Systematic Studies of Oryzomyine Rodents (Muridae): Definitions of *Oryzomys villosus* and *Oryzomys talamancae*

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ABSTRACT

The holotype of the Colombian *Oryzomys villosus* is shown to be a composite: the skull is an example of *Oryzomys albigularis,* the skin from an *Oryzomys talamancae*. The latter, usually included within the species definition of *O. capito,* appears to be a distinct biological species with a geographic range extending from eastern Costa Rica through Panama to the valleys and lower Andean slopes of Ecuador, Colombia, and western Venezuela; its habitat is evergreen and deciduous tropical forest from near sea level up to about 5000 ft. Identifying *villosus* and *talamancae* is part of systematically revising the genus *Oryzomys,* a task that can be accomplished by study of the many specimens now housed in collections of natural history institutions.

INTRODUCTION

We identify *Oryzomys villosus* and sketch the morphological and geographic boundaries of *Oryzomys talamancae*. From the time it was named and described by J. A. Allen in 1899, *O. villosus* has been known by only two specimens from Colombia; its morphological, distributional, and ecological characteristics have eluded taxonomists; and despite its postulated tie to four other taxa of South American muroids by four authors writing at different times, its phylogenetic relationships with other species of *Oryzomys* were unresolved and enigmatic.

Our concern is with *O. talamancae* because one of the two specimens identified as *O. villosus* turns out to be an example of *O. talamancae,* and the other, the holotype, consists of a skull from *O. albigularis* and a skin of *O. talamancae*. Although the species boundary of *O. albigularis* is incompletely known, it and its close allies are understood better than many other species of *Oryzomys*.

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The characteristics of *O. talamancae,* however, have been considered part of the imprecise and undiagnostic limits of *O. capito.* In reality, the two are not the same; *O. talamancae* has unambiguous morphological and distributional features distinguishing it from *O. capito.*

The two subjects contribute to a systematic revision of the genus *Oryzomys.* Estimated to contain more than 100 species by some biologists (Haiduk, Bickham, and Schmidly, 1979), about half that number by others (Honacki et al., 1982); thought to be composed of several distinctive subgenera in some checklists (Cabrera, 1961, for example), subgenera which others would divorce from the genus (Gardner and Patton, 1976; Carleton and Musser, 1984); the generic limits of *Oryzomys* remain obscure, the number and characteristics of the species actually a part of the genus are still unresolved, and the position of *Oryzomys* within the pattern formed by phylogenetic relationships among New World muroid rodents is currently unknown. We do know that *Oryzomys* is now placed in the subfamily Sigmodontinae, which contains more than 70 genera and 360 species, many of them Neotropical in geographic distribution. Carleton and Musser (1984, p. 310) have pointed out that "the systematics of an assemblage so speciose and anatomically and ecologically diverse still requires much attention. Specific and generic level revisionary studies are needed, particularly for South American groups." *Oryzomys* is one of those groups and a clarification of its contents and generic definition "would help resolve, to a greater or lesser degree, many of the nettlesome taxonomic problems within the South American sigmodontine fauna."

Our report is the first of a projected series documenting the identities of specimens of oryzomyine rodents in the collections of the American Museum of Natural History and the National Museum of Natural History, Smithsonian Institution. Collections at other institutions will be used for some subsequent papers and other systematists will participate in authorship. The holdings of oryzomyines at the American Museum are extensive and much of the material has been sitting in cabinets unidentified and unreported from the time it was brought into the Museum.

Through the years we have assembled the material, sorted it into kinds, and made the specimens more accessible to study by biologists than they ever were before. Many persons have expressed interest in systematically revising *Oryzomys* and its allies, a few have made forays into clarifying the species (Gardner and Patton, 1976; Myers and Carleton, 1981), and some have promised to visit the American Museum of Natural History to identify specimens, and publish their results.

But visitors to the *Oryzomys* collection have been few and far between, and the genus remains unrevised. Being impatient, we began to study the specimens. These kinds of preserved materials, consisting of study skins with associated skulls and sometimes skeletons, as well as examples preserved in fluid, are a primary source of data, the only source available for samples of many species of *Oryzomys* from the Neotropical region. At first we were concerned only with the collections at the American Museum but later turned to those at the National Museum of Natural History because their lots represented species and localities that supplemented our specimens. The morphological and geographic scope represented in just the two collections is rich enough so that by sorting specimens into groups based on features of skins, skulls, and dentitions, plotting on a map the places of capture of those examples, then looking at holotypes to associate scientific names with sorted clusters, significant hypotheses about definition, contents, and phylogenetic relationships of *Oryzomys* can be made. Our report is a contribution to that goal.

INSTITUTIONS AND METHODS

Specimens we examined or refer to are in collections at the American Museum of Natural History, New York (AMNH); the British Museum (Nat. Hist.), London (BM); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Values from measurements are in millimeters. Figures for total length, lengths of tail, hind foot, and ear are those recorded on labels attached to skins. We subtracted length of tail from total length to obtain head and body length. Cranial and dental measure-

ments were taken with dial calipers graduated to tenths of millimeters. Limits of cranial measurements are defined in Musser (1979); those for dental by Myers and Carleton (1981).

Sexual size dimorphism is trivial (Goldman, 1918) and sexes are combined in the samples from which values were derived that are listed in table 2.

ACKNOWLEDGMENTS

We are indebted to several persons for helping us understand the taxonomy and natural history of oryzomyine rodents. Foremost has been Dr. Alfred L. Gardner, who has examined most holotypes associated with the genus and either in manuscript or thought came to some kind of understanding about species-limits, generic boundaries, and habitats. He shared his information with us, pointed out many of the features he relied on to distinguish species, and urged us to test his hypotheses. His generosity, given in the context of impartial inquiry, has formed an important part of the foundation of our report. Drs. Michael D. Carleton, Philip Myers, James L. Patton, and Robert S. Voss have discussed with us results of their studies and viewpoints about the taxonomic problems with *Oryzomys*. Our paper is stronger, due to their insights and experience shared with us. Dr. Charles O. Handley, Jr., allowed us to study the large collections of *Oryzomys* he made in Panama and Venezuela with teams under his supervision. We are most grateful for his help. Dr. Sydney Anderson turned over to us his material from Bolivia so that our knowledge of the species occurring in that country would be more complete and our sketch of *O. talamancae* more accurate than would have otherwise been possible. Figures 4 and 5 were drawn by Ms. Patricia J. Wynne. Photographs are the work of Messrs. Peter Goldberg and Jim Coxe. We appreciate the fine efforts of these artists.

Oryzomys villosus

In a report on new rodents from Colombia and Venezuela, Allen (1899, p. 195) wrote that through "the liberality of Mr. Morris K. Jesup, President of the American Museum of Natural History, the Museum has been placed in possession of one of the most extensive and best prepared collections of mammals that has probably ever been brought together from a single limited locality in South America." That part of the collection from Colombia was obtained under the direction of Mr. Herbert H. Smith and was "made mainly in the vicinity of Santa Marta, Colombia, in the coast region below an altitude of 500 feet; a part, however, was collected in the lower portion of the Sierra region, at altitudes varying from 4000 to 6000 feet." And the Venezuelan specimens "are from a small collection of mammals made by Mr. F. W. Urich, in the mountainous district situated about ninety miles from Cumana."

Named and described by Allen were one new species of rabbit, 17 new species of caviomorph and muroid rodents, and two new subspecies of squirrels. Among the muroid rodents were 10 new species in the genus *Oryzomys*:

O. maculiventer—p. 204; holotype, AMNH 15306; adult male from Sierra El Libano, 6000 ft, Santa Marta District, Colombia; collected May 17, 1899 by H. H. Smith.

O. trichurus—p. 206; holotype, AMNH 15328; adult male from El Libano plantation, near Bonda, 500 ft, Santa Marta District, Colombia; collected June 29, 1899 by H. H. Smith.

O. sanctaemartae—p. 207; holotype, AMNH 15312; adult female from Bonda, Santa Marta District, Colombia; collected June 5, 1899 by H. H. Smith.

O. mollipilosus—p. 208; holotype, AMNH 15323; adult female from Valparaiso, 4500 ft, Santa Marta District, Colombia; collected May 10, 1899 by H. H. Smith.

O. magdalenae—p. 209; holotype, AMNH 15318; adult female from Minca, 2000 ft, Santa Marta District of Magdalena Province, Colombia; collected August 3, 1899 by H. H. Smith.

O. villosus—p. 210; holotype, AMNH 15321; adult female from Valparaiso, 4500 ft, Santa Marta District, Colombia; collected April 15, 1899 by H. H. Smith.

O. palmarius—p. 210; holotype, AMNH 14733; adult male from Quebrada Secca, Venezuela; collected December 10, 1898 by F. W. Urich.

O. tenuicauda—p. 211; holotype, AMNH 14737; adult male from Los Palmales, Venezuela; collected December 5, 1898 by F. W. Urich.

O. modestus—p. 212; holotype, AMNH 14734; adult female from Campo Alegre, 3000 ft, Venezuela; collected by F. W. Urich.

O. fuliventer—p. 212; holotype, AMNH 14735;

adult female from Quebrada Secca, Venezuela; collected November 23, 1898 by F. W. Urich.

We have examined the holotypes upon which these 10 taxa are based and can associate nine of the names with species currently recognized in the literature or in unpublished taxonomic revisions. The first of Allen's new *Oryzomys, O. maculiventer,* is based upon an example of *O. albigularis.* Cabrera (1961, p. 382) recognized *maculiventer* as a subspecies of *O. albigularis* and that allocation currently prevails (Gardner and Patton, 1976).

Oryzomys trichurus was regarded by Hershkovitz (1960, p. 545) as one of the many names applying to *Oecomys concolor* (which Hershkovitz called *Oryzomys concolor*). The holotype of *trichurus,* however, is really an example of *Oecomys speciosus.* In a manuscript in preparation, Musser and Carleton will show that *speciosus,* rather than being a subspecies of *O. concolor* as treated by Hershkovitz, is a distinctive species sympatric with part of what Hershkovitz identified as *O. concolor.*

The next of Allen's names, *O. sanctaemartae,* should be associated with the genus *Zygodontomys* as Cabrera (1961, p. 464) listed it, not with *Oryzomys.* Whether *sanctaemartae* designates a separate species or will be absorbed in the synonymy of a well-known species of *Zygodontomys,* such as *Z. brevicauda,* can be determined by careful taxonomic revision of the genus.

