

SYSTEMATIC STUDIES OF
ORYZOMYINE RODENTS
(MURIDAE, SIGMODONTINAE):
A SYNOPSIS OF *MICRORYZOMYS*

MICHAEL D. CARLETON AND GUY G. MUSSER



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A SYNOPSIS OF *MICRORYZOMYS*

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ABSTRACT

The genus *Microryzomys* contains certain small-bodied, long-tailed oryzomyine rodents that are endemic to the northern and central Andes, their distribution describing an arc from northern Venezuela, through Colombia, Ecuador, and Peru, to central Bolivia.

Based on the examination of over 900 museum specimens representing 105 principal collecting localities, two species, without subspecific divisions, are recognized: *M. minutus* (*dryas* Thomas, *d. humilior* Thomas, *fulvirostris* Allen, and *aurillus* Thomas in synonymy) and *M. altissimus* (*a. hyalaeus* Hershkovitz and *a. chotanus* Hershkovitz in synonymy). *Microryzomys minutus* can be distinguished from its congener *altissimus* by a combination of size and proportional differences, which were underscored in principal component analysis of 16 craniodental and 3 external variables using representative population samples of each species. These results, together with 14 locality records of sympatry (or parapatry) in the mountains of Colombia, Ecuador, and Peru, support an interpretation of only two biological species.

Populations of *Microryzomys altissimus* are more restricted geographically, altitudinally, and perhaps ecologically than are those of *M. minutus*. The geographic limits of *M. minutus* define the distributional boundaries of the genus, whereas, *M. altissimus* occurs only in the Cordillera Central of Colombia, throughout the Andes of Ecuador, to the highlands of central Peru. Locality records document that *M. altissimus* occupies a higher altitudinal zone (mostly from 2500 to 4000 m) compared to *M. minutus* (mostly from 1500 to 3500 m); most instances of sympatry occur within the 2500 to 3500 m interval. Information gleaned from specimen tags and fieldnotes suggests that the two species inhabit different morphoclimatic vegetation zones consistent with the altitudinal belts they occupy. *Microryzomys minutus* dwells in a variety

of wet, cool Andean forests ranging from lower and upper montane rain forest to subalpine rain forest; at its upper altitudinal limits, it may frequent various habitats found at the ecotone between upper Andean forests and páramo. *Microryzomys altissimus* is more regularly associated with páramo environments, the forest-páramo ecotone, and subalpine rain forest. Both species range on either side of the Huancabamba Depression in northern Peru without evidence of appreciable differentiation. Neither species penetrates the Altiplano biome in southern Peru and Bolivia; the southernmost distribution of *M. minutus* adheres to wet forest along Amazon-facing slopes east of the Altiplano.

Examination of external, cranial, dental, and gastric morphology revealed a suite of qualitative traits, apparently unrelated to overall size, by which species of *Microryzomys* can be distinguished from those of *Oligoryzomys* and from *Oryzomys palustris*, the type species of *Oryzomys*. The concordance of these discrete character states contradicts the notion that *Microryzomys* and *Oligoryzomys* are artificial constructs used to segregate the smaller species within a speciose genus highly varied in body size. Instead, such character associations support the monophyly of species assigned to *Microryzomys* and to *Oligoryzomys* relative to other groups of oryzomyine rodents. Emended diagnoses, framed at the generic level, are provided for these two taxa. Evaluation of 20 qualitative characters reveals that *Oryzomys palustris* is highly differentiated from both *Microryzomys* and *Oligoryzomys*, which share many traits thought to be plesiomorphic. Certain derived character states suggest that *Microryzomys* and *Oligoryzomys* are sister taxa, but the evidence for a close relationship is weak, and this possibility must await further corroboration and the study of a broader array of oryzomyines.

INTRODUCTION

In discussing the difficulty of rendering a clear decision on the generic status of the Andean mouse *minutus*, Osgood (1933: 3), with his usual acuity, encapsulated the basic problem impeding our comprehension of higher taxonomic relationships within Neotropical Sigmodontinae: "Such species are all too numerous among South American rodents and the combination of characters they offer runs from one extreme to another so it is clear that no ultimate generic and subge-

neric classification will be possible until all these species are thoroughly understood." One of the more intractable South American groups in terms of understanding species limits consists of *Oryzomys* and its relatives, the oryzomyine rodents. They constitute the largest tribal-level assemblage among the diverse radiation of Neotropical Sigmodontinae, whose South American members number about 50 genera and 250 species (see, for example, Reig, 1986). Estimates of the number

of valid species in *Oryzomys* alone range from approximately 55 (Honacki et al., 1982; Corbet and Hill, 1986) to over 100 (Haiduk et al., 1979), a discrepancy partly due to disagreement over which of several distinct taxa should be included as subgenera or maintained separately. The species *minutus*, which prompted Osgood's reflection, and its close relative *altissimus* represent one of those distinctive units: *Microryzomys*, a group of small-bodied, long-tailed oryzomyines that inhabit intermediate to high elevations in mountains stretching from northern Venezuela through the Andes of Colombia, Ecuador, and Peru to central Bolivia.

Our primary objectives are to substantiate the specific recognition of *minutus* and *altissimus*, to summarize their geographic distributions, and to document the uniformity of their diagnostic characteristics with respect to other groups of oryzomyines. This contribution represents a somewhat tardy continuation of a series of reports aimed at clarifying the definition of oryzomyine species and ultimately achieving a more rigorous diagnosis of *Oryzomys* itself (Musser and Williams, 1985). Our approach involves the examination of extant museum series, of which many hundreds more specimens now exist in collections than at the time of Osgood's writing. We believe that a fresh synthesis of this material will significantly enhance our current knowledge of oryzomyine species and their geographic occurrence and will serve to focus future studies of oryzomyines that use other analytical tools and are asking broader phylogenetic questions.

Correlative objectives of our paper relate to this last point. In view of the extensive morphological variation among oryzomyines, and especially given the confusing and inconsistent definition of the morphological boundaries of *Oryzomys* itself and the groups it embraces, we consider it important to establish the morphological identity of *Microryzomys* with respect to the genotype of *Oryzomys*, *Mus palustris* Harlan, as designated by Baird (1858). By using *Oryzomys palustris* as the focus of comparison in this and subsequent studies on oryzomyines, we hope to lay a firmer groundwork for the unambiguous diagnosis of *Oryzomys*, a task which forms the crux of improved phylogenetic understanding of oryzomyine rodents

and attendant decisions regarding the taxonomic rank of allied forms. In addition, we shall contrast specimens of *Microryzomys* to those of *Oligoryzomys*, since the two taxa have been occasionally synonymized (Gyldenstolpe, 1932; Tate, 1932d, 1932e) and since their members are frequently confused due to their small size and superficial resemblance.

MATERIALS AND METHODS

We examined approximately 900 specimens of *Microryzomys*, principally study skins with associated skulls, from the following collections, each preceded by the museum acronym adopted throughout this paper.

AMNH	American Museum of Natural History, New York City
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History), London
CM	Carnegie Museum of Natural History, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
LSU	Museum of Zoology Louisiana State University, Baton Rouge
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MSU	The Museum, Michigan State University, East Lansing
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C.
UVB	Universidad del Valle, Departamento de Biología, Colombia

Specimens were assigned to one of four broad age classes based on dental wear: juvenile (J)—upper third molars unerupted or if erupted, essentially unworn; young adult (Y)—molars little worn, primary cusps conical and secondary lophs and styles distinct; adult (A)—moderate wear, primary cusps still well-defined but bluntly rounded and lophs and styles indistinct; and old adult (O)—heavy wear, primary cusps obliterated and crown basin-shaped. The distinction between juvenile and young adult cohorts based on up-

per third molar eruption constituted a more objective criterion than did the assignment of individuals among the three adult classes based on relative wear. Specimens with unerupted or unworn third molars are also clothed in a qualitatively recognizable juvenile pelage, which is much shorter, finer to the touch, and conspicuously paler than that of adults. In some specimens with erupted but unworn third molars, replacement hairs of the brighter adult coat are evident beneath the juvenile pelage. Specimens in the categories young-to-old adults exhibit full adult pelage.

Values for external and cranial measurements are in millimeters (mm). Total length, lengths of tail (TL), hind foot (HFL), and ear are those recorded by the collector on the skin label; tail length was subtracted from total length to obtain length of head and body (HBL). Fourteen cranial and two dental dimensions were measured to the nearest 0.1 mm using hand-held dial calipers accurate to 0.05 mm. These measurements, and their abbreviations as used herein, include: occipitonasal length (ONL); greatest zygomatic breadth (ZB); interorbital breadth (IOB); length of rostrum (LR); breadth of rostrum (BR); breadth of braincase (BBC); height of braincase (HBC); breadth of zygomatic plate (BZP); length of diastema (LD); length of bony palate (LBP); postpalatal length (PPL); breadth of bony palate across first upper molars (BM1s); length of incisive foramina (LIF); breadth of incisive foramina (BIF); crown length of maxillary tooththrow (LM1-3); width of first upper molar (WM1). The limits of these measurements are the same as defined by Musser (1979), except that the breadth of the bony palate (=palatal bridge) is the distance between the labial edges of the first molars. Since the development of the incisive foramina has been used to discriminate *M. minutus* and *M. altissimus*, we measured (to 0.01 mm) their termination relative to the anterior face of the first molars using a craniometer mounted to a binocular microscope.

Anatomical terminology follows Reig (1977) for the dentition, Bugge (1970) for the cephalic arteries, Wahlert (1985) for the cranial foramina, and Carleton and Musser (1984) for general features of the murid skull. For verification of the trenchant features of *Oryzomys palustris*, we relied on large skin-

and-skull series of the nominate subspecies from New Jersey and Virginia in the AMNH and USNM. Cranial and external traits of *Oligoryzomys* were examined in representative samples of the following nominal species also in the AMNH and USNM: *andinus* (Bolivia, Peru); *arenalis* (Peru); *chacoensis* (Argentina, Bolivia, Paraguay); *delticola* (Uruguay); *destructor* (Bolivia, Ecuador, Peru); *eliurus* (Brazil); *flavescens* (Argentina, Uruguay); *fulvescens* (Mexico, Central America); *longicaudatus* (Chile); *microtis* (Bolivia, Brazil); *nigripes* (Paraguay); and *vegetus* (Panama).

The stomachs, each fully distended with food, of the following species and specimens were extracted for comparisons of gross gastric morphology.

Microryzomys altissimus: Ecuador, near Papallacta (AMNH 248277, 248279–80, 248497); Peru, Junín (AMNH 232630).

M. minutus: Ecuador, San Francisco (AMNH 63385–6), near Papallacta (AMNH 248278); Colombia, Antioquia (AMNH 149282).

Oryzomys palustris: Georgia, St. Catherine's Island (AMNH 239256–61, 239263–4); Florida, Marion Co. (AMNH 243113).

Oligoryzomys andinus: Peru, Lima (AMNH 213675).

O. chacoensis: Paraguay, Chaco (AMNH 248399).

O. delticola: Brazil, Rio Grande del Sur (AMNH 235422, 235424–6, 235968, 235970).

O. destructor: Peru, Junín (AMNH 213677–8, 213680).

O. eliurus: Brazil, Minas Gerais (AMNH 80375, 91491).

O. flavescens: Uruguay, Rocha (AMNH 206010).

O. sp. B, flavescens Group: Peru, Junín (AMNH 213685–6).

O. fulvescens: Venezuela, Sucre (AMNH 257246, 257248, 257250–2).

O. longicaudatus: Chile (AMNH 213694–7).

O. microtis: Bolivia, Santa Cruz (AMNH 263326–8, 263334–5, 263340, 263369).

O. nigripes: Paraguay, Misiones (AMNH 234788).

Because of the high proportion of damaged skulls encountered, 16 geographically cohesive OTUs were identified to augment sample sizes for statistical analyses. In view of the highly dissected nature of Andean topography and the probable isolation of many populations of *Microryzomys*, we were conservative in combining specific localities (numbers refer to Gazetteer listing below).

The OTUs recognized are:

	N	Area
<i>Microryzomys altissimus</i>		
OTU 1 Locs. 75–77	25	central Peru
OTU 2 Locs. 97, 98	13	southern Ecuador
OTU 3 Locs. 86, 87, 102	17	northern Ecuador
OTU 4 Locs. 91, 106	15	central Colombia
<i>Microryzomys minutus</i>		
OTU 5 Locs. 6, 7	22	southern Peru
OTU 6 Loc. 93	12	central Peru
OTU 7 Loc. 22	15	northern Peru
OTU 8 Locs. 101	9	central Ecuador
OTU 9 Locs. 39, 40	16	western Colombia
OTU 10 Locs. 43, 46	17	western Colombia
OTU 11 Locs. 48–50	11	central Colombia
OTU 12 Loc. 57	29	central Colombia
OTU 13 Loc. 61	17	western Venezuela
OTU 14 Loc. 65	102	western Venezuela
OTU 15 Loc. 69	17	western Venezuela
OTU 16 Locs. 71, 72	12	northern Venezuela

Standard descriptive statistics (mean, range, standard deviation) were computed for the OTUs. One- and two-way analyses of variance were performed to assess the effects of age and sex on nongeographic population variation in our largest population sample (OTU 14, N = 102). Principal components were extracted from a variance-covariance matrix and computed using three external variables (HBL, TL, HFL) and the 16 cranial variables, all of which were first transformed to natural logarithms. Loadings are expressed as Pearson product-moment correlation coefficients of the principal components with the original external and cranial variables. All analytic procedures were carried out using Systat (Version 4.0, 1988), a series of statistical routines programmed for microcomputers.

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and associated data acquired during the Smithsonian Venezuelan Project, Dr. Sydney Anderson permitted us to use specimens collected for his project on the mammals of Bolivia, and Ms. Lynn J. Barkley provided specimens and data from her Peruvian collections. Dr. Robert S. Voss provided unrestricted use of his fieldnotes and habitat photos, all of which have enhanced the quality of our final report. Significant contributions have been made by Ms. Marina Williams, who collated much of the mensural and locality data and drew preliminary distributional maps, and Mr. Dave F. Schmidt, who also verified distributional records and whose care and skill are evident in the maps and graphical figures. Mr. Helmut Sommer carefully prepared the specimens on which figures 8 and 21 are based. The clear illustrations of skulls and hind feet reflect Ms. Patricia J. Wynne’s craftsmanship and intelligent eye. The cranial photographs are the work of Mr. Peter Goldberg, whose dedication to excellence has helped us to visually convey observations that are not easily expressed by the written word. SEM micrographs were made by Ms. Joan Whelan. Dr. Lee H. Herman offered his insights on the cladistic relevance of the character variation we studied. Finally, Drs. Robert S. Voss, Philip Myers, and G. Ken Creighton contributed to the final version through their critical reviews; we are grateful for their time and interest.

GAZETTEER OF PRINCIPAL COLLECTING LOCALITIES

The specimens examined represent 105 principal collecting localities (figs. 1, 2), which are listed below according to the sole occurrence of each species and to their co-occurrence in sympatry or parapatry. We consulted several sources to verify the placement of these sites, the most useful being: the series of South American ornithological gazetteers available through the Museum of Comparative Zoology (Paynter, 1982; Paynter and Traylor, 1977, 1981; Paynter et al., 1975; Stephens and Traylor, 1983); the gazetteers produced by the U.S. Board of Geographic Names, Dept. of Interior; and certain expedition and collection accounts (Allen, 1916a; Chapman, 1926; Handley, 1976; Osgood, 1914; Thomas 1920, 1926a,b, 1927). Localities and their coordinates were further checked for geographic plausibility against various topographic maps (mostly 1:250,000 to 1:1,000,000 scale). Coordinates for distance and elevational modifiers that were interpolated from topographic maps are preceded by circa (= ca.); otherwise, the coordinates given are those obtained from gazetteers. A National Geographic Society map of South America (October, 1950) served as our base map (1:8,000,000), but secondary political boundaries and their names accord with the Defense Intelligence Agency Manual on Geopolitical Data Elements (March, 1984). To avoid visual congestion on the maps, some nearby trapping sites, as indicated in parentheses, are included under the principal localities plotted. However, specific locality information, with distances and altitudes as given by the collector, and corresponding catalog numbers for each museum specimen studied are listed below under Taxonomic Summary.

Our attribution of localities as sympatric or parapatric requires comment. Few field workers who collected *Microryzomys* were aware of the possible coexistence of the two forms in the same local habitat; in fact, specimens of *altissimus* have been regularly identified as *minutus* in museum holdings. Because of this problem, coupled with the inconsistency of locality designations and the incompleteness of original fieldnotes, we cannot always be certain that specimens bearing the same skin-tag provenance actually lived

in syntopy, or its operational field equivalent of having been taken in the same trap line. Our categorization of such localities as sympatric or parapatric reflects this reservation, although we are confident that careful fieldwork at each such place would reveal the two species as syntopic.

Microryzomys minutus

Bolivia

Departamento Santa Cruz

1. Siberia, 25 and 30 km W Comarapa, 2800 m, ca. 17°51'S/64°42'W.

Departamento La Paz

2. Río Aceramarca (including 1 mi S Yerbani), 2600 and 3290 m, 16°18'S/67°53'W.
3. Nequejahuira, near Pongo, 2440 m, 16°20'S, 67°50'W.
4. Unduavi, 15 km NE, 2400 m, ca. 16°16'S/67°48'W.
5. Zongo, 30 km N, 2000 m, ca. 15°54'S/67°59'W.

Peru

Departamento Cuzco

6. Marcapata (including Limacpunco and Amacho), 2400–3350 m, 13°30'S/70°55'W.
7. Torontoy, 2895 m, 13°10'S/72°30'W.
8. Machu Picchu, 3655 m, 13°07'S/72°34'W.
9. Tocopquey, Ocobamba Valley, 2775 m, 12°53'S/72°21'W.

Departamento Ayacucho

10. Puncu, 30 km NE Tambo, 3370 m, 12°47'S/73°49'W.

Departamento Junín

11. Río Tarma, Yano Mayo, 2590 m, 11°25'S/75°42'W.

Departamento Pasco

12. Acobamba, 45 mi NE Cerro de Pasco, 2440 m, ca. 10°28'S/75°52'W.
13. Carpath Pass, trail to Hacienda Paty, 2165 m, ca. 09°42'S/76°09'W.
14. Huaylaspampa, south of, 2745 m, ca. 09°42'S/76°02'W.

Departamento Amazonas

15. San Pedro, 2620–2865 m, 06°38'S/77°42'W.
16. Ventilla (including 10 mi E Molinopampa), 2485 m, 06°11'S/77°33'W.
17. Uchco, 1525 m, ca. 06°07'S/77°20'W.
18. Lake Pomacochas, 6 km SW, 1830 m, 05°53'S/77°57'W.
19. Cordillera Colán, 3260 m, ca. 05°30'S/78°10'W.

Departamento Cajamarca

20. Taulís, 2700 m, 06°54'S/79°03'W.

Departamento Piura

21. Canchaque, 15 km E, 1750 m, 05°24'S/79°36'W.

22. Cerro Chinguela (including Machete and Batán), 2200–2700 m, 05°07'S/79°23'W.

Ecuador*Provincia El Oro*

23. Taraguacocha, Cordillera de Chilla, 2970 m, 03°40'S/79°40'W.

24. El Chiral, 1630 m, 03°38'S/79°41'W.

Provincia Azuay

25. Molleturo, 2315 m, 02°48'S/79°26'W.

Provincia Chimborazo

26. Huigra, Paujchi, 02°17'S/78°59'W.

Provincia Tungurahua

27. Mount Tungurahua, 3500 m, 01°27'S/78°26'W.

28. Baños, 01°24'S/78°25'W.

29. San Rafael, 2745 m, 01°22'S/78°29'W.

Provincia Napo

30. Baeza, 1980 m, 00°27'S/77°53'W.

Provincia Pichincha

31. Pintag, above Chillo, 3050 m, 00°22'S/78°23'W.

32. Tumbaco (including Río Machángara), 2135–2500 m, 00°13'S/78°24'W.

33. Verdecocha, 3100 m, 00°06'S/78°36'W.

34. Santa Rosa, via Mindo, 1800 m, 00°03'S/78°35'W.

35. Pelagallo, 00°09'N/78°32'W.

36. Perucho, Guailabamba, 1980 m, 00°07'N/78°25'W.

37. Guallea, (including west of and road to Guallea), 1220–1800 m, 00°07'N/78°50'W.

38. Pacto, 1400 m, 00°12'N/78°52'W.

Colombia*Departamento Huila*

39. Santa Marta, San Agustín, 2700 m, ca. 01°57'N/76°34'W.

40. San Antonio (including Río Magdalena and Río Ovejeras), 2200–3100 m, 01°57'N/76°29'W.

Departamento Cauca

41. Valle de Las Papas (including Páramo del Las Papas), 3050 m, 01°55'N/76°36'W.

42. Gabriel López, 3000 m, 02°29'N/76°18'W.

43. Cerro Munchique, 1500–2500 m, 02°32'N/76°57'W.

44. La Gallera, 1735 m, 02°35'N/76°55'W.

45. Charguayaco (including Sabanetas and coastal range W of Popayán), 2000–2200 m, 02°40'N/76°57'W.

46. Río Mechengue, 800 m, 02°40'N/77°12'W.

Departamento Cundinamarca

47. Fusagasugá (including El Roble), 1750–2195 m, 04°21'N/74°22'W.

48. San Cristóbal, Bogotá region, 2900 m, 04°34'N/74°05'W.

49. Bogotá (including San Francisco), 2700–3500 m, 04°36'N/74°05'W.

50. Guasca, Río Balcones, 04°52'N/73°52'W.

51. Quipile, 04°45'N/74°32'W.

52. San Juan de Río seco, 04°51'N/74°38'W.

Departamento Tolima

53. Río Toche, 2070 m, 04°26'N/75°22'W.

Departamento Quindío

54. Laguneta, 3140 m, 04°35'N/75°30'W.

55. Salento, 2135 m, 04°38'N/75°34'W.

Departamento Antioquia

56. Las Palmas (including 1 mi NW Las Palmas), 2440–2600 m, 06°10'N/75°33'W.

57. Páramo Frontino (including Santa Bárbara, Guapanal, Ríos Ana and Urrao), 2200–3300 m, 06°28'N/76°04'W.

58. Ventanas, Valdivia, 3000 m, 07°05'N/75°27'W.

Departamento Magdalena

59. Sierra Nevada, near Mamancarnaca, 3300–3600 m, 10°43'N/73°39'W.

60. Macotama (including El Mamón), 2440–2745 m, 10°55'N/73°30'W.

Venezuela*Estado Tachira*

61. Buena Vista, 41 km SW San Cristóbal, 2350–2420 m, 07°27'N/72°26'W.

Estado Mérida

62. Páramo Tambor (including El Tambor), 2440–2680 m, 08°36'N/71°24'W.

63. La Carbonera, 12 km SE La Azulita, 2180 m, 08°38'N/71°21'W.

64. Río Mucujun (including Lago Mucubají and Santa Rosa), 2345 m, 08°36'N/71°09'W.

65. Tabay, 4–9 km SE, 2127–3810 m, 08°36'N/71°01'W.

66. La Culata, 3000 m, 08°45'N/71°05'W.

67. Nudo de Apartaderos, 4000 m, 08°48'N/70°51'W.

68. Páramo de los Conejos (including El Conejo), 2925 m, 08°50'N/71°15'W.

69. Paramito, 3–4 km SW Timotes, 3050–3345 m, 08°59'N/70°46'W.

Estado Trujillo

70. Haciendas Misísí, 15 km E Trujillo, 2360 m, 09°21'N/70°18'W.

Estado Miranda/Distrito Federal

71. Alto de No León, 33 km WSW Caracas, 1996 m, 10°26'N/67°10'W.

72. Pico de Avila, 5–6 km NNE Caracas, 2081–2241 m, 10°33'N/66°52'W.

Estado Sucre

73. Turumiquire (including Mount Turumiquire), 1705 and 2410 m, 10°07'N/63°52'W.

74. Cerro Negro, 10 km NW Caripe, 1630–1690 m, 10°12'N/63°32'W.

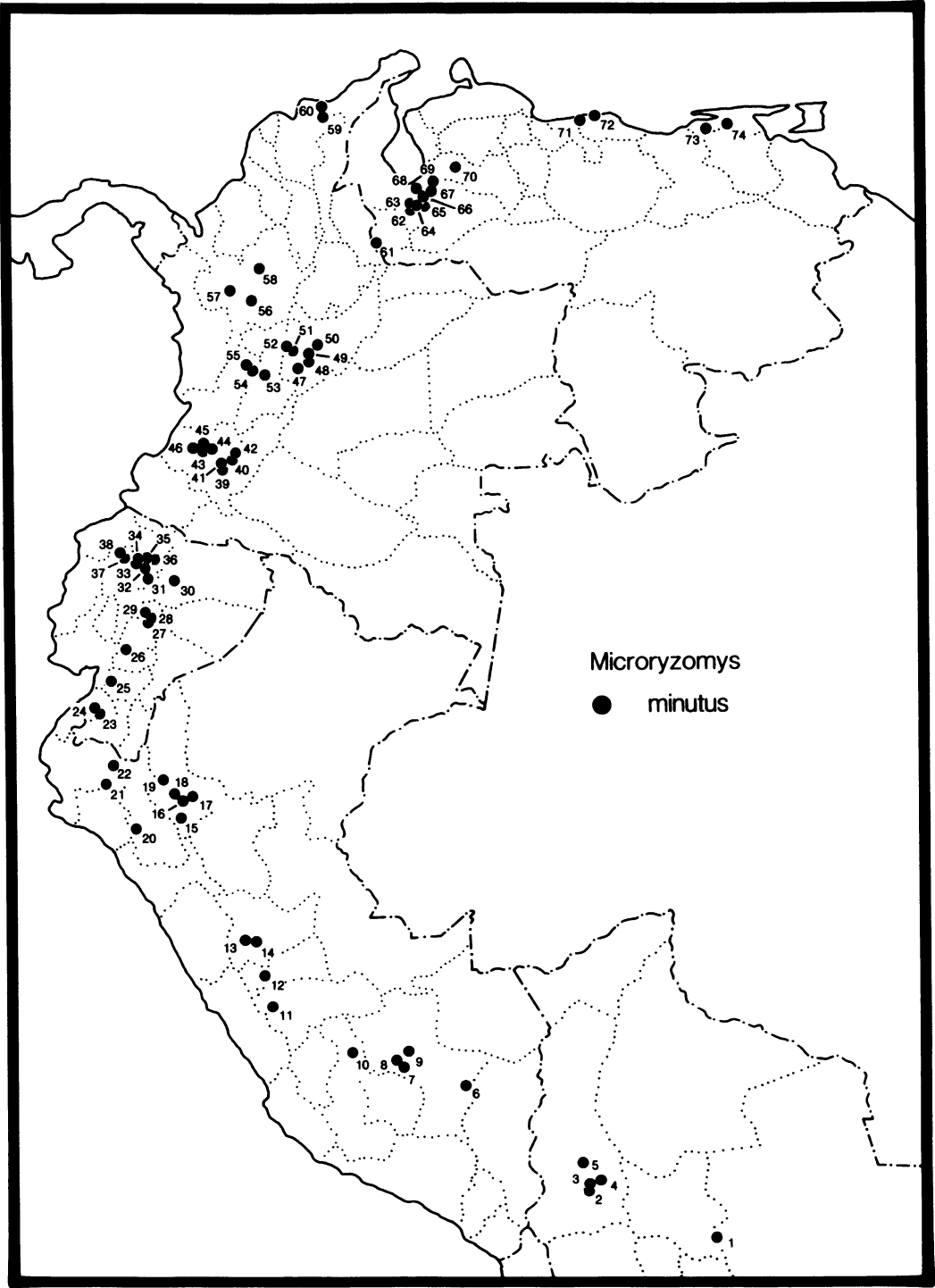


Fig. 1. Geographic distribution of *Microryzomys minutus*. Key to numbered localities listed in Gazetteer of Principal Collecting Localities.

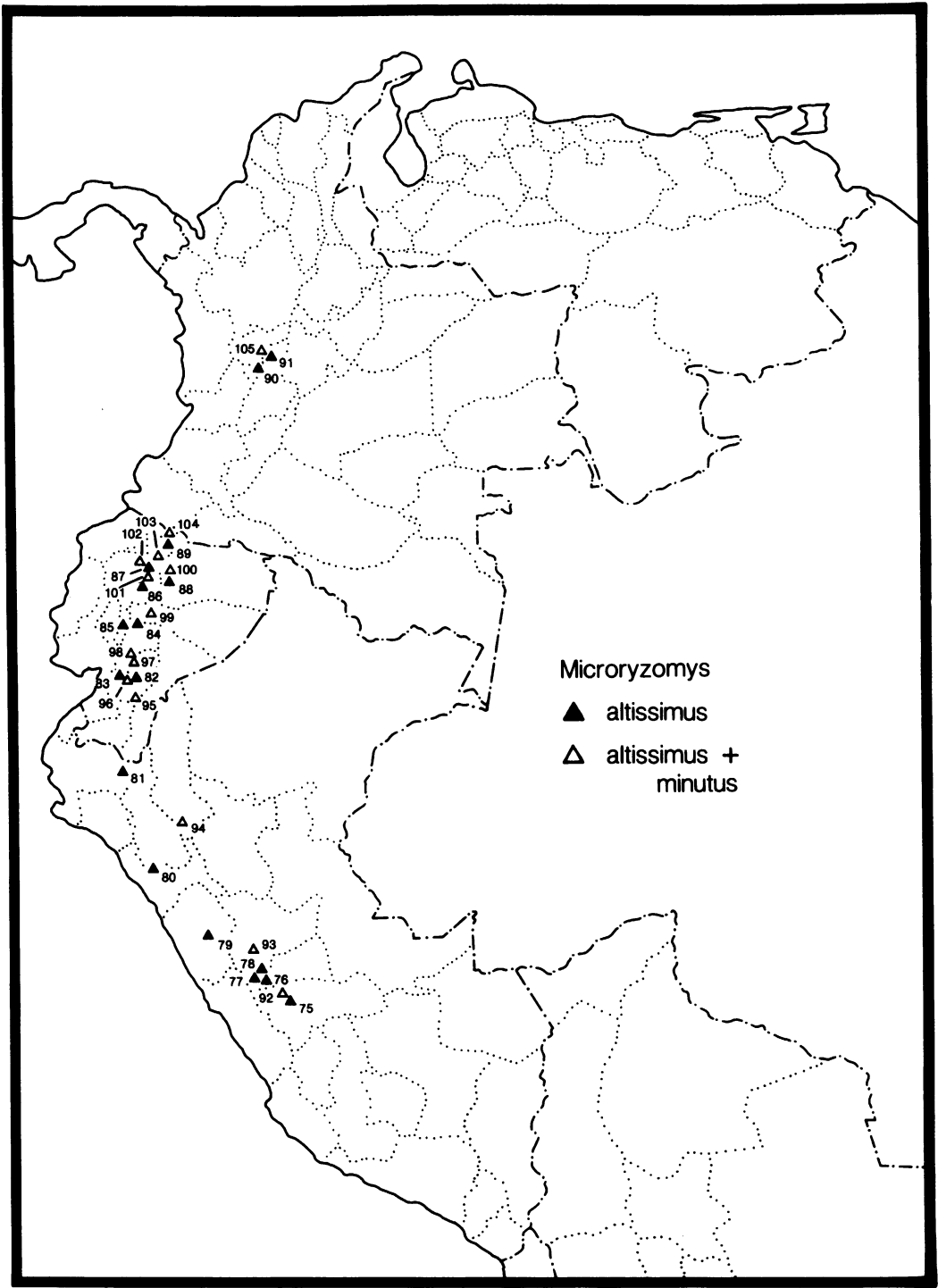


Fig. 2. Geographic distribution of *Microryzomys altissimus* and localities of parapatry or sympatry with *M. minutus*. Key to numbered localities listed in Gazetteer of Principal Collecting Localities.

*Microryzomys altissimus***Peru***Departamento Junín*

75. Maraynioc, 45 mi NE Tarma, 3655–3960 m, 11°22'S/75°24'W.

Departamento Pasco

76. Chipa, 3780 m, 10°42'S/75°57'W.

77. La Quinua (including Chiquirín), 3415–3535 m, 10°36'S/76°10'W.

78. Huariaca, 2745 m, 10°27'S/76°07'W.

Departamento Ancash

79. Quilcayhuanca (including Tullparaju), 4300 m, ca. 09°30'S/77°25'W.

Departamento Libertad

80. Otuzco, mountains NE of, 3050 m, ca. 07°45'S/78°35'W.

Departamento Piura

81. Huancabamba (including SW of), 3000 m, 05°14'S/79°28'W.

Ecuador*Provincia Azuay*

82. Sinicay, 2530 m, 02°50'S/79°00'W.

83. Las Cajas, Cuenca (including Contrayerbas, Lake Luspa, Chaudiurcu, Lake Torreadora), 3355–4000 m, ca. 02°48'S/79°17'W.

Provincia Chimborazo

84. Urbina, 3650 m, 01°30'S/78°44'W.

Provincia Bolívar

85. Sinche, 3385–4000 m, 01°32'S/78°59'W.

Provincia Pichincha

86. Cerro Corazón (including Páramo N of Corazón) 3355 m, 00°32'S/78°39'W.

87. Quito (including Guápulo), 2680–3505 m, 00°13'S/78°30'W.

Provincias Pichincha-Napo

88. Antisana (including Antisanilla and southern slopes), 3505–4115 m, 00°30'S/78°08'W.

Provincia Imbabura

89. Pimampiro, Chota Valley, 2000 m, 00°26'N/77°58'W.

Colombia*Departamento Quindío*

90. Finca La Cubierta, 6 km N Salento-Cocora rd, 3670 m, ca. 04°42'N/75°28'W.

Departamentos Tolima-Caldas

91. Nevado del Ruiz (including Páramo del Ruiz and Tabacal del Ruiz, 3300–4000 m, 04°54'N/75°18'W.

Sympatry or Parapatry**Peru***Departamento Junín*

92. Tarma, 22 mi E, 2225 m, ca. 11°16'S/75°32'W.

Departamento Huánuco

93. Huánuco, 3200–3720 m, 09°55'S/76°14'W.

Departamento Amazonas

94. Balsas, mountains east (including Tambo Jenes), 3050–3660 m, ca. 06°45'S/77°50'W.

Ecuador*Provincia Azuay*

95. Bestion, 3080 m, 03°25'S/79°01'W.

96. Lake Llaviuco, Cuenca, Las Cajas, 3100 m, 02°51'S/79°08'W.

Provincia Cañar

97. San Antonio, N of Cañar and S of Tambo, 2038–3355 m, 02°29'S/78°57'W.

98. Naupan Mountains (including Chical and Pinangu), 3050–3660 m, 02°24'S/78°58'W.

Provincia Tungurahua

99. San Francisco, 2440 m, 01°18'S/78°30'W.

Provincia Napo

100. Papallacta (including Río Papallacta and Río Papallacta Valley), 3125–3660 m, 00°22'S/78°08'W.

Provincia Pichincha

101. Río Pita (including Chillo), 2745–3355 m, 00°18'S/78°28'W.

102. Pichincha (including its eastern slopes, Chaupicruz, Santa Rosa, and San Ignacio), 2925–3800 m, 00°10'S/78°33'W.

103. Mojanda Mountains (including Cochasqui and Piganta), 2285–3355 m, 00°08'N/78°16'W.

Provincia Carchi

104. Atal, Montufar, 2900 m, 00°36'N/77°49'W.

Colombia*Departamento Tolima*

105. Río Termale, 3200–3500 m, 04°58'N/75°23'W.

TAXONOMIC HISTORY

The distinctiveness of mice that later mammalogists have come to recognize as *Microryzomys* initially went unnoticed. Tomes (1860) described *minutus* under the genus

Hesperomys, at that time a loosely defined taxon which encompassed both South and North American muroid rodents that systematists today classify among many genera.

