera Central of northern Nicaragua and possibly adjacent south-central Honduras.

Specimens examined.—*Scotinomys teguina stenopygius*: Santa Maria de Ostuma, 12 km N Matagalpa, Matagalpa, Nicaragua, 4 (UCLA). *S. t. teguina*: Humuya, La Paz, Hon-

duras, 5 (AMNH). *S. t. cacabatus*: Lajas, Villa Quezada, Costa Rica, 3 (AMNH); Tapesco, Alajuela, Costa Rica, 2 (AMNH). *S. t. endersi*: Canas Gordas, Costa Rica, 1 (AMNH); 10.5 mi N San Isidro, Costa Rica, 1 (LACM). *Scotinomys* sp.: Cerro de La Muerte, 4.6 mi S La Georgina, Costa Rica, 1 (LACM). Abbreviations refer to specimens in the collections of the American Museum of Natural History, the Los Angeles County Museum of Natural History, and the University of California, Los Angeles.

Discussion

As the genus *Scotinomys* is restricted to the mid-montane regions between the Isthmus of Tehuantepec and the Isthmus of Panama, its disjunct distribution is not surprising in view of the topographic diversity of that region. The characteristic habitat of these mid-montane regions, cloud forest or "subtropical wet forest," is likewise discontinuous in Central America, and the lowlands of southern Nicaragua constitute the principal interruption in the distribution of this habitat. A brief review of the distribution of the genus *Scotinomys* and its relationship to the distribution of this habitat brings forth some interesting zoogeographic questions.

There are four currently recognized species of *Scotinomys*. *S. harrisi*, *S. longipilosus*, and *S. xerampelinus* are known only from their respective type localities in the higher (2400 to 3200 m) montane regions of Costa Rica and western Panama. The fourth species, *S. teguina*, is a polytypic form with 11 previously described subspecies; it has been recorded only at elevations between 1000 and 2200 m (Hall and Kelson, 1959: 668–671). Eight of the subspecies of *teguina* are known only from Costa Rica and Panama (*apricus, cacabatus, endersi, episcopi, escazuensis, garichensis, irazu,* and *leridensis*). Three subspecies have been previously described from the northern segment of the range of the species from Chiapas (*subnubilus*), Guatemala and Honduras (*teguina*), and Honduras (*rufoniger*); the presently described subspecies from north-central Nicaragua (*stenopygius*) thus brings to four the number of forms known from Central America north of the Nicaraguan gap. Although Hall and Kelson (1959: map 383, 670) extrapolated the range of *S. t. cacabatus*, known only from the vicinity of Tapesco, Costa Rica, to extend north across Nicaragua into southern Honduras, we know of no evidence for this assumption. It is highly improbable that *Scotinomys* occurs in the lowlands of southern Nicaragua. The contemporary range of the species *teguina* may thus be regarded as divided into at least two major parts—one north of, and one south of this lowland gap in southern Nicaragua. In view of the rather circumscribed altitudinal limits of *teguina*, other discontinuities in the distribution of the species are to be expected; however, there are no other wide, transcontinental gaps in mid-montane elevations elsewhere within the range of *teguina*. The significance of the southern Nicaraguan lowlands in the present disjunct distribution of the species is therefore clear.

One would expect that a comparison of the morphological characters of *stenopygius* with similar characters in other populations of *teguina* both to the north and to the south of the Nicaraguan lowlands would give some indication

of the relative duration of the major interruption in the range of the species. Thus, two principal alternatives would normally be expected: 1) *stenopygius* represents a form morphologically intermediate between the northern and southern populations of the species, or 2) *stenopygius* represents the termination of a cline in linear measurements from *subnubilis* in Chiapas through *teguina* in Guatemala and Honduras, with the Costa Rican populations showing characteristics that disrupt the cline. The first of these alternatives would suggest a shorter separation, the second a longer separation. Table 1 shows the relationships between linear measurements of *stenopygius* and its next adjacent population to the north, *teguina*, and to the two most northern races of the southern complex, *cacabatus* and *endersi* of Costa Rica. Certain tendencies are evident in this comparison. The subspecies *cacabatus* and *endersi* are, in general, larger than the northern populations in total length, tail, and hind foot measurements, but not in the length of the ear from notch. Measurements of *stenopygius*, however, do not show it to be a connecting morph between northern and southern populations of *teguina*, and it does not fall in line with the trends mentioned above. The single male of *stenopygius* is approximately equal in size to the largest of the three females. All four examples of *stenopygius* are small in total length, but there is no reduction in skull size, tail, hind foot, or ear from notch measurements; the latter two structures even tend to be large in comparison with those of adjacent populations. It is clear that the relatively short total length in *stenopygius* results from a marked reduction in postcranial body size, for the dimensions of the skull and the extremities have not been correspondingly reduced. Even apart from this peculiar feature, *stenopygius* does not fit into a general size trend from north to south as it has a longer tail, hind foot, and ear from notch. Thus, the characters of *stenopygius* do not fit either of the two alternatives mentioned above. The occurrence of *stenopygius* near the mid-point in the range of the species, and its morphologically discordant variation, justifies some zoogeographic comment.

The three species of *Scotinomys* known only as isolated populations at high elevations (*harrisi, longipilosus,* and *xerampelinus*) present a familiar pattern of discontinuous distribution characteristic of montane isolation. However, the discontinuous distribution of *S. teguina*, and in particular its interruption in the low Nicaraguan gap, invites further explanation. An obvious suggestion is that the range was once continuous and that orogenic changes involving subsidence and inundation resulted in extensive separation of the populations. It is entirely possible, however, that the area now called the Nicaragua gap has not been elevated much, if any, above the present level during the latter part of the Cenozoic. Thus, a continuity of montane habitat may have never existed. If separation of the contemporary northern and southern populations of *teguina* had occurred earlier than the late Cenozoic, one would expect that clear differentiation into two distinct species would have taken place. An alternative explanation is that at some time in the late Cenozoic, probably in the Pleistocene, relatively cool conditions permitted a continuity of the favored habitat of

Scotinomys across an area of low elevation. Subsequent warming and resulting ecological changes in the lowlands would require either adaptation to new conditions or a retreat to higher elevations where some condition close to the original habitat might exist. It is possible, of course, that such ecological changes may have been accompanied by increased competition from other cricetid rodents, most especially the oryzomines; an expansion of geographic range of such forms, already adapted to warm, lowland conditions, may have furthered the restriction of *Scotinomys* to a montane environment.

In studies of the distribution of Middle American vertebrates, much emphasis is usually placed on the significance of two isthmian regions—Tehuantepec and Panama (Stuart, 1957; Duellman, 1960; Baker, 1963; B. E. Harrell, unpublished data). The possible importance of the Nicaraguan region as a gap or a terminal area in the range of many species, although by no means ignored (Griscom, 1945: 133–134), seems less widely recognized by students of mammalian distribution. For example, an examination of the tabular data given by Baker (1963: 213) discloses that of the 61 polytypic species of Middle American mammals (excluding chiroptera) that are also found in South America, two-thirds of those that do not range north of the Isthmus of Tehuantepec are not known to occur north of Nicaragua. One reason for the relative neglect of the Nicaraguan region in distributional analyses is that, in terms of published specimen records, Nicaragua is very poorly known; even some common and widely distributed species are as yet unrecorded there. Future collecting in Nicaragua will fill in some apparent gaps, but many of the interruptions and terminations in distribution that occur there are undoubtedly real and not artifactual. One of the purposes of the present paper is to call attention to such a situation and to stimulate further interest in the Nicaraguan region.

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