Two of Allen's names, *O. mollipilosus* and *O. magdalenae,* refer to the same species; holotypes of each are examples of *Oryzomys talamancae,* an identification we justify in the pages to follow.

Two other names, *O. palmarius* and *O. fulviventer,* were listed by Hershkovitz (1960, p. 553) as synonyms of *Oryzomys* (subgenus *Oecomys*) *concolor speciosus.* The holotypes of *palmarius* and *fulviventer* are not examples of *Oecomys speciosus* but of *Oecomys trinitatis,* which is the oldest name that should be applied to part of what Hershkovitz treated as *O. concolor.* True *concolor* (based on our examination of the holotype) is the name to use for another large-bodied species of *Oecomys,* an arrangement that will be discussed by Musser and Carleton (MS).

The holotype of Allen's *O. tenuicauda* is an example of a species in the genus *Rhipidomys,* not *Oryzomys.* Among holotypes of *Rhipidomys* stored in the American Museum, we note that the holotype of *R. caucensis,* named and described by Allen in 1913, is similar in morphology to the holotype of *R. tenuicauda* and represents the same species. Cabrera (1961) lists *caucensis* as a synonym of *R. latimanus similis* (p. 419) and *tenuicauda* as a subspecies of *R. mastacalis* (p. 423). But in the collections of *Rhipidomys* at the American Museum, none of the material labeled either *R. latimanus* or *R. mastacalis* is similar to the holotypes of *tenuicauda* and *caucensis* in features of skins and skulls. We checked Handley's report on the mammals collected during the tenure of the Smithsonian Venezuelan Project (Handley, 1976) and found that neither *tenuicauda* or *caucensis* were listed there. The reason, according to Dr. Handley, who kindly permitted us to include some of his findings based on examination of most holotypes of *Rhipidomys,* is that *R. fulviventer* is the oldest name for the small-bodied species that is represented by the holotypes of *tenuicauda* and *caucensis.* So Allen's *Oryzomys tenuicauda* really applies to *Rhipidomys fulviventer,* named and described by Thomas in 1896.

The next of Allen's new species, *O. modestus,* is based upon a holotype, which is an example of what is currently recognized as *O. capito.* Cabrera (1961, p. 387) lists *modestus* as a synonym of *O. c. velutinus.* The holotypes of *modestus* and *velutinus* (the latter was named by Allen and Chapman in 1893) clearly represent the same species, and that species is now called *O. capito.*

So of the 10 new species described by Allen in 1899, nine proved to be invalid, represented by holotypes of species already described in the literature. The tenth, *Oryzomys villosus,* has been the only one to stand recognized as a species from 1899 up to the present. For example, in the taxonomic and geographic reference to mammalian species of the world published by the Association of Systematics Collections in 1982 (Honacki, Kinman, and Koeppl, 1982), *O. villosus* is listed as a species with its geographic distribution encompassing northern Colombia. Earlier, in 1961, Cabrera (p. 396) had listed

O. villosus as a valid species in the subgenus *Oryzomys.* Between 1961 and 1982, the only other references to the species we could locate was that of Hershkovitz (1966, fn. on p. 137) who considered *O. villosus* to be a "representative" of *O. albigularis,* and the view of Gardner and Patton (1976, p. 38) who regarded *O. villosus* to closely resemble *O. capito.*

As far as we know, *O. villosus* is known only by the holotype and one other specimen. It is another of those species whose identity and relationship to other species of *Oryzomys* has remained ambiguous from the time it was described. One reason lies in Allen's undiagnostic description. Of *O. villosus,* Allen (1899, p. 210) wrote:

This is a long-tailed, rather large species, with rather large ears and a remarkably soft, short, velvety pelage throughout. (The pelage, however, seems rather worn.) The skull is short, broad, and massive, with the coronoid very low and broad, forming merely an obtuse angle without a sharp point; yet the two sides are alike and the structure seems normal. It is apparently nearly related to *O. meridensis* Thomas, but is smaller, with a relatively longer tail, very much smaller ears, and a quite different coloration. It is perhaps still nearer *O. vestitus* Thomas, also from Merida, from which its smaller size and dissimilar coloration should distinguish it.

The name *meridensis,* is currently considered to be a subspecies of *Oryzomys albigularis* (Cabrera, 1961, p. 382) and *vestitus* refers to a species of *Thomasomys,* not *Oryzomys* (Cabrera, 1961, p. 434; Handley, 1976, p. 51).

Why is it so peculiar that *Oryzomys villosus* has been related to *Oryzomys albigularis, O. capito,* and *Thomasomys vestitus*? Simply because the holotype of *O. villosus* is a composite: the skin is an example of *O. talamancae,* the skull is from a specimen of *O. albigularis.* Let's examine the identities of the two elements.

Oryzomys albigularis, according to Gardner and Patton (1976, p. 38),

is an assemblage of closely related species of large, terrestrial rodents inhabiting humid forests at middle to upper elevations. Most have variable amounts of white on the venter. Usually the white is restricted to the throat, but it may cover the entire ventral surface (e.g., in

some *maculiventer*). All have relatively large, robust skulls, usually with broad incisive foramina and moderately developed supraorbital ridges. The second upper molars lack an enamel island separating the first primary fold and the major fold (first internal fold coalesced with first primary fold).

The taxon *maculiventer* is the representative of *O. albigularis* from Departamento Magdalena in the Santa Marta District of Colombia. When Allen (1899) described *maculiventer,* he had examined 47 specimens. There are 27 now in the collection at the American Museum of Natural History. Five (AMNH 15288–15291, 23263) are from Valparaiso, 4500 ft, collected during April and June, 1899. Twenty-two, including the holotype (AMNH 15300, 15302–15309, 15293–15297, 23261, 23262, 23265, and 23267–23271), are from Sierra El Libano, 6000 ft, and were collected during May 1899. In figure 1, the cranium of *O. villosus* is contrasted with that of the holotype of *O. magdalenae* (which represents *O. talamancae*), an adult *maculiventer* from Valparaiso, and the holotype of *maculiventer*—an old adult from El Libano. The cranium of *O. villosus* is clearly unlike the smaller *magdalenae* and closely similar to the specimens of *maculiventer,* especially the adult from Valparaiso which, judged from wear of the molars, is similar in age to *villosus.* We could not find any qualitative features that would separate the cranium of *villosus* from specimens of comparable age in the series of *maculiventer* from either Valparaiso or El Libano. Measurements of size, expressed by values of lengths of skull and molar row, also support our identification (table 1): the cranium of *villosus* is simply an example of *maculiventer,* a taxon which is now associated with *O. albigularis.*

The skin of the holotype of *O. villosus* does not resemble that of *maculiventer* but is similar to specimens of the species that Allen described as *O. mollipilosus* and *O. magdalenae* (fig. 1, table 1). The series of *O. mollipilosus,* including the holotype, is represented by seven specimens (AMNH 15320, 15322–15327) from Valparaiso, 4500 ft, collected during April–June 1899. The type-series of *O. magdalenae* consists of the holotype (AMNH 15318) and one other specimen (AMNH 15319) from Minca, 2000 ft, col-
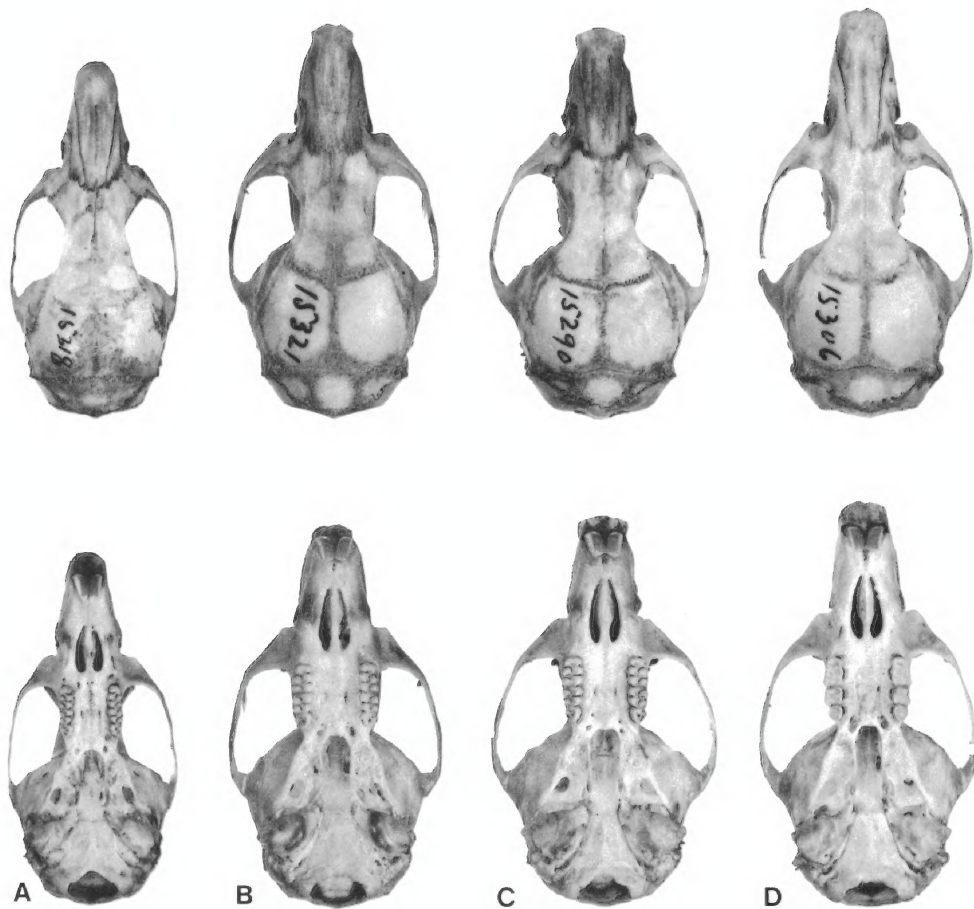
FIG. 1. Views of crania from adult *Oryzomys*: A, holotype of *O. magdalenae* (=*talamancae*) (AMNH 15318); B, holotype of *O. villosus* (AMNH 15321); C, *O. maculiventer* (=*albigularis*) from Valparaiso (AMNH 15290); D, holotype of *O. maculiventer* (AMNH 15306). All approximately ×1.5.

lected in July and August 1899. Holotypes of both taxa are adults and about the same age, as judged by wear of molars and cranial features. The skull of *magdalenae* is intact and illustrated in figure 1, that of *mollipilosus* is fragmented with the only pieces remaining being part of the rostrum and upper incisors, a portion of the maxillary with both molar rows, and the mandible. The skins of both holotypes are complete. We cannot detect any significant qualitative or quantitative differences between the holotypes of *mollipilosus* and *magdalenae* in features of either skin or skull and conclude that they represent the same species. *Oryzomys talamancae* is the proper name of that species and our reasons for tying Allen's two names to *talamancae* will be presented in a following section.