In the late 1800s and early 1900s, three other species-group taxa currently associated with *Microryzomys*, namely *dryas* and *humilior* (Thomas, 1898) and *fulvirostris* (Allen, 1912), were diagnosed under Baird's (1858) genus *Oryzomys*. The so-called pygmy forms of *Oryzomys* were first grouped together by Bangs (1900), who erected *Oligoryzomys* as a subgenus (type species = *Oryzomys navus*) and assigned to it forms such as *dryas*, as Allen (1912) did later for his new species *fulvirostris*. In 1914, Osgood recorded *minutus* and *dryas* from separate localities in northern Peru. He was the first to remark on the closeness of their relationship and to emphasize their differentiation from other dwarf *Oryzomys* assigned to the subgenus *Oligoryzomys*. Osgood (1914: 158) forecasted the essential diagnostic traits of *Microryzomys*, noting that *minutus* and *dryas* "... differ from *O. stolzmanni* and allies in having more delicately formed skulls, with very small teeth, a non-projecting zygomatic plate, and a full rounded relatively broad braincase." In light of their soft, luxuriant pelage and ochraceous underparts, he continued: "The resemblance of this diminutive mouse [in this case, *dryas*] both externally and cranially to certain species of *Rhipidomys* is noteworthy. Its slender hind foot and its laterally pitted palate are the only obvious objections to stating that it is an exact miniature, for example, of *R. fulviventer*."

Osgood's observations may have spurred Thomas to reconsider the status of these particular pygmy forms, which he (1917c) set apart from other *Oryzomys* in a new subgenus, *Microryzomys* (type species = *Hesperomys minutus* Tomes, 1860). At the same time, he also named another species, *aurillus*, belonging to the subgenus. Thomas' brief characterization of *Microryzomys* cited their small teeth and lack of an anterior projection on the zygomatic plate. In a later paper, he (1920) expanded the description of his new subgenus and species and acknowledged Osgood's 1914 comments. Thomas reported (1920: 229) that "... an examination of the young type of *O. minutus* received with the Tomes collection in 1907 (B.M. 7.1.1.112) ... shows the characters of *Microryzomys* in all respects."

The genus-group nomenclatural history of *Microryzomys* might have ended in 1920 were

it not for an inexplicable reversal of opinion by Oldfield Thomas. Whereas earlier he was confident of the identity of Tomes' *minutus* as a *Microryzomys* and its closeness to *dryas* and *aurillus*, he (1926b: 612–613) later faulted his previous determination. "In this statement I was wrong, for a renewed examination of this type [*minutus*] ... and especially of its teeth, ... shows that it is not a *Microryzomys*, in the sense then used, but an *Oryzomys*, no doubt of the '*Oligoryzomys*' group. ..." His conclusion in this regard seemingly hinged on reevaluation of the specific distinction between *stolzmanni* and *minutus*, as in the same paper he had previously remarked (pp. 611–612) that "... an alteration in the name of the common species usually called '*Oryzomys stolzmanni*' is necessitated, for there seems to be no tangible difference between *stolzmanni* of Peru and *minutus* of Ecuador. ..." Accordingly, Thomas used the species name *Oryzomys minutus* for the Peruvian mice and created the genus *Thallomyscus* for *dryas*, the new taxon's type species, and *aurillus*. *Microryzomys* was relegated to a synonym of *Oryzomys*, specifically of the subgenus *Oligoryzomys*, an interpretation followed by Gyldenstolpe (1932) and Tate (1932d, 1932e).

This taxonomic rearrangement persisted only a short time before Osgood (1933) resurrected the whole issue of *Microryzomys* and *Thallomyscus*. After personally studying the holotypes of *minutus* and *dryas*, Osgood concluded that the two represent one and the same species collected at nearly the same time, by the same collector (Louis Fraser), from the same place (near Pallatanga, Ecuador), and therefore placed *Thallomyscus* as a junior synonym of *Microryzomys*. From our perspective, shaped by examination of the same material available to Thomas and Osgood plus hundreds of additional specimens, we fully concur with Osgood's final assessment: the holotype of *minutus* (BMNH 7.1.1.112) is a juvenile, that of *dryas* (BMNH 59.11.1.11) an old adult, and each is an example of the same species. Osgood retained *Microryzomys* as a subgenus of *Oryzomys* only after some deliberation that again (1933: 2–3) revealed his impression of its uniqueness: "... what may now be called *Microryzomys* is far better distinguished from *Ory-*

zomys than is *Oligoryzomys* . . .,” and “. . . if it were not for the rather long palate and marked lateral pits, there could be no objection to regarding *minutus* as a diminutive *Thomasomys*.”

Most subsequent authors have followed Osgood's (1933) treatment of *Microrizomys* as a subgenus of *Oryzomys* and one distinct from *Oligoryzomys* (Ellerman, 1941; Hershkovitz, 1940, 1944; Cabrera, 1961; Honacki et al., 1982; Reig, 1986). Nevertheless, the notion has persisted that *Microrizomys* and especially *Oligoryzomys* are basically artificial constructs that unify the extremely small species within a genus highly variable but evenly graded in body size. For instance, in his revision of North American rice rats, Goldman (1918: 88) noted that “*Oligoryzomys* . . . departs from the subgenus *Oryzomys* mainly in a combination of relative rather than absolute characters.” Later, Tate (1932e: 9) wondered “. . . whether *Oligoryzomys* represents a natural division or is merely a phylogenetic assemblage of small forms descended from independent oryzomyine stocks . . .” and candidly employed the subgenus for convenience. In similar fashion, Hershkovitz (1944: 13) asserted that “. . . the long-tailed *Microrizomys* and *Oligoryzomys* represent hardly more than size gradations leading to the larger *Oryzomys* . . .” However, Myers and Carleton (1981: 12) presented additional qualitative features that distinguish *Microrizomys* from *Oligoryzomys* and considered both to be well-circumscribed subgenera, as did Gardner and Patton (1976) based on karyological information. Carleton and Musser (1984) viewed *Microrizomys* as a genus but included *Oligoryzomys* under *Oryzomys*, and Reig (1986) listed both as subgenera. As we shall document below, a suite of cohesive traits portrays both *Microrizomys* and *Oligoryzomys* as more concrete phylogenetic entities

within the oryzomyine radiation than the comments of Goldman, Tate, and Hershkovitz would suggest.

The species-group nomenclatural history of *Microrizomys* has been less clouded than the issue of its genus-group priority. By the time of Osgood's (1933) synopsis, four species and one subspecies of *Microrizomys* had been proposed: *minutus* (Tomes, 1860); *dryas* and *dryas humilior* (Thomas, 1898); *fulvirostris* (Allen, 1912); and *aurillus* (Thomas, 1917c). Osgood (1933: 3) doubted the consistency of traits used to diagnose the various species and considered them only “. . . to indicate no more than subspecific importance.” Consequently, he recognized the one polytypic species *M. minutus* with five subspecies: *minutus* (with *dryas* in synonymy), *aurillus*, *humilior*, *fulvirostris*, and *altissimus*, a new geographic race which he described from Peru. Osgood admitted that *altissimus* might deserve specific rank; nevertheless, in spite of evidence of near sympatry and ecological segregation, he favored its status as a subspecies.

Hershkovitz (1940) later collected both *minutus* and *altissimus* in syntopy and consequently elevated the latter to a species, while describing two new Ecuadorean subspecies, *hylaesus* and *chotanus*, of *M. altissimus*. The occurrence of two species of *Microrizomys* has been conventionally acknowledged (Cabrera, 1961; Voss and Linzey, 1981; Honacki et al., 1982; Corbet and Hill, 1986), although some workers have continued to maintain *altissimus* as a subspecies of *M. minutus* (Gardner and Patton, 1976; Reig, 1986). As discussed below, the evidence for their specific distinction is incontrovertible, there being at least 14 instances of sympatry or contiguous allopatry in the material we have seen from the high mountains of Peru, Ecuador, and Colombia (fig. 2).

INTRASPECIFIC AND INTERSPECIFIC VARIATION OF *MICRORYZOMYS ALTISSIMUS* AND *M. MINUTUS*

As judged by the results of the two-way analyses of variance in our largest sample (OTU 14, N = 102), crania of *Microrizomys* exhibit little sexual dimorphism but display

appreciable age-related size differences. For only one variable (BIF) are sex effects statistically significant, reflecting the larger mean values of males (table 1). Whether this rep-

TABLE 1
Results of Two-Way Analyses of Variance
(For 16 cranial measurements of 102 specimens
of *Microroryzomys minutus* from Tabay,
Venezuela; also see table 2)

Variable	F (Sex)	F (Age)	F (Interaction)
ONL	0.25	23.65***	6.21*
ZB	3.83	24.88***	9.86**
IOB	3.34	2.16	2.25
LR	0.97	21.53***	6.59*
BR	0.59	14.18***	3.97*
BBC	0.69	3.52	2.33
HBC	0.36	2.63	2.61
BZP	1.04	5.44*	3.29
LD	0.21	33.48***	6.17*
LBP	0.01	3.61	0.40
PPL	0.97	27.12***	8.16**
BM1S	0.03	4.22*	0.16
LIF	0.61	9.67**	0.85
BIF	8.32**	26.03***	16.57***
LM1-3	0.24	0.13	0.01
WM1	0.36	0.72	0.88

* = $P \leq .05$; ** = $P \leq .01$; *** = $P \leq .001$.

resents a Type I sampling error or a possible functional correlate (e.g., size of Jacobsen's organ) cannot be ascertained without further study. In contrast, about half of the variables increase significantly in mean size with the three age cohorts recognized (tables 1, 2), particularly the three largest dimensions (ONL, ZB, PPL) and those of the facial region (LR, BR, LD, LIF, BIF). Measurements describing the size of the toothrow (LM1-3, WM1) and neurocranium (BBC, HBC, IOB), however, reveal neither sex nor age effects (tables 1, 2). Although disparate age distributions could bias morphometric comparisons among OTUs, we did not adjust for such inequalities because our samples of intact crania are already small and regretfully imbalanced with regard to sex and age representation. Furthermore, we assume that such age-related variation is inconsequential relative to the magnitude of interspecific differentiation. Since the cranial features that principally account for morphometric separation of the species (see below) are those that display negligible age-related effects, we feel that this assumption is defensible.

In his description of *minutus altissimus*, Osgood (1933) emphasized the paler color-

ation of his new form but considered it unremarkable compared to *minutus* in size and cranial features. Although Osgood underappreciated the cranial distinctiveness of *altissimus*, Hershkovitz (1940), in raising the form to a species, brought attention to certain proportional differences, among them its more inflated braincase, longer maxillary toothrow, and development of the incisive foramina.

The significance of these traits is generally borne out by the results of our principal component analyses, in which the four samples that we recognize as *M. altissimus* (OTUs 1-4) are set apart from those we identify as *M. minutus* (OTUs 5-16) on the first component (fig. 3). This segregation is due largely to contrasts in length and robustness of the molar rows, size of the braincase, and length of the incisive foramina, which are all proportionately greater in *M. altissimus* (table 3). Except for length of the incisive foramina, these variables were found to be largely unaffected by age-class in the analyses of variance. Cranial dimensions that exhibit marked change with age typically, but not exclusively, loaded more heavily on principal component II. Of the three external variables included, only tail length contributed strongly to the separation of species samples on the first principal component (table 3). The tail is both absolutely and relatively longer in examples of *M. minutus*, approximately 145 percent of head and body length compared to 137 percent in *M. altissimus* (see Appendix).

Considerable between-sample dispersion exists on components II and III, particularly as observed among the OTUs of *M. minutus* and in the divergence of the Colombian example of *M. altissimus*. Some of this variation may stem from the problem of unequal age representation in deriving sample means. Alternatively, the dispersion may convey real interlocality differentiation associated with isolation of organisms inhabiting a complex montane setting. We regret that the inadequacy of our OTUs, both in terms of their size and sampling density, prevents a closer look at the possible congruence of intraspecific morphological divergence and Andean geography. Nonetheless, the separation of the four OTUs of *M. altissimus* from the 12 of *M. minutus* exceeds that seen between other

TABLE 2
Mean Cranial Size for Sex and Age Cohorts of *Microryzomys minutus*
(OTU 14, N = 102; also see table 1)

Variable	Males			Females		
	Y (N = 20)	A (N = 41)	O (N = 17)	Y (N = 7)	A (N = 8)	O (N = 9)
ONL	21.3	22.2	23.1	21.0	21.3	21.7
ZB	11.0	11.3	11.9	11.0	11.2	11.2
IOB	3.5	3.4	3.4	3.3	3.5	3.4
LR	6.5	6.9	7.2	6.5	6.5	6.8
BR	3.8	3.9	4.2	3.7	3.8	3.9
BBC	10.2	10.3	10.3	10.2	10.3	10.1
HBC	7.1	7.2	7.2	7.0	7.1	6.9
BZP	1.7	1.7	1.8	1.7	1.7	1.7
LD	5.3	5.7	6.1	5.2	5.4	5.6
LBP	3.3	3.4	3.5	3.3	3.3	3.5
PPL	7.0	7.4	7.9	6.9	7.1	7.2
BM1S	3.9	4.0	4.1	3.9	4.0	4.1
LIF	3.6	3.8	4.0	3.5	3.6	3.7
BIF	1.6	1.6	1.7	1.6	1.6	1.6
LM1-3	2.9	2.9	2.9	2.9	2.8	2.9
WM1	0.9	0.9	0.9	0.9	0.9	0.9

taxa that had been recognized as species distinct from *M. minutus*, such as *aurillus* (OTU 5) and *fulvirostris* (OTU 10). We interpret these results, together with the distributional records of sympatry, as indicative of only two biological species.

HersHKovitz (1940: 83) first underscored the development of the incisive foramina as a means to identify the two species of *Microryzomys*: “In *altissimus* the palatine [= incisive] foramina extend posteriorly beyond the level of the molars; in *minutus* these foramina terminate anterior to the level of the molars.” To corroborate the utility of this characteristic (see fig. 4) for species discrimination, we measured the distance between the caudal end of the incisive foramina and the frontal plane intersecting the anterior border of the first upper molars. The incisive foramina do clearly project between the first molars in most *M. altissimus*, approximately 85 percent of the 97 specimens measured, but their termination relative to the first molars varies broadly in *M. minutus* (table 4). In only 50 percent of the latter do the foramina end discernibly anterior to the first molars, and in some 20 percent, they extend between the toothrows. Although the incisive foramina average longer in samples of *M. altissi-*

mus, a condition which contributes substantially to its morphological differentiation from *M. minutus*, their position with respect to the first molars cannot be used as a facile landmark for species assignment. As with other closely related muroid species, the nature of individual character variation requires that additional features be consulted in rendering species determinations.

Shape of the incisive foramina is a qualitative, although not absolute, discriminator of the two species. The sides of the foramina are parallel or nearly so in most examples of *M. altissimus*, slightly broader at midsection in a few. The incisive foramina of some *M. minutus* resemble those of *M. altissimus*, but the foramina of most expand widely in their posterior third, giving the openings an ovate rather than oblong outline (fig. 4).

In addition to the size of the molar rows, the occurrence of a protolophid on the lower first molars may aid species discrimination. As observed in specimens with slight dental wear, a protolophid is regularly absent or small in *M. minutus* but usually present and distinct in *M. altissimus* (fig. 5, arrow). Otherwise, occlusal configuration of the enamel structures, folds, and fossettes is similar in the two species.

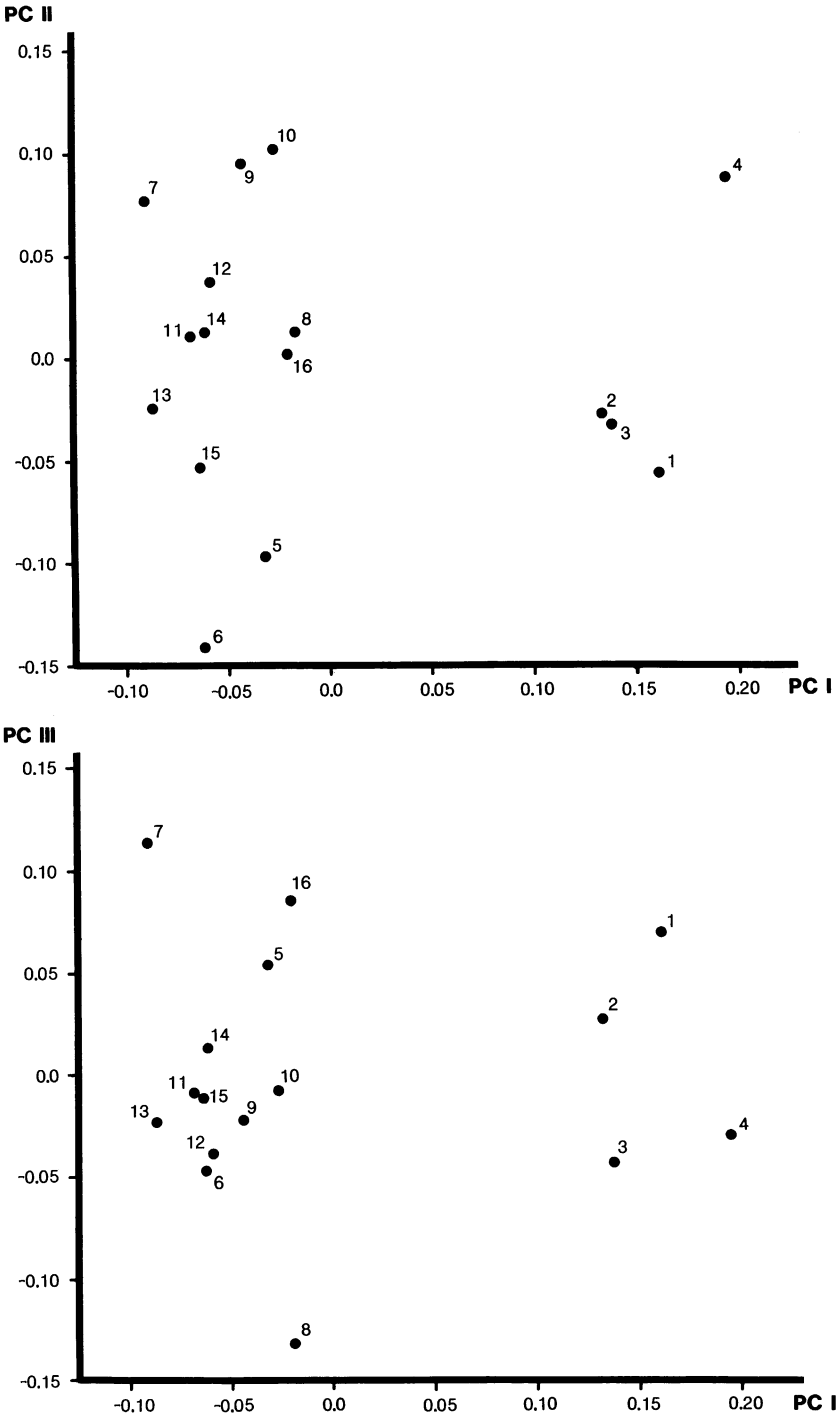


Fig. 3. Sample means of *Microryzomys altissimus* (Nos. 1-4) and *M. minutus* (Nos. 12-16) projected onto the first three principal components extracted from the covariance matrix of their log-transformed measurement data. See table 3.

TABLE 3
Results of Principal Components Analysis of
Microryzomys
(Performed on log-transformed means of the 3
external and 16 cranial variables of all 16
OTUs; see text and figure 3)

Variable	PC I	PC II	PC III
Correlations			
HBL	-.43	.24	-.32
TL	-.83	.26	.40
HFL	-.18	.48	.29
ONL	.27	.78	.01
ZB	-.04	.84	-.06
IOB	-.13	.68	-.41
LR	-.08	.31	.05
BR	-.50	.47	-.37
BBC	.80	.37	.15
HBC	.50	-.07	-.30
BZP	.00	.54	.21
LD	-.60	.57	.03
LBP	.08	.70	-.56
PPL	-.18	.48	-.13
BM1S	.69	.35	.04
LIF	.80	.26	.46
BIF	-.08	.37	.85
LM 1-3	.96	.21	.01
WM1	.89	.19	-.09
Eigenvalue	.009	.005	.004
% Variance	35.7	18.4	13.8

HersHKovitz (1940) noted another qualitative characteristic, the size of the incisor tubercle on the dentary, as helpful for separating the species. In adult specimens of *M. minutus*, this tubercle or capsular process, which represents the posterior limit of the incisor alveolus, forms a distinct lateral projection from the ascending ramus (figs. 4, 6). The tubercle is smaller and indistinctly developed in adult *M. altissimus*. This distinction is best appreciated when examining specimens of comparable age and seems useful in conjunction with other features; however, the nature of this trait disallows a quantitative assessment of its discriminatory reliability.

In addition to the greater length of tail, specimens of *M. minutus* also possess broader hind feet, especially as observed in the metatarsal region. Perhaps associated with their broader metatarsum, the proximal plantar pads (thenar and hypothenar) of *M. minutus* appear larger and fleshier, compared to the more gracile and elongate pads of *M. altissimus* (fig. 7). These interspecific distinctions are evident only between fluid-preserved specimens of equivalent age; plantar pad development is obscured on the shriveled hind feet of dried museum skins.

TABLE 4
Termination of Incisive Foramina in *Microryzomys*
(Distance measured, to 0.01 mm, relative to the anterior border of the first molars)

Sample	N	Anterior			Even	Posterior		
		> .30	.30-.15	.15-.05	.00 ± .05	.05-.15	.15-.30	> .30
<i>altissimus</i>								
Peru	33	0	0	1	5	5	16	6
Ecuador	49	0	0	0	7	5	20	17
Colombia	15	0	0	0	1	2	10	2
<i>minutus</i>								
Peru	44	1	3	11	15	6	7	1
Ecuador	21	3	1	7	6	2	2	0
Colombia	73	8	23	15	16	7	1	3
W Venezuela	151	14	39	31	41	12	14	0
N Venezuela	12	0	0	0	2	0	7	3
Totals:								
<i>altissimus</i>	97	0	0	1	13	12	46	25
<i>minutus</i>	301	26	66	64	80	27	31	7
Frequencies:								
<i>altissimus</i>	97	0.0	0.0	1.0	13.4	12.4	47.4	25.8
<i>minutus</i>	301	8.6	21.9	21.3	26.6	9.0	10.3	2.3



Fig. 4. Views ($\times 3$) of the crania and mandibles of adult *Microryzomys* from Ecuador. Top row: *M. minutus* (AMNH 63037). Bottom row: *M. altissimus* (AMNH 155675).

Other than proportional contrasts of the tail and hind feet, external features that distinguish the two species are chromatic ones, notably the amount of dorsoventral pelage contrast, the bicolouration of the tail, and the dusky saturation of the tops of the feet. *Microryzomys altissimus*, as Osgood (1933: 5) observed, has "... the upper and under parts well distinguished, the tail broadly and completely bicolor, the feet wholly whitish without dusky markings." The species has overall slightly paler pelage: the head is grayish and the dorsal body fur contains more yellow than

tawny highlights; the ventral coat is pale to warm grayish buff, not rich ochraceous-tawny. The dorsum and venter are thus clearly demarcated in pelage tone in most specimens at hand. The tail is dark brown above and unpigmented below, usually appearing sharply bicolor for its entire length; in some individuals, the ventral surface of the distal one-fourth is mottled or dusky. Tops of the front and hind feet are white; some specimens have traces of brown in the skin but not enough to mask the whitish appearance.

At localities in Peru and Ecuador where

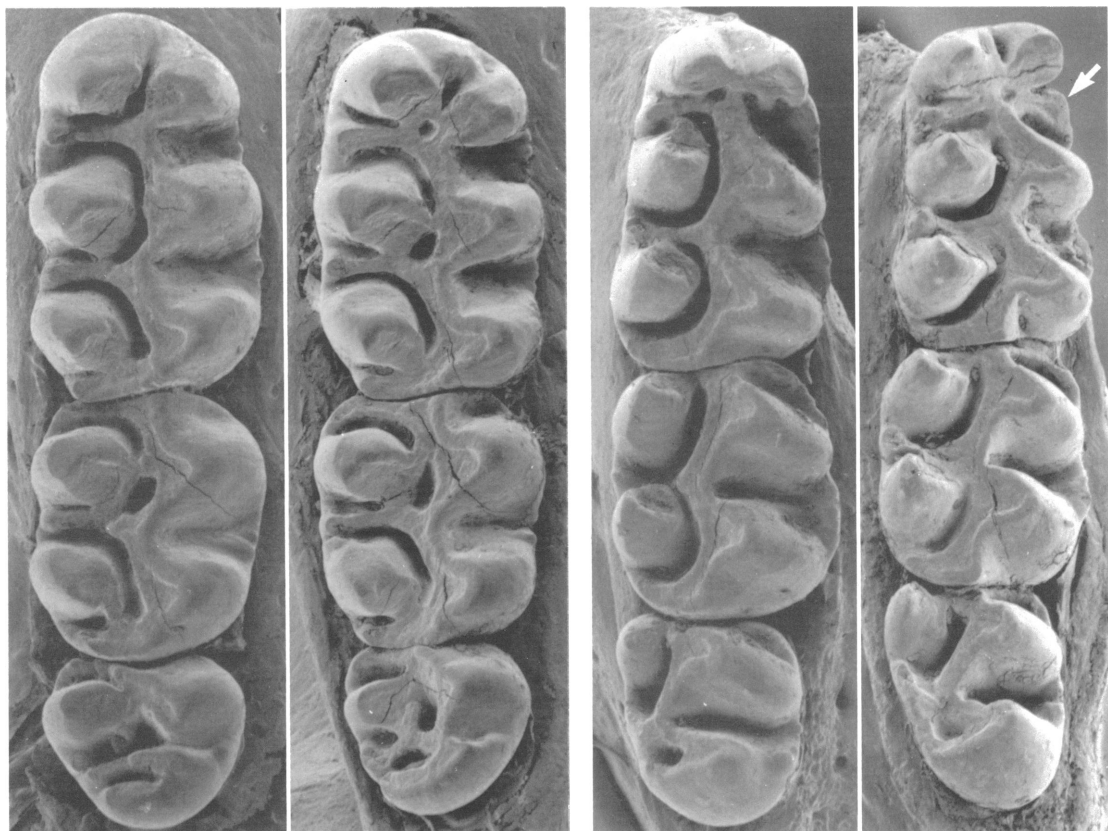


Fig. 5. Occlusal view of upper (left pair) and lower (right pair) right molar rows of *Microroryzomys*. In each pair, the left photograph is *M. minutus* (AMNH 66527; LM1-3 = 3.0 mm, Lm1-3 = 3.1 mm), and the right photograph is *M. altissimus* (AMNH 231055; LM1-3 = 3.1 mm, Lm1-3 = 3.3 mm). The arrow indicates the protolophid, a structure more frequently observed in specimens of *M. altissimus*.

the two species have been caught together, examples of *M. minutus* may be usually recognized by the darker and richer hue of both their dorsum and venter. The upper and underparts are typically colored ochraceous-tawny, presenting little chromatic distinction between the dorsal and ventral coats. Still, in any large series of the two from the same area, some specimens of each are inseparable in ventral coat color and in the contrast, or lack of it, between dorsum and ventrum. The tails of most specimens of *M. minutus* are dark brown all around; some individuals show a pale or mottled undersurface, either extending nearly the full length or just near the base. Dorsal surfaces of the front and hind feet are darker in *M. minutus* compared to *M. altissimus*, appearing brownish rather than whitish.

Most specimens of *M. minutus* and *M. altissimus* have a bright orange-buff patch of fur behind their pinnae, although this trait is frequently difficult to verify in museum skins with the pinnae appressed flat to the nape. In any sample of each species, these postauricular patches are sharply evident on most specimens, while faint or lacking on others. We could not detect significant interspecific differences in the expression of this feature or its frequency of occurrence.

Of the color patterns surveyed, tail pigmentation and coloration of the feet provide the most consistent distinctions between *M. minutus* and *M. altissimus*. Differences in pelage tone and degree of dorsal-ventral contrast, although generally apparent between large series, can be misleading if used alone. These chromatic traits, combined with dis-

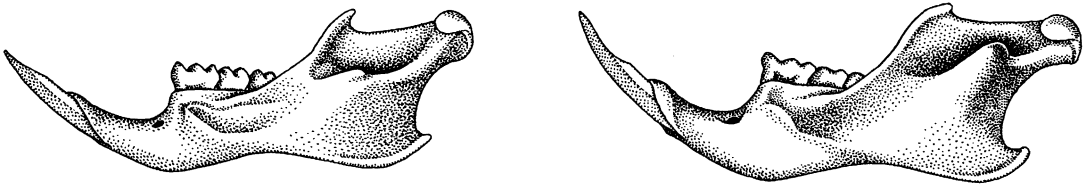


Fig. 6. Lateral view of dentaries of adult *Microryzomys* contrasting size of the incisor capsule. Left, *M. altissimus* (AMNH 63058); right, *M. minutus* (AMNH 67562).

tinctions in tail length, size of braincase, length and robustness of molar rows, definition of the protolophid on m1, length and outline of incisive foramina, and size of the incisor tubercle, offer a reliable phenotypic suite for discriminating the two species.

The overlap of *M. minutus* and *M. altissimus* in their ventral fur color underscores the range of variation within the genus that extends from buffy gray to ochraceous-tawny. The former is typical of *M. altissimus*, the latter of *M. minutus*. Nevertheless, this chromatic range may be observed not only within a locality sample but between samples from different geographic regions, and such regional differences have formed the primary basis for past recognition of subspecies within each of the species (Herskovitz, 1940; Osgood, 1933).

In his 1933 publication clarifying the status of *Thallomyscus* and *Microryzomys*, Osgood also delineated the geographic races of *M. minutus* that, except for the elevation of *altissimus* to species rank, have since been recognized (for example, Cabrera, 1961). Together with the nominative form from Pallatanga, Ecuador, Osgood (1933) associated *aurillus* (Thomas, 1917c) from central Peru, *humilior* (Thomas, 1898) from the Bogota region of Colombia, and *fulvirostris* (Allen, 1912) from Munchique in western Colombia, as formal subspecies of *M. minutus*. In Osgood's view, *aurillus* and *humilior* were similar in color, both slightly paler than *minutus* proper, and *fulvirostris* was indistinguishable from *humilior*.

This is the general pattern we detect. The only difference in external features among all samples of *M. minutus* is the intensity of ochraceous versus buffy saturation of the ventral fur. Specimens from the mountains of Ecuador are the darkest: most have ochraceous buff or tawny venters and lack demar-

cation between the upperparts and underparts. Some examples from Bolivia, Peru, Colombia, and Venezuela also possess ochraceous-tawny underparts, yet many have buffy gray venters such that the upper and underparts noticeably contrast. Between these extremes, the average saturation of buffy and ochraceous hues of most mice in a sample is less than that typical of the Ecuadorean series. However, as Osgood earlier emphasized, the chromatic difference is slight, and we have found the variation among our larger samples of *M. minutus* to be extensive and highly localized throughout its broad Andean distribution. Nor can we discern any clear correspondence between cranial morphology and the average and minor contrasts in ventral pelage tone. As observed above, considerable dispersion exists among OTUs of *M. minutus* on principal components II and III, but that spread does not suggest any geographic pattern concordant with variation in venter color. Because we are unable to extract information from our analyses that would allow us to consistently recognize and unambiguously diagnose geographic subunits within *M. minutus*, we have abandoned subspecific divisions of this species.

Differences in coat color as well as cranial size have been used to divide *M. altissimus* into subspecies. Herskovitz (1940), after documenting its sympatry with *M. minutus*, elevated Osgood's (1933) *altissimus* to a species and described two subspecies of the latter from the northern Andes of Ecuador: *chotanus* from 2000 m in the Chota Valley, Provincia Imbabura, and *hylaesus* from 2900 m in the eastern cordillera, Provincia Carchi. Although Herskovitz had only one specimen of *chotanus* and two of *hylaesus*, he characterized the former as larger and paler, lacking bright postauricular patches, and having larger infraorbital foramina, wider incisive

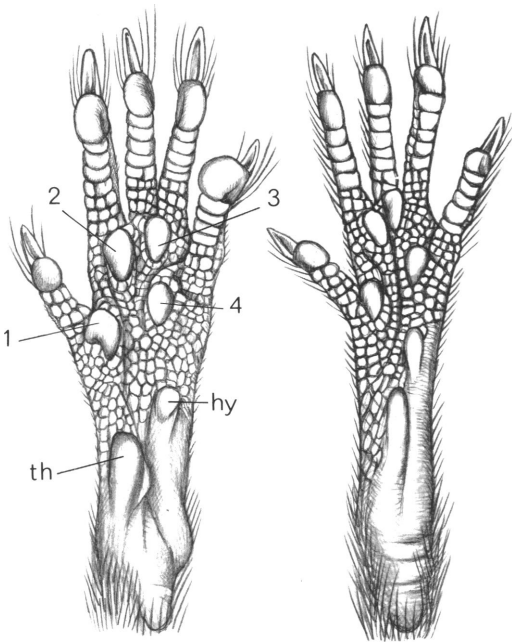


Fig. 7. Plantar view of left hind foot in species of adult *Microryzomys*. Left: *M. minutus* (AMNH 248278); right, *M. altissimus* (AMNH 248280). hy, hypothenar pad; th, thenar pad; 1–4, first through fourth interdigital pads.

foramina, and a heavier rostrum than *hylaesus*. The definition of postauricular patches, as discussed previously, varies in both *M. altissimus* and *M. minutus*, and no significant geographic variation in fur color or external proportions is otherwise apparent among our examples of *M. altissimus* from Peru, Ecuador, and Colombia. When measured against the amount of population and individual variation observed over a broader geographic sweep, the chromatic distinctions ascribed to *chotanus* and *hylaesus* seem insignificant.

Additional perspective on these taxa (whose holotypes we have not seen) is supplied by Dr. Robert S. Voss (personal research notes),

who compared them to the specimens of *M. altissimus* he collected around Papallacta, Ecuador.

Differences in coat color between the holotype of *chotanus* and the two specimens of *hylaesus* are slight, fall within the range of pelage tones exhibited by Papallacta mice, and may be attributable to an artifact of preparation: the two specimens of *hylaesus* are understuffed and the brownish, dorsal guard hairs are therefore crowded closer together than in the better-stuffed specimen of *chotanus*. Bright patches of postauricular fur are evident on the holotype of *hylaesus* as remarked by Hershkovitz, but appear no more conspicuous on the paratype of that taxon than on the single example of *chotanus*, and such patches are of variable development among Papallacta mice. Insofar as measurements are retrievable from the damaged skulls of *hylaesus* and *chotanus*, differences in cranial dimensions appear commensurable with the range of variation of the same measurements among mice of similar ages from Papallacta. Differences in size between the two races are correlated with shape differences that usually accompany ontogenetic development, and from toothwear I judge the type of *chotanus* to have been fully adult while examples of *hylaesus* are subadult (UMMZ 77223) or young adult (UMMZ 77224). Thus the distinctions between Hershkovitz's (1940) examples of *altissimus* from Imbabura and Carchi appear less trenchant by comparison with ontogenetic and individual variation in the larger Papallacta sample; geographic differentiation among northern Ecuadorean populations of this species remains to be convincingly demonstrated, and the use of subspecific nomenclature does not appear warranted by the available data.

We concur but draw attention to one problem yet to be resolved concerning the degree of differentiation among populations of *M. altissimus*. The sample from Colombia (OTU 4) is set apart in cranial morphometry from other OTUs of *altissimus*, but this separation does not reflect the distribution of named subspecies; the sample from the type locality of *altissimus* in Peru (OTU 1) and the two from Ecuador are phenetically very close (fig. 3). The extent of the divergence of the Colombian mice and their level of relationship to other *altissimus* populations warrant further study.