The skin of *O. villosus* is from an adult female. The upperparts are dark tawny brown, the underparts grayish white, the pelage soft, short, and somewhat velvety. The hind feet and tail are short. None of these features are characteristic of *O. albigularis maculiventer*. The latter is larger in body size (table 1), has long and soft pelage, dark brown upperparts and grayish white underparts that are broken up by some expression of a white patch.

In figure 2, we contrast views of the underparts of the holotype of *villosus* with the holotype of *magdalenae* and three adults of *maculiventer,* including the holotype. Most specimens of *maculiventer* have grayish white bellies with a distinct white pectoral patch (fig. 2C); some have a more extensive area of white, similar to that seen in figure 2D; and

a few have mostly white bellies, similar to the holotype of *maculiventer* (fig. 2E). For example, we examined 104 specimens of *maculiventer* from Magdalena District (which is just south of Santa Marta District) that are in the National Museum of Natural History and found that 88 specimens have a pectoral patch similar in area or smaller to that in figure 2C, 15 have a patch like that shown by figure 2D, and only one has an all white belly. Not a single specimen lacked some expression of a white patch.

In contrast to those of *maculiventer,* all specimens from the type-series of *O. mollipilosus* and *O. magdalenae* have grayish white underparts and no white patches, a feature that is typical of *O. talamancae* in general. In characteristics of pelage texture and coloration, as well as body size, the skin of the holotype of *O. villosus* is indistinguishable from adults of comparable age from the type-series of *mollipilosus* and *magdalenae,* especially AMNH 15322, an adult female *mollipilosus* from Valparaiso.

It is clear to us why Allen could relate *O. villosus* to both the *albigularis*-like form, *O. meridensis,* and a *Thomasomys*; the skull resembled *meridensis* and, at least to Allen, the skin a *Thomasomys* (Dr. R. S. Voss told us that up until the 1960s, the only specimen of *Thomasomys vestitus* was in London and Allen probably knew it only by the description in the literature). And why Hershkovitz (1966) could write that *villosus* was related to *O. albigularis,* whereas Gardner and Patton claim that it most closely resembled *O. capito,* which in features of body size and pelage resembles *O. talamancae,* is now evident. Because the locality data for the holotype of *O. villosus* is associated with the skin of AMNH 15321, we regard it as the holotype of *Oryzomys villosus* Allen, 1899, p. 210. That scientific name becomes a subjective synonym of *Oryzomys mollipillosus* Allen, 1899, p. 208, which is one of the names applied to *Oryzomys talamancae* Allen, 1891, p. 193. Either in the field or museum, the skull of a specimen of *maculiventer* from either Valparaiso or El Libano was wrongly associated with the skin of a *mollipilosus* from Valparaiso.

When Allen (1899, p. 210) named and described *O. villosus,* he referred to the "Type

TABLE 1
Measurements (in Millimeters) from Adults of *Oryzomys mollipilosus, Oryzomys magdalenae, Oryzomys villosus,* and *Oryzomys maculiventer* in the American Museum of Natural History

Taxon and Specimen	Lengths			
	Tail	Hind Foot	Skull	Maxillary Toothrow
Holotypes				
15323 *O. mollipilosus*	110	27	—	4.5
15319 *O. magdalenae*	130	29	31.4	4.5
15321 *O. villosus*	140	28	32.7	5.4
15306 *O. maculiventer*	170	32	34.7	5.3
O. mollipilosus (=*talamancae*)				
Valparaiso				
15322	120	28	—	4.6
O. maculiventer (=*albigularis*)				
Valparaiso				
15290	170	31	32.4	5.4
15288	165	31	34.0	5.4
23263	181	33	34.7	5.6
El Libano				
15294	170	32	34.7	5.3
23270	173	31	35.0	5.6
23271	163	32	33.9	5.4
23267	175	32	34.5	5.6
23268	183	32	33.3	5.3
23262	176	32	33.5	5.8
15309	150	31	33.1	5.4
15308	171	33	35.0	5.6
15307	191	34	35.2	5.7
15304	172	31	34.1	5.5
15303	162	32	34.2	5.3
15302	168	31	34.8	5.4
15300	176	33	34.1	5.7
15296	182	31	33.5	5.6

and only specimen." Later, however, in a general report on the mammals from the District of Santa Marta, Allen (1904, p. 436) noted two specimens of *O. villosus,* one from Valparaiso, obviously the holotype, and the other from Don Diego. We found five skins from Don Diego in the collection: two adults (AMNH 23284, 23285) and three juveniles (AMNH 23287–23289). "*Oryzomys mollipilosus*" was the original identification written on the skin labels of all but one; that specimen, AMNH 23284, had been identified as "*Oryzomys villosus.*" It, as well as the
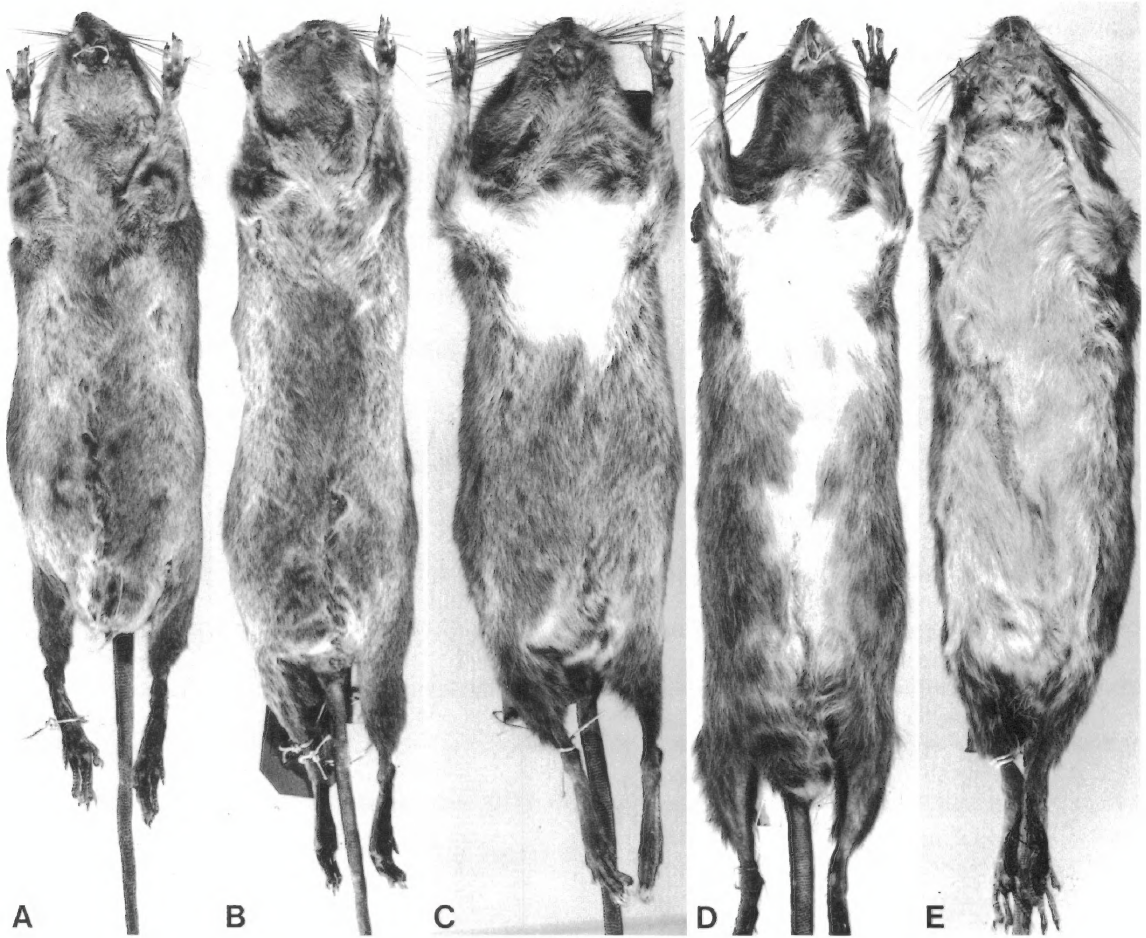
FIG. 2. Views of underparts from adult *Oryzomys*: A, holotype of *O. villosus* (AMNH 15321); B, *O. magdalenae* (=*talamancae*) from Valparaiso (AMNH 15322); C (AMNH 15328) and D (AMNH 15329), *O. maculiventer* (=*albigularis*) from Valparaiso; E, holotype of *O. maculiventer* from El Libano (AMNH 15306).

other four specimens, are simply examples of what Allen had called *O. mollipilosus,* which is the same as *O. talamancae,* as we explain in the next section.

Oryzomys talamancae

In the previous section, we associated the names *mollipilosus, magdalenae,* and *villosus* with *Oryzomys talamancae*; here we discuss aspects of that species; its taxonomic history, geographic distribution, general habitat, morphology, and comparison with some other species of *Oryzomys.* Our picture of the species is really a sketch, intended to identify

some specimens we examined that represent *O. talamancae,* show why it should be separated from *O. capito* with which it had been united, and stimulate others to provide a more complete picture of its taxonomy, distribution, and natural history by further research in the field and museum.

Oryzomys talamancae was named and described by Allen in 1891. An adult male (USNM 12222/22742), the holotype, and a second specimen (USNM 12227) were the basis for the description. The animals had been collected from Talamanca (which is "probably near Sipurio, in the valley of the Rio Sicsola," according to Goldman, 1918,

p. 73), southeastern Costa Rica by W. M. Gabb. Allen gave values of measurements made on the skin, skull, and teeth. He also wrote this description (p. 193), which turns out to be accurate for the species throughout its geographic range:

Pelage short, thick, soft, velvety. Above, russet-brown medially, mixed with blackish brown, passing gradually into clear yellow-brown on the sides; beneath, grayish white, the hairs being white or faintly yellowish white at the tips and gray beneath the surface, the basal gray portion showing through the surface, giving the effect of grayish white with a faint yellowish cast. Cheeks, sides of the neck, and flanks deep yellowish brown or golden cinnamon. Sides of the muzzle, dull soiled grayish white. Upper surface of fore and hind feet, dull pale yellowish gray, very scantily haired, and the toes nearly naked, except at the base of the claws. Soles entirely naked, tubercles 6. Ears large, blackish naked. Tail about as long as head and body, naked, blackish above, dark brown below, hence indistinctly bicolored.