ANATOMICAL COMPARISONS WITH OTHER ORYZOMYINES

In the descriptive accounts that follow, we first present the development of a feature as observed in *Microryzomys*. Comparisons to *Oryzomys palustris* and species of *Oligory-*

zomys emphasize qualitative differences to the condition found in *Microryzomys*; if not mentioned, the trait's development resembles that described for *Microryzomys*. We

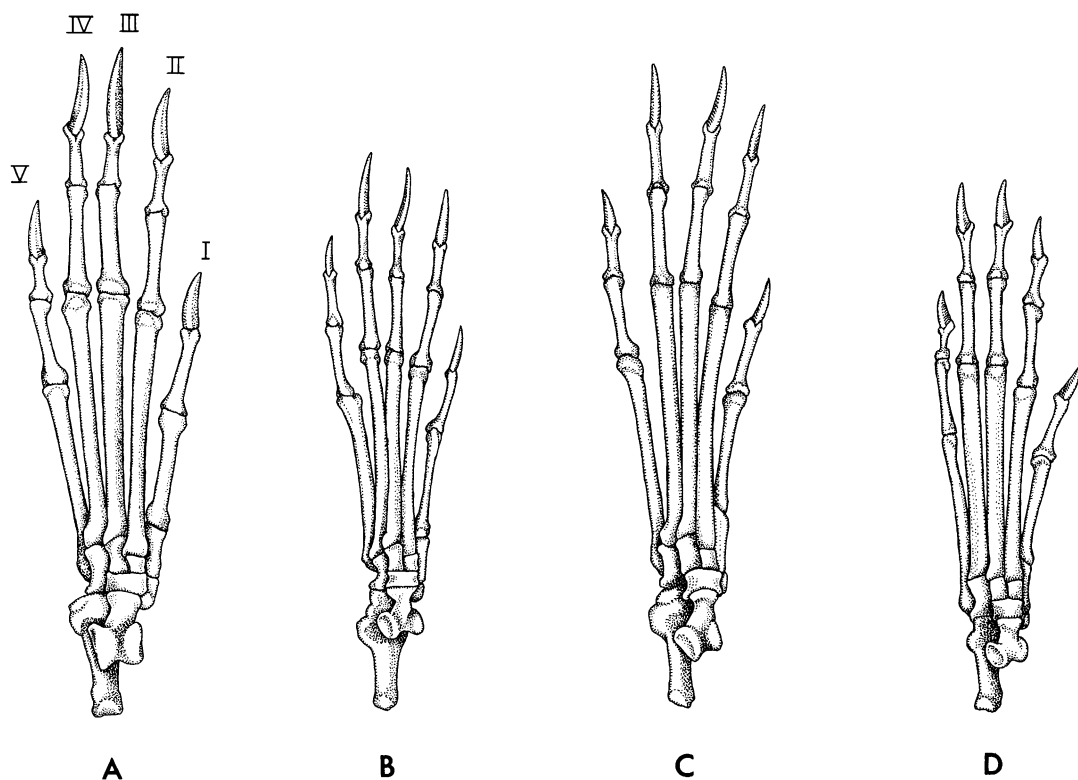


Fig. 8. Dorsal view of metatarsal proportions among species of adult oryzomyines. A, *Oryzomys palustris* (AMNH 239265); B, *Microryzomys minutus* (AMNH 248278); C, *Oligoryzomys longicaudatus* (AMNH 262233); D, *Oligoryzomys microtis* (AMNH 213695). Note the longer metatarsal V relative to IV in *Microryzomys* as compared to *Oryzomys* and *Oligoryzomys*.

based most of our cranial and external comparisons on the condition observed in fully adult animals.

EXTERNAL FORM

PELAGE AND PINNAE

Microryzomys: The texture of the fur is soft and wooly. Individual overhairs (not guard hairs) of the dorsal coat exhibit an agouti banding pattern, the basal three-fourths plumbeous, followed by an ochraceous band, then a blackish tip. Guard hairs are either entirely black or silver-tipped and not much longer than the regular coat except on the rump. The tops of the front and hindfeet are covered with fine white hairs. The end of each digit bears a cluster of silvery hairs that arch over the claw, nearly obscuring it; the terminal hairs overhang the claws of the manus but rarely extend beyond the claws of the pes.

In addition to the mystacial array, there are superciliary, genal, submental, and a small cluster of interrampal vibrissae, the last associated with a small but conspicuous sebaceous gland evident even on study skins (see Brown, 1971, for vibrissal descriptions and terminology). There are also ulnar carpal vibrissae just above the wrists, but we could not locate other forelimb sets or calcaneal vibrissae on the hindlimbs (Brown and Yalden, 1973, describe limb vibrissae). The tail is relatively long, about 55 to 60 percent of total length, thinly covered with hair (denser in *altissimus*) such that the scutellation is evident, lacks a terminal pencil, and is sharply to weakly bicolored (*altissimus*) or basically monocolored (*minutus*).

The moderate size pinnae are dark, each clothed externally and along the internal rim with blackish hairs.

Oryzomys palustris: The fur is thick and

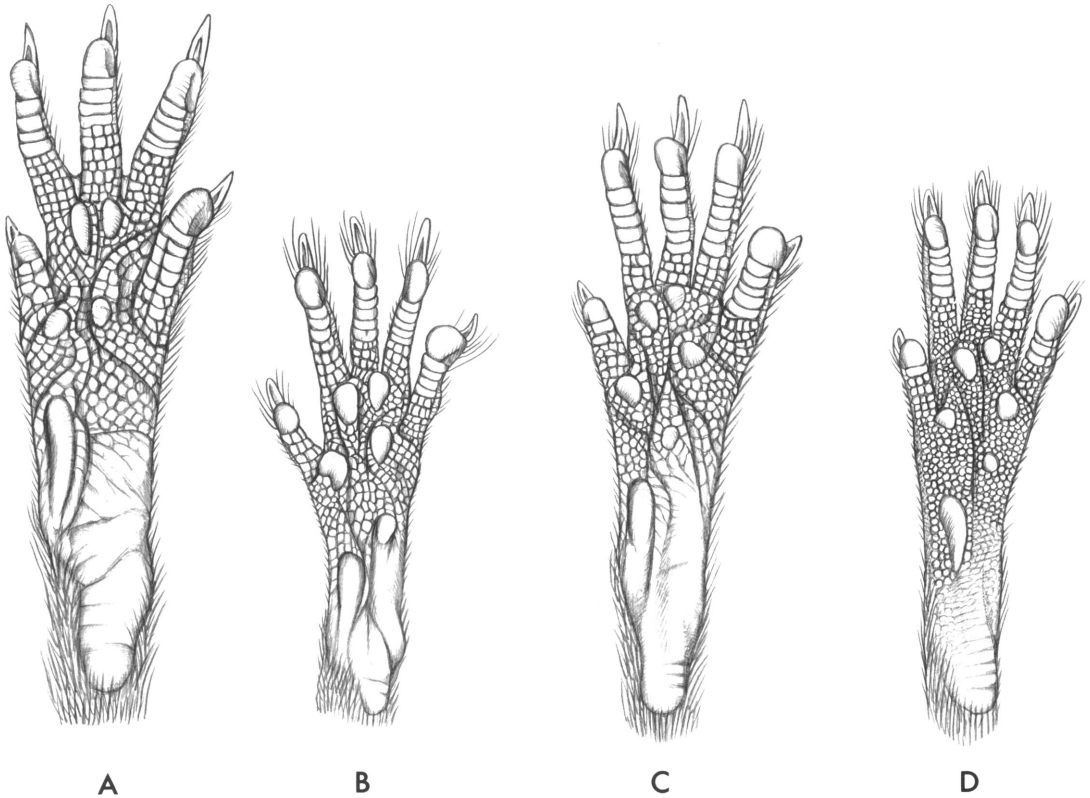


Fig. 9. Plantar view of left hind foot in species of adult oryzomyines. A, *Oryzomys palustris* (AMNH 239265); B, *Microryzomys minutus* (AMNH 248278); C, *Oligoryzomys longicaudatus* (AMNH 213694); and D, *Oligoryzomys microtis* (AMNH 263334).

short. In texture, it is sleeker and coarser to the touch, lacking the soft, woolly resiliency of *Microryzomys* fur. The guard hairs extend farther beyond the body fur, and most of those on the rump have unpigmented silvery tips, a marked contrast to the high density of entirely black guard hairs in *Microryzomys*. Upperparts and underparts are always sharply delineated, more so even than in *M. altissimus*. Dorsal surfaces of the front and hind feet are more densely covered with white hairs; the terminal hairs of the digits cover only the proximal half of each claw. The tail is stout and relatively shorter, subequal to head and body length.

The pinnae are paler and do not contrast sharply with the dorsal coat as seen in species of *Microryzomys*. A tuft of white or pale buff hairs occurs at the anterior base of each pinna and extends onto their lower internal margin; comparable tufts are absent in *Mi-*

croryzomys, although most individuals of both species possess buffy or ochraceous postauricular patches.

Oligoryzomys: The fur feels coarser and sleeker, not as fine and woolly. The textural contrast is greatest between *Microryzomys* and lowland species of *Oligoryzomys* (such as *microtis*, *nigripes*, and *chacoensis*); Andean forms (such as certain populations of *longicaudatus* and *destructor*) approach *Microryzomys* in pelage length and softness.

MAMMARY GLANDS

Microryzomys: Females uniformly possess eight mammae arranged in four pairs—two inguinal, one axillary, and one pectoral.

Oryzomys palustris: Condition as in *Microryzomys*.

Oligoryzomys: Condition as in *Microryzomys*.



Fig. 10. Dorsal view ($\times 3$) of adult crania. Left, *Oryzomys palustris* (AMNH 222367); middle, *Microryzomys minutus* (AMNH 63037); right, *Oligoryzomys microtis* (AMNH 211781).

FOREFEET AND HINDFEET (figs. 8, 9)

Microryzomys: The manus has a nail-bearing, stubby pollex; the palmar surface is naked with five close-set palmar pads, consisting of three moundlike interdigital pads and two larger, oblong metacarpal pads. The hindfoot is relatively long and narrow (for example, as compared to species of *Oecomys*) and conforms to the terrestrial-scansorial type recognized by Hershkovitz (1960: 524, fig. 4). The first and fifth digits are shorter than the three central ones; the hallux (with claw) reaches the middle of the first phalanx of digit II and the fifth digit (with claw) nearly reaches the distal end of the second phalanx of digit IV. Metatarsal V is shorter than metatarsals II–IV, about 75 percent of their length (fig. 8B). White hairs clothe the dorsal metatarsus and barely extend over the sides of the foot. The entire plantar surface from the phalanges to the heel lacks hairs and bears six prominent plantar pads. Four interdigital pads occur at the base of the phalanges and cluster

near one another, pads 2 and 3 forming a pair set slightly anterior to pads 1 and 4. Toward the heel are located, in alternation, the hypothenar, which matches the interdigitals in size and fleshiness, and the large oblong thenar, which forms a conspicuous landmark on the ventral metatarsus (fig. 9B).

Oryzomys palustris: The hindfeet are relatively broader with slight but discernible interdigital webbing (fig. 9A). The claw of the fifth digit extends only to the base of the second phalanx of digit IV, and the fifth metatarsal is conspicuously shorter than metatarsals II–IV, about two-thirds their length (fig. 8A). The fur covering the metatarsus is denser and appreciably overlaps the sides of the foot to form moderately developed fringes. The interdigital plantar pads are much smaller, unlike the fleshy mounds observed in *Microryzomys*, and are nearly obscured by epidermal creases. The thenar pad is relatively longer and narrower and barely elevated above the plantar surface. A hypothenar pad is either absent, the usual condition, or so



Fig. 11. Ventral view ($\times 3$) of crania shown in figure 10. Left, *Oryzomys palustris*; middle, *Microryzomys minutus*; right, *Oligoryzomys microtis*.

diminutive that it is difficult to detect, even on fluid-preserved specimens (fig. 9A).

Oligoryzomys: The hindfeet are broader with fifth digits relatively shorter; the claw of digit V reaches only to the base of the second phalanx of digit IV (fig. 8C, D). Relative to plantar area, the interdigital pads are conspicuously smaller and not as fleshy. Like the interdigitals, the thenar and hypothenar pads are also smaller, the latter a round pimple compared to the oblong mound found in both species of *Microryzomys* (fig. 9C, D).

CRANIUM

ROSTRUM (figs. 10, 14)

Microryzomys: The rostrum is narrow, delicate, and relatively short (about 28–30% of ONL). As seen in dorsal view, the rostral sides taper gradually forward from the nasolacrimal capsules, such that the distal portion of the premaxillary bones are hidden beneath the nasals.

Oryzomys palustris: Specimens possess a

wide and short rostrum that appears stocky compared to that of *Microryzomys*. The greater width results from the relatively more inflated nasolacrimal capsules and the broader premaxillaries. The rostrum also tapers anteriorly but the premaxillary bones can be seen to extend for almost their entire length along the nasal margins.

Oligoryzomys: Compared to *Microryzomys*, the rostrum is heavier. The size of the premaxillaries relative to the nasal bones imparts a stocky shape more closely resembling that of *O. palustris*.

ZYGOMATIC ARCHES AND PLATES (figs. 10, 12, 14, 15)

Microryzomys: In both species, the zygomatic plate is narrow with only a slight forward extension that does not overlap the thin bony capsule for the nasolacrimal duct. As a consequence, the zygomatic notch is shallow and the anterior ends of the zygoma appear squared-off in dorsal view (figs. 10, 14). The



Fig. 12. Lateral view ($\times 3$) of crania and mandibles of specimens shown in figures 10 and 11. Top left, *Oligoryzomys microtis*; top right, *Microryzomys minutus*; bottom, *Oryzomys palustris*.

lightly built zygomatic arches are parallel-sided or only slightly convergent anteriorly. This configuration contributes to the squared-off appearance as does the narrow breadth of the zygoma relative to the braincase—the arches either align with or extend slightly beyond its lateral contours. The midportions of the zygoma dip ventrally but remain discernibly above the level of the orbital floor, as seen in lateral view. The jugal is extremely reduced such that the zygomatic processes of the maxillary and squamosal contact one another or remain separated by a sliver of jugal bone (fig. 15B–D).

Oryzomys palustris: The zygomatic plate is broader, and its anterior margin projects forward to appreciably overlap the nasolacrimal capsule and to form a conspicuous zygomatic notch (fig. 14). This configuration, together with the laterally bowed arches that sweep outward beyond the sides of the braincase, gives a more elongate, curving appearance to the zygoma as viewed dorsally, rather than the squared outline seen in *Microryzomys*. The zygomatic arches of *O. palustris* are sturdy and robust with compact but distinguishable jugals. The jugal spans only a short segment of each mid-arch but distinctly separates



Fig. 13. Occipital view ($\times 4$) of crania shown in figure 12. Plane of the foramen magnum is vertical in *Oryzomys palustris* (top) and *Oligoryzomys microtis* (bottom) but oriented posteroventrally in *Microryzomys minutus* (middle).

the zygomatic extensions of the maxillary and squamosal bones (fig. 15A). In contrast to *Microryzomys*, the middle part of the arches is slung lower, their ventralmost projection approximately even with the floor of the orbit (fig. 12).

Oligoryzomys: The zygomatic plates are broader, and their anterior borders extend forward to slightly overlap the capsular inflation for the nasolacrimal canal and to form a distinct zygomatic notch, which is not as

deep as that of *O. palustris*. This forward projection of the plate eliminates the "squared-off" appearance of the zygomatic arches and rostrum as observed in *Microryzomys*. The zygomatic arches bow more laterad and dip strongly ventrad, approaching more the condition observed in *O. palustris* than that of *Microryzomys* (fig. 12). The development of the jugal is similar to that of *Microryzomys*: this bone is either absent or is represented by irregular slivers compressed between the maxillary and squamosal processes of the arch (fig. 15B–D).

INTERORBIT (fig. 10)

Microryzomys: In both species the interorbit is narrow, its edges smooth and shaped like an hourglass, without supraorbital shelves or ridges.

Oryzomys palustris: The interorbit is wide with a well-defined supraorbital shelf outlined by either weakly beaded edges or ridges at the posteromedial aspect of each orbit. This arrangement imparts a more elongate appearance to the braincase in dorsal view.

Oligoryzomys: The dorsal contour of the narrow interorbit also recalls an hourglass shape, but the edges are sharper, not rounded as in specimens of *Microryzomys*.

BRAINCASE (figs. 10, 12, 13)

Microryzomys: This cranial region dominates the dorsal aspect of the skull, seeming disproportionately large relative to the orbital and facial areas (fig. 10). The walls of the broad braincase are rounded and smooth, lacking temporal and lambdoidal ridges. The frontal bones meet posteriorly at a 90° angle, imparting a distinct flexion to the frontoparietal border; the interparietal is short anteroposteriorly but transversely broad, nearly equaling the caudal border of the parietals. In lateral view, the cranial roof is observed to slope sharply downward toward the occiput, the highest point of this flexion occurring above the postglenoid foramina (fig. 12). As a result of this pronounced cranial flexion, the foramen magnum is oriented posteroventrally (fig. 13) and the occipital condyles are inconspicuous viewed from above.

Oryzomys palustris: In contrast to that of *Microryzomys*, the braincase appears pro-

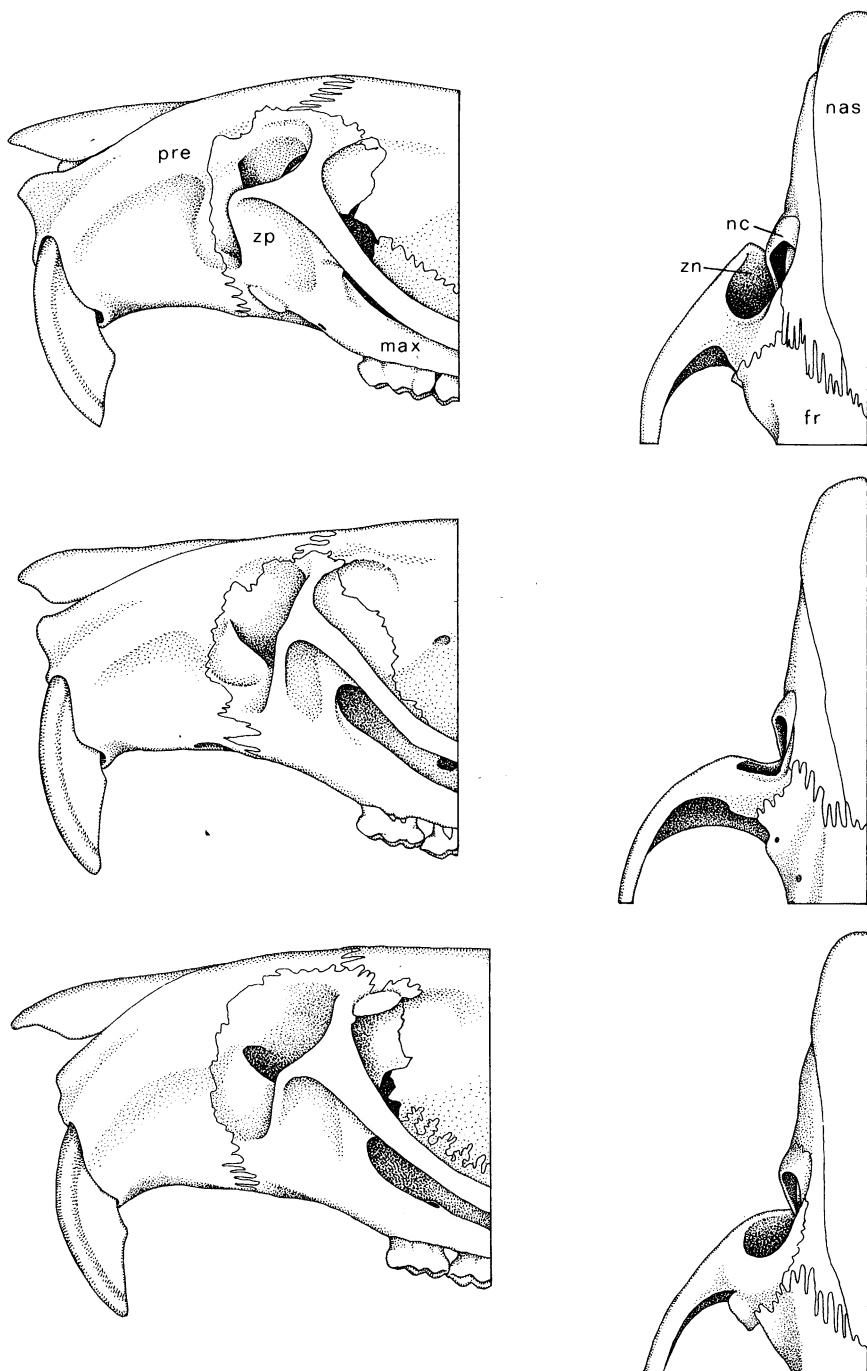


Fig. 14. Rostral and zygomatic regions of species of adult oryzomyines. Top, *Oryzomys palustris* (AMNH 242523); middle, *Microrizomys minutus* (AMNH 46808); bottom, *Oligoryzomys microtis* (AMNH 248993). **fr**, frontal; **max**, maxillary; **nc**, nasolacrimal capsule; **nas**, nasal; **pre**, premaxillary; **zn**, zygomatic notch; **zp**, zygomatic plate.

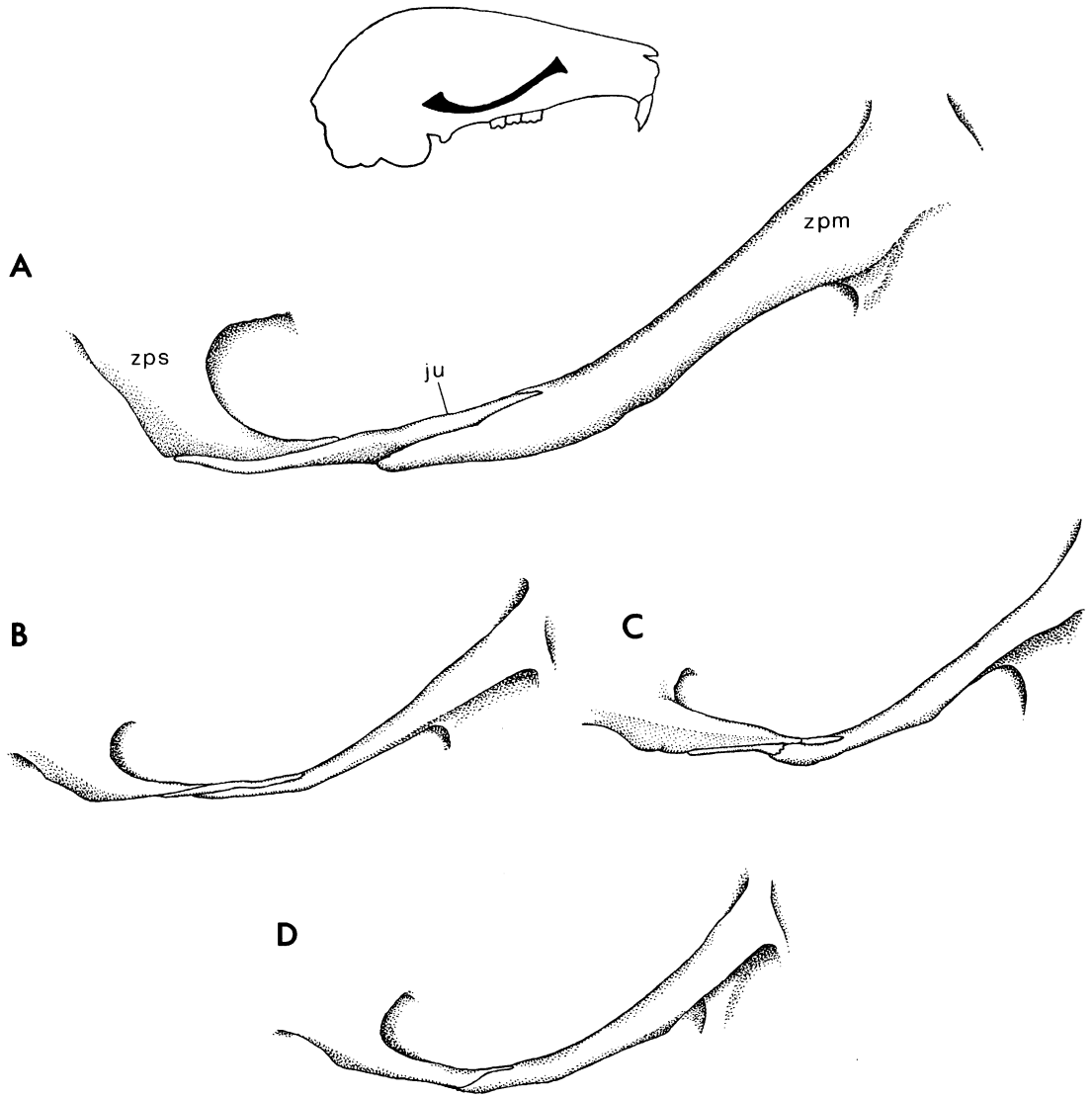


Fig. 15. Lateral view of right zygomatic arch showing jugal development in species of adult oryzomyines. A, *Oryzomys palustris* (AMNH 242669); B, *Microryzomys altissimus* (AMNH 231064); C, *M. altissimus* (AMNH 63047); D, *M. minutus* (AMNH 260419). Views B–D illustrate the range of jugal formation observed in species of both *Microryzomys* and *Oligoryzomys*. ju, jugal; zpm, zygomatic process of maxillary; zps, zygomatic process of squamosal.

portionately integrated with the remainder of the cranium. It is relatively narrower, box-like, and angular due to the temporal and lambdoidal ridges that become prominent in adult and older animals. The interparietal is relatively smaller, its width covering about one-half of the caudal border of the parietals.

The cranial vault is nearly flat from the interorbit to the occipital border, such that the rear of the braincase forms a more vertical wall and does not overhang the occipital condyles, portions of which are evident in dorsal view. With the lack of a strong cranial flexion, the plane of the foramen magnum is clearly

vertical, its opening directed caudad not ventrad (fig. 13).

Oligoryzomys: The calvarium is relatively narrow, its dorsal profile flatter than in examples of *Microryzomys*. The foramen magnum is oriented more posteriorly than ventrally, although still not visible from dorsal view.

PALATAL REGION (figs. 4, 11, 16, 17)

Microryzomys: The incisive foramina (= anterior palatine), which span about 70 percent of the diastemal length, are either nearly parallel-sided and oblong in outline (most *altissimus*) or conspicuously broader in their posterior third and ovate (most *minutus*). They terminate just anterior to (most *minutus*) or beyond (most *altissimus*) the anterior face of the upper first molars (figs. 4, 16).

The bony palate of *Microryzomys* is longer than the molar rows but barely so, terminating slightly behind the upper third molars and pierced by a pair of simple posterolateral palatal pits. Posterior palatine foramina exit in the maxillopalatine suture from a level even with the anterior third of the second upper molars to the posterior third of the first molars. The short and broadly U-shaped mesopterygoid fossa lacks any projection from the palatines and is perforated dorsally by moderately sized sphenopalatine vacuities that expose approximately equal lengths of the basisphenoid and presphenoid. In ventral view, three-fourths to the entire length of the vacuities is visible within the mesopterygoid fossa (fig. 16).

The lateral pterygoid plates (= pterygoid fossae, parapterygoid fossae) are shallow and narrow, usually perforated by a fontanelle between the pterygoid and sphenoid parts of the plate as well as by the posterior end of the alisphenoid canal. A groove usually marks the rear of the plate where the infraorbital branch of the stapedial artery crosses to enter the alisphenoid canal (fig. 17). Above the pterygoid plates, the alisphenoid strut is uniformly absent, creating an oblong concavity that represents the confluence of the foramen ovale accessorius and the masticatory-buccinator foramen. The medial wall of this con-

cavity is perforated by a large foramen ovale and, toward the front, the small anterior opening of the alisphenoid canal (fig. 20B).

Oryzomys palustris: The long and slitlike incisive foramina consistently extend between the first upper molars and generally terminate acutely at both ends.

In specimens of *O. palustris*, bony palatal length exceeds that of *Microryzomys*, the segment projecting beyond the end of the tooth-rows about equal in length to the third molars, not less than. Perhaps correlated with the greater caudal extension of the bony palate, the posterolateral palatal pits are larger and usually more complex with smaller foramina contained within (figs. 16, 17). Other supernumerary foramina are frequently distributed between the posterolateral pits and the posterior palatine foramina. The latter exit at a level around the middle to front of the upper second molars. The sphenopalatine vacuities are set farther forward, bordering mostly the presphenoid and a short section of basisphenoid. As a result of their anterior placement as well as the greater postmolar projection of the palate, only the posterior third of the vacuities are visible ventrally through the mesopterygoid fossa.

The lateral pterygoid plates are more heavily ossified, and each lacks a medial fontanelle and groove on the rear margin (fig. 17).

Oligoryzomys: Size of the incisive foramina and anatomy of the pterygoid plates resemble the condition observed in *Microryzomys*. The expanse of the hard palate and condition of the palatal pits varies: in *O. microtis*, the configuration corresponds closely to that of *Oryzomys palustris*; whereas in all others, the development resembles that typical of *Microryzomys*.

Approximately 90 percent of the specimens examined of most species of *Oligoryzomys* lack an alisphenoid strut. However, in at least one species, *O. microtis*, about one-third of the specimens from any locality possess struts (Olds and Anderson, 1987). If present, the strut defines, to its front, the masticatory-buccinator foramen, from which emerges the masticatory-buccinator branch of the maxillary nerve, and, to its rear, the foramen ovale accessorius (fig. 20D). In spec-

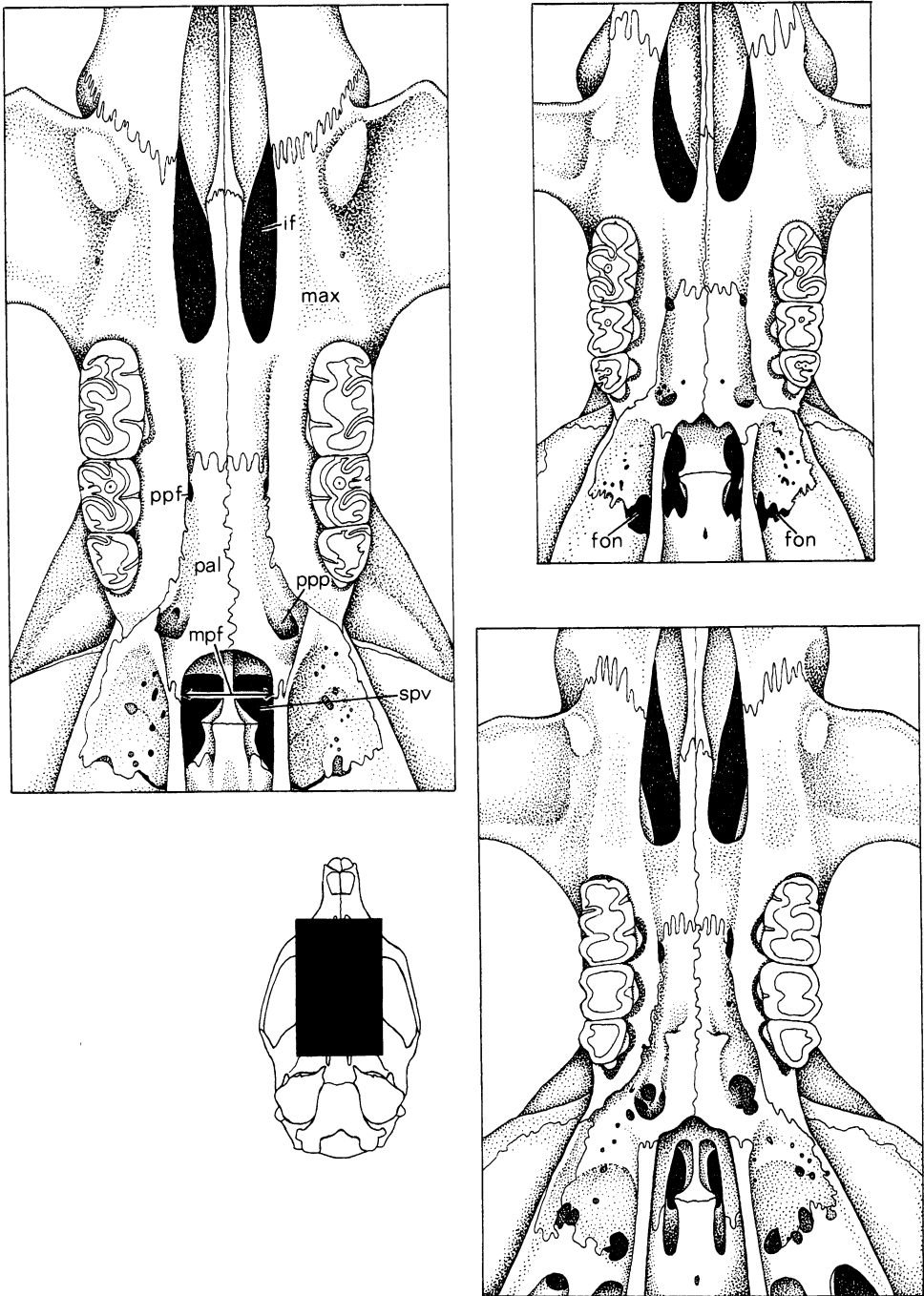


Fig. 16. Diastemal and palatal regions of specimens illustrated in figure 14. Top left, *Oryzomys palustris*; top right, *Microryzomys minutus*; bottom right, *Oligoryzomys microtis*. fon, fontanelle; if, incisive foramen; max, maxillary; mpf, mesopterygoid fossa; pal, palatine; ppf, posterior palatine foramen; ppp, posterolateral palatal pit; spv, sphenopalatine vacuity.