A few years later, Allen (1897, p. 36) again examined the holotype of *O. talamancae,* compared it with Thomas's *O. melanotis,* which had been described in 1893, and gave values for a few more skull measurements.

Originally thought to be a species of eastern Costa Rica, *O. talamancae* was found to occur in Panama also (Anthony, 1916, p. 369) and by 1918, when his monograph on rice rats of North America was published, Goldman (1918, p. 73) could write that the distribution of the species was known to be "heavily forested regions from eastern Costa Rica eastward through Panama to near Colombian frontier; altitudinal range from sea level to 3,000 feet; Arid and Humid Lower Tropical Zones." From 1918 until 1960, *O. talamancae* was regarded by biologists to be a valid species of *Oryzomys* and a common part of the Costa Rican and Panamanian faunas (Goldman, 1920; Goodwin, 1946).

By 1960, the picture of *O. talamancae* had changed. In a footnote to a section in his systematic revision of the subgenus *Oecomys,* genus *Oryzomys,* Hershkovitz (1960, p. 544) wrote that *O. laticeps* was the older name for the species known by *talamancae,* and included several other scientific names

as well; furthermore, *laticeps* itself was antedated by the name *capito* (see also Hershkovitz, 1966, and fn. on p. 137). The proper name for the rice rat of Costa Rica and Panama appeared to be *O. capito talamancae,* and designated a geographic segment of what was a species widely distributed throughout northern and central South America. The replacement of *laticeps* by *capito* was accepted by Cabrera (1961) and other workers whose reports were published later. By 1981, the segment of *O. capito* in Costa Rica and Panama was treated as two subspecies: *O. c. carrikeri* from the Caribbean coast of eastern Costa Rica and western Panama, and *O. c. talamancae* from southeastern Costa Rica and the rest of Panama (Handley, 1966, p. 780; Hall, 1981, p. 618). And in any report on the biology of Panamanian rodents published up to 1983, *O. capito* was the name used to refer to the medium-sized terrestrial rice rat that was formerly called *O. talamancae* (see, for example, Fleming, 1970, 1971; Eisenberg and Thorington, 1973).

Then one year ago, Gardner (1983, p. 485) presented a key to the Costa Rican species of *Oryzomys* and there returned to the name *O. talamancae.* His action, he told us, came from studying the *Oryzomys capito* complex and discovering that the samples from Costa Rica and Panama were not the same as most of the samples from South America that were commonly called *O. capito.* That there is great morphological and chromosomal heterogeneity in what Hershkovitz (1960) and Cabrera (1961) considered to be *O. capito* was evident to Gardner and Patton (1976) because they could distinguish at least four species among the named forms Hershkovitz (1960) had listed within *O. capito.* Gardner told us that *O. talamancae* was one of these, and he described some of the characters he used to distinguish *O. talamancae* from *O. capito.* We then worked through the collection of *Oryzomys* at the American Museum of Natural History to test Gardner's results and in the process came not only to agree with him, but to identify specimens from regions outside of Costa Rica and Panama as *O. talamancae* and provide information on the geographic distribution of the species as well as other qualities.
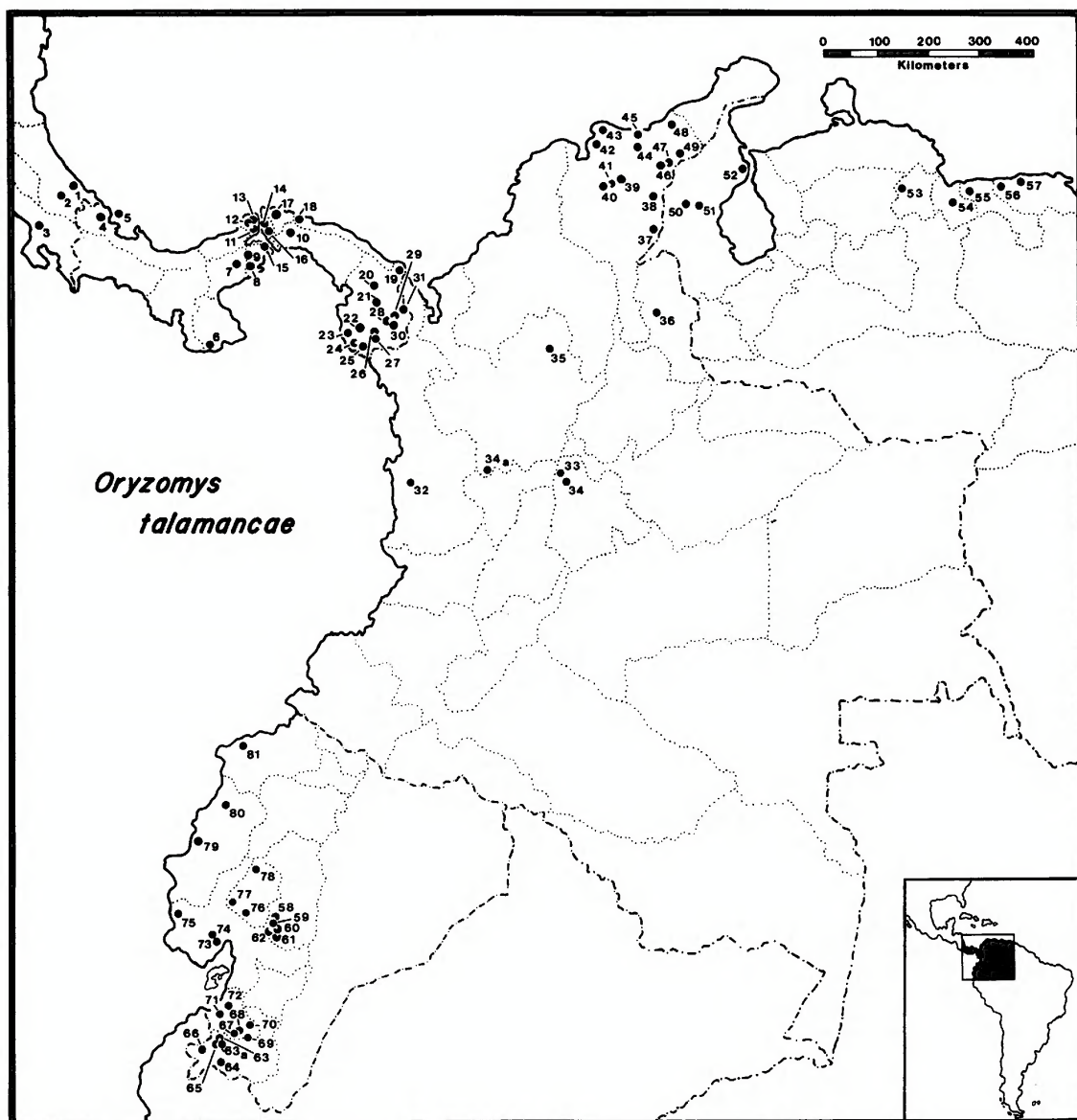
FIG. 3.   Geographic distribution of *Oryzomys talamancae*. Numbers key to numbered localities listed in text.

SPECIMENS, LOCALITIES, RANGES, AND HABITAT

The specimens we identify as *Oryzomys talamancae* and the localities at which they were collected are listed below. The number preceding each place corresponds to the numbered dot on the map in figure 3. We list only specimens from the American Museum of Natural History and the National Museum of Natural History.

COSTA RICA

1. Provincia Limón, Estrella (including Pandora and Fortuna, which is 8 miles west of Pandora, both in the Estrella Valley): USNM 284656 and 284657.

2. Provincia Limón, Talamanca; "probably near Sipurio, in the valley of the Río Sicsola" (also spelled Sixaola), according to Goldman (1918, p. 73): AMNH 25976 (holotype of *Oryzomys carrikeri*), AMNH 25974 and 25975; USNM 12227 and USNM 12222/22742 (holotype of *Oryzomys talamancae*).
3. Provincia Puntarenas, Palmar (Pacific): AMNH 139426–139428.

PANAMA

4. Provincia Bocas del Toro, Almirante (including 10 kilometers northwest of Almirante): USNM 293127 and 315991.
5. Provincia Bocas del Toro, Boca del Drago (including Drago): USNM 315992 and 315995.
6. Provincia Los Santos, Cerro Hoya: USNM 323864–323869, 323871–323879, 323912–323922.
7. Provincia Coclé, El Valle (including 6 miles east of El Valle): USNM 303430, 304803–304808, 304811 and 304812.
8. Provincia Panamá, La Campana (including Cerro Campana, 3000 ft): USNM 298716, 302673, 303421–303429, 304802.
9. Provincia Panamá, Maxon Ranch (Río Trinidad): AMNH 36794, 36797, 36798.
10. Provincia Panamá, Cerro Azul (including La Zumbadora): USNM 302493, 302496, 302674–302677, 303102–303104, 303260, 303261, 302497–302506, 302667, 305703, 305704, 306952–306955, 306957, 306959, 310568, 310569, 310571–310574.
11. Provincia Canal Zone, Gatún: USNM 170978–170983.
12. Provincia Canal Zone, Fort Sherman (including Fort Sherman, 6 miles west of Cristóbal, 5 m; and Mohinga Valley, 3 miles south of Fort Sherman): USNM 457263–457319, 296304.
13. Provincia Canal Zone, Fort Gulick: USNM 396457.
14. Provincia Canal Zone, Buena Vista Peninsula, 1–2 km northwest of Frijoles: USNM 503717.
15. Provincia Canal Zone, Rodman Naval Ammo Depot, 8 km west of Balboa, 50 m: USNM 457230–457262.
16. Provincia Canal Zone, Madden Lake and Madden Dam (including Madden Road): USNM 300342–300344, 300346–300351, 301168–301170.
17. Provincia Colón, Cerro Bruja: USNM 171530.
18. Provincia San Blas, Mandinga: USNM 305645, 305646, 305699, 305700, 305702.
19. Provincia San Blas, Armila (including Quebrada Venado): USNM 335567–335630.