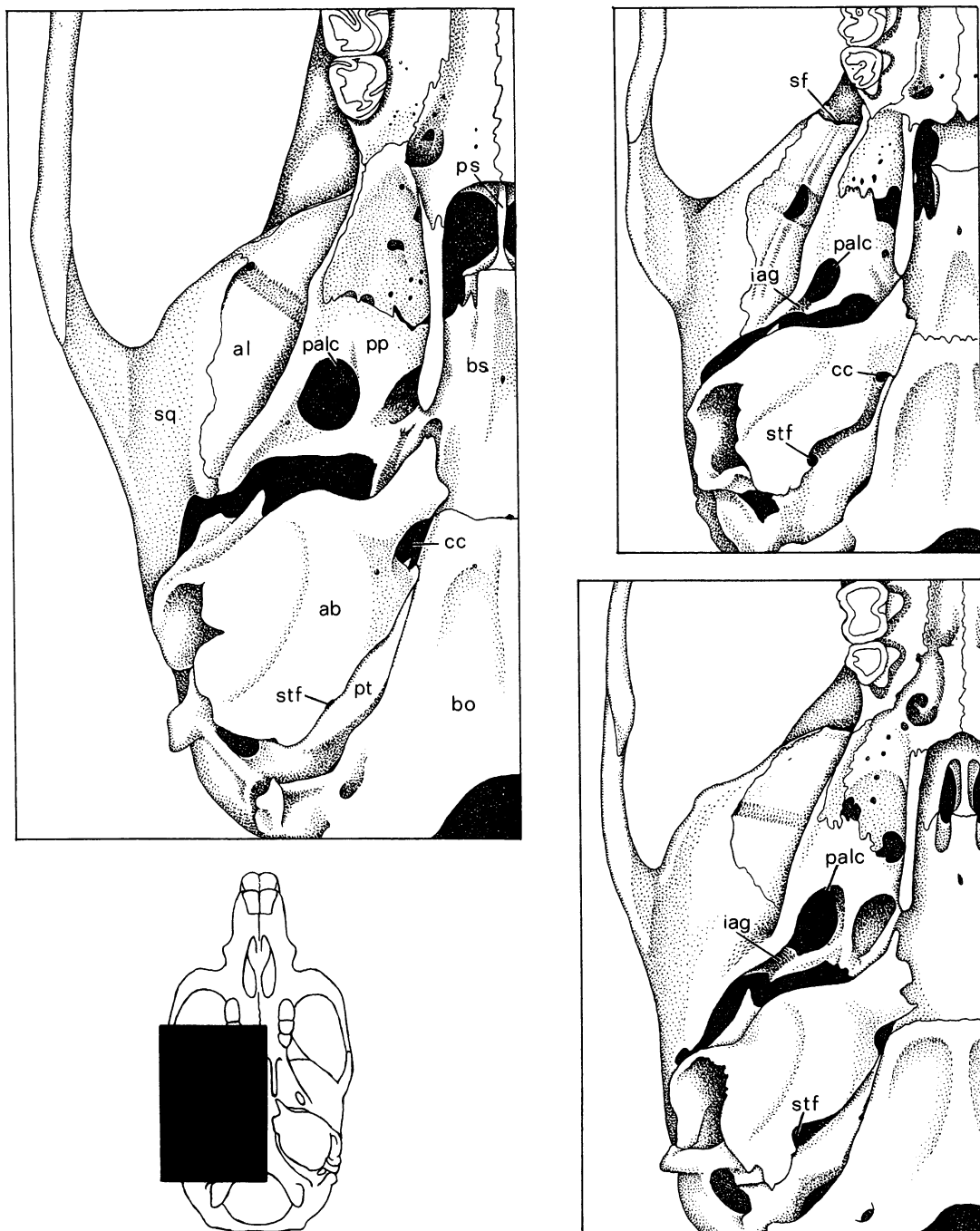


Fig. 17. Mesopterygoid fossa and right lateral pterygoid plate of specimens illustrated in figure 14. Top left, *Oryzomys palustris*; top right, *Microryzomys minutus*; bottom right, *Oligoryzomys microtis*. **ab**, auditory bulla (ectotympanic); **al**, alisphenoid; **bo**, basioccipital; **bs**, basisphenoid; **cc**, carotid canal; **iag**, groove for the infraorbital branch of stapedia artery; **palc**, posterior opening of the alisphenoid canal; **pp**, pterygoid plate; **ps**, presphenoid; **pt**, pteriotic; **sf**, sphenofrontal foramen; **sq**, squamosal; **stf**, stapedia foramen.

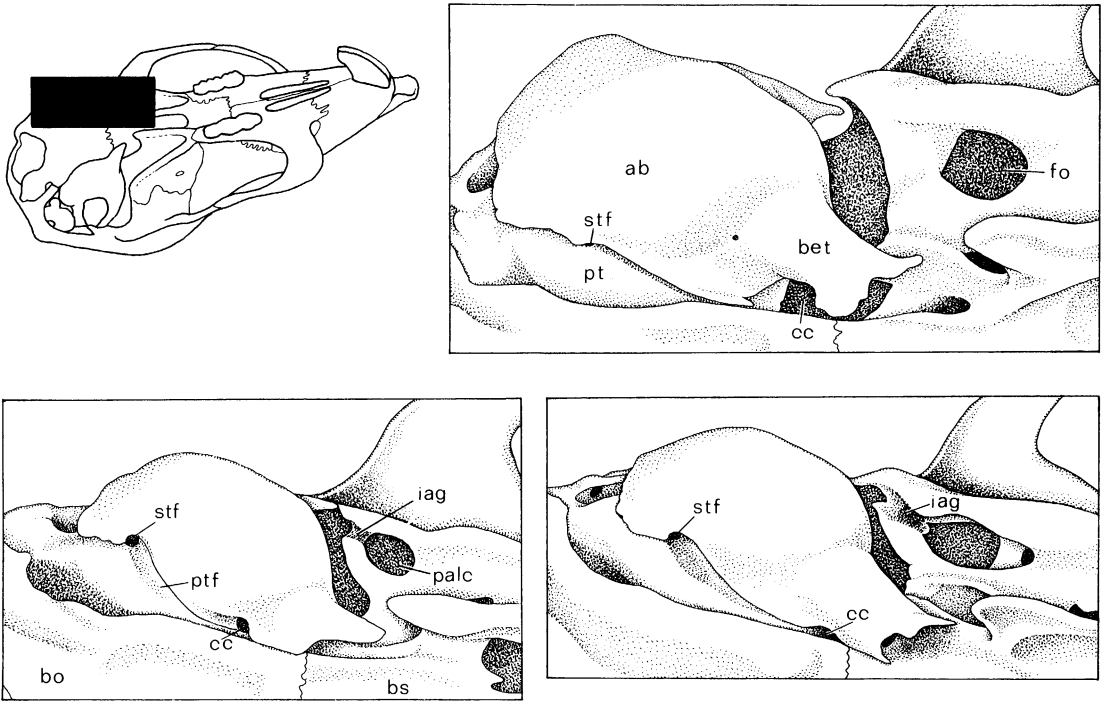


Fig. 18. Right otic capsule of oryzomyines based on specimens illustrated in figure 14. Top right, *Oryzomys palustris*; bottom left, *Microrizomys minutus*; bottom right, *Oligoryzomys microtis*. **ab**, auditory bulla (ectotympanic); **bet**, bony eustachian tube; **bo**, basioccipital; **bs**, basisphenoid; **cc**, carotid canal; **iag**, groove for the infraorbital artery; **palc**, posterior opening of the alisphenoid canal; **pt**, pteriotic; **ptf**, petrotympanic fissure; **stf**, stapedial foramen.

imens of *Oligoryzomys* lacking a strut (fig. 20C), the morphology of the alisphenoid region resembles that of *Microrizomys* (fig. 20B).

OTIC CAPSULES AND ASSOCIATED FORAMINA (figs. 12, 18, 19)

Microrizomys: The subsquamosal (= squamosomastoid) fenestra is present and spacious, incising, along with the postglenoid foramen, a narrow hamular process (= post-tympanic hook) of the squamosal bone on the lateral wall of the braincase (fig. 19). The large, nearly semicircular postglenoid foramen is usually continuous with the middle lacerate foramen, or nearly so, such that the otic capsules appear loosely attached to the lateral wall of the braincase.

The small ectotympanic bullae do not cover the entire ventral surface of the periotic (= petromastoid, petrosal) bone, leaving ex-

posed a wide posteromedial segment and a thin, tapered flange that extends between the ectotympanic and basioccipital (fig. 18). This flange of the periotic typically reaches forward to the carotid canal and partially forms its medial wall. The bony eustachian tube is relatively broad, having a ventromedial tab that defines the ventral part of the carotid canal. The internal carotid artery scores an impression at the crease between the ectotympanic and periotic, and the large stapedial foramen occurs toward the posterior end of the petrotympanic fissure.

The mastoid (= mastoid bulla, mastoid portion of the petromastoid, periotic capsule of petrosal) is squarish, its lateral wall thin and perforated by a large fenestra. Except where the mastoid foramen exits, the dorsal and posterior edges of each mastoid evenly abut the exoccipital in a gently curving line (fig. 19).

Oryzomys palustris: The ectotympanic

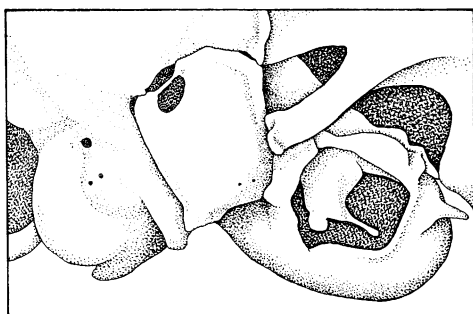
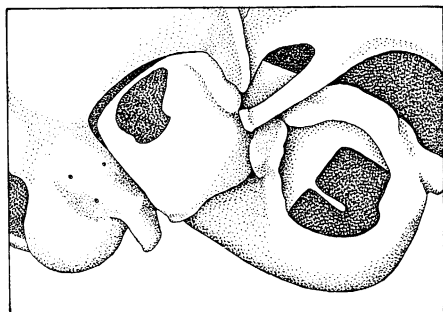
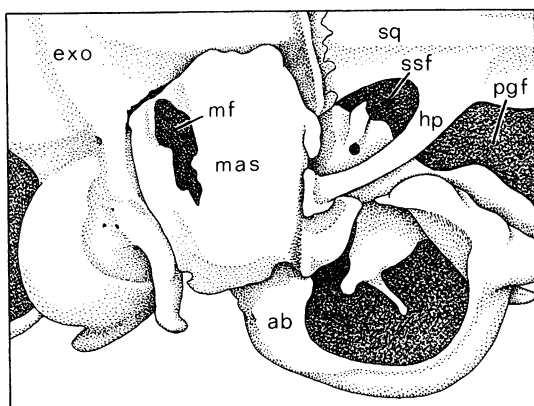


Fig. 19. Mastoid-exoccipital region of crania shown in figure 14. Top, *Oryzomys palustris*; middle, *Microryzomys minutus*; bottom, *Oligoryzomys microtis*. **ab**, auditory bulla (ectotympanic); **exo**, exoccipital; **hp**, hamular process of squamosal; **mas**, mastoid; **mf**, mastoid fenestra; **pgf**, postglenoid foramen; **sq**, squamosal; **ssf**, subsquamosal fenestra.

bullae are more extensive, shielding more of the ventral periotic surface. Thus, the exposed wedge of periotic bone is shorter, narrower, and usually obscured by the antero-

medial portion of the ectotympanic, which exclusively forms the dorsal rim of the carotid canal; the basioccipital defines the medial edge of the canal (fig. 18). The bony eustachian passage is more tubular and its medial edge does not enfold the carotid canal as much as in *Microryzomys*, nor does the internal carotid artery impress a long groove along the bullar wall. A stapedial foramen is present but barely evident as a minute hole in the posteromedial petrotympanic fissure.

The outer wall of the mastoid is thicker and the fenestra relatively smaller. Instead of even contact, the anterodorsal edge of the mastoid projects over the exoccipital such that the dorsal junction of the mastoid-exoccipital appears to arch more strongly (fig. 19).

Oligoryzomys: The size and construction of the otic capsules generally conform to those of *Microryzomys*, except that the flange of periotic bone is narrower and forms less of the medial depression of the internal carotid artery.

The shape of the mastoid, thickness of its outer surface, and relative size of its fenestra resemble the condition of *Microryzomys*, but the anterodorsal configuration of the mastoid and exoccipital is more like that of *O. palustris*.

CRANIAL FORAMINA AND CEPHALIC ARTERIAL PATTERNS (figs. 20, 21)

Significant variation of the cephalic arterial circulation underlies the pattern of occurrence of certain cranial foramina in *Microryzomys*, *Oligoryzomys*, and *Oryzomys palustris*, as Bugge (1970) detailed for the superfamily Muroidea. Of these three taxa, Bugge only studied examples of *O. palustris*, but the pertinent cranial foramina of *Oligoryzomys* and *Microryzomys* are sufficiently like other muroid species he examined to permit reconstruction of their basic circulatory plan, particularly with regard to the stapedial artery and its major branches. Furthermore, we verified basic circulatory patterns in all three taxa by dissecting fluid-preserved specimens and by tracing the dried and blackened blood vessels that adhere to poorly cleaned skulls, of which there exist adequate numbers in most museum collections.

Microryzomys: Specimens uniformly possess a squamosal-alisphenoid groove clearly visible through the translucent braincase, usually with a perforation where it crosses the depression for the masticatory nerve. This groove leads to the small sphenofrontal foramen located at the junction of the orbito-sphenoid, alisphenoid, and frontal bones. This arrangement, together with a large stapedial foramen (fig. 18) and posterolateral groove on the pterygoid plate (fig. 17), indicates that the cephalic blood supply in *Microryzomys* conforms to the primitive murid pattern like that found in *Peromyscus*, many other sigmodontines, and Old World hamsters (Klingener, 1968; Bugge, 1970; Carleton, 1980).

In this condition, a large stapedial artery enters the otic capsule through the stapedial foramen and passes through the crus of the stapes and tympanic cavity to exit from a stapedial canal deep to the anterior end of the otic capsule (fig. 21B). There the stapedial divides into two main branches. One is the supraorbital branch, which passes across the squamosal and alisphenoid bones, scoring the squamosal-alisphenoid groove, and emerges at the sphenofrontal foramen (figs. 20B, 21B). The second primary stapedial branch is the common trunk of the mandibular and infraorbital arteries: the former supplies the lower jaw; the latter passes along the groove on the pterygoid plate, enters the posterior end of the alisphenoid canal, and emerges into the orbit through the anterior alar (= sphenoidal) fissure (fig. 21B). In contrast to the pattern in *Microryzomys*, the stapedial artery plays a modified role in the orbital circulation of both *Oligoryzomys* and *Oryzomys palustris*.

Oryzomys palustris: Individuals of *palustris* lack a sphenofrontal foramen as well as the squamosal-alisphenoid groove (figs. 20A, 21A); the stapedial foramen is minute. As documented by Bugge (1970), the stapedial artery of *Oryzomys palustris* has lost its three primary branches, such that the supply of the orbit and upper jaw is taken over by a secondary connection (anastomotic artery A5 per Bugge's figures) to the internal carotid and the external carotid serves the mandibular circulation. The greatly reduced stapedial persists as the middle meningeal artery to the floor of the braincase.

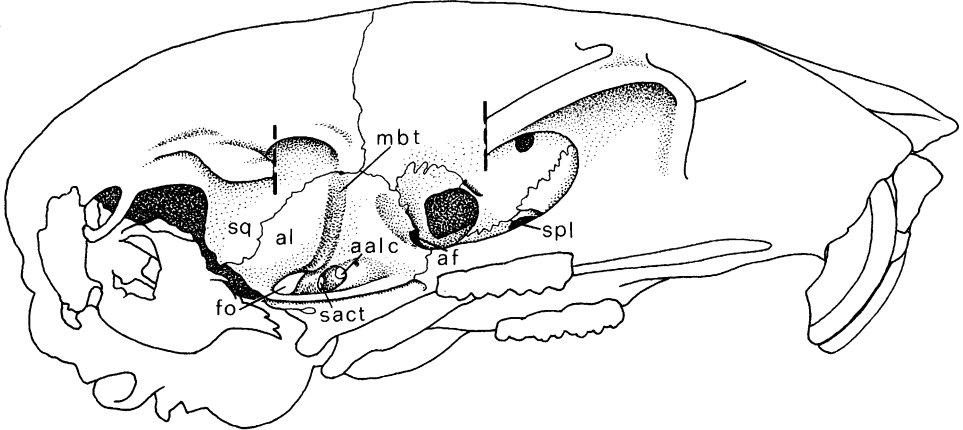
The secondary connection to the orbital-maxillary circulation branches from the internal carotid artery after the latter passes through the carotid canal (fig. 21A). This branch next crosses diagonally over the dorsal surface of the pterygoid plate to enter the anterior end of the short alisphenoid canal and finally exits the braincase through the anterior alar fissure (fig. 21A). The diagonal groove in the pterygoid and tunnel-like medial entrance to the alisphenoid canal are clearly evident in dorsal view with the roof of the braincase removed (fig. 21A), and the medial tunnel entrance can be seen in lateral view to lie between the foramen ovale and anterior opening of the alisphenoid canal (fig. 20A).

Oligoryzomys: All species of *Oligoryzomys* examined lack a sphenofrontal foramen and the accompanying squamosal-alisphenoid groove but possess a stapedial foramen similar in size to that of *Microryzomys* (fig. 18). This configuration indicates, as does the course of dried blood vessels, that the supraorbital branch of the stapedial artery is absent and that the orbital supply arises instead from the distal part of the infraorbital branch. As in *Microryzomys*, the infraorbital continues as an extension of the stapedial through the alisphenoid canal and emerges onto the orbital floor through the anterior alar fissure (fig. 21C). The infraorbital's passage ventral to the posterior edge of the pterygoid plate is marked by an external groove, where a dried blood vessel can often be found in poorly cleaned specimens. In a dissection of two specimens, we could not find a mandibular branch diverging from the infraorbital; presumably, it has developed a secondary anastomosis from the external carotid (both variations occur in Muroidea).

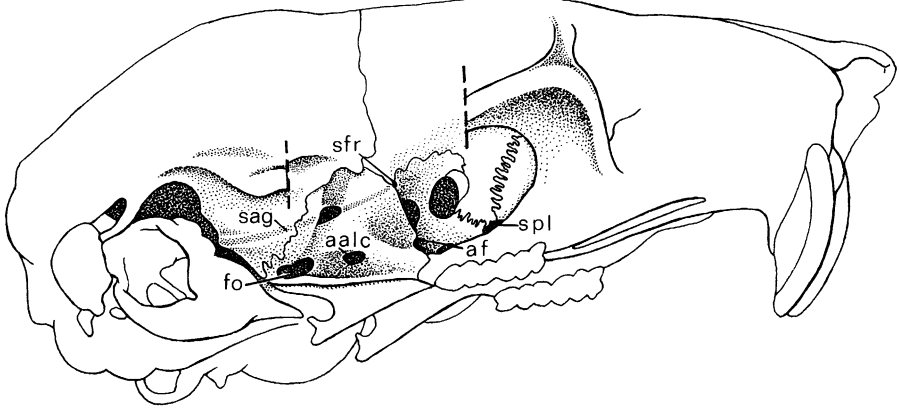
LOWER JAW (fig. 12)

Microryzomys: The short coronoid process extends dorsally to the same height as the condyloid process, outlining a shallow sigmoid notch between them. The concavity of the angular notch is shallow, and the angular process ends well anterior to the condyloid process. The terminus of the incisor alveolus projects from the lateral face of the ascending ramus as a distinct capsule (larger in *minutus*)

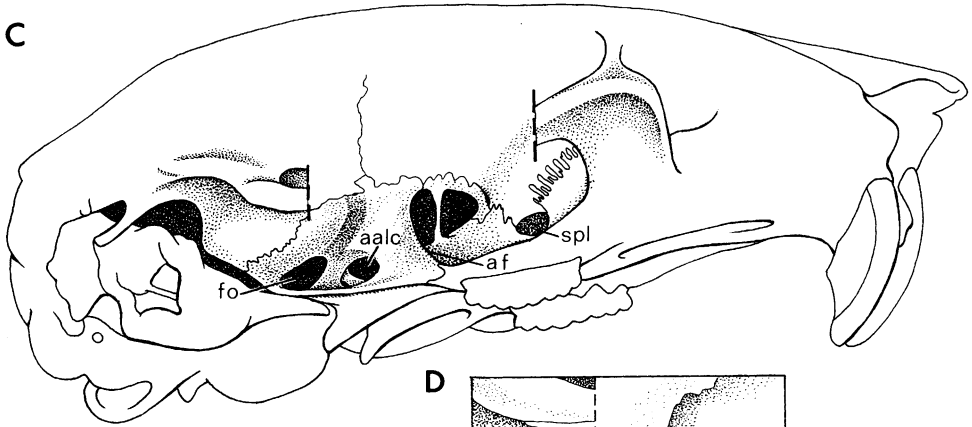
A



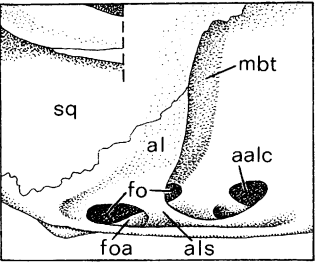
B



C



D



that nearly extends dorsally to the sigmoid notch. The upper and lower masseteric crests converge at their anterior ends, which are reflected slightly upwards to terminate near the anterior root of the lower first molar.

Oryzomys palustris: The coronoid process is much larger and the sigmoid notch accordingly deeper. The angular notch is more deeply excavated and the angular process is located almost even with the condyloid process. Relative to the size of the dentary, the incisor capsule is smaller and does not project upward as far as observed in *Microryzomys*.

Oligoryzomys: The morphology of the dentary generally resembles the condition described for *O. palustris*.

DENTITION

Identification of the enamel elements of oryzomyine molar topography follows Reig (1977) whose terminology is schematically illustrated in figures 22 and 24. Determination of coronal structure was based on observations of young animals with erupted third molars that have little or no wear. We consulted series of specimens to qualitatively characterize the typical condition of a taxon but did not score individual dental variation.

INCISORS (fig. 14)

Microryzomys: Both upper and lower incisors are delicate, lack grooves, and have yellow-orange to deep orange enamel; the enamel color of the lower incisors is paler. The upper incisors are orthodont in most specimens but approach opisthodonty in a few.

Oryzomys palustris: The incisors are appreciably sturdier, the uppers strongly opisthodont.

Oligoryzomys: The upper incisors are regularly opisthodont rather than orthodont, but

otherwise resemble those of *Microryzomys* in proportion and enamel pigmentation.

FIRST UPPER MOLAR (M1) (figs. 5, 22, 23)

Microryzomys: The molars are tuberculate and brachyodont with two rows of cusps arranged in opposite labial-lingual pairs.

The anteromedian flexus is distinct and deep in young animals, setting off prominent anterolingual and anterolabial conules, which are about two-thirds the size of the primary cusps. The flexus becomes isolated as an anteromedian island with increased wear and is finally obliterated in old individuals. The separation of the conules produces a wide procingulum, nearly as wide as the posterior two-thirds of the molar; this configuration imparts a rectangular occlusal outline. Behind the anterolabial conule, an elongate anteroloph extends, usually as an isolated ridge, to the labial edge of the molar; a short and shallow anteroflexus persists between the anteroloph and anterolabial conule until obscured by heavy wear.

The protocone is connected at its anteromedial corner to the anterocone and at its midsection to the paracone. At its posteromedial corner, the protocone joins the proximal section of the mesoloph and, via the median mure, the hypocone. The metacone attaches to the posteroloph by means of a posteriorly directed enamel bridge. The posteroloph is free at its terminal end, which remains separated from the metacone by a narrow, short posteroflexus until obscured by moderate wear.

An elongate mesoloph extends from the median mure between protocone and hypocone to the labial margin where it forms a low style. The mesoloph is connected in its proximal third by an enamel lophule from the paracone to form a fossettus from the medial segment of the mesoflexus, a pattern evident until the molar is heavily worn.

Fig. 20. Squamosal-alisphenoid region of specimens illustrated in figure 14. A, *Oryzomys palustris*; B, *Microryzomys minutus*; C, *Oligoryzomys microtis*; D, *O. microtis* (AMNH 260416). aalc, anterior opening of alisphenoid canal; af, anterior alar fissure; al, alisphenoid; als, alisphenoid strut; fo, foramen ovale; foa, foramen ovale accessorius; mbt, trough for masticatory-buccinator nerve; sact, tunnel for secondary arterial connection between internal carotid and orbital-maxillary circulation; sag, squamosal-alisphenoid groove; sfr, sphenofrontal foramen; spl, sphenopalatine foramen; sq, squamosal.

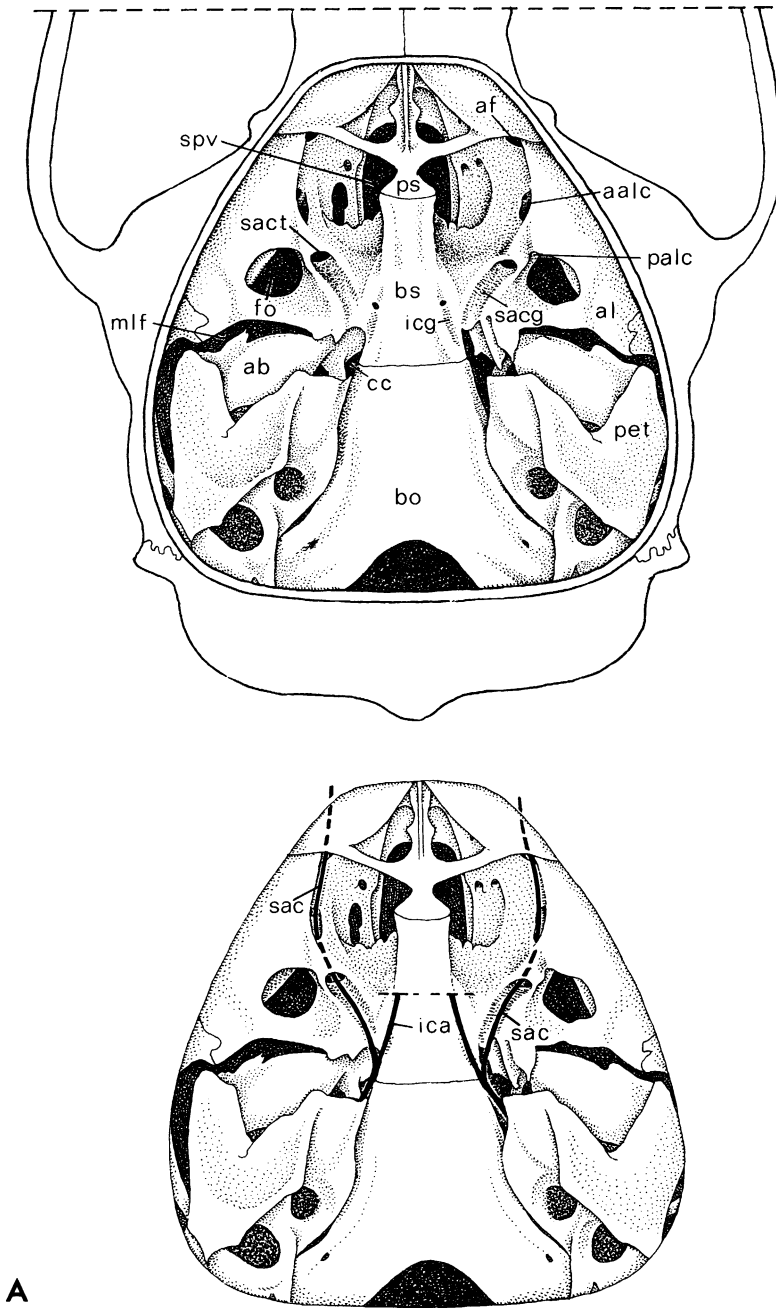
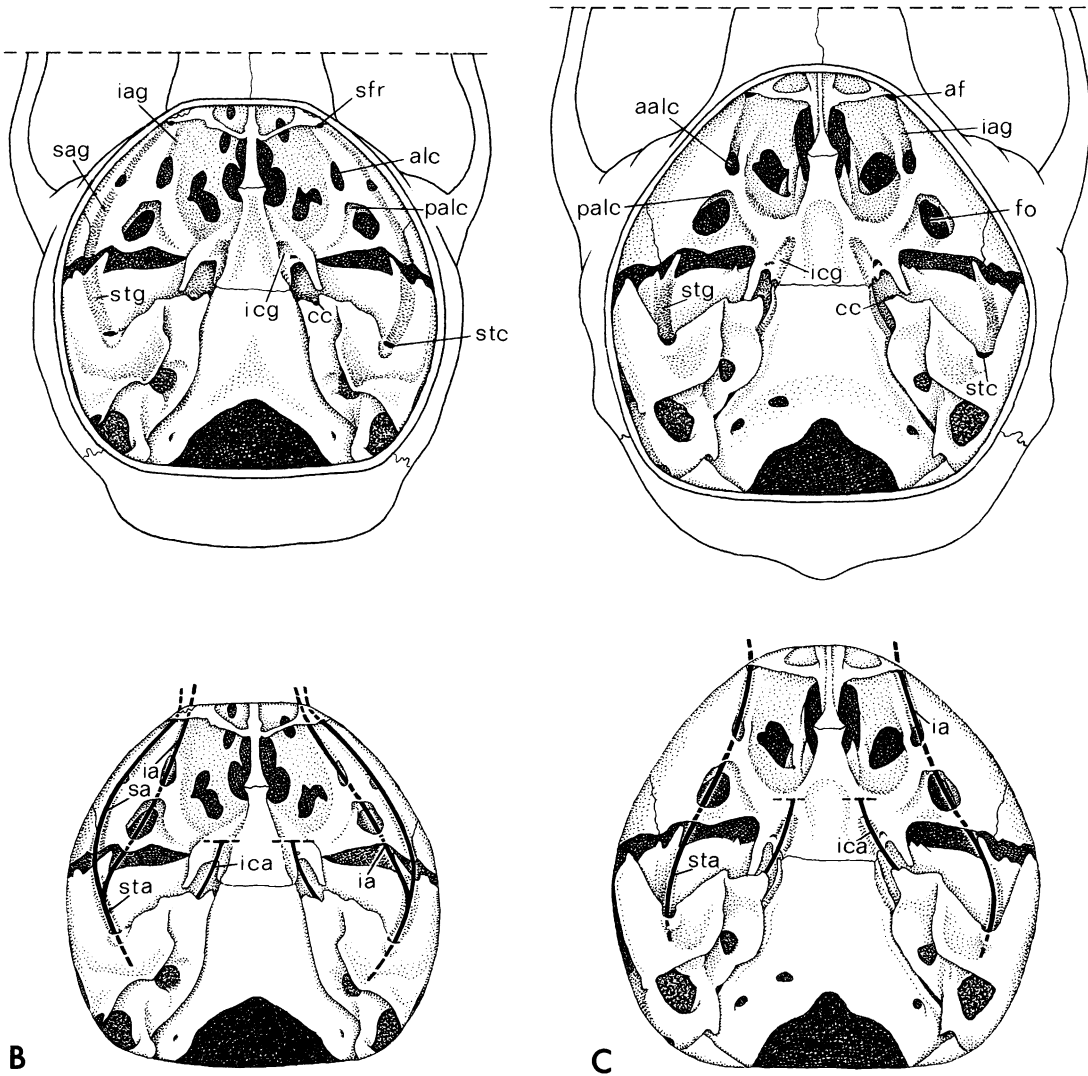


Fig. 21. Dorsal view of the basicranial region (roofing bones of braincase removed) of oryzomyines. **A**, *Oryzomys palustris* (AMNH 242835); **B**, *Microrizomys minutus* (AMNH 231038); **C**, *Oligoryzomys destructor* (AMNH 231882). **aalc**, anterior opening of alisphenoid canal; **ab**, auditory bulla (ectotympanic); **af**, anterior alar fissure; **al**, alisphenoid; **bo**, basioccipital; **bs**, basisphenoid; **cc**, carotid canal; **fo**, foramen ovale; **iag**, groove for the infraorbital branch of the stapedial artery; **ia**, infraorbital branch of stapedial artery; **ica**, internal carotid artery; **icg**, groove for internal carotid artery; **mlf**, middle lacerate foramen; **palc**, posterior opening of the alisphenoid canal; **pet**, petrosal; **ps**, presphenoid; **sa**, supraorbital branch of stapedial artery; **sag**, squamosal-alisphenoid groove; **sac**, secondary arterial connection between



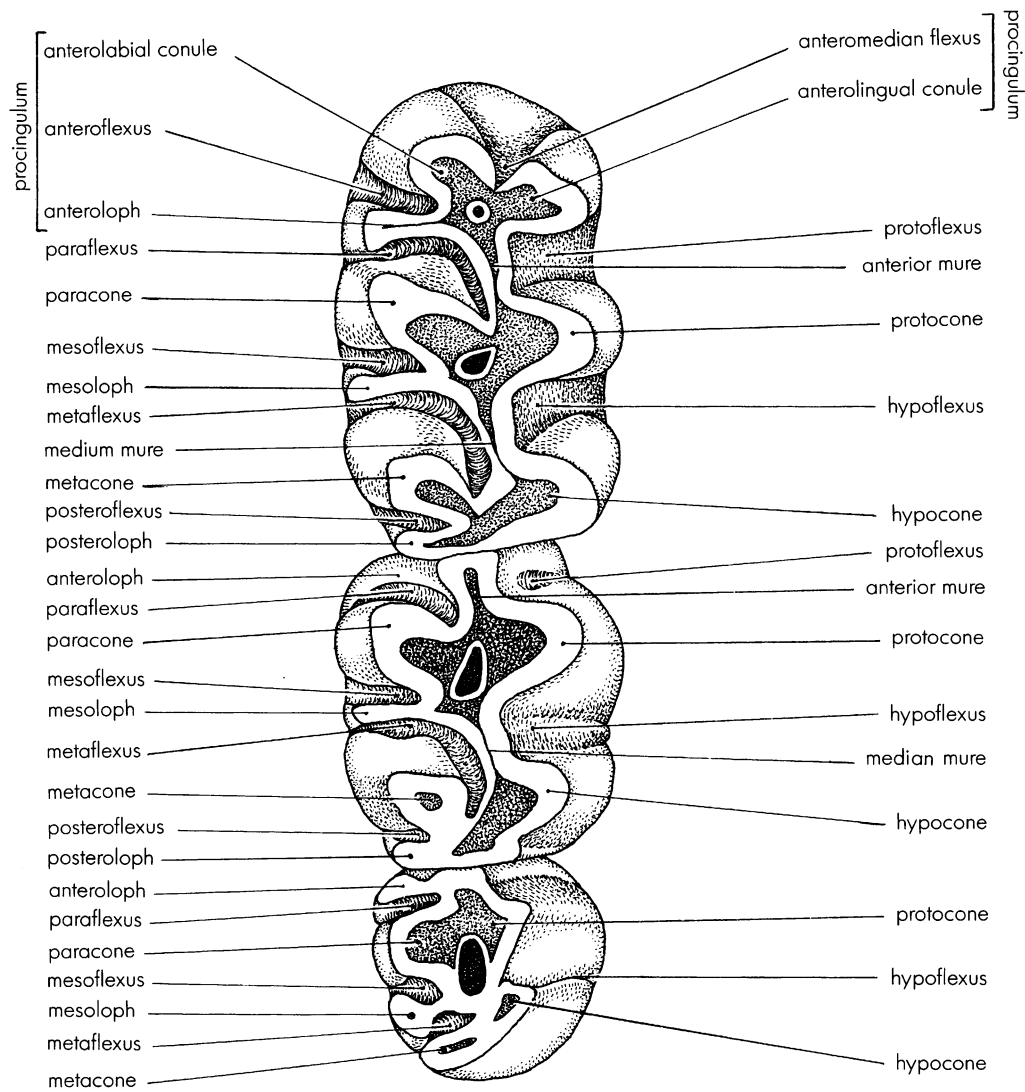
internal carotid and orbital-maxillary circulation; **sacg**, groove for secondary arterial connection; **sact**, tunnel-like medial entrance to alisphenoid canal for secondary arterial connection; **sfr**, sphenofrontal foramen; **spv**, sphenopalatine vacuity; **sta**, stapedial artery; **stc**, stapedial artery canal; **stg**, groove for stapedial artery.

The minor and major labial folds are open at the labial margin of the tooth and lack lophs and styles. The deep and wide lingual folds (protoflexus and hypoflexus) are also free of conspicuous cingular structures; in some specimens, however, a slight enamel crinkle or shelf at the lingual margin may be seen.

Oryzomys palustris: The molars are more

robust with heavier enamel and higher crowns.

In contrast to the rectangular outline of the M1 in *Microryzomys*, that in *O. palustris* is oval, a shape due to the relatively narrower procingulum and larger protocone that forms a bulge on the lingual border. An antero-medial indentation is lacking in unworn molars; instead, the chunky anterolingual and



LABIAL

LINGUAL

Fig. 22. Schematic drawing of the upper right molar row of *Microryzomys altissimus* (AMNH 321055); terminology follows Reig (1977).

anterolabial conules coalesce at their antero-medial edges to form a broad, undivided anterior rim. The posteromedial margins of the conules remain separated by a hollow, which apparently corresponds to the deep portion of the anteromedian flexus and which, in young specimens, is confluent with the narrow and convoluted anteroflexus. Only the hollow can be identified in later wear stages,

but it too is obliterated in old animals. The anteroloph bows anteriorly from the mure, nearly meeting the back of the anterolabial conule, and does merge with the posterolabial margin of the conule; with moderate wear, conule and loph appear as one solid structure. Certain enamel connections between the cusps and lophs are oriented differently in *O. palustris* as compared to *Microryzomys*. For

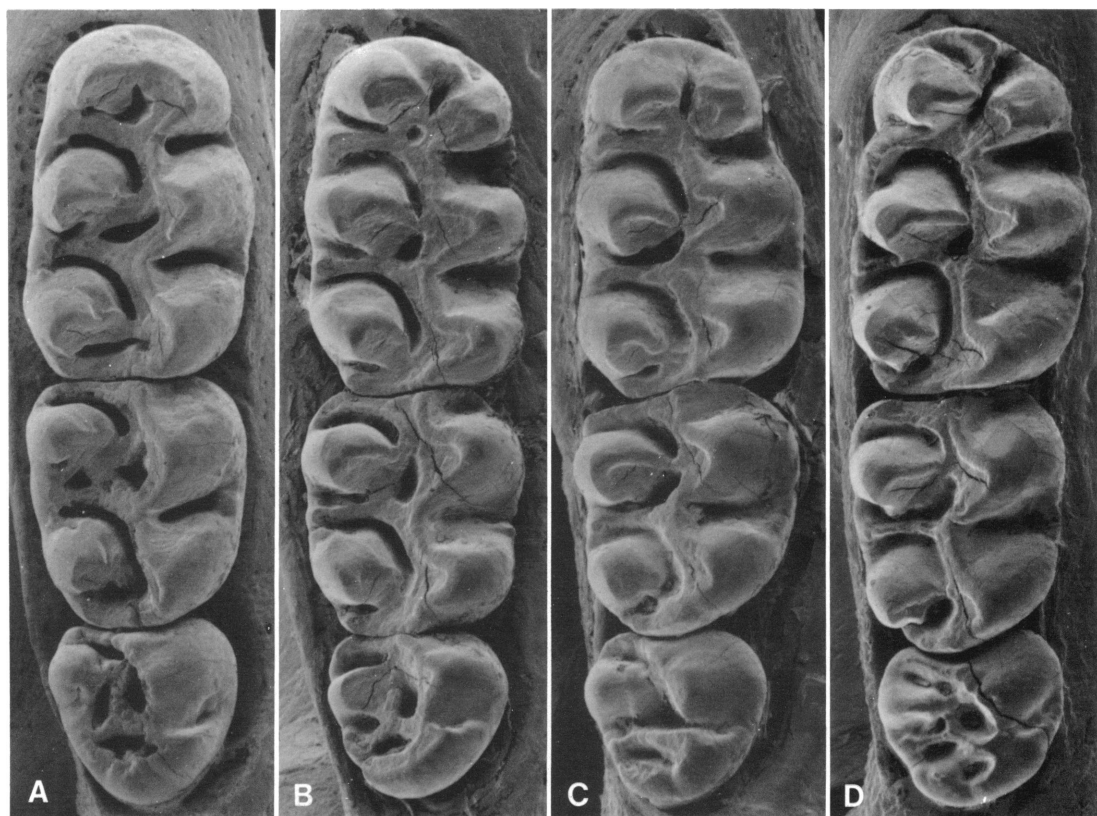


Fig. 23. Occlusal view of right upper molar rows of species of oryzomyines. A, *Oryzomys palustris* (AMNH 234836, LM1-3 = 4.3 mm); B, *Microryzomys altissimus* (AMNH 231055, LM1-3 = 3.0 mm); C, *Oligoryzomys fulvescens* (AMNH 181446, LM1-3 = 3.0 mm); D, *Oligoryzomys* sp. B, *flavescens* group (AMNH 231117, LM1-3 = 3.3 mm).

one, the posterior bridge from the paracone to the mesoloph is displaced more laterally; this configuration divides the mesoflexus into a short labial cleft and an elongate, curved fossettus that forms a prominent landmark in the center of the tooth. The short labial portion of the mesoflexus exists only in very young specimens because slight wear transforms it into a small hollow bordered by the high labial cingulum. For another, an enamel bridge links the metacone to the middle of the hypocone rather than the posteroloph. The more anterior placement of this connection, together with the fusion of the labial end of the posteroloph with the metacone, isolate the posteroflexus as a narrow, elongate basin. In some specimens, two connections are found, the anterior one and a posterior one as in *Microryzomys*. The broad poster-

oloph forms a high wall across the back of the molar, instead of a low, posterolabial orientation as seen in *Microryzomys*.

The wide mesoloph extends from the median mure to the labial margin where it merges with the high labial cingulum between the paracone and metacone. This cingulum also seals the entrance to the metaflexus. The protoflexus and hypoflexus are much narrower in *O. palustris* than in *Microryzomys*, correlated with the more robust size of the protocone and hypocone in the former taxon.

Oligoryzomys: Crown height and occlusal topography basically resemble the condition in *Microryzomys*. The anterocone (anterolabial and anterolingual conules), however, is narrower than the posterior two-thirds of the molar (as in *Oryzomys palustris*), such that the tooth appears oval in outline. The distal

segment of the posteroloph is set closer to the metacone in most species, fused with the metacone in some (for example, *O. chacoensis*). The protoflexus and hypoflexus are not as broad, and cingular ridges and styles regularly occur at the lingual openings of these folds in some species.

SECOND (M2) AND THIRD (M3) UPPER MOLARS (figs. 5, 22, 23)

Microryzomys: The M2 is nearly square in occlusal outline and closely resembles the M1 except for the obvious lack of the procingulum. The protoflexus exists either as a slight indentation or deeper cleft at the anterolingual margin of M2.

The M3 is almost circular in outline and comprises about half the area and two-thirds the length of M2. The protocone and paracone remain distinct, but the hypocone and especially the metacone are smaller. Together they form an arcuate posterior heel set off by the metaflexus. No posteroloph is evident. The ridgelike mesoloph is discrete and in some specimens expands into a broad labial style. The labial reentrant folds (paraflexus, mesoflexus, and metaflexus) are conspicuous, but the hypoflexus occurs as a shallow indentation between the protocone and vestigial hypocone. A protoflexus is absent.

Oryzomys palustris: Instead of squarish, the M2 is a truncated oval in outline. Conspicuous in the M2 is its intact high labial margin that seals off the openings to the various folds. The protoflexus is indistinct.

The M3 is larger, especially in area, relative to the M2, rather than being distinctly smaller as it is in *Microryzomys*. The heavy enamelization and higher crown renders the cusps less distinct; the moundlike protocone and paracone are discernible but the posterior rim of the tooth is defined by a continuous wall curving from the paracone to the protocone. The structural boundaries of the hypocone and metacone (and posteroloph?) are scarcely observable within this posterior heel. Four hollows congested in the center of the tooth presumably represent serial homologs of the folds and fossettes of the M2.

Oligoryzomys: The shape of M2 resembles a truncated oval rather than a square. The

paraflexus between paracone and anterolabial cingulum is shallow in some species compared to the usual deep fold in species of *Microryzomys*.

The paraflexus of M3 is less well defined, appearing as a shallow hollow or trough, such that the paracone presses tightly against the anterolabial cingulum.

FIRST LOWER MOLAR (m1) (figs. 5, 24, 25)

Microryzomys: The anteromedian flexid is a deep cleft, such that the anterolingual and anterolabial conulids are as well defined as their counterparts in M1. Their separation produces a broad procingulum and a rectangular occlusal outline for the tooth. In molars with little wear, the anterolophid is seen as a slightly bent or straight ridge extending from the anterior murid. The anteroflexid is shallow and often barely distinguishable because the loph fuses with the anterolingual conulid after light wear. In some specimens, an enamel lophulid connects the anterolophid to the metaconid, subdividing the metaflexid. Opposite the anterolophid is a bulky structure that originates from the anterior murid and broadens distally to occupy most of the labial margin between the anterolabial conulid and protoconid. We interpret this as a protolophid. It is evident in juvenile to young adult *altissimus* (fig. 5) but unites with the anterolabial conulid with further wear; in *minutus*, however, a well-defined protolophid is frequently absent (fig. 5) or is smaller than that observed in *altissimus*, being visible only in very young animals.

The mesolophid is always present, usually as a wide ridge originating from the median murid and extending to the lingual edge where it forms a stylid. The posterior margin of the mesolophid fuses to the large entoconid, which faces anteromedially. The posterolophid is sharply defined by a long posteroflexid, which reaches the mesolophid at its origin from the murid.

The mesoflexid and posteroflexid typically open to the lingual margins except in some specimens where the end of the mesolophid contacts the metaconid. The wide and deep hypoflexid is either flat or bears a low stylid

on its labial margin, a minor variation encountered on the m2 and m3 as well.

Oryzomys palustris: In unworn mls, discrete anterolabial and anterolingual conulids are not evident but have seemingly merged to form a single broad cusp. Their merger is suggested by a small anteromedian island behind the front rim of the anteroconid. The procingulum curves back lingually as a high ridge to join with the metaconid and labially as a lower cingulum to join the protoconid; the outline of the anterior one-third of the tooth recalls a ship's rounded bow, a marked contrast to the squarish anterior of the m1 in *Microryzomys*. A protolophid is occasionally present, and, if so, extends from the midline of the tooth to merge with the high labial margin. The anterolophid is variably developed: in some, it extends intact from the murid to the wall-like lingual cingulum; in others, it is broken into irregular enamel crenulations and is unrecognizable as a linear element (fig. 25); in a few, it seems to extend posteromedially to meet the metaconid.

The metaconid and protoconid, as well as the entoconid and hypoconid, join at their midregions via transverse enamel lophulids, not at their respective anteromedial aspects as seen in examples of *Microryzomys*.

High lingual and labial cingula bound the circumference of the tooth, preventing the valleys between cusps and lophids from opening to the margins. The distal portion of the posterolophid, even in young rats, is continuous with the posterolingual edge of the entoconid, thereby enclosing the posteroflexid as a long, narrow valley.

Oligoryzomys: The anteroconid (anterolabial and anterolingual conulids) is generally not as broad as in *Microryzomys*, for the anteromedian flexid is less pronounced and the conulids lie closer together. In other cases, the conulids are more discrete (for example, *O. sp. B*, *flavescens* group); whether such variation represents consistent differences among species of *Oligoryzomys* is uncertain at this stage. Still, the compact anteroconid has a rounded anterior contour and gives the m1 an ovoid shape compared to a nearly rectangular outline in *Microryzomys*. A ridgelike anterolophid, the configuration found in *Microryzomys*, is rarely observed in *Oligory-*

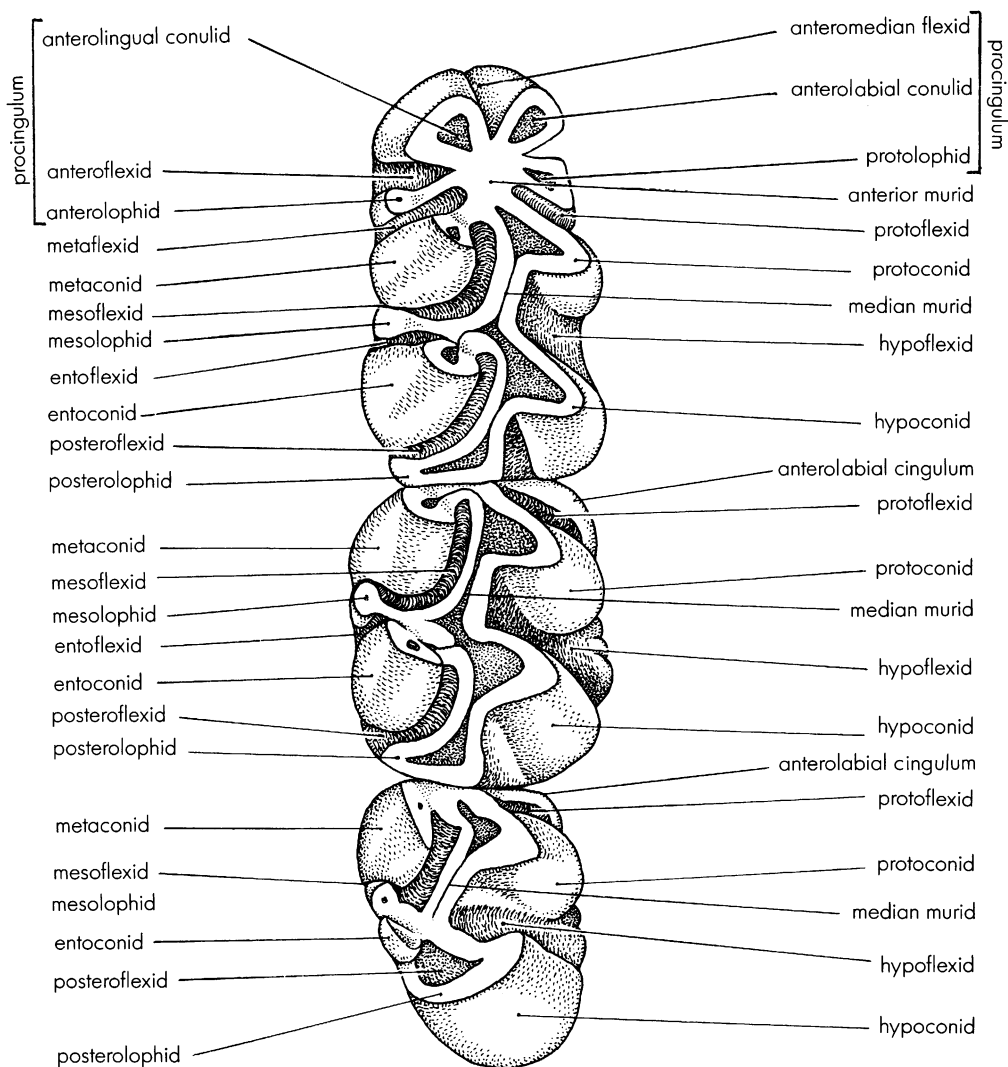
zomys. More often, it is absent or perhaps fused to the anterolingual conulid, its free end represented by the lingual cingulum arising from the rear margin of this conulid.

SECOND (m2) AND THIRD (m3) LOWER MOLARS (figs. 5, 24, 25)

Microryzomys: The m2 is nearly square in outline and except for the lack of procingular elements; its occlusal surface closely matches that of m1. A conspicuous anterolabial cingulum, incised by a discrete protoflexid, arises from the anterior corner of the protoconid.

The m3 is approximately two-thirds the size of the m2. The posterolophid of the m2 abuts the front of the metaconid and protoconid of the m3, or occasionally its anterolabial cingulum instead of the protoconid (fig. 5). Metaconid, protoconid, and hypoconid are distinct cusps, and a small entoconid can be distinguished in some young animals. In most instances, however, the entoconid cannot be separated from the stout posterolingual cingulum, which apparently represents a fusion of the posterolophid and hypoconid; its corresponding fold, the entoflexid, is similarly indistinct or lost. The mesolophid persists as a short spur from the median murid or is inseparably united with the lingual cingulum or, in some specimens, the entoconid. A mesoflexid and posteroflexid are present, but the latter is little more than a hollow that disappears in later wear stages. A distinct, shelflike cingulum embellishes the anterolabial corner of the tooth.

Oryzomys palustris: The m2 is rectangular and longer relative to the m1 than is the same molar, which is basically square, in *Microryzomys*. This proportional difference may partly result from the presence in *palustris* of an anterolophid, which interconnects the anterior margins of the protoconid and metaconid to form the forward wall of the m2. Unlike the condition in *Microryzomys*, a metaflexid is therefore present but usually divided into smaller fossetids by a bridge between the anterolophid and metaconid. The anterolophid and accompanying metaflexid lose their definition after slight to moderate wear and become inseparable from the metaconid-protoconid. Other structural dissimi-



LINGUAL

LABIAL

Fig. 24. Schematic drawing of the lower right molar row of *Microroryzomys altissimus* (AMNH 321055); terminology follows Reig (1977).

larities between the second lower molars of *O. palustris* and *Microroryzomys* parallel those noted for the m1s.

The m3 is subequal in length to the m2, rather than distinctly shorter as in *Microroryzomys*. As in the m2, an anterolophid apparently forms part of the anterior border of the tooth, but its definition is less satisfactory to conclude serial homology. Its presence is

suggested by the large C-shaped fossetid, which anatomically corresponds to the confluence of a metaflexid and mesoflexid. The serial homology of the two posterolingual fossetids is likewise obscure, but their position intimates that they represent an entoflexid and posteroflexid. The mesolophid usually persists as a recognizable ridge. The labial cones, the protoconid and hypoconid, are

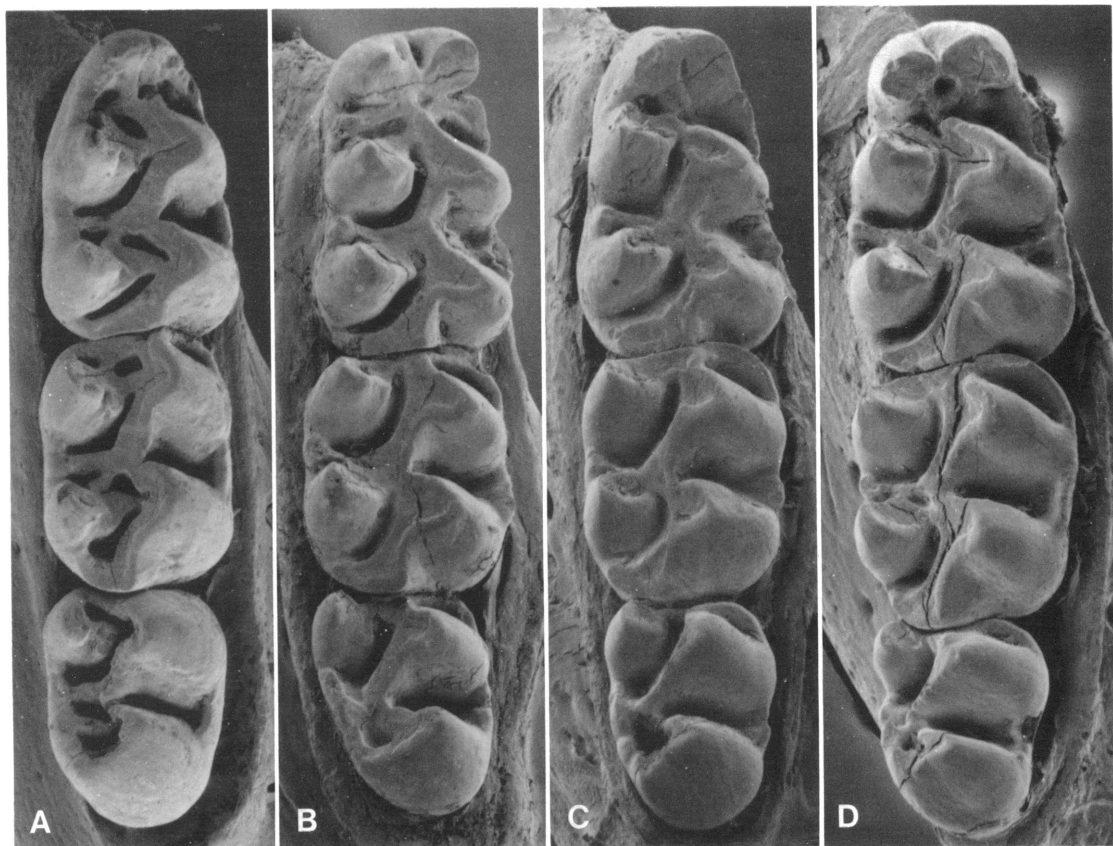


Fig. 25. Occlusal view of right lower molar rows of specimens of oryzomyines illustrated in figure 23. A, *Oryzomys palustris* (Lm1-3 = 4.5 mm); B, *Microryzomys altissimus* (Lm1-3 = 3.3 mm); C, *Oligoryzomys fulvescens* (Lm1-3 = 3.2 mm); D, *Oligoryzomys* sp. B, *flavescens* group (Lm1-3 = 3.4 mm).

much more massive than the lingual counterparts, the metaconid and entoconid, the last only a ridge extending from the walled lingual cingulum to the medial face of the hypoconid. The size of the hypoconid may be compounded by its coalescence with the posterolophid; the structural limits of these features are unidentifiable. The rounded anterolabial margin of the m3 usually lacks a shelllike cingulum, a structure so prominent in *Microryzomys*.

Oligoryzomys: In species such as *O. longicaudatus*, a thin anterolophid appears to occur on the m2 and abut the posterolophid of the m1. A corresponding metaflexid is present as a transient, narrow fold or small hollow between the anterolophid and metaconid. In other species, for example *O. ful-*

vescens (fig. 25C), an anterolophid and metaflexid are undeveloped, the m2 appearing as in *Microryzomys*. The stability of this characteristic within and between species of *Oligoryzomys* requires further evaluation. Relative to molar size, the anterolabial cingulum is higher and more prominent than its counterpart in *Microryzomys*, and the protoflexid is deeper and wider.

The m3 is similar to that of *Microryzomys*, except the anterolabial, shelllike cingulum is again relatively larger.

MOLAR ROOTS (figs. 26, 27)

Microryzomys: Each upper molar is anchored by three roots, each lower one by two.

Oryzomys palustris: Most specimens pos-

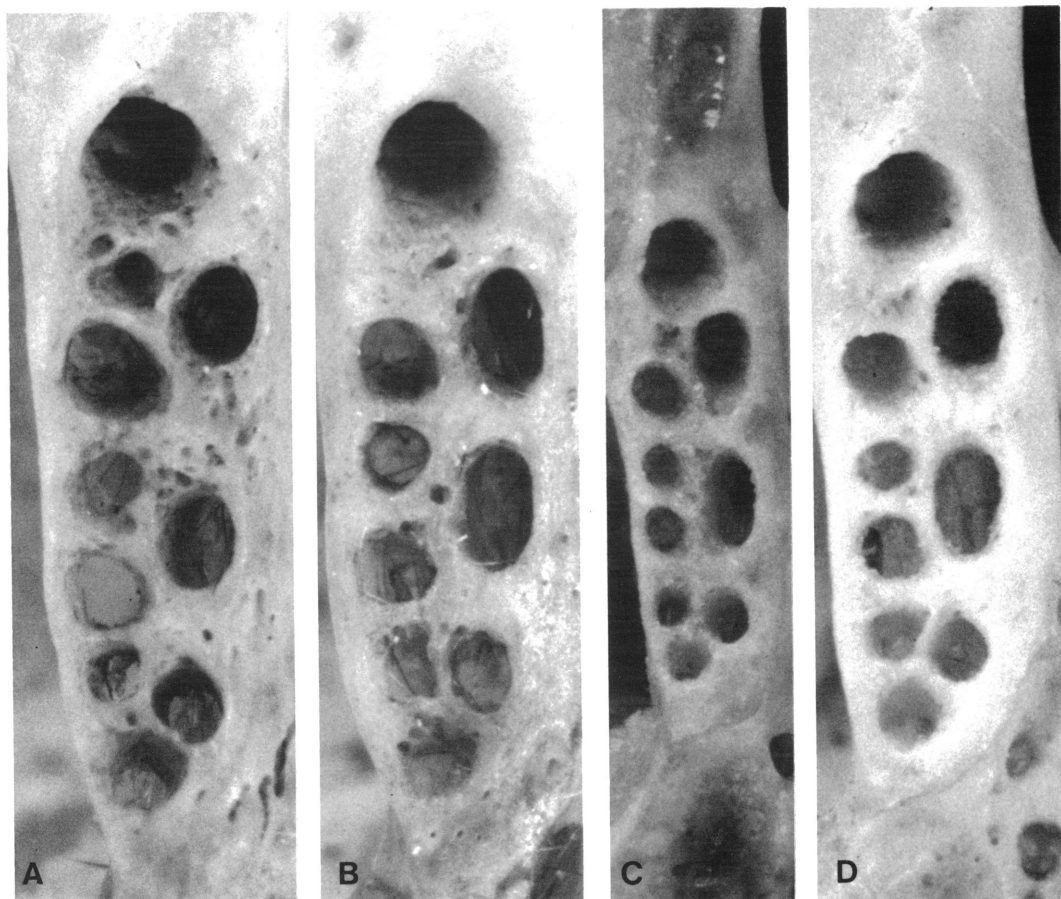


Fig. 26. Ventral view ($\times 20$) of the alveoli of right upper molars of oryzomyines. A, *Oryzomys palustris* (AMNH 245480a); B, *O. palustris* (AMNH 245480b); C, *Microryzomys minutus* (AMNH 66558); D, *Oligoryzomys longicaudatus* (AMNH 93297). Note the variation in *O. palustris*.

sess delicate satellite roots on their upper first molars so that the tooth is secured by three primary roots and an accessory rootlet beneath the paracone. In like manner, the lower molars of most specimens possess accessory roots, having one or two satellite roots on m1 (total equals three-four) and another small lingual root on m2 and m3 (total equals three). Some specimens, however, exhibit only two large roots on each lower molar.

Oligoryzomys: The number of roots equals that of *Microryzomys*.

OTHER ORGAN SYSTEMS

Our anatomical comparisons have been confined mainly to study skins, skulls, dentitions, and the feet of fluid-preserved spec-

imens. To thoroughly explore variation in other anatomical systems among *Microryzomys*, *Oligoryzomys*, and *Oryzomys palustris* is beyond the scope of our present inquiry, and the information garnered from published studies is too limited for meaningful taxonomic insights concerning the three. For example, although species of Sigmodontinae, especially South American taxa, formed the subject of broad anatomical surveys of the stomach (Carleton, 1973), phallus (Hooper and Musser, 1964), and male accessory reproductive glands (Voss and Linzey, 1981), examples of *Microryzomys* were sampled in only one of those endeavors, namely the study of the male accessory glands.

In their investigation of accessory reproductive glands, Voss and Linzey (1981) had

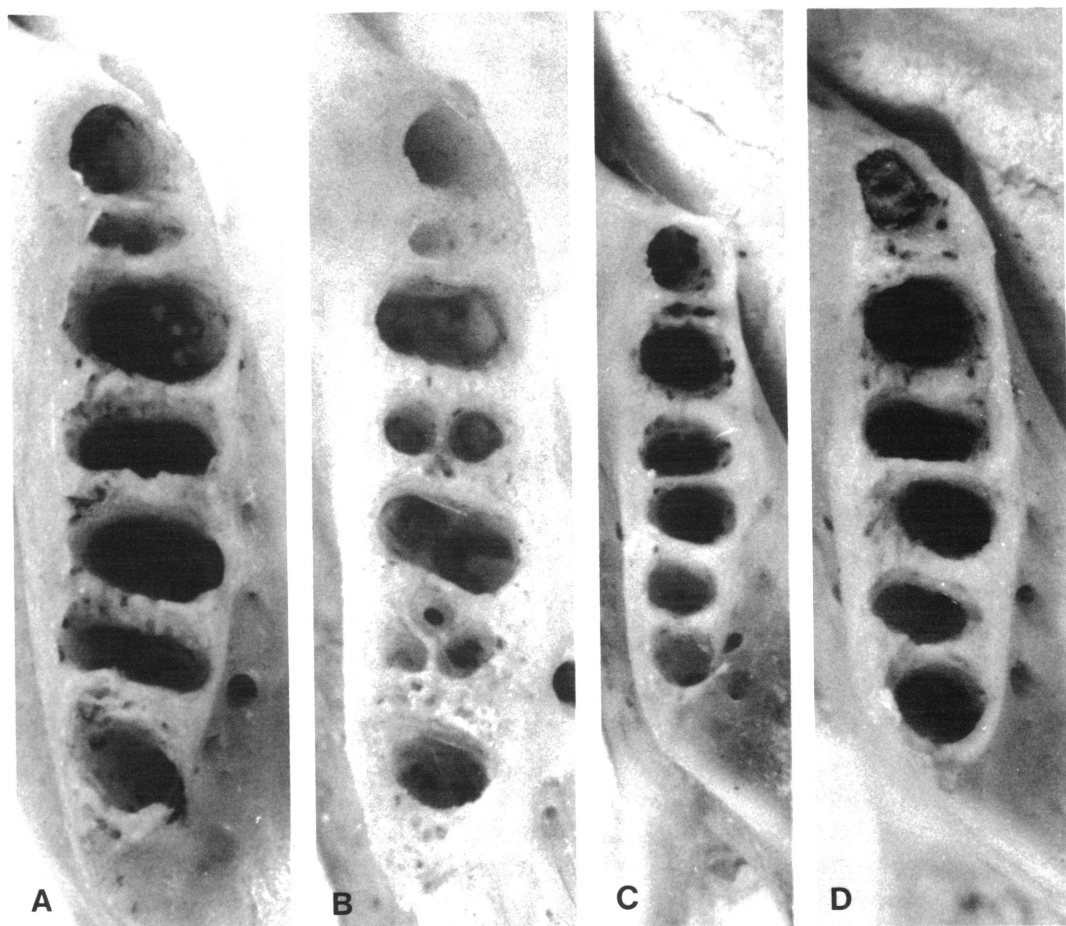


Fig. 27. Dorsal view ($\times 20$) of the alveoli of right lower molars of the same specimens shown in figure 26. A, *Oryzomys palustris*; B, *O. palustris*; C, *Microryzomys minutus*; D, *Oligoryzomys longicaudatus*. Note the contrast between A and B with regard to the occurrence of satellite roots on m1 and the two large roots on m2 and m3.

available only one specimen of *Microryzomys*, an individual of *M. altissimus* from Ecuador. A fluid specimen of *M. minutus* has been examined herein, and its glandular composition matches the description given for *M. altissimus*. Species of *Microryzomys* possess a full complement of accessory glands similar to those of most other species of oryzomyines they sampled (which included *O. palustris*) except *Oligoryzomys fulvescens* and *Oryzomys albicularis*, both of which lacked preputials. However, the absence of these glands in *fulvescens* cannot be considered a consistent distinction between *Microryzomys* and *Oligoryzomys*, for Myers and Carleton (1981) reported that specimens of *O. fornesi* (= *microtis*), *O. flavesceus*, and *O. longicaudatus*

possess large preputials, whereas examples of *O. nigripes* and *O. chacoensis* have either minute glands or none at all.

Clearly, both species of *Microryzomys* and other forms of *Oligoryzomys* merit detailed examination of their alimentary canal and reproductive system before the phylogenetic significance of this variation, and perhaps other differences still undiscovered, can be fully assessed. One anatomical survey that we have amplified involves gastric morphology, as reported below.

STOMACH (fig. 28)

Microryzomys: Examples of *altissimus* and *minutus* are indistinguishable in gross mor-

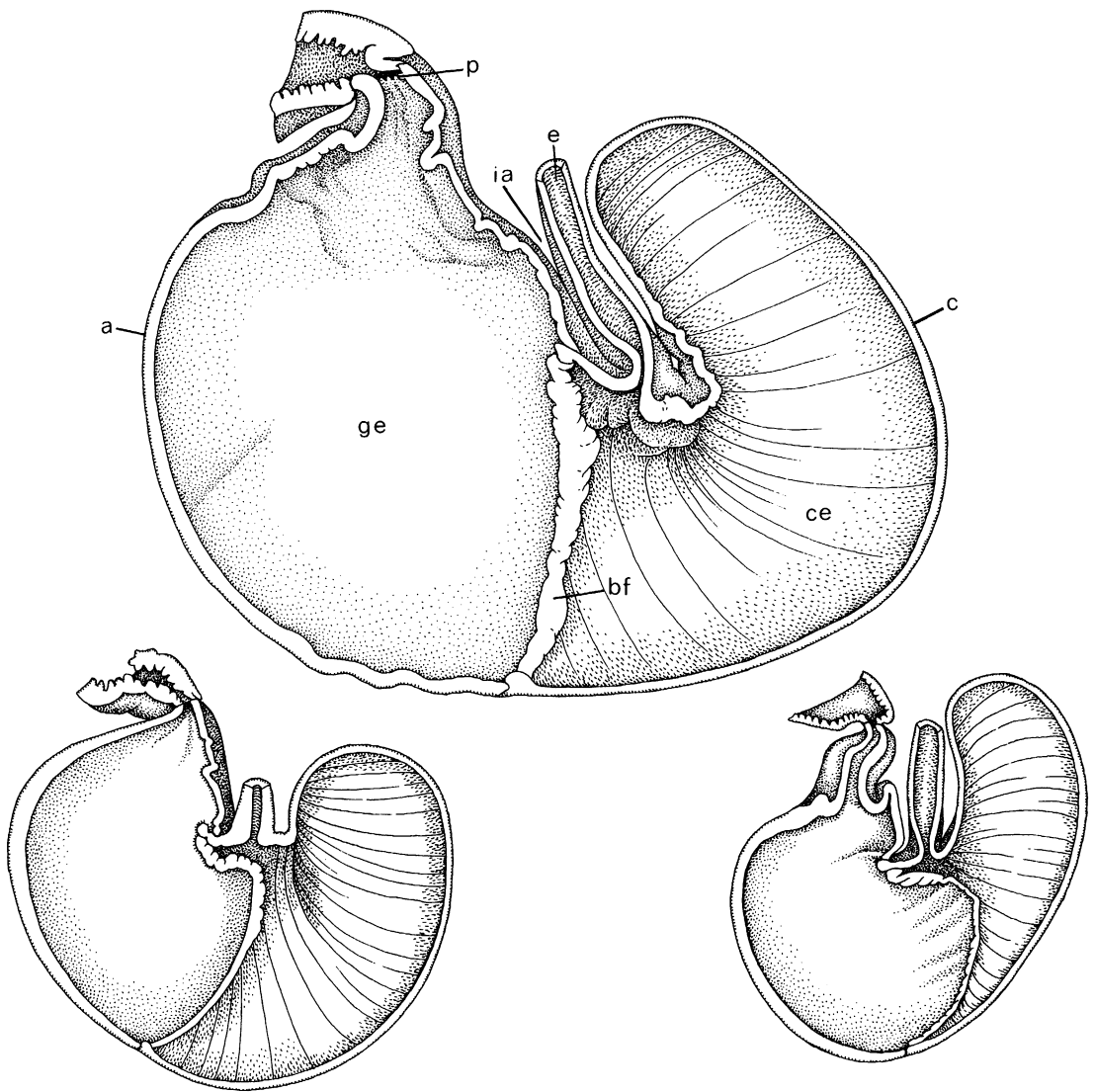


Fig. 28. Ventral view of oryzomyine stomachs (in midfrontal section) showing variation in extent of gastric glandular epithelium. Top, *Oryzomys palustris* (AMNH 239256); bottom left, *Microroryzomys altissimus* (AMNH 248497); bottom right, *Oligoryzomys microtis* (AMNH 263328). a, antrum; bf, bordering fold; c, corpus; ce, cornified squamous epithelium; e, esophagus; ge, glandular epithelium; ia, incisura angularis; p, pylorus.

phological features of their stomach, which conforms to the unilocular-hemiglandular scheme as characterized by Carleton (1973). Within that broad anatomical design, specimens of *Microroryzomys* more closely resemble certain other South American genera that possess a more extensive distribution of glandular epithelium. In this configuration, the bordering fold, which marks the junction of

glandular and cornified mucosa, extends from the incisura angularis and recurves to the left past the esophageal orifice. Some glandular epithelium thus covers the proximal area of the corpus in addition to all of the antrum; this glandular distribution resembles that figured for *Chilomys* by Carleton (1973: 13).

Oryzomys palustris: The fully distended stomach of this species also recalls the uni-

locular-hemiglandular plan, but one in which the bordering fold approximately bisects the stomach on a line from the incisura angularis to a point opposite it on the greater curvature. This is the more commonplace unilocular-hemiglandular variant among the South American sigmodontines surveyed by Carleton (1973).

Oligoryzomys: All of the species samples

available exhibited the basic unilocular-hemiglandular design, but the expanse of glandular lining surpasses that observed in *Oryzomys palustris*, either matching the area of glandular covering as seen in *Micoryzomys* (*Oligoryzomys chacoensis*) or slightly exceeding it (*Oligoryzomys delticola*, *O. longicaudatus*, and *O. microtis*).