20. Provincia Darién, Río Chucunaque: USNM 306960 and 306961.
21. Provincia Darién, El Real: AMNH 37584.
22. Provincia Darién, Pelisa (on Río Pavarando?): AMNH 19710 and 19711.
23. Provincia Darién, Punta Piña (including Piña): USNM 314727–314729, 324959, 396458–396463.
24. Provincia Darién, Jaqué (including Amayal which is near Jaqué): AMNH 19726–19728; USNM 363201–363216.
25. Provincia Darién, Guayabó Bay (including Guayabó): AMNH 19693–19700, 19713–19723.
26. Provincia Darién, Cana (including Escucho Ruido and Río Escucho Ruido, both in Cana), 2000–3000 ft: AMNH 19704, 19705, 19712, 19724, 19725; USNM 178655, 179599, 179601–179603, 179606.
27. Provincia Darién, near Río Setegenti, 1800 ft: USNM 318172–318176.
28. Provincia Darién, Cituro: AMNH 38168.
29. Provincia Darién, Tapaliza, 1000 ft: AMNH 37916–37922, 37928, 37929.
30. Provincia Darién, Paya (including Boca de Río Paya and Río Paya): USNM 306962, 310567, 310570, 314581.
31. Provincia Darién, Tacarcuna (including Tacarcuna Village Camp and Tacarcuna Casita Camp), 2650 ft and 3200 ft: AMNH 37915; USNM 310497, 310503, 310504, 310553–310565, 310575–310584, 339057.

COLOMBIA

32. Departamento Chocó, Baudó, 3500 ft: AMNH 33187 and 33188.
33. Departamento Cundinamarca, Río Guatequi: AMNH 38406.
34. Departamento Cundinamarca, Cundinamarca, which is in Caparrapi, Volcanes: USNM 282115.
34a. Departamento Antioquia, Valparaíso: AMNH 15323 (holotype of *Oryzomys mollipilosus*).
35. Departamento Antioquia, Zaragoza (including 24 km south and 21 km west of Zaragoza La Tirana), 620 m: USNM 499560–499573, and 500000.
36. Departamento Norte de Santander, Río Tarra which is in San Calixto: USNM 283090.
37. Departamento Magdalena, El Salado, which is on the southeastern slope of Sierra Nevada de Santa Marta: USNM 280626, 283080–283082.
38. Departamento Magdalena, Don Diego (also spelled San Diego): AMNH 23284, 23285, 23287–23289, 23622 and 23624.

39. Departamento Magdalena, Pueblo Bello: USNM 280623–280625.
40. Departamento Magdalena, Colina Agricola de Caracolicite, which is in Santa Marta, 400 m: USNM 280597–280604, 280607–280616, 280619–280620, 280622.
41. Departamento Magdalena, Manzanares, 3000 ft: AMNH 15496 and 23279.
42. Departamento Magdalena, Pueblo Viejo: AMNH 38936–38940.
43. Departamento Magdalena, Minca: AMNH 15318 (holotype of *Oryzomys magdalenae*) and 15319.
44. Departamento Magdalena, Pueblo Viego, northern slope of the Sierra Nevada de Santa Marta: USNM 85536.
45. Departamento Magadalena, Palamino: AMNH 38941.
46. Departamento Magdalena, Villaneva which is in the Río Ceasar Valley: USNM 283084 and 283085.
47. Departamento Magdalena, Sierra Negra which is on the western slope of Sierra de Perijá: USNM 283083.
48. Departamento Magdalena, Barbacoas: AMNH 34219.
49. Departamento Magdalena, Fonseca, which is in Las Marimondas in the East Andes: USNM 283086–283088.

VENEZUELA

50. Estado Zulia, Machiques (including 13 km south and 19 km west of Machiques), 1131 m: USNM 442132.
51. Estado Zulia, San Julian, 8 miles east of La Guaira: USNM 105405 (holotype of *Oryzomys medius*) and 143791–143792.
52. Estado Zulia, Maracaibo (including Hacienda El Tigre which is 17 km north and 55 km west of Maracaibo), 80 m: USNM 442134 and 442135.
53. Estado Yaracuay, Aroa (which is 8 km north and 18 km west of San Felipe, near Minas de Aroa), 403–404 m: USNM 442109 and 442129–442131.
54. Estado Carabobo, La Cumbre de Valencia: AMNH 31550.
55. Estado Aragua, Rancho Grande: AMNH 183156.
56. Distrito Federal, Caracas (including 3 km south and 46 km west of Caracas near El Limón), 398 m: USNM 387857.
57. Distrito Federal, Macuto, near sea level: USNM 102735.

ECUADOR

58. Provincia Chimborazo, Rios Chimbo-Coco, 2400 ft: AMNH 62314, 62315, and 62317.
59. Provincia Chimborazo, Hacienda Chaquarapata, which is near Rio Chimbo and is north of Bucay and south of Pallatanga, 2300 ft: AMNH 61628–61636.
60. Provincia Chimborazo, Ventura, which is 7 km north of Bucay, 1400 ft: AMNH 61637–61654 and 63093–63098.
61. Provincia Chimborazo, Bucay, 1000 ft: AMNH 61345 and 61346.
62. Provincia Chimborazo, Puente de Chimbo (including Puente de Chimbo in Bucay) 1200–2400 ft: AMNH 62301–62304, 62307–62309, 62311, 62312, 62318–62326, 62328, 62329, 62331, 62335–62337, 62340–62346, 62348–62355, 63103–63111, 63313.
63. Provincia Loja, La Puente, 2500 ft: AMNH 61322–61327.
63a. Provincia Loja, Alamor, 4500–4550 ft: AMNH 48426 and 61334–61339.
64. Provincia Loja, Los Pozos: AMNH 67377–67394.
65. Provincia Loja, Cebollal (also spelled "Seboyal") which is near Alamor, 3100 ft: AMNH 61352–61354.
66. Borders of Provincia Loja and Provincia El Oro, Río Puyango (also named Río Túmbez), 1000 ft: AMNH 61328–61333.
67. Provincia El Oro, Portovelo, 2000 ft: AMNH 48249 and 48250, 48420–48424, 48444.
68. Provincia El Oro, Río Pindo, which is 6 miles east of Portovelo, 1850 ft and 3650 ft: AMNH 48425 and 48446–48450.
69. Provincia El Oro, Zaruma (including Loja Trail) near Punta Santa Ana, 3650 ft: AMNH 47834–47849, 48413–48419, 48427–48441.
70. Provincia El Oro, Salvias, which is at the Río Salvias (also named Río Armarillo) in the Cordillera de Chilla, 3500 ft and 4000 ft: AMNH 47806 and 48445.
71. Provincia El Oro, Santa Rosa (including 4 km southeast of Santa Rosa), 60 ft and 100 ft: AMNH 61347–61351; USNM 513562–513568.
72. Provincia El Oro, Pasaje, 200 ft: AMNH 61340–61342.
73. Provincia Guayas, Chongoncito: AMNH 63092.
74. Provincia Guayas, Cerro Bajo Verde which is in the Cordillera de Chongón: AMNH 63112–63122.
75. Provincia Guayas, Cerro Manglar Alto (including Manglar Alto), 1200 ft and 1500 ft: AMNH 64791–64796, 64798–64806, 64808, 64809, 64811–64816, 64818, 64819, 64821, 64824–64836, 66363–66365.

76. Provincia Los Riós, El Recreo, near Río Nue-
vo: USNM 534357 and 534360.
77. Provincia Los Riós, Vinces (including Ange-
lica, Pijigual, Carmen, and Abras de Monte-
quilla, which is 13 km northeast of Vinces):
AMNH 63101–63102; USNM 513558.
78. Provincia Los Ríos, Limón: AMNH 66947,
66949, 66950, 66952, 66954, and 66955.
79. Provincia Manabi, Bahia de Caráquez (in-
cluding Río Briseño): AMNH 64733, 64780–
64783, 64785–64790.
80. Provincia Manabi, Cuaque (including Cerro
de Cuaque and "El Destino"), 300 ft: AMNH
64760–64770, 64773–64779.
81. Provincia Esmeraldas, Esmeraldas, 3 km
northwest of Majua, 640 ft: USNM 513546,
513549–513552, 513554 and 513555.

We also examined a specimen from Ha-
cienda El Refugio, Provincia Guayas (USNM
53456) but did not map the locality.

The geographic range of *O. talamancae* ex-
tends from eastern Costa Rica through Pan-
ama into western and northern Colombia,
northeastern Venezuela, and western Ecua-
dor. The clumped nature of localities on the
map (fig. 3) probably reflects places where
collectors have worked and not the actual
geographic distribution of the species. Ad-
ditional collecting, as well as study of speci-
mens in other museums, will certainly fill in
some of the large gaps now seen on our map.
Still, the localities from which we examined
specimens do form a pattern, however in-
complete, that may be a reasonable estimate
of the real range of *O. talamancae*. South and
east of Costa Rica and Panama, the localities
we mapped are in the intermontane valleys
and lower slopes of the Ecuadorian, Colom-
bian, and Venezuelan Andes. We have not
seen specimens of *O. talamancae* from east
of the Cordillera Occidental in Ecuador, the
Cordillera Oriental in Colombia, and the
Cordillera de Merida in western Venezuela,
or south of the Cordillera de la Costa in
northern Venezuela. East of the Andean
chains from Ecuador to northern Venezuela,
tropical habitats in the vast Amazon Basin,
Venezuelan and Colombian Llanos, and
Guiana Highlands are inhabited by popula-
tions of *O. capito* and such species as *O. mac-
connelli* and *O. nitidus* that were once united
with *O. capito* (see Gardner and Patton, 1975);

O. talamancae is apparently absent. And in
suitable tropical habitats in the valleys and
foothills of the Andes south of Ecuador, either
O. capito or some of the other species once
submerged in it—*O. nitidus, O. macconnelli,
O. yunganus*—are the species encountered,
not *O. talamancae*.

From just above sea level up to about 5000
ft is the general altitudinal range of *O. tala-
mancae* judged by published information and
data from skin labels and field notes.

Throughout this range, tropical forest, both
evergreen and deciduous, is the primary hab-
itat of *O. talamancae*. Many of the specimens
we studied were taken in virgin forest, es-
pecially what is called "hill tropical forest"
and "tropical rain forest" in field notes, as
well as "monte." The animals can also sur-
vive in places where original forest cover has
been altered. Some samples, for example, had
been collected from scrub around settle-
ments, in agricultural fields and pastures next
to either virgin or thinned forest, and in coffee
groves.

NAMES AND HOLOTYPES

The scientific names associated with *O.
talamancae*, as well as information about ho-
lotypes upon which they are based, are listed
below.

Oryzomys talamancae Allen, 1891, p. 193, July
24: holotype, USNM 12222/22742; an adult
male from Talamanca, Costa Rica; collected by
W. M. Gabb.
Oryzomys mollipilosus Allen, 1899, p. 208, De-
cember 20: holotype, AMNH 15323; adult fe-
male from Valparaiso, 4500 ft, Santa Marta Dis-
trict, Colombia; collected May 10, 1899 by H.
H. Smith.
Oryzomys magdalenae Allen, 1899, p. 209, De-
cember 20: holotype, AMNH 15318; adult fe-
male from Minca, 2000 ft, Santa Marta District,
Colombia; collected August 3, 1899 by H. H.
Smith.
Oryzomys villosus Allen, 1899, p. 210, December
20: holotype, AMNH 15321; adult female from
Valparaiso, 4500 ft, Santa Marta District, Co-
lombia; collected April 15, 1899 by H. H. Smith.
Oryzomys sylvaticus Thomas, 1900, p. 272, March:
holotype, BM 0.1.1.21; Santa Rosa, southern
Ecuador, 10 m; collected June 30, 1899 by Perry
O. Simons.

Oryzomys panamensis Thomas, 1901, p. 252, September: holotype, BM 0.5.1.67; female from City of Panama, Panama; collected by E. Andre on February 25, 1899.

Oryzomys castaneus Allen, 1901, p. 406, November 30: holotype, BM 1.3.19.11; adult female from St. Javier, northern Ecuador, 60 ft; collected by G. Flemming and R. Miketta on July 28, 1900.

Oryzomys medius Robinson and Lyon, 1901, p. 142: holotype, USNM 105405; young adult male from San Julian, 8 miles east of La Guaira, Venezuela; collected on August 8, 1900 by Wirth Robinson.

Oryzomys carrikeri Allen, 1908, p. 656, October 13: holotype, AMNH 25976; adult female from Rio Sicsola, Talamanca, Costa Rica; collected by M. A. Carriker, Jr. on August 18, 1904.

We did not focus on detecting any significant geographic variation in the traits analyzed among samples of *O. talamancae* available to us so we do not know if some of the scientific names listed above might apply to subgroups of the species. We do know that specimens of comparable age and pelage condition look closely similar to one another no matter where they were collected, and are also similar in measurements (table 2). The most conspicuous variation is within samples and reflects differences in body size due to age and differences in pelage coloration due to age and possibly season. A more careful analysis of the species, however, may reveal some significant geographic variation.

Goldman (1918) did not recognize geographic variants when he revised the taxonomy of *O. talamancae* from Costa Rica and Panama. He regarded the names *panamensis* and *carrikeri* to be subjective synonyms of *O. talamancae*. Later reports separated *carrikeri* as a valid subspecies (Handley, 1966; Hall, 1981) but after looking at the holotypes we go along with Goldman for each of the specimens could have been drawn from the same population.

Of the other names, we regard *villosus* to be a subjective synonym of *mollipilosus* and we would add *magdalenae* as well. Also, these holotypes and that of *medius* are closely similar to each other in features of skins and skulls.

We have not examined the holotypes of either *sylvaticus* or *castaneus*. Dr. Alfred

Gardner reports to us that both have the characteristic cranial and dental features of *O. talamancae* and the published descriptions of coloration and body size certainly fit with that species. We have examined specimens from Santa Rosa, the type-locality of *sylvaticus*, and they are clearly examples of *O. talamancae*. We suspect the name *castaneus* will prove to be a synonym of *sylvaticus*, and therefore of *talamancae*.

CHARACTERISTICS AND CONTRASTS

The terrestrial *O. talamancae* is of medium body size with a tail about as long as the combined length of head and body (table 2). Goldman (1918) has provided an adequate general description of the external features, pelage, skull, and dentition. Basically, the pelage is dense, short, and soft. The upperparts are tawny brown and darker along the back than along the sides, which tend to be bright yellowish brown. Underparts are grayish white, without white pectoral or abdominal patches or strips. Ears are dark brown. Dorsal surfaces of front and hind feet are white or pale yellow. Digits of the hind feet are covered by silvery hairs that extend conspicuously beyond the claws. Top and sides of the tail are dark brown or tan, the undersurface is paler from base to about the distal half to three-fourths and so appears bicolored.

Conformation of the skull is basically like that depicted for the holotype of *magdalenae* in figure 1A. The rostrum is moderately long and broad, the interorbital region wide. The incisive foramina are short and do not extend posteriorly between the molar rows. The palatal bridge is long and that part of it posterior to the molar rows is sculptured by small foramina and pits. Sphenopalatine vacuities tend to be short slits in the walls of the mesopterygoid fossa. Pterygoid fossae are bony, often penetrated by numerous small nutrient foramina in their anterior halves. The auditory bullae are small.

Two cranial and one dental feature of *O. talamancae* are especially significant. In every specimen of *O. talamancae* we examined, the configuration of the alisphenoid region re-

TABLE 2

Measurements (in Millimeters) from Samples of Adult *Oryzomys talamancae* from Costa Rica, Panama, Colombia, and Ecuador.

(Mean plus or minus one standard deviation, observed range in parentheses, and size of sample are listed for each measurement.)

Measurement	Panama[a]	Colombia[b]	Ecuador[c]	Holo-type[d]
Length of head and body	124.4 ± 9.2 (101–136) 22	135.2 ± 8.1 (120–151) 13	124 ± 4.6 (118–136) 20	—
Length of tail	124.7 ± 9.9 (110–143) 22	125.2 ± 9.5 (114–140) 13	128.5 ± 5.8 (118–137) 19	—
Length of hind foot	29.2 ± 1.6 (27–32) 22	29.5 ± 1.3 (27–32) 13	29.1 ± 1.0 (28–31) 20	—
Length of ear	21.1 ± 2.7 (16–25) 22	19.0 ± 1.1 (18–22) 13	—	—
Greatest length of skull	31.9 ± 0.9 (30.2–33.8) 22	31.7 ± 1.3 (29.7–34.3) 13	30.7 ± 0.8 (29.2–32.1) 20	31.4
Zygomatic breadth	15.8 ± 0.5 (15.1–16.8) 22	15.6 ± 0.6 (14.7–16.8) 13	15.2 ± 0.5 (14.2–16.3) 20	15.4
Interorbital breadth	5.0 ± 0.2 (4.8–5.4) 22	5.1 ± 0.2 (4.9–5.6) 13	4.9 ± 0.2 (4.7–5.2) 19	5.1
Length of rostrum	10.4 ± 0.4 (9.6–11.2) 22	10.1 ± 0.5 (9.3–11.2) 13	9.7 ± 0.4 (8.9–10.4) 20	10.4
Breadth of rostrum	5.9 ± 0.4 (5.3–6.4) 22	5.9 ± 0.4 (5.4–6.7) 13	5.6 ± 0.3 (5.2–6.0) 20	5.9
Breadth of braincase	12.6 ± 0.3 (12.1–13.3) 22	12.3 ± 0.4 (11.7–13.0) 13	12.3 ± 0.3 (11.5–12.9) 20	12.5
Height of braincase	9.1 ± 1.9 (8.0–9.2) 22	8.5 ± 0.4 (7.9–9.3) 12	8.4 ± 0.3 (8.0–9.0) 20	8.5
Breadth of zygomatic plate	3.1 ± 0.3 (2.4–3.5) 22	3.1 ± 0.3 (2.6–3.7) 13	3.2 ± 0.2 (2.8–3.4) 20	2.6
Depth of zygomatic notch	1.5 ± 0.2 (1.2–1.9) 22	1.5 ± 0.2 (1.1–1.9) 13	1.4 ± 0.2 (1.1–1.8) 20	1.6
Length of diastema	8.3 ± 0.4 (7.8–9.3) 22	8.3 ± 0.6 (7.5–8.9) 13	7.6 ± 0.3 (7.2–8.5) 20	8.1
Length of incisive foramina	4.5 ± 0.4 (3.8–5.4) 22	4.4 ± 0.4 (3.6–5.1) 13	4.4 ± 0.3 (3.7–4.8) 20	4.5
Breadth of incisive foramina	2.4 ± 0.2 (2.1–2.7) 22	2.5 ± 0.3 (2.2–2.9) 13	2.2 ± 0.2 (1.9–2.5) 20	2.3
Length of palatal bridge	6.8 ± 0.3 (6.2–7.4) 20	6.8 ± 0.4 (6.2–7.3) 13	6.7 ± 0.5 (6.0–7.6) 20	7.8
Breadth of PB at M^1	2.9 ± 0.3 (2.3–3.5) 22	2.9 ± 0.3 (2.4–3.1) 13	2.6 ± 0.3 (2.1–3.3) 20	2.6
Breadth of mesopterygoid fossa	2.4 ± 0.1 (2.2–2.6) 20	2.3 ± 0.2 (2.1–2.6) 13	2.1 ± 0.2 (1.7–2.7) 20	2.3
Postpalatal length	10.7 ± 0.6 (9.9–11.9) 19	10.9 ± 0.6 (9.9–12.1) 12	10.6 ± 0.4 (10.0–11.2) 20	10.2
Length of bulla	3.2 ± 0.1 (3.1–3.5) 22	3.2 ± 0.1 (3.0–3.4) 13	3.6 ± 0.2 (3.2–3.8) 20	3.2
Crown length of M$^{1-3}$	4.5 ± 0.2 (4.2–4.8) 22	4.5 ± 0.1 (4.3–4.7) 13	4.4 ± 0.1 (4.1–4.6) 20	4.4
Crown breadth of M^1	1.3 ± 0.1 (1.2–1.4) 13	1.3 ± 0.1 (1.2–1.4) 22	1.3 ± 0.1 (1.2–1.4) 20	1.2

[a] Provincia Darien: USNM 306960, 310553–310567, 310570, 310584, 363201, 363202, and 363205.
[b] Departamento Antiguia: USNM 499560–499571, and 499573.
[c] Provincia El Oro: AMNH 47831–47833, 47836–47839, 47841, 47844, 47846–47848, 47850, 48413, 48415, 48417, 48418 and 48427–48429.
[d] Costa Rica: USNM 12222/22742.

sembles that in the genus *Rattus*. In *Rattus*, according to Musser (1982, p. 30)

> the lateral alisphenoid strut is missing. The foramen ovale accessorius is merged with the buccinator-masticatory foramina. The anterior opening of the alisphenoid canal, the channel-like canal itself, and the foramen ovale are exposed. The masticatory and buccinator branches of the maxillary nerve emerge directly from the foramen ovale. The internal maxillary artery, but not the internal maxillary vein, passes along the bottom of the open alisphenoid canal and then through the anterior opening of the canal into the sphenoidal fissure.[3]

This configuration is illustrated in Musser (1982, p. 29) for *Rattus exulans* and contrasted with the pattern in *Apomys insignis*, which has the lateral strut of alisphenoid bone. The conformation of the alisphenoid region in *O. talamancae* can also be seen in figure 4.