DIFFERENTIATION AMONG ORYZOMYINE TAXA STUDIED

SUMMARY OF QUALITATIVE CHARACTER VARIATION

From the foregoing morphological comparisons, we have abstracted the following list of qualitative characters (table 5) whose variation lends itself to consistent definition, recognition of homology, and polarization as discrete character states. The alphabetic order of character states within characters 1–14 and 16–20 presents our hypothesized sequence of primitive-derived conditions, in which all transformations (from a to b, or from a to b to c) are linear. States b and c of character 15 are each derived from character state a. Discussion of many of these same characters and evaluation of their polarity may be found in the studies of Carleton (1980), Carleton and Musser (1984), Hershkovitz (1962), Musser and Newcomb (1983), and Voss (1988). At this time, we are not prepared to rigorously defend our choice of primitive-derived sequences beyond the arguments contained in the aforementioned papers. Nevertheless, these character definitions provide a useful framework for discussing the morphological differentiation among the taxa we studied and for grasping at least preliminary insight to their level of relationship.

Character 1. Conformation of hind feet:

(a) metatarsals II–IV slightly longer than V; nail of fifth digit extends to terminal phalanx of fourth digit;

(b) metatarsals II–IV conspicuously longer than V; nail of fifth digit extends to second phalanx of fourth digit.

Character 2. Conformation of plantar pads:

(a) pads large and fleshy, interdigitals set close together, hypothenar conspicuous;

(b) pads smaller, interdigitals 2 and 3 set apart from 1 and 4 as pairs, hypothenar present but small;

(c) pads distributed as above but diminutive and of low relief, hypothenar pad absent or minute.

Character 3. Development of interdigital webbing on pes:

(a) none;

(b) small interdigital webs present.

Character 4. Development of terminal hair tuft on digits:

(a) large, hairs arch beyond tip of nail;

(b) small, hairs cover about half of nail.

Character 5. Development of zygomatic plate and notch:

(a) plate narrow, notch indistinct;

(b) plate intermediate, notch distinct but shallow;

(c) plate broad, notch well incised.

Character 6. Development of interorbit and cranial ridges:

(a) interorbit hourglass-shaped, braincase smooth even in old adults;

(b) interorbit constricted, supraorbital shelf with reflected edges present; temporal and lambdoidal ridges evident, especially in old adults.

Character 7. Development of jugal:

(a) present and well defined; maxillary and squamosal processes of zygoma never in contact;

(b) absent or represented by slivers of bone; maxillary and squamosal processes of zygoma frequently in contact.

The irregular development or absence of the jugal bone in *Microryzomys* and *Oligo-*

ryzomys suggests that the expression of this trait relates to their small size. However, examination of other Sigmodontinae reveals that the jugal is regularly present, irrespective of general body size, and spans a significant segment of the middle zygoma. For example, genera smaller than or equal to *Microryzomys* and *Oligoryzomys* in body size—such as *Baiomys*, *Calomys*, *Neacomys*, *Reithrodontomys*, and small *Peromyscus*—all possess a distinct jugal; in particular, that observed in *Baiomys* is large for its diminutive proportions. At the other end of the size range, the tylomyine genera *Tylomys* and *Otodylomys* typically lack a jugal element in their zygomatic arches.

Character 8. Basicranial flexion:

(a) weakly pronounced, foramen magnum oriented mostly caudad;

(b) strongly pronounced, foramen magnum oriented posteroventrally.

Character 9. Size of interparietal:

(a) broad, strap-shaped, nearly as long as caudal border of frontals;

(b) narrow, wedge-shaped, about half as long as caudal border of frontals.

Character 10. Size of incisive foramina:

(a) relatively short, terminating short of, even with, or slightly beyond front of first molars;

(b) relatively long and slitlike, span much of diastemal palate and conspicuously project between first molars.

Character 11. Development of bony palate and posterolateral palatal pits:

(a) palate extends little beyond third molars, pits small and simple;

(b) palate extends well beyond third molars, pits large and perforated.

Character 12. Size of ectotympanic bullae:

(a) relatively small, exposed flange of periotic extends to carotid canal;

(b) relatively large, exposed wedge of periotic not contributing to wall of carotid canal.

Character 13. Carotid circulatory pattern and cranial foramina:

(a) primitive pattern, stapedia foramen and posterior opening of alisphenoid canal large, squamosal-alisphenoid groove and sphenofrontal foramen present;

(b) derived pattern 1, stapedia foramen and posterior opening of alisphenoid canal

large, squamosal-alisphenoid groove and sphenofrontal foramen absent;

(c) derived pattern 2, stapedia foramen and posterior opening of alisphenoid canal small, squamosal-alisphenoid groove and sphenofrontal foramen absent, secondary branch crosses dorsal surface of pterygoid plate.

Character 14. Configuration of molar crowns:

(a) molars brachyodont, cusps tuberculate, labial and lingual folds wide and margins open, enamel connections between principal cusps oriented more obliquely;

(b) molars higher crowned, cusps more bunodont, labial and lingual folds narrow and margins closed by cingular connections between cusps and lophs(ids), enamel connections oriented more transversely.

Character 15. Development of procingulum on first molars:

(a) anteromedian flexus(id) present, labial and lingual conules(ids) of procingulum distinct but small and closely joined, occlusal outline ovate;

(b) anteromedian flexus(id) present, labial and lingual conules(ids) of procingulum large and strongly separated, occlusal outline rectangular;

(c) anteromedian flexus(id) absent, anterior rim of procingulum entire, occlusal outline ovate (derived from state a).

Character 16. Development of anterolophid on m2 and m3:

(a) anterolophid absent or weakly expressed;

(b) anterolophid and companion metaflexid distinct.

Character 17. Presence of anterolabial cingulum on m3:

(a) anterolabial cingulum present, typically developed as broad flange;

(b) anterolabial cingulum absent, or developed as narrow ridge.

Character 18. Relative size of upper and lower third molars:

(a) subequal in size to second molars, principal coronal features of posterior half of third molars recognizable;

(b) noticeably smaller than second molars, posterior half of third molars more reduced.

Character 19. Number of molar roots:

(a) upper and lower molars each anchored by three and two major roots, respectively;

(b) satellite rootlets variably developed, especially on upper and lower first molars.

Character 20: Area of gastric glandular epithelium:

(a) gastric mucosa covering proximal portion of corpus near esophageal opening as well as antrum;

(b) gastric mucosa limited to antrum, not extending left beyond the incisura angularis.

DISCUSSION

A survey of the character-state distribution among *Microryzomys*, *Oligoryzomys*, and *Oryzomys palustris* for these 20 characters (table 5) underscores several points about these oryzomyines.

Firstly, the genus-group taxa *Microryzomys* and *Oligoryzomys* are each characterized by several discrete morphological traits whose variation appears unrelated to overall size. For instance, the configuration of the pes and plantar pads, zygomatic plate, jugal, interorbit, carotid circulation, and dentition offers a combination of qualitative features that serves to objectively delimit the species membership of each (see diagnoses under Taxonomic Summary below). This finding contradicts the notion that the two taxa are artificial constructs, or taxonomic grades, that circumscribe the smaller mice in a speciose genus highly varied in body size, for example, as suggested by Tate (1932e) and Hershkovitz (1944). In contrast, we regard the evidence based on discrete character variation as supportive of the hypothesis that *Microryzomys* and *Oligoryzomys* are each monophyletic. Until refuted by other data, this interpretation is more compelling than their portrayal as polyphyletic entities.

Secondly, species of *Microryzomys*, and to a lesser extent those of *Oligoryzomys*, retain many ancestral conditions within the framework of our hypothesized character polarities (table 5). Of the 14 character states which *Microryzomys* and *Oligoryzomys* share, 12 are considered to be primitive (3a, 4a, 6a, 9a, 10a, 11a, 12a, 14a, 16a, 17a, 19a, 20a); whereas, only two of their similarities—a reduced jugal (7b) and small third molars (18b)—are synapomorphies. Of the six traits unique to *Microryzomys* (among the taxa

TABLE 5
Matrix of Character States Among Three
Oryzomyine Taxa
(see text)

Character	<i>Micro- ry- zomys</i>	<i>Oligo- ry- zomys</i>	<i>Ory- zomys palus- tris</i>
1. Pes	a	b	b
2. Plantar pads	a	b	c
3. Interdigital webbing	a	a	b
4. Digital hair tufts	a	a	b
5. Zygomatic plate	a	b	c
6. Interorbit and ridges	a	a	b
7. Jugal	b	b	a
8. Basicranial flexion	b	a	a
9. Interparietal	a	a	b
10. Incisive foramina	a	a	b
11. Bony palate	a	a	b
12. Ectotympanic bullae	a	a	b
13. Carotid circulation	a	b	c
14. Molar crowns	a	a	b
15. Procingulum	b	a	c
16. Anterolophid	a	a	b
17. Anterolabial cingulum	a	a	b
18. Size of m3	b	b	a
19. Molar roots	a	a	b
20. Glandular mucosa	a	a	b

studied), four constitute ancestral states—conformation of the hind feet (1a) and plantar pads (2a), narrow zygomatic plate (5a), and carotid circulation (13a)—and two are derived—a strong basicranial flexion (8b) and wide procingulum (15b).

Thirdly, the type species of *Oryzomys*, *Mus palustris* Harlan, is strongly removed morphologically from *Oligoryzomys* and especially *Microryzomys*. It is particularly noteworthy that much of the differentiation of *Oryzomys palustris* relects its large number of apparently derived conditions, involving 16 of the 20 characters surveyed (2c, 3b, 4b, 5c, 6b, 9b, 10b, 11b, 12b, 13c, 14b, 15c, 16b, 17b, 19b, 20b). Examples of *Oryzomys palustris* possess no derived features in common with species of *Microryzomys*, but do share four predicted modifications with those of *Oligoryzomys*—a short metatarsal V (1b), small plantar pads (2b, c), wider zygomatic plate (5b, c), and derived carotid pattern (13b,

c). For three of the presumed synapomorphies (2b, 5b, and 13b), species of *Oligoryzomys* exhibit the annectant step of three-state characters leading to the autapomorphic condition observed in *Oryzomys palustris*.

Although we have summarized the discrete character variation encountered in a cladistic context, the absence of other species more broadly representative of oryzomyines, as well as other Sigmodontinae, precludes a meaningful phylogenetic assessment of relationship. Inclusion of additional species would doubtlessly affect not only the number of characters treated but also our interpretation of polarities, the amount of homoplasy predicted, and the pattern of relationships supported. We do believe that the hypothesis that *Microryzomys* and *Oligoryzomys* are sister taxa which originated early relative to the evolution of *Oryzomys palustris* merits special attention. The evidence for this conjecture, however, is weak and shaped more by the joint retention of so many primitive states by *Microryzomys* and *Oligoryzomys* than by the few synapomorphic traits they display. The refinement of *palustris*' hierarchical position within the oryzomyine radiation also must await further evaluation. Nevertheless, the derived condition of so many of its features cautions that the uncritical use of North American *Oryzomys palustris* as an outgroup representative of oryzomyines, or South American sigmodontines as a whole, may severely compromise phylogenetic insights.

We have chosen to recognize the differentiation of *Microryzomys* and *Oligoryzomys* as genera based on the unique combination of qualitative features shared by species contained within each taxon. In view of the incomplete picture of their kinship to *Oryzomys*-like forms and to other sigmodontines, their continuation as subgenera might be as easily argued. In the absence of phylogenetic information of such broader scope, however, we defend our preference for generic recognition in an operational way. With the suite of qualitative characters now of potential use in estimating muroid relationships (see, for example, Carleton, 1980; Musser and Newcomb, 1983; Voss, 1988), we can more objectively discern the lower bounds of this supraspecific character covariation and prefer to use the genus category to identify and di-

agnose these distinctive morphologies. If *Microryzomys* and *Oligoryzomys* must be maintained as subgenera, then the task of drawing the morphological boundary of a genus like *Oryzomys* becomes, for us, fraught with greater arbitrariness, for other oryzomyine taxa conventionally recognized at this level—such as *Neacomys*, *Nectomys*, *Nesoryzomys*, and *Oecomys*—exhibit discrete character-state contrasts of a similar nature and could as rationally be subsumed under one genus. We acknowledge that such a protocol for generic treatment is an interim expediency to be followed until more rigorous, inclusive studies can put our designation of taxonomic categories on a firmer phylogenetic basis.

To this point, we have informally referred, without explication, to *Microryzomys* as an "oryzomyine," a grammatical construction connoting a tribal-level assemblage of genera. Indeed, recent works formally recognize Oryzomyini as the largest tribe, containing over 40 percent of the approximately 250 South American species, among seven in the subfamily Sigmodontinae (Vorontsov, 1959; Reig, 1980, 1984). The other six tribes are the Ichthyomyiini, Akodontini, Scapteromyiini, Phyllotini, Wiedomyiini, and Sigmodontini. Here we review both the evidence for the tribal association of *Microryzomys* and the historical development of the tribal constructs that now comprise formal categories in our classification of New World muroids.

Osgood (1914, 1933) explicitly drew attention to features of *Microryzomys* that recall the smaller-bodied species of *Rhipidomys* or *Thomasomys*. This resemblance so impressed Osgood that he clearly wrestled with the idea of recognizing *Microryzomys* as a genus allied to those forms. These similarities include such traits as low-crowned molars, inflated braincase, amphoral interorbit, narrow zygomatic plate, and long, soft pelage. Nevertheless, he finally elected to retain *Microryzomys* as a subgenus of *Oryzomys* on the basis of its relatively long palate and rudimentary palatal pits. His decision in this regard was influenced by the earlier papers of Thomas (1906b, 1917b), who first emphasized the utility of palatal construction for segregating the many dentally complex, long-tailed, sylvan forms that had been indiscriminantly lumped under *Oryzomys* and *Rhip-*

idomys into two groups. Thomas thus delineated the association of genera that later systematists have recognized, usually informally, as the oryzomyines and thomasomyines (for example, Hershkovitz, 1962, 1966a; Hooper and Musser, 1964). The number of mammary glands, six in thomasomyines and eight in oryzomyines, has also been advanced as a trait for distinguishing the two groups (Thomas, 1906b; Hershkovitz, 1966a).

The level of affinity of *Microryzomys* to oryzomyines versus thomasomyines has been, in one sense, rendered superfluous by Reig (1980: 262), who synonymized Thomasomyini under Oryzomyini because "the distinction . . . of a thomasomyine group does not seem to be well warranted." Although his taxonomic action may eventually prove justified, some presentation of character evaluation would have better served our understanding of the interrelationship of forms composing the two assemblages. In the meantime, we merely note that species of *Microryzomys* exhibit the trenchant features that Thomas advanced for his grouping of *Oryzomys*-like forms: a bony palate that projects beyond the end of the molar rows; the presence of posterolateral palatal pits; and the possession of eight mammae. We therefore continue to view *Microryzomys* as an oryzomyine, possibly representing a cladistically early lineage, not a member of the thomasomyine complex as denoted by Thomas (1906b, 1917a) and Hershkovitz (1962, 1966a).

The irresolution surrounding the placement of *Microryzomys* as oryzomyine or as thomasomyine epitomizes the situation involving the generic-level taxonomic arrangement within Sigmodontinae as a whole. Our lack of confidence in this regard stems, at least partially, from the manner in which these suprageneric groupings have emerged to become formal taxonomic categories.

In the descriptive phase of South American mammalogy, authors naturally crafted their diagnoses and comparisons in terms of the taxa already known. For example, Thomas (1901: 183) characterized his new species *Oxymycterus mimus* as "A member of the group of small *Akodon*-like *Oxymycteri* [sic], the nearest ally being *O. bogotensis*"; diagnosed

(1902: 137) *Akodon fumeus* as "A dark-coloured species of the *A. mollis* group"; and announced (1906a: 421) his discovery of *Rheomys* as "A third genus of the *Ichthyomys* group." Knowledge of higher-order relationships during this period grew by an accretive, phenetic process, with earlier-described genera—such as *Oryzomys*, *Akodon*, and *Phyllotis*—serving as foci of comparison and contrast. In particular, the term "group" was applied in a loose and vague manner to a variety of supraspecific aggregations that by current standards are explicitly stratified in our taxonomic hierarchy as species groups, subgenera, genera, or tribes. In the early 1900s, Thomas (1906b, 1916a, 1916b, 1917b) sorted out some of this inconsistency by listing related genera and their species and briefly discussing character traits justifying their association. These "groupings" were essentially equivalent to our present-day Oryzomyini, Thomasomyini, Phyllotini, and Akodontini, the four largest tribes of South American Sigmodontinae.

Tate's series (1932a–h) of papers on the taxonomic histories of South American rodents further solidified the contents and number of basic generic aggregations among them. His bibliographic collations marked an important contribution toward synthesizing the voluminous and far-flung taxonomic literature on South American rats, and although not primarily revisionary in intent, his treatment entailed considerable awareness of anatomical variation and decisions on the taxa recognized and their rank. Moreover, Tate's publications conferred further identity to the generic-level groupings through the joint consideration of genera under a single title and through the introduction of collective terms like "oryzomine," "akodont," and "fish-eating rats." Other treatises on the South American rats and mice during this era, such as those of Gyldenstolpe (1932) and Ellerman (1941), provided little insight to higher-order relations. Ellerman (1941: 327) gloomily assessed the situation: "But directly Panama is passed, an enormous list of names described for the most part binomially, and in appalling chaos, is reached."

The next stage in the emergence of our tribal entities issues largely from the work of Philip Hershkovitz of the Field Museum of

Natural History. His revisionary studies of *Nectomys* (1944) and *Oecomys* (1960), *Holochilus* (1955), *Phyllotis* and allies (1962), and *Scapteromys* and *Kunsia* (1966a) were framed within diagnoses of their respective generic groups (oryzomyine, sigmodont, phyllotine, and scapteromyine) and accompanied by evolutionary scenarios of their geographic and ecological diversification. Whereas Tate consolidated the taxonomic literature involving Thomas' groupings of South American muroids, Hershkovitz consolidated the vast empirical data for their basis. His investigations refined and expanded the morphological diagnoses of previously defined genera, improved systems of comparative terminology, and interpreted anatomical differences within an evolutionary context of ancestral-derived modifications. Hershkovitz's collective efforts have elevated our appreciation of sigmodontine diversity and evolution far above the "appalling chaos" that existed in the early 1940s. Still, his diagnoses of the various suprageneric taxa represented little more than extended summaries of the morphological variation embraced by the genera that Thomas had previously associated. Hershkovitz's own comments (1966a: 82), apropos of characterizing the scapteromyine group, reflected the tentative basis for their usage:

The non-technical term scapteromyine is employed here in the sense of a supergenus or generic group coordinate with oryzomyine, phyllotine, sigmodont, akodont, peromyscine, etc. With fuller knowledge of cricetine origin, dispersal, and radiation one or another of these natural aggrupations of closely related and nominal genera may be consolidated within a single, well defined genus. Others may be accorded formal tribal rank within the subfamily [Sigmodontinae].

The nomenclatural formalization of tribes followed swiftly thereafter. Vorontsov (1959), in a sometimes overlooked paper, satisfied the canons of zoological nomenclature by selecting type genera, attaching prescribed suffixes, and defining the generic contents for several tribes of New World muroids. More recently, Reig (1980, 1984, 1987) has acknowledged many of Vorontsov's tribes and presented them within his own classification of Muroidea and Sigmodontinae (*sensu stricto*, that is, exclusive of the neotomine-peromyscines or Neotominae).

This review highlights, from our perspective, the basic weakness that has hindered formulation of a more credible higher-order taxonomy of South American muroids. Although the many genera are today arranged within a neat tribal classification, the empirical basis for these tribes has advanced little since Oldfield Thomas' first attempts to group the genera. The tribal associations have acquired their identity as much from the inertia of repetition and nomenclatural formalization as from processes of rigorous character evaluation, alpha-level revisionary attention, and enhanced comprehension of supraspecific phylogeny. In our Introduction, we offered Osgood's (1933: 3) assessment that "... no ultimate generic and subgeneric classification [of South American rodents] will be possible until all these species are thoroughly understood." Paradoxically, in the course of "Defining the Tribe Akodontini," Reig (1987: 364) echoed a similar shortcoming: "To arrive at this definition satisfactorily would require revision of the whole tribe and other related groups of the subfamily Sigmodontinae." He then proceeded to give "the intensional meaning of the polythetic concept of the Akodontini."

After a half-century, we question the value of continuing attempts to adjust such tribal-level constructs if divorced from much needed studies on species variation and their morphological limits and from the interdependence between these research activities and the elucidation of discrete character variation and improved diagnoses of genera. For South American sigmodontines, the time is past due for renewed species-level attention, the results of which will provide a better foundation for phylogenetic studies among species, genera, and tribes, and classifications derived therefrom. In our opinion, stipulation of tribal arrangements without this foundation has proven a barren research focus, or at least the return in terms of added systematic understanding has diminished markedly since Thomas' earliest forays.

We believe that a refined species taxonomy bears more pragmatically on the substance of investigations aimed at resolving higher-order relationships than conventionally acknowledged. For one, it supplies more insight for the interpretation of polymorphisms of

discrete traits, be they of crania, chromosomes, or proteins. Unfortunately, for many South American rats and mice, one is often-times uncertain whether such variation, encountered either within a locality or among geographic samples, in fact represents a single, highly plastic species or a composite of morphologically similar species. For another, a dependable species framework allows the unambiguous choice of exemplars of supraspecific taxa to serve as OTUs in phylogenetic studies. The correct species identity of such exemplars, especially those designated as type species of subgenera and genera, is crucial to any taxonomic recommendations that devolve from the study. As recounted by Reig

(1987), much of the difficulty surrounding the recognition of *Bolomys* has issued from the inconsistent and vague definition of its type species *Akodon amoenus*. Numerous cases having lesser and greater taxonomic ramifications pervade the alpha-level systematics of South American sigmodontines. We are by no means sanguine that improvement of the current species taxonomy will remove ambiguity and contention over the supraspecific classifications of Sigmodontinae eventually put forth. We are convinced, however, that this research agenda constitutes an important, perhaps even necessary, step to determine whether we can.

ALTITUDINAL, ECOLOGICAL, AND GEOGRAPHIC DISTRIBUTION

The genus *Microryzomys* is autochthonous to the northern and central Andes, its distribution describing an arc from northern Venezuela, through Colombia, Ecuador and Peru, to central Bolivia. We believe that the known locality records of *Microryzomys* accurately convey the broad outlines of its geographic range, although the greater number of *minutus* samples more convincingly document its distributional limits compared to those of *altissimus* (see figs. 1, 2).

The known elevational range of the genus is broad, extending from 800 (*minutus* in southwestern Colombia) to 4300 m (*altissimus* in southcentral Peru). The altitudinal records of *minutus* under 1000 m are possibly to be considered suspect, particularly the 900-m record for the Río Cosanga, Ecuador, an Olalla site of imprecise altitude. Of the almost 200 collecting stations where altitude was indicated (131 representing *minutus* and 67 *altissimus*, as tallied from the Taxonomic Summary), over 80 percent of the sites fall within the 2000 to 4000 m range (fig. 29).

Although the sampling effort reflected by the locality data must be admitted as highly uneven and altitudinal figures in some cases inaccurate, the broad pattern suggests that *minutus* generally occupies a lower altitudinal belt than does *altissimus*. About 75 percent of the places where *minutus* has been taken occur between 2000 and 3500 m, an

interval which closely matches Handley's (1976) well documented trapping results for *minutus* in Venezuela. In contrast, over 80 percent of the records of *altissimus* are concentrated in the 2500 to 4000 m range. Osgood (1933) first drew attention to the altitudinal superposition of *altissimus* relative to *aurillus* (= *minutus*) based on their occurrence at certain localities in Peru, and the same pattern is repeated for many nearby samples representing successively descending altitudes in Colombia and Ecuador. The greatest altitudinal overlap of *minutus* and *altissimus* collecting localities, 2500 to 3500 m, encompasses most instances of sympatry that we have encountered (see Gazetteer of Principal Collecting Localities). This collective locality information probably exaggerates the extent of altitudinal overlap of the two species in a local area because differences in slope aspect and inclination greatly influence local temperatures, rainfall regimes, and the consequent distribution of plant communities (Grubb, 1977; Sarmiento, 1986). We anticipate that regional transect studies would disclose a pattern of altitudinal parapatry with only a narrow zone of syntopy.

The altitudinal data for *minutus* intimate that it inhabits a variety of wet and cool Andean forests. This is consonant with the typical habitat notations gleaned from skin tags, faunal accounts, and gazetteers, which asso-

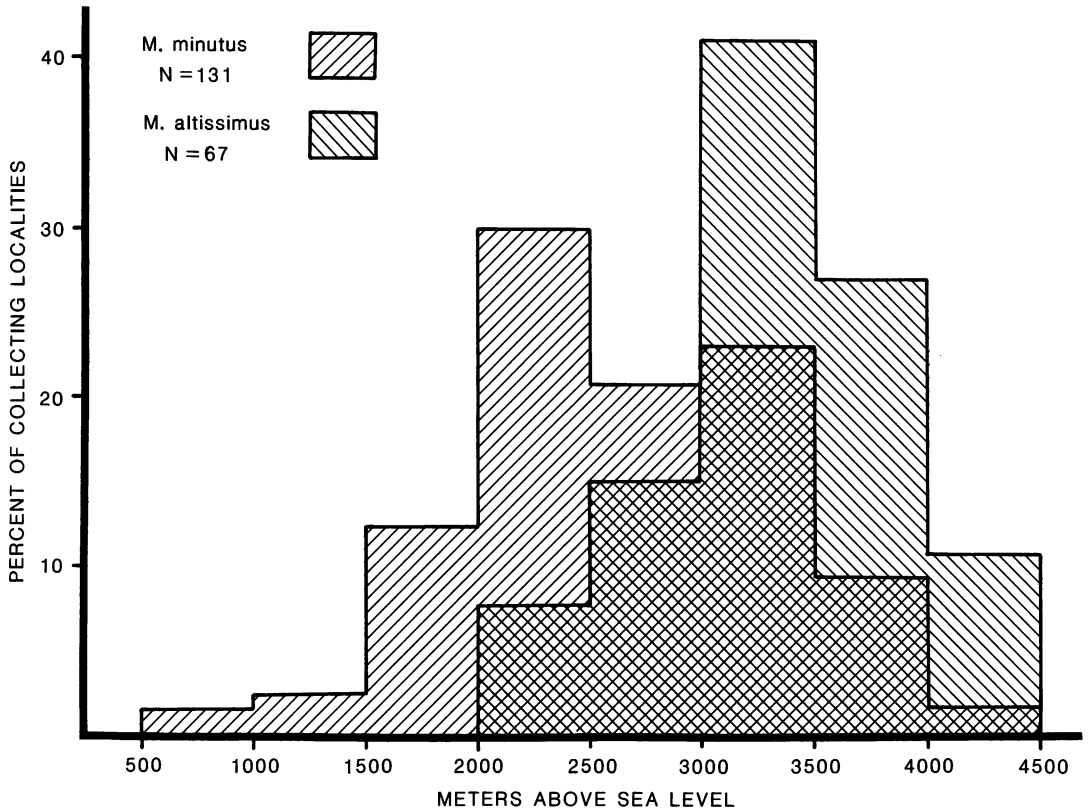


Fig. 29. Frequency histogram of the altitudinal occurrence of the two species of *Microryzomys*, based on all locality records for which collectors recorded altitude.

ciate *minutus* with areas described as lower subtropical forest, lower montane moist forest, humid temperate forest, mossy subtropical forest, scrubby cloud forest on ridge, heavy cloud forest, elfin forest, and páramo. In Peru and Ecuador, Osgood (1933) characterized *aurillus* (= *minutus*) as a forest animal confined to the more humid ranges of the Andes. The field crews of the Smithsonian Venezuelan Project trapped most examples of *minutus* in cloud forest, with small numbers obtained from páramo and agricultural lands (Handley, 1976). Cloudforest cover in Venezuela spans vegetative life zones classified (after Grubb, 1977) as lower montane rain forest, upper montane rain forest (in which *minutus* is most common), and subalpine rain forest. At its upper altitudinal limits in Venezuela, *minutus* appears to occur rarely in grassy páramo, instead living in various habitats found at the ecotone between upper Andean forest and páramo. Some of

these habitats, such as certain low-canopied *Polylepis* woodlands and shrubby *Espeletia* stands, are considered part of the páramo zone (Simpson, 1986; van der Hammen and Cleef, 1986).

While gathering data on ichthyomyine rodents, Robert S. Voss visited Venezuela in 1979 and collected *Microryzomys minutus* near some of Handley's (1976) field stations. Voss's fieldnotes, which he has kindly abstracted for us, more graphically detail the plant composition and microclimate where *M. minutus* lives. The three places mentioned below are located in the Merida Andes, Estado Merida: near Lago Mucubaji and Laguna Negra, 3500–3700 m, both in the Serranía de Santo Domingo; and near La Mucuy, 4–5 km ESE Tabay, 2400–2600 m, in the Sierra Nevada.

Near Lago Mucubaji [fig. 30] I trapped six *Microryzomys* on the ground along the shrubby, moss-covered banks of a small stream bordered by a heathlike

vegetation that is typical of open páramo landscapes throughout the Andes of Venezuela and Colombia. The locally dominant species in this community are a large, arborescent rosette plant, *Espeletia schultzei* (Compositae), and a tough, small-leaved shrub, *Hypericum laricifolium* (Guttiferae). Individual *Espeletia* . . . may be 2 m or more in height, but other plants in this habitat are seldom more than a meter high. Jumbled boulders, bunch grass, cushion plants, and moss fill in the spaces among the dominant species. The vegetation is almost always wet from dense fogs and misting rain, and there was one light snowfall during our work here.

Eight additional specimens of *Microryzomys* were taken . . . near Laguna Negra in dense thickets of *Polylepis sericea* (Rosaceae), a low sprawling tree with shaggy, reddish bark . . . The canopy of such thickets (which also include *Espeletia* . . .) is broken and discontinuous, and only about 3 to 4 meters high. Under the canopy, the ground is jumbled with boulders and tangled with roots and prostrate trunks; all exposed surfaces, vegetable or mineral, are covered with dense, cold mats of wet moss. Small runways crisscross the mossy ground among the roots and rocks, and I caught *Microryzomys* in these tiny paths as well as in open spaces under rocks that I found by pulling away fistfuls of matted moss.

[In the vicinity of La Mucuy (fig. 31)] The cloud forest habitat . . . is basically the same as that at similar elevations where *M. minutus* occurs throughout the northern Andes. The forest canopy is about 25 to 30 m high; the trees are unbuttressed and they bear heavy loads of epiphytic orchids, bromeliads and ferns in their upper branches. Thin, rope-like vines are festooned through the canopy and loop through the subcanopy, but woody lianas (common in lowland forests) are absent. The understory vegetation consists chiefly of treeferns, sapling trees, and shrubs (there are no giant herbaceous monocots here in contrast with forests at lower elevations). Dense thickets of dwarf bamboo (one or more species of *Chusquea*) are ubiquitous wherever treefalls or landslides have torn openings in the forest canopy. Fallen trunks and branches litter the steep mountain slopes on which this forest grows, and everything near ground level is covered with moss, ferns, and a variety of other small epiphytes. The ground is thickly leaf-littered and there is a deep underlying humus layer . . . *Microryzomys minutus* were taken on the ground beneath a mossy pile of fallen branches beside a stream at 2500 m.

Microryzomys altissimus, on the other hand, may be more regularly associated with páramo environments. Habitat remarks frequently reference páramo, as well as *Polylepis* forest, arid scrub, and humid temperate forest just below timberline. In the mountains around Huánuco, Peru, Osgood (1933) noted that both *altissimus* and *aurillus* (= *minutus*) were captured at a lower site where forest and páramo habitats intermix, but at the upper station where páramo alone occurs, only *altissimus* was taken. In northern Ecuador,

Hershkovitz (1940: 83) trapped both *altissimus hylaeus* and *minutus* at 2900 m "at the edge of a small cornfield entirely surrounded by virgin forest."

Our best habitat descriptions of places where species of *Microryzomys* occur sympatrically again derive from the meticulous field observations of Voss, who, in 1978 and 1980, collected them together in the vicinity of Papallacta, Ecuador, on the eastern slopes of the Cordillera Oriental.

The Papallacta region is cold and wet . . . Above the town, where many of the *Microryzomys* specimens were collected between 3600 and 3900 m, ground frost is common in the early mornings and stream sides are often rimed with ice. Páramo habitats . . . extend from about 4000 m down to 3600 m, the upper limit of continuous forest cover. This open landscape consists of rolling hillsides and low rocky peaks dissected by narrow ravines or divided by broad cirques with flat marshy bottoms. The páramo here is dominated by wet grasslands, the grass growing in dense, wiry clumps about a meter high [fig. 32] . . . Large bromeliads (*Puya* sp.) are scattered on hillsides, but *Espeletia* is uncommon here and rarely seen. Dense stands of *Polylepis* sp. occur in sheltered valleys.

Between 3700 and 3600 m the traveller passes through a narrow ecotone of mixed bunch grass and waist-high shrubs, and enters a distinctive, dwarfed forest of low, bent and twisted trees (Subalpine Rain Forest of Grubb, 1977) . . . The forest canopy at this elevation seldom exceeds 5 or 6 meters [fig. 33]. There is no appreciable understory, but horizontal limbs, sprawling trunks, and fallen logs limit foot travel and visibility. Epiphytic orchids and bromeliads are absent here, but wet mats of moss, liverworts, and ferns completely cover tree trunks and branches. A few, thin vines are present, but not palms, bamboo, or treeferns. Herbaceous dicots, ferns, and horsetails (*Equisetum*) provide a sparse ground cover above the moss and littered leaves. Matted roots and a deep, peaty humus make the soil soft and springy underfoot.

Descending the mountain slopes, below about 3400 m, the forest grows gradually taller and assumes the characteristics of Upper Montane Rain Forest (Grubb, 1977); a variety of vascular epiphytes (Orchidaceae, Bromeliaceae, Ericaceae, Piperaceae) become very abundant. In the immediate vicinity of Papallacta, between 3200 and 3000 m, this taller forest has been cleared from all but the most inaccessible slopes and there remain only a few wet stands of dense secondary growth surrounded by lush pastures and potato fields.

Specimens of *Microryzomys altissimus* were taken from about 3100 to almost 3900 m elevation. All 14 were trapped on the ground. One was taken at the edge of stream in a cow pasture, and one in a nearby stand of secondary growth; these were the only captures below 3200 m. The rest were taken above 3600 m, three in Subalpine Rain Forest, six in the shrubby ecotone between forest and páramo, two in páramo grassland, and one along the grassy edge of a *Polylepis* thicket. Away from streams . . . the commonest mi-



Fig. 30. Páramo near Lago Mucubají, 3500–3700 m elevation, in the Merida Andes of Venezuela and northern Colombia, where *Microoryzomys altissimus* does not range, this open landscape is the habitat of *Microoryzomys minutus*. Photographed 9 March 1980 by Paul Kaarakka.

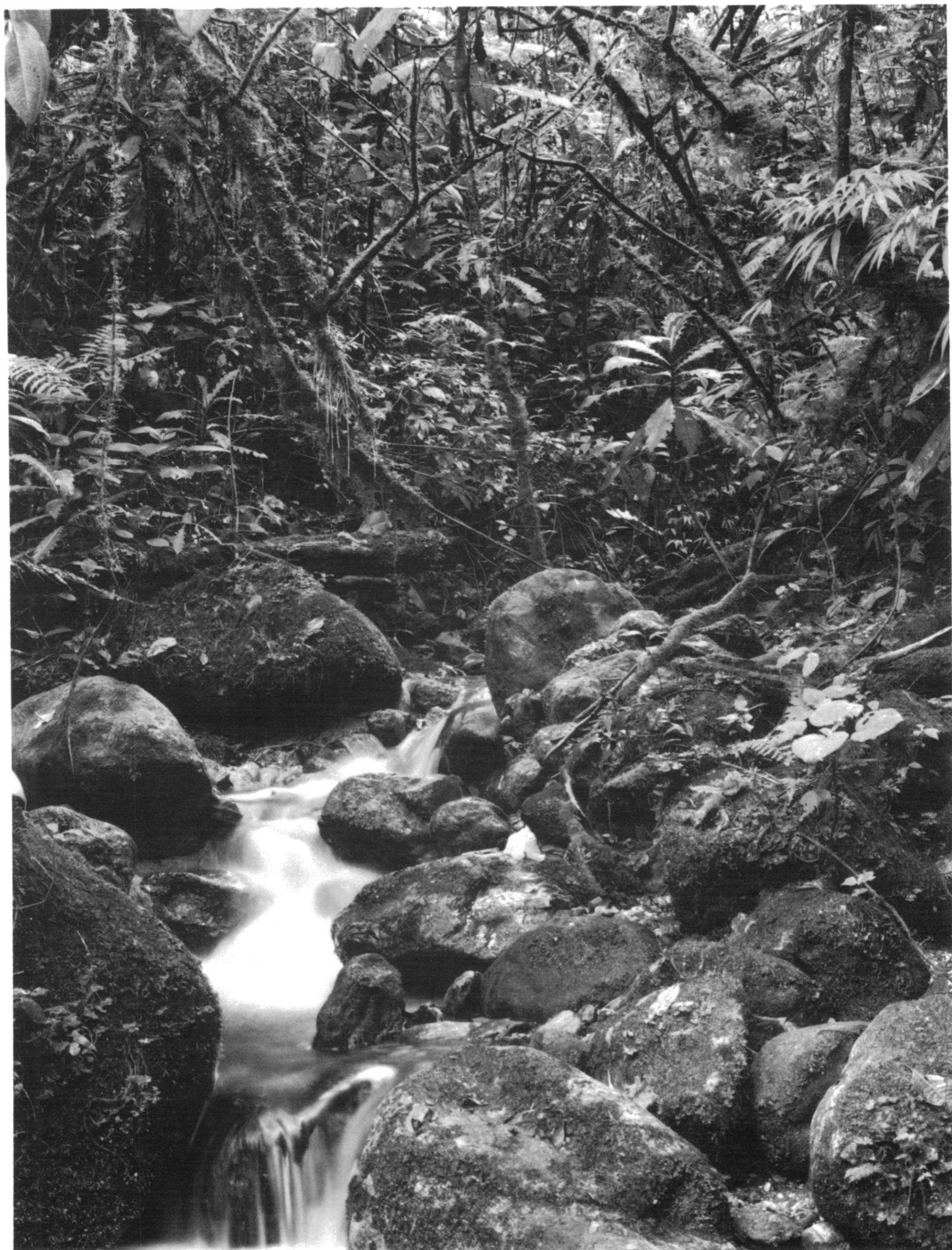


Fig. 31. Streamside habitat in cloud forest near La Mucuy, about 2500 m elevation, in the Merida Andes of Venezuela. *Microryzomys minutus* commonly occurs in this environment. Photographed 1 January 1980 by Paul Kaarakka.



Fig. 32. Páramo, about 3800 m elevation, above Papallacta, in the Cordillera Oriental of Ecuador. In the Andes south of Venezuela and northern Colombia, *Microoryzomys altissimus* lives in such páramo habitats apparently to the exclusion of *M. minutus*. Photographed 19 April 1980 by Paul Kaarakka.



Fig. 33. Subalpine rain forest below treeline, about 3400 m elevation, near Papallacta, Ecuador. Where the distributions of the two *Microoryzomys* overlap, *M. minutus* is found primarily in forest habitats and is absent from páramo where *M. altissimus* occurs.

crohabitat where I found *M. altissimus* was in runways through grass. Of the six specimens of *M. minutus* that I collected . . . , three were taken below 3200 m, on the ground, in patches of dense secondary vegetation. Two were collected in Subalpine Rain Forest at about 3400 m, one inside a hollow tree and another under a pile of mossy branches on the ground. At 3600 m I caught one specimen in the forest on a mossy horizontal limb over a stream. I never caught this species in páramo habitats near Papallacta.

In summary, the available distributional and ecological data depict *minutus* as an intermediate to high-altitude species inhabiting a variety of cool, wet forests, and *altissimus* as a high-altitude form occurring in subalpine rain forest to open páramo habitats. Limited evidence suggests that in mountains where *altissimus* is absent, such as the Venezuelan Andes, *minutus* occupies *Polylepis* forest and other habitats above the treeline of continuous forest. However, in ranges where the two co-occur, such as the Ecuadorean Cordillera Oriental, *minutus* is confined to the upper edges of subalpine rain forest, whereas *altissimus* is found in subalpine rain forest, along forest-páramo ecotones, and upwards into grassy páramo. Even at its upper altitudinal extremes, *minutus* seems to require an arborescent habitat structure, preferring to dwell in dwarfed woodlands rather than among the bunch grasses of open páramo where *altissimus* has been captured. The longer tail, broader hind feet, and larger metatarsal pads of *minutus* and the more pronounced counter-shading of the body and tail of *altissimus* may reflect adaptation to these different microhabitats and concomitant differences in the degree of arboreality. On the basis of such differences, and the very late development of páramo environments following mostly Quaternary uplift and glacial retreat (Simpson, 1975; van der Hammen and Cleef, 1986), the *altissimus* morphotype can perhaps be argued as the more derived form. Still, our knowledge of the microhabitat associations of *minutus* and *altissimus*, in both sympatric and allopatric situations, is limited to a few geographic areas, an inadequacy which signals the need for basic autecological studies of both species coupled with carefully designed altitudinal transects in other parts of their ranges.

The distributional boundaries of *minutus* define the geographic limits of the genus,

whereas the range and altitudinal occurrence of *altissimus*, as currently understood, are more restricted (fig. 34). The absence of *altissimus* in northern Colombia and Venezuela seems sufficiently well documented in view of the sampling at high altitudes in the Cordillera Oriental, Sierra Nevada de Santa Marta, and Cordillera de Merida, all of which support habitats where it might be expected to occur. Floristic and geomorphological evidence indicates that the eastern cordillera of Colombia underwent much of its developmental history quite independently from that of the central chain (Cuatrecasas, 1986; Simpson, 1975; van der Hammen and Cleef, 1986). As a result, the alpine habitats of these two Colombian cordilleras were discontinuous during much of the Pleistocene, a history which may explain the northern terminus of *altissimus* in the Cordillera Central. No records of *altissimus* are known from the Cordillera Occidental of western Colombia, nor from southern Colombia at the convergence of the three cordilleras. A wide gap thus separates the central Colombian populations, which proved to be the most divergent of the *altissimus* samples we compared morphometrically, from those in Ecuador and Peru, where the species reaches its southern terminus in the high mountains of Pasco and Junín. Additional fieldwork must decide whether the southern Colombian hiatus reflects the inadequacy of collections from high altitudes or the absence of preferred habitats. Nonetheless, even presuming our present knowledge of *Microryzomys* distribution to be complete, the depression of vegetation zones by as much as 1300 to 1500 m during Pleistocene glacial episodes (Simpson, 1975; van der Hammen and Cleef, 1986) would probably have created a corridor of suitable habitat to link these moieties of *altissimus*.

The distribution of *minutus* is practically coterminous with the Andean vegetation zone that Vuilleumier (1986) identified as Wet Montane, broadly synonymous with the popular, nontechnical term "cloud forest." Such a broad distribution for a single species, assuming that we are correct in this interpretation, contrasts with the usual pattern documented for other Andean organisms, which generally exhibit more restricted ranges within this ecogeographic region. Allopatric re-

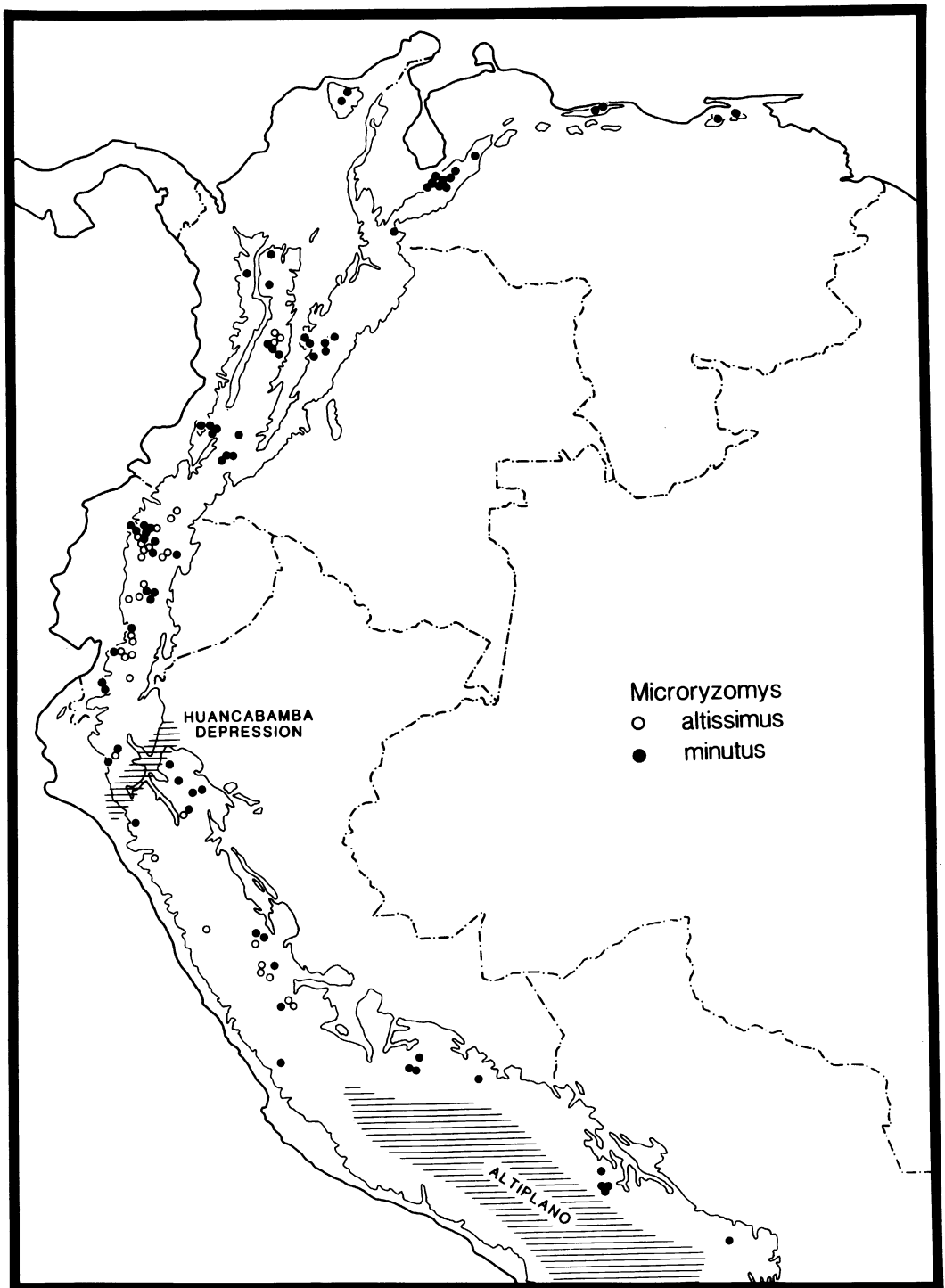


Fig. 34. Geographic distribution of species of *Microryzomys* in relation to the 1000-meter contour line of the Andes and Caribbean Coastal Ranges. The region of the Huancabamba Depression and general limits of the Altiplano (after Simpson, 1975) are indicated by cross-hatching (see text for discussion).

placement of closely related species endemic to specific mountain systems is more often the case (Lynch, 1986; Simpson, 1975, 1986; Vuilleumier, 1986), although the distributions of some bats of the genera *Sturnira* and *Vampyrops* nearly approach the geographic sweep of *Microryzomys minutus* (Koopman, 1982). The northern and central Andean occurrence of *minutus* is substantively delimited, but its southern reaches still require amplification. Current evidence suggests that the presence of *minutus* follows the flange of moist forest along the eastern flanks of the Cordillera Oriental from southern Peru into Bolivia, and it may occur farther south than presently documented.

Both species range on either side of the Huancabamba Depression in northwestern Peru, a zone of low mountain passes and arid inter-Andean valleys which demarcate the distributional limits of many other Andean organisms (Lynch, 1986; Parker et al., 1985; Simpson, 1975). The effectiveness of this area as a geographic barrier has been emphasized for animals living at high altitudes, particularly those restricted to humid montane forest and páramo. Yet neither *minutus* nor *altissimus* displays appreciable differentiation across this region, although the populations of each are likely disjunct there. In this regard, the distributional pattern of *Microryzomys* conforms to that of certain other Andean groups with species that occur in both the western and eastern cordilleras of Peru and extend north of the Huancabamba Depression into Ecuador (Simpson, 1975; Parker et al., 1985). If both species came to occupy their current distributions from more restricted ranges, then the presence of *minutus* on either side of the Depression can be readily accommodated since its populations occur broadly over middle Andean altitudes and a mosaic of forest communities; however, the presence of *altissimus*, a form confined to upper forest fringes and páramo, north and south of this barrier is more problematic. The apparent insignificance of this region with regard to *Microryzomys* biogeography and morphological divergence therefore suggests that the two species were already established and relatively widely distributed prior to the increasing aridity and fluvial dissection of the Huancabamba area.

Despite some past references associating *Microryzomys* and puna habitat, neither species is known to penetrate that vegetational zone as it is conventionally recognized in the central and southern Andes (e.g., by Simpson, 1975). As Pearson (1951) and Reig (1986) have remarked, Osgood (e.g., 1933) loosely used the term "puna" to identify the belt of open Andean habitats above timberline. Reig's (1986: 413, table 16-3) reference to *Microryzomys minutus* living in puna sites is evidently in error, for the source cited (Thomas, 1926a) contains a locality record in Departamento Junín at 2600 m, not Cuzco at 4200 m. Furthermore, more extensive surveys of mammals inhabiting the Altiplano of southern Peru and its western slopes have not uncovered *Microryzomys* as a constituent member of this faunal region (Dorst, 1958; Pearson, 1951; Pearson and Ralph, 1978). Instead, the southern geographic range of *Microryzomys* seems to adhere to very moist forests, which in some sectors extend above 3500 m, of Amazonian-facing slopes (Cordilleras Oriental, Vilcabamba, Real), thereby skirting the eastern reaches of the Altiplano and true puna (fig. 34).

The distributional pattern and oryzomyine affinity of *Microryzomys* are consistent with Reig's (1986) perception of northern versus southern foci of evolutionary differentiation for several of the larger tribes of Sigmodontinae. Namely, the phyletic diversification of oryzomyines (including thomasomyines) generally corresponded with the uplift and formation of northern Andean montane forest and páramo; whereas, the radiation of phyllotine and akodontine rodents was principally connected with orogenic processes that created southern Andean highlands and the puna biome. Compared to puna, páramo comprises largely unexploited habitats as far as mammals are concerned perhaps due to the newness of its formation, a contrast noted by Hershkovitz (1972) and developed more thoroughly by Reig (1986) for Rodentia. Although rigorous comparisons of the level of endemism and diversification within these morphoclimatic realms must await much needed specific and generic revisions of many sigmodontine rodents, the distinction, as a generality, seems well drawn. In particular, the exploitation of páramo vegetation as a

dietary resource seems not to have occurred to the extent observed in the puna. Many of the phyllotine genera endemic to the Altiplano (*Andinomys*, *Chinchillula*, *Galenomys*, *Punomys*), or common there (*Neotomys*, *Phyllotis*), possess strikingly hypsodont dentitions and remodeled cranial architectures that suggest adaptation for largely herbivorous food habits (Hershkovitz, 1962). Such modifications are lacking among the fewer sigmodontine species restricted to true páramo, with the possible exception of *Sigmodon inopinatus* in the high Andes of Ecuador.

We close this essay by again stressing that the fragmented condition of so many crania and the consequent insufficiency of our samples from broad areas of *Microryzomys* dis-

tribution have disallowed a more rigorous assessment of populational differentiation and its correspondence to Andean geography. With this weakness in our data, the species taxonomy presented must be considered a rough framework from which to pursue more detailed analyses of variation using better samples drawn from critical regions and using other kinds of data. In view of the complex and dynamic nature of Andean geology and its biota, *Microryzomys* potentially offers an exciting biological system, with a reasonable chronological framework, for studies of morphologic and genic differentiation, both between the two (or more?) species and among populations of each separated to varying degrees by topography, altitude, and ecology.

TAXONOMIC SUMMARY

Microryzomys Thomas

Oryzomys (*Microryzomys*) Thomas, 1917c: 1 (type species, *Hesperomys minutus* Tomes, 1860).

Thallomyscus Thomas, 1926b: 613 (type species, *Thallomyscus dryas* Thomas, 1898).

EMENDED DIAGNOSIS: A genus of sigmodontine rodent characterized by the following combination of traits—soft and luxuriant fur, small body size with tail notably longer than head and body, hind feet short and slender with six fleshy plantar pads, hypothenar pad large and oblong; skull delicately built having a short, attenuate rostrum, hourglass-shaped interorbit and smooth, rounded braincase devoid of ridges; foramen magnum directed posteroventrad; zygomatic arches parallel-sided and only slightly broader than braincase, jugal reduced or absent; zygomatic notch rudimentary and zygomatic plate narrow, its leading edge not reaching the nasolacrimal capsules; bony palate only slightly extended beyond end of third molars, posterolateral palatal pits simple; stapedia foramen present and large, posterior opening of alisphenoid canal large, and squamosal-alisphenoid groove leading to sphenofrontal foramen present (primitive cephalic arterial supply); alisphenoid strut absent; incisors narrow, asulcate, and typically orthodont; molar teeth diminutive, crowns brachyodont with labial and lingual folds broad and open on margins,

each upper molar anchored by three roots and each lower two; anterocone (id) strongly bifurcated and wide, giving rectangular shape to the first molars; anteroloph (id) usually distinct, mesoloph (id) present, metacone (entoconid) linked to posteroloph (id) instead of middle of hypocone (id), anterolabial cingulum present on lower third molar.

CONTENTS: Two species are recognized, *M. minutus* (Tomes, 1860) and *M. altissimus* Osgood, 1933.

Microryzomys minutus (Tomes)

Hesperomys minutus Tomes, 1860: 215 (type locality, Ecuador, probably near Pallatanga; holotype, BMNH 7.1.1.112).

Oryzomys dryas Thomas, 1898: 267 (type locality, near Pallatanga, Ecuador; holotype, BMNH 59.11.1.11).

Oryzomys dryas humilior Thomas, 1898: 268 (type locality, plains of Bogotá, 8750 ft, Colombia; holotype, BMNH 98.7.3.3).

Oryzomys (*Oligoryzomys*) *fulvirostris* Allen, 1912: 86 (type locality, Munchique, 8325 ft, Colombia; holotype, AMNH 32567).

Oryzomys (*Microryzomys*) *aurillus* Thomas, 1917c: 1 (type locality, Torontoy, Peru; holotype, USNM 194795).

EMENDED DIAGNOSIS: A species of *Microryzomys* characterized by the prevalence of ochraceous-tawny pelage tones, faint or no contrast of dorsal from ventral body fur, tail

basically monocolored and usually longer than 110 mm, and dusky markings on tops of fore and hind feet; hind feet slightly wider and plantar pads more robust; skull more delicate with narrower braincase, shorter and ovate incisive foramina, and shorter tooth-row (usually less than 3.0 mm); dentary with distinct incisor tubercle.

DISTRIBUTION: Lower montane to subalpine wet forests and páramo fringes of the Caribbean Coastal Ranges and Merida Andes of Venezuela; Sierra Nevada de Santa Marta, Cordilleras Oriental, Central, and Occidental of Colombia; Cordilleras Oriental and Occidental of Ecuador; Cordillera Occidental of northwestern Peru; Cordillera Oriental and its eastern flanks of Peru into westcentral Bolivia; excluding the Altiplano region and coastal ranges of southwestern Peru. Known altitudinal occurrence from 800 to 4265 m, over 80 percent of the collecting localities from 2000 to 3500 m.

SPECIMENS EXAMINED: 642, as listed below.

BOLIVIA: *Departamento Santa Cruz*, Siberia, 25 km (by road) W Comarapa, 2800 m (UMMZ 155892, 156216–28); 30 km (by road) W Comarapa, 2800 m (AMNH 260419). *Departamento La Paz*, 15 km (by road) NE Unduavi, 2400 m (UMMZ 156210); Río Aceramarca, 10,800 ft (AMNH 72733); Río Aceramarca, 1 km S Yerbani, 2600 m (UMMZ 156211–5); 30 km (by road) N Zongo, 2000 m (UMMZ 156209); Nequejahuirá, near Pongo, 8000 ft (AMNH 72723).

PERU: *Departamento Cuzco*, Marcapata, Amacho, 2750 and 3350 m (FMNH 75226–7, 75334–46, 75581, 78722–7); Marcapata, Limacpunco, 2400 m (FMNH 75333); 1 km below Marcapata, 9000 ft (LSU 19287–94); Torontoy, 9500–14,000 ft (BMNH 22.1.1.42–5; USNM 194795, 194867–8, 194870); Machu Picchu, 12,000 ft (USNM 194872); Occabamba Valley, Tocopuquen, 9100 ft (BMNH 22.1.1.46–7; USNM 194874, 194877, 194879). *Departamento Ayacucho*, Puncu, 30 km NE Tambo, 3370 m (LSU 15700). *Departamento Junín*, Province Tarma, 22 mi E Tarma, 7300 ft (AMNH 231036, 231038, 231041, 231070, 231093); Yano Mayo, Río Tarma, 8500 ft (BMNH 26.2.1.12–5). *Departamento Pasco*, Acobamba, 45 mi NE of Cerro, 8000 ft (BMNH 27.11.1.120–1). *Departamento Huánuco*, Huánuco,

10,500–12,200 ft (FMNH 23692–8, 23700–16); trail to Hacienda Paty, below Carpisah Pass, 7100 ft (LSU 19286); Bosque Cutirragra, S Huaylaspampa, 9000 ft (LSU 18439). *Departamento Amazonas*, Tambo Jenés, 12,000 ft (BMNH 26.4.1.32–4); 10 mi E Molinopampa (FMNH 19772–7); Tambo Ventilla, 8150 ft (BMNH 26.5.3.68); Uchco, Tambo Almirante, 5000 ft (FMNH 19785); 6 km (by road) SW Lake Pomacochas, 6000 ft (LSU 19264); San Pedro, 8600–9400 ft (AMNH 73207); Cordillera Colán, northeast of La Peca, 10,700 ft (LSU 21872). *Departamento Cajamarca*, Taulís, 8850 ft (AMNH 73152). *Departamento Piura*, 15 km (by road) E Chanchaque, 5700 ft (LSU 19261, 19263, 20312); Cerro Chinguela, 5 km NE Zapalache, 2700 m (LSU 26972–3, 27120); above Machete on Zapalache-Carmen trail, 2200 m (LSU 26959–61, 27119); Batán, on Zapalache-Carmen trail, 2250 m (LSU 26962–71).

ECUADOR: *Provincia El Oro*, Taraguacocha, Cordillera de Chilla, 9750 ft (AMNH 47602); El Chiral, 5350 ft (AMNH 47626). *Provincia Azuay*, Bestion, 10,100 ft (AMNH 47622–3); Molleturo, 7600 ft (AMNH 61914–5); Cuenca, El Cajas, Saraicho Valley, Lake Llaviuco, 3100 m (BMNH 82.731, 84.311). *Provincia Cañar*, San Antonio, N of Cañar and S of Tambo, 6727 ft (AMNH 67553, 67561–6); Chical, Naupan Mountains, 10,000 ft (AMNH 63032–4, 63037). *Provincia Chimborazo*, Paujchi, near Huigra (AMNH 63071); Pallatanga (BMNH 59.11.1.11, 7.1.1.112). *Provincia Tungurahua*, Páramo de Mount Tungurahua, 3500 m (FMNH 47598); San Francisco, east of Ambato, 8000 ft (AMNH 63385–6, 67549–50, 67552, 67555, 67558–9); Baños (FMNH 47597); San Rafael, 9000 ft (AMNH 66527–33). *Provincia Napo*, Oriente, Río Cosanga, 900 m (MCZ 37918–9); Baeza, 6500 ft (BMNH 15.7.12.7); Baeza arriba (AMNH 63845); Papallacta, 11,000 ft (AMNH 46804; BMNH 34.9.10.125); near Papallacta, 10,480 ft (AMNH 248278); Río Papallacta Valley, 11,100 ft (UMMZ 155679, 155801); 1.4 km (by road) E Papallacta, 9980 ft (UMMZ 155797); 1.6 km E Papallacta, 10,250 ft (UMMZ 127126); 6.2 km W Papallacta 11,700 ft (UMMZ 155678). *Provincia Pichincha*, Santa Rosa via Mindo, 1800 m (FMNH 93142); Santa Rosa, 9600 ft (AMNH

66585, 66587–97); Pelagallo, S of Nanegal and N of Catacoli (AMNH 46806); Gualea, Ilambo Valley, 1800 m (FMNH 95001, 95081); west of Gualea, 1300 m (FMNH 53285); Gualea, road to, 4000 ft (AMNH 46808, 47011); Machángara, Río Machángara, 8200–8500 ft (AMNH 46779, 47010); Tumbaco, 7000 ft (BMNH 98.9.4.3–4, 98.10.26.6); Canyon de Río Pita, 9700 ft (AMNH 66570–4); Pintag, above Chillo, 10,000 ft (BMNH 98.5.1.6); Perucho, 7000 ft (BMNH 98.9.4.6, 98.10.26.5); Guailabamba, Perucho, 6500 ft (AMNH 46781); Pichincha, 11,200–12,500 ft (BMNH 34.9.10.124, 34.9.10.126, 34.9.10.220, 34.9.10.285, 54.461; FMNH 53280); Pichincha, 10,790 ft (UMMZ 127127); Pichincha, eastern slopes, 3700–3800 m (FMNH 92009); San Ignacio, Pichincha, 11,150 ft (AMNH 66548–51, 66556–9, 66561, 66563–5, 66567); Santo Domingo Trail, forest northwest of Corazón (AMNH 66534–8); Old Santo Domingo Trail 7000–8750 ft (UMMZ 127128–9, 155803–4); Cerro Verde Cocha-west, 3100 m (FMNH 53279); Guaramos-west, 2000 m (FMNH 53281–3); Pacto, 1400 m (FMNH 53284); Mojanda Mountains, Cochasqui, 11,000 ft (AMNH 47007); San Fadeo-west, 1700 m (FMNH 53278). *Provincia Carchi*, Montufar, near San Gabriel, Hacienda Indujel del Vinculo, 2900 m (UMMZ 77216–7).

COLOMBIA: *Departamento Huila*, San Agustín, Santa Marta, 2700 m (FMNH 71956–8); Valle de Las Papas, Central Andes, 10,000 ft (AMNH 33872–3); San Agustín, San Antonio, 2200–2350 m (FMNH 71948–53, 71961–6); San Agustín, Las Bardas, 3100 m (FMNH 71960); San Agustín, Río Magdalena, 2350 m (FMNH 71959); San Agustín, Río Ovejeras, 2350 m (FMNH 71954). *Departamento Cauca*, Gallera, northwest of Popayán, 5700 ft (AMNH 32605); Munchique, 8325 ft (AMNH 32567, 181449); Cerro Munchique, 1500–2500 m (FMNH 86868–70, 89288–90, 89292, 89295–6; USNM 303845–9); Coastal Range west of Popayán, 10,340 ft (AMNH 32621); Charguayaco, 2200 m (AMNH 181456); Sabanetas, 2000 m (FMNH 89284, 89287, 89289); Río Mchengué, 800 m (FMNH 90275–9); Gabriel López, 3000 m (FMNH 89298); no locality (AMNH 32927). *Departamento Cundina-*

marca, San Cristóbal, Bogotá region, 2900 m (FMNH 71986–8, 72007–8); Bogotá, 2700–3500 m (FMNH 71978, 71980–2; BMNH 98.7.3.3, 99.10.3.31–3); Fusagasugá (BMNH 32.7.14.20); El Roble, 7200 ft (AMNH 32918); Boquerón, San Francisco, 3000 m (FMNH 71983–5, 72006); Laguna del Verjon, (AMNH 62775–6); Guasca, Río Balcones (FMNH 71990–2, 72009–10); San Juan de Río seco (AMNH 71348, 71366); Quipile (AMNH 71349). *Departamento Tolima*, Río Toche, 6800 ft (AMNH 32906–10, 32912–3, 32915, 32926; BMNH 13.5.27.24); Río Termes, 3200 m (FMNH 72004). *Departamento Quindío*, Salento, 7000 ft (AMNH 32923–4); La Guneta, 10,300 ft (AMNH 32919; BMNH 13.5.27.23). *Departamento Antioquia*, Las Palmas, SW Medellín, 2600 m (FMNH 70542, 70547–8); 1 mi NW Las Palmas, 8000 ft (AMNH 149277); Urrao, Santa Barbara, 2700–2800 m (FMNH 71935–36, 71941–3, 72005); Urrao, Guapanal, 2200 m (FMNH 71932–4); Urrao, Páramo Frontino, 3300 and 3500 m (FMNH 71920–31, 71997–2003); Urrao, Río Ana, 2200 m (FMNH 71937); Urrao, Río Urrao, 2200 and 2400 m (FMNH 71938–40); Valdivia, Ventanas, 3000 m (FMNH 70541). *Departamento Magdalena*, Sierra Nevada, near Mamanacarna, 3300–3600 m (FMNH 69217–8); Macotama, 8000 ft (AMNH 38927–32; BMNH 9.4.15.7; MCZ 8232–4, 8240–1, 8254; USNM 85540); El Mamón, 9000 ft (MCZ 8321).

VENEZUELA: *Estado Tachira*, Buena Vista, near Páramo de Tama, 41 km SW San Cristóbal, 2350–2420 m (USNM 442200–34, 456331–2). *Estado Mérida*, Páramo Tambor, 8000 ft (FMNH 22113–5, 22122, 22134–5); El Tambor, 8800 ft (AMNH 96164–5); La Carbonera, 12 km SE La Azulita, 2180 m (USNM 387902–6); Sierra de Mérida (FMNH 22112); Culata, 3000 m (BMNH 5.2.5.16); Santa Rosa, 1–2 km N Mérida, 1870–2055 m (USNM 387904–6); Nudo de Apartaderos, 4000 m (AMNH 131025); Páramo de los Conejos, 9600 ft (AMNH 96166–8); Río Mucujun (BMNH 29.3.17.50–1; FMNH 22096–7, 22099, 22101–11); vicinity of Lago Mucubaji, 7700 ft (UMMZ 156395–402); 4–9 km SE Tabay, 2127–3810 m (USNM 374364–5, 374369, 374372, 374375, 374377–8, 374380, 374382–4, 374386–90, 374392–4,

374396–8, 374402–3, 374405–7, 374410–1, 374414–27, 374429, 374431–2, 374434–6, 374438, 374442, 374446–8, 374452–5, 374457, 374459–63, 374466–8, 374471, 374474–5, 374479–82, 374484–5, 374489–90, 374492–4, 374496, 374500, 374502–3, 374506, 374508–11, 374514–5, 374517, 374519, 374521, 387891–6, 387899–901); Paramito, 3–4 km W Timotes, 3050–3345 m (USNM 374340–8, 374350, 374353–4, 374356–60). *Estado Trujillo*, Hacienda Misísí 15 km E Trujillo, 2360 m (USNM 374331, 374333, 374338). *Estado Miranda/Distrito Federal*, Alto de No León, 33 km WSW Caracas, 1996 m (USNM 374329); Pico Avila, 5–6 km NNE Caracas, 2081–2241 m (USNM 371168–72, 371174–5, 372519, 372521–3). *Estado Sucre*, Cerro Negro, 10 km NW Caripe, 1630–1690 m (USNM 409914–5, 416698, 416701); Carapas, Turumiquire, 5600 and 7900 ft (AMNH 69894–6); Mount Turumiquire (FMNH 38057, 38059). *Estado indeterminate*, Deyrolle (FMNH 7046); Galipuis, 6000 ft (BMNH 14.7.27.7).

Microryzomys altissimus (Osgood)

Oryzomys (Microryzomys) minutus altissimus Osgood, 1933: 5 (type locality, La Quinua, mountains north of Cerro de Pasco, 11,600 ft, Peru; holotype, FMNH 24699).

Microryzomys altissimus hylaeus Hershkovitz, 1940: 81 (type locality, Atal, Hacienda Indujel del Vincula, near San Gabriel, Montufar, 2900 m, Carchi Province, Ecuador; holotype, UMMZ 77224).

Microryzomys altissimus chotanus Hershkovitz, 1940: 82 (type locality, southern slopes of Chota Valley, parish of Pimampiro, 2000 m, Imbabura Province, Ecuador; holotype, UMMZ 77222).

EMENDED DIAGNOSIS: A species of *Microryzomys* characterized by more buff in the upper body fur and grayish buff in the underparts such that the dorsum and venter are clearly demarcated, grayish head, tail bicolor and usually shorter than 110 mm, and tops of fore and hind paws whitish; hind feet and metatarsal pads narrower; skull slightly heavier with broader braincase, longer incisive foramina, and longer (usually greater than 3.0 mm), more robust toothrows; incisor tubercle of dentary small.

DISTRIBUTION: Páramo and assorted subalpine forest ecotones of the central and

northern Andes, including the Cordillera Central of central Colombia; Cordilleras Occidental and Oriental of Ecuador; Cordilleras Occidental and Oriental of northern Peru southward to the vicinity of Departamento Junín. Known altitudinal occurrence from 2000 to 4300 m, most collecting localities from 2500 to 4000 m.

SPECIMENS EXAMINED: 273, as listed below.

PERU: *Departamento Junín*, Province Tarma, 22 mi E Tarma, 7300 ft (AMNH 231035, 231055, 231064, 231068–9, 231071, 231073, 232630); Maraynioc, 45 mi NE Tarma, 12,000–13,000 ft (MCZ 38576–86); Ccorimachay Rockshelter (UMMZ 122632). *Departamento Pasco*, Chipa, 12,400 ft (AMNH 60577–9); La Quinua, mountains north of Cerro de Pasco, 11,600 ft (FMNH 24578–9, 24683, 24685–6, 24688–91, 24693–705; USNM 259586); Chiquirín, 11,200 ft (FMNH 27406–10, 27412; USNM 259587); Huariaca, 25 mi N Cerro de Pasco, 9000 ft (BMNH 27.11.1.109, 27.11.1.113). *Departamento Huánuco*, Huánuco, 10,500–12,200 ft (FMNH 23691, 23699). *Departamento Ancash*, Huarás, Tullparaju, 4300 m (FMNH 81432); Huarás, Quilcayhuanca, 4300 m (FMNH 81433–4); 4 mi S, 8 mi E Recuay, 12,500 m (MVZ 137924). *Departamento Libertad*, mountains northeast Otuzco, 10,000 ft (FMNH 19358–9). *Departamento Amazonas*, mountains east of Balsas, 10,000 ft (FMNH 19769–71). *Departamento Piura*, Huancabamba, 3000 m (FMNH 81439–41); 33 km (by road) SW Huancabamba, 10,000 ft (LSU 19257).