The other significant cranial feature also occurs in all the examples of *O. talamancae* we studied. In each side of the braincase, there is a sphenofrontal foramen at the junction of the frontal, alisphenoid, and orbitosphenoid bones, and a squamosoalisphenoid groove leading from that foramen back to the postglenoid foramen (fig. 4). In some specimens there is a hole formed where the groove passes behind the shallow depression in which the masticatory and buccinator branches of the maxillary nerve course (fig. 4). The foramen and groove are associated with a large stapedial foramen and a basicranial carotid circulation in *O. talamancae* similar to the pattern diagrammed and described by Carleton (1980, pp. 42–43): "the stapedial artery divides inside the tympanic bulla [Dr. R. S.

Voss wrote us that the stapedial artery actually "passes through the stapes and exits the bulla entire through a small fissure, then, inside the braincase near the anterior edge of the bulla, the stapedial divides"; also, see Bugge, 1970] forming the ophthalmic and internal maxillary arteries; these exit to the orbit via the sphenofrontal foramen and sphenoidal fissure respectively. The passage of the ophthalmic artery imparts a faint groove, which is generally evident on cleaned skulls, upon the inner surface of the squamosal bone."

The cusp pattern forming the occlusal surface of each second upper molar is an important distinguishing feature in *O. talamancae* and other species of *Oryzomys* (Goldman, 1918; Gardner and Patton, 1976). The occlusal configuration characteristic of *O. talamancae* is diagrammed on the left in figure 5. In each second upper molar, the first primary fold is coalesced with the first internal fold so no enamel island exists between the first primary fold and the major fold (terminology is taken from Hershkovitz, 1960, pp. 522–523, where readers can also see the structures illustrated; also, see Reig, 1977, for another nomenclature of molars, a system that many think is a better standard for description). In other species of *Oryzomys*, the first internal fold is narrowly connected to the first primary fold in young animals and as the tooth wears the first internal fold becomes isolated as an enamel island between the first primary fold and the major fold, a configuration illustrated on the right in figure 5. Goldman (1918, p. 72) described this enamel island as situated along the "postero-internal base of the paracone." There is a small enamel island occurring in *O. talamancae* but it is the remnant of the first secondary fold, which can also be seen in species with the larger enamel island derived from the first internal fold (fig. 5).

The configuration of the alisphenoid region, presence of a sphenofrontal foramen and squamosoalisphenoid groove, occlusal pattern of each second upper molar, bright tawny upperparts, grayish white underparts, partially bicolored tail, and geographic range distinguish *O. talamancae* from other species of *Oryzomys*, especially *O. capito* and those which were once included within that species

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[3] The sphenoidal fissure has been assumed to be the anterior termination of the alisphenoid canal because most people, as Wahlert (1983, p. 2) explained for his own action, have "followed Hill (1935) in naming the fissure in the posterior part of the orbital depression the sphenoidal fissure." Wahlert elaborates: "Hill claimed that this opening corresponds to the superior orbital fissure and foramen rotundum in primates, and he did not observe that their homologues are still present in an inner layer of the alisphenoid that invests the brain. The fissure is, in fact, the anterior end of the alisphenoid canal. I have chosen a new name, the anterior-alar fissure, to express its unique position and morphology and its distinctness from the orbital fissure."
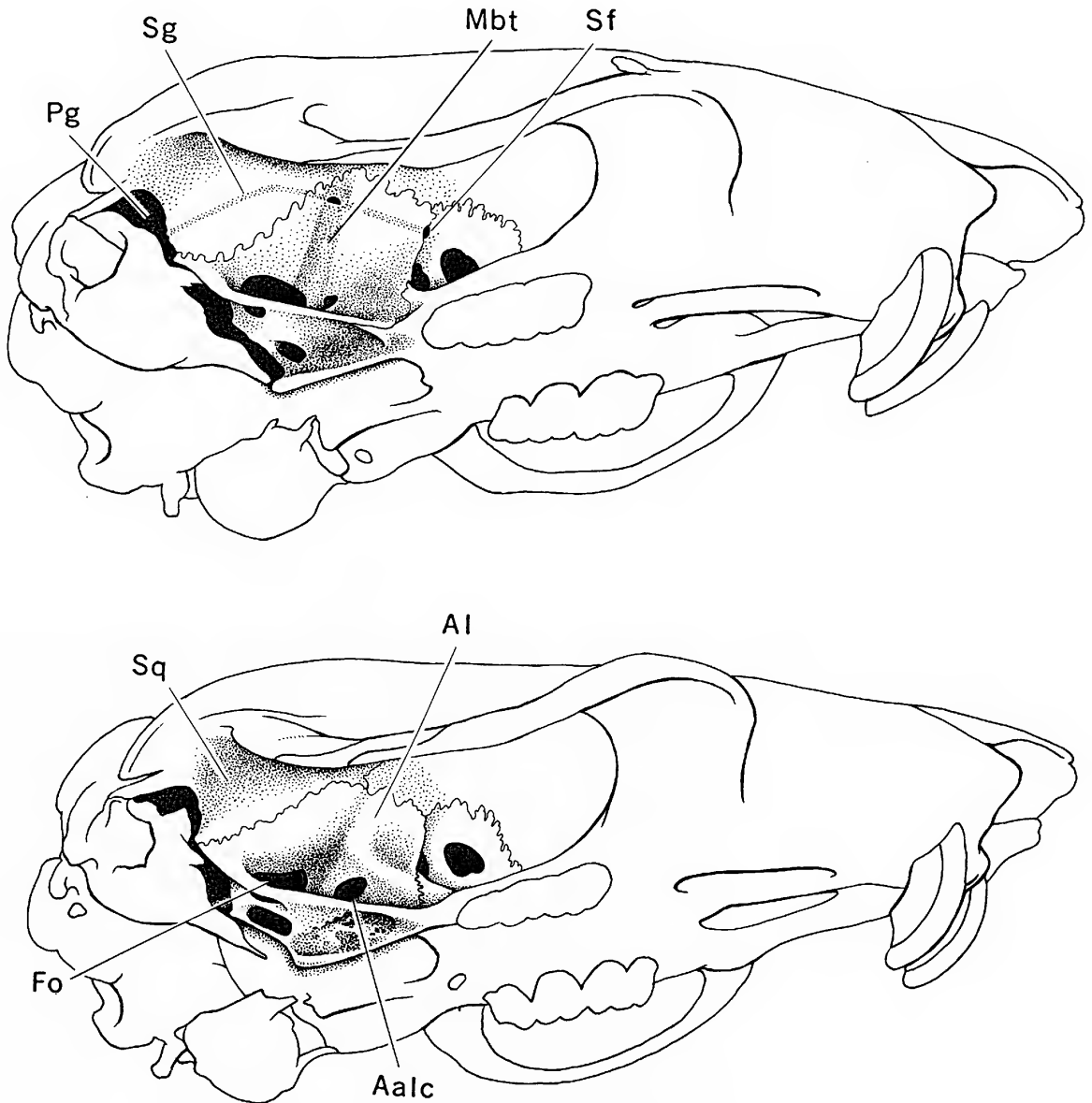
FIG. 4. Cranial views of *Oryzomys*. TOP, *O. nitidus* (AMNH 211736): the squamosoalisphenoid groove (**Sg**) and sphenofrontal foramen (**Sf**) are present. Note opening in trough where masticatory-buccinator branch of maxillary nerve (**Mbt**) courses, which reflects underlying groove. BOTTOM, the configuration in *O. capito* (AMNH 231911): squamosoalisphenoid groove and sphenofrontal foramen are absent. Abbreviations: **Aalc**, anterior opening of the alisphenoid canal; **Al**, alisphenoid bone; **Fo**, foramen ovale; **Pg**, postglenoid foramen; **Sq**, squamosal bone.

but have been extracted and characterized by Gardner and Patton (1976): *O. nitidus, O. macconnelli,* and *O. yunganus* (table 3). *Oryzomys capito* is the first of these that we contrast with *O. talamancae.*

The morphological and geographic bound-

aries of *O. capito* are still unresolved and will remain so until specimens from Paraguay, the type-locality, are studied and their diagnostic characters identified and looked for in samples from other regions of South America. Until the time that happens, Gardner and
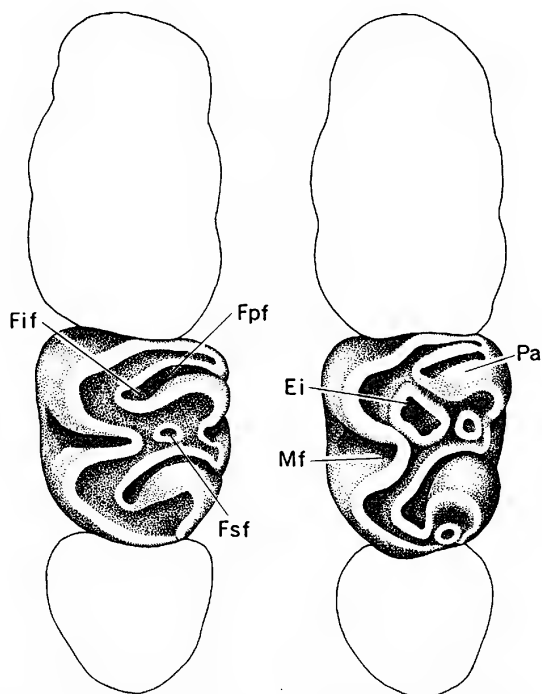
FIG. 5. Occlusal views of second upper molars in *Oryzomys*. LEFT, *O. talamancae* (AMNH 23622): the first internal fold (**Fif**) and first primary fold (**Fpf**) are broadly joined and there is no enamel island (**Ei**) between the first primary fold and the major fold (**Mf**). The only island present is that formed from the first secondary fold (**Fsf**). RIGHT, *O. nitidus* (AMNH 211740): a conspicuous enamel island occurs between the first internal fold and major fold at the posteromedial base of the paracone (**Pa**).