ECUADOR: *Provincia Azuay*, Bestion, 10,100 ft (AMNH 47613–21); Contrayerbas, El Cajas, 11,000 ft (AMNH 61916–21); Sinicay, 8300 ft (AMNH 61922); Cuenca, Lake Luspa, Las Cajas, 3700 m (BMNH 82.733–6, 82.739–49, 82.823, 84.316); Cuenca, El Cajas, Lake Llaviuco, Saraucho Valley, 3100 m (BMNH 82.729, 84.301); Cuenca, Chaudiurcu, near Angas, 3750 m (BMNH 84.312–4); Cuenca, Lake Torreadora, El Cajas, 4000 m (BMNH 82.732, 84.309–10, 84.317–8). *Provincia Cañar*, San Antonio, N of Cañar and S of Tambo, 11,000 ft (AMNH 63051–5, 63057–64, 63074–6); Pinangu, 10,000 ft (AMNH 63043–50); Chical, Naupan Mountains, 10,000 ft (AMNH 63031, 63035–6, 63578). *Provincia Chimborazo*, Urbina and

Cochaseca (AMNH 63040-2, 66540). *Provincia Tungurahua*, San Francisco, east of Ambato, 8000 ft (AMNH 67560). *Provincia Bolívar*, Sinche, 11,100 ft (AMNH 66897-9); Sinche, Guaranda, 4000 m (BMNH 99.9.9.30). *Provincia Napo*, Papallacta, 11,000-12,000 ft (AMNH 47068-9, 47071); near Papallacta, 10,480 ft (AMNH 248277, 248279; UMMZ 127125); 6.2-10.6 km W Papallacta, 11,700-12,600 ft (UMMZ 155672-7, 155798-9, 155802); 6.9 km (by road) W Papallacta, 12,020 ft (AMNH 248280, 248497); Antisana, páramo on southern slope, 13,500 ft (MSU 3705). *Provincia Pichincha*, Cerro Corazón, 11,000 ft (AMNH 47017-8); Páramo north of Corazón, 11,500 ft (AMNH 66598-66600, 66604); Quito, 9400-10,000 ft (AMNH 46880, 47025-6, 47031, 47033-7, 47039, 47042, 47055, 47057); 15 km S Quito, 10,000 ft (AMNH 213549); Chillo, near Río Pita, 9000-11,000 ft (AMNH 47046-53, 47056); Canyon de Río Pita, 9700 ft (AMNH 66575-6, 66569); Santa Rosa, 9600 ft (AMNH 66586, 66605-7); Upper Río Pita, (AMNH 66539); Guápulo, 8800 and 9200 ft (AMNH 47027, 47032); Pichincha, San Ignacio, 11,150 ft (AMNH 46638, 47059, 47061-4, 47066, 66545-7, 66552-5, 66560, 66562, 66566, 66568, 66608-9); Pichincha, 9500-10,500 ft, (BMNH 98.5.1.7-8, 98.9.4.5, 34.9.10.218-9); Pichincha, Pichan, 3500 m (BMNH 54.460); Chaupicruz (AMNH 47022); Pichincha, Volcan, 3300 m (BMNH 54.462); Pichincha, eastern slopes, 3700-3800 m (FMNH 92008); Pichincha, Hacienda Garzón, 10,500 and 12,000 ft, (ANSP 12688-91, 12693); Antisana and Antisanilla, 11,500-13,600 ft (AMNH 66577-82, 66584); Mojanda Mountains, Piganta, 7500 ft (AMNH 47019); Mojanda Mountains, 10,000 ft (AMNH 46862). *Provincia Imbabura*, Pimampiro, southern slopes of the Chota Valley, 2000 m (UMMZ 77222). *Provincia Carchi*, Montufar, near San Gabriel, Hacienda Indujel del Vinculo, 2900 m (UMMZ 77223-4).

COLOMBIA: *Departamento Quindío*, Finca La Cubierta, 6 km north of Salento-Cocora road, 3670 m (UVB 3363-5). Border of *Departamentos Tolima* and *Caldas*, Páramo del Ruiz, 3300-4000 m (FMNH 71904-6, 71912-5); Tabacal del Ruiz, 3400-3600 m

(FMNH 71903, 71908-11, 71917-8). *Departamento Tolima*, Río Termales, 3500 m (FMNH 71907, 71916).

Oligoryzomys Bangs

Oryzomys (*Oligoryzomys*) Bangs, 1900: 94 (type species, *Oryzomys navus* Bangs, 1900).

EMENDED DIAGNOSIS: A genus of sigmodontine rodent characterized by the following combination of traits—small body size, tail longer than head and body, and short and broad hind feet; plantar tubercles six but smaller than in *Microryzomys*, not so fleshy, hypothenar pad small and round not oblong; skull small but with stout appearance, rostrum relatively broad and stocky, interorbit hourglass-shaped with squared edges; braincase more elongate and smooth, dorsal profile flatter than in *Microryzomys* with foramen magnum directed posteriorly; zygomatic arches bowed laterad, jugal reduced or absent; zygomatic notches distinct, zygomatic plates broad such that the anterior edge reaches the nasolacrimal capsules; stapedia foramen large, posterior opening of alisphenoid canal large, squamosal-alisphenoid groove and sphenofrontal foramen absent (derived cephalic arterial supply); incisors opisthodont, asulcate; molars brachyodont, cuspidate, uppers with three roots each and lowers two roots each; first molars ovate, anterocone (id) narrower than in *Microryzomys*, antero-medial flexus (id) shallow, anterolabial and anterolingual conules (ids) smaller and set closer together; anteroloph and mesoloph (id) present, metacone (entoconid) linked to posteroloph (id) instead of middle of hypocone (id); anterolabial cingulum well developed on lower third molar.

CONTENTS: The species diversity within *Oligoryzomys* requires much needed substantiation based on detailed, regionally focused, revisions. Tate (1932e) listed approximately 30 nominal species, many of them known from a single locality or from one to a few specimens. At the other extreme, Hershkovitz (1966a: 137) seemed to imply that most South American forms are geographic races of *nigripes* and that *fulvescens* may even qualify as a Central American subspecies of it. That supposition severely underestimates the diversity within *Oligo-*

ryzomys, for recent regional investigations have repeatedly documented the sympatric or parapatric occurrence of three to four species (Massoia, 1973; Myers and Carleton, 1981; Contreras and Berry, 1983; Olds and Anderson, 1987). Authors of faunal accounts have recognized a dozen species more or less (Cabrera, 1961; Honacki et al., 1982; Reig, 1986). Entangled with uncertainty over the number of valid species are issues of nomenclatural priority among geographic forms whose relationship has been inconsistently interpreted. Specific names such as *nigripes* and *longicaudatus* or *fulvescens* and *delicatus* often appear in the literature and in collections in reference to the same populations from the same place.

With this cautionary preamble, we tender the following list of species and stress its provisional nature. The species tentatively recognized herein stem not only from evaluation of the relevant literature but also from our examinations of all specimens of *Oligoryzomys* contained in AMNH and USNM, as well as selected series in other museums (CM, FMNH, LSU, MSU, MVZ). This approach does not meet the standards of a sound revision but does enhance our systematic interpretations beyond the information currently available in the literature.

We discuss the species diversity within *Oligoryzomys* under five subsections: the *fulvescens* Group, the *microtis* Group, the *andinus* Group, the *flavescens* Group, and the *nigripes* Group. Broad distributional boundaries are outlined for each species, usually referenced by publications or specimen numbers to document its occurrence in a particular region. Probable synonymies are provided for most South American forms; however, readers are referred to Hall (1981) for the many synonyms and subspecies recognized under Central American *O. fulvescens* and to Cabrera (1961) for those associated with Andean *O. longicaudatus*. The information presented here should be considered a series of hypotheses that can eventually be tested by rigorous inquiry into the systematics of *Oligoryzomys*.

FULVESCENS GROUP
Oligoryzomys fulvescens

DISTRIBUTION: Mexico, Central America, and northern South America. The range in

Mexico and Central America, as outlined by Hall (1981: 621), encompasses eastern and western Mexico as two coastal arms that join in eastern Oaxaca and Veracruz and extends to the Canal Zone in Panama. In northern South America, the species is distributed throughout the western, central, and eastern cordilleras of Colombia, into the mountains of eastern and northern Venezuela, and eastward to the island of Trinidad. To the southeast, *O. fulvescens* occurs in savannas and along the base of the tepuis in eastern Venezuela, nearby Brazil (Mount Roraima), southern Guyana (Kanuku Mountains), and throughout Surinam (Husson, 1978). To the southwest, *O. fulvescens* ranges into eastern Andean foothills in Napo Province, Ecuador, near the Colombian border (KU 112879, Santa Cecilia, 340 m, 00°03'N/76°58'W) and down western Andean foothills and Pacific lowlands to the coastal plain of southwestern Ecuador (AMNH 61309, Santa Rosa, 100 m, 03°27'S/79°58'W). Altitudinal occurrence is from near sea level to above 3000 m. Based on current evidence, *Oligoryzomys fulvescens* does not occur east of Surinam or south of the Río Negro, Río Amazonas, and Río Napo. Nor is it known to inhabit the strip of wet forest along the Pacific lowlands and adjacent Andean foothills from northern Ecuador and Colombia (the Choco), northward through Panama and Costa Rica, to eastern Nicaragua and Honduras.

SCIENTIFIC NAMES: Names, authors, and dates of publication that apply to Mexican and Central American *O. fulvescens* are listed by Hall (1981). We associate the following names with South American samples of the species: *delicatus* Allen and Chapman (1897); *navus* Bangs (1900); *messorius* Thomas (1901b); *tenuipes* Allen (1904); *munchiquensis* Allen (1912); and *griseolus* Osgood (1912).

Oligoryzomys arenalis

DISTRIBUTION: Known from the arid and semiarid coastal plain of Peru where it has been reported from the departments of Lambayeque (Thomas, 1913) and La Libertad (Osgood, 1914) in the north. Specimens that we have identified as *O. arenalis* document its range along the coastal plain of southern Peru, near Matarani, Departamento Arequipa (MVZ 150165–6). From the Pacific coastal plain, *O. arenalis* extends inland to the west-

ern Andean slopes (1500 to 2150 m) of northwestern Peru in the departments of Piura (AMNH 63712; LSU 19256, 19258–9, 19262; USNM 304519, 304521–2, 551642) and Cajamarca (MVZ 137918–9), and occurs in the high northern Peruvian inter-Andean valleys (1950 to 2850 m) near Chachapoyas, Departamento Amazonas (AMNH 73204–6, 73208–10). The distributional limits of *O. arenalis* and the level of its relationship to *O. fulvescens* are unknown.

SCIENTIFIC NAMES: Described by Thomas (1913), *O. arenalis* is the only name that has been applied to samples from this region.

Oligoryzomys vegetus

DISTRIBUTION: Known only from highlands between 1200 and 1500 m in northwestern Panama; possibly occurs in nearby Costa Rica.

SCIENTIFIC NAMES: Bangs (1902) described the species and no other names have been applied to it.

MICROTIS GROUP

Oligoryzomys microtis

DISTRIBUTION: The known range extends as a belt across northern Brazil and Peru south of the Río Amazonas, from near Belem (Capim) in the northeast (reported as *O. delicatus* by Pine, 1973) to the south side of the Río Curary where it joins the Río Napo in northern Loreto Province, Peru (AMNH 71505–14). South of the Río Curary, *O. microtis* inhabits the eastern Andean foothills of Peru (including LSU 16695–6, 16699 from Departamento Ayacucho, and LSU 14360, MVZ 136581, 136594, 136596–8, 136600, 136602–4, 136606–8, 136610–12, 136615 from Departamento Loreto, which Gardner and Patton, 1976, listed as *O. longicaudatus*); of Bolivia east to the lowlands of northern Bolivia (Olds and Anderson, 1987); and the adjacent segment of Mato Grosso (Utiarity, AMNH 37159, 37542). The species continues south through eastern Bolivia and nearby Mato Grosso (Alho et al., 1986, as *O. fornesi*) to the eastern parts of the Argentine provinces of Formosa (Massoia, 1973, as *O. fornesi*) and Chaco (Contreras and Berry, 1983, as *O. fornesi*) and to northeastern Corrientes Province (Contreras, 1982, as *O. fornesi*). The eastern distributional limits of *O. microtis* in

south-central Brazil are unknown. It does occur as far east as Anapolis in Estado Goiás (AMNH 202664), and Mares et al. (1989) recorded it (as *O. fornesi*) from south of Brasília in the Federal District. Myers and Carleton (1981) erroneously included samples from eastern Brazil (Sao Paulo and Minas Gerais) under the name *fornesi*, but we allocate those specimens to either *O. eliurus*, *O. flavescens*, or a population related to the latter. Most samples of *O. microtis* have been collected at localities below 500 m elevation. Even along the eastern foothills of the Andes, specimens are not known from localities above 725 m in Peru (AMNH 231002, 231016, 231048, 231066, 231078–9, 231089–90, 231096) or above 640 m in Bolivia (Olds and Anderson, 1987—their record of *O. microtis*, AMNH 72700, from Ticunhuaya, La Paz, at 4800 ft is a juvenile *O. destructor*).

SCIENTIFIC NAMES: Allen (1916b) gave the name *microtis* to eight specimens collected along the lower reaches of the Río Solimoes, about 50 mi above its confluence with the Río Negro. It is the oldest name available for the species otherwise designated as *matto-grossae* Allen (1916b), *chaparensis* Osgood (1916), and *fornesi* (Massoia, 1973).

ANDINUS GROUP

Oligoryzomys andinus

DISTRIBUTION: Peruvian and Bolivian Andes. Formerly known only from the holotype collected at 1830 m on the semiarid western slope of the Peruvian Andes in Departamento La Libertad (Osgood, 1914), the distribution of *O. andinus*, as determined by our identifications, extends north of La Libertad to 2135 m in Departamento Lambayeque (Porcula Pass, MVZ 137920) and south of La Libertad along the western flanks of the Andes in Peru to the departments of Ancash between 2750 and 3950 m (E Pariacoto, MVZ 135651–4; vicinity of Huaras, MVZ 135648–50; near Yupash, MVZ 139216–8) and Lima between 2750 and 3650 m (W Casapalca, AMNH 213675, 230982–92; Colcabamba, MVZ 121156; Zarate, MVZ 119921; San Mateo, MVZ 119920; below Huaros, MVZ 119911; E Yaugas, MVZ 141302). Farther south, the range includes the Andes of Bolivia in the departments of Oruro at 3730 m (near Huancarama, on the altiplano, AMNH

26405–6) and Potosi at 3370 m (SE Pocoata, AMNH 255946—identified as *O. longicaudatus* by Olds and Anderson, 1987). Although most records are from Pacific flanks of the Andes and on the western puna of Peru and altiplano of Bolivia, there is a sample from the eastern Peruvian Andes in Departamento Cuzco at 1700 m (94 km W Cuzco, LSU 19253–5). Geographic and altitudinal limits of *O. andinus* are unknown but its documented distribution is complementary to that of *O. chacoensis*.

SCIENTIFIC NAMES: No other names have apparently been tied to the species.

Oligoryzomys chacoensis

DISTRIBUTION: Caatinga, cerrado, chaco, and relatively dry forests of Brazil, Paraguay, Argentina, and Bolivia. The most northern records are from caatinga habitats in the states of Ceara (Santanopole, Sitio Cancao, USNM 304583) and Pernambuco (Exu, USNM 528416) of northeastern Brazil. Other distributional records cluster in and around the chaco: southwestern Mato Grosso (Myers and Carleton, 1981); Paraguay west of the Río Paraguay (Myers and Carleton, 1981); the chaco of southeastern Bolivia and Andean foothills of southern Bolivia (Olds and Anderson, 1987—including MVZ 119918 from NW Tarija and USNM 271411–2 and 271432 from Entre Ríos, which they listed as *O. longicaudatus*); and the northern Argentine provinces of Jujuy (Olds and Anderson, 1987; also CM 43843–7, 43849), Formosa, Chaco (Myers and Carleton, 1981; Contreras and Berry, 1983), and Salta (CM 43857, 43860–2, 43864–6, 43868–82, 43884–5, 43887–93, 43941, 43943, 86605—reported as *O. nigripes* by Mares et al., 1981). Known altitudinal occurrences range between 200 and 1800 m.

SCIENTIFIC NAMES: The species was described by Myers and Carleton in 1981. The level of its differentiation from *O. andinus* requires evaluation.

FLAVESCENS GROUP

Oligoryzomys flavescens

DISTRIBUTION: Brazil, Uruguay, and Argentina. Our most northern locality record is from Minas Gerais in eastern Brazil (Parque

Nacional de Serra de Canastra, MSU 27302, 29254). From there, the range extends southward through Sao Paulo (Vieira, 1953; Myers and Carleton, 1981, as *O. fornesi*) and Río Grande do Sul of Brazil, to Uruguay (Langguth, 1963; Barlow, 1969) and Argentina. In Argentina, specimens and reliable literature reports document the occurrence of the species in the provinces of Misiones (Massoia et al., 1987), Chaco (Contreras and Berry, 1983), Salta (CM 43859, 43883, 43886, 43942, 86604—reported as *O. nigripes* by Mares et al., 1981), Tucuman (Myers and Carleton, 1981; de Fonollat, 1984), Mendoza, Cordoba, San Luis, and Buenos Aires (Contreras and Rosi, 1980; Myers and Carleton, 1981). In their guide to the mammals of Argentina, Olrog and Lucero (1981) delimited the southern extent of *O. flavescens* just north of Río Negro Province, but we have seen an adult (LSU 16882) taken in northwestern Chubut Province at Colonia Cushamen (42°12'S/70°50'W). The southern limit of *O. flavescens* in Argentina as well as its northern limit in eastern Brazil remain undefined. The known altitudinal range extends from near sea level to 2150 m.

SCIENTIFIC NAMES: Waterhouse described *flavescens* in 1837; *antoniae* Massoia (1979) and *occidentalis* Contreras and Rosi (1980) have been recognized as subspecies.

Oligoryzomys sp. A

DISTRIBUTION: Minas Gerais, eastern Brazil (Río Caparao, Serra do Caparao, 3000 ft; AMNH 80371, 80373–4, 91490, 91492).

Oligoryzomys sp. B

DISTRIBUTION: Bolivian and Peruvian Andes. Specimens we assign to this undescribed species are from the eastern puna and flanks of the Bolivian Andes between 2150 and 3650 m from as far south as Departamento Tarija (E Tarija, AMNH 262933–4), north through the departments of Santa Cruz (W Comarapa, MVZ 119917; AMNH 260396–403), Cochabamba (SE Epizana, AMNH 246726; El Choro, AMNH 119405; Incachaca, AMNH 35827–8, 35831–3, 35835–6, 35838, 35840, 35842; Parotani, AMNH 38543–4; E Totorá, MVZ 119916), and La Paz (Río Aceramarca, AMNH 72693–4; Pongo, AMNH 72702–3,

72706–14, 72726, 81283, 241612; Caracato, AMNH 248977–81; Tacacoma, AMNH 91540). Specimens from most of the above localities were identified as *O. longicaudatus* by Olds and Anderson (1987). In Peru, the species occurs in the eastern puna and Amazonian slopes of the Andes between 2250 and 3950 m from Puno in the south (W Yanahuaya, MVZ 172630; SW Ollachea, MVZ 172603–8; near Limbani, MVZ 116060, 116062, 116068–9), northward through Cuzco (NW Ollantaytambo, MVZ 173979–83; N Paucartambo, MVZ 115638–42, 115644, 115646–7, 171479–80; Cuzco, AMNH 38822) and Apurimac (NE Abancay, MVZ 173984), to Junín (N La Oroya, AMNH 231101–5, 231108–17, 231049–50, 231768, 231692, 231884, 213683–6). Records are also from the Pacific side of the southern Peruvian Andes between 3350 and 4175 m in the departments of Arequipa (S Callalli, MVZ 173978) and Ayacucho (near Puquio, MVZ 116012, 139219—identified as *O. longicaudatus* by Gardner and Patton, 1976; Tapuna Pass, AMNH 208095–6). Its distribution north of Departamento Junín in Peru and south of Departamento Tarija in southern Bolivia has yet to be determined. The geographic and altitudinal range of this form suggests that it is the Andean counterpart of *O. flavescens*.

Oligoryzomys sp. C

DISTRIBUTION: Altiplano of southern Peru in Departamento Puno (Purina, NW Tira-pata, 3940 m, MVZ 172600; NE San Antonio, 4000 m, MVZ 172601).

NIGRIPES GROUP *Oligoryzomys nigripes*

DISTRIBUTION: Paraguay east of the Paraguay River and the departments of Misiones, Formosa, and Chaco in northern Argentina (Myers and Carleton, 1981; Contreras and Berry, 1983). Throughout this region, the altitudinal range of the species is from 100 to 500 m. The relationship of *O. nigripes* to other species we refer to the *nigripes* group and the extent of its geographic distribution have yet to be determined. Mares et al. (1981) reported *O. nigripes* from Provincia Salta in northwestern Argentina, but their samples

consist of *O. flavescens* and *O. chacoensis* (see those accounts).

SCIENTIFIC NAMES: Myers and Carleton (1981) regarded *Mus nigripes* Olfers (1818) as the oldest available name for this species instead of *tarso nigro* Fischer (1814) as advocated by Langguth (1966), selected a neotype for *nigripes*, and fixed its type locality. Rengger's (1830) *longitarsus* may be a synonym (Cabrera, 1961).

Oligoryzomys eliurus

DISTRIBUTION: Central and eastern Brazil. The species has been recorded from the caatinga region in the states of Ceara and Pernambuco, northeastern Brazil (Mares et al., 1981; Streilen, 1982—these series may contain examples of *O. chacoensis*), and south through eastern Brazil to the states of Parana (Vieira, 1955; Mares et al., 1981; Myers and Carleton, 1981) and Santa Catarina (AMNH 75895). *Oligoryzomys eliurus*, sometimes classified under *O. nigripes*, is considered a common element of the Cerrado of central Brazil (Mares et al., 1985; Alho et al., 1986; Nitikman and Mares, 1987) and has been recorded from Estado Goias and from as far west as Utiariti in northern Mato Grosso (AMNH 37540–1) and as far south as Maracaju in southern Mato Grosso (AMNH 134541–6, 134551, 134833, 134838, 134900, 134902–3). The degree of isolation of this form from *O. nigripes* to the south and from *O. destructor* to the west, both of whose ranges it complements, requires investigation. The altitudinal range extends from about 100 to 1000 m.

SCIENTIFIC NAMES: Wagner described *eliurus* in 1845; *pygmaeus* Wagner (1845) and *utiaritensis* Allen (1916b) are possible synonyms.

Oligoryzomys destructor

DISTRIBUTION: Andes of southern Colombia, Ecuador, Peru, and Bolivia. As documented by specimens we examined, the northernmost record of *O. destructor* is at 1250 m on the Pacific slopes of the Andes in Departamento Narino, Colombia (Ricaurte, near the Ecuadorean border, AMNH 34223–4—identified as *munchiquensis* by Allen, 1916a). The species is found on both Ama-

zonian and Pacific slopes of the Ecuadorean Andes, including the provinces of Imbabura (near Intag, AMNH 46772, 46788–91, 47024), Pichincha (Gualea, AMNH 36279, 36298, 36305–8, 46770, 46772, 46774, 46800, 46992; Nanegal, AMNH 46766, 46792; Guapulo, AMNH 47058; Mojanda region, AMNH 46793–6, 46769, 46783, 47020, 47070; near Mount Illiniza, AMNH 46768), Chimborazo (San Antonio, AMNH 63056, 63065–6, 63978, 63314; Pauchi, AMNH 63067–70; Pallatanga, AMNH 61626–7), El Oro (Zaruma-Loja trail, AMNH 47625, 47845; Río Pindo, AMNH 47612; Pinas, AMNH 61356), Loja (Guainche, AMNH 61359–60; Celica, AMNH 47627; San Bartolo, AMNH 61357; Alamor, AMNH 47628, 61358; Loja, AMNH 213193), and Zamora-Chinchi (Zamora, AMNH 36564–5, 47624). The altitudinal range in Ecuador extends from 600 to 3350 m.

In Peru, *O. destructor* apparently occupies only the Amazonian drainage and eastern slopes of the Andes between 700 and 2750 m: from the northern department of Amazonas (near Lake Pomacochas, LSU 19265–8; Santa Rosa de Huayabamba, AMNH 11821/10113; Uscho, AMNH 73197–203; near Pomacochas, MVZ 135646–7); south through the departments of Huanuco (Cordillera Carpish, LSU 14361), Junín (NNE Palca, MVZ 172633–5; Valle del Perene, AMNH 61817; Utcuyacu, AMNH 63875, 63878; N La Merced, AMNH 231001; near San Ramon, many AMNH specimens; E Tarma, many AMNH specimens), Cuzco (Marcapata, LSU 19252; above Huyro, LSU 19285; San Luis, LSU 19284), Ayacucho (San Jose, LSU 16700; Huanhuachayo, LSU 16701, 16697; all recorded as *O. longicaudatus* by Gardner and Patton, 1976), and Apurimac (SSE Abancay, MVZ 115650); to Puno (W Yanahuaya, MVZ 172631–2; Sandia, MVZ 116070; near Limbani, MVZ 116063, 116065–7, 116643, 114631, 171510; NNE Ollachea, MVZ 172609–29).

In Bolivia, records of *O. destructor* are also restricted to the eastern flanks of the Andes, between 1450 and 3050 m: Departamento La Paz in the north (Cocapunco, AMNH 72644; Ticunhuaya, AMNH 72700; Okara, AMNH 72704–5; Sorata, AMNH 91536–9; Neque-

jahuira, AMNH 72722–3, 72725; Pitiguaya, AMNH 72716, 72729–31); south to the departments of Cochabamba (Incachaca, AMNH 38526, 38529–30, 38534–5, 38537, 38539, 38541), Santa Cruz (Vallegrande, USNM 290901–2), and Chuquisaca (Tola Orka, USNM 271588, 271590, 545229), the southernmost record of the species. All of these Bolivian specimens were recorded as *O. longicaudatus* by Olds and Anderson (1987).

SCIENTIFIC NAMES: We believe that *destructor* Tschudi (1844) is the oldest name available for these series. Other names that apply to the species are *melanostoma* Tschudi (1844), *stolzmanni* Thomas (1894), possibly *maranonicus* Osgood (1914), and *spodiurus* Hershkovitz (1940).

Oligoryzomys longicaudatus

DISTRIBUTION: Chile, from the province of Atacama in the north to Tierra del Fuego, and Argentina, from the northern province of Tucuman south along the eastern flanks of the Andes to Santa Cruz (Osgood, 1943; Greer, 1965; Mann, 1978; Olrog and Lucero, 1981; Pearson, 1983). The altitudinal range is from about 200 to 2000 m. Samples from the Andes of Bolivia and Peru have been traditionally identified as *O. longicaudatus* (Cabrera, 1961; Honacki et al., 1982; Olds and Anderson, 1987), but all specimens we have examined from these areas represent either *O. andinus*, *O. destructor*, or indeterminate species of the *O. flavescens* group; the latter two are sympatric at some places in both Peru and Bolivia. Although the systematic status and relationships of *longicaudatus* need much refinement, particularly with regard to *O. nigripes* and *O. destructor*, current evidence indicates that the form does not occur north of Chile and Argentina.

SCIENTIFIC NAMES: The epithets *longicaudatus*, *philippii*, and *magellanicus* are conventionally assigned to geographic segments in Chile and Argentina; authors and dates of publication of these names, along with others considered synonyms, are listed by Osgood (1943) and Cabrera (1961). Recently, Gallardo and Patterson (1985) suggested that *philippii* and *magellanicus* are separate species.

Oligoryzomys delticola

DISTRIBUTION: Uruguay (Langguth, 1963; Barlow, 1969; Ximenez et al., 1972), the adjoining regions of Provincia Corrientes in northeastern Argentina (Massoia, 1973) and of Estado Río Grande do Sul in Brazil (NW Alegrete, Candelaria, Quinta, Santa Maria; AMNH 235419–26, 235968–71, 235973), and islands in the Delta del Parana (Cabrera, 1961; Langguth, 1963; Olrog and Lucero,

1981). Primarily a lowland species, from sea level to about 500 m. Range limits are undetermined but as presently understood, it is allopatric to *O. eliurus* to the north, *O. nigripes* to the northwest, and *O. longicaudatus* to the south.

SCIENTIFIC NAMES: Described by Thomas in 1917a, no other names have been associated with the species.

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APPENDIX
Descriptive Statistics for
Selected Variables and OTUs of *Microryzomys*

Species and OTU	N	Mean	Range	SD
Head and Body Length				
<i>M. altissimus</i>				
Peru (OTU 1)	22	74.6	62–84	6.4
Ecuador (OTU 3)	11	77.8	66–84	5.4
Colombia (OTU 4)	15	80.6	73–89	4.7
<i>M. minutus</i>				
Peru (OTU 5)	21	77.9	62–94	6.7
Colombia (OTU 12)	29	80.6	67–92	6.3
Venezuela (OTU 14)	38	82.1	64–99	8.5
Tail Length				
<i>M. altissimus</i>				
Peru (OTU 1)	22	108.0	95–122	7.4
Ecuador (OTU 3)	11	99.6	94–107	3.8
Colombia (OTU 4)	15	105.8	100–112	3.6
<i>M. minutus</i>				
Peru (OTU 5)	21	114.9	98–133	9.7
Colombia (OTU 12)	29	117.6	99–128	7.2
Venezuela (OTU 14)	35	116.4	101–129	7.0
Hindfoot Length				
<i>M. altissimus</i>				
Peru (OTU 1)	22	21.4	18–23	1.6
Ecuador (OTU 3)	11	21.5	21–23	0.8
Colombia (OTU 4)	15	22.3	21–24	0.7
<i>M. minutus</i>				
Peru (OTU 5)	21	23.3	22–26	1.0
Colombia (OTU 12)	29	21.9	20–24	1.1
Venezuela (OTU 14)	38	21.9	20–24	1.0
Occipitonasal Length				
<i>M. altissimus</i>				
Peru (OTU 1)	13	22.2	20.0–24.9	1.38
Ecuador (OTU 3)	17	22.3	20.4–23.6	0.76
Colombia (OTU 4)	8	22.4	21.4–24.1	0.93
<i>M. minutus</i>				
Peru (OTU 5)	22	21.6	19.9–23.8	1.09
Colombia (OTU 12)	27	22.3	20.8–24.3	0.81
Venezuela (OTU 14)	102	22.0	20.1–24.3	0.94
Zygomatic Breadth				
<i>M. altissimus</i>				
Peru (OTU 1)	15	11.3	10.7–12.4	0.46
Ecuador (OTU 3)	12	11.5	11.0–11.9	0.29
Colombia (OTU 4)	5	11.8	11.5–12.2	0.30
<i>M. minutus</i>				
Peru (OTU 5)	17	11.3	10.3–12.7	0.72
Colombia (OTU 12)	25	11.7	11.1–12.5	0.41
Venezuela (OTU 14)	102	11.3	10.1–12.4	0.48

APPENDIX—(Continued)

Species and OTU	N	Mean	Range	SD
Interorbital Breadth				
<i>M. altissimus</i>				
Peru (OTU 1)	22	3.29	3.0–3.6	0.13
Ecuador (OTU 3)	17	3.25	3.0–3.4	0.12
Colombia (OTU 4)	14	3.49	3.4–3.8	0.11
<i>M. minutus</i>				
Peru (OTU 5)	22	3.32	3.1–3.5	0.13
Colombia (OTU 12)	29	3.43	3.1–3.8	0.16
Venezuela (OTU 14)	102	3.43	3.0–3.8	0.15
Length of Rostrum				
<i>M. altissimus</i>				
Peru (OTU 1)	17	6.35	5.5–7.6	0.55
Ecuador (OTU 3)	16	6.29	5.5–6.9	0.32
Colombia (OTU 4)	14	6.76	6.2–7.4	0.38
<i>M. minutus</i>				
Peru (OTU 5)	22	6.12	5.3–7.1	0.54
Colombia (OTU 12)	29	6.36	5.9–7.4	0.37
Venezuela (OTU 14)	102	6.80	6.0–7.8	0.40
Breadth of Braincase				
<i>M. altissimus</i>				
Peru (OTU 1)	18	10.8	10.2–11.2	0.24
Ecuador (OTU 3)	16	10.6	10.1–11.3	0.34
Colombia (OTU 4)	6	11.1	10.9–11.2	0.14
<i>M. minutus</i>				
Peru (OTU 5)	19	10.4	10.0–11.0	0.30
Colombia (OTU 12)	26	10.4	9.8–10.8	0.22
Venezuela (OTU 14)	102	10.3	9.6–10.7	0.24
Length of Diastema				
<i>M. altissimus</i>				
Peru (OTU 1)	21	5.38	4.8–6.2	0.39
Ecuador (OTU 3)	17	5.40	4.9–5.7	0.20
Colombia (OTU 4)	14	5.40	5.0–6.0	0.34
<i>M. minutus</i>				
Peru (OTU 5)	22	5.24	4.6–6.2	0.39
Colombia (OTU 12)	29	5.54	5.0–6.3	0.31
Venezuela (OTU 14)	102	5.63	5.0–6.6	0.35
Length of Bony Palate				
<i>M. altissimus</i>				
Peru (OTU 1)	23	3.48	3.1–4.0	0.22
Ecuador (OTU 3)	17	3.45	3.1–3.8	0.19
Colombia (OTU 4)	14	3.70	3.4–4.1	0.21
<i>M. minutus</i>				
Peru (OTU 5)	22	3.23	3.0–3.6	0.17
Colombia (OTU 12)	29	3.70	3.3–4.1	0.23
Venezuela (OTU 14)	102	3.41	2.9–3.9	0.19

APPENDIX—(Continued)

Species and OTU	N	Mean	Range	SD
Postpalatal Length				
<i>M. altissimus</i>				
Peru (OTU 1)	20	7.24	6.3–8.1	0.44
Ecuador (OTU 3)	16	7.52	6.7–8.0	0.39
Colombia (OTU 4)	10	7.38	6.8–7.9	0.33
<i>M. minutus</i>				
Peru (OTU 5)	22	7.24	6.3–8.3	0.49
Colombia (OTU 12)	28	7.35	6.4–8.8	0.46
Venezuela (OTU 14)	102	7.36	6.4–9.0	0.48
Breadth of Palate across M1s				
<i>M. altissimus</i>				
Peru (OTU 1)	21	3.96	3.4–4.4	0.26
Ecuador (OTU 3)	16	4.01	3.8–4.3	0.11
Colombia (OTU 4)	14	4.31	4.2–4.6	0.10
<i>M. minutus</i>				
Peru (OTU 5)	13	3.95	3.5–4.2	0.18
Colombia (OTU 12)	16	3.84	3.5–4.1	0.18
Venezuela (OTU 14)	102	4.00	3.6–4.3	0.15
Length of Incisive Foramen				
<i>M. altissimus</i>				
Peru (OTU 1)	20	4.13	3.5–4.6	0.27
Ecuador (OTU 3)	16	3.96	3.6–4.1	0.19
Colombia (OTU 4)	13	4.19	3.7–4.6	0.25
<i>M. minutus</i>				
Peru (OTU 5)	22	3.69	3.2–4.1	0.24
Colombia (OTU 12)	29	3.74	3.4–4.1	0.19
Venezuela (OTU 14)	102	3.74	3.2–4.4	0.23
Length of Maxillary Tooththrow				
<i>M. altissimus</i>				
Peru (OTU 1)	25	3.12	2.8–3.3	0.10
Ecuador (OTU 3)	17	3.15	3.0–3.4	0.13
Colombia (OTU 4)	15	3.29	3.1–3.5	0.09
<i>M. minutus</i>				
Peru (OTU 5)	22	2.86	2.6–3.0	0.11
Colombia (OTU 12)	29	2.90	2.7–3.1	0.13
Venezuela (OTU 14)	102	2.86	2.6–3.0	0.09
Width of M1				
<i>M. altissimus</i>				
Peru (OTU 1)	25	0.90	0.8–1.0	0.03
Ecuador (OTU 3)	17	0.90	0.8–1.0	0.05
Colombia (OTU 4)	15	0.97	0.9–1.0	0.05
<i>M. minutus</i>				
Peru (OTU 5)	22	0.85	0.8–0.9	0.05
Colombia (OTU 12)	29	0.85	0.7–0.9	0.06
Venezuela (OTU 14)	102	0.86	0.8–0.9	0.05

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