Patton (1976, p. 39) have given us their characterization of *O. capito* as "dorsal adult coloration usually buffy brown to yellowish brown (but rufous in some individuals), usually with a broad, darker, mid-dorsal stripe, and with gradation to paler and grayer laterally (immatures dark gray-brown dorsally); ears clothed externally with dark brown hairs and internally with a mixture of whitish and dark brown hairs; incisive foramina comparatively short, broad, and teardrop-shaped; sphenopalatine pits simple; bony excrescences (palatal bridge) usually present on palate; enamel island lacking the second upper molars (first primary fold coalesced with first internal fold." In the collection of the American Museum of Natural History, these traits are characteristic of several hundred specimens from Trinidad, Venezuela, Surinam, Guyana, Colombia, Brazil, Ecuador, Peru, and Bolivia.

Although similar to each other in body size and general aspects of skins and skulls, *O. capito* is separated from *O. talamancae* by several features. The pelage is darker and has flat color tones in *O. capito,* not bright and tawny as it is in most specimens of *O. talamancae.* In *O. capito,* the range of variation in tail coloration extends from monocolored dark brown to tails that are slightly paler or sparsely mottled on the ventral surfaces; the tails of *O. talamancae* are sharply and conspicuously bicolored for up to three-fourths of their length. In contrast to *O. talamancae,* *O. capito* does not have sphenofrontal foramina or squamosoalisphenoid grooves.

Oryzomys yunganus, while possessing different chromosomal features from *O. capito,* is, according to Gardner and Patton (1976, p. 40), "nearly identical with *O. capito,* especially externally, but may be distinguished by the comparatively narrow incisive foramina and the presence of an enamel island in the second upper molars separating the first primary and major folds." Those two characteristics also separate *O. yunganus* from *O. talamancae.* *Oryzomys yunganus* contrasts further with *O. talamancae* by its dark and flat-toned pelage, monocolored tail, and no sphenofrontal foramina and squamosoalisphenoid grooves. The only examples of *O. yunganus* we have studied are from Peru, a region outside the known geographic range of *O. talamancae.*

In chromosomal features, *O. nitidus* is sharply distinct from *O. capito,* and in the words of Gardner and Patton (1976, p. 39), has these external, cranial, and dental characters: "dorsal adult coloration reddish brown, grading on the sides to cinnamon along the lateral line (immatures a mixture of gray and reddish brown dorsally); ears clothed internally and externally with black hairs; incisive foramina comparatively long and narrow; sphenopalatine pits usually simple; palatal excrescences (incipient palatal bridge) present in most individuals; enamel island present in the second upper molars between the medial portion of the first primary fold and the major fold."

TABLE 3

Distribution of Some Distinguishing Features Among Species of _Oryzomys_ Associated with the _Oryzomys capito_ Complex[a]

Trait	Species of _Oryzomys_				
	O. talamancae	_O. capito_	_O. yunganus_	_O. nitidus_	_O. macconnelli_
Dorsum	Bright, tawny	Dark, flat tones	Dark, flat tones	Bright, tawny	Bright, tawny
Tail	Bicolored	Monocolored to slightly paler or mottled underneath	Monocolored	Bicolored	Bicolored
Alisphenoid strut	Absent	Absent	Absent	Present in 21 out of 34 specimens	Absent
Sphenofrontal foramen	Present	Absent	Absent	Present	Present
Squamosoalisphenoid groove	Present	Absent	Absent	Present	Present
Enamel island in M²	Absent	Absent	Present	Present	Present

[a] Based on specimens in the American Museum of Natural History. See text for details.

Our specimens of _O. nitidus_ are from Brazil, Bolivia, and Peru, areas east and south of the range of _O. talamancae. Oryzomys nitidus_ and _O. talamancae_ resemble one another very closely in that both have bright tawny upperparts, grayish white underparts, a sharply bicolored tail for some part of its length, sphenofrontal foramina and squamosoalisphenoid grooves. _Oryzomys nitidus_ is a larger animal; has an enamel island between the two folds in the second upper molar (fig. 5), a character absent in _O. talamancae;_ and of the 34 examples of _O. nitidus_ we examined in the American Museum of Natural History, 21 have a distinct strut of alisphenoid bone on the left, right, or both sides, a feature not present in _O. talamancae._

Oryzomys macconnelli is represented in the American Museum of Natural History by specimens from Peru, eastern Ecuador, Venezuela, and Guyana. Gardner and Patton (1976) claim this species to be distinct from _O. capito_ and "in some respects" to resemble members of the _O. albigularis_ group of species. We agree. For Gardner and Patton (1976, p. 40), _O. macconnelli_ is characterized as: "long and lax, dark reddish brown dorsal pelage; large incisive foramina, widest in the middle and tapering anteriorly and poste-

riorly; palatal excrescences obsolete; sphenopalatine pits compound; cheek teeth comparatively simple; second upper molars with short first and second primary folds, and with a shallow enamel island between the first primary and major folds (first internal fold discrete, but lost early in wear); and third upper molars with persistent first internal fold and comparatively well-developed major fold."

Except for its larger body size and longer, softer pelage, _O. macconnelli_ resembles _O. talamancae_ in external characters, especially the tawny upperparts, grayish white underparts, and sharply bicolored tails. Some series of _O. macconnelli,_ those from Venezuela, for example, appear as larger-bodied versions of _O. talamancae._ In general aspects of the crania, the two species are also similar. Both, for example, do not have alisphenoid struts but do have sphenofrontal foramina and squamosoalisphenoid grooves. _Oryzomys talamancae_ has a much smaller skull and molars than does _O. macconnelli_ and does not have the enamel island in each second upper molar, which is present in _O. macconnelli._

These are the entities—_O. capito, O. nitidus, O. yunganus,_ and _O. macconnelli_—that had to be contrasted with _O. talamancae_ to help define that species (table 3). Each of these

groups have yet to be carefully studied. More than one species may be represented in some, particularly in what we now refer to as *O. capito*. In the collection at the American Museum, for example, there are several lots of specimens that are distinguished from one another by distinctive morphological features; these samples may represent species rather than geographic variants of *O. capito*. Also, there may be older scientific names to apply to each of these groups. But no matter what the results of further taxonomic study, each of the entities is distinct from *O. talamancae* and genetically isolated from it, as estimated by characteristics of skins, skulls, and dentition.

FUTURE INQUIRY

The holotype of *Oryzomys villosus* is now identified and a definition of *O. talamancae* is proposed. Both identification and definition were accomplished by studying skins, skulls, and entire animals preserved in fluid—the kind of material stored in collections of natural history museums. Estimating the morphological and geographic boundaries of *O. talamancae* provides a foundation allowing questions to be formulated about it and contributes toward a taxonomic revision of the genus *Oryzomys*.

The localities of *O. talamancae* we mapped indicate a distribution from eastern Costa Rica through Panama into the Andes of Colombia, Ecuador, and Venezuela. Are there other species of *Oryzomys*, other muroid rodents, caviomorph rodents, other groups of mammals, other vertebrates (especially birds), or forest assemblages that also have distributions coinciding with that of *O. talamancae*? Among oryzomyine rodents, there are four other species with ranges similar in broad outline to that of *O. talamancae* but different in details. *Oryzomys (Melanomys) caliginosus* occurs farther west in Central America, to Honduras (Hall, 1981), and is spread in South America from Colombia east to western Venezuela and south to southern Ecuador (Cabrera, 1961; Dr. R. S. Voss, personal commun.). *Oryzomys alfaroi,* judged from specimens in the American Museum of Natural History and the National Museum, ranges from eastern Mexico through Central America into Colombia, and down to Ecuador. Its

distribution in South America is Andean and similar to that of *O. talamancae*.[4] *Oryzomys aphrastus,* originally known only from the Pacific foothills of Costa Rica, also occurs in similar situations in western Panama and the Andes of northwestern Ecuador (Hall, 1981; Drs. R. S. Voss and R. Pine, personal commun.). Finally, the range of *Sigmodontomys alfari* extends from southeastern Honduras through eastern Nicaragua and Costa Rica into Panama, Colombia, western Venezuela, and northern Ecuador (Cabrera, 1961; Hall, 1981; Handley, 1976). We would like to know if *O. talamancae* is part of a special fauna and flora with an evolutionary history different from that which now surrounds the species and habitats in which it is found. This distinctive distribution was obscured when the outlines of *O. talamancae* were hidden within the broad and vague definition of *O. capito*.

Why is *O. talamancae* apparently absent from forests east of the Andes and south of Ecuador? Is it because suitable habitats in those regions are occupied by *O. capito, O. nitidus, O. yunganus,* and *O. macconnelli* and other members of the *O. capito* group? Is the geographic range of *O. talamancae* entirely allopatric to the ranges of these other species or are there narrow areas of overlap? What are the relationships between *O. talamancae* and the other species at places where their ranges abut or overlap?

Finally, what is the phylogenetic position of *O. talamancae* relative to other species of *Oryzomys*? What we know about its morphology indicates *O. talamancae* to be a member of the subgenus *Oryzomys* (Goldman, 1918; Hooper and Musser, 1964), but what its closest relative may be within that large assemblage is not known. To adequately answer the question requires that other species of *Oryzomys* be defined and samples of them compared with those of *O. talamancae*, essentially a revisionary study of the genus. Now is the time for this endeavor because *Ory-*

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[4] The geographic distribution we outline is for true *O. alfaroi*. There are at least four species in what is now called *O. alfaroi*. One of these is *O. alfaroi* and the oldest scientific names for the other three are *O. chapmani, O. hylocetes,* and *O. rhabdops*. *Oryzomys alfaroi* is the only one occurring in South America (Musser and Carleton, MS).

zomys is well represented in collections by large samples from many localities throughout the New World. Furthermore, some populations of not only *Oryzomys* but of oryzomyine rodents are being analyzed by chromosomal and biochemical approaches (Gardner and Patton, 1976; Koop, Baker, and Genoways, 1983; Baker, Koop, and Haiduk, 1983; Maia et al., 1984), which are supplying data that can be used along with that obtained from careful study of skins, skulls, and teeth to assess phylogenetic relationships among species of *Oryzomys* in particular and among genera of oryzomyines in general.